C. DEJOUX and A. ILTIS / Editors

Lake Titicaca

A Synthesis of Limnological Knowledge



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Lake Titicaca

A Synthesis of Limnological Knowledge

Edited by

C. DEJOUX and A. ILTIS



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Editors' Note

This work is a compilation of more than a century of limnological work on Lake Titicaca, to which has been added much original data obtained over the last few years.

We have wanted this compilation to be as exhaustive as possible in order to combine the dispersed and often difficult-to-find information in a single volume. It is possible that some documents which were impossible to find or have escaped the literature search, have not been included. We apologize to both our readers and to the authors involved for any such omissions. Nonetheless we consider that we have, either directly or indirectly, reported almost all the scientific information existing at present on the lake.

The author(s) of each chapter were entirely responsible for the scientific content of their papers and the changes that we occasionally made only concerned the style and length of the texts, with the aim of bringing more consistency and homogeneity to the book. We have however left the choice of place names up to individual authors, as the spelling of certain geographical sites can vary according to sources of reference. For this reason, you will sometimes find the Río Suchez spelt with a z and sometimes with an s (Suches), although these are the same watercourse. There are also synonyms: Huiñaimarca, Lago Menor and Lago Pequeño are the same body of water as are Lago Chucuito, Lago Mayor and Lago Grande, corresponding respectively to the smaller, shallow southern basin of Lake Titicaca, and the vast, deep northern basin. Some chapters mentioning place names do not include a map showing their location. We suggest the reader refer to the general map of the lake at the inside of the front cover of this book for this purpose.

The reader may also find slight differences from chapter to chapter in the altitude, surface area and maximum depth of the water body. It is evident that these are measurements that vary over the course of time and unfortunately it has not always been possible for authors to give a precise reference date to accompany these data. Only those chapters dealing specifically with these variables systematically associate a date with the values mentioned.

The original version of this work is in English. The loose translation into Spanish is mainly intended for the two Latin American countries in which the lake lies. The original texts were written either in English, Spanish or French. The translation into Spanish was carried out by Mrs Rina Risacher and that into English by Mr Bob Britton. Our North American colleagues, and particularly Heath Carney, have kindly provided us with help on certain very technical texts.

We would also like to thank all the authors who have agreed to participate in this synthesis volume by writing chapters summarising their specialist knowledge of Lake Titicaca. Our thanks also go out to the Rector of the Universidad Mayor de San Andres (UMSA) in La Paz who has accepted to preface this book and to the Director General of ORSTOM* who provided finance from this organisation for all of this work.

We would finally like to express our gratitude to the heads of the Departments of Geology and Biology of the UMSA in La Paz who, within the framework of an agreement signed between the UMSA and ORSTOM, provided the opportunity for staff from this institute to discover and work on a high altitude tropical lake, which is undoubtedly one of the most unusual and beautiful in the world.

C. Dejoux and A. Iltis

*Institut Français de Recherche Scientifique pour le Développement en Coopération; previously: Office de Recherche Scientifique et Technique Outre-Mer.

Preface

Research on Lake Titicaca is essential for the conservation and development of the entire Bolivian Altiplano ecosystem. The influence of Titicaca is not restricted to the area adjoining the shoreline, but covers a vast region where animal and plant life depends on the climatic conditions which are to a large extent determined by the relationship between the water and atmosphere existing at the lake's surface.

The heavy concentration of human population around the shores demonstrates the major life-supporting function of the lake, for the economy of the shoreline communities is one of the most prosperous of those living on the Altiplano. In addition, the beauty of the landscape makes it one of the main tourist attractions both nationally and internationally. For all these reasons, Lake Titicaca forms part of the Bolivian Republic's most valuable heritage, a part shared by the neighbouring Republic of Peru.

However, as our knowledge and understanding of the Altiplano grows as a result of rigorous research, the fragility of this ecosystem becomes increasingly evident. For this reason, the exploitation of the economic potential of such a large water body as Lake Titicaca is not possible without adopting precautionary measures, essential for preserving the equilibrium.

A few decades ago when the accumulated knowledge was still rudimentary, it was thought that the possibilities for irrigation using the lake's water were practically unlimited and that all that was needed was to create the infrastructure required to transport the water over several hundreds of kilometres of distance. Nowadays opinions have changed because we have arrived at the scientifically-based conclusion that the potential is in fact limited. We now know precisely what terrible effects would be brought about by an accelerated drop in the water level. It is no exaggeration to say that just a 10% a decrease in the volume of water could provoke a rapid desertification of the Altiplano and a highly unfavourable climatic change for animal and plant life.

As research progresses and new understanding is achieved, the importance of the lake becomes more evident. At the same time an increasing need is felt for the adoption of policies aimed at precise and rigorous management of the entire basin. Human errors can cause irreversible damage in a short space of time.

The book "LAKE TITICACA" will be of immense help in bringing about this new awareness. The two scientists Claude Dejoux and André Iltis have here compiled the main scientific works recently carried out in the varied disciplines concerning this important life-support system. By the same token, it constitutes an intellectual heritage which will enrich the people of Bolivia.

It must be stressed that French and Bolivian scientists have for a long time been working diligently, observing and analysing the various aspects of the lake. On reading this book, the great value of the results is confirmed, and it is certain that this book will in future be the essential reference work for scientists wanting to make progress in revealing the lake's secrets. We can state unequivocally that this work constitutes a complete review of the present state of knowledge on Lake Titicaca and that it provides the latest results of research on this habitat.

Of course, science has no final resting point; what we see now is just the culmination of a certain stage, but others will follow which will represent the next episode and an advance on present knowledge. Despite this, anyone wishing to make progress must analyse the contents of this book. In the same way, those responsible for economic and social policy must base themselves on its conclusions in setting up and implementing actions which could in any way compromise the spheres of influence of Lake Titicaca.

The Universidad Mayor de San Andrés thanks ORSTOM (Institut Français de Recherche Scientifique pour le Développement en Coopération) for having contributed in such an effective manner in the study of Lake Titicaca. The research workers of the ORSTOM have left and continue to leave a deep impression by their scientific work, both at UMSA and in the country as a whole. The most important aspect of the activities of this Institute is that they are undertaken in a coordinated way, in complementarity with those of Bolivian research workers, which contributes in consolidating the national capacity to acquire new knowledge.

I would like to thank Claude Dejoux and André Iltis for this important contribution to Bolivian culture, and at the same time thank them for having given me the opportunity to write these few lines in which I express the sentiments of the teaching staff, researchers and students of the Universidad Mayor de San Andrés, who are constantly striving to obtain an ever deeper understanding of the true nature of our nation.

Pablo Ramos Sanchez, rector

Universidad Mayor de San Andrés LA PAZ

Introduction

CLAUDE DEJOUX and ANDRÉ ILTIS

At the latitude of 14° S, the Andes chain divides into two Cordilleras which enclose a high plateau, the Altiplano, covering about 200,000 square kilometres and with an altitude varying between 3700 and 4600 metres above sea level.

Lake Titicaca occupies the northern part of this plateau. It is both vast and deep and is designated as the highest navigable lake in the world.

It is divided into two lake basins: the Lago Pequeño (or Huiñaimarca) and the Lago Grande, more rarely known as the Chucuito. These two parts are connected by the approximately 800 metres wide Tiquina Strait. The maximum depth of the Lago Grande is 285 metres whereas that of the Lago Pequeño is only 40 metres. More than two-thirds of the former has a depth greater than 150 metres whereas the latter is only 5 to 10 metres deep over most of its area.

Because of its geographical location, the lake is subject to the climatic conditions belonging to the tropical zone, especially insofar as insolation remains relatively stable throughout the year. Because of its high-altitude situation, it is influenced by conditions belonging to montane climates (high luminous intensity, low temperatures, low air humidity) which interfere with those factors related to its tropical nature. To this is added the unusual morphometry of the lake basin, in which coexist, often poorly connected to one another, large shallow areas (Lago Pequeño, and the large Puno, Ramis and Achacachi Bays) and deep areas, more typical of alpine type lakes.

The entire hydrological system of the Altiplano is endorheic, with all the consequences that such a system can have on the biological components of the habitat. The lake itself functions almost as a closed system; its only outflow river under the present hydrological situation accounts for less than 5 % of the total water losses. The lake water is subject to strong evaporation, has a retention time of the order of 63 years and has a total dissolved salt content of close to one gram per litre, which distinguishes it from the much fresher waters of the majority of the Andean mountain lakes.

It should finally be noted that it stands at the transition point between two very distinct geographical regions: the desert fringe of the Pacific coast to the west and the great Amazonian forest extending to the Atlantic coast to the east.

In addition to its unusual limnological features, it is, according to Indian mythology, one of the birthplaces of mankind. The sun, the moon and the stars were born within its bounds according to the wishes of Viracocha, creator of the world. Here, after the Great Flood that destroyed the world, mankind took its first steps. The lake was a sacred site for the Incas, who saw it as the end of the earth and a point of fusion where the two concepts of time and space came to be expressed.

Although the Spaniards had for a long time roamed over the Altiplano, it was probably a Frenchman, Alcide D'Orbigny, who was the first scientist to take an interest in Lake Titicaca and he brought back biological collections to Europe following one of his expeditions to South America from 1826 to 1833. The first descriptions of the molluscs came from these samples.

At about the same period, another scientist, J.B. Pentland, at the time British Consul in Bolivia, studied the unusual aquatic habitat during two expeditions undertaken at ten years' interval (1827–28 and 1837–38). As a geographer he made the first precise maps of the lake and its region and also collected biological specimens, which he sent back to Europe. Among these were fish which were used by Cuvier and Valenciennes to describe the first species of *Orestias*. Other collections of biological specimens arrived in Europe following the visits of Castelnau and Weddel (1843–47). Further visitors (Squier, 1870; Orton, 1873; Marcoy, 1877; Puente, 1892; Tovar, 1892 and Basadre, 1894) only paid scant attention to the true study of the lake. But in 1875, over a period of less than two months, Agassiz and Garman carried out the first coordinated study of this environment, including bathymetric, hydrographic and biological surveys, which were published in 1876 and 1877.

It was not before the start of the twentieth century that more structured expeditions were organised, and particularly that of Créqui-Montfort and Sénéchal De La Grange (1903), in which the zoologist Neveu-Lemaire participated. It is to him that we owe the first extensive faunal inventory, which, after all the species collected had been identified, confirmed the low species diversity already reported by Agassiz and Garman (1876).

The first expedition whose aim wasn't simply to bring back further collections of specimens, but rather to study the relationships existing between the flora and fauna, was organised under the direction of H.C. Gilson in 1937. The publications resulting from the collections made by this British expedition did not however provide a very detailed ecological description of the various ecosytems studied – in particular that of Lake Titicaca. In many cases the publications were restricted to species lists with brief descriptions of the sampling locations. This 'Percy Sladen Trust Expedition to Lake Titicaca' did nevertheless have the merit of including a hydrologist, a chemist, three zoologists, an entomologist and a botanist and their full and detailed publications are still authoritative to the present day; in many fields they represent one of the main sources of reference for this synthesis.

After a hiatus of ten years because of the Second World War, a number of specialised studies were carried out providing further information to that already acquired on the biology of the lake (Vellard, 1951 to 1954; Niethammer, 1953; Brundin, 1956; Ueno, 1967) and on its geology, physicochemistry and general limnology (Newell, 1945; Schindler, 1955; Monheim, 1956; Löffler, 1960; Derkosch and Löffler, 1961).

It was not until 1972, the year of the setting up of the laboratory of the Instituto del Mar del Perú (IMARPE) at Puno, that coordinated studies started to be carried out again. From 1973 the University of Davis (California) carried out a regular programme of observations in Puno Bay and in the Peruvian part of the Lago Grande, in liaison with this institute. In 1974, the Universidad Mayor de San Andrés (UMSA) at La Paz and ORSTOM (then known as the Office de la Recherche Scientifique et Technique Outre-Mer, but later to become the Institut Français de Recherche Scientifique et Technique pour le Développement en Coopération) started a joint limnological research programme on the Bolivian part of the lake, firstly on the Huiñaimarca and then on the Lago Grande. This began with morphometric and sedimentological studies before going on to cover biological subjects.

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In spite of the setting up of cooperative research arrangements and the relative ease of access to the Andes and its aquatic habitats, scientific expeditions have not yet become a thing of the past. In June-July 1978, North American scientists organised a scientific expedition known as the 'Catherwood Bolivian-Peruvian Altiplano Expedition' involving two invertebrate specialists, an entomologist, an algologist and a botanist. Their main results were published a few years later (Roback *et al.*, 1980; Roback and Coffman, 1983) and represent a major contribution to our knowledge of the aquatic insects of this region of Latin America.

A Peruvian-Bolivian programme of assessment of Lake Titicaca's resources was carried out from 1983 to 1985, under the auspices of SELA (Sistema Economico Latino-Americano) and OLDEPESCA (Organización Latino-americana de Desarollo Pesquero). The University of La Paz then developed research on the spatio-temporal variations in physico-chemical variables and on the plankton during 1984–1985. The Instituto del Mar del Perú at Puno turned its work towards estimating the present fish stocks.

We should also mention the setting up in 1988 of an experimental pisciculture station on the edges of Lago Pequeño near the Tiquina Strait, as part of the economic cooperation programme between Japan and Bolivia. This is particularly aimed at the production of trout fry and at the study of the biology of this species in the lake.

It is certain that increasingly extensive understanding of Titicaca will be required in the forthcoming years, especially as this area is the subject of several present and future regional development projects. For this reason, it seemed to us essential in this work to take stock of the data accumulated from over a century of work on this lake basin, as the results of the numerous studies carried out up until now were very disconnected, fragmentary and scattered over several countries.

We have therefore attempted to make an exhaustive as possible review of current knowledge from the existing literature and from the results of more recent observations, the aim being to produce a sort of database on this unusual ecosystem. This synthesis, which highlights gaps and imperfections in existing knowledge, should help in guiding future research. Future work should aim at filling in the gaps of the descriptive part of this work and then go on to study the dynamics of the relationships between the various communities and their habitat, an aspect that has scarcely been touched up until now.

The following chapters describe the lake's animal and plant populations and their high degree of endemism which has frequently been reported in the literature. This concept of endemism needs to be qualified and used with a certain amount of discretion, as it only in fact concerns certain groups. It shows itself to its fullest extent in the molluscs, of which the majority of species (*Taphius montanus* excluded) are only known from Lake Titicaca. The same is true for the amphipods among which only *Hyalella inernis* is found in other habitats on the Altiplano. The fish occurring in the lake also have a high degree of endemism, with only a few species of *Orestias* and *Trichomycterus* being recorded in other aquatic habitats neighbouring the lake.

For the majority of other taxonomic groups the flora and fauna consist of species that are widespread either throughout the Andes or South America, or are even cosmopolitan. Although some newly named species are only currently known from Lake Titicaca, it is highly likely that more intensive and extensive surveys will widen their distribution range.

The more motile species occurring in Lake Titicaca have often colonised other habitats around the lake, but in contrast, animal species living in neighbouring aquatic habitats are not always capable of adapting to the slightly saline waters of the lake, this being particularly the case with the insect fauna.

In terms of population dynamics, the older data are too short-term and too scanty to provide a description of the temporal changes and especially long-term changes that have occurred to the flora and fauna of the lake. However, some species previously recorded as dominant are now only recorded sporadically (certain molluscs and amphipods) and other taxa have not been found recently. In the last case, insufficient sampling may be the cause, but it is certain that the changes in dominance have more complex causes. With the exception of the fish fauna which has been and continues to be highly influenced by fishing pressure and species introductions, it is unlikely that human activities are the direct cause of the radical changes that have occurred to the species composition. Perhaps internal rhythms belonging to Lake Titicaca itself could be cited, although for many groups it is difficult to demonstrate marked intra-annual seasonal cycles. At the interannual level, the few studies covering at least two years demonstrate frequently acyclical variations which seem to be the direct consequence of the variability of abiotic factors rather than major rhythms of a biological nature.

In the applied field, three subjects appear to have been given particular attention, the study of the beginnings of pollution being the most important. Although the closure for economic reasons of most of the mining operations in the catchment is a positive factor on this front, the increase in the human population along the shoreline recorded in recent years is already leading to contamination in certain almost enclosed bays.

The second applied subject to be studied with great attention is the longterm changes to the lake's hydrology. Several development projects envisage the taking of sometimes large quantities of water from this environment, and it is important to know with precision the variations in the potential available water resources caused by meteorological variability.

Finally, estimates of the overall fish production and its variability are still, if not quite non-existent, at least very approximate for a system which contributes greatly to feeding the population of the neighbouring areas. The population dynamics of trout and pejerrey (since they were introduced into the lake more than forty years ago) are still practically unknown over the lake as a whole and knowledge of the indigenous fish species is scarcely better. Information needed for a rational management of the fish resources should be collected as soon as possible.

Publicising the value of further developing research on this very special lake is also one of the aims of this book, and we sincerely hope that this objective will be fulfilled.

References

AGASSIZ (A.), GARMAN (S.W.), 1876. Exploration of Lake Titicaca. Bull. Mus. Comp. Zool., Harvard, 3: 273–349.

- BASADRE (M.), 1894. Los lagos de Titicaca. Bol. Soc. Geogr., Lima, 3.
- BRUNDIN (L.). 1956. Die bodenfaunistychen Seetypen und ihre Anwendbarkeit auf die Sudhalbkugel. Zugleich ein Theorie der produktionbiologischen Bedeutung der glazialen Erosion. Rep. Inst. Freshw. Res., Drottningholm, 37: 186–235.
- CASTELNAU (F. de). 1855. Expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro à Lima et de Lima au Para. Paris, 6 vol.
- CREQUI-MONTFORT (G. de), SENECHAL DE LA GRANGE (E.), 1904. Rapport sur une mission scientifique en Amérique du Sud (Bolivie, République Argentine, Chili, Pérou). Nouvelles Arch. des Missions Scientifiques, 12, 81.
- DERKOSCH (I.), LÖFFLER (H.), 1960. Spektrochemische Spurenanalyse Südamerikanischer Binnengewasser. Ark. Geofysik, 3: 337–345.
- D'ORBIGNY (A.), 1835-47. Voyages dans l'Amérique méridionale. Pitois-Levrault et Cie., Paris, 7 tomes, 11 volumes.

- GILSON (H.C.), 1939-40. The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1: 1-357.
- LÖFFLER (H.), 1960. Limnologische Untersuchungen an Chilenischen und Peruanischen Binnengewassern. Ark. Geofysik, 3: 155–254.
- MARCOY (P.), 1877. Voyage dans la région du Titicaca et dans les vallées de l'est du Bas-Pérou. Le Tour du Monde, 257 p.

MONHEIM (), 1956. Beitrage zur Klimatologie und Hydrologie des Titicacabeckens. *Sellbstverl. d. Geograph. Heidelberg*, 1: 1–152.

- NEVEU-LEMAIRE (M.), 1906. Les lacs des hauts plateaux de l'Amérique du Sud. Imprimerie Nationale, Paris, 197 p.
- NEWELL (N.D.), 1945. Geology of the Lake Titicaca region. Geological Society of America, Mem. 36, 111 p.
- NIETHAMMER (G.), 1953. Vogelleben am Titicaca See. Natur. V. Volk., 83: 409-416.
- ORTON (J.), 1873. The Andes and the Amazon. New York, 645 p.
- PENTLAND (J.B.), 1948. The Laguna of Titicaca and the valleys of Yukai, Collao and Desaguadero in Peru and Bolivia from geodesic and astronomic observations made in the years of 1827 and 1828, 1837 and 1838. British Admiralty Chart, n° 1268, London.
- PUENTE (I. la), 1892. Estudio monográfico del lago Titicaca bajo su aspecto físico y histórico. *Bol. Soc. Geogr.*, Lima, 1: 363.
- ROBACK (S.S.), COFFMAN (W.P.), 1983. Results of the Catherwood Bolivian-Peruvian Altiplano Expedition. Part 2: Aquatic Diptera including montane Diamesinae and Orthocladiinae (Chironomidae) from Venezuela. Proc. Acad. Nat. Sci. Philadelphia, 135: 9–79.
- ROBACK (S.S.), BERNER (L.). FLINT (O.S.), NIESER (N.), SPRANGLER (P.J.), 1980. Results of the Catherwood Bolivian-Peruvian Altiplano Expedition. Part 1. Aquatic insects except Diptera. Proc. Acad. Nat. Sci. Philadelphia, 132: 176–217.
- SCHINDLER (O.), 1955. Limnologische Studien im Titicacasee. Arch. Hydrobiol., 51 (1): 42– 53.
- SQUIER (E.G.), 1870. On the basin of Lake Titicaca. Rep. Brit. Ass., Trans. of Sections: 175.
- TOVAR (A.), 1892. Lago Titicaca. Observaciones sobre la disminución progresiva de sus aguas. *Bol. Soc. Geogr.*, Lima, 1: 163–167.
- UENO (M.), 1967. Zooplankton of Lake Titicaca on the Bolivian side. *Hydrobiologia*, 29: 547–568.
- VALENCIENNES (A.), 1839. Rapport sur quelques poissons d'Amérique rapportés par M. Pentland. L'Institut, 7: 118.
- VALENCIENNES (A.), 1846. Des Orestias. In: Histoire naturelle des poissons. Cuvier et Valenciennes 18: Bertrand, Paris: 221–244.
- VELLARD (J.), 1951. Estudios sobre batracios andinos. 1: El grupo *Telmatobius* y formas afines. Memor. Mus. Hist. Nat. Javier Prado, Lima, 1: 90 p.
- WEDDEL (H.A.), 1852. Aperçu d'un voyage dans le nord de la Bolivie et dans les parties voisines du Pérou. L. Martinet, Paris, 28 p.

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A. ABIOTIC ASPECTS

I. ORIGINS I.1. Formation and geological evolution

ALAIN LAVENU

The Altiplano is a vast intermontane basin in the Central Andes of Peru, Bolivia and Argentina, lying between the Western and Eastern Cordilleras (Fig. 1). It is about 2000 km long and 200 km wide with an altitude varying from 3700 to 4600 metres. It is an endorheic basin. The north and centre of the Altiplano are occupied by large permanently flooded lakes: Lakes Titicaca and Poopo. The southern part is more arid and is the site of "salares"*: Coipasa and Uyuni.

Since the early Quaternary, the Altiplano has always been occupied by lakes, but these have not always had the same extent as the present-day lakes. Studies of ancient lake sediments have enabled the history of these lakes to be studied (Orbigny, 1835–1847; Neveu-Lemaire, 1906; Bowman, 1909; Troll, 1927–1928; Moon, 1939; Ahlfeld, 1946; Newell, 1945; Ahlfeld and Branisa, 1960).

Although the Pliocene is characterised by fluviatile and lacustrine deposits corresponding to a relatively warm environment, the transition to the Quaternary is marked by a major climatic change. The climate underwent a sudden cooling and glaciation appeared at about 3 million years BP. Glaciation developed throughout the Quaternary. The climatic change led to profound changes in the type of deposits. The Quaternary sediments of the Altiplano take the form of high altitude facies: glacial and interglacial deposits in the Cordillera and on the piedmont, torrential fluviatile deposits on the piedmont and high plain and lacustrine evaporite deposits in the centre of the basin.

Studies of these ancient lakes and of the main glacial stages in the Eastern Cordillera have allowed the establishment of relationships between the three lake formations and the three most recent stages of glacial recession (Servant, 1977; Servant and Fontes, 1978) (Fig. 2). Recently, the discovery in the north of the Altiplano of two ancient lacustrine episodes has established the

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^{*} Vast saltpans with a more or less thick crust of salt covered locally or periodically with shallow water.

4 A. Lavenu



Figure 1. Situation of the Altiplano in the Central Andes chain (from Lavenu *et al.*, 1984). C: Cochabamba; CR: Crucero: LP: Lake Poopo; LPZ: La Paz; LT: Lake Titicaca; SC: Salar de Coipasa; SU: Salar d'Uyuni.

same relationships between lake levels and the two first Quaternary glaciations (Lavenu *et al.*, 1984) (Fig. 3).

Periods of maximum lake extent correspond to the end of glaciations or to the end of glacial stages and are due to the melting of glaciers (Servant and Fontes, 1978). Discontinuities between different stages are marked by ablation surfaces which coincide with the end of the morphological evolution of each interglacial stage.

Quaternary deposits postdate a polygenic ablation surface S6 of complex history. On the piedmont of the Eastern Cordillera this surface follows a volcanic layer (Chijini tuff) dated at 2.8 million years BP (Lavenu *et al.*, 1989).

The extent and limits of these water bodies are directly related to climatic and tectonic changes (Fig. 3). For this reason the various lacustrine deposits are not superimposed but rather inset one another. The study of the lake levels will be done in chronological order from the most ancient to the most recent.



Figure 2. Correlations between Pleistocene glacial and lacustrine formations in the northern Altiplano (from Servant and Fontes, 1978).

AGE (Ma)*	EPOCH	SURFACES	LACUSTRINE EVENTS	GLACIAL AND INTERGLACIAL EVENTS	TECTONIC EVENTS
	PRESENT	tO	TITICACA	Moraines	
0.01 -	HOLOCENE	tl	TAUCA		
	UPPER			CHOQUEYAPU II	
		ť2	MINCHIN	CHOQUEYAPU I	
	PLEISTOCENE				
0.5 -					NS
		U	BALLIVIAN		EXTENSION
	LOWER		(OLLOWAT.)	SORATA	Littletoit
		S4			
			CABANA		
1				KALUYO	
	PLEISTOCENE	S5	MATARO	Purapurani F. (1.6 Ma)	
				CALVARIO	
1.6 ·		64			N S COMPRESSION
ļ		30	LA PAZ		EW
			Chijini tu	ff (2.8 Ma)	COMPRESSION
1	PLIOCENE			PATAPATANI	
			FORMATION		
* fr	om Berggren et al. 1985				

Figure 3. Stratigraphical, morphological and tectonic relationships during the Pleistocene.

The Lower Pleistocene

The existence of the two most ancient lake levels is clearly evident to the north-west of Lake Titicaca in both Peru and Bolivia (Lavenu *et al.*, 1984). The outcrops are marked by coarse torrential and fluviatile sediments at the basin margins and by fine lacustrine deposits towards the centre of the basin (Fig. 4).

The most ancient deposits, called Mataro (Fig. 4), take the form of a series of fluviatile detrital deposits showing alternating beds of ochre-coloured clayey sand and gravelly sand. This incomplete series outcrops over a thickness of about 50 metres. The presence of a fossil deer antler indicates an undifferentiated Quaternary age. The top of the Mataro deposits is an ablation surface developed at a present-day altitude 3950 metres around the paleo-basin (surface S5) (Fig. 5). This lake reached its maximum extension after the Calvario glaciation (Dobrovolny, 1962) after 2.8 My BP (Lavenu *et al.*, 1989). It is the equivalent of the Purapurani Formation of the La Paz basin dated from the lower Pleistocene at 1.6 My BP (Lavenu *et al.*, 1989)



Figure 4. The extent of lakes in the north and centre of the Altiplano (from Lavenu *et al.*, 1984). 1: Lake Mataro; 2: Lake Cabana; 3: Lake Ballivian (Ulloma and Azangaro formations); 4: Lake Minchin; 5: Glacial and fluvio-glacial formations in the piedmont and Eastern Cordillera. A: Ananca; AA: Ayo Ayo; C: Callapa; CR: Crucero; D: Desaguadero; DC:Deustua-Cabana; E: Escoma; EP: Estacion Pando; J: Juliaca; LPZ: La Paz; MC: Mataro Chico; UL: Ulloma; UM: Umala; UU: Ulla Ulla; V: Viacha. Lakes Escara and Tauca are not represented. In the area of Lake Poopo and Salar de Coipasa, the limits of Lake Tauca are included within the boundaries of Lake Minchin. In the north, the limits of Lakes Minchin and Tauca are almost the same as those of the present-day Lake Titicaca.



Figure 5. Spatial relationships of various lake levels in the north of the Altiplano (from Lavenu *et al.*, 1984).

and the equivalent of the Ayo Ayo lower Pleistocene deposits further south (Hoffstetter *et al.*, 1971).

The Cabana Formation, which formed after the Kaluyo glaciation (Servant, 1977), insets the previous series. This spatial relationship shows that the Cabana water body had a smaller area and volume than the previous one. The lacustrine deposits, which again include fluviatile beds, outcrop over a thickness of about 50 metres. This formation has been eroded to form the surface S4 at an altitude of 3900 metres.

On the piedmont and in the Cordillera, the surfaces S5 and S4 usually stand above the valleys of the present-day streams by several tens of metres. The existence of these two surfaces in the north and centre of the Altiplano suggests that the Ulloma-Callapa sill, now crossed by the river Desaguadero in a gorge, did not exist in the lower Pleistocene and that the two lakes, Mataro and then Cabana, thus each formed a single water body on the Altiplano (Fig. 6).

The Upper Pleistocene

The sediments of Lake Ballivian, which formed after the Sorata glaciation (Ulloma Formation in Bolivia and Azangaro Formation in Peru), insets the Cabana deposits (Bowman, 1909).

These deposits are very fossiliferous and recent works have enabled them to be attributed to the lower Pleistocene age: Ensenadian or lower Lujanian in the South American chronology (Hoffstetter, 1986; Marshall *et al.*, 1991; Marshall and Salinas, 1991). A comparable fauna exists in the Tarija basin in southern Bolivia, where a volcanic stratum has been given an Ensenadian age of 0.7 My BP (McFadden *et al.*, 1983). The sediments of Lake Ballivian correspond to a water body situated at a present-day altitude of 3860 metres. At the foot of hills and in the Cordillera, the ablation surfaces corresponding



Figure 6. Communications between the Northern and Central Altiplano (from Lavenu et al., 1984).

to these sediments form alluvial terraces (t3) covering considerable areas. These terraces usually lie 5 to 6 metres above the level of present-day streams.

A few signs of lacustrine terraces around Lake Titicaca at an altitude of 3840 metres could correspond to a postglacial episode of the first Choqueyapu stage.

In the southern Altiplano, the lacustrine layers of the Escara formation could correspond to those of Lake Ballivian (Servant, 1977). These layers are at a lower present-day altitude (3780 metres) and demonstrate the existence of the Ulloma-Callapa sill.

The end of the Pleistocene is marked by the Lake Minchin deposits which inset those of Lake Ballivian. This water body is characterised by an ablation surface and terraces (t2) situated at 3825 metres altitude, between 10 and 15 metres above the present level of Lake Titicaca. Upstream on the Altiplano these terraces form alluvial terraces situated 3 to 4 metres above the present-day streams.

This lake, divided into two water bodies by the Ulloma-Callapa sill, was very reduced in extent in the north of the Altiplano, but greater in area in the south. Incomplete fossils have enabled it to be assigned to the undifferentiated Lujanian age (Lavenu, 1984; Marshall and Sempéré, 1991; Marshall *et al.*, 1991). In the south, an intermediate lacustrine terrace has been dated to 27,000 years BP (Servant and Fontes, 1978).

The Holocene

The Holocene of the Altiplano is characterised by Lake Tauca (Servant, 1977), also divided into two water bodies by the Ulloma-Callapa sill. Its area was reduced compared to Lake Minchin. Low alluvial peaty terraces are found all around this paleolake throughout the Altiplano and in the Cordillera. This is the t1 system, situated 1 metre above the level of the thalwegs. In the centre of the Altiplano, Servant and Fontes (1978) have assigned it an age of between 12,500 and 10,000 years BP.

Lakes Minchin and Tauca are related to the melting of the glaciers of the Choqueyapu glaciation which included two main stages, (Troll, 1930; Troll and Finsterwalder, 1935) Choqueyapu I before Minchin and Choqueyapu II before Tauca.

Lake Tauca stabilised at 5 metres above the present level of Lake Titicaca. In the north of the Altiplano, it was at a level of 3815 metres, and in the south at 3720 metres. The area of the lake can be estimated at a minimum of about 52,000 km². Servant and Fontes (1978) gave it an area of 43,000 km² in the south of the Altiplano. In the north the Tauca water body must have covered about 9000 km². These water bodies progressively reduced in size, so that all that remains is Lake Titicaca (8560 km²) at 3810 metres altitude in the north of the Altiplano, Lake Poopo (3686 m) in the centre and the salares (3650 m) in the south. Over the same period the glaciers have also decreased in volume and area.

Neotectonics

The Andean Cordillera had practically acquired its present-day altitude in the Pliocene. Between 2 and 3 My BP the upper Pliocene deposits were subjected to tectonic compression. This shortening, trending NE-SW to E-W, was responsible for reverse faulting and folding (Lavenu, 1988; Lavenu and Mercier, 1992). In the early Quaternary a second minor compressional deformation affected deposits aged from the upper Pliocene to the early


Figure 7. Structural diagram of the Eastern Cordillera piedmont between La Paz and Lake Titicaca (from Lavenu, 1981). 1: undifferentiated pre-Pleistocene formations; 2: Quaternary volcanic formations; 3: pre-Sorata glacial formations; 4: (a) Sorata moraines, (b) Ulloma Formation; 5: Choqueyapu moraines; 6: Recent Quaternary.

Quaternary. This deformation led to the formation of reverse faults resulting from a N-S shortening.

Following these compressional events, the Altiplano and particularly the piedmonts of the Western and Eastern Cordilleras were affected by tectonic extension in a N-S to NNE-SSW direction. This deformation, which has affected all Quaternary deposits up to the present, is due to a high topography effect. This special state of stress is described for the Central Andes of Peru by Sébrier *et al.* (1985).

These deformations caused major fracturing in the Plio-Quaternary deposits between Lake Titicaca and La Paz. The normal faults have a WNW-ESE to NW-SE trend (Fig. 7).



Figure 8. Cross-section of the Eastern Cordillera north-west of Peñas. Quaternary faults with throws of hundreds of metres (from Lavenu, 1981). 1: undifferentiated pre-Pleistocene formations; 2: lower Pleistocene formations; 3: recent Quaternary.

After the formation of surfaces S6 and S5 and the accumulation of Purapurani interglacial deposits dated at 1.6 My BP (Lavenu *et al.*, 1989), the extensional deformation trending N-S affected lower Pleistocene deposits (Fig. 8). Steep scarps in the La Paz region demonstrate the existence of a first period of extension in the Pleistocene (before S6 and S5). Near La Paz the vertical throw of some normal faults trending 120°E attains 400 metres (Fig. 9; points 1 and 2 on Fig. 7). The same is true on the shores of the lake to the west of Huarina, at the foot of the Eastern Cordillera, where deposits of Pliocene age are uplifted to abnormally high altitudes. On the north-east shores of the lake at Escoma the S4 surface is situated at altitude between S5 and S4 of 200 metres and between S5 and S6 of 100 metres are also abnormally high compared to those in the centre of the Altiplano where they are only 50 metres.

Before the development of S4, an extensional tectonic movement occurred at the foot of the Eastern Cordillera, which caused the Cordillera to be uplifted relative to the Altiplano. This extensional deformation, by causing sinking of the land surface, favoured the establishment of Lakes Mataro and Cabana. It was certainly at this epoch that the lowest part of the Altiplano, the trough in which Lake Titicaca is now situated, was really created. The deepest part of the present lake reaches nearly 284 metres near to Soto Island in Peru (Boulangé and Aquize, 1981).



Figure 9. Section of the Quebrada Minasa (point 1 *Figure 7*) (from Lavenu, 1988). squares: Sorata moraines; circles: pre-Sorata glacial formations; dots: La Paz Pliocene formation.



Figure 10. Spatial relationships of ablation surfaces in the central Altiplano (Pando) and on the Eastern shore of Lake Titicaca (Escoma) (from Lavenu *et al.*, 1984).

A later extensional tectonic deformation affected the S4 surface. In the Eastern Cordillera the moraines of the Sorata glaciation intrude deeply into the valleys, another sign of the relative uplifting by comparison with the Altiplano.

The extensional deformations of the upper Pleistocene and the Holocene are weaker and the morphological displacements less important. Numerous indicators show that this N-S extension is continuing: at Llojeta (point 3 on Fig. 7), the S3 surface which represents the topographic surface of the Altiplano has a vertical throw of nearly one metre; to the east of Peñas the Choqueyapu moraines are cut by normal faults; on Cojata island, the level of Lake Minchin deposits is raised by faulting to more than 17 metres above the present lake level.

Conclusion

The present lake system on the Altiplano is the result of the evolution of a more ancient system which began from the lower Pleistocene, with the transition at the end of the Pliocene from a relatively warm climate to a cool damp climate.

The presence and size of the lakes are directly related to the recession of glaciers at the start of the interglacial periods. As in the case of the glaciers, the areas of successive lacustrine water bodies decreased considerably over the course of the Quaternary.

Plio-Quaternary tectonic deformations fractured the piedmont of the Eastern Cordillera. Neotectonic extensional activity trending N-S has typified all the Quaternary. The tectonic trough which was to be occupied by the presentday Lake Titicaca was created in the lower Pleistocene, following Lake Cabana and before Lake Ballivian.

References of chapter I

- AHLFELD (F.), BRANISA (L.), 1960. Geología de Bolivia. Instituto Boliviano del Petróleo. Ed. Don Bosco, La Paz, 245 p.
- BERGGREN (W.A.), KENT (D.V.), FLYNN (J.J.), 1985. Cenozoic geochronology. Geol. Soc. Amer. Bull., 96: 1407–1418.
- BOWMAN (I.), 1909. Physiography of the Central Andes. Amer. Journ. Sci., ser. 4–28, 197–217: 373–402.
- DOBROVOLNY (E.), 1962. Geología del valle de La Paz. Departamento Nacional de Geología, Bolivia, 3: 153 p.
- HOFFSTETTER (R.), 1986. High Andean mammalian faunas during the Plio-Pleistocene. *In*: High altitude tropical biogeography, Vuilleumier and Monasterio eds., Oxford Univ. Press: 278–345.
- HOFFSTETTER (R.), MARTINEZ (C.), MUÑOZ-REYES (J.), TOMASI (P.), 1971. Le gisement d'Ayo-Ayo (Bolivie), une succession stratigraphique Pliocène-Pléistocène datée par des mammifères. C. R. Acad. Sciences, Paris, 273: 2472–2475.
- LAVENU (A.), 1984. Age pliocène de la Formation Remedios dans l'Altiplano bolivien. Caractères de la tectonique Pliocène. C. R. Acad. Sciences, Paris, 299: 1051-1054.
- LAVENU (A.), 1988. Etude tectonique et néotectonique de l'Altiplano et de la Cordillère Orientale des Andes boliviennes. Travaux et Documents Microfichés, ORSTOM, Paris, 28: 420 p.
- LAVENU (A.), BONHOMME (M.G.), VATIN-PERIGON (N.), DEPACHTERE (P.), 1989. Neogene magmatism in the Bolivian Andes between 16°S and 18°S: Stratigraphy and K/Ar geochronology. *Journal of South American Earth Sciences*, 2 (1): 35–47.
- LAVENU (A.), FORNARI (M.), SEBRIER (M.), 1984. Existence de deux nouveaux épisodes lacustres quaternaires dans l'Altiplano péruvo-bolivien. *Cah. ORSTOM, sér. Géol.*, 14 (1): 103–114.
- LAVENU (A.), MERCIER (J.L.), 1992. Evolution du régime tectonique de l'Alhplano et de la Cordillère orientale des Andes de Bolivie du Miocène à l'Actuel. Géodynamique (in press).
- McFADDEN (B.J.), SILES (O.), ZEITLER (P.), JOHNSON (N.M.), CAMPBELL (K.E. Jr.), 1983. Magnetic polarity stratigraphy of the Middle Pleistocene (Ensenadan) Tarija Formation of Southern Bolivia. *Quat. Res.*, 19: 172–187.
- MARSHALL (L.G.), SALINAS (P.), 1991. The Lorenzo Sundt collection of Pleistocene mammals from Ulloma, Bolivia in the Museo Nacional de Historia Natural, Santiago, Chile (in press).
- MARSHALL (L.G.), SEMPERE (T.), 1991. The Eocene to Pleistocene vertebrates of Bolivia and their stratigraphic context: a review (in press).
- MARSHALL (L.G.), SWISHER (C.), LAVENU (A.), HOFFSTETTER (R.), CURTIS (G.), 1991. Geochronology of the mammal-bearing Late Cenozoic on the northern Altiplano, Bolivia. *Journal of Geology* (in press).
- MOON (H.P.), 1939. 3. The geology and physiography at the Altiplano of Peru and Bolivia. *In*: The Percy Sladen Trust Expedition to Lake Titicaca in 1937. *Trans. Linn. Soc. London*, ser. 3, 1 (1): 27–43.
- NEWELL (N.D.), 1945. Geology of the Lake Titicaca region. Geological Society of America, Mem. 36, 111 p.
- SEBRIER (M.), MERCIER (J.L.), MEGARD (F.), LAUBACHER (G.), CAREY-GAIL-HARDIS (E.), 1985. Quaternary normal and reverse faulting and the state of stress in the Central Peru. *Tectonics*, 4 (7): 739–780.

- SERVANT (M.), 1977. Le cadre stratigraphique du Plio-Quaternaire de l'Altiplano des Andes tropicales en Bolivie. Bulletin AFEQ, Recherches françaises sur le Quaternaire, INQUA, 1, 50: 323–327.
- SERVANT (M.), FONTES (J.C.), 1978. Les lacs quaternaires des hauts plateaux des Andes boliviennes. Premières interprétations paléoclimatiques. *Cah. ORSTOM*, sér. Géol., 10 (1): 9-23.
- STEINMANN (G.), 1929. Geologie von Peru. Karl Winter, Heidelberg, 448 p.
- TROLL (C.), 1927. Forschungsreisen in den zentralen Anden von Bolivia und Peru. Peterm. Mitt., 73: 41–43; 218–222.
- TROLL (C.), FINSTERWALDER (R.), 1935. Die Karten der Cordillera Real und des Talkessels von La Paz. Peterm. Mitt., 81: 393–399; 454–455.

II. GEOMORPHOLOGY ANDSEDIMENTATIONII.1. Morphology and bathymetry

DENIS WIRRMANN

At an altitude of 3809 metres above sea level, Lake Titicaca, the northern lake basin on the Altiplano (a high endorheic plateau in Peru and Bolivia) is the largest navigable water body in the world lying at over 3000 metres.

Following brief descriptions by Spanish chroniclers, the first scientific observations were undertaken by A. d'Orbigny during his voyage in South America (1826–1833). Until the turn of the century the map considered to be the most reliable was that made by Pentland, following two voyages on the lake (1827–28/1837–38). Further brief or multidisciplinary expeditions then took place, notably those of Agassiz and Garman (1876) and Créqui de Montfort and Sénéchal de la Grange, reported by Neveu-Lemaire in 1906. Each of these attempted to describe the precise geographical setting, with greater or lesser success. Following the last great multidisciplinary expedition, the Percy Sladen Trust Expedition (1936–39), more specialised studies started to be carried out.

Only the most recent data are taken into account in this synthesis chapter. The main reference work is that of Boulangé and Aquize Jaen (1981), the cartographic material used being the 5 maps at 1/100,000 published in 1978 by the Hydrological Services of Peru and Bolivia (Hidronav, 1978) which were drawn from 7000 soundings to the nearest 0.1 m, based on the average measurements over 41 years of observations.

The catchment area

This is shared unequally between the Republics of Peru and Bolivia, with its long axis running NNW-SSE, the coordinates of its extreme points being as follows (Fig. 1):

14°09'06"-17°08'29" latitude south

68°03'34"-71°01'42" longitude west

To the north, the catchment area is bounded by the Vilcanota Cordillera culminating at 5480 m, at a point where the eastern and western Cordilleras join and which marks the limit of the Altiplano.

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Figure 1. The Lake Titicaca catchment area (adapted from Boulangé and Aquize Jaen, 1981).

The eastern boundary follows the line of the summits of the Carabaya and Aricoma Cordilleras (altitudes over 4800 m) then curves in towards the south to follow the Cordillera Apolobamba whose general level slopes down to 4800 m.

Further south, the limits of the catchment approach within 10 km of the lake and the altitude is of the order 4500 m. This narrowing of the catchment area is related to the heavy erosion on the Amazonian flanks by the Rio Beni, which penetrates the Cordillera up to the foot of the Illampu peak (highest point of the catchment at 6322 m), between the Apolobamba and

Real Cordilleras. The eastern boundary continues along the Cordillera Real and then follows the edge of the Altiplano in the La Paz region (4000 m altitude).

The southern flank of the catchment area runs along summits ranging in height between 4500 and 4800 m and is open to the south by the sole outflow from the lake, the river Desaguadero, which then flows south to drain into Lake Poopo.

The western boundary runs north-west – south-east along the western Cordillera, whose summits do not exceed 5000 m altitude.

The lake basin

The Lake Titicaca basin, having the same orientation as that of the catchment area, is divided into two sub-basins (Fig.2):

-in the north the Lago Grande or Great Lake,

-in the south, the Lago Menor or Lago Huiñaimarca, joined by the Tiquina strait which is about 850 metres wide with a maximum depth of 21 metres. The geographical limits of the lake are as follows:

15°13'19"-16°35'37" latitude south and 68°33'36"-70°02'13" longitude west.

The 915 km long shoreline is poorly defined to the north and west where it merges with the flood plains of the main inflow rivers. The eastern shoreline, in contrast, is better defined since it follows a fault line.

The greatest length over water measured between the furthest points on the shore along NNW-SSE line passing through the Tiquina strait is 178 km, and the greatest width at right angles to this axis is 69 km in Lago Grande and 41 km in Lago Huiñaimarca.

Measurements of the area and volume of Lake Titicaca vary slightly depending on the methods of calculation used -planimetry (Tables 1 and 2) or direct calculation from the Hidronav data (Table 3). These differences lead to estimates which are not incompatible with one another, since a drop in water level of 1 m from the current level (3809 m above sea level) would lead to a decrease in water area of 1000 km² and a decrease in volume of about 8 km³.

From direct calculations from cartographic data, the total area of the lake is 8562 km² and the volume of water 903 km³, the area of the islands being negligible (1.3 % of the total area).

Lago Grande

Block diagrams made from sounding points enable 4 bathymetric zones in Lago Grande to be differentiated (Figs 2 and 3): (Figure 3 can be found as a separate figure at the end of the book)

- a deep water zone over 200 metres deep in the central part of the lake;



Figure 2. Bathymetry of Lake Titicaca (adapted from Boulangé and Aquize Jaen, 1981).

the deepest point measured by Boulangé and Aquize Jaen (1981), situated near Soto island, was 284 m deep;

- a zone of moderate depths of between 100 and 200 metres depth, best developed along the western margins of Lago Grande;
- a zone of intermediate depths of between 100 and 20 metres, occupying parts of Puno and Achacachi Bays;
- and finally the littoral margins, with less than 20 metres water depth, very narrow along the eastern shore but well developed in the Puno, Rio Ramis and Achacachi Bays.

As a general rule, Lago Grande is characterised by a steeply shelving

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	Lago Mayor	Puno Bay	Total	Lago Menor	Lake Titicaca
A km²	6542	589	7131	1428	8559
A _l km²	49	1	50	61	111
A _l / A %	0.7	0.1	0.7	4.2	1.3
A _E km²	6493	588	7081	1367	8448
L km	151	41		62	178
I _M	69	30		41	69
I _m	43	14	47	23	48
Z _M	284	51		42	284
Z _m	135	8	125	9	105
Z _m / Z _M	0.47	0.16	0.44	0.21	0.37
C km	455	155	610	305	915
$DC \simeq C / \sqrt{\pi}$, A	1.59	1.80	2.04	2.28	2.79
V x 10 ⁹ m ³	878.7	4.8	883.5	12.36	895.86

Table 1. Morphological parameters of the lake (from Boulangé and Aquize Jaen, 1981)

Table 2.	Relation	between	surface	area/depth	and	volume/depth	(from	Boulangé	and	Aquize
				Jaen,	198	1)				

Lago Mayor and Puno Bay							
Depth in m	Water s km²	urface area %	Volume m ³ x 10 ⁹ %				
0 20 50 100 150 200 250 284	6493 5407 4816 3886 3332 1948 800	100 76.3 68 54.8 47 27.5 11.3	124.5 153.3 217.2 180.3 130.5 66.6 11.1 883.5	14.1 17.4 24.6 20.4 14.8 7.5 1.2			
Puno Bay							
0 5 10 20 50 52	588 221 146 75 2	100 37.6 24.8 12.8 0.3	1.95 0.91 1.09 0.89 0.002 4.84	40.3 18.8 22.5 18.4 0 100			
		Lago Meno	or .				
0 5 10 20 30 40 42	1367 768 434 167 44 4	100 56.2 31.7 12.2 3.2 0.3	5.27 2.97 2.90 0.98 0.20 0.04 12.36	42.7 24.0 23.5 7.9 1.6 0.3 100			

Lake Titicaca							
Depth in m	AR	EAS	Volume				
	km²	%	m ³ x 109	%			
	9562 7	100	002.7	100			
1	7541.5	88	805.7				
2	7304.7	85	888.0	08			
3	70527	82	881.8	97.5			
4	6889 5	80	875	97			
5	6754	79	868.2	96			
10	6269.5	73	836	92.5			
15	5963	70	805.5	89			
20	5714	67	776.5	86			
25	5606.5	65	748.2	83			
30	5500.7	64	720.5	80			
35	5411.2	63	693.3	77			
40	5320.7	62	666.5	74			
45	5249.2	61	640.1	71			
50	5167.2	60	614.1	68			

Table 3. Relation between surface area/depth and volume/depth (from Boulangé and Aquize Jaen, 1981)

bottom from straight off the shore and its mean depth is 135 metres. The islands represent less than 1 % of the total area of 7132 km², which itself represents 84% of the total area of lake Titicaca. The volume of Lago Grande is 889 km³, or 98.5% of the total water volume.

Lago Huiñaimarca

From the figures given above it can be seen that Lago Huiñaimarca only makes up a very small proportion of the total water volume, although its area of about 1470 km² represents 16 % of the area of Lake Titicaca. This reflects its shallow mean depth (9 m) and the large area (of the order of 56%) less than 5 m in depth.

Three bathymetrical zones are differentiated (Figs 2 and 3):

- the deepest zone down to 41 m in the north, known as the Chua trough,
- a central basin in the centre-west beyond the line of islands with a maximum depth of 20 metres,
- a shallow area extending between and around these two zones, with a sill about 7 metres deep between the Chua trough and the central depression.

As a general rule, the slopes are very gentle, with the exception of the eastern margin of the Chua trough. The outflow of the Rio Desaguadero is not deeply cut, but forms a sill (5 metres deep) so it is only when the lake level is at 3804 m or higher that the lake and the upper reaches of the Desaguadero are in communication. The current at the outflow from Lake Huiñaimarca is slight, and sometimes even reversed (Carmouze and Aquize Jaen, 1981), the true outlet being situated further south at Aguallamaya (Fig. 2).

At the point where the Tiquina Strait enters Lago Huiñaimarca there is

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a sill 21 m deep. Lago Huiñaimarca would thus appear to be a basin that could have functioned as an entity independent of the Lago Grande in the past and in which two separate basins could have existed (see Chapter III).



II.2. General aspects of present-day sedimentation

LUIS A. RODRIGO and DENIS WIRRMANN

The two principal parameters that control the distribution of the sediments in the lake are on one hand, the relation between allochothonous elements of dertrial origin, and autochothonous elements of bio-geochemical origin, on the other, the nature of bio-chemical sedimentation. Therefore, the different facies of the actual sediments will be defined in function of their carbonate concentration, determined by the Bernard Calcimeter, in organic matter measured by the ashing and insoluble residues left after the acid attack (left in acid solution).

The synthesis is a summary of the results presented by Boulange *et al.* (1981). These authors analyzed some 20 samples taken from the mouths of the main tributaries of the lake, and some from the affluents up river, as well as superficial sediments (top 20 cm) taken by Ekman grab in depths of less than 40 meters and by dredging in deeper water. Samples were taken from a total of 100 stations spread over the Lago Menor and the Lago Mayor.

Riverine inputs

These have been classified by attempting to take into account the homogeneity of the sources of each input (Fig. 1); four types of sand have been distinguished:

- Sands of volcanic origin: three types of mineral, occurring in variable proportions, are predominant: monoclinal pyroxene, hypersthene and green and brown hornblendes. The proportion by weight of heavy minerals is always greater than 1% (samples 21, 7 and 5). The light fraction is composed of quartz, labradorite and traces of mica.
- Sands from Devonian formations are characterised by a high proportion of tourmaline and weathered zircon associated with metamorphic minerals such as hornblende and andalusite (sample 9). The quartz, which dominates the light fraction, is associated with small quantities of plagioclases, kaolinite and smectites.
- Sands from Carboniferous formations have as their main characteristic

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Figure 1. Geology of the catchment of Lake Titicaca and location of the sampling sites in inflow rivers used by Boulangé *et al.* (1981).

the presence of beautiful, clear, unworn andalusites with a salmon pink pleochroism (samples 2, 11 and 13). The light fraction contains quartz associated with traces of micas, plagioclases, kaolinite and smectites.

- Sands from Cretaceous formations are characterised by the abundance of very worn zircons and tourmaline (samples 10 and 19), sometimes associated with titanaugite (sample 14). The light fraction contains quartz and traces of plagioclases and smectites.

In terms of the lake inflow rivers, only the dominant characteristic of the catchment area are recognisable:

- The Río Ramis and its tributaries drain the four formations described above, but the volcanic formations are the one that determine the sand type;
- The Río Huancane has a relatively homogeneous catchment area draining Cretaceous landscapes;
- The Ríos Ilave and Coata transport sands characteristic of volcanic formations with a clay fraction dominated by montmorillonite associated with a little illite;
- The Río Suchez brings to the lake a sandy fraction formed mainly of quartz (due to the presence of aeolian dunes along its banks); the fraction in suspension is dominated by illite associated with a little montmorillonite and traces of kaolinite.

Lacustrine sedimentation

Six sedimentary facies have been defined (Fig. 2) in terms of their concentrations of insoluble residues, carbonates and organic matter.

A) The detrital facies (I)

These are sediments containing more than 70% of clastic components, less than 25% of organic matter and very little carbonate. They are distributed along the lake shores, at the mouths of inflows and in the the deep water zone of Lago Grande, with local differences in granulometry.

On the whole, the most coarse type consists of pebbles of sandstone, quartzite or volcanic rocks coming directly from the Plio-Quaternary formations bordering the lake and deposited on the beaches adjoining these outcrops (Fig. 1). Sandy beaches occur along the west coast of Lago Huiñaimarca and Lago Grande at the mouths of the Río Ilave and Suchez. In the latter, the sandy bottom extends for 5 km, reaching a depth of 50 m. Silty muds form homogeneous compact deposits, coloured brown by the presence of haematite. These occur at the mouths of inflow rivers, and form two large detrital fans in Lago Grande in the bay of the Río Ramis and in Puno Bay (Río Coata). The finest detrital deposits are silty-clay muds forming the superficial sediments in the central depression of Lago Grande.

B) The carbonate detrital facies (II)

These sediments contain less than 25% organic matter and 20 to 70% of carbonates. They are localised in the littoral zone, occurring between the



Figure 2. Distribution map of the surface sediment facies, adapted from Boulangé et al. (1981).

detrital (I) and organic (VI) facies. Despite similarities in facies between Lago Grande and Lago Huiñaimarca, the following differences should be noted:

- because of the abundant aquatic vegetation related to the shallowness of the water column, the organic content is higher in Lago Huiñaimarca (mean 17% compared to 12%) as is the $CaCO_3$ content (mean 44% compared to 34%).
- The residual, more sandy fraction, is greater in Lago Grande.

C) The carbonate facies (III)

These are sediments containing more than 60% of carbonates (calcite and aragonite) and less than 25% organic matter derived from plankton decompo-

sition. These fluids, homogeneous sediments contain remains of macrophytes, mollusc shells and crustacean carapaces. The silty-clay fraction, making up 80% of the total sediment, is formed mostly of grains of calcium carbonate, associated with a small proportion of illite and montmorillonite. This facies occurs particularly in the zone occupied by Characeae, that is to say in depths of 4 to 10 metres and is better represented in Lago Huiñaimarca.

D) The organo-detrital facies (IV)

This facies, characterised by an organic matter content of between 25 and 50% and by less than 15% of carbonates, occurs in the deeper water areas of Lago Huiñaimarca (between 20 and 40 m) and between 80 and 100 m in Lago Grande. These are dark, gelatinous muds with a strong odour of hydrogen sulphide and contain very few shells.

E) The carbonate organo-detrital facies (V)

These are also gelatinous muds made of 95% silt and clay, containing some shells and plant remains and in which the organic matter and carbonate contents vary between 25-50% and 15-50%, respectively. It is intermediate between the carbonate (III) and organo-detrital (IV) facies and has only been recorded in Lago Huiñaimarca on flat bottoms between 10 and 20 m depth.

F) The organic facies (VI)

This is the sediment occurring in bays in shallow water areas (<2 m) where totora is abundant. The organic matter content exceeds 50% and there is very little carbonate. The detrital fraction (25 to 45%) is made up of medium and fine sands, silt and a high proportion of clay.

The spatial distribution of the various facies is related to water depth, as this controls the distribution of the aquatic vegetation, which plays an important role as filter for the allochthonous input. For example, in going from the shore to the centre of the basin in Lago Huiñaimarca, the following succession is recorded: in the shallow water areas (<2 m) either a detrital facies (I) in areas close to inflow rivers, or an organic facies (VI); then between 2 and 4 metres, the sediments are of the carbonate detrital facies (II), grading into the carbonate facies (III) in the zone of maximum development of Characeae. Between depths of 10 and 20 metres, the superficial sediments are of the carbonate organo-detrital type (V). Beyond the zone colonised by aquatic vegetation the sediments are organo-detrital (IV), the detrital phase having a finer grain size than at the lake margins.

The same sequence is found in the main bays of Lago Grande, but in the central basin itself the most common sequence is as follows:

- a zone of sediments of detrital origin, which can extend down to 50 m depth depending on the slope, with the grain size classification being of finer sands at the margins and of medium sands at between 20 and 50 metres depth.
- carbonate detrital sediments (or organo-detrital) between 50 and 100 metres depth and beyond this depth, fine detrital deposits.

The sedimentation dynamics are still poorly known, but the sedimentation rates vary according to the facies and between Lago Grande and Lago Huiñaimarca. For example in the case of carbonate deposits (III), Boulangé *et al.* (1981) give a velocity of sedimentation rate of 0.5 mm y⁻¹ for Lago Grande, whereas in Lago Huiñaimarca this rate was 10 times higher (Wirrmann *et al.*, 1988). According to the latter, the sedimentation rate for the organo-detrital facies in Lago Huiñaimarca was of the order of 0.2 mm y⁻¹.

Plate 2. Above: very accidented reliefs resulting from the Andes formation occur at the altitude of the Lake Titicaca. They form high islands or steep margins as in many places along the Lago Grande shoreline. Center: view from the Tiquina Strait towards the Lake Huiñaimarca and the Taquiri and Paco Islands; Down: the lake region receives in sommer heavy rainfalls. Rain and hail are frequent but, despite the altitude, snowfalls are very occasional. (Photos Claude Dejoux.)



II.3. Temporal sedimentation patterns in the nearshore littoral of Lago Huiñaimarca

MICHAEL W. BINFORD, MARK BRENNER and DANIEL R. ENGSTROM

Historical changes in material delivery to a lake are measurable by stratigraphic study of dated lake sediment cores (Binford et al., 1987). In some lakes, broad littoral areas lie between the shoreline and open water, where sediment cores are usually collected. Biological and physical processes in the littoral zone transform materials delivered to the lake from land (e.g. uptake of dissolved nutrients by macrophytes), and can function as a sink for materials that arrive in dissolved or particulate form. Dense macrophyte stands in the littoral zone serve a regulatory function for the entire lacustrine ecosystem (Wetzel, 1983), in part by influencing the movement of nutrient (C, N, and P) and non-nutrient (e.g. silts) materials from the land to openwater areas of the lake (Howard-Williams, 1985; Howard-Williams and Lenton, 1975). Sequestering of material in the nearshore littoral can affect paleoecological inferences that are based on study of mid-lake sediment profiles. The vast littoral area of the smaller, southeastern basin of Lake Titicaca (Huiñaimarca) undoubtedly controls material flux from the terrestrial to the limnetic environment, and lutimately to open-water sediments. Seventy percent of the 1430 km² lake is <10 m deep, and 58% of the lake bottom is covered by macrophyte beds (bathymetry from 1:100,000 scale map produced by the "Dirección de Hidrografía de la Marina de Bolivia" and the "Instituto Geografico Militar del Perú" (Anon, 1978); macrophyte data from Collot et al., (1983).

Sediment accumulation rates in the littoral zone of this lake are major components of material budgets for the whole system, and their measurements are necessary for studies of long-term ecological alterations of the lake caused by climatic fluctuation and human activities. Net accumulation of nutrients and silts in the nearshore, shallow region of the lake represents intercepted material that might otherwise be deposited in deep water.

This study reports measurements of changing material accumulation rates in nearshore sediments of Lago Huiñaimarca during the last 150 years. We present results of ²¹⁰Pb dating and sediment chemistry based on analysis of a 98 cm sediment-water interface core taken in a small bay near the archaeological site of Lukurmata, on the north side of the Taraco peninsula

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Figure 1. Map of Lago Huiñaimarca showing the location of Lukurmata mud-water interface core 22-VIII-86-1 on the north side of the Taraco peninsula, Bolivia.

(Fig. 1). Sediment accumulation rates in the littoral zone of Lake Titicaca are compared with measurements made in other tropical and subtropical lakes, and we discuss the implications with respect to ecological processes in open water.

Materials and methods

Sediment-water interface core 22-VIII-86-1 was taken with a 4 cm diameter, 1.9 m long, plastic-barrel piston corer. The core was extruded in the field at 2 cm intervals to 10 cm depth, at 1 cm intervals to 30 cm depth, and at 4 cm

intervals thereafter to the base of the section. Dry weight and water content of the sediment were determined by weight loss on drying for 24 hours at 105°C. Organic matter content was measured by weight loss on ignition for 2 hours at 550°C (Håkanson and Jansson, 1983). Total C was measured coulometrically (Huffman, 1977), with a Coulometrics Inc. model 5011 coulometer and a System 120 prep line set at 950°C. Selected levels were analyzed for inorganic carbon with the coulometer and a System 140 prep line using 2N HClO₄.

Ash samples were digested in 1N HCl for total P (Andersen, 1976), total S and cation analyses. Total P was determined on a Coleman Model 14 spectrophotometer after blue color development with ascorbic acid-ammonium molybdate reagent (Anon, 1975). Cations were read on a Jarrell-Ash ICP 9000 and sulfur was measured turbidometrically on the spectrophotometer (Anon, 1975). Total N was determined by autoanalyzer following a modified Kjeldahl digestion (Nelson and Sommers 1975). ²¹⁰Pb assay was done by distillation extraction of the granddaughter radionuclide ²¹⁰Po, dissolution of the condensate in weak HCl, and plating on a silver planchette for alpha spectrometry (modified from Eakins and Morrison, 1978). A known amount of ²⁰⁸Po was added to samples as a yield tracer. Dates were calculated with the Constant Rate of Supply (CRS) Model (Appleby and Oldfield,1978), without mixing terms.

Results

Physical and chemical characteristics of Lukurmata core 22-VIII–86-1 are presented in Fig. 2. Bulk density (ρ) and percent dry weight increase with depth in the core. Organic matter (L.O.I. 550°C) constitutes between 23.6% and 51.2% of the sediment dry weight and is highly correlated with total C content (r = 0.96, p < 0.0001). Total C is virtually all organic C, as inorganic (carbonate) carbon levels are negligible. Nitrogen content in sediments (11.2–31.4 mg g⁻¹) is higher than levels found in upland soils (<2.0 mg g⁻¹): Brenner unpublished data). Mean total P content in the sediments (0.82 ± 0.28, n = 19) is comparable to values measured in upland soils (1.10 ± 0.24, n = 9). Total S in sediments is variable (1.3–35.9 mg g⁻¹) and uncorrelated with total C (r = -0.31, p > 0.05). Ca ranges from 8.4 to 15.1 mg g⁻¹ and Na ranges between 0.2 and 13.4 mg g⁻¹. Both Ca and Na are correlated with organic matter (r = 0.58, p < 0.001 and r = 0.80, p < 0.0001, respectively). Mg, K, Mn and Fe concentrations are intercorrelated and probably bound, for the most part, in clays.

Under the assumptions of the CRS dating model, log unsupported ²¹⁰Pb activity versus core depth (Fig. 3a) is linear if: 1) flux of ²¹⁰Pb to the sediments has remained constant over the past 150 years; 2) there has been no post-depositional ²¹⁰Pb mobility; 3) sediments have not been mixed physically; 4) net sediment accumulation rate has remained unchanged during the past 150









Figure 3(a). Unsupported ²¹⁰Pb activity plotted against depth in Lukurmata sediment-water interface core 22-VIII-86-1. Vertical bars indicate the ²¹⁰Pb activity in the interval and horizontal bars show the counting error. (b). Age vs. depth and age vs. cumulative mass plots. Ages computed by interpolation between analysed intervals. (c) Bulk sediment accumulation rate vs. age with sedimentation rates plotted at the basal age of each dated interval.

years; and 5) bulk density (ρ) is constant over the length of the core. There is no evidence that ²¹⁰Pb flux has fluctuated in the recent past, and postdepositional migration of ²¹⁰Pb is unlikely because lead is bound tightly to sedimented particles at the high pH of Titicaca waters and muds. Sediment mixing and homogenization are ruled out by strongly variable concentrations of chemical constituents, even in the topmost sediments (Binford *et al.*, 1988; and see Fig. 2 above). Deviations from the straight line in Fig. 3a are thus attributable to changing bulk density (Fig. 2) and changing net sediment accumulation rates (Fig. 3c). These two factors also determine the age/depth plot in Fig. 3b. The age/cumulative mass plot in Fig. 3b illustrates variable sedimentation rates.

Bulk sediment accumulation rate over the ²¹⁰Pb-dated section of the core has ranged from a low of 0.003 g cm⁻² yr⁻¹ for the intervals starting at 143 and 65 years ago, to 0.018 g cm⁻²yr⁻¹ for the period starting 106 years ago (Fig. 3c). The mean net sedimentation rate for the last 143 years is 0.009 g cm⁻² yr⁻¹. Most recently, net sediment accumulation from 1984–1986 has averaged 0.015 g cm⁻² yr⁻¹, and is close to the highest values recorded. Total residual unsupported ²¹⁰Pb accumulation at the core site is 2.76 pCi cm⁻², which is equivalent to a ²¹⁰Pb flux rate to the sediments of 0.09 pCi cm⁻² yr⁻¹. The radiocarbon date at the base of the section is 1950 ± 80 BP (GX-13052), yielding a mean sediment accumulation rate over the last two millennia of 0.011 g cm⁻² yr⁻¹ (Binford and Brenner, 1989).

Discussion

Organic-rich surface sediments of Lukuramta core 22-VIII-86-1 resemble nearshore surficial deposits mapped previously north of the Taraco Peninsula

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Lake	Country	Accumulation rate (mg cm ⁻² yr ⁻¹)	Time span (years)	Dating method
1. Titicaca	Bolivia	9.0	143	²¹⁰ Pb
2. Titicaca	Bolivia	10.7	1950	¹⁴ C
3. Miragoane	Haiti	11.0	129	²¹⁰ Pb
4. Yaxha	Guatemala	38.0	420	pollen
5. Sacnab	Guatemala	45.0	420	pollen
6. Quexil	Guatemala	16.0	420	pollen
7. Chimaj	Guatemala	15.0	146	²¹⁰ Pb
8. Chilonche	Guatemala	47.0	153	²¹⁰ Pb

Table 1. Mean bulk sediment accumulation rates in Lake Titicaca (Lukurmata Core 22-VIII-86-1) and other tropical lakes.

(Boulange *et al.*, 1981). Most of the organic matter is probably composed of macrophyte and algal remains that were produced near the site of deposition. The remainder of the sediment is comprised largely of carbonate-free silts and clays.

The 210 Pb deposition rate computed from the Titicaca core, 0.09 pCi cm⁻² yr^{-1} , is low compared with the value of ~0.5 pCi cm⁻² yr^{-1} measured in many areas of the northern hemisphere, which apparently have greater upwind ²²²Rn sources (El-Daoushy, 1988). Low fallout ²¹⁰Pb deposition rates reported for other tropical lakes (e.g. Lake Miragoane, Haiti = 0.09 pCi cm⁻² yr⁻¹ [Brenner and Binford, 1988]; Lakes Chilonche and Chimaj, Guatemala = $0.134 \text{ pCi cm}^{-2} \text{ yr}^{-1}$ and $0.085 \text{ pCi cm}^{-2} \text{ yr}^{-1}$, respectively [Brenner et al., 1990]) are attributed to low rates of ²²²Rn exhalation from the nearby sea surface. The low ²¹⁰Pb inventory at the Lukurmata site may be a consequence of low radon emission rates from the surrounding land and lake surface, post-depositional loss of sediment and associated ²¹⁰Pb from the core site, or a sedimentation hiatus. Drving of the core site may have occurred in the recent past when the lake level dropped. Site desiccation would not only interrupt sediment and ²¹⁰Pb deposition, but would result in loss of previously deposited material. Low lake stages between 1910 and 1920, and again in the 1940s would be the most probable times for drying of the core locality. The most recent lower level was in 1972-1974, when the lake was about 3 m shallower and the site should have been barely covered with water. Nevertheless, sedimentary discontinuities are not evident (Figs 2 and 3), and a low ²¹⁰Pb fallout rate probably accounts for the small total residual ²¹⁰Pb.

Net sediment accumulation rate is influenced by many factors including: watershed-lake ratio, drainage geology and soils, lake and watershed morphometry, vegetation coverage and human disturbances, lake productivity, sediment diagenesis, location of the core site, etc. The long-term mean bulk sediment accumulation rate at the Lukurmata site is compared with accumulation rates measured in six other tropical lake basins (Table 1). Although the lowest net sediment accumulation rate was measured in Lake Titicaca (9.0 mg cm⁻² yr⁻¹ for the past 143 years), the value is similar to



Figure 4. Accumulation rates of organic matter, C, N, and P vs. age in Lukurmata mudwater interface core 22-VIII-86-1. Rates are plotted at the basal age of each dated interval. Accumulation rates were computed by multiplying the bulk sediment accumulation rate in the interval by the fraction of the bulk sediment that each variable comprises. Where sedimentary concentrations were unavailable for dated intervals, the mean concentation for the two contiguous intervals was used.

rates measured in Lakes Miragoane, Quexil and Chimaj (11.0, 16.0 and $15.0 \text{ mg.cm}^{-2}.\text{yr}^{-1}$, respectively).

Contemporary (1984–1986) bulk sediment accumulation rate measured at the Lukurmata site is low relative to recent (2–10 years) lake-wide mean values recorded in Florida, USA lakes (Table 2). Likewise, the accumulation of organic matter, carbon, nitrogen and phosphorus proceeds more slowly at the Lukurmata site than in Florida lakes (Table 2).

Nearshore sediment accumulation rate has not been constant over the last 143 years (Figs 3c and 4). The magnitude of changes in the net sediment accumulation rate over time exceeds the magnitude of changes in stratigraphic concentration of organic matter and nutrients (C, N, and P). Furthermore, organic matter, C, N, and P all show generally increasing concentrations progressing upward over the ²¹⁰Pb-datable portion of the core. Therefore, shifting patterns of organic matter and elemental accumulations (Fig. 4) display similar trends to those for bulk sediment (Fig 3c).

During the past century there have been two general trends in sediment

Table 2. Recent sediment accumulation rates $(mg.cm^{-2}.yr^{-1})$ in Lake Titicaca (Lukurmata core 22-VIII-86-1) and 34 subtropical Florida lakes. Florida data are for mid-lake samples and represent average lake-wide sedimentation rates for the past 2–10 years (Binford and Brenner 1986). Titicaca data are site-specific accumulation rates for the topmost 2 cm of the core (1984–1986).

	Bulk	Organic	Carbon	Nitrogen	Phosphorus
		matter			
Titicaca	15.2	7.8	3.8	0.48	0.024
Florida					
Mean	234.	39.8	20.0	1.83	0.171
s.d.	407.	19.3	10.3	1.07	0.134
range	32-2080	15.3-88.9	6.9-46.7	0.56-4.42	0.024-0.586

Accumulation Rates

accumulation rate. First, there was a decline in sediment accumulation over four decades, starting at a high point 106 years ago. Then, after the low that began about 1920, there was a general rise in the sediment accumulation rate that began about 1950. The causes for increasing sediment accumulation in the complex Titicaca littoral are not obvious, but several mechanisms could be responsible. Two major events, one terrestrial and one lacustrine, coincide with rising sediment accumulation since the 1940s. Agrarian reforms in the 1950s (Ponce Sangines 1989) probably altered land use practices in the vicinity of Lukurmata. Increased riparian construction and cultivation normally increases the flux of nutrient and non-nutrient materials from the land to the lake. Second, following the low lake stage of the mid-1940s, Lake Titicaca rose again, with two minor declines in the late 1950s and early 1970s, into the mid-1980s. The highest recorded lake level of the past century was in 1985–1986, at 3811.5 m a.s.l. (Ponce Sangines 1989). Higher lake level corresponds with higher rainfall and increased discharge from the canal surrounding the Cerro Wilakollu. In this seasonally arid drainage system, increased discharge would probably have delivered more eroded material to the sediments at the core site during wetter years.

Preliminary results from Lukurmata core 22-VIII-86-1 demonstrate that the Lukurmata littoral area has accumulated organic-rich sediment for nearly two millennia (Binford *et al.*, 1988). Increased rates of bulk sediment accumulation and nutrient sequestering during the last 40 years are correlated with lake level change and agrarian reform. Nevertheless, until details of historical land use at Lukurmata are known and effects of lake-level fluctuation are better understood, the quantitative impact of these events on nearshore sedimentation cannot be evaluated.

Sediment data from the Lukurmata site suggest that extensive macrophyte beds dominated by *Schoenoplectus tatora*, *Potamogeton*, *Myriophyllum*, *Elodea*, *Chara* and associated filamentous Chlorophytes, use dissolved nutrients and trap suspended particulates, thereby sequestering nutrient and non-nutrient materials in the nearshore environment. Nutrient scavenging in the littoral zone probably limits nutrient delivery to open-water regions of Lake Titicaca, thus limiting phytoplankton standing crops and maintaining high water transparencies with Secchi disk depths ranging from 2 to 7 m (Lazzaro 1985). Macrophyte growth occurs year-round, so there is no seasonal dieback and nutrient release as occurs in temperate lakes (Carpenter and Lodge 1986). Lake-level change and harvesting by local inhabitants probably keeps the macrophyte community in an aggrading phase (*sensu* Bormann and Likens 1979, Vitousek and Reiners 1975, Gorham *et al.* 1979), which results in the littoral being a net sink of nutrients that enter the lake by overland or nearshore groundwater flow.

Preliminary age/depth data from deep-water Titicaca cores indicate that total sediment accumulation rates in nearshore areas are of the same order of magnitude as those recorded at open-water sites. An 8.36 m core taken in 8.5 m of water near Huatajata has a sedimentation rate of 0.22 cm yr^{-1}

(3430 yrs B.P. at 7.55 m). A 3.27 m core collected in 8.3 m of water near Guaqui has a sediment accumulation rate of 0.10 cm yr⁻¹ (3160 yrs B.P. at 3.20 m). At Lukurmata, 20 cm of sediment accumulated during the past 143 years (0.14 cm yr⁻¹), and 96 cm accumulated in 1950 years (0.05 cm yr⁻¹).

Data from the Lukurmata core suggest the importance of the Titicaca littoral zone in controlling open-water productivity and sedimentation. Future work will be directed at comparing the Lukurmata core with other nearshore profiles and sampling cores throughout Lago Huiñaimarca to assess lake-wide sediment deposition patterns.

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References of chapter II

- AGASSIZ (A.), GARMAN (S.W.), 1876. Exploration of Lake Titicaca. Bull. Mus. Comp. Zool., Harvard, 3: 273-349.
- ANDERSEN (J.M.), 1976. An ignition method for determination of total phosphorus in lake sediments. *Wat. Res.*, 10: 329–331.
- Anon., 1975. Standard methods for the examination of water and wastewater. APHA (American Public Health Association). 14th ed.
- Anon., 1978. Lago Titicaca. Mapas al 1/100,000, PERU-BOLIVIA, HIDRONAV N○ 3100– 3200–3300–3400–3500. Instituto Geográfico Militar, Lima, Perú.
- APPLEBY (P.G.), OLDFIELD (F.), 1978. The calculation of Lead-210 dates assuming a constant rate of supply of unsupported ²¹⁰Pb to the sediment. *Catena*, 5: 1–8.
- BINFORD (M.W.), BRENNER (M.), 1986. Dilution of ²¹⁰Pb by organic sedimentation in lakes of different trophic states, and application to studies of sediment-water interactions. *Limnol. Oceanogr.*, 31: 584–595.
- BINFORD (M.W.), BRENNER (M.), 1989. Resultados de estudios de limnología en los ecosistemas de Tiwanaku. In: Arqueología de Lukurmata, Alan Kolata ed., Vol. 2. Instituto Nacional de Arqueología y Producciones Pumapunku, La Paz, Bolivia: 213–236.
- BINFORD (M.W.), BRENNER (M.), WHITMORE, (T.J.), HIGUERA-GUNDY (A.), DE-EVEY (E.S.), LEYDEN (B.), 1987. Ecosystems, paleoecology and human disturbance in subtropical and tropical America. *Quat. Sci. Rev.*, 6: 115–128.
- BINFORD (M.W.), BRENNER (M.), LEYDEN (B.), 1988. Paleolimnology of Tiwanaku ecosystems: results of second-year studies. Unpubl. report, 47 p.
- BORMANN (F.H.), LIKENS (G.E.), 1979. Pattern and Process in a Forested Ecosystem. Springer Verlag, New York, 253 p.
- BOULANGE (B.), VARGAS (C.), RODRIGO (L.A.), 1981. La sédimentation actuelle dans le lac Titicaca. *Rev. Hydrobiol. trop.*, 14 (4): 299–309.
- BOULANGE (B.), AQUIZE JAEN (E.), 1981. Morphologie, hydrographie et climatologie du lac Titicaca et de son bassin versant. *Rev. Hydrobiol. trop.*, 14 (4): 269–287.
- BRENNER (M.), BINFORD (M.W.), 1988. A sedimentary record of human disturbance from Lake Miragoane, Haiti. J. Paleolimnol., 1: 85–97.
- BRENNER (M.), LEYDEN (B.), BINFORD (M.W.), 1990. Recent sedimentary histories of shallow lakes in the Guatemalan savannas. J. Paleolimnol., 4: 239–252.
- CARMOUZE (J.P.), AQUIZE JAEN (E.), 1981. La régulation hydrique du lac Titicaca et l'hydrologie de ses tributaires. *Rev. Hydrobiol. trop.*, 14 (4): 311–328.
- CARPENTER (S.R.), LODGE (D.M.), 1986. Effects of submerged macrophytes on ecosystem processes. *Aquatic Botany*, 24: 341–370.
- COLLOT (D.), KORIYAMA (F.), GARCIA (E.), 1983. Répartitions, biomasses et productions des macrophytes du lac Titicaca. *Rev. Hydrobiol. trop.*, 16 (3): 211–318.
- DEEVEY (E.S.), RICE (D.S.), RICE (P.M.), VAUGHAN (H.H.), BRENNER (M.), FLANNERY (M.S.). Mayan urbanism: impact on a tropical karst environment. *Science*, 206: 298–306.
- D'ORBIGNY (A.), 1835-1847. Voyage dans l'Amérique méridionale. Pitois-Levrault et Cie., Paris, 7 tomes, 11 vol.
- EAKINS (J.D.), MORRISON (R.T.), 1978. A new procedure for the determination of Lead-210 in lake and marine sediments. *Int. J. appl. Radiat. Isotopes*, 29: 531–536.
- EL-DAOUSHY (F.), 1988. A summary on the Lead-210 cycle in nature and related applications in Scandinavia. *Envir. Int.*, 14: 305–319.
- GILSON (H.C.), 1939–1940–1955. The Percy Sladen Trust Expedition to Lake Titicaca in 1937. *Trans. Linn. Soc. London*, 1: 357 p.
- GORHAM (E.), VITOUSEK (P.), REINERS (W.), 1979. Ecosystem succession and nutrient retention. Annu. Rev. Ecol. and System., 10: 53-84.
- HÅKANSON (L.), JANSSON (M.), 1983. Principles of lake sedimentology. Springer Verlag, New York, 316 p.

- HOWARD-WILLIAMS (C.), 1985. Cycling and retention of nitrogen and phosphorus in wetlands: a theoretical and applied perspective. *Freshw. Biol.*, 15: 391-431.
- HOWARD-WILLIAMS (C.), LENTON (G.M.), 1975. The role of the littoral zone in the functioning of a shallow tropical lake system. *Freshw. Biol.*, 5: 445–459.
- HUFFMAN (E.W.D., Jr.), 1977. Performance of a new automatic carbon dioxide analyzer. *Microchemical Journal*, 22: 567–573.
- LAZZARO (X.), 1985. Poblaciones, biomasas y producciones fitoplanctónicas del Lago Titicaca. Rev. Inst. Ecol., La Paz, 7: 23–64.
- NELSON (D.W.), SOMMERS (L.E.), 1972. A simple digestion procedure for estimation of total nitrogen in soils and sediments. J. Environ. Qual., 1: 423–425.
- NEVEU-LEMAIRE (M.), 1906. Les lacs des hauts-plateaux de l'Amérique du Sud. Imprimerie Nationale, Paris. 197 p.
- PENTLAND (J.B.), 1838. The laguna of Titicaca and the valleys of Yukai. Collao and Desaguadero in Peru and Bolivia, from geodesic and astronomic observations made in the years of 1827 and 1828, 1837 and 1838. British Admiralty Chart, no 1268. London.
- PONCE SANGINES (C.), 1989. Lukurmata: investigaciones arqueológicas en un asentamiento urbano de la cultura Tiwanaku. Ensayo de historiación del avance científico (1895–1988). In: Arqueología de Lukurmata. Alan Kolata ed., Vol. 1. Instituto Nacional de Arqueología y Producciones Pumapunku. La Paz, Bolivia: 11–85.
- VITOUSEK (P.L.), REINERS (W.M.), 1975. Ecosystem succession and nutrient retention: a hypothesis. *Bioscience*, 25: 376–381.
- WETZEL (R.G.), 1983. Limnology (2nd ed.). W.B. Saunders Company, Philadelphia, 767 p.
- WIRRMANN (D.), MOURGUIART (P.), de OLIVEIRA ALMEIDA (F.), 1988. Holocene sedimentology and ostracodes repartition in Lake Titicaca. Paleohydrological interpretations. *In:* Quaternary of South America and Antartic Peninsula, Rabassa ed., A.A. Balkema, 6: 89–127.

III. PALEOHYDROLOGYIII.1. A 20,000 years paleohydrological record from

Lake Titicaca

DENIS WIRRMANN, JEAN-PIERRE YBERT and PHILIPPE MOURGUIART

The Bolivian Altiplano is an endorheic basin which extends from 16° to 20° S. Lat. and from 65° to 69° W. Long., with altitudes ranging from 3700 to 4600 metres, covering 200,000 km² between the Western and Eastern Cordilleras which are 6500 m high (Fig. 1). From north to south, three major lacustrine areas occupy this high plateau:

- Lake Titicaca at 3809 metres above sea level, covering 8562 km²;
- Lake Poopo at 3686 m.a.s.l. covering 2530 km²;
- Coipasa-Uyuni, a group of dry salt lakes, covering 11,000 km² at 3653 m.a.s.l.

Over the last 1.8 million years these basins have registered episodes of greatly enlarged lake areas. According to Lavenu *et al.* (1984) and to Servant and Fontes (1978, 1984), the Pleistocene record of Titicaca lake level fluctuations can be summarised as follows:

- during the Early Pleistocene the paleolake Mataro rose with a water level established at 140 metres above the present level. This stage is related to the end of the Calvario glaciation (Servant, 1977) and the corresponding deposits are recognisable mainly at the NW edge of the basin;
- the paleolake Cabana occurred during the middle Pleistocene with a water level established at 90 metres above the present Lake Titicaca level; the associated sediments are present on the eastern and western shores of the basin;
- then with the retreat of the Sorata glaciation (Servant, 1977) the Ballivian stage occurred with a paleolake in which the water level was 50 metres higher than the present level; its deposits are located in the southern and western coasts of the basin;
- a lacustrine terrace, located at 15 metres above the present lake level, is attributed to the paleolake Minchin (Upper Pleistocene, between 27,000 and 21,000 years BP), according to correlations with the Central Altiplano;
- the last Pleistocene lacustrine episode, at approximately 10 500 BP, corresponds to the Tauca stage, giving rise to a paleolake slightly larger in area than the Lake Titicaca. According to Hastenrath and Kutzbach (1985) and Kessler (1985) this stage is attributed to an increase of 50% to 30% in the rainfall over the Altiplano.

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Figure 1. The Bolivian Altiplano showing the extent of the Tauca lacustrine phase (modified after Servant and Fontes, 1978):

- 1: over 4500 m
- 2: 4000-4500 m
- 3: 3500-4000 m
- 4: below 3500 m
- 5: extent of Lake Tauca
- 6: dry salt lakes

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In this paper we will describe the Titicaca lake level oscillations occurring during the final stages of the Upper Pleistocene and the Holocene. This study is part of the GEOCIT programme (Géodynamique du Climat Intertropical) developed by the ORSTOM and was carried out in Bolivia with the collaboration of the Universidad Mayor de San Andrés (UMSA) at La Paz.

Materials and methods

Several sediment core samples have been collected using various coring devices depending on the water depth (Fig. 2) in the different areas recognised in Lago Grande and Lago Huiñaimarca (Chapter. II.1).

Firstly, a number of transects were made with a Züllig corer with a maximum core length 180 cm and a diameter of over 33 mm (Vargas, 1982; Wirrmann, 1982). 17 cores were later collected using a 6 metre Mackereth corer (Barton and Burden, 1979) to provide sedimentological records covering a longer time period. After that the characteristics of the present distribution of the ostracod fauna (Chapter.VI.4.f) and pollen content (Ybert 1988 and in prep.) in the superficial sediments and sediment-water interface was studied by analysing Mondsee core samples (maximum length 80 cm with a diameter of over 60 mm). A total of 56 cores samples were collected in 1981–1983 and 1986–1988.

The sedimentological results are based on a detailed lithological description of the core sections (texture, colour after the Munsell Soil Color Charts ed. 1975, faunal contents) and on quantitative and/or qualitative determination of the main components (geochemistry, X-ray, microgranulometry, binocular and microscopic observations). Exhaustive descriptions of the core samples are available in de Oliveira Almeida (1986), Wirrmann (1987) and Wirrmann *et al.* (1988).

The paleontological data relating to the ostracod fauna are presented in Mourguiart (1987) and those concerning the pollen record in the two Mackereth cores (TD, TD1) are available in Ybert (1988).

The paleoenvironmental interpretations are made in reference to qualitative changes in the sedimentological records, in the ostracod fauna and in pollen composition and their comparison with the present distribution.

We will present here paleohydrological data back to 20,000 BP, based on a radiochronology obtained by dating organic matter or ostracod carapaces (¹⁴C Accelerator Mass Spectrometry methodology) or the bulk sediment (classical ¹⁴C method).

Results

Comparative analysis of the sedimentological and paleological data based on this chronology and assuming the absence of turbid or biological perturbation



Figure 2. Core localities in Lake Titicaca: Mackereth core: ▼ Züllig core: ● Mondsee core: ★

in the core samples, allows us to propose the following interpretative curves for lake level fluctuations (Fig. 3).

The Upper Pleistocene

There is only one core, TD1, which provides a partial radiochronology for this period. The ages obtained span a time interval of between 18,000 and 21,000 BP (Wirrmann, 1991), but the base of the core may roughly corre-



Figure 3. Composite curves of lake level fluctuations. From top to bottom:

- the empirical extreme values of the water level are indicated for the western central depression of Lago Huiñaimarca, based on palynological evidence;

- based on sedimentology and ostracod associations for Lago Huiñaimarca and Lago Grande:

– ¹⁴C dates with error intervals: \perp
spond to an estimated age of 24,000 BP, assuming a constant sedimentation rate.

The palynological records argue in favour of a very low lake level in comparison with the present level:

- before 21,000 BP, pollen contents are equivalent to those from the *Isoetes* zone of present-day high altitude glacial lakes of the Hichu Kkota valley (Ybert in prep.). They imply a water depth of between 0.4 to 4 metres;
- from about 21,000 to 20,000 BP, a stage of very shallow water depth (less than 0.2 metres) is inferred by the very low amounts of algae;
- from 20,000 to 19,100 BP the water depth increases to 4 metres;
- from about 19,100 to 18,000 BP, the water depth is estimated at between 1 and 8 metres.

The overall trend in sediment composition up until 18,000 BP (i.e. very fine mineral deposits of 71 to 47 % of clay, containing scattered grains of vivianite, greigite and framboidal pyrite from the base of the core to the top of this section and with a mean amount of 10 % carbonates), does not allow lake level fluctuations to be determined during this time interval. Moreover these deposits have no present equivalent in Lake Titicaca or in the glacial lakes. The absence of evaporites during this period of very low lake level, when the Desaguadero outlet could not have been functioning, is still not explained. Hence it is difficult to be precise about the paleobathymetrical environment from sedimentological evidence.

No dating has been obtained for the TD1 core between 18 185 BP and 7700 BP. The palynological characteristics of the corresponding core section (only 54 cm in length) argue in favour of a higher lake level than during the preceding stage, but lower than the present level at first, and then exceeding it. The presence of diatoms of deep, freshwater environments (S. Servant-Vildary, pers. comm.) at the top of this section confirms this final high lake level. From correlations with the Central Altiplano lacustrine basins, this stage can be attributed to the Tauca phase. Despite the lack of lithological unconformities, a hiatus in sedimentation is likely to have occurred. It is only with a more detailed chronology that it will be possible to be precise about the timing of this event.

From the age of 9600 BP obtained at a level of 291.5–295.5 cm, the base of the TD core (core section 320–483 cm) dates from the ultimate Upper Pleistocene. From palynological evidence, these azoic, clayey non-carbonate sediments, containing framboidal pyrite, are attributed to a lake level established between 5–10 metres below the present for the 483–420 cm, section, then quite similar to the present level and finally from 360 cm, slightly higher than at present. The top of this core section may represent the Tauca lacustrine phase, which is defined with more precision in the Central Altiplano, although still not totally reliably (Servant and Fontes, 1978, 1984).

From their lithology, cores TB and TB2 taken in the Chua hollow in Lago Huiñaimarca belong to this time period, but have not been dated radiochronologically up until now. Unfortunately the specific environmental

conditions in Lago Huiñaimarca make it difficult to propose sedimentological correlations with cores TD and TD1. Here again, more ¹⁴C datings are needed to clarify the chronology of lake level changes.

The Holocene

For this period the chronology is documented with more precision: 8 datings for Lago Grande and 16 datings for Lago Huiñaimarca. Five major stages are defined:

- from approximately 10,500 BP to 7700 BP, a decrease in lake area took place after the Tauca episode. Lake Titicaca registered a severe drop in level, progressive at the beginning and becoming more and more drastic afterwards. This decrease is well recorded in core TD: at 9600 BP the water level was established at around 15 metres below the present level (high amounts of terrestrial and wetland pollen and of miscellaneous algae, but with very few *Pediastrum* and *Botryococcus*). The sediments became coarser and richer in carbonates and in organic matter;
- from 7700 BP to 7250 BP, the lake level dropped by at least 50 metres in the Lago Grande, as inferred from the basal evaporites in core TJ. Gypsum precipitation also occurred in Lago Huiñaimarca: it is observed in the lower core sections of cores TB2, TC, TC1 and TE and in cores TD and TD1. Titicaca was characterised by very shallow, small and scattered individual basins in Lake Huiñaimarca (Chua hollow and western central depression) and around the central depression of Lago Grande. The consequence of this drought episode was the reduction of 42% in the water area of the lake and a loss of 30% of its water volume (Fig. 4). The communications between Lago Grande and Lago Huiñaimarca, and between the Chua hollow and the western central depression in the latter, were cut off;
- from about 7250 BP to 4000 BP, from the evidence on continuing individual basins, there was at first a stage of a very low lake level established around 10–45 metres below the present level. From the evidence of the ostracod fauna and diatom flora associations, the dissolved salts concentration rose to more than 40 g l^{-1} in the western central depression of Lago Huiñaimarca. Then, the occurrence of oligohaline to freshwater ostracod species and pollen types indicate a progressive and slight rising of the water level. The sediments belong to the carbonate facies, including variable quantities of shells and Characeae remains. The waters were oligohaline in both the Lago Grande and in the Chua hollow;
- from about 4000 BP to 2000 BP, after a short but notable phase of decrease, a progressive rise in lake level took place, giving a water depth established about 10 metres below the present level. Major inflows of water enriched in Na⁺ and Cl⁻ are noted, but the waters were fresh from 3600 BP. The communication between the Lago Grande and Lago Huiñaimarca was re-established at the end of this period;



Figure 4. Block diagram of the present Titicaca basin showing the emerged land (hatched), the state of water level during the maximum lowering (50) and the corresponding water area (after Wirrmann, 1987 and Wirrmann *et al.*, 1988).

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- after 2000 BP and before 1000 BP, Lake Titicaca assumed its present state and the Desaguadero became an effective outlet. Lake level oscillations of 5-10 metres amplitude are noted. According to historical chroniclers (Ramos Gavilán, 1621) a slight rise in level occurred around 350 BP. This event is not recorded in all the Mackereth cores, because the majority of them have been sampled beyond the water depth which allows the recording of such interannual lake level fluctuations. It is only in four cores (TC, TC1, TE and TF) and also in two Züllig cores (B1 and D4) that this event is recognisable.

III.2. Ancient lake environments as deduced from pollen analysis

JEAN-PIERRE YBERT

Studies carried out on two cores from Lago Huiñaimarca, TD and TD1 (see Chapter III.1), have demonstrated great variations in the palynological content of sediments and reveal the presence in the lower layers of large quantities of *Isoetes*, an aquatic fern not recorded at present in Lake Titicaca, but abundant in the high Bolivian valleys at between 4250 and 4750 m altitude (Collot, 1980).

To interpret the fossil spectra in paleoclimatological terms, it is therefore necessary to know the present-day pollen sedimentation pattern in lakes whose environment would appear to correspond as closely as possible to that which Lake Titicaca experienced in the past. The lakes selected for this study were, firstly, those in the Hichu Kkota valley close to Lake Titicaca and situated in a botanically high altitude environment (Fig. 1 A and B) and secondly, Lake Poopo, characterised by a halophytic flora (Figs 1 A and C).

The paleobathymetric interpretations are derived from the comparison of present-day spectra obtained from analysing superficial samples taken along transects across these lakes as well as in Lake Titicaca with a Mondsee corer (Figs 1 and 2).

The fossil samples analysed were taken at 10 cm intervals on cores TD and TD1 and were then processed using the following steps:

- treatment with 10% HCl, with boiling 15% KOH, acetolysis, densimetric separation using bromoform with d = 2, mounting in glycerine/gelatine.

The palynomorphs identified in the analyses were lumped into 4 large groupings in terms of their dominant ecological origin: terrestrial habitats or wetland habitats (marshes, bogs, flood-plains bordering the lake) or their biological origin: aquatic macrophytes or planktonic organisms.

The taxa making up these groupings are given in the legends to the pollen diagrams.

Location of the sampling transects for the present-day samples and their corresponding environments

The Hichu Kkota valley, situated to the east of Lake Titicaca, belongs to the Puna region, a high Andean province also known as the "Puna Brava"

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which is typified by its very sparse vegetation dominated by tussock-forming grasses. The mean annual temperature is 5.4°C at 4310 m altitude and the thermal gradient is of the order of 0.53°C per 100 metres (Ostria, 1987). Annual precipitation averages 834 mm, with a peak in January-February.

Ostria (1987) and Collot (1980) have studied the vegetation of this valley and have established the altitudinal distribution of the various plant species. Among the taxa recognised in the palynological preparations are:

Nototriche violacea recorded above 4900 m; Valeriana, present between 4650 and 4750 m in dry areas; Caryophyllaceae and liguliflorous Compositae, which are especially abundant above 4500 m; Gentiana present between 4300 and 4800 m, but most abundant around 4500 m; Juncaceae which make up most of the vegetation of the bogs (known as "bofédales") above 4550 m, where they are associated with numerous mosses and liverworts; Plantago, abundant below 4500 m in the bottom of damp valleys; Elodea, Myriophyl-lum, Lilaeopsis, Ruppia and Schoenoplectus tatora, whose upper limits of occurrence are respectively 4700, 4500, 4400 and 4300 m; Isoetes, present in all the lakes between 4250 and 4750 m.

The phytoplankton (Iltis, 1984) is represented by *Botryococcus braunii*, *Spirogyra*, *Zygnema*, *Staurastrum*, *Mougeotia* and *Pediastrum*, to mention only those taxa recognisable in our preparations. It should be noted, however, that *Pediastrum* is absent from Jankho Kkota, the highest lake.

One transect was studied for each of the main lakes in the valley (Fig. 1): Khara Kkota (4310 m), Khotia (4450 m) and Jankho Kkota (4690 m), lakes with mean water temperatures of 9.6°C, 8.8°C and 7°C respectively (Iltis, 1988).

Lake Titicaca is situated in the province of Puna *sensu stricto*, at a mean altitude of 3810 m; it is subject to a cold and semi-arid climate with a mean annual temperature of 8°C and rainfall of between 790 and 950 mm per year. The herbaceous vegetation is dominated by Gramineae, but Compositae and Chenopodiaceae are also well represented. Trees are infrequent, the main species being *Polylepis tomentella*, *Buddleya incana*, *Cantua dependens* and *Eucalyptus* sp. introduced in the last century.

The aquatic macrophytes recognised in our preparations were Lilaeopsis, Hydrocotyle, Myriophyllum, Elodea, Schoenoplectus tatora, Potamogeton and a small amount of Ruppia. It is noteworthy that Lilaeopsis, which flowers regularly in Lakes Khara Kkota and Khotia, has never been found flowering in Lake Titicaca.

The phytoplankton found in our preparations is composed mainly of *Botryococcus braunii*, *Pediastrum*, *Ankistrodesmus*, *Spirogyra*, *Mougeotia*, *Zygnema* and *Staurastrum*.

The mean surface water temperature is 12 to 14°C for Lago Grande and 10 to 16°C for Lago Huiñaimarca (Iltis, 1987).

Three transects were studied (Fig. 2), the first in Lago Grande extending from Achacachi Bay in the direction of Sun Island, the two others in Lago Huiñaimarca, from Suana Island in a southerly and south-westerly direction



Figure 1. Map showing location of study lakes.



Figure 2. Map showing location of transects in Lake Titicaca.

respectively. The deepest samples ($D \times 6$ and $D \times 7$) were taken with a Züllig type grab (Figs 2 and 3).

Lake Poopo, situated at 3690 m altitude, is also in the province of Puna *sensu stricto*, but is in an area with a colder and more arid climate than Lake Titicaca. The mean annual temperature is 6 to 8 °C and rainfall is between 300 and 400 mm per year.

The surrounding vegetation is a mountain steppe dominated by Gramineae and Compositae, with frequent cactuses in rocky areas. Because of the saline soils, the vegetation around the lake itself is composed mainly of Chenopodiaceae.

The water is generally saline (up to 50 g 1^{-1}), so *Myriophyllum* and *Schoenoplectus* are rare. The most abundant aquatic plant is *Ruppia* which covers nearly 60 % of the lake area. The phytoplankton is dominated by the genera



Figure 3. Composite palynological diagram of the Lake Titicaca transect.

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Nodularia, Oscillatoria, Dictyosphaerium, Peridinium and Cyclotella (Iltis et al., 1990).

One transect was studied in the southern part of the lake, extending northwest from Quillacas (Fig. 1).

Present-day distribution of palynomorphs in relation to water depth and environmental factors

Analysis of superficial samples (Ybert, in prep.) has demonstrated a direct relationship between the distribution of the palynomorphs and the zonation of aquatic macrophytes, which itself is related to water depth (Collot, 1980).

The main features of this distribution, which is well marked on the transect in Lago Grande (Fig. 3), can be summarised as follows:

The taxa from terrestrial environments are on the whole abundant (12 to 35%) from the lake shore down to 1 m depth, with a maximum of 60 to 80% at about 40 cm. Their proportion then decreases rapidly to 5 to 15% between 1 and 2 m and then stays around 5% down to 8 to 10 m depth. After 10 m it increases again (10%) as a result of the input of allochthonous components and wind-dispersed taxa;

The taxa from wetland habitats are very abundant in the shoreline zone, where fungal spores dominate. They remain abundant (15 to 35%) from 40 cm to 2 m depth, where they are made up essentially of fungal spores and Cyperaceae pollen. They then decrease rapidly so as to represent only 2 to 5% of the palynological spectrum from 4 m onwards;

Aquatic macrophytes occur at less than 4% in the shoreline zone (between 0 and 40 cm depth), then increase to 15 to 40% in the *Myriophyllum* zone (between 40 cm and 2 m), then decrease rapidly so as to disappear almost completely from 4 m depth;

Algae are poorly represented (5%) down to 40 cm depth where they are made up essentially of *Spirogyra*. *Botryococcus* appears between 0 and 20 cm, increases slightly (3 to 10%) down to 2 m and then becomes dominant (80 to 90%) after 10 m. *Pediastrum* appears around 60 cm depth and remains at levels of between 2 and 10% until about 4 m, then becomes dominant between 4 and 10 m (50 to 70%) and then decreases (<5%). *Ankistrodesmus* (10 to 15%) is common in the *Myriophyllum* zone but not abundant elsewhere.

On the whole, this distribution was found to be almost identical in all the transects studied; however, the composition of the 4 main groupings of palynomorphs varies in relation to the ambient environment and characterises certain abiotic factors.

The altitudinal factor (Fig. 4) is characterised by:

- much higher percentages of Valeriana at Jankho Kkota (2%) than at Khotia (<0.2%);
- progressively higher percentages of Amaranthaceae-Caryophyllaceae (0.1

to 0.4%), liguliflorous Compositae (<0.1 to 1%) and Juncaceae going from Lake Titicaca to Lake Jankho Kkota;

- the absence of *Valeriana*, *Gentiana* and Juncaceae from the superficial sediments of Lake Titicaca;
- the proportion of *Gentiana* ranging 2 to 4% at Khotia and less than 1% at Jankho Kkota and Khara Kkota;
- high percentages of *Isoetes* at Khara Kkota (21% on average for all spectra, 80% between 0.1 and 3.5 m depth) but lower at Khotia and Jankho Kkota (2 and 10% respectively) and very low in Titicaca (<0.2%);
- high percentages of *Plantago* in the shallow water samples at Khara Kkota (33%) and Khotia (20%), but very low at Jankho Kkota (<1%) and Titicaca (<2%);
- high percentages (>25%) of Cyperaceae between 1.8 and 4 m depth in Titicaca, less than 5% in Khara Kkota and Khotia and less than 1% at Jankho Kkota;
- the absence of *Pediastrum* in Jankho Kkota, percentages of less than 3% in Khotia and Khara Kkota and greater than 20% in Titicaca;



Figure 4. Composite palynological histograms of the lakes arranged according to altitude.



The salinity factor is characterised by:

- high percentages (10 to 20%) of *Ruppia* in Lake Poopo, less than 0.2% in Titicaca and absence from the high altitude lakes;
- high percentages (up to 70%) of Chenopodiaceae in Lake Poopo, around 10% in Titicaca and less than 2% in the Hichu Kkota valley;



Figure 6. Composite palynological diagram of core TD1.



- percentages of *Myriophyllum* exceeding 40% in Achacachi Bay (Titicaca) and less than 0.2% in Lake Poopo;
- percentages of *Pediastrum* of less than 0.6% in Lake Poopo, but at times exceeding 60% in Titicaca.

Deductions concerning the Lake Titicaca environment over the last twenty thousand years

Interpretation of the palynological diagrams for cores TD and TD1 (Figs 5 and 6), in comparison with the present-day data summarised above, leads us to propose the following succession of environmental conditions in the central-west basin of Lago Huiñaimarca:

Palynological zone E, at the base of core TD1, before 21,000 BP.

The presence of *Valeriana*, *Gentiana*, *Isoetes* and Juncaceae is evidence of a 'Puna Brava' environment, with a temperature close to that currently occurring at about 4500 m altitude, or 3 to 5°C below present temperatures.

The lake was shallow and the shorelines were occupied by "bofédales" identical to those occurring in the Hichu Kkota valley above 4500 m. The lake bottom was vegetated by *Isoetes* and not by totora as is the case now (Photos 1 and 2).

Palynological zone D, base of core TD, 400-200 cm on TD1, between about 21,000 and 17,500 BP.

In general terms the environment stays the same, but there is firstly a drop in lake level (sub-zone D3), then a progressive rise from 3 to 15 metres.

The presence of *Valeriana* and Juncaceae, and the total absence of *Pedias-trum* in the sub-zone D2, indicates an environment comparable to that of Lake Jankho Kkota. The temperature was therefore 5 to 7°C lower than at present, and then 2 to 5°C lower in D1.

Palynological zone C, 425–320 cm on TD, 200–150 on TD1, between about 17,500 and 11,000 BP.

Isoetes is still numerous in sub-zone C2, *Pediastrum* and *Plantago* are present, but *Valeriana* and Juncaceae have disappeared. This association is equivalent to that of the superficial sediments in Lake Khara Kkota. The temperature has increased to reach values close to those at present and at the same time the lake level has risen significantly to 2 to 10 m below the present level. The "bofédales" with Juncaceae have disappeared from the margins to be replaced by meadows with *Plantago*.

During the period corresponding to sub-zone C1, *Isoetes* and the wetland palynomorphs disappear completely and *Pediastrum* increases. The lake environment becomes more or less the same as at present. Temperatures are the same as or slightly higher than at present and the lake level is about 5 m higher.

There is then the start of a drop in temperature and lake level from 12,000 or 11,500 BP (corresponding to the top of the C zone).

Palynological zone B, 320–110 cm on TD, 150–85 cm on TD1, between about 11,000 and 4100 BP.

The drop in level started in C1 is accentuated, and from about 10 500 BP the depth of the lake decreases rapidly so as to become of the order of 2 to 5 m only. The depth then decreases even more and varies between 0 and 1 m, the lowest levels being between about 7700 and 6500 BP and then about 4500 BP.

The temperature was lower than at present by 1 to 3° C during the period corresponding to sub-zone B5 (about 11,000–9500 BP), close to the present value between 9500 and 5500 BP, with slight cooling at about 8700 and 6500 BP, and then again 1 to 2° C cooler from about 5000 BP.

The predominance of fungal spores, *Spirogyra* and Chenopodiaceae pollen, the presence of *Ruppia* and the rarity of *Myriophyllum* and *Pediastrum* indicate a saline environment comparable to that of Lake Poopo.

Palynological zone A, top of TD and TD1, from about 4100 BP.

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This zone is marked by a rapid increase in the percentage of algae and the almost complete disappearance of wetland palynomorphs, which indicates a major rise in lake level.

The water level was 10 to 15 m below the present level between about 3000 and 2000 BP, then at the same level from 2000 to 1500 BP. A well-marked drop occurred about 2500 BP together with oscillations of an amplitude of about 5 m marked by sharp increases in the percentage of *Pediastrum*.

Temperatures were close to those at present, but slight cooling could have taken place at about 3000, 1200 and 600 BP.

The absence of *Pediastrum* during the first half of the period corresponding to the sub-zone A3 (before 3600 BP) indicate that the waters were still saline. The proportion of Cyperaceae then increased at the start of the sub-zone A2 and it is only from about this period (about 3000 years BP) that totoras must have developed, giving Lake Titicaca the appearance by which it is known today.

References of chapter III

- BARTON (C.E.), BURDEN (F.R.), 1979. Modification to the Mackereth corer. *Limnol. Oceanogr.*, 24: 977–983.
- COLLOT (D.), 1980. Les macrophytes de quelques lacs andins (lac Titicaca, lac Poopo, lacs des vallées d'Hichu Kkota et d'Ovejhuyo). ORSTOM, La Paz: 115 p., multigr.
- HASTENRATH (S.), KUTZBACH (J.), 1985. Late Pleistocene climate and water budget of the South American Altiplano. *Quat. Res.*, 24: 249–256.
- ILTIS (A.), 1984. Algues du lac Titicaca et des lacs de la vallée d'Hichu Kkota (Bolivie). *Cryptogamie, Algologie*, 5 (2-3): 85-108.
- ILTIS (A.), 1987. Datos sobre la temperatura, el pH, la conductibilidad eléctrica y la transparencia de las aguas de superficie del lago Titicaca boliviano (1985–1986). UMSA. ORSTOM, La Paz, Informe 3: 19 p., multigr.
- ILTIS (A.), 1988. Datos sobre las lagunas de altura de la región de La Paz (Bolivia). UMSA.OR-STOM, La Paz, Informe 4: 50 p., multigr.
- ILTIS (A.), DEJOUX (C.), WASSON (J.G.), 1990. Datos hidrobiológicos referentes al lago Poopó (Bolivia). UMSA. ORSTOM, La Paz, Informe 21: 19 p., multigr.
- KESSLER (A.), 1985. Zur Rekonstruktion von spätglazialem Klima und Wasserhaushalt auf dem peruanisch-bolivianischen Altiplano. Zeitsch. für Gletscherkunde und Glazialgeologie, 21: 107–114.
- LAVENU (A.), FORNARI (M.), SEBRIER (M.), 1984. Existence de deux nouveaux épisodes lacustres dans l'Altiplano péruano-bolivien. *Cah. ORSTOM, sér. Géol.*, 14 (1): 103–114.
- MOURGUIART (P.), 1987. Les Ostracodes lacustres de l'Altiplano bolivien. Le polymorphisme, son intérêt dans les reconstitutions paléohydrologiques et paléoclimatiques de l'Holocène. Thèse Univ. Bordeaux 1, 263 p.
- OLIVEIRA ALMEIDA (L.F. de), 1986. Estudio sedimentológico de testigos del lago Titicaca. Implicaciones paleoclimáticas. Tesis UMSA, La Paz: 136 p.
- OSTRIA (C.), 1987. Phytoécologie et paléoécologie de la vallée alto-andine de Hichu Kkota (Cordillère orientale, Bolivie). Thèse Univ. Paris 6, 180 p.
- RAMOS GAVILAN (Fray A.), 1621 (1976). Historia de Nuestra Señora de Copacabana. La Paz, Academia Boliviana de la Historia.
- SERVANT (M.), 1977. Le cadre stratigraphique du Plio-Quaternaire de l'Altiplano des Andes tropicales en Bolivie. Supp. Bull. AFEQ, 1, 50: 323–327.
- SERVANT (M.), FONTES (J.C.), 1978. Les lacs quaternaires des hauts plateaux des Andes boliviennes. Premières interprétations paléoclimatiques. *Cah. ORSTOM*, sér. Géol., 10 (1): 9–23.
- SERVANT (M.), FONTES (J.C.), 1984. Les basses terrasses fluviatiles du Quaternaire récent des Andes boliviennes. Datations par le ¹⁴C. Interprétation paléoclimatique. *Cah. ORSTOM*, sér. Géol., 14 (1): 15–28.
- VARGAS (C.), 1982. La sédimentation subactuelle d'un bassin intramontagneux: le lac Titicaca (Partie lac Huiñaimarca, Bolivie). Thèse Univ. Bordeaux 1, 91 p.
- WIRRMANN (D.), 1982. Primeros resultados sobre el estudio de los testigos del lago Huiñaimarca. ORSTOM, La Paz: 34 p., multigr.
- WIRRMANN (D.), 1987. El lago Titicaca: sedimentología y paleohidrología durante el Holoceno (10.000 años B.P. Actual). UMSA.ORSTOM, La Paz, Informe 6: 61 p.
- WIRRMANN (D.), 1990. The Lake Titicaca. Bolivia-Peru. *In*: "Global Geological Record of Lake Basins" Kelts and Gierlowski Kordesch eds., Cambridge Univ. Press, Cambridge (in press).
- WIRRMANN (D.), MOURGUIART (P.), OLIVEIRA ALMEIDA (L.F. de), 1988. Holocene sedimentology and ostracodes repartition in Lake Titicaca. Paleohydrological interpretations. *In*: Quaternary of South America and Antartic Peninsula, Rabassa ed., A.A. Balkema, 6: 89-127.
- YBERT (J.P.), 1988. Apports de la palynologie à la connaissance de l'histoire du lac Titicaca

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(Bolivie-Pérou) au cours du Quaternaire récent. Inst. fr. Pondichery, Trav. sec. sci. techn., 25: 139-150.

- YBERT (J.P.), Sédimentation palynologique actuelle dans les lacs d'altitude de Bolivie. Relations avec la bathymétrie et avec l'altitude. (en préparation).
- YBERT (J.P.), Evolution bathymétrique du lac Titicaca au cours des vingt derniers millénaires d'après les données palynologiques (en préparation).

IV. CLIMATOLOGY AND HYDROLOGY IV.1. Climatology and hydrology of the Lake Titicaca basin

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Two separate active hydrological systems are present within the endorheic basin of the Altiplano: (i) Lake Titicaca (3809.5 m altitude) which overflows via the Río Desaguadero into Lake Poopo (3686 m), which itself overflows into the Salar de Coipasa (3657 m) during periods of high water level. (ii) The Salar de Uyuni (3653 m) into which flows the Río Grande of the Lipez (Fig. 1). These two systems can communicate with one another, but only at water levels higher than those recorded in 1986. At the present day Lake Titicaca is the only large and truly perennial surface water body.

The total area of the Lake Titicaca basin, to the offtake of the Desaguadero and including the area of open water, is $57,500 \text{ km}^2$, a quarter lying in Bolivia and three-quarters in Peru.

The catchment area covers 49,010 km², or 85% of the total basin, 1/5 being in Bolivia and 4/5 in Peru. Three-quarters of the catchment area is drained by six rivers (Table 1): The Rios Ramis (31%), Ilave (15%), Coata (11%), Catari (7%), Huancane (7%) and Suchez (6%).

4% of the basin lies at an altitude of between 5000 and 6400 m. The plain of the Altiplano makes up 28%, whereas the lake itself covers 15% of the area. The average gradient of the inflow rivers can vary from 35 m km⁻¹ in the upper parts of the basin to 0.8 m km^{-1} in the lower reaches. The main water courses are between 120 and 180 km long, but the Río Ramis measures 283 km long.

The lake shoreline is 915 km long. If it is assumed that the maximum inter-annual fluctuation in lake size is ± 200 m from the mean position of the shoreline around all its perimeter, this corresponds, over a total area of 8490 km², to a change in area of $\pm 2.0\%$ for the period 1968–1987. Because this figure lacks accuracy and calibration, this correction has not been applied to the hydrological calculations on the lake.

Functioning and hydrological balance of Lake Titicaca

In addition to an annual fluctuation in level, Lake Titicaca also undergoes

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Figure 1. Hydrological systems of the Bolivian-Peruvian Altiplano. Hydrography of the Lake Titicaca basin.

changes in level of a time-scale of several years. Since 1914, the range of variation has been 6.37 metres.

Lake Titicaca is fed by inflows from the surrounding rivers around its margins and by rain falling directly onto the lake. Losses are due to evaporation and surface drainage leaving via the Desaguadero. Certain authors (Carmouze, 1981; Lozada, 1985) believe there is infiltration of water through the lake bed, which contributes to the removal of dissolved salts, in addition to removal by surface outflow via the Río Desaguadero and physico-chemical and biochemical sedimentation within the lake itself. However, the water table along the shorelines lies above the level of the open water (Guyot *et al.*, 1990) and the aquifer contributes to the lake inflows.

Variations between years in precipitation and evaporation in the basin determine the water level of the lake. Water losses are also regulated by topographical sills occurring between the start of the Río Desaguadero (at Puente Internacional) and the downstream end of a broad section of the river known as the Laguna Lucuchala, extending some 30 km from the lake (to Aguallamaya). At the exit from the lake, the cross-section of the outlet forms a V-shaped sill whose bottom lies at an altitude of about 3803 m. This does not always form the sill controlling the outflow of water, which can be further downstream. The water flowing out of the lake flows south along the course of the Desaguadero which also receives water from other catchments on the Altiplano. The hydrological system of sills and water levels which controls the outflow of water from the lake therefore seems to be complex, especially at periods of low water level.

If inputs from rainfall and rivers make the level of the Laguna Lucuchala rise more quickly than that of the lake, water can flow out from both ends of the lagoon: southwards down the Desaguadero and northwards towards the lake. This supply of water to the lake will continue until the level of the lake reestablishes a new equilibrium. The current is then reversed and the Desaguadero regains its normal course. It should be stressed that this current reversal is a rare and transient phenomenon, only involving relatively small volumes of water in terms of mean values and overall lake balance.

The hydrological balance of Lake Titicaca can be expressed as:

$$P + Qt + Qn = Qd + Qi + Qe + dH$$

where:

P = Precipitation on the lake,

Qt = Inflows to the lake from rivers Qt = Pt - Et - Qef + n, where

Pt: is the precipitation on the inflow catchments,

Et: true evapo-transpiration,

Qef: any artificial exports out of the catchment, via water courses,

- n: changes in the quantity of water stored in the aquifer, whose value can be positive or negative
- Qn = Inflows to the lake from aquifers,
- E = Evaporation from the lake surface,
- Qd = Surface losses via the outflow, the Río Desaguadero,
- Qi = Infiltration through the lake bed, if such exists,
- dH = Changes in lake storage, whose value can be positive or negative.

The climate of Lake Titicaca basin

All the data used for both climatic and hydrological calculations are derived from records collected by the National Hydrology and Meteorology Services (SENAMHI) of La Paz and Puno.

Air temperatures

Mean annual temperatures

In areas lying below 4000 m altitude, the mean annual temperatures are between 7 and 10°C. Around the lake itself, however, they remain above 8°C. Boulangé and Aquize (1981) calculated that the mean annual temperature in the area of the lake should be 0°C and attributed the temperature difference to the thermal effects of the water body. The map of mean annual temperatures for Bolivia (Roche *et al.*, 1990) also shows values of close to 8°C over all the eastern half of the Bolivian Altiplano (7.3°C at Uyuni) and over Lake Poopo which has less thermal influence. The temperatures at stations lying between 3900 and 4000 m in the extreme south and north of the lake region are also of the order of 7°C. The lake makes the climate more temperate by decreasing the temperature range, but it does not seem to cause an increase of mean annual temperature of more than 2°C around its margins.

The isotherm map of the basin (Fig. 2) has been drawn using a correlation between temperature and altitude. Data from some stations outside the basin have also been used in order to obtain as wide a range of altitude as possible. The temperature gradient is 0.76° C 100 m⁻¹. For the area lying between 3800 and 4000 m, the temperature dispersion is great because of the effects of slope, shelter and distance from the lake. On the high peaks forming the margins of the basin, the mean annual temperature falls to below zero at around 5100 m.

Over the entire basin, the lowest temperatures occur in July, in the winter, whereas the highest temperatures occur between December and March, frequently being centred on February (Fig. 2).

Mean maximum and minimum temperature and temperature range

Figure 2 shows the changes in mean, maximum and minimum monthly temperatures and thus the temperature range over the course of the year for various stations in the basin.

The lowest mean minimum monthly temperature occurs in July. Values of 1.8° C are recorded at Copacabana (3810 m, on the lake shore) and -11.8° C at Charaña (4069 m, very far from the lake).

The mean maximum monthly temperatures for these stations are 15.3°C and 3.6°C, respectively. These occur in October or November when cloud cover is less than at the height of summer, when maximum rainfall occurs. For the same reason a second peak is recorded in March-April. In contrast the minimum temperature occurs in mid-winter since this takes place at end of night and therefore does not depend on the amount of sunshine.

Temperature range increases with distance from the lake, being $10.7^{\circ}C$ on the shoreline.

Climatology and hydrology of the Lake Titicaca basin

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Figure 2. Map of mean annual temperatures (°C) in the Lake Titicaca basin. Seasonal changes in average monthly mean and maximum temperatures, January to December.

Relative humidity

The mean annual relative humidity around the lake varies between 50 and 65%, at temperatures of 8 to 10°C. Lower values of 50 to 45% are recorded in the south of the basin. As a general rule, humidity increases with altitude, with a maximum value of 83% at Chacaltaya (5200 m). Variation over the year follows the rainfall pattern, with a maximum in January or February and a minimum in July. The values at Copocabana for these two periods are 70% and 52%, respectively.

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Sunshine duration

The annual sunshine duration near to the lake is 2915 h yr⁻¹ at Belen and 3000 h yr⁻¹ at Puno. Monthly minima of 167 and 180 h respectively are recorded at these two stations in January or February, during the height of the rainy season, whereas the maximum monthly values of 298 and 296 h occur in the middle of winter. The mean value for total solar luminous flux measured on the Altiplano at Viacha and Patacamaya is 8.8 mm day⁻¹ (Vacher *et al.*, 1989).

Winds

The dominant winds, usually of moderate strength and often affected by local breezes, are from the north-east in the rainy season and from the west to south-west the rest of the year.

Precipitation

All the rainfall data has been homogenised on a monthly and annual basis by a spatio-temporal vector method (VECSPAT, CLIMAR2 computer program); this is a matrix calculation based on pseudo-proportionality of the data (Hiez, 1972; Roche, 1988). This method provides automatic data processing and allows missing values to be estimated or entirely calculated.

The period subject to homogenisation and used to draw up the hydrological balance is 1968–1987; there were very few meteorological stations before 1968.

Spatial distribution of precipitation and rainfall mechanisms

The map of mean isohyetes for the period in question shows the spatial distribution of precipitation (Fig. 3).

On the whole, isohyetes are concentric around the lake, in the centre of which the maximum rainfall of over 1000 mm is recorded. Rainfall tends to decrease with distance from the lake, falling to minimum values of 500 to 600 mm. It then increases again towards the summits of the Eastern Cordillera, where extreme values can exceed 800 mm and towards the west, as far as the summit of the Pecajes Caranjas chain where maximum values can exceed 1000 mm.

This spatial distribution is determined by the regional air circulation patterns, by the influence of orography and by the major body of water formed by the lake.

On occasions, and almost exclusively during the rainy season, humid



Figure 3. Mean annual precipitation (mm) for the Lake Titicaca basin (period 1968-1987).

Amazonian air spills over the peaks of the Eastern Cordillera which rise to between 4500 and 6400 m. The north-east trade winds thus bring considerable quantities of water into the hydrological system, although much smaller quantities fall on the Altiplano than on the Amazonian slopes. As the air descends towards the lake, its pressure and temperature increase, leading to a decrease in relative humidity and a decrease in rainfall.

The rain shadow effect produced by the highest summits is particularly noticeable. The humid Amazonian airmass frequently remains blocked behind the highest mountains but manages to pass over the lower crests around the rest of the basin. The area around Suchez, sheltered by the Cordillera Apolobamba rising to over 6000 m, is for example particularly dry. The

lowest rainfall in the basin occurs to the south-west of Illampu and the Cordillera Apolobamba, where Escoma has only 507 mm and Belen 452 mm.

The influence of the lake is due to its extremely large surface area and its large volume caused by its depth. Its strong capacity to absorb solar radiation leads to water temperatures that are significantly higher (10 to 14°C) than those of the surrounding air and land. The lake is therefore continuously giving out heat to its surroundings. Air passing over the lake is warmed and picks up water vapour at the same time. It is subject to strong convection, particularly during the night when the temperature difference is accentuated. leading to thunderstorms which are heavier over the lake than on the land. Rainfall over the lake is greater than 800 mm and can reach 1000 mm. The maximum recorded is on Taquili Island; but the value of 1535 mm, much higher than elsewhere in the basin, would appear to be excessive - the calculated value is only 1272 mm. The humid air from the Lago Grande can cross the Yunguyo-Copocabana isthmus or the Tiquina Strait into the Lago Huiñaimarca, so that rainfall is also high over the western part of this basin, such as at Desaguadero (797 mm) and Tiquina (1050 mm). In contrast, in the south-eastern parts of the lake, the NE winds are deviated by the Illampu massif or are affected by down-drafts along its western flank and do not cross or only partially cross the Lago Grande, so the south-eastern parts of both the Lago Grande and Lago Huiñaimarca are relatively dry.

Weighted mean precipitation over the catchment areas and on Lake Titicaca

The quantities of monthly, annual and long-term rainfall were calculated by computer, by weighting the rainfall recorded at each meteorological station by its area of influence (Thiessen polygons), over the 20 year period (1968–1987). These quantities were calculated for each of the 82 individual catchments and for the main grouped catchments, using homogenised data in which missing data had been estimated and using entirely calculated data. Only the former will be presented in detail.

The lowest long-term average rainfall in this data set was 585 mm yr^{-1} for the catchment of the Río Keka and the highest was 811 mm yr^{-1} for the Río Coata catchment and 889 mm yr^{-1} over the Lago Grande. The long-term mean precipitation for the main catchments are given in Table 1.

The average precipitation over the whole basin is 758 mm yr⁻¹, or a total volume of 43.6×10^9 m³ yr⁻¹. The long-term average rainfall over the entire lake is 880 mm yr⁻¹, or a total volume of 7.47×10^9 m³ yr⁻¹, equivalent to a discharge of 236.7 m³ s⁻¹, The long-term average rainfall of the Lago Grande is 889 mm yr⁻¹ and that of the drier Lago Huiñaimarca 829 mm yr⁻¹. In terms of volumes, these values (6.42 and 1.05×10^9 m³ yr⁻¹) mean that 86% and 14% respectively of the total inputs to each of the two parts of the lake come from rainfall.

	AREAS km²	RAINFALLS mm	m ³ s-1	MODULE 10 ⁶ m ³	%	mm	ls ^{−1} km ^{−2}	KE %	DE mm
Ramis*	15 060	795.4	78.1	2464.1	29.0	163.6	5.2	22.2	632
Coata*	4 650	885.5	46.6	1470.9	17.3	316.4	10.0	35.7	569
llave*	7 290	699.6	42.7	1346.2	15.8	184.8	5.9	26.4	515
Huancane*	3 580	714.4	20.8	655.7	7.7	183.3	5.8	25.7	531
Zapatilla*	440	823.2	2.3	71.3	0.9	161.7	5.2	19.6	661
Peruvian basin*	31 010	769.0	190.4	6007.3	70.6	193.7	6.1	25.2	575
Complement	18 000	628.4	79.3	2501.1	29.4	139,0	4.4	22.0	489
Total basin	49 010	736.2	269.7	8508.4	100.0	173.6	5.5	23.6	563

Table 1. Water balance of the catchments of rivers flowing into Lake Titicaca (1968-1987)

* observed

Rainfall in the Bolivian part of the catchment amounts to 664 mm yr⁻¹, of which 635 mm yr⁻¹ falls on the land and 753 mm yr⁻¹ on the Bolivian part of the lake. Similarly, the Peruvian part of the catchment receives 786 mm yr⁻¹, of which 762 mm yr⁻¹ falls on the land and 964 mm yr⁻¹ on the Peruvian part of the lake. Expressed in terms of volume these values are equivalent to 9.01×10^9 m³ yr⁻¹, 6.48×10^9 m³ yr⁻¹ and 2.54×10^9 m³ yr⁻¹ for Bolivia and 34.5×10^9 m³ yr⁻¹, 29.4×10^9 m³ yr⁻¹ and 4.94×10^9 m³ yr⁻¹ for Peru. It can thus be seen that the Bolivian and Peruvian parts of the lake receive 34% and 66% respectively of the quantity of rainfall falling directly on the water surface.

The five catchments in Peru for which the discharge is known, together have a mean long-term precipitation of 769 mm yr^{-1} , whereas the rest of the basin receives 682 mm yr^{-1} .

Seasonal distribution of precipitation

The rainy season is centred on January (Fig. 4). The rains usually start in December and end in March. The middle of the dry season, which lasts from May to August, is in June. Two transitional periods separate these seasons, one in April and the other from September to November. Figure 4 shows the monthly variation in long-term average rainfall for the main catchments. Depending on the individual catchment, 65 to 78% of the annual precipitation falls during the four months of the rainy season, but only 3 to 8% in the dry season. The two intermediate periods account for 18 to 29%. Over the entire dry land part of the catchment, these values are 70%, 5% and 25%, respectively. They are the same for the lake itself and therefore for the entire Lake Titicaca basin.

The maximum monthly rainfall recorded over the lake reaches values of 300 to 450 mm, depending on the station, with a weighted mean of 353 mm in January 1984, a particularly rainy month.



Figure 4. Monthly rainfall distribution in the Lake Titicaca basin (period 1968-1987).

Hydrology of the Lake Titicaca basin

The hydrology of Lake Titicaca, and particularly the inputs and outputs of its water balance, have been studied previously by several workers (Monheim, 1956; Bazoberry, 1968; Kessler, 1970; Richerson *et al.*, 1977 and Carmouze *et al.* 1977, 1982). The balance can produce very different results depending on the precision of the data, its processing and on the period taken into consideration.



Figure 5. Map of the hydrographic network in the Lake Titicaca catchment and location of gauging stations. A histogram of the mean monthly discharge and the value for the mean annual discharge $(m^3 s^{-1})$ calculated over the observation period is shown for each station.

Discharges of the inflow rivers

Spatial distribution of riverine inputs to the lake

Mean monthly discharges are available from seven gauging stations in Peru, five of them providing direct measurements of river inputs into the lake. These stations are on the Río Ramis, Río Ilave, Río Huancane at Puente Carretera, Río Coata at Maravillas and the Río Zapatilla at Puente Carretera (Fig. 5). The first four measure the discharges of the most important water courses of the system. Two stations within the Coata catchment are installed on the Río Lagunillas at Lagunillas and on the Río Verde at Verde. The proportion of the catchments gauged in comparison to the total catchment area in Peru is 80.3%, and is 63.5% of the entire terrestrial catchment of the lake. Measurements generally started in 1956.

Seven catchments have been taken into consideration in Bolivia: The Río Suchez at Escoma, the Río Huaycho at Puerto Acosta, the Río Keka at Achacachi, the Río Catari at Tambillo, the Río Sehuenca at Villa Iquiaca, the Río Jacha Jahuira at Hichu Kkota and the Río Tiwanacu at Tiwanacu (Fig. 5). These data cover shorter periods than those from Peru. Bolivia gauges 6470 km² of the catchment at these stations, of which 1630 km² is in Peru. Bolivia therefore obtains measurements on 47.4% of the catchment lying within its own territory and 13.3% of the total lake catchment. Overall, discharges are recorded for 76% of the total catchment in the two countries.

For the rest of the area for which no direct measurements are available, 4400 km^2 are occupied by river catchments similar to those monitored (Rios Pallina, Batallas, etc.) and 7100 km² are made up of small coastal catchments for which run-off was calculated from rainfall. Using this method of calculation, the volume flowing into the lake each year between 1968 and 1978 varied from $3.11 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$ in 1983 to $15.78 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$ in 1986, the mean being about $8.90 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$. On the basis of the discharges measured in the five main catchments, the mean inflow over the period 1956–1987 was $8.09 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$, equivalent to a mean discharge of 256 m³ s⁻¹.

Another method of calculation was also used. After homogenising the data using the VECSPAT method, the unknown discharges were calculated from those of the gauged Peruvian catchments, by taking into account the ratios of their areas, rainfall and the given annual run-off coefficients. The values obtained, assuming a mean run-off coefficients of 22% for the non-measured catchments, gave an annual mean inflow over the period 1968–87 of 8.51×10^9 m³ yr⁻¹, equivalent to 270 m³ s⁻¹, a value close to the previous calculation. The proportion of the total discharge actually measured is therefore 71%. This river inflow represents a water depth of 1002 mm over the entire lake surface. The results in Table 1 which should be compared with those of Table 2 have therefore been obtained for different groupings of catchments. The estimated discharges with run-off percentages of 15 to 25% for those catchments not measured directly, varies between 250 and 290 m³ s⁻¹, equivalent to a depth of water of between 930 and 1080 mm over the entire lake surface.

Run-off and specific discharge

The mean run-off coefficient over all the gauged catchments in Peru is 25.2%, with a maximum of 38.3% in the Coata catchment and a minimum of 19.6% in the Zapatilla catchment. Previous assessments have given a mean run-off coefficient for the whole lake catchment of 23.6%.

In terms of specific discharges the catchments can be divided into two areas:

- The north and west where the specific discharges are close to 5.5 l s⁻¹ km⁻², with the exception of the Coata which has a specific discharge of $10 \text{ l s}^{-1} \text{ km}^{-2}$.
- The south and east, covering mostly the area within Bolivia, where the specific discharges are of the order of 3 to $41 \text{ s}^{-1} \text{ km}^{-2}$, with the exception of the Sehuencas which reaches $61 \text{ s}^{-1} \text{ km}^{-2}$.

The lowest inputs come from the driest areas situated on the eastern fringes and from catchments situated on the Altiplano where the low gradients favour infiltration and evapotranspiration rather than run-off. In the heavy rainfall catchments with steep gradients, the specific discharges are of the order of $15 \ 1 \ s^{-1} \ km^{-2}$. In high altitude catchments such as that of the Suchez this discharge can be relatively low however $(3.71 \ s^{-1} \ km^{-2})$, because of the low rainfall and the heavy retention of water by the fluvio-morainic soils and by peat. Relief therefore has an influence on run-off, both by the gradient and by the head of water it produces. This explains why the discharge per unit area of the Río Sehuencas, which runs directly off the Cordillera into the lake, is higher than that of the Río Keka which wanders over the plain.

Despite the relief, the maximum daily specific discharges are not very high. For a median year they range between 20 and 60 l s⁻¹ km⁻². The spatial distribution of discharges per unit area is identical to that of river discharges.

Temporal variation in discharge

The histogram of mean monthly discharges (Fig. 6) shows a maximum in February, except for the Río Ramis, where a slight peak is evident in the month of March. 80% of the lake inputs occur between January and April. Late or early rains have practically no effect on run-off.

Year-to-year variation in annual discharge (Fig. 7) shows the low values for the periods 1956–1958, 1964–1967 and especially 1983, a year affected by an exceptional El Niño event. Similarly, the high discharges of the years 1962–1963, 1974–1976 and 1984–1986, when inputs were 1.5 to 2 times higher than the mean, are also evident. Together with the amount of rain falling directly on the lake, these variations in river input to the lake influence long-term changes in lake level. The period 1956–1987 was a dry period which lasted until 1974 and was followed by a much wetter period, particularly from 1984–1986.

Statistical analysis of the distribution of mean annual discharges over the period 1956–1987 provides estimates of the various return times (Table 2).

Statistical analysis of the annual mean monthly maximum discharges gives



Figure 6. Variation in the total mean monthly discharges $(m^3 s^{-1})$ for the lake's five largest inflow rivers (Ramis, Coata, Ilave, Huancane and Suchez) over the period 1956–1987.

an indication of the probability of exceptional discharges (Table 3) and shows in the case of the Ilave and the Ramis, which have the same median value, that the value for the 100-year flood is twice as high in the former although its catchment area is only half that of the latter.

Discharge of the outflow from Lake Titicaca

The many gaps in the measurements of the discharge of the Desaguadero made at Puente Internacional at the outflow from the lake have been filled



Figure 7. Total mean annual discharges $(m^3 s^{-1})$ for the lake's five largest inflow rivers (Ramis, Coata, Ilave, Huancane and Suchez) over the period 1956–1987.

	Ramis	llave	Coata	Huancané	Suchez
Surface (km²)	15 060	7 290	4 650	3 580	3 170
Minimum	25	10	11	5	4
Medium	74	38	47	19	11
Maximum	121	90	99	40	20
Dry fifty	36	13	15	8	6
Middle	70	37	36	19	12
Wet fifty	140	100	90	42	24

Table 2. Measured and adjusted mean annual discharge (m³ s⁻¹) for the period 1956–1987.

by interpolation. The mean annual discharge over the period 1968–1987 has thus been estimated at $30.6 \text{ m}^3 \text{ s}^{-1}$.

The discharge has been correlated with the lake level at Puno over the period 1957–1988, then reconstituted as a function of the level to reduce the strong heterogeneity that exists between periods. The mean annual discharge for the period 1968–1987 based on this correlation is $48.5 \text{ m}^3 \text{ s}^{-1}$.

In order to overcome the inaccuracy of the discharge values measured at this station, discharges were also estimated from those measured at Calacoto, situated 150 km downstream, after making allowances for the inputs from the intervening catchments. The mean annual discharge estimated this way for the same period is $37.5 \text{ m}^3 \text{ s}^{-1}$.

It should be noted that the discharges measured directly at the lake outflow and those estimated by one of the above two methods can differ by a factor of two. Figure 8 shows the changes in mean annual discharge from the lake for the period 1956 to 1987.

The annual outflow increased in successive cyles over the entire observed time scale to reach a maximum mean annual discharge of $169 \text{ m}^3 \text{ s}^{-1}$ in 1986. The maximum recorded daily discharge of $250 \text{ m}^3 \text{ s}^{-1}$ occurred in April of the same year. The discharge is highly variable and can be almost zero or even negative in some years (1971–1973), whereas it can exceed $100 \text{ m}^3 \text{ s}^{-1}$ in other years (1986–1987) when the lake level is high. The mean therefore only has relative significance, because if the four highest years from 1985 to 1988 are excluded, the value is reduced to $19.5 \text{ m}^3 \text{ s}^{-1}$.

The period 1956–1989, and especially from 1974 onwards, was a wet one in comparison to the entire period for which records are available, which starts in 1916 and includes the particularly dry years from 1935 to 1945. The median value for the outflow discharge is $15 \text{ m}^3 \text{ s}^{-1}$ for the period 1956–1989 but falls to less than $5 \text{ m}^3 \text{ s}^{-1}$ when the entire period is taken into consider-

	Ramis	llave	Coata	Huancané	Suchez
Average	350	350	270	130	60
20 years	550	800	580	240	140
100 years	660	1 130	810	320	220

Table 3. Return frequencies of maximum daily discharges $(m^3 s^{-1})$ for the period 1956–1987.



Figure 8. Mean annual discharge $(m^3 s^{-1})$ calculated for the Desaguadero at the exit from Lake Titicaca (Puente Internacional) for the period 1956–1989.

ation. The mean annual discharge of 10 m³ s⁻¹ would only be reached in one year out of three. Statistical analysis of the discharges gives a 100-year maximum value of 250 m³ s⁻¹. For the maximum daily discharge the 100-year value is 350 m³ s⁻¹.

Because of the lake inertia and meteorological conditions, the maximum outflow discharge occurs in April (Fig. 9), the month of highest lake level, whereas the maximum for inputs from the catchment is in February. The fall in lake level is therefore gradual, so that the volume flowing out in May is greater than in March. Because of this regulatory effect of the lake, only



Figure 9. Seasonal changes in mean monthly discharge $(m^3 s^{-1})$ calculated for the Desaguadero at the exit from Lake Titicaca (Puente Internacional) for the period 1956–1989.

60% of the total annual volume flows out down the Desaguadero between January and June, whereas river inputs over the same period amount to 85% of the annual total.

Lake Titicaca levels

Figure 10 shows the changes in daily records of lake level at Puno from 1914 to 1989. The zero datum on the scale is at 3809.93 m altitude.

Changes over the year are determined by the balance between water inputs and losses. The maximum level is generally centred on April, at the end of the rainy season and the period of high river inputs. The minimum usually occurs in December, just before the start of the rains.

Over the entire period the total inter-annual range in level has been 6.37 m, with an absolute minimum of -3.72 m below datum in December 1943 and an absolute maximum of 2.56 m above datum in April 1986.

The annual range of level has varied between 1.80 m (in 1986) and 0.04 m (in 1983);

Differences in level during a month are usually maximum in February, with a mean value of 0.26 m. This corresponds to the major rise in water level caused by the maximum inputs from rivers and direct rainfall. The minimum monthly differences in water level generally occur in December and April, corresponding to the stable periods of annual minimum and maximum levels. The rise in water level occurs more quickly than the fall because the inputs are concentrated almost exclusively over 5 months, whereas the losses by evaporation are more evenly spread over the year.



Figure 10. Changes in the level of Lake Titicaca at Puno.

Volume of water in Lake Titicaca

Boulangé and Aquize Jaen (1981) estimated the volume of the lake to be $895.9 \times 10^9 \text{ m}^3$ during the period 1964–1979 when the water level was on average 0.46 m lower than during the period 1968–1987. The increase in level is equivalent to $3.89 \times 10^9 \text{ m}^3$. We therefore adopt a lake volume of $900 \times 10^9 \text{ m}^3$ for this latter period. Taking into account the mean inputs, the turnover rate for the water is 1.79%, or an average retention time of 55.8 years. The volume of the Lago Grande ($887.5 \times 10^9 \text{ m}^3$) is much greater than that of the Lago Menor ($12.5 \times 10^9 \text{ m}^3$).

The actual evapotranspiration and evaporation are generally the most difficult terms to measure in the hydrological cycle. This is the case for Lake Titicaca and its basin where uncertainties exist in the values to be used. The spot measurement or estimation of these terms and their extension to the whole catchment are very complicated. One of the interests in calculating the water balance is to provide an estimate of the losses other than those due to surface flows from the basin. Such losses are considered as an approximate value for evaporation. From the balance equation (paragraph 2), these losses are equal to the algebraic sum of the other terms.

In the case of Lake Titicaca and its basin, the interest is all the greater because it involves the evaluation of the actual evaporation from a very large body of water and the actual evapotranspiration from a high-altitude mountainous soil-vegetation complex lying within the tropics.

Any losses by infiltration through the lake bed and any inputs to the lake from aquifers could also be included in the balance without problems, if their values were known. This is not the case, since these phenomena are poorly understood, although it is likely that subterranean inputs such as those from aquifers surrounding the lake and which are evident in the form of springs and seepages, are greater than any underground losses under the Desaguadero in the direction of Lake Poopo. These possible inputs and losses have not therefore been taken into consideration in the calulations. Any input from aquifers would tend to lead to an under-estimate of overall losses and therefore of the approximate value for evaporation. The opposite is true in the case of infiltration.

Various attempts have been made to estimate evaporation on the Altiplano using several methods. Among these were Carmouze and Aquize Jaen (1981) who, from a water balance, estimated total losses at 1880 mm yr⁻¹ and after estimating infiltration of 160 mm yr⁻¹ from a dissolved chloride balance, calculated an evaporation of 1720 mm yr⁻¹. Carmouze *et al.* (1983) arrived at a figure of 1720 mm yr⁻¹ for evaporation based on a heat balance. In contrast, Vacher *et al.* (1989), after measuring the terms of the radiation balance, calculated potential evapotranspiration on the Altiplano using the Penman formula and arrived at figures of 1300 mm yr⁻¹ at Belen and 1350 mm yr⁻¹ at Patacamaya. These values are lower than those above because of the low net radiation.
Mariaca (1985) using type A tanks obtained values of 1860 mm yr⁻¹ and 1955 mm yr⁻¹ for Desaguadero (Peru) and Patacamaya, respectively. These values were reduced to 1490 mm yr⁻¹ and 1565 mm yr⁻¹ after applying a tank correction factor of 0.8. At Belen evaporation is lowest in June, with a value of 110 mm and highest in October with 154 mm. The annual total at this site is 1692 mm. At Isla del Sol, on the lake itself, but at a height of 150 m above the lake level, the annual value is 1606 mm. After applying the tank correction factor, these two values become 1355 mm and 1285 mm.

Actual evapotranspiration of the Lake Titicaca catchment

Overall, the terrestrial part of the catchment receives 736 mm yr⁻¹ of rain, or a volume of 36.1×10^9 m³ yr⁻¹ (Table 2).

Over the long term, the actual evapotranspiration over the catchment is equivalent to the difference between rainfall and run-off. In the case of Titicaca, however, an uncertainty remains because account has to be taken of changes in the groundwater reserves in the catchment. As is the case with the lake, it is likely that the volume of groundwater has increased up to the end of the period in question, as a result of the very wet period from 1984 to 1986. Evapotranspiration calculated from a water balance would therefore be overestimated. Actual evapotranspiration in the various river catchments varies between 490 and 660 mm yr⁻¹, with a value of 563 mm for the entire terrestrial part of the catchment (Table 2). This represents a volume of 27.6×10^9 m³ yr⁻¹, or a loss of 76.4%, the highest component of losses in the catchment.

The terms of the water balance and actual evaporation from Lake Titicaca

As has been shown above, several methods have been used to evaluate each term in the water balance, each giving significantly different results. It is worth mentioning these various results on a long-term average scale, since the method of estimation, used for the first time, provides an estimate of the degree of uncertainty that is attached to the final accepted values.

- Two values for average precipitation over the lake have been obtained using the Vecspat method: 7.47×10^9 m³ yr⁻¹ with missing values estimated and 7.07×10^9 m³ yr⁻¹ with calculated values.
- Two values are given for river inputs: firstly $8.90 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$ based on the observed results plus correlations and the other $8.51 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$ with missing values estimated by Vecspat and with a run-off coefficient of 22% for the non-measured catchments. The discharges calculated by Vecspat give the same overall results. The values vary between $7.86 \times 10^9 \text{ m}^3$ yr⁻¹ and $9.11 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$, if a range of values for run-off coefficient of between 15 and 25% is used for the non-measured part.

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Units	Rainfalls	Rivers	Effluent	Evaporation	Lake storage
Height mm Volume 10 ⁹ m ³ %	880 7.47 46.8	1 002 8.51 53.2	160 1.36 8.9	1 628 13.82 91.1	94 0.80

Table 4. Mean annual hydrological balance for Lake Titicaca over the period 1968-1987.

- The value for the volume flowing out by the Desaguadero derived from actual data plus interpolation for missing values is 0.965×10^9 m³ yr⁻¹, that obtained by correlations with lake levels is 1.53×10^9 m³ yr⁻¹ and that estimated from the disharge at the Calacoto gauging station (Bourges *et al.*, 1991) is 1.18×10^9 m³ yr⁻¹.
- Changes in lake volume derived from 5 day running means of lake level give an annual increase in volume of 0.802×10^9 m³ yr⁻¹, or 94 mm per year over the 20 year period in question.

Different combinations of the results given above could thus be applied to the calculation of overall losses resulting from the balance.

A minimum figure of $12.6 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$, or 1485 mm is obtained by taking the lowest values for inputs and the highest figure for the Desaguadero discharge and a maximum value of $14.8 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$ or 1745 mm is obtained by doing the converse. The mean of these two values is 1615 mm with an error of $\pm 8\%$.

Two estimates based on the median and mean of the available values of each term give figures for overall losses of 14.0×10^9 m³ yr⁻¹ and 13.9×10^9 m³ yr⁻¹ or 1650 mm and 1630 mm, respectively.

On the basis of discharge by Vecspat, outflow discharge deduced by correlations with lake levels, and rainfall figures with estimated missing values, the overall losses are estimated at 13.6×10^9 m³ yr⁻¹ or 1610 mm and those from calculated rainfall figures at 13.2×10^9 m³ yr⁻¹ or 1560 mm, the mean of these two figures being 1585 mm.

From measured discharge values with missing values calculated by correlations, outflow measurement estimated from discharge at Calacoto and rainfall with missing values calculated by Vecspat, the overall losses are estimated at 14.4×10^9 m³ yr⁻¹, or 1695 mm. The same calculation, but using rainfall values calculated by Vecspat gives overall losses of 14.0×10^9 m³ yr⁻¹, or 1645 mm.

If we had to give one value for the terms of the water balance, we would adopt rainfall and discharges with missing values estimated by Vecspat and the mean of the two calculated values for the Desaguadero (Table 4). For the overall losses other than those leaving by the Desaguadero, a volume of 13.8×10^9 m³ yr⁻¹, or 1628 mm yr⁻¹ is therefore proposed. By taking into account a margin of uncertainty of $\pm 3\%$, a value is obtained which is close to most estimates of actual evaporation.

The overall hydrological balance of the basin

Using the values for the terrestrial part of the basin and for the lake, the total precipitation over the basin was 43.6×10^9 m³ yr⁻¹. A volume of 0.80×10^9 m³ yr⁻¹ was stored in the lake and 41.4×10^9 m³ yr⁻¹ was evaporated. Exportation out of the basin towards Lake Poopo by the Desaguadero was 1.36×10^9 m³ yr⁻¹. Evaporation and evapotanspiration therefore represent 96.8% of the water losses whereas surface outflow was only 3.2%.

Conclusions

The climate of the Lake Titicaca basin, temperate by day and cold at night, is that of a high mountain region subjected by its geographical situation to a tropical regime. The influence of the impressive body of water is felt by a reduction in temperature range and to a lesser extent by higher mean temperatures than those that should occur at such altitudes. The lake, with water warmer than the surrounding air also influences precipitation, which is greatest at the lake's centre. Rain falls almost exclusively between December and March and amounts can vary by a factor of two from one year to another.

The hydrological regime is therefore tropical, but river discharges are spread out over the year in the eastern rivers where glaciers cover the higher summits. Mean annual discharge can vary by a factor of three between years, reflecting in an amplified manner the inter-annual irregularity in rainfall. The maximum river inputs occur in the second half of summer one to two months after the rainfall peak; 80% of run-off occurs in 4 months.

The irregularity of rainfall and river inputs between years, combined with a relative stability in evaporation and a slight surface outflow, are the cause of the great variations recorded in lake level. The range of \pm 3.18 m recorded since 1914 has led to a change in lake volume of \pm 3%. Because of the great difference in their volumes, this variation accounts for \pm 2.6% in the Lago Grande and \pm 33% in the Lago Menor. The stability of the lake environment is therfore very variable according to the particular area.

Direct rainfall onto the lake amounts to 880 mm, or 7.47×10^9 m³ yr⁻¹, whereas inputs from rivers are equal to 1002 mm, or 8.51×10^9 m³ yr⁻¹. Evaporation (including unknown groundwater inputs or losses) removes 1628 mm $\pm 3\%$, or 13.8×10^9 m³ yr⁻¹, whereas the Desaguadero only drains away 160 mm yr⁻¹, or 1.36×10^9 m³ yr⁻¹. Direct rainfall therefore accounts for 47% of the inputs and the inflow rivers 53% of inputs. Evaporation accounts for 91% of the total losses and outflow via the Desaguadero only 9%. The up-to-date, entirely computerised way of processing the rainfall and hydrological data guarantees a better precision of the values. It is certain that the period 1968–1987 was wetter than those periods studied previously by other workers and that this has led to changes in the relative importance of the terms in the water balance by increasing the contribution of the inflow

rivers and that of the Desaguadero and decreasing that of direct rainfall and evaporation. In comparison Carmouze (1982) for the period 1956–1978, which was drier than 1968 to 1987, gave a figure for evaporation of 1720 mm and of 0.22×10^9 m³ yr⁻¹ for outflow via the Desaguadero.

Lake Titicaca, because of its area and volume and its situation at high altitude within the tropics, remains a hydrological site unique in the world.

References of chapter IV

- AMBROGGY (R.), 1965. Cuencas acuíferas del lago Titicaca. *In*: Hidrología del Altiplano de Bolivia. La Paz. Min. Agric: 11 p.
- Anon., 1955. Estudio del lago Titicaca. Ingenieros Ejecutivos S.A., Lima, multigr.
- Anon., 1956. Segundo Informe sobre la instalación de estaciones meteorológicas y de aforos en la cuenca del lago Titicaca. Ingenieros Ejecutivos S.A., Lima, multigr.
- Anon., 1965. Programa de inventario y evaluación de los recursos naturales del Departamento de Puno. Sector de Prioridad I; Cap. 2: Climatología; Cap. 3: Geología y Rec. Mineros; Cap. 4: Hidrología, vol. 2; Cap. 5: Suelos, vol. 3; Cap. 6: Ecología y Agrostología, vol. 4; Cap. 7: Diagnóstico Económico, vol. 5. INP/ONERN/CORPUNO, Lima.
- Anon., 1971. Informe sobre estudio físico-químico realizado en el lago Titicaca. Dic. 1969. Of. de Investig. Min. Marina. nº 124, Lima: 10 p.
- Anon., 1972. El Altiplano de Puno. Estudios agroclimáticos por cuencas. Dir. Agrometeorología. SENAMHI. Lima. Climatología, multigr.
- Anon., 1973 a. Estudio de las sequías en la Hoya del Titicaca. Dir. Agrometeorología; 1 y 2: Climatología, Hidrología, SENAMHI., Lima: 42 p.
- Anon., 1973 b. Evaluación agroclimática del Departamento de Puno. Dir. Agrometeorología, SENAMHI., Lima, multigr.
- Anon., 1981. Estudio de la cuenca del río Ilpa. Min. Agric., Puno PGAS Proy. Manejo de cuencas. Tomo 1: diagnóstico de la cuenca, 114 p. Tomo 2: plan de manejo de la cuenca, 102 p.
- AQUIZE JAEN (E.), 1980. Clima de la cuenca del lago Titicaca. UNTA, Puno.
- AQUIZE JAEN (E.), 1983. La sequía en Puno. Alternativas Institucionales, Tecnológicas y Populares: El lago Titicaca, Inundaciones y Sequías. IISDA, Convenio UNTA. NUFFIC, Puno.
- ARCE (B.), 1966. El clima de la cuenca del Titicaca y su influencia en la producción agrícola. Tesis UNSAA, Cuzco.
- BAZOBERRY (A.), 1969 a. Anteproyectos y alternativas sobre la utilización de las aguas del lago Titicaca, Desaguadero y Poopó con fines de energía e irrigación. Imp. Artist., La Paz: 50 p.
- Bazoberry (A.), 1969 b. Balance hídrico del lago Titicaca. Dir. Irrig. Minist. Fom., Lima, multigr.
- BAZOBERRY (A.), 1971. Aprovechamiento de las aguas del lago Titicaca: Proyecto conjunto Bolivia-Perú. Imp. Artist., La Paz: 63 p.
- BOULANGE (B.), AQUIZE JAEN (E.), 1981. Morphologie, hydrographie et climatologie du lac Titicaca et de son bassin versant. *Rev. Hydrobiol. trop.*, 14 (4): 269–287.
- BOULANGE (B.), VARGAS (C.), RODRIGO (L.A.), 1981. La sédimentation actuelle dans le lac Titicaca. *Rev. Hydrobiol. trop.*, 14 (4): 299–309.
- BOURGES (J.), CARRASCO (M.), CORTES (J.), 1991. El lago Titicaca. Aportes en aguas superficiales y desagüe. PHICAB, La Paz (in press).
- CAMPOS (R.), 1977. Evaluación del potencial eólico en la Hoya del lago Titicaca. Tesis Prog. Ciencia, UNA – La Molina, Lima: 150 p.

- CANAZA MAMANI (V.), 1988. Análisis de consistencia de datos hidrometeorológicos de la cuenca del río Ramis. Tesis UNTA, Puno: 127 p.
- CARI (A.), 1977. Caracterización hidrológica de la cuenca del río Ilave. Tesis Ing. Agron. UNTA, Puno: 106 p.
- CARO (M.), 1980. Determinación de la evotranspiración potencial a gran altitud. Tesis Ing. Agron. UNA – La Molina, Lima: 77 p.
- CARMOUZE (J.P.), AQUIZE JAEN (E.), 1981. La régulation hydrique du lac Titicaca et l'hydrologie de ses tributaires. *Rev. Hydrobiol. trop.*, 14 (4): 311–328.

CARMOUZE (J.P.), ARZE (C.), QUINTANILLA (J.), 1977. La régulation hydrique des lacs Titicaca et Poopó. *Cah. ORSTOM, sér. Hydrobiol.*, 11 (4): 269–283.

- CARMOUZE (J.P.), ARZE (C.), QUINTANILLA (J.), 1978. Circulación de materia (aguas, sales disueltas) a través del sistema fluvio-lacustre del Altiplano. *Cah. ORSTOM.*, *sér. Géol.*, 10 (1): 49–68.
- CARMOUZE (J.P.), ARZE (C.), QUINTANILLA (J.), 1981. Régulation hydrochimique du lac Titicaca et l'hydrochimie de ses tributaires. *Rev. Hydrobiol. trop.*, 14 (4): 329–348.
- CARMOUZE (J.P.), ARZE (C.), QUINTANILLA (J.), MIRANDA (J.), 1978. Estudio de la regulación hídrica del sistema fluvio-lacustre del Altiplano. *Rev. Boliviana de Química*, 2 (1): 2–22.
- CARMOUZE (J.P.), MIRANDA (L.), 1978. Estudio de los factores de control de los carbonatos disueltos en las aguas del lago Titicaca. Proceso de precipitación de calcita. *Rev. Boliviana de Química*, 2 (1): 57–67.
- CARMOUZE (J.P.), AQUIZE JAEN (E.), ARZE (C.), QUINTANILLA (J.), 1983. Le bilan énergétique du lac Titicaca. *Rev. Hydrobiol. trop.*, 16 (2): 135-144.
- CASTRO (M.), 1970. El lago Titicaca. Rev. de Marina, Lima, 4 (326): 371-382.
- CEHAK (K.), KESSLER (A.), 1976. Varianzspektrumanalyse der seespisgelschwankungen des Titicaca Sees (Sudamerica). Arch. Met. Geoph. Biokl., ser. B, 24: 201–208.
- CHOQUEHUANCA CORNEJO (P.), 1978. Calidad de agua de los principales afluentes del río Ramis (1978). Tesis Ing. Agron. UNTA, Puno: 66 p.
- CHURATA (J.), 1977. Caracterización hidrológica del río Ramis. Tesis Ing. Agron. UNTA, Puno.
- CHURATA SALLUCA (J.), MAMANI HUANCA (L.A.), 1977. Hidrología de la cuenca del río Ramis. Tesis Ing. Agron. UNTA, Puno: 173 p.
- COLQUE ROJAS (Z.S.), 1983. Primera evaluación de la radiación solar en Puno. Tesis Ing. Agron. UNTA, Puno: 82 p.
- CUTIPA LUQUE (J.), 1973. Predicción de sequías e inundaciones en base a precipitaciones pluviales a través del análisis ondulatorio hasta el año 2000 en el distrito de Puno. Tesis 1ng. Agron. UNA – La Molina, Lima: 30 p.
- DAVILA (R.), 1957. Problemas meteorológicos e hidrológicos del lago Titicaca. 1. Algunas sugerencias sobre observaciones de circulaciones terciarias y problemas de tiempo en la cuenca del Titicaca. 2. Algunas consideraciones sobre el balance hidrológico del Titicaca. *Rev. Inst. Geogr. Lima*, 3: 6–25.
- DEL CASTILLO (A.), 1977. Ciclos del lago Titicaca en función de manchas solares y desplazamiento del centro de alta del Pacífico. Carta no publicada. Inst. Mar Perú, Puno.
- FERNANDEZ JAUREGUI (C.A.), ROCHE (M.A.), ALIAGA (A.), PEÑA (J.), 1987. Los recursos hídricos en Bolivia. PHICAB, CONAPHI, IHH.UMSA, ORSTOM, SENAMHI, La Paz: 20 p., multigr.
- FONTES (J.), BOULANGE (B.), CARNIYGE (J.), FLOROWSKI (T.), 1979. Preliminary oxygen-18 and deuterium study of the dynamics of Lake Titicaca. *In* : Meeting International Atomic Energy Agency, AIEA, Vienna: 145–150.
- FUSE (J.), 1964. Informe sobre radiación solar total que debe incidir en la Bahía de Tamán del lago Titicaca. Instit. Geofís. Univ. S. Agustín, Arequipa.
- GILSON (H.C.), 1939. The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1: 1–357.
- GILSON (H.C.), 1964. Lake Titicaca. Verh. Internat. Verein. Limnol., 15: 112-127.

- GILSON (H.C.), HOLMES (P.), 1939. 2. Meteorology. In: The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1 (1): 21–26.
- GOMEZ (J.), 1972. Estudio del lago Titicaca para aprovechamiento de sus aguas. Tesis. Ing. Agron. UNA. La Molina, Lima: 118 p.
- GOMEZ BRAVO (J.A.), 1979. Calidad de los recursos hídricos de la cuenca de Pamacanchi. Tesis UNTA, Puno: 138 p.
- GONZALES GONZALES (V.A.), 1985. Capacidad erosiva de las precipitaciones en la localidad de Juli. Tesis UNTA, Puno: 51 p.
- GUEVARA (A.), 1953. El clima de Puno. Boletín de la Direc. Gral de Agric., Lima: 78-87.
- GUYOT (J.L.), GUMIEL (D.), 1990. Premières données sur l'hydrogéologie et l'hydrogéochimie du nord de l'Altiplano bolivien. *Hydrogéologie*, 3: 159–164.
- GUYOT (J.L.), ROCHE (M.A.), NORIEGA (L.), CALLE (H.), QUINTANILLA (J.), 1990. Salinities and sediment transport in the bolivian highlands. J. Hydrol., 113: 147–162.
- GUYOT (J.L.), ROCHE (M.A.), QUINTANILLA (J.), CALLICONDE (M.), NORIEGA (L.), CALLE (H.), CORTES (J.), 1989. Cargas en suspensión, salinidades y transportes de materia sobre el Altiplano boliviano. PHICAB, IIQ.UMSA, ORSTOM, SENAMHI, La Paz: 20 p., multigr.
- HANN (J.), 1903. Zum Klima des Hochlandes von Peru and Bolivia. Peterm. Geogr. Mitteil, 49 (5): 280–282.
- HIEZ (G.), 1977. L'homogénéité des données pluviométriques. Cah. ORSTOM, sér. Hydrol., 14 (2): 129–172.
- HOLLOWAY (A.), 1957. Reporte de un reconocimiento del agua dulce del Perú. Lago Titicaca. SCIPA, Lima: 77 p.
- HUTCHINSON (G.E.), 1957. A treatise on Limnology. I. Geography, Physics, and Chemistry. John Wiley & Sons, New York, 1015 p.
- JIMENEZ (A.), 1967. El plan nacional de agua potable rural en Puno, estudio de fuentes. Tesis UNI, Lima.
- KESSLER (A.), 1947. Atmospherische Zirkulationsanomalien und Spiegelschwankungen des Titicaca Sees. Klimat. Forsch., 17: 361–372.
- KESSLER (A.), 1963. Über Klima und Wasserhaushalt des Altiplano (Bolivien-Peru) während des Hochstandes der letzten Vereisung. Erdkunde, Arch. für Wissenschaft. Geogr., Bonn, 17: 165–173.
- KESSLER (A.), 1966. Junge Laufaderung des Desaguadero und die Entstehung des Uru Sees (bolivianischer Altiplano). Erdkunde, Arch. für Wissenschaft. Geogr., Bonn, 20: 194-204.
- KESSLER (A.), 1970. Über den Jahresgang der potentiellen Verdunstung im Titicaca Becken. Arch. Met. Geoph. Biokl., Ser. B, 18: 239–252.
- KESSLER (A.), MONHEIM (F.), 1967. El balance hidrológico del lago Titicaca, una contribución al aprovechamiento de sus aguas. Serv. Nac. Planif. Coord., La Paz: 6 p.
- KESSLER (A.), MONHEIM (F.), 1968. Der Wasserhaushalt des Titicaca Sees nach neueren Messergebnissen. Erdkunde, Arch. f
 ür Wissenschaft. Geogr., Bonn, 22 (4): 275–283.
- KIRKISH (M.), TAYLOR (M.), 1978. Micrometeorological Measurements at Lake Titicaca (Peru-Bolivia). Verh. Internat. Verein. Limnol., 20: 1203-1209.
- LA PUENTE (I.), 1982. Estudio monográfico del lago Titicaca. Bol. Soc. Geogr. Lima, 1: 263– 391.
- LOZA ANCCO (C.F.), 1983. Determinación de la precipitación efectiva en la cuenca del río Ramis. UNTA, Puno: 38 p.
- LOZADA (G.A.), 1985. Balance hídrico superficial de la cuenca del lago Poopó y los salares de Uyuni y Coipasa, Bolivia. PHICAB, IHH.UMSA, ORSTOM, SENAMHI, La Paz: 158 p., multigr.
- MARCA AROCUPITA (P.), 1984. Curvas escala gastos de los ríos Ramis y Huancané. Tesis UNTA, Puno: 109 p.
- MARCOY (P.), 1877. Voyage dans la région du Titicaca et dans les vallées de l'est du Bas Pérou. Le Tour du Monde, 257 p.
- MARIACA (J.J.), 1985. Balance hídrico superficial de la cuenca del lago Poopó y los salares

de Uyuni y Coipasa, Bolivia. PHICAB, IHH.UMSA, ORSTOM, SENAMHI, La Paz: 203 p., multigr.

- MERCADO (R.), (no dated). Clima y agua del Titicaca. Dir. Irrigación, Min. Agric., Lima, 4 p., multigr.
- MEYBECK (M.), 1979. Concentrations des eaux fluviales en éléments majeurs et apports en solution aux océans. *Rev. Géol. Dynam. et Géogr. Phys.*, 21 (3): 215–246.
- MONHEIM (F.), 1955. Bericht über Forschungen in den zentralen Anden insbesondere im Titicaca Becken. Erdkunde, Arch. für Wissenschaft. Geogr., Bonn, 9: 204–216.
- MONHEIM (F.), 1956 a. Beiträge zur Klimatologie und Hydrologie des Titicacabeckens. Sellbstverl. d. Geograph. Heidelberg, 1: 1–152.
- MONHEIM (F.), 1956 b. Contribución a la climatología e hidrología de la cuenca del lago Titicaca. Traducción Carlos Pecka, UNTA, Puno: 232 p.
- MORLON (P.), 1979. Apuntes sobre el problema agronómico de las heladas. El aspecto meteorológico. CIDA.Min. Agric. Alim., Puno: 54 p., multigr.
- MORLON (P.), BANEGAS (M.), 1980. Evapotranspiración y aridez. Estudio agroclimatológico de la cuenca del lago Titicaca. CIDA.Min. Agric. Alim., proyecto colza y cereales, región 10, Puno, multigr.
- NEVEU-LEMAIRE (M.), 1906. Les lacs des hauts plateaux de l'Amérique du Sud. Imprimerie Nationale, Paris, 197 p.
- ORTEGA BAILON (G.F.), 1974. Determinación de la evotranspiración y balance hidrológico en el altiplano. Tesis Ing. Agron. UNTA, Puno: 68 p.
- PALOMINO (P.), 1983. La sequía en Puno. Alternativas institucionales tecnológicas y populares: cultura popular y predicciones de sequía. IIDSA, Convenio UNTA.NUFFIC. Puno.
- PAUCAR PACHECO (A.), 1977. Frecuencia de sequías del Altiplano. Tesis UNTA, Puno: 35 p.
- PEGUY (C.P.), 1970. Précis de Climatologie. Masson, Paris, 468 p.
- PONCE VILCAPAZA (D.B.), 1982. Hidrograma unitario sintético de la cuenca del río Ilave. Tesis UNTA, Puno: 54 p.
- POSNANSKY (A.), 1911. El clima del Altiplano y la extensión del lago Titicaca, con relación a Tihuanacu en épocas prehistóricas. Tipografía comercial de Ismael Argote, La Paz, 29 p.
- POSNANSKY (A.), 1928. La remoción del ángulo climatérico en el Altiplano de los Andes como factor del despueble de la gente interandina. 23th Inter. Congr. of Americanist, New York, S. 235, 246 p.
- QUINTANILLA (J.), CALLICONDE (J.), GUYOT (J.L.), ROCHE (M.A.), NORIEGA (L.), CALLE (H.), CORTES (J.), 1989. Cargas en suspensión, salinidades y transportes de materia sobre el Altiplano boliviano. *Rev. Ingeniería Sanitaria*, 4 (5): 54–59.
- QUINTANILLA (J.), GUMIEL (D.), GUYOT (J.L.), 1991. Evaluación preliminar de la hidrogeología en hidrogeoquímica del Norte del Altiplano boliviano. Congreso boliviano de Química, La Paz, August 1990 (in press).
- QUISPE ZAPARA (L.L.), AMAN UI (A.A.), 1978. Caracterización hidrológica de la cuenca del río Coata. Tesis Ing. Agron. UNTA, Puno: 143 p.
- RICHERSON (P.J.), WIDMER (C.), KITTEL (T.), 1977. The limnology of Lake Titicaca (Peru-Bolivia). Univ. California, Davis, Inst. Ecology, 14: 78 p., multigr.
- ROCHE (M.A.), 1986. Distribuciones espacio-temporales de los parámetros climatológicos sobre Bolivia. Premier Symposium de la Recherche française en Bolivie, La Paz, Sept. 1986: 29–32, multigr.
- ROCHE (M.A.), 1987. Les bilans hydriques des Andes et de l'Amazonie, Bolivia. Symp. Paléolacs et Paléoclimats en Amérique latine et en Afrique, ORSTOM, Bondy, Janvier 1987. *Géodynamique*, 2 (2): 97–98.
- ROCHE (M.A.), 1988. CLIMAR 2, logiciel d'exploitation de données pour l'étude des variations climatologiques spatio-temporelles. PHICAB.ORSTOM, La Paz, 76 p., multigr.
- ROCHE (M.A.), 1989. Présentation générale des études sur la physicochimie des eaux à l'ORSTOM. Quatrièmes Journées hydrologiques de l'ORSTOM, Montpellier, Septembre 1988: 3–9.

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- ROCHE (M.A.), FERNANDEZ JAUREGUI (C.), 1986. Los balances hídricos de Bolivia. Premier Symposium de la Recherche française en Bolivie, La Paz, Sept. 1986: 44–47, multigr.
- ROCHE (M.A.), ROCHA (N.), 1985. Mapa pluviométrico de Bolivia y regiones vecinas, 1/4.000.000. PHICAB, ORSTOM, SENAMHI, La Paz.
- ROCHE (M.A.), FERNANDEZ JAUREGUI (C.), ABASTO (N.), ALIAGA (A.), 1989. Mapa de temperaturas anuales de Bolivia. 1/5.000.000. PHICAB, ORSTOM, SENHAMI, La Paz.
- SERVANT (M.), VILLARROEL (R.), 1979. Le problème paléoclimatique des Andes boliviennes et de leurs piedmonts amazoniens au Quaternaire. C.R. Acad. Sciences, Paris, 288: 665–668.
- STENZ (E.), 1950. Condiciones climatológicas del Altiplano de Bolivia. Nimbus, Soc. Met. Bolivia, 2 (6-7): 24-53.
- TAYLOR (M.), AQUIZE JAEN (E.), 1984. A climatological energy budget of Lake Titicaca (Peru-Bolivia). Verh. Internat. Verein. Limnol., 22: 1246–1251.
- TEJADA CARI (A.), 1977. Caracterización hidrológica de la cuenca del río Ilave. Tesis Ing. Agron. UNTA, Puno: 104 p.
- TEJADA CARI (J.R.), 1980. Caracterización hidrológica de la cuenca del río Huancané. Tesis Ing. Agron. UNTA, Puno: 101 p.
- TERRY (B.), 1966. Estudio de la precipitación pluvial, de la temperatura y las manchas solares en el Dpto. de Puno. Tesis Ing. Agron. UNA La Molina, Lima.
- VACHER (J.), 1989. Third International Conference in Southern Hemisphere. Meteorology and Oceanography. Buenos Aires. Abstracts: 169–172.
- VEGA (L.), 1968. Primera aproximación del balance hidrológico del lago Titicaca con fines de futuros aprovechamientos de sus aguas. Dir. Irrig. Min. Fom. Obr. Públ., Lima, multigr.
- VEGA (L.), 1970. Estudio de niveles del lago Titicaca. 5° Seminario Latinoamericano de Irrigación en Caracas, Venezuela, 1968. SENAMHI, 1 (1), Lima.
- WASSON (J.G.), GUYOT (J.L.), DEJOUX (C.), ROCHE (M.A.), 1989. Régimen térmico de los ríos de Bolivia. PHICAB, ORSTOM, SENAMHI, UMSA, La Paz: 35 p., multigr.
- YEPES (J.), 1950. Definición de ambientes naturales en el Altiplano. Nimbus, Soc. Met. Bolivia, 2 (6-7): 3-23.

V. PHYSICO-CHEMISTRY V.1. Physico-chemical properties of the water

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The physical and chemical properties of the water of Lake Titicaca have been subject to spot measurements during scientific expeditions and more recently have been measured over much more extended time periods. Works covering this field include Gilson (1939–40, 1964), Monheim (1956), Löffler (1960), Kessler and Monheim (1968), Widmer *et al.* (1975), Richerson *et al.* (1975, 1977), Hegewald *et al.* (1976), Lazzaro (1981), Hegewald and Runkel (1981), Carmouze *et al.* (1981, 1983, 1984), Richerson *et al.* (1986), Iltis (1987) and Quintanilla *et al.* (1987).

Although the data of these workers on the hydroclimate provide valuable information on spatial and seasonal differences, the absence of long-term measurements means that we are still uninformed at present about any between-years variation.

The water temperature, dissolved oxygen content and transparency are the three factors for which there are currently most measurements. All the data collected demonstrate marked individualities in the major morphological regions of the lake. The Lago Menor, with its shallow depth, and which is similar in many respects to the large shallow bays in the Lago Grande such as Puno Bay and Achacachi Bay, is very distinct from Lago Grande, typified by seasonal stratification and a greater thermal inertia.

Water temperature

Seasonal changes in surface temperature

The mean monthly surface temperatures measured in the Lago Grande between 1977 and 1979 (Carmouze *et al.*, 1983) varied between 11.25 and 14.35°C, the lowest temperature being in August and the highest in March (Table 1). The mean annual temperature (1977–1979) was 13.0°C.

Occasional measurements made in Lago Grande (Gilson, 1964; Iltis, 1987) give minimum values of 10.9°C (end of July) and maximum values of 17.0°C

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Table 1. Seasonal changes in air temperature, surface water temperature in the Lago Grande, wind speed at 2 m above the ground (Carmouze *et al.*, 1983), hours of sunshine per day (Boulangé and Aquize Jaen 1981) and daily total incident radiation in $J \text{ cm}^{-2} d^{-1}$ (Lazzaro, 1981). With the exception of water temperatures measured in the Lago Grande data come from the Puno (Peru) meteorological station.

Parameters	J	F	м	Α	м	J	J	A	s	0	N	D	Mean
Air temp.	9.95	9.77	9.33	8.44	8.71	5.26	5.07	6.43	7.90	9.40	10.10	10.15	8.21
Water temp.	13.85	14.30	14.35	13.85	13.0	12.0	11.5	11.25	11.75	12.9	13.35	13.85	13.0
Wind speed	1.14	1.03	0.96	0.95	0.97	1.08	1.06	1.23	1.32	1.42	1.39	1.28	1.15
Solar duration	5.8	5.8	6.6	8.5	9.1	9.4	9.7	9.1	9.0	9.2	8.5	6.8	8.12
Global radiation J-1	2.144	2.065	2.006	2.190	1.969	1.940	1.860	2.195	2.320	2.412	2.420	2.307	2.152

(February), whereas the extreme values recorded in the Lago Menor are 8.5°C (June) and 18.5°C (February).

In Lago Grande the annual range of mean monthly temperature has a mean value of 3.1° C with an observed maximum of 6° C. In Lago Menor, where mean monthly data are absent, the recorded range of extremes is 10° C.

The factors likely to affect changes in the water temperature over the year are the air temperature, the wind speed and the total incident solar radiation (Fig. 1). Measurements made at Puno show that the mean air temperatures range between 5.07° C in July and 10.15° C in December. Wind speeds are rather low throughout the year, the average varying from 0.95 m s^{-1} in April to 1.42 m s^{-1} in October; winter can be considered as the most windy season. Daily sunshine hours vary between 9.7 h d^{-1} in July and 5.8 h d^{-1} in January and February and total incident radiation varies between $2420 \text{ J cm}^{-2} \text{ d}^{-1}$ in November and $1860 \text{ J cm}^{-2} \text{ d}^{-1}$ in July (Lazzaro, 1981). As a result, wind



Figure 1. Seasonal changes in: top: air temperature at Puno (solid line) and surface water temperature in the Lago Grande (dashed line); bottom: sunshine hours (solid line) and wind speed at 2 m above the ground at Puno (dotted line) (from Carmouze *et al.*, 1983).

action can be considered as negligible and air temperature and incident radiation are the two factors which are most influential in causing changes in water temperature.

The seasonal range of variation at the surface is closer to that of the air in the shallower areas and particularly in the Lago Menor, because of the lower inertia related to a shallower mean depth.

Although the seasonal range and seasonal changes are closely correlated with those of the air, the fact that the mean annual temperature of both Lago Grande and Lago Menor is 13°C, whereas that of the air at Puno (1964–1978) is only of the order of 8.1°C, implies that heat exchanges and heat processes are occurring that are not found in more usual climatic and altitudinal conditions.

Horizontal variations

The different behaviours of surface temperatures are reflected in variations in temperature from one part of the lake to another: Lago Menor is colder than Lago Grande in winter and warmer in summer. Between 1985 and 1987, for example, five series of observations over the entire Bolivian part of the lake (Iltis, 1987) showed that the mean surface temperature in Lago Menor was 1°C higher in summer and 1.5°C colder in winter than in Lago Grande. These differences obviously disappear at transitional seasons (April and September-October).

Vertical variations

Published data referring to the temperature in the top hundred metres over the period 1976–1978 (Carmouze *et al.*, 1984) show that the surface waters in the Lago Grande start to warm up from October onward. This warming spreads gradually downwards until a well-defined thermocline is established in December. The thermocline gets deeper until the month of May before disappearing from June to September (Fig. 2). It would appear however that turnover does not take place right to the bottom of the lake, or else that water circulation is very slow there, because at the end of the period of mixing (September) the temperature at 180 m depth was 11 °C and the oxygen saturation was only 70%.

From the available data, Lake Titicaca can be placed in the class of warm monomictic lakes of Hutchinson's (1957) classification, the greater part of Lago Menor and the shallow bays (down to 20 m) being of the polymictic type.



Figure 2. Mean monthly vertical profiles of dissolved oxygen concentration in the water. The shaded area indicates the position of the thermocline (Carmouze *et al.*, 1984).

Dissolved oxygen

The main factors controlling the dissolved oxygen concentration are atmospheric pressure and temperature.

The mean atmospheric pressure at the altitude of Lake Titicaca is 646 hPa (compared to about 1010 hPa at sea level). The relatively low water temperature compensates in part for this effect of pressure so that the resulting saturation concentration is of the order of 7 mg l^{-1} . A saturation curve for the range of temperature encountered in the lake, calculated from Montgomery *et al.* (1964), is given in Fig. 3.

The surface waters of the Lago Menor have concentrations close to saturation all the year round (\geq 95% saturation). The highest values are recorded in winter and are due to an increase in solubility of oxygen caused by the



Figure 3. Relationship between mean monthly dissolved oxygen concentrations in the surface water expressed in mmol l^{-1} and water temperature in °C. The diagonal line divides the area of supersaturation to the right and under-saturation to the left (Carmouze *et al.*, 1984).

drop in water temperature. During summer stratification, the hypolimnion in the Chua Depression becomes isolated and only contains 1 to 2 mg l^{-1} (Lazzaro, 1981) with anoxia in the bottom layers in March 1979 and 1980.

Data published for Lago Grande for the period 1976–78 (Carmouze *et al.*, 1984) show an unusual temporal pattern in the percentage saturation of the surface water (Fig. 3): the water is significantly more saturated during vertical mixing than during the period of stratification. The opposite generally occurs in temperate lakes when the cold season coincides most often with the rainy season. Here, in contrast, most precipitation takes place between December and March. This possible correlation does not however explain the supersaturation that occurs in July, August and September.

The regular oxygen profile indicates that the hypolimnion in the Lago Grande becomes deficient in oxygen during the period of stratification. The vertical circulation from July to September over the period 1976–78 (Carmouze *et al.*, 1984) was insufficient to reoxygenate the deeper water layers. It is possible that variation in the main meteorological factors between years is reflected in a variable efficiency in the overturn of the water body.

Transparency

The transparency as measured by Secchi disk is greater in Lago Grande than in Lago Menor. There is however great spatial and temporal variability in both basins.

The extreme values recorded in Lago Menor are 1.2 and 9 metres (Lazzaro, 1981; Iltis, 1987), with lower transparencies in summer and autumn and higher values in winter. As an example, five series of measurements, each carried out at 28 stations in the Lago Menor gave mean values of 4.7 m in June 1985, 4.5 m in December 1985, 5.6 m in April 1986, 5.4 m in October 1986 and 3.2 m in February 1987.

The relationship between Secchi disc transparency (S in metres) and the photosynthetic available radiation m^{-1} K (PAR, Ln base, flat receptor) is K.S = 1.12.

The euphotic depth therefore reaches to the bottom over most of the Lago Menor, except in the deepest areas (the Chua Depression). At Chua, light attenuation is closely correlated with the phytoplankton concentration. In other, shallower stations, other particles in suspension also play an important role (Lazzaro, 1981).

In the Lago Grande, Richerson *et al.* (1977) give Secchi disc values of between 4.5 and 10.5 m. Observations made in 1982 gave a maximum value of 13.3 m, whereas in 1984–85, the mean value was 15.7 m (Alfaro and Roncal, unpublished data). Five series of measurements, each taken at 19 stations in the Bolivian part of Lago Grande, gave mean values of 11.8 m in June 1985, 11.9 m in December 1985, 13.2 m in April 1986, 12.4 m in October 1986 and 13.9 m in February 1987 (Iltis, 1987). These values are in agreement with those of a series of 4 observations (Quintanilla *et al.*, 1987) made between August 1984 and May 1985 where the means were between 11.3 and 14.6 metres.

Chemical properties

pH

The pH values of the surface waters are relatively stable. Lazzaro (1981) recorded values of between 8.55 and 8.65 in the Lago Menor in 1979–80. Mean values at 28 stations between 1985 and 1987 gave mean values of 8.68 in December 1985, 8.40 in April 1986, 8.38 in October 1986 and 8.31 in February 1987; the extreme values were 8.06 and 9.38 (Iltis, 1987).

Richerson *et al.* (1977) gave pH values of 8.6 in the stratified period and 8.5 in the period of isothermy in the Peruvian part of the Lago Grande. The means recorded at 19 stations in the Bolivian part of the lake were 8.48 in December 1985, 8.30 in April 1986, 8.31 in October 1986 and 8.20 in February 1987 (Iltis, *loc. cit.*).

pH is therefore on average a little higher in the Lago Menor than in the Lago Grande, possibly because of the greater photosynthetic activity of phytoplankton and very abundant benthic macrophytes.

Total dissolved solids (TDS)

This has been measured in terms of the electrical conductivity at 25°C. The mean of 16 measurements made in April 1985 in the Lago Menor was 1343

	NEVEU- LEMAIRE 1903	POSNANSKY 1908	GILSON 1937	LÖFFLER 1954	RICHERSON et al. 1973	HEGEWALD et al. 1974-77	CARMOUZE et al. 1977
Ca	64,6	68,7	65,4	54,3	64,0	62,0	65,2
Mg	18	16	34,5	41	36	36,4	35
Na	261	240	167,7	176	-	205,0	178,9
к	8	4	14,9	14	-	21,7	15,4
SO4	392	285	246,2	251	282	265,7	253,4
CI	287	339	247	244	260	272,0	253,8

Table 2. Ionic composition (in mg l^{-1}) of the waters of Lake Titicaca published by various workers (the dates given are the sampling dates).

 μ S cm⁻¹. A later series of 28 measurements gave the following values: 1521 in December 1985, 1368 in April 1986, 1490 in October 1986 and 1366 in February 1987. The means recorded at 19 stations in the Bolivian part of the Lago Grande were 1501 μ S cm⁻¹ in December 1985, 1448 in April 1986, 1490 in October 1986 and 1409 in February 1987 (Iltis, *loc. cit.*).

As for temperature, the means recorded showed more marked changes in Lago Menor, where dilution by water in the rainy season and evaporation during the dry season had greater effects than in Lago Grande. At intermediate seasons such as in October 1986, the conductivity was identical in both basins. Stations situated close to the mouths of the Rios Catari, Tiwanaku and Suchez had conductivities 100 to 300 μ S lower than those of other stations.

The directly measured TDS in Lake Titicaca vary according to sources from 1.2 g l^{-1} (Lazzaro, 1981), to 1.03 (Hegewald *et al.*, 1976) and 0.78 g l⁻¹ (Richerson *et al.*, 1977).

Chemical composition of the water

This has been measured by various workers: Neveu-Lemaire (1906), Posnansky (1911), Gilson (1964), Löffler (1960), Richerson *et al.* (1977), Hegewald *et al.* (1976, 1980) and Carmouze *et al.* (1981) (Table 2).

The waters are dominated by chloride, sulphate and sodium ions, the ranking of cations being Na > Ca > Mg > K.

The concentrations of nitrate and phosphate are the subject of a separate chapter (Chapter V.6).

For silica, the majority of published values lie between 0 and 2.6 mg l^{-1} , with a representative mean value of $1.8 \text{ mg } l^{-1}$ (Carmouze *et al.*, 1981). Concentrations of silica in the top five metres of the water column in Lago

Menor vary between 0.2 and 1.8 mg l^{-1} over the annual cycle. Maximum values occur during the winter turnover in deep stations. In areas where the depth is less than 5 metres, the concentrations remain low throughout the year.

Löffler (1960) gave values varying of between 0.5 and $1 \text{ mg } l^{-1} \text{ Si} 0_2$ for Puno Bay. Richerson *et al.* (1977) measured silica concentrations throughout the annual cycle in the Peruvian part of the Lago Grande and found that concentrations in the epilimnion were between 0.49 and 1.18 mg l^{-1} from January to the end of May, but then fell rapidly to 0.18 mg l^{-1} . Concentrations in the hypolimnion in this period (January to 15 June) varied between 1.82 and 2.60 mg l^{-1} . In July, at the onset of isothermal conditions, the silica concentration of the surface waters was between 0.28 and 0.46 mg l^{-1} , whereas the concentration in the deep waters fell to 0.34 mg l^{-1} . The silica concentration in the surface waters then increased slowly from September to the end of the year but in the deeper water this increase was faster and the highest value (3.7 mg l^{-1}) was reached at 150 m depth at the end of the year.

Among the trace elements, Derkosh and Löffler (1961) mentioned the presence of boron, iron and lead and traces of chromium, manganese, aluminium and arsenic. Cobalt, nickel and vanadium were absent. Gilson (1964) recorded the presence of lithium $(0.9 \text{ mg} \text{ I}^{-1})$ and aluminium $(0.4 \text{ mg} \text{ I}^{-1})$. Hegewald *et al.* (1976) and Hegewald and Runkel (1981) recorded traces of iron, copper and zinc and $0.26 \text{ mg} \text{ I}^{-1}$ of aluminium in the water of Puno Bay.

Conclusions

Analysis of the physico-chemical properties of the waters of Lake Titicaca shows a low seasonal variability. The lake environment can thus be considered as fairly stable.

The range of variation of surface temperature during the year is rather low (3°C) in comparison with that recorded in African lakes at the same latitude (Talling, 1969). This is partly explained by the altitude, but also by the climate: the rainy season and maximum cloud over occur in the summer and thus winter sunshine partly compensates for the lowering of the air temperature.

The deep areas (Lago Grande, Chua Depression) behave as warm monomictic lakes, whereas the shallow areas (Lago Menor and Puno Bay) can be classified as rather independent environments with a polymictic cycle and with more marked seasonal changes.

There are few data on the oxygen concentration at the bottom of the Lago Grande and at Chua in the Lago Menor for periods of more than a year. The variation between years in the oxygen concentrations at the bottom, both in periods of stratification and isothermy, is therefore unknown.

The rather high total dissolved salt concentration is attributed to heavy chemical weathering of the catchment area. Its stability is a result of the long retention time of water in the lake.

The range of variation in the values of some variables can be greater in the vast shallow areas such as the Lago Huiñaimarca and Puno Bay, which are relatively isolated from the central body of water in the Lago Grande, especially as these regions are influenced by special local conditions (such as inflow rivers and the presence or absence of macrophytes), which makes them spatially heterogeneous. As a result, most of the variables studied have a greater range than in the Lago Grande.

V.2. Hydrochemical regulation of the lake and water chemistry of its inflow rivers

JEAN-PIERRE CARMOUZE, CARLOS ARZE and JORGE QUINTANILLA

The first data on the chemical composition of major dissolved elements in Lake Titicaca date from the beginning of the century (Neveu-Lemaire, 1906; Posnansky, 1911). These were followed by those of the Percy Sladen Trust Expedition in 1937 (Gilson, 1939–1940, 1964). Recently, more complete studies have been carried out on the Lago Grande (Richerson *et al.*, 1977) and on the whole lake (Carmouze *et al.*, 1977).

After a preliminary assessment of the main dissolved salts, a more precise assessment is given here for the Lago Grande and Lago Pequeño by means of new data on river and lake hydrology (Carmouze and Aquize Jaen, 1981) and on river water chemistry.

River water chemistry

The chemical composition of the waters of the lower courses of the main inflow rivers (Ramis, Coata, Ilave, Huancane and Suchez) and of that of secondary rivers (Pallina, Catari, Tiwanaku, Challa Jahuira, Chilla, Batallas Chicas, Keka, Huaycho and Zapatilla) was studied from samples collected between 1976 and 1979 (Table 1 and Fig. 1).

A less detailed study of the chemistry of the upper reaches of certain rivers, in relation to the geology of the corresponding part of the catchment area, enables us to make some general remarks on the origins of dissolved salts.

The Río Ramis

The mean total dissolved salt content is 5.52 mmol l^{-1} , with the following composition of main ions:

 $HCO_3 = 28.4\%$, $SO_4 = 13.94\%$, Cl = 11.58%, Na = 18.46%K = 1.23%, Ca = 18.55%, Mg = 5.72%, $SiO_4H_4 = 2.08\%$

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	HCO ₃	(HCO _→)	SO4	$^{2}(SO_{\downarrow})$	CI	(CI)	Na	(Na)	K	(K)	Ca	(Ca)	Mg	(Mg)	SiO4 Hy	$(SiO_4^{-3}Hy)$
Huancanć, lit. Moho	1.75	1.266	1.295	0.931	2.85	2.065	2.82	2.045	0.105	0.076	1.56	1.13	0.485	0.35	0.091	0.066
Ramis, lit. Arapa and Capachica	1.57	4.17	0.77	2.046	0.64	1.70	1.02	2.71	0.068	0.18	1.025	2.725	0.315	0.839	0.115	0.306
Ilpa	1.78	0.388	1.25	0.272	10.20	2.376	10.75	2.343	0.465	0.101	1.38	0.30	1.15	0.251	0.056	0.125
Coata, lit. Puno and Ilave	0.895	1.23	0.39	0.566	1.865	3.568	1.875	2.583	0.118	0.162	0.63	0.871	0.15	0.206	0.185	0.255
Zapatilla and lit. Juli-Tiquina	0.85	0.488	0.94	0.54	1.18	0.678	1.22	0.70	0.121	0.069	0.865	0.50	0.455	0.262	0.28	0.161
Lit. Tiquina-Desaguadero	0.29	0.059	0.40	0.103	0.025	0.006	0.12	0.030	0.065	0.008	0.28	0.072	0.15	0.038	0.218	0.058
llave	1.47	1.565	0.595	0.631	1.55	1.65	1.49	1.586	0.121	0.128	1.06	1.128	0.345	0.366	0.292	0.311
Lit. Desaguadero-Guaqui	1.775	0.036	0.245	0.005	0.645	0.013	1.05	0.020	0.107	0.004	0.815	0.016	0.232	0.005	0.246	0.005
Tiwanaku, lit. Taraco	1.915	0.354	0.59	0.109	0.276	0.051	0.53	0.095	0.076	0.014	1.155	0.213	0.27	0.05	0.153	0.028
Catarict Pallina	1.95	1.057	1.89	1.025	2.57	1.39	2.89	1.55	0.16	0.086	1.92	1.04	0.68	0.368	0.131	0.07
Batallas Chicas, lit. Watajata-																
Tiquina	0.25	0.033	0.13	0.017	0.025	0.003	0.20	0.025	0.03	0.04	0.09	0.012	0.06	0.008	0.103	0.013
Keka, lit. Tiquina-Achacachi, lit.																
Achacachi-Escoma	0.35	0.128	0.08	0.029	0.03	0.011	0.30	0.11	0.03	0.011	0.100	0.037	0.07	0.025	0.072	0.026
Suchez	0.64	0.151	0.251	0.059	0.025	0.006	0.19	0.043	0.032	0.007	0.305	0.071	0.16	0.038	0.06	0.014
Huaycho	0.67	0.116	0.71	0.123	0.955	0.165	1.22	0.103	0.085	0.013	0.67	0.116	0.217	0.038	0.19	0.033

Table 1. Mean annual salt concentrations [i], and mean annual inputs (i) of waters from inflowing rivers and from streams along the shoreline (lit). [i] is expressed in mmol l^{-1} and (i) in mol $\times 10^9$.



Figure 1. Geological formations in the catchment area of Lake Titicaca and water sampling locations. (r = Ramis, h = Huancane, c = Coata, i = Ilave, s = Suchez).

The calcium and bicarbonate are slightly dominant.

The total dissolved salt content shows seasonal variations, with the waters at the start of the rainy season being more heavily mineralised (10.43 mmol l^{-1}) and those at the height of the flood the least mineralised (1.27 mmol l^{-1}). The former have a double bicarbonate-calcium and chloride-sodium character, while calcium and bicarbonate dominate in the the latter.

The Río Coata

The mean total dissolved salt content of the Río Coata is 6.10 mmol l^{-1} , with sodium and chloride dominating.

 $HCO_3 = 14.6\%$, $SO_4 = 6.35\%$, Cl = 30.58%, Na = 30.7%K = 1.9%, Ca = 10.35%, Mg = 1.45%, $SiO_4H_4 = 3.03\%$

Variations in dissolved salt content are both:

- very marked over the course of the year (the waters at the start of the flood reach a salt content of 18.4 mmol l^{-1} and those at the height of the flood 4.55 mmol l^{-1});
- very great from one year to another at the same season (18.4 mmol l^{-1} on 15 November 1976, 7.55 mmol l^{-1} on 26 November 1978).

There are also great seasonal changes in the chemical composition. Na + Cl make up 70% of the total dissolved salts at the start of the flood and 59 % at the height of the flood.

The Río Ilave

The mean total dissolved salt content of the Río Ilave is 5.50 mmol l^{-1} . The waters are of a mixed chloride-sodium and bicarbonate-calcium character:

 $HCO_3 = 21.2\%$, $SO_4 = 8.57\%$, Cl = 22.4%, Na = 21.53%K = 1.75%, Ca = 15.34%, Mg = 4.35%, $SiO_4H_4 = 4.22\%$

Seasonal changes in salt content are relatively slight. The waters at the start of the flood have a salt content of 9.5 mmol 1^{-1} and those at the height of the flood 4.35 mmol 1^{-1} . Sodium and chloride dominate slightly in the former (Na + Cl = 51% of total dissolved salts), whereas the latter have a more marked bicarbonate-calcium character (HCO₃ + Ca = 41.4%). Nevertheless, qualitative variations in salt content are slight, irrespective of discharge.

The Río Huancane

The mean total dissolved salt content of the Río Huancane is 10.95 mmol 1^{-1} . The waters are of a predominantly sodium-chloride type:

$$HCO_3 = 15.96\%$$
, $SO_4 = 11.73\%$, $Cl = 26.11\%$, $Na = 25.75\%$
K = 0.96\%, Ca = 14.24\%, Mg = 4.41\%, SiO_4H_4 = 0.83\%

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There are great seasonal variations. The waters at the start of the flood can reach a salt concentration of 26.84 mmol l^{-1} , whereas those at the height of the flood have a salt content three times lower (8.45 mmol l^{-1}). The between-years variation for any given season is also very marked because of irregularities in the hydrological regime (26.8 mmol l^{-1} in November 1976 against 10.3 mmol l^{-1} in November 1978). Variations have also been recorded on a much shorter time scale, associated with hydrological irregularities between months (23.3 mmol l^{-1} on 15 December 1976; 6.3 mmol l^{-1} on 15 January 1977; 16.9 mmol l^{-1} on 6 February 1977).

Qualitatively, the waters at the start of the flood have a clear chloridesodium character (Na and Cl represent 70.5% of the total dissolved salts, whereas this percentage is only 46% at the height of the flood).

The Río Suchez

The waters of the Río Suchez are only very slightly mineralised. The mean total dissolved salt content is 1.66 mmol l^{-1} and the percentage composition as follows:

 $HCO_3 = 88.48\%$, $SO_4 = 15.09\%$, Cl = 1.5%, Na = 11.42%K = 1.92%, Ca = 18.34%, Mg = 9.6%, $SiO_4H_4 = 3.6\%$

Bicarbonate and calcium predominate throughout the year (HCO_{3 +} Ca = 57% of total dissolved salts). Seasonal variations in salt content are slight. The waters at the start of the flood have less than twice the salt content of those at the height of the flood (2.5 mmol l^{-1} against 1.40 mmol l^{-1}).

Secondary rivers

From results based on only two samples, the Río Zapatilla would appear to have a highly variable composition over the course of the year, both quantitatively and qualitatively. At the end of December 1976, the salt content was 7.95 mmol 1^{-1} and at the start of February 1977 it was 19.95 mmol 1^{-1} . At times of high discharge, chloride and bicarbonate concentrations are roughly equal (HCO₃ = 18.6%, SO₄ = 18.2% and Cl = 15.3%). At low discharge sodium and chloride dominate greatly (Na + Cl = 67.5%).

The Ríos Challa Jahuira and Chilla have similar compositions at the time of the floods, the salt content of the former being 4.61 mmol l^{-1} and that of the latter 5.55 mmol l^{-1} . Bicarbonate and calcium dominate in both.

The Río Tiwanaku is typified by waters that change little in chemical composition over the course of the year. The salt content at the time of flood is 4.75 mmol 1^{-1} and that at low water is 9.05 mmol 1^{-1} . Bicarbonate and calcium predominate at all seasons.

The Ríos Pallina and Catari have relatively heavily mineralised waters. At the season of low water the salt content of the Río Pallina is 23.9 mmol l^{-1} and that of the Río Catari 9.55 mmol l^{-1} . Chloride and sodium predominate in these waters.

In the rainy season, the salt content of the waters of the Río Catari (9.55 mmol 1^{-1}) are of the mixed bicarbonate-calcium and chloride-sodium type. The same must be true of the flood waters of the Río Pallina.

The Ríos Batallas Chicas and Keka are very little mineralised (0.925 mmol 1^{-1} and 1.05 mmol 1^{-1} , respectively); bicarbonates predominate whereas the chloride concentration is low or else is absent.

The Río Huaycho has a salt content of $4.7-6.2 \text{ mmol } l^{-1}$, with bicarbonates, chlorides and sulphates all well represented.

General observations on the origins of dissolved salts in river waters

The problem of the origin of dissolved salts in the waters of the catchment area of Lake Titicaca is rather complex. The geology of the catchment contains a rather high number of different formations each with a number of distinct rock types.

This problem has been dealt with in a very simple manner by collecting water samples at the point where they run off the main formations i.e.: the Silurian-Devonian, lower Carboniferous, the lower middle and upper Cretaceous, the lower and middle Tertiary and the Pleistocene. The last two formations are of volcanic origin, whereas the others are sedimentary rocks (Fig. 1).

A certain number of observations can be made from the analyses carried out.

- (a) Rivers, such as the Suchez, Keka and Batallas Chicas, flowing off granite massifs and then crossing short plains have poorly mineralised waters (1 to 2 mmol l⁻¹). Chlorides occur at low concentrations or are absent.
- (b) Rivers in the upper part of the Ramis catchment (above 4000 m) and mainly crossing Palaeozoic sedimentary formations of Silurian-Devonian and Carboniferous age (schists and marls in the former and mainly sandstones in the latter) have little or no chlorides. As the waters of the Río Ramis entering the lake have a chloride content of roughly the same magnitude as that of bicarbonates and sulphates it is therefore thought that there is an enrichment in chlorides in the lower reaches of this river.
- (c) The rivers forming the Huancane mainly derive from Cretaceous formations. Their total dissolved salt content does not exceed 6.2 mmol l⁻¹ in which bicarbonate and calcium dominate. In contrast the salt content of the Huancane itself is always significantly greater than this value (between 8.5 and 27 mmol l⁻¹) and chloride and sodium dominate very clearly. The waters are markedly enriched in sodium and chloride in the lower reaches. In addition, in the eastern part of the catchment there

are a few small lakes which function as differential concentration basins for dissolved salts (relative enrichment in NaCl).

(d) The upper reaches of the Ríos Coata and Ilave cross lower Tertiary sedimentary formations and also middle Tertiary and Pleistocene volcanic rocks. The chemical composition of water derived from any one formation is very variable, but it seems that the waters are poorer in chlorides the closer they are sampled to the rock formation. It would therefore appear that the waters are very quickly enriched in chloride in the downstream Quaternary areas.

Hydrochemical regulation in the lake

The water flowing into Lake Titicaca has the following mean annual chemical composition in mmol l^{-1} (R = river, L = lake):

$$[HCO_3]_R = 1.31, [SO_4]_R = 0.76, [Cl]_R = 1.51, [Na]_R = 1.65$$

 $[K]_R = 0.11, [Ca]_R = 0.98, [Mg]_R = 0.34, [SiO_4H_4]_R = 0.16$

whereas the lake's water has the following characteristics:

 $[HCO_3/CO_3]_L = 2.19, [SO_4]_L = 2.64, [Cl]_L = 7.11, [Na]_L = 7.78$ $[K]_L = 0.395, [Ca]_L = 1.63, [Mg]_L = 1.44, [SiO_4H_4]_L = 0.03$

It can thus be seen that the Na concentration increases by a factor of 4.7 in the lake and that of Ca by 1.7, whereas the dissolved silica concentration decreases by a factor of 5.3.

To understand these changes in the concentrations of each of the dissolved ions in the lake the values of the fluxes at the boundaries of the lake have to be evaluated for each ion. These fluxes include those associated with water currents (river inflows and outflows, infiltration, etc.) and fluxes associated with bio-geochemical reactions. These fluxes vary in both space and time, leading to local spatial heterogeneity and temporal fluctuations.

For this reason two approximations have been made:

- to reduce the spatial variation, the lake has been divided into two environments of lower heterogenity, the Lago Mayor and Lago Menor, which are very distinct entities (identified as LM and Lm, respectively),
- by considering a long time period, the hydrochemical conditions in the lake vary around a mean state since the inputs and outputs of dissolved salts approximately balance.

We have chosen the longest time period possible in relation to the available data, i.e. 1964–1978 to establish a mean annual balance for each of the dissolved ions.

The mean annual composition of the inflow rivers was calculated from data covering the period 1976–79. The mean input of dissolved salts was

calculated from this composition and values for the mean annual volumes of water covering the period 1964-79. The salt regulation figures derived from these data are certainly more representative than those that would have been obtained using just the 1976-79 data.

The terms of the annual balance are as follows:

- for the lake as a whole: $(i)_F = (i)_I + (i)_S + (i)_D + \delta(i)^L$ for the LM: $(i)_F^{LM} = (i)_I^{LM} + (i)_S^{LM} + (i)_T + \delta(i)^{LM}$ for the Lm: $(i)_F^{Lm} + (i)_T = (i)_I^{Lm} + (i)_S^{Lm} + (i)_D + \delta(i)^{Lm}$

Where (i)_F, (i)_F^{LM} and (i)_F^{Lm} are the river inputs of ions into the lake, LM and Lm, respectively; (i)_I, (i)_I^{LM} and (i)_I^{Lm} are the losses of i by infiltration from the lake, LM and Lm; (i)_S, (i)_S^{LM} and (i)_S^{Lm} are the losses by sedimentation from the lake, LM and Lm; $(i)_D$ the losses of i via the Desaguadero; (i)_T the quantity of i passing from Lm to Lm via the Tiquina strait and $\delta(i)^{L}$, $\delta(i)^{LM}$ and $\delta(i)^{Lm}$ are variations in the reserve of i in the lake, the Lm and Lm.

Inputs of dissolved salts by the rivers

To calculate the mean annual inputs of dissolved salts into the lake, the mean annual composition of the waters in each hydrological area was first calculated. Then these were weighted in relation to the mean discharges of each river (Carmouze and Aquize Jaen 1981) (Table 1).

The absence of data for some rivers forced us to make the following approximations:

- water draining in along the Huancane shoreline was assumed to have the same chemical composition as the waters of the Río Huancane;
- water draining in along the Arapa-Capachica shoreline was assumed to have the same chemical composition as the waters of the Río Ramis;
- water draining in along the shoreline between Puno and Tiquina was assumed to have a chemical composition intermediate between those of the waters of the Río Zapatilla and those of sampling point 8 (Fig. 1);
- water draining in along the Desaguadero-Guaqui shoreline was assumed to have a chemical composition intermediate between that of the Río Challa Jahuira and Río Chilla:
- water draining in along the Taraco shoreline was assumed to have the same chemical composition as the waters of the Río Tiwanaku;
- water draining in along the Wuatajata Tiquina shoreline was assumed to have the same chemical composition as the waters of the Río Batallas Chicas:
- water draining in along the Tiquina-Achacachi-Escoma shoreline was assumed to have the same chemical composition as the waters of the Río Keka.

The mean annual inputs to the whole lake, the Lago Mayor (LM) and Lago Menor (Lm) were than calculated for the period 1964–1978 using the mean annual volumes of water discharged by the rivers over the period 1964 and 1978 (moles $\times 10^9$):

$$\begin{split} (\text{HCO}_3)_{\text{F}}^{\text{L}} &= 11.04, \, (\text{SO}_4)_{\text{F}}^{\text{L}} = 6.43, \, (\text{Cl})_{\text{F}}^{\text{L}} = 12.69, \, (\text{Na})_{\text{F}}^{\text{L}} = 13.93 \\ (\text{K})_{\text{F}}^{\text{L}} &= 0.90, \, (\text{Ca})_{\text{F}}^{\text{L}} = 8.23, \, (\text{Mg})_{\text{F}}^{\text{L}} = 2.84, \, (\text{SiO}_4\text{H}_4)_{\text{F}}^{\text{L}} = 1.37 \\ (\text{HCO}_3)_{\text{F}}^{\text{LM}} &= 9.50, \, (\text{SO}_4)_{\text{F}}^{\text{LM}} = 5.167, \, (\text{Cl})_{\text{F}}^{\text{LM}} = 11.23, \, (\text{Na})_{\text{F}}^{\text{LM}} \\ &= 12.20 \\ (\text{K})_{\text{F}}^{\text{LM}} = 0.74, \, (\text{Ca})_{\text{F}}^{\text{LM}} = 6.88, \, (\text{Mg})_{\text{F}}^{\text{LM}} = 2.38, \, (\text{SiO}_4\text{H}_4)_{\text{F}}^{\text{LM}} = 1.20 \\ (\text{HCO}_3)_{\text{F}}^{\text{Lm}} = 1.54, \, (\text{SO}_4)_{\text{F}}^{\text{Lm}} = 1.26, \, (\text{Cl})_{\text{F}}^{\text{Lm}} = 1.46, \, (\text{Na})_{\text{F}}^{\text{Lm}} = 1.72 \\ (\text{K})_{\text{F}}^{\text{Lm}} = 0.15, \, (\text{Ca})_{\text{F}}^{\text{Lm}} = 1.35, \, (\text{Mg})_{\text{F}}^{\text{Lm}} = 0.47, \, (\text{SiO}_4\text{H}_4)_{\text{F}}^{\text{Lm}} = 0.17 \end{split}$$

The Lagor Mayor therefore receives on average nearly 85% of the total inputs of dissolved salts as against only 15% for the Lago Menor.

Losses of dissolved salts by the desaguadero

Hydrological studies of the lake (see Chapter IV.1) have shown that the Desaguadero can become an inflow river in January and February in certain years. The waters which enter the lake through the Desaguadero have a chemical composition similar to that of the lake itself in neighbouring areas, since it is water of lacustrine origin stored in the adjacent flood plain that is forced back into the lake.

The net losses of dissolved salt by the Desaguadero can therefore be calculated with satisfactory precision by using the mean chemical composition of the lake water in the proximity of the Desaguadero (see Table 2) and the mean annual net volume of water flowing out over the period 1964–1978, i.e. 0.217×10^9 m³.

The net losses in moles $\times 10^9$ are as follows:

$$\begin{array}{l} (\mathrm{HCO_3/CO_3})_\mathrm{D} = 0.415, \ (\mathrm{SO_4})_\mathrm{D} = 0.575, \ (\mathrm{Cl})_\mathrm{D} = 1.725, \ (\mathrm{Na})_\mathrm{D} \\ = 1.855 \\ (\mathrm{K})_\mathrm{D} = 0.095, \ (\mathrm{Ca})_\mathrm{D} = 0.33, \ (\mathrm{Mg})_\mathrm{D} = 0.325, \ (\mathrm{SiO_4H_4})_\mathrm{D} = 0.004 \end{array}$$

It should be noted that the mean annual input from rivers over the period 1964 to 1978 amounts 46.5×10^9 moles, whereas the losses from the outflow river only amount to 5.3×10^9 moles. The Desaguadero therefore only evacuates 11.4% of the riverine inputs, the rest being eliminated by infiltration, biogeochemical sedimentation or stored in the lake.

Table 2. Chemical composition of the waters of the whole lake $[i]^L$, the Lago Mayor $[i]^{LM}$, Lago Menor $[i]^L$ m and Desaguadero $[i]^D$ in mmol 1⁻¹. Changes in the mean annual salt reserves from 1964 to 1978 in the whole lake $\delta(i)^L$, the Lago Mayor $\delta(i)^{LM}$ and the Lago Menor $\delta(i)^{Lm}$ in moles $\times 10^9$. Transport of dissolved salts through the Tiquina strait $(i)^1$, in moles 10^9 year^{-1} .

$M \times 10^3$	$(i)^{L}$ M × 10 ³	(i) ^L %	R ¹ Years	T^{L} M × 10 ³	$(i)^{LM}_{\Lambda}$ $M \times 10^3$	(i) ^{LM} %	R ^{LM} Years	T^{LM} $M \times 10^3$	$(i)^{Lm}$ M × 10 ³	(i) ^{Lm} %	R ^{Lm} Years	T^{Lm}
HCO ₂ /CO ₂	1964	11.60	0.59	169	1940	9.66	0.49	200	24	1.57	6.5	
So ⁴	2365	6.65	0.28	355	2330	5.36	0.23	435	35	1.30	3.7	27
Cl	6370	13.30	0.21	479	6275	11.73	0.19	537	95	1.57	1.6	60
Na	6970	14.60	0.21	382	6865	12.78	0.19	537	105	1.84	1.7	57
К	355	0.93	0.26	174	348	0.77	0.22	452	5.5	0.15	2.7	37
Ca	1460	8.37	0.57	435	1441	7.00	0.48	206	19	1.37	7.2	14
Mg	1290	2.97	0.23	20	1271	2.49	0.20	510	19	0.49	2.6	39
SiO₄H₄	27	1.37	5.1		7.35	1.20	0.16	6	0.10	0.17	170	0.6

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Losses by infiltration

We assume that infiltrating water has a mean chemical composition similar to the water of the lake itself (Table 2). The mean volume of water infiltrating has been estimated from the Cl balance (Carmouze and Aquize Jaen, 1981). This volume is equal to $1.36 \times 10^9 \text{ m}^3 \text{ year}^{-1}$ for the whole lake, $0.93 \times 10^9 \text{ m}^3 \text{ year}^{-1}$ for the LM and $0.44 \times 10^9 \text{ m}^3 \text{ year}^{-1}$ for the Lm, which give the following losses in 10⁹ moles for the whole lake (i)^L, the LM (i)^{LM} and Lm (i)^{Lm}:

$$(\text{HCO}_{3}/\text{CO}_{3})_{1}^{L} = 2.985, (\text{SO}_{4})_{1}^{L} = 3.595, (\text{Cl})_{1}^{L} = 9.68, (\text{Na})_{1}^{L} = 10.59$$

$$(\text{K})_{1}^{L} = 0.54, (\text{Ca})_{1}^{L} = 2.22, (\text{Mg})_{1}^{L} = 1.96, (\text{SiO}_{4}\text{H}_{4})_{1}^{L} = 0.041$$

$$(\text{HCO}_{3}/\text{CO}_{3})_{1}^{\text{LM}} = 2.035, (\text{SO}_{4})_{1}^{\text{LM}} = 2.43, (\text{Cl})_{1}^{\text{LM}} = 6.53, (\text{Na})_{1}^{\text{LM}} = 7.139$$

$$(\text{K})_{1}^{\text{LM}} = 0.36, (\text{Ca})_{1}^{\text{LM}} = 1.510, (\text{Mg})_{1}^{\text{LM}} = 1.325, (\text{SiO}_{4}\text{H}_{4})_{1}^{\text{LM}} = 0.022$$

$$(\text{HCO}_{3}/\text{CO}_{3})_{1}^{\text{Lm}} = 0.825, (\text{SO}_{4})_{1}^{\text{Lm}} = 1.175, (\text{Cl})_{1}^{\text{Lm}} = 3.190, (\text{Na} = 3.530)$$

$$(K)_{I}^{Lm} = 0.180, (Ca)_{I}^{Lm} = 0.645, (Mg)_{I}^{Lm} = 0.640, (SiO_{4}H_{4})_{I}^{Lm} = 0.013$$

Overall, infiltration eliminates 40% of the dissolved salts brought in by the rivers. It accounts for 56% of the losses of Na and Cl, 43% of the loss of K, 40% of the loss of SO₄, 34% of the loss of Mg, 20% of the losses of HCO_3/CO_3 and Ca and scarcely 2% of the losses of SiO_4H_4 .

Losses by biogeochemical sedimentation

These are obtained by subtraction using the balance equations:

- for the lake as a whole: $(i)_S^L = (i)_F^L (i)_I^L \delta(i)_L^L$ for the LM: $(i)_S^{LM} = (i)_F^{LM} (i)_I^{LM} (i)_T \delta(i)_L^{LM}$

- for the Lm: $(i)_{S}^{Lm} = (i)_{F}^{Lm} + (i)_{T} = (i)_{I}^{Lm} (i)_{D} + \delta(i)^{Lm}$ The values of $(i)_{T}$, $(i)^{L}$, $(i)^{LM}$ and $(i)^{Lm}$ must first be calculated. The quantity of salts passing through the Tiquina strait is equal to $(i)_T =$ $(v)_T \times [i]^{GL}$, where $(v)_T$ = the volume of water flowing through Tiquina = $0.515 \text{ m}^3 \times 10^9 \text{ year}^{-1}$ (Carmouze and Aquize Jaen, 1981). The results are given in Table 2.

The variations of the reserves of i in the lake, LM and Lm are: $\delta(i)^{L} =$ δ (v)^L × [i]^L, δ (i)^L = δ (v)^{LM} × [i]^{LM} and δ (i)^{Lm} = δ (v)^{Lm} × [i]^{Lm}, respectively. $\delta(v)^{L}$, $\delta(v)^{LM}$ and $\delta(v)^{Lm}$ which represent the changes in the volume of the entire lake, the Lm and Lm are equal to 0.18, 0.15 and 0.03×10^9 m³, respectively (results in Table 2).

It is therefore possible to calculate $(i)_{S}^{L}$, $(i)_{S}^{LM}$ and $(i)_{S}^{Lm}$; the results, expressed in moles $\times 10^{9}$, are as follows:

$$\begin{aligned} (\text{HCO}_3/\text{CO}_3)_{\text{S}}^{\text{L}} &= 7.245, \ (\text{SO}_4)_{\text{S}}^{\text{L}} &= 1.785, \ (\text{Cl})_{\text{S}}^{\text{L}} &= 0.0, \ (\text{Na})_{\text{S}}^{\text{L}} &= 0.04 \\ (\text{K})_{\text{S}}^{\text{L}} &= 0.195, \ (\text{Ca})_{\text{S}}^{\text{L}} &= 5.385, \ (\text{Mg})_{\text{S}}^{\text{L}} &= 0.295, \ (\text{SiO}_4\text{H}_4)_{\text{S}}^{\text{L}} &= 1.32 \\ (\text{HCO}_3/\text{CO}_3)_{\text{S}}^{\text{LM}} &= 6.00, \ (\text{SO}_4)_{\text{S}}^{\text{LM}} &= 0.98, \ (\text{Cl})_{\text{S}}^{\text{LM}} &= 0.0, \ (\text{Na})_{\text{S}}^{\text{LM}} \\ &= 0.0 \\ (\text{K})_{\text{S}}^{\text{LM}} &= 0.12, \ (\text{Ca})_{\text{S}}^{\text{LM}} &= 4.28, \ (\text{Mg})_{\text{S}}^{\text{LM}} &= 0.10, \ (\text{SiO}_4\text{H}_4)_{\text{S}}^{\text{LM}} &= 1.15 \\ (\text{HCO}_3/\text{CO}_3)_{\text{S}}^{\text{Lm}} &= 1.38, \ (\text{SO}_4)_{\text{S}}^{\text{Lm}} &= 0.785, \ (\text{Cl})_{\text{S}}^{\text{Lm}} &= 0.0, \ (\text{Na})_{\text{S}}^{\text{Lm}} \\ &= 0.08 \\ (\text{K})_{\text{S}}^{\text{Lm}} &= 0.065, \ (\text{Ca})_{\text{S}}^{\text{Lm}} &= 1.17, \ (\text{Mg})_{\text{S}}^{\text{Lm}} &= 0.20, \ (\text{SiO}_4\text{H}_4)_{\text{S}}^{\text{Lm}} &= 0.15 \end{aligned}$$

It is assumed that Cl is not sedimented. The sedimentation values given for Na are not significant taking into account the uncertainties in the terms in the balance equation. The losses by sedimentation of HCO_3/CO_3 , SO_4 , K, Ca, Mg and SiO_4H_4 are 65.6%, 27.7%, 21.6%, 67.8%, 10.2% and 96.3%of the river input, respectively. Sedimentation of SiO_4H_4 , HCO_3/CO_3 , Ca, K and SO_4 is 7.7, 5.3, 4.6, 2.9 and 2.25 times greater in the LM than in the Lm, respectively, but that of Mg is twice as great in the Lm than in the LM.

Overall, losses by sedimentation represented 28.5% of the river input between 1964 and 1978, 77.5% occurring in the LM and 25% in the Lm.

The partial removal of SiO_4H_4 in the lake is to a great extent due to use of silica by diatoms and the removal of HCO_3 and Ca is mainly due to the precipitation of calcium carbonate (Carmouze and Miranda, 1978; Boulangé *et al.*, 1981). SO₄ is partially reduced under reducing conditions. K and Mg are taken up by macrophytes and it should be noted that the sedimentation of Mg was greater in the Lm than in the LM where macrophyte development is less extensive.

Although they were calculated separately, the sum of the balances for the LM and Lm is close to the balance for the lake as a whole.

The stocks of dissolved salts in the lake and their turnover rate and retention time

The stocks of dissolved salts in the lake are continually being renewed, their annual turnover rate being equal to the quantities of salts brought in $(i)_A$ or eliminated $(i)_P$ each year divided by the corresponding stocks (i). The inverse of this value, T, is the mean retention time of the dissolved substance in the lake; it is another way of giving an idea of the time taken for matter to circulate through the environment.

The calculation is simple

- For the whole lake $(i)^{L} = (v)^{L} \times [i]^{L}$; $R_{i}^{L} = (i)^{L}_{A}/(i)^{L} = (i)^{L}_{P}/(i)^{L}$; $T_{i}^{L} = 1/R_{i}^{L}$

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	HCO ₃ /C	$O_3 SO_4$	CI	Na	Κ	Ca	Mg	SiO ₄ H ₄
(i) ^L	1964	2365	6370	6970	355	1460	1290	27
$(i)_{A}^{L}$	11.60	6.65	13.30	14.60	0.93	8.37	2.97	1.37
R^{L} (%)	0.59	0.28	0.21	0.21	0.26	0.57	0.23	5.10
T ^L (Years)	169	355	479	479	382	174	435	20
(i) ^{LM}	1940	2330	6275	6865	348	1441	1271	20
$(i)_{A}^{LM}$	9.66	5.36	11.73	12.78	0.77	7.00	2.49	1.20
R^{LM}	0.49	0.23	0.19	0.19	0.22	0.48	0.20	0.16
T^{LM}	200	435	537	537	452	206	510	6
(i) ^{Lm}	24	35	95	105	5.5	19	19	0.10
$(i)^{Lm}_A$	1.57	1.30	1.57	1.84	0.15	1.37	0.49	0.17
R ^{Lm}	6.5	3.7	1.6	1.7	2.7	7.2	2.6	170
T^{Lm}	15	27	60	57	37	14	39	0.6

Table 3. Stocks of dissolved salts (i), mean annual inputs or losses (i)^{\wedge}, annual turnover rate of the stocks Rⁱ and retention time Tⁱ in the whole lake, LM and Lm. (from Carmouze *et al.*, 1981).

- For the LM $(i)^{LM} = (v)^{LM} \times [i]^{LM}$; $R_i^{LM} = (i)^{LM}_A/(i)^{LM} = (i)^{LM}_P/(i)^{LM}$; $T_i^{LM} = 1/R_i^{LM}$
- For the Lm $(i)^{Lm} = (v)^{Lm} \times [i]^{Lm}$; $R_i^{Lm} = (i)_A^{Lm}/(i)^{Lm} = (i)_P^{Lm}/(i)^{Lm}$; $T_i^{Lm} = 1/R_i^{Lm}$

The results are given in Table 3. Over the period in question $(i)_A^A$ was slightly greater than a $(i)_P$, so an intermediate value was used in the calculations.

The mean annual turnover rates of dissolved salts are low in the LM, with the exception of SiO_4H_4 . They vary between 0.5 and 0.2% for all dissolved ions, except for SiO_4H_4 for which it is 16%. These rates are about 10–12 times higher in the Lm. In other terms, the retention time for a substance is 10–12 times shorter in the Lm than in the LM, being 30 years on average for the Lm and 350 years in the LM.

Fluctuations in the chemical composition of the water between years

Comparison between the data on the chemical composition of the waters of Lake Titicaca obtained from the beginning of the century by the workers cited in the introduction and those of the present day shows that there are no significant differences, if allowance is made for the different methods of analysis used. In other words, the major changes in water level of the lake have hardly affected the chemical composition of the water. This can be verified by a rough calculation and a comparison between analyses made at a time of low water level (1971) and high water level (1978), compared to a normal situation (1967).

(a) Low water level

From 1967 to 1971 the volume of the lake fell from 896×10^9 m³ to 887×10^9 m³. The stocks of dissolved salts decreased by a quantity approximately equal to the product of the deficit in river discharge, i.e. 4.5×10^9 m³ and the mean chemical composition of the river waters.

Stocks of dissolved salts at low water level (i)_d in moles $\times 10^3$:

 $(HCO_3/CO_3)_d = 1958, (SO_4)_d = 2360, (Cl)_d = 6359, (Na)_d = 6958, (K)_d = 354, (Ca)_d = 1455, (Mg)_d = 1288, (SiO_4H_4)_d = 26.27$

The corresponding concentration in mmol:

$$[HCO_3/CO_3]_d = 2.21, [SO_4]_d = 2.26, [CI]_d = 7.17, [Na]_d = 7.84$$

 $[K]_d = 0.40, [Ca]_d = 1.64, [Mg]_d = 1.45, [SiO_4H_4]_d = 0.029$

(b) At high water level

From 1967 to 1978 the volume increased from $896 \times 10^9 \text{ m}^3$ to $904 \times 10^9 \text{ m}^3$. River discharge had an excess of $4.0 \times 10^9 \text{ m}^3$.

Stocks of dissolved salts at high water level (i)_c in moles $\times 10^3$:

 $(HCO_3/CO_3)_c = 1970, (SO_4)_c = 2369, (Cl)_c = 6380, (Na)_c = 6980, (K)_c = 356, (Ca)_c = 1464, (Mg)_c = 1292, (SiO_4H_4)_c = 27.65$

The corresponding concentration in mmol:

 $[HCO_3/CO_3]_c = 2.18, [SO_4]_c = 2.62, [CI]_c = 7.06, [Na]_c = 7.72$ $[K]_c = 0.393, [Ca]_c = 1.62, [Mg]_c = 1.43, [SiO_4H_4]_c = 0.035$

From these results it can be seen that the chemical composition of the water varies little between periods of high and low water level, at least in the LM. The changes in concentration do not exceed 2%. In the Lm, however, judging just from the change in volume of water, these must reach 10-15%.

Conclusions

The total dissolved salt contents of the rivers flowing into Lake Titicaca are usually between 5 and 10 mmol l^{-1} . These are relatively high values compared to the mean value of 2 mmol l^{-1} given for inland waters by Meybeck (1979). They reflect heavy chemical erosion.

Most of the water originates from volcanic and sedimentary formations

and has total dissolved salt contents of between 5 and 20 mmol 1^{-1} , with strong seasonal variations. Concentrations can be three times higher at low water than during floods, but no one chemical ion dominates. HCO₃ SO₄ and Cl are present in roughly equal proportions. Nevertheless, at low water or at the start of the rainy season chloride and sodium may dominate due to a clear enrichment in sodium chloride in the lower reaches of the rivers.

Water coming directly off the Eastern Cordillera is less mineralised (less than 5 mmol 1^{-1}). The dominance of bicarbonates, calcium and sodium is characteristic of chemical erosion of crystalline rocks.

The hydrological regime of the lake is such that the dissolved salts in the river waters should on average be enriched by a factor of 4.7. This is true for Na and Cl, but for other dissolved ions this factor is lower because of chemical sedimentation. This mainly affects dissolved silica (used by diatoms), bicarbonate, carbonate and calcium (precipitated as $CaCO_3$), and to a lesser extent sulphate (reduction in deep stratified water), potassium and magnesium (uptake by macrophytes).

Overall, sedimentation losses amounted to 28.5% of the riverine inputs between 1964 and 1978. 77.5% of this sedimentation occurred in the Lago Mayor and 22.5% in the Lago Menor. Losses by infiltration amounted to 40% of the riverine input: 68% in the Lago Mayor and 32% in the Lago Menor. The Desagaudero only removed 11.4% of the riverine inputs.

The annual turnover of the stocks of dissolved salts is very low in the Lago Mayor; for the major ions it varies between 0.20 % (Na and Cl) and 0.50% (Ca and HCO₃). It is much higher in the where it varies between 1.6-1.7% (Na and Cl) and 6.5-7.2% (Ca and HCO₃).

As a consequence Lake Titicaca is a very stable environment. Irregularities in the inputs of water and dissolved salts do not change the composition of its waters to any notable extent, at least in the Lago Mayor.

V.3. Dissolved matter and suspended sediment loads in some inflow rivers and in the Rio Desaguadero

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The hydrology and hydrochemistry of Lake Titicaca and of its main inflows have been the subject of many studies and a preliminary balance for lake inputs has been drawn up from a series of ten sampling campaigns between 1976 and 1979 (Carmouze *et al.*, 1978, 1981). Although the present rate of sedimentation is known from sedimentological studies in the Lago Huiñaimarca (see Chapter II.3), the direct inputs of riverine sediments have only been studied qualitatively (Boulangé *et al.*, 1981), and the seasonal changes in these inputs (dissolved and suspended) are still poorly known.

A recent typological study on water courses in the La Paz region, based on a regional ecological approach (Wasson and Marin, 1988) provided a series of data on the hydrology, hydrochemistry and suspended matter concentrations on two small Bolivian inflows into Lake Titicaca, the Rios Tiwanaku and Jacha Jahuira (or Keka). These two streams have similar mean annual discharges of about $1 \text{ m}^3 \text{ s}^{-1}$, but originate from very different catchment areas, since the former (TI) is situated entirely on the Altiplano, whereas the latter (JJ) flows down a glacial valley from the Eastern Cordillera. Each stream was sampled every ten days throughout an entire hydrological cycle. Chemical analyses of the major ions were carried out and the concentration of suspended matter was measured by filtering 1 1 of water through a Whatman GF/C filter followed by drying at 105 °C for 2 hours.

These data provide new information on the spatio-temporal variation of dissolved and suspended matter inputs to Lake Titicaca, in relation to the nature of the catchment areas and the hydrological season. These data are supplemented by observations on the Rios Suchez and Desaguadero (Guyot *et al.*, 1990a), in order to determine the seasonal cycle and annual balances of matter entering the lake and then exported by the Rio Desaguadero (Fig. 1).



Figure 1. Simplified hydrographic and geological map of the Bolivian catchment area of Lake Titicaca, from the geological map of Bolivia at 1: 1000,000 (YPFB-GEOBOL, 1978). 1: Palaeozoic, 2: Cenozoic, 3: Quaternary, 4: Granite massifs. See station codes in Table 1.

The seasonal cycle

Hydrology

Under the influence of the same pattern of precipitation, typified by a marked rainy season from December to March, the lake inflows generally have a period of high water levels lasting from January to March (Fig. 2A). In



Figure 2. Seasonal cycle from January to December of suspended and dissolved matter. 2A: mean monthly discharges (Q, in $m^3 s^{-1}$). 2B: mean monthly flux of suspended matter (QS, in t d^{-1}). 2C: mean monthly flux of dissolved matter (QD, in t d^{-1}).

contrast, in the Rio Desaguadero, whose discharge is directly influenced by the level of water in Lake Titicaca, the period of high water levels extends until May because of the inertia related to the volume of water in the lake (Guyot *et al.*, 1990a).

Concentrations

The concentrations of total dissolved solids (TDS) and total suspended sediments (TSS) have very different seasonal cycles in the Rios Tiwanaku and Jacha Jahuira. In the former, changes in river discharge lead to great variations in the concentrations of suspended and dissolved matter, whereas in the latter the concentrations remain very low and remarkably stable throughout the seasonal cycle.

These differences are related to the geological and geomorphological characteristics of the catchment areas. In the case of the Rio Jacha Jahuira, only Palaeozoic rocks occur, dominated by the granite massifs of the Cordillera, which explains the very low concentrations of TDS. The profile in the form of a series of terraces, leading to the presence of a series of lakes upstream of the sampling station, contributes to decreasing the concentration of TSS carried. In contrast, the Rio Tiwanaku drains the Quaternary sedi-



Figure 3. Seasonal changes over the period 1987–1988 in discharge at Tiwanaku (Q, in $m^3 s^{-1}$), suspended sediments (SM, in g l^{-1}) and electrical conductivity (Cond., in mS cm⁻¹ at 25 °C) at Tiwanaku (TI) and Hichu Kkota (JJ).

ments of the Altiplano, which are very easily transported during floods (Fig. 3).

Flux

As a consequence, the cycles of the flux of dissolved and particulate matter are very different in these two water courses. In the Rio Jacha Jahuira, fluctuations in the TSS load are barely significant and the TDS load are directly related to river discharge. In contrast, in the Rio Tiwanaku, the TSS load is very high in the four months of high water level and practically zero in the dry season. Variations in the TDS load are much lower, because of a degree of dilution during the floods (Fig. 3).

The seasonal cycle of TSS in the Rios Suchez (at Escoma) and Desaguad-
		Sites char	Hydrology				
Codes	Rivers	Siles	Altitude of the sites (m)	Basin ereas (km²)	Observation poriods	Mean annual discharges (m-3 s-1)	Specific discharges (I.s ⁻¹ km ⁻²)
SU JJ TI DE	Suchez Jacha Jahuira Tiwanaku Dosaguadero	Escoma Hichu Kkota Tiwanaku Calacolo	3.850 4.320 3.850 3.790	3.100 63 320 9 800 + SL*	1976-1982 1945-1975 1987-1988 1976-1982	10 1.1 1.2 52	3.4 17 3.8 -

Table 1. Characteristics of the sampling stations and quantities of matter transported.

SL* = Lake Titicaca basin (57.100 km²))

		Suspen	ded sediments		Dissolved sediments					
Codes	Observation periods	N* sample	Contents (mg i-1)	Solid discharges (10 ³ t yr ⁻¹)	Eresion rates (t km ⁻² γr ⁻¹)	Observation periods	N* sample	Contents (mg !-1)	Dissolved discharges (10 ³ t yr ⁻¹)	Erosion rates (t km ⁻² yr ⁻¹
SU JJ TI DE	1976-82 1987-88 1987-88 1987-88 1976-82	52 39 40 100	180 9 330 250	65 0.3 34 580	21 5 110 59	1983-88 1987-88 1987-88 1983-88	5 39 40 788	60 34 280 670	30 1.2 6.6 1800	9 9 10 -

ero (at Calacoto) have one characteristic in common with the Rio Tiwanaku: most of the transport of suspended matter takes place during the period of high water levels (Fig. 2B). This is not surprising in the case of the Rio Desaguadero where the TSS come from tributaries situated between Lake Titicaca and the sampling station and which drain catchments on the Altiplano of the same type as that of the Rio Tiwanaku. In the case of the Rio Suchez, this indicates that the Cenozoic and Quaternary sedimentary deposits traversed by the water course after leaving the Palaeozoic formation must have a significant influence on the TSS dynamics.

TDS and TSS budgets

An assessment of the flux of matter transported has been calculated from the available data (Table 1). For the Hichu Kkota station (JJ) for which the hydrological data come from an old series of observations (S.N.D.C. – G.T.Z., 1981), calculations were carried out from monthly averages corresponding to various periods, because of the absence of regular discharge records. In this particular case, this method does not present any major inconvenience because of the stability of the measured concentrations. On the other hand, in the case of a water course such as the Rio Tiwanaku, where major variations in concentrations are recorded over the seasonal cycle, calculation of the quantity transported from annual means (discharge and concentration) would result in an underestimate of the flux of suspended matter and an overestimate of the flux of dissolved matter.

The results given in Table 1 demonstrate the apparent uniformity of the rates of chemical erosion (dissolution), calculated after allowance for atmospheric inputs (bicarbonates in solution). These rates are of the order of 10 t km^{-2} yr⁻¹ in all three inflows to the lake studied, despite the dissimilarities in their geographical situations.

Conversely, the rates of mechanical erosion are very variable depending on whether the catchments are situated on the Altiplano or in the Cordillera. In the Rio Jacha Jahuira, for example, the flux of dissolved matter is about twice as high as the flux of suspended matter and the rate of mechanical erosion (5 t km⁻² yr⁻¹) is one of the lowest ever recorded in the Bolivian Andes. In the Rio Suchez, this rate although four times higher is still rather low for an Andean water course (Guyot *et al.*, 1988, 1989, 1990a, 1990b). In contrast, in the Rio Tiwanaku, although the mean concentrations of TSS are of the same order as those of TDS, the flux of TSS is five times higher because of the great temporal variation in concentrations. The rate of mechanical erosion in this water course is 110 t km⁻² yr⁻¹ and that recorded in the Rio Desaguadero is about half this value.

This area of the Altiplano would therefore seem to be characterised by a total erosion rate (solution + suspension) of the order of 60 to 120 t km⁻² yr⁻¹, whereas the data obtained for the Rios Suchez and Jacha Jahuira give results that are four times lower for the western slopes of the Eastern Cordillera.

Consequences for Lake Titicaca

These data provide the first indication of the spatio-temporal variations in the regimes of dissolved and suspended materials entering and leaving Lake Titicaca.

As far as the export of material via the Rio Desaguadero is concerned, analyses carried out along this water course have shown that the dissolved content at Calacoto is the same as that of Lake Titicaca (Guyot *et al.*, 1990a); it is therefore valid to use this gauging station in drawing up the lake balance. Obviously, only the flux of dissolved matter $(1800 \times 10^3 \text{ t yr}^{-1})$, which is directly related to discharge, can be taken into consideration. In addition, a flux of total organic carbon (mainly in the dissolved form) of $18 \times 10^3 \text{ t yr}^{-1}$ leaving the lake has been estimated for the period 1976–1982 (Wasson *et al.*, 1991).

Estimating the flux entering the lake is a much more complex problem, because it is essential that the variability demonstrated be taken into account in drawing up the total quantities of matter. The rivers draining the Tertiary and Quaternary sedimentary deposits show great variations in their concentrations of dissolved salts and particularly in TSS during the seasonal cycle.

A regional approach by type of catchment basin, and from a sufficiently long series of measurements would appear to be essential to produce precise estimates, particularly for the suspended matter flux. At this time, the absence of data on the TSS in other inflows into Lake Titicaca prevents the drawing up of a total figure (TDS + TSS) for the flux of matter entering the lake. The results given here are a start in this direction and are of value in studies of present-day sedimentation in Lake Titicaca. They also form part of a wider study on the transport of matter and of erosion in the Bolivian Andes.

V.4. The thermal stratification regime in Lake Titicaca

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Temperature stratification in lakes creates density differences that play a key role in regulating vertical mixing. Vertical mixing in turn regulates the distribution of chemical ions and suspended particles, including phytoplankton, with respect to depth. Because of the relatively high attenuation of light with depth, photosynthesis is restricted to surface waters. Under stratified conditions, sinking particles carry nutrient ions from the euphotic photosynthetic zone into the hypolimnion, and recycling is limited by reduced vertical mixing. Under unstratified conditions, nutrients are returned to the surface, but plankton populations may be mixed so deeply that they are limited by low average light levels. Typically, production is highest under conditions of weak stratification, or just after a period of deep mixing as stratification is reestablished. Thus, the stratification regime is the single most important hydroclimatological factor regulating biotic processes in lake ecosystems.

Stratification is driven by the heat budget (see Chapter V.5). During periods of low solar radiation and high evaporation lakes cool. When the heat income increases due to high solar radiation and lower evaporation, most of this heat is gained at the surface due to the low transparency of water. If heat is gained faster than it can be mixed downward by the wind, a warm, buoyant epilimnetic layer is formed with a strong density and a temperature gradient between the epilimnion and the cooler hypolimnion. On this gradient, buoyancy forces counteract the tendency of turbulent diffusion to mix the lake. Warm, wind-driven eddies cannot be driven into the hypolimnion because the denser underlying water forces them back upwards (Csanady, 1973).

There are four important time scales of variation in stratification that are important in lakes: interannual, annual, within-year polymictic, and diurnal. Each is influenced by different facets of the driving climate and weather variables.

Classically, the seasonal time scale has received the most attention from limnologists, but the special conditions of tropical lakes may make both the longer and shorter time scales more important. The reason is that lowlatitude lakes like Titicaca have relatively small annual variations in heat

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content due to the relatively small seasonal variations in solar radiation, air temperature and evaporation in the tropics. Hutchinson and Löffler (1956) predicted that the low annual heat budget of tropical lakes would lead to many cases of oligomixis (mixing on time scales longer than a year) at low elevation and polymixis (frequent mixing within a year) at high elevation. In fact, most tropical lakes of moderate depth are basically of the warm monomictic type; they circulate more or less completely once a year during the coldest season (Talling, 1969; Baxter *et al.*, 1965).

However, the low annual heat budget does appear to make the other time scales of variation relatively more important. Lewis (1973), Kittel and Richerson (1978), and Taylor and Aquize Jaen (1984) have shown that variations of heat gain and loss, and hence stratification strength, vary substantially at the polymictic time scale. Variations between years in degree of mixing are important in deeper lakes like Titicaca (see below), but there is no evidence that they differ significantly from deep temperate lakes like Tahoe (Goldman, 1981; Goldman *et al.*;, 1989) in this regard, contrary to the hypothesis of Kittel and Richerson (1978), who thought that variations in the small heat budget of tropical lakes would lead to qualitative differences in stratification in different years. Due to the typically short period of isothermy in tropical lakes, however, a significantly greater tendency toward oligomixis in the tropics may yet be demonstrated.

The relatively high radiation load of the tropics will tend to ensure that diurnal stratification is strongly marked. On each daily cycle, the surface few meters will gain substantial heat during the day, only to lose most of this heat during the night. This same phenomenon is of course important in the temperate summer. Even in the relatively strongly mixed oceanic case, diurnal stratification is often observed (Howe and Tait, 1969).

Methods

Temperature measurements by our group were obtained with a thermistor (occasionally a water bottle thermometer) in Lago Grande during the years 1973–1976 and 1981–1982. All thermometers were calibrated against laboratory thermometers (1973–76) or tank-tested deep-sea reversing thermometers (1981–82). In the 1973–76 study, data were collected from a station 7 km east of the village of Capachica in 175–200 m of water. In 1981–1982 measurements were also obtained from a station in the middle of Puno Bay with a water depth of 24–25 m. Short-term studies of diurnal stratification were made in 1981–1982 using the themistor instrument at stations near the island of Taquile in Lago Grande and at the main station in mid-lake. Carmouze *et al.* (1984) conducted a similar study in 1979, measuring temperature stratification at monthly intervals at a deep-water station in Lago Grande. The study of Lazzaro (1981) documents the stratification at a 40 m



Figure 1. Temperature profiles from Lake Titicaca, 1973 (Richerson et al., 1977).

deep station in the Chua Depression in Lago Pequeño. Details of methods are given in the papers referenced below.

Annual cycle of stratification in Lago Grande

The basic monomictic pattern of stratification in Lake Titicaca is illustrated in Fig. 1 for the year 1973. All the years studied to date in both Lago Grande and Lago Pequeño show qualitatively similar patterns. Stratification is present except for a brief period of near-isothermy in July, during the height of the dry season. During the main period of stratification, epilimnetic tempera-



Figure 2. Isotherms in^oC versus depth and time for the 1973–1976 period (Taylor and Aquize Jaen, 1984).

tures are around $13-15^{\circ}$ C and hypolimnetic temperatures about 11.1° C. In temperate lakes, temperature differences between the hypolimnion and the epilimnion would typically exceed 10° C.

Figure 2 illustrates the pattern of stratification for a period of 39 months in 1973–1976. The basic pattern of stratification is very regularly monomictic (see also Chapter VI.1d), with a brief period of isothermy in July and August. A significant thermocline forms in August and September, with the thermocline deepening to about 50 m by December. From late December until late April or early May the lake remains stratified with surface temperatures of 13°C or greater. The thermocline deepens and weakens during the main cooling period in May and June.

The work of Lazzaro (1981) shows that the 40 m deep Chua Depression in Lago Pequeño (Huiñaimarca) also has the basic warm monomictic pattern. During the wet season period of strongest stratification, the top of the thermocline in Lago Pequeño is only about half as deep as in Lago Grande.

Deep mixing is often incomplete in Lago Grande. Note in Fig. 1 that all of the profiles in July and August show some stratification at depths of 60–100 m. Oxygen profiles (Richerson *et al.*, 1975) from 1973 indicate a failure to mix below 100 m. Mixing was also incomplete in 1980 and 1981. A 0.1° C temperature discontinuity was present at 110 m in early 1981. The temperature and oxygen profiles obtained by Carmouze *et al.* (1984) in 1979 also suggest incomplete mixing. Figure 3 shows oxygen levels at three depths for 1981–1982, and Fig. 4 shows the progressive decline in oxygen at depth



Figure 3. Dissolved oxygen concentrations at three depths in Lago Grande. 20 m, \blacktriangle ; 50 m, \bigcirc ; 150 m, \blacksquare (Vincent *et al.*, 1985).



Figure 4. Vertical profiles from monthly measurements of dissolved oxygen in Lago Grande, 1979. The stippled zone indicates the location of the thermocline (Carmouze *et al.*, 1984).

resulting from incomplete mixing in June and July 1979. The anomalously depleted oxygen at 150 m until the isothermal period in 1981 confirms that mixing must have been incomplete the previous year. During the first half of 1981, Lago Grande was anoxic below 200–210 m. This level of oxygen depletion has not been observed in any other year and perhaps resulted from incomplete mixing in 1979, as observed by Carmouze *et al.* (1984), as well as in 1980. The volume of anoxic and low oxygen water was great enough to prevent full oxygenation of the deep waters during the 1981 period of isothermy, and a small volume of water below 250 m remained anoxic until the 1982 mixing period (See Chapters V.6 and VI.1d for discussions of the consequences for the nitrogen budget of this failure of deep circulation).

Carmouze *et al.* (1984) computed the relative thermal resistance to mixing for their profiles for 1979. This computation expresses the density difference between the top and bottom of a stratum of water, 10 m thick in the case of their calculation, relative to the density difference between 4 and 5°C, the temperature change for which density change is minimal. Figure 5 shows the results of this computation. Resistance to mixing is, of course, more closely related to density differences than to temperature *per se.* Note the relatively rapid creation and destruction of the density stratified layer, and its relative stability for many months during the stratified season. Note also that a rather long period with quite low density gradients (June–September) was not sufficient for complete mixing to occur.

Carmouze et al. (1984) estimated the consequences of stratification for the recycling of biologically important materials using calculations based on the dissolved O_2 and CO_2 budgets. The primary production estimated by Richerson *et al.* (1977) for 1973 was 1.5 g C m⁻² d⁻¹, or 300×10^9 mol C year⁻¹ for the whole of Lago Grande. Using a respiration coefficient of 0.87, they estimate that only 35×10^9 mol C year⁻¹ of CO₂ was produced in the hypolimnion. Thus, nearly 90% of the respiration and recycling of carbon and other nutrients appeared to have taken place in the epilimnion (or if it took place in the hypolimnion, was balanced by the diffusion of O₂ downwards and presumably of nutrients upwards). The amount of carbon lost from the epilimnion is large in terms of phytoplankton standing stock, which is about 3 g C m⁻² or 1.5×10^9 mol. Thus the equivalent of approximately 20 times the epilimnetic instantaneous standing stock of biomass carbon is mineralized below the hyppolimnion. If the ratio of C:N is 7 in the biomass, the potential loss of nitrogen from the epilimnion due to settling of organisms or material with a similar N:P ratio would be of the order of 20 µmol N 1^{-1} year⁻¹. This figure is rather large, given that it exceeds hypolimnetic concentrations of available N (NO₃ + NH₄) by a factor of 3 to 4 (Vincent et al., 1985). During the annual destratification, the euphotic zone must start with a total available nitrogen content of approximately 5–7 μ mol l⁻¹. It seems likely that recycling of nitrogen is even more efficient than for carbon, although cyanobacterial N-fixation might supply roughly $4-10 \mu$ mol N l⁻¹ $vear^{-1}$ (Chapter V.6). It does make sense that the C:N ratio of sinking



Figure 5. Vertical profiles of physical stratification of the water column, expressed in units of relative thermal resistance (defined in the text, Carmouze *et al.*, 1984).

detritus would rise with depth and that the average depth of nitrogen mineralization would be shallower than for carbon. Thus nitrogen is probably more likely to be mineralized in the epilimnion or just below it, compared to carbon. See Vincent *et al.* (Chapter V. 6) for a more extensive analysis of the nitrogen budget of the lake.



Figure 6. Temperature and stratification in Puno Bay. Bottom water temperature (24 m), \bullet ; temperature difference between 4m (below the diurnal thermocline) and 24 m, \Box ; depth of maximum temperature gradient, \bigcirc (Vincent *et al.*, 1986).

Polymictic patterns of stratification of Puno Bay and Lago Grande

Puno Bay has a mean depth of 14 m and a maximum depth of 37 m. Given that the main thermocline in Lago Grande lies at 50 m during the period of most intense stratification, a thermocline as strong and permanent as that in the main basin is unlikely to form. Even if density-driven exchanges between Lago Grande and Puno Bay were weak, we would expect the top of the seasonal thermocline around 25 meters as in Lago Pequeño. Puno Bay is too shallow over most of its extent to show the annual cycle of stratification. However, a marked pattern of more ephemeral stratification does play an important role in the Bay (Fig. 6). The Bay frequently has a temperature gradient of from a few tenths to 2°C. The depth of maximum gradient ranges from near the bottom at our station to shallower than 10 meters. In the two years for which we have data, the most persistent stratification events occurred during the main heat storage phase of the annual cycle from October to December. During the middle of the warmest season, episodes of strong stratification were interrupted by essentially complete mixing. The main period of heat loss in April and May results in convective mixing that prevents stratification, and the cool season period of modest changes in overall heat storage resulted in episodes of weak stratification, especially in 1982. In each episode of stratification, there was a tendency for the thermocline to begin near the bottom, rise to shallower depths during the period of maximum stratification, and then descend again to near the bottom.

In Lago Grande a pattern of complex subdivision of the epilimnion sometimes occurs on the polymictic time scale. Such temporary sub-stratification of the epilimnion can be seen in Fig. 1, especially on February 24 and November 30. Several complex episodes of thermocline depth change and variation in internal structure are apparent in Fig. 2. Lewis (1973) described a similar pattern from Lake Lanao and called the process *atelomixis*. Taylor and Aquize Jaen (1984) developed a non-dimensional measure of the variability in heat flux, S* where

$$S^* = \frac{r_s}{(B/T)}$$

 r_s is the standard deviation of the average monthly storage fluxes about the annual mean, B is the Birgian heat budget (Hutchinson, 1957), and T is the time interval from the lake's seasonal minimum heat storage to its maximum. They compared the values of S* for 5 temperate and two tropical lakes. The value for Titicaca was considerably higher than for the temperate lakes, and that for Lake Valencia (Lewis, 1983) was considerably higher than for Titicaca in the low heat budget and weaker stratification of tropical lakes does indeed exaggerate the importance of events on the polymictic time scale.

Diurnal stratification

Powell et al. (1984) studied the formation and erosion of the diurnal thermocline in Lake Titicaca. Two examples of the diurnal cycle are given in Fig 7. During the night, wind mixing and convection usually make the epilimnion isothermal to considerable depths, typically to the top of the seasonal thermocline. Shortly after sunrise, the surface few meters of water begin to heat, with maximum temperatures and temperature gradients right at the surface. Surface skin temperatures become ca. 1°C warmer than the underlying epilimnion temperatures at 10-15 m. By early afternoon, a diurnal mixed layer begins to form. By sundown, the mixed layer reaches 5-7 m depth with temperatures 0.3-0.4°C above those of the deeper epilimnion. Detectable diurnal heating reaches to about 10 m at this point. After dark, the loss of heat is fairly rapid, and nearly isothermal conditions obtain by about midnight. Neale and Richerson (1987) made detailed observations on ten examples of diurnal stratification in Lago Grande. The increase in surface skin temperature ranged from 0.06 to 2.41°C (average 1.08°C). The afternoon mixed layer depth ranged from 1.5 to 9.5 m (average 4.7 m), while the depth penetration of a recognizable diurnal thermocline ranged from 5 to 13 m (average 8.6 m).

Powell *et al.* (1984) computed coefficients of vertical eddy diffusivity for two time periods during the afternoon and evening heat loss phase of stratification for the data shown in Fig. 7. The calculation is based on measuring the rate at which turbulent diffusion is driving heat downward from layer to layer, after correcting for the direct effects of heating by absorption of solar radiation. Minimum diffusivities in the region of the maximum diurnal stratification were about a factor of 10 lower than at shallower and deeper weakly stratified depths. Mixing of the epilimnion is thus very strongly in-



Figure 7. The daily cycle of near-surface heating and cooling for two days in Lake Titicaca. The dates are 3 September 1981 (246–81) and 22/23 July 1982 (203/204/82). The time the profile was obtained is noted next to each curve (Powell *et al.*, 1984).

hibited by diurnal stratification. The reduced mixing has quite substantial effects on photosynthesis (See Chapter VI.1d).

Conclusions

Despite its high elevation and low mean temperatures, the patterns of stratification in Lake Titicaca are typical for large, deep tropical lakes. Differences between epilimnetic and hypolimnetic temperatures are relatively small (ca. 3°C), but persistent throughout most of the year in Lago Grande. Lago Grande is a warm monomictic lake in Hutchinson's (1957) classification, with a brief period of isothermy or near isothermy in July and August. The relatively weak annual pattern of stratification makes patterns at other time scales relatively more conspicuous. There is a marked variation in the degree of deep mixing during the annual isothermal event that causes major differences in lake chemistry between years. There is irregular variation in the strength of stratification and depth of free mixing during the stratified period in Lago Grande and a polymictic circulation pattern in shallow Puno Bay. There is a pattern of strong diurnal stratification and nocturnal mixing on all but the cloudiest and windiest days.

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This paper is dedicated to the memory of Carl Widmer who began the modern study of the limnology of Lake Titicaca in 1973 and introduced me to this most fascinating lake. Special thanks also Victoria Valcárcel who helped us in so many ways.

V.5. The energy balance

JEAN-PIERRE CARMOUZE

Lake Titicaca is a unique example of a large, deep, tropical lake (between latitudes $15^{\circ}25$ and $16^{\circ}35$ south) located at 3810 m altitude. A priori one might think that this high altitude location may confer a special type of thermal regulation upon it. The various studies that have been carried out on this subject (Kessler, 1970; Carmouze *et al.*, 1983; Richerson *et al.*, 1977 and Taylor and Aquize Jaen, 1984) provide:

- 1) a better undertanding of the micro-climate created by the lake on the surrounding region,
- 2) a definition of the factors which control the temperature of the lake and its thermal stratification,
- 3) an estimate of the rate of evaporation which is one of the terms of the hydrological balance.

The energy balance of the water body contains two terms which should balance. The first is the algebraic sum of two components: the short wavelength radiation balance, Q_s , and the long wavelength radiation balance, Q_T . The second term represents the exchanges by conduction within the water mass Q_L , by convection at the water atmosphere interface Q_C , and by evaporation, Q_E .

The total balance is represented by:

$$Q_s + Q_T = Q_c + Q_L \tag{1}$$

The heat provided by inputs from rainfall and rivers and thermal phenomena associated with biogeochemical reactions, convection through the lake bed and geothermal energy are ignored. These various heat flows are closely related to one another. The thermal balance is subjected to the external forcing factors of solar radiation and the state of the atmosphere (temperature, air humudity, cloud cover, wind speed, etc.), the latter also being influenced by the thermal response of the water body itself, that is to say the microclimate it creates. In the final analysis, it is the water temperature (or the total heat content of the lake) which adopts a value so that the sum of the terms of the energy balance tends towards zero. The water temperature represents one of the main readjustment factors influencing the long wave-

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Figure 1. Location of Lake Titicaca and the Puno meteorological station. The dominant winds are indicated.

length radiation emitted by the lake, the evaporation and the thermal convection.

Because the solar radiation and the atmospheric conditions vary continuously on a daily, seasonal and annual basis, a succession of energy balances tends to becomes established at the water-atmosphere interface and within the water mass. The effect of changes in the inputs and outputs of energy at these levels, is either to draw in energy from the environment or to release energy into it, leading to changes in the total quantity of heat stored and its distribution within the lake.

In this chapter we will describe the exchanges occurring at the wateratmosphere interface and their consequences on the changes in the heat reserves of the lake. The vertical distribution of these reserves reflected in the thermal stratification is described in Chapter V.4.

Any hydrological or energy balance is typified by the period chosen. The balance that is to be described is based on meteorological data recorded at Puno (Peru) between 1954 and 1987 and temperature data in the Lago Grande collected between 1976 and 1979. It should be noted that the Puno meteorological station is exposed to the dominant winds (Fig. 1). These data

are insufficient on a small time-scale for analysis of diurnal changes, and refer to too short a time period for annual variations in energy flux to be evaluated. Nevertheless, a monthly energy balance can be drawn up.

Radiation balance within the lake

Solar radiation absorbed at short wavelengths

The total solar radiation, which represents the light energy from direct and diffuse solar radiation falling on a horizontal surface, can be easily calculated in relation to the latitude of the site of observation and the state of the overlying atmospheric layer.

We have used the method of calculation developed by Perrin de Brichambaut and Lamboley (1968). These workers start with the daily total of solar radiation incident at the top of the earth's atmosphere, G_0 , averaged for each month, and then calculate the solar radiation at the earth's surface in fine weather, G_{max} . This calculation requires that a certain number of assumptions be made relating to the altitude, the transparency of the atmosphere, the quantities of condensable water vapour and ozone. The following assumptions were made in the calculation of Gmax: atmospheric pressure, P = 1000 mb; quantity of condensable water vapour, w = cm, coefficient of atmospheric transparency B = 0.07.

At 15°S, the latitude of Lake Titicaca, the values for total incident radiation at sea level in J cm⁻² d⁻¹ are:

Month	J	F	Μ	A	М	J	J	А	S	0	N	D	
G _{max}	3200	3125	2950	2650	2250	2075	2125	2375	2750	3050	3200	3250	

Corrections need to be made to take into account the true environmental conditions. At the altitude of the lake (3810 m) the total radiation must be increased by 4% just because of decreased scattering from gas molecules (1% per 1000 m altitude). The quantity of condensable water vapour, w, was determined from the water vapour pressure at the lake's surface, fa, using Hann's formula:

$$\mathbf{w} (\mathbf{cm}) = 0.17 \times \mathbf{fa} (\mathbf{mb}) \tag{2}$$

fa being on average equal to 5.8 mb and $w \approx 1$ cm. This value introduces a correction of +3%. The transparency coefficient, B, which defines the quantity of aerosols contained in the column of atmosphere above the observation point is of the order of 0.025 for a pure atmosphere. This factor decreases with altitude according to the formula Bp = B × P/1000, where P = the atmospheric pressure in mb. At Lake Titicaca this value must be close to 0.015. The influence of B on G_{max} is slight, because the decrease in direct radiation

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is partially compensated by an increase in diffuse radiation. However, because of the effect of scattering of solar radiation by the water body, this influence is indirectly increased. For an albedo of water close to 0.07 and B = 0.015, according to Perrin de Brichambaut and Lamboley, G_{max} must be increased by +6%. In total for Lake Titicaca, the values of G_{max} must then be increased by 13%.

A figure for total mean radiation, G, is derived from the corrected values, taking into account the duration of sunshine. To do this Perrin de Brichambaut and Lamboley have drawn up a table of correspondence between the proportion of sunshine hours (i.e. the ratio between the mean measured hours of sunshine, S, and the maximum theoretical sunshine hours, S_{max} , for continuous fine weather) and the ratio G/G_{max} , based on Angström's formula:

$$G/G_{max} = 0.76 \times S/S_{max} + 0.24$$

S/S _{max}	0	0.2	0.4	0.5	0.6	0.8	1.0
G/G _{max}	0.24	0.42	0.58	0.65	0.73	0.86	1.0

The values of G have thus been calculated from sunshine duration data recorded at Puno (Table 1).

Part of the solar radiation, G, is dispersed in all directions by reflection and scattering from the water body surface. This fraction, or albedo, is close to 0.07 in the case of a lake. The energy absorbed by Lake Titicaca in the form of short wavelength radiation can therefore be estimated as: $Q_s = G$ (1 - 0.07).

The values obtained vary between $2628 \text{ J cm}^{-2} \text{ d}^{-1}$ in October and $1864 \text{ J cm}^{-2} \text{ d}^{-1}$ in June, the mean annual value being $2190 \text{ J cm}^{-2} \text{ d}^{-1}$ (Fig. 2).

Long wavelength radiation from the earth

This radiation includes two components of long wavelength radiation; one is the radiation emitted by the water body and the other the radiation emitted by the atmosphere away from the lake, both representing losses of energy for the lake.

Emission from the lake

Water has a behaviour close to that of a black body. The energy emitted by the lake is estimated from the Stefan-Boltzmann equation:

$$Ml = \epsilon \times \sigma \times Te^4$$
(3)

Table 1. Monthly means for: maximum and minimum air temperatures near the water body Θ_{amoy} , Θ_{amax} , $\Theta_{$

$\theta_{a,m,a}$ in °C	14.5	14.2	14.1	14.3	13.7	13.2	13.0	13.8	14.3	15.6	15.9	15.1	_
$\theta_{a \text{ mun}}$ in °C	5.0	5.2	4.8	3.4	1.0	-0.9	-1.3	Ø.2	2.0	3.2	4.0	4.8	_
$\theta_{a mean}$ in °C (1)	9.95	9.77	9.33	8.44	6.71	5.26	5.07	6.43	7.90	9.4	10.10	10.15	8.21
θ _e in °C	13.85	14.3	14.35	13.85	13.0	12.0	11.5	11.25	11.75	12.9	13.35	13.85	13.0
f _a in num.	7.5	7.9	7.7	6.5	4.9	4.0	4.0	4.6	5.4	5.5	5.9	6.8	5.89
F _c in num.	15.90	16.34	16.40	15.90	15.02	14.06	13.60	13.38	13.82	14.06	15.34	15.90	15.05
P in num.	646	646.1	646.7	647.1	647.1	646.7	646.5	646.3	646.3	645.7	645.4	645.4	646.2
S in %	44	45	54	72	80	83	80	75	74	66	52	67.5	
δ max													
N in octets	6.9	6.7	6.0	4.4	3.1	2.5	2.4	3.0	4.0	4.6	5.4	6.3	4.5
Uin m s ⁻¹	1.14	1.03	Ø.96	0.95	0.97	1.08	1.06	1.23	1.32	1.42	1.39	1.28	1.15



Figure 2. Mean monthly values of components of the Lake Titicaca energy balance expressed in $J \operatorname{cm}^{-2} d^{-1}$.

Q_S = short wavelength solar radiation absorbed

 $Q_T = long$ wavelength radiation from the lake

 $Q_N = Q_S - Q_T$ = radiation balance

Q_E = evaporation losses

 $Q_C =$ losses by conduction

Mean monthly changes in the heat content of the lake, expressed in $J \text{ cm}^{-2} d^{-1}$: δQ_L

Where ϵ = the emissivity of water = 0.97; σ = the Stefan-Boltzmann constant = 4.9 × 10 J cm⁻² K⁻⁴ d⁻¹ and Te = the surface water temperature in °Kelvin.

The mean monthly values of Ml calculated from the values of Θe , taken from Table 1, vary between $-3240 \text{ J cm}^{-2} \text{ d}^{-1}$ in March and $-3102 \text{ J cm}^{-2} \text{ d}^{-1}$ in August; the mean annual value being $-3181 \text{ J cm}^{-2} \text{ d}^{-1}$.

Atmospheric radiation under clear skies

This is the most difficult to estimate term in the radiation balance. Among the various formulae and graphical solutions used to estimate this term, we have chosen that of Brunt, which is statistically valid in the case of clear skies. This formula considers the emission of the atmosphere to be that of a black body at the air temperature at ground level, corrected by a factor taking into account the partial pressure of water vapour at ground level, since this plays a major role in the absorption and re-emission of terrestrial radiation.

$$Ma = \epsilon \times \sigma \times Ta^{4}(a + b \times \sqrt{fa})$$
(4)

Where: Ma = the energy emission by the atmosphere towards the lake in J cm⁻² d⁻¹; ϵ = the emissivity of the atmosphere; σ = the Stefan-Boltzmann constant; Ta = the temperature of the air at ground level in °K, and fa = the water vapour pressure at ground level in mb. The values of the constants a and b are rather uncertain. We have used the values recommended by M. and R. Berliande (*in* Ivanoff, 1975): a = 0.61 and b = 0.051.

The mean monthly values of Ma were thus calculated from the Θa and Fa data in Table 1. Ma varies from -2288 J cm⁻² d⁻¹ in February to -2021 J cm⁻² d⁻¹ in July, the mean value being -2179 J cm⁻² d⁻¹ (Table 2).

The long wavelength terrestrial radiation balance

In fine weather, the terrestrial radiation balance Q_{To} is equal to Ma – Ml. This value is reduced under cloudy conditions because the radiation by the atmosphere increases the greater the cloud cover and the lower the cloud ceiling.

Among the various proposed empirical formulae relating the mean value for terrestrial radiation under cloudy conditions, Q_T , to that of the mean value under clear skies Q_{To} and to cloud cover N, we have chosen that of Berliande (*in* Ivanoff, 1975): $Q_T = Q_{To}$ (1 – c. Nm), where m = 1.75 and c = 0.57 (value adopted for latitude 15°S). Values for cloud cover in octets, N, from Table 1, have been rescaled from 0 to 1.

The long wavelength radiation balance for each month calculated using this method shows that there is a loss of energy which is at a maximum in June $(-1025 \text{ J cm}^{-2} \text{ d}^{-1})$ and a minimum in January $(-518 \text{ J cm}^{-2} \text{ d}^{-1})$, the mean loss over the year being $-782 \text{ J cm}^{-2} \text{ d}^{-1}$ (Table 2, Fig. 2).

The radiation balance

The radiation balance, R_N , which is the quantity of energy available, is equal to the difference between Q_S and Q_T . It varies from 839 J cm⁻² d⁻¹ in June to 1903 J cm⁻² d⁻¹ in November, the mean value over the whole year being 1409 J cm⁻² d⁻¹ (Fig. 2).

The heat content of the lake, evaporation, conduction

The quantity of energy in the form of radiation available at the lake surface determines the exchanges of energy between the water and atmosphere by evaporation, Q_E , and by thermal convection, Q_C , and within the water itself

by changes in the energy content of the lake, δQL , according to the following equation:

$$R = \delta Q_L + Q_c + Q_E$$

The terms of this equation, including the monthly evaporation rates, E, will be calculated from values of Q_E and we will propose a semi-empirical formula for the estimation of E.

Changes in the heat stored in the lake

The heat content of the lake per unit area has been calculated as follows: the lake was divided into layers of equal depth in which the heat content was calculated. This content is equal to the product of the proportional area that each layer represents in terms of the total lake area, the thickness of the layer and its mean temperature. The sum of values for each layer gives the total quantity of heat contained in the lake (Dussard, 1966).

The calculation was carried out using temperature profiles that we recorded in the Lago Grande from 1977 to 1979 and the bathymetric profile drawn up for the lake by Boulangé and Aquize Jaen (1981).

After estimating the quantities of heat stored in the lake, Q_L , in each month, the changes from month to month δQ_L were calculated (Tables 2 and 3, Fig. 3). The lake has a maximum loss of heat in June of 667 J cm⁻² d⁻¹ and a maximum heat gain in October of 378 J cm⁻² d⁻¹. It should be noted that the maximum monthly change in heat reserves of the lake is of the order of 50×10^3 J month⁻¹ and only represents 8% of the mean annual value of the reserves.

It is not easy to compare the changes in heat content over the course of a year from one lake to another, since these changes depend not only on the climatic conditions of the region, but also on the morphology of the lake and of its catchment. To overcome this difficulty, Taylor and Aquize Jaen (1986) have proposed a dimensionless index, S, which they call the stored heat flux:

$S = \sigma S / \beta / T$

Where: σS = standardised monthly changes in stored heat. β = the difference between the maximum and minimum monthly values of stored heat T = the time (months) between the month with the lowest heat content and that with the highest content. From the data in Table 3: σS = 10 417 J cm⁻²; β = 50 995 J cm⁻² and T = 8 months; from which S = 1.63.

Taylor and Aquize Jaen (1984) from their own data and those of Richerson *et al.* (1977), calculated values of 1.45 and 1.54, respectively, and noted that values normally found in lakes in temperate regions are lower, of the order

Table 2. Components of the mean monthly energy balance within the Lago Grande. The results are expressed in J cm⁻² d⁻¹. $Q_S =$ solar energy absorbed; M_L = energy emitted by the lake surface; M_a = energy emitted by the atmosphere towards the lake under clear skies; Q_T = quantity of heat lost by terrestrial radiation; R_n = radiation balance; δQ_L = changes in the heat content of the lake. Q_E = heat lost by evaporation; Q_C = heat lost by turbulent convection. B = Bowen ratio.

	J	F	М	А	М	J	J	А	S	0	N	D	Annual mean
Qs	2.070	2.046	2.132	2,171	2.025	1.864	1.947	2.142	2.399	2,628	2.581	2.296	2.190
M_L	-3.215	-3.236	-3.240	-3.215	-3.177	-3.135	-3.114	-3.102	-3.122	-3.148	-3.194	-3.215	-3.181
M.,	2.290	2.288	2.267	2.203	2.100	2.027	2.021	2.083	2.155	2.206	2.243	2.268	2.179
QT	-518	-552	-637	-809	-956	-1.025	-1.016	-914	-803	-737	-678	-741	-782
R,	1.552	1.494	1.494	1.361	1.065	839	930	1.228	1.596	1.890	1.903	1.554	1.409
ΔQ_1	190	232	182	-53	-478	-667	-399	-73	169	378	349	182	-
В	0.192	0.226	0.243	0.241	0.259	0.258	0.282	0.227	0.190	0.155	0.145	0.168	0.215
Q	-1.142	-1.029	-1.055	-1.139	-1.225	-1.197	-1.036	-1.060	-1.199	-1.309	-1.357	-1.174	-1.160
$Q_{t}\cdot$	-219	-232	-256	-274	-317	-309	-292	-240	-228	-203	- 197	- 197	-248

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Table 3. Heat content of the Lago Grande in the first month, Q_L , and the mean monthly changes δQ_L . The results are expressed in J cm⁻². (Note that the monthly values of δQ_L are expressed in mean daily values for each month in Table 2).

	J	F	м	А	М	J	J	А	s	0	N	D
Q	613.310	619.205	625.750	631.395	629.815	615.015	595.015	582.650	580.400	585.475	597.190	607.665
ΔQ_L	5.095	0.545	5.045	-1.560	-14.600	-20.000	-12.370	-2.230	5.075	11./1.	10.475	0.040

of 1.15, thus underlining the wider range of changes in heat content in tropical lakes.

Exchanges by evaporation and convection

Exchanges by evaporation and convection are difficult to estimate. Various semi-empirical formulae exist, but one of the best ways of estimating them is to derive the sum of their values from the energy balance, and then calculate their separate values from Bowen's ratio, B. This ratio reflects the fact that the coefficients of the transfers of water vapour and of heat at the air-water interface are very close to another.

$$B = Q_c/Q_E = C_p \cdot P/0.621 \cdot L \times \Theta_e - \Theta_a/F_e - f_a$$

Where: Θ_a = the air temperature; Θ_e = the water temperature; C_P = the specific heat capacity of air at atmospheric pressure = 1005 J g⁻¹; L = the latent heat of evaporation of water in J g⁻¹ (This is a function of the surface water temperature Θ_e : L = 2495 - 2.38 Θ_e); P = the atmospheric pressure; F_e = the partial pressure of water vapour at saturation at the temperature Θ_e and f_a = the actual pressure of water vapour in the air just above the lake's surface.



Figure 3. Mean monthly values for evaporation rates from Lake Titicaca in mm d^{-1} .

(1) Curve obtained from the energy balance

(2) Curve derived from the relationship E = 0.477 $(F_e-f_a)\;U_{2m}$

(3) Curve derived from the relationship $E = 0.17 + U_m (F_e - f_a)$

E being the mean monthly evaporation rate in mm d^{-1} , $F_e - f_a$ the humidity deficit in mb and U_{2m} the wind speed 2 m above ground level in m s⁻¹.

The mean monthly values of $Q_E + Q_C$ were thus calculated from equation (1) and those of B from data presented in Table 1. The separate values of Q_E and Q_C (Table 2) were obtained from equation (5).

Losses by evaporation range from $-1357 \text{ J cm}^{-2} \text{ d}^{-1}$ in November to $-1029 \text{ J cm}^{-2} \text{ d}^{-1}$ in February and those by turbulent convection from $-309 \text{ J cm}^{-2} \text{ d}^{-1}$ in June to $-197 \text{ J cm}^{-2} \text{ d}^{-1}$ in November (Fig. 2).

Evaporation rates derived from the energy balance, semi-empirical formulae

The mean monthly evaporation rate, E, was derived from the relationship $E = Q_E/L$; where E is expressed in cm d⁻¹; Q_E in J cm⁻² and L, the latent heat of evaporation in J g⁻¹.

The results (Fig. 3) show that the evaporation rates range from 4.2 to 5.3 mm d^{-1} , the minimum being in May and the maximum in November. The mean annual rate of 1720 mm is very close to the value of 1740 mm/year obtained from the hydrological balance of the Lago Grande by Carmouze and Aquize Jaen (1981).

Kessler (1970) and Richerson *et al.* (1977) have also calculated rates of evaporation of 1714 and 1900 mm/year, respectively, from the heat balance and values of 1480 and 1344 mm/year from the hydrological balance. The most recent estimate made by Taylor and Aquize Jaen (1984) from the heat balance is 1350 mm/year.

The semi-empirical formulae which are used to calculate the evaporation rates are mostly derived from the approximate expression for this variable derived from the general aerodynamic model:

$$E = D_a/A_a \times C_Z 0.622/P (F_e - f_a) U_Z$$
P

Where: $D_a =$ the coefficient of turbulent diffusion of the atmosphere in the vertical plane; $A_a =$ the coefficient of turbulent viscosity of the atmosphere in the vertical plane; $C_Z =$ the friction coefficient at distance Z at which the wind speed, U_Z , is measured.

These variables are difficult to measure. Jacobs (1951) chose to determine a mean value for this group of variables by combining the energy balance method giving QE and equation (6):

$$\mathbf{E} = \mathbf{Q}_{\mathbf{E}}/\mathbf{L} = \mathbf{k}(\mathbf{F}_{\mathbf{e}} - \mathbf{f}_{\mathbf{a}}).\mathbf{U}_{6m}$$
(7)

Taking the 4 oceanic regions, he obtained values of k varying between extremes of 0.11 and 0.20 (E being expressed in mm d - 1, F and f in mb and U in m s - 1 at 6 m above the water surface). Using the same method for Lake Titicaca, a mean annual value of k of 0.477 was obtained. It should be noted that these values of k are not directly comparable, because for



Figure 4. Monthly values for the humidity deficit of the air, $F_c - f_a$, at Puno and the wind speed at 2 m above ground level.

Titicaca, U was measured at 2 m above ground level. Equation (7) thus becomes:

$$E = 0.4777 (F_e - f_a) U_{2m}$$

The mean monthly evaporation rates were calculated from this equation using the data presented in Table 1. The graph obtained shows wide deviations from that obtained from the energy balance (Fig. 3). The deviations are to a large extent due to the variable U, because the slope of the monthly evaporation curve given by the balance method (Fig. 3) is close to that of $F_e - f_a$ and different from that of U (Fig. 4). To obtain a better agreement between the two methods it is therefore necessary to use formulae giving less weight to the wind factor, such as: $E = (k1 + k2 U_{2m}) \times (F_e - f_a)$. A satisfactory adjustment was obtained by taking the following values for k1 and k2:

$$k1 = 0.17, k2 = 0.30$$

which give

$$E = (0.17 + 0.30 \text{ U}_{2m}) \times (F_e - f_a)$$
(9) (Fig. 3)

Note that Laevastu (*in* Ivanoff, 1975) used values of k1 = 0.26, k2 = 0.077 in oceanic environments. These values are different from ours, but they referred to wind speeds at 10 m above the water surface and not at 2 m as in our case. It is therefore probable that the use of meteorological data from another station around the lake would lead to a change in values of k1 and k2.

The unusual nature of the energy balance

- Because of its high altitude situation, Lake Titicaca receives 13% greater solar radiation during fine weather than it would receive if it were at sea level. On the other hand, the sunshine duration $(245 \text{ h month}^{-1})$ is not very high; at the same latitude higher values can occur, such as at Lake Chad at 13°N which has 288 h month⁻¹. However, this increase in sunshine only amounts to an increase in solar energy of 3 to 4%. In total, the solar radiation received by Lake Titicaca, with a mean annual value of 2190 J cm⁻² d⁻¹, is higher than that received by other environments at approximately the same latitudes.

The seasonal variations in solar radiation are in part attenuated by the fact that in the season when the solar radiation reaching the top of the atmosphere is at its lowest (i.e. June-July-August) the sunshine hours are at their greatest. The between-month variation in incident radiation, which amounts to 42% of the mean value in fine weather, is reduced to 32% because of seasonal changes in cloud cover.

– The losses by terrestrial long wavelength radiation, Q_T , at the lake surface are greatest when the difference between the surface water temperature, Θ_e and the temperature of the overlying air, Θ_a , is slight. However, in the case of Lake Titicaca, the difference between Θ_e and Θ_a (expressed as the daily average) varies between 3.5°C and 5°C throughout the year. If the water temperature were to fall to that of the air, the radiation losses would be 20% less. In addition, Θ_e and Θ_a are on average 10 to 15°C lower than they would be at sea level at the same latitude. Under the conditions occurring at low altitude, the terrestrial solar radiation losses would be reduced by 10 to 15%.

Overall, at Lake Titicaca, again because of its high altitude, the long wavelength radiation losses are 30 to 35% higher than those which would occur if it were situated at sea level. Seasonal variations in terrestrial radiation are very pronounced, with extreme values differing by + 32% from the annual mean value. These variations are nevertheless attenuated by the fact that the differences in water and air temperatures are greatest when the partial pressure of water vapour is at its lowest in the southern winter, whereas the reverse occurs in summer. The seasonal variations are still much less than the diurnal changes (which are not dealt with in this chapter) due to the wide range of Θ and especially Θ a over the 24 hours.

- The radiation balance provides the value for the energy available within the water body. In the case of Lake Titicaca, the increase in the gain in short wavelength radiation (ca. 10%), because of its situation at 3800 m altitude, is roughly compensated for by an increase in losses by long wavelength radiation (ca. 30 to 35%). This implies that the sum of the losses by evaporation and conduction is of the same order of magnitude as that recorded in low-altitude lakes. - The energy losses by evaporation, averaging $1160 \text{ J cm}^{-2} \text{ d}^{-1}$ over the year, correspond to an evaporation rate of 1720 mm year⁻¹. This value is of the same order of magnitude as that recorded in other tropical lakes. It should be recalled that the evaporation rate is mainly a function of the water vapour deficit, $F_a - f_e$, and of the wind speed U. $F_a - f_e$ is on average 9.16 mb, a relatively high value, although the water and air temperatures are low compared to those occurring at low altitudes. This value is explained by the low relative humidity (the mean annual value of fe = 50%) and by the fact that the daily mean water temperature is always 4 to 5°C above that of the air. A simple calculation shows in fact that if the water temperature were reduced to that of the air, the water vapour deficit, $F_a - f_e$, would be 5.15 mb, a value that when substituted in formula (8) would lead to a decrease in the evaporation rate of 40 to 45%. The wind speed, which is not very high on average (1.15 m s⁻¹ at 2 m above ground level), has nevertheless an effective action in renewing the air mass which would otherwise tend to become saturated on contact with the water, since the temperature gradient at the surface of the water body is such that it leads to the formation of an unstable stratification for most of the time.

The changes in evaporation rates over the year reflect those in the humidity deficit, $F_a - f_e$, the wind speed playing a minor role. However, the winds, which are lighter in May-June, tend to reduce the increase in evaporation at this period due to the strong humidity deficit.

- Exchanges by thermal convection represent losses of heat from the lake throughout the year, when the day is taken as the time unit.

The Bowen ratio, B, is inversely proportional to the atmospheric pressure (see equation (5)). At 3800 m altitude, however, this is only 640 mb, so that the value of B is 36% lower than what it would be at the normal pressure of 1000 mb. But the relatively low air and water temperatures have the reverse effect. By taking the example of a tropical lake at low altitude with the same difference between the air and water temperatures of 4.5° C, but with values of around 26°C and the same relative humidity (50%), it can be seen from formula (4) that B decreases by 40%. In general, the altitude factor on its own does not systematically favour heat exchanges by evaporation in a lake compared to those by thermal convection and vice versa.

– The last term of the energy balance to be analysed is that of the changes in the heat reserves of the lake provoked by the uneven distribution of solar energy over the course of the year. These changes (631 500 J cm⁻² at the end of March against 580 500 J cm⁻² at the end of August) represent thermal control by the lake since they result from the absorption of excedent solar energy in summer and its restitution in winter, the season of deficit in winter, thus attenuating the fluctuations caused by the other energy fluxes.

Thermal regulation is a function of the amplitude of seasonal changes in solar radiation, directly related to the latitude of the site, and also of the capacities of the lake itself to exchange heat energy with the atmosphere. This capacity is related to the depth of the water column involved in heat exchanges at different seasons. In deep lakes the transport of heat with depth depends on the intensity of vertical mixing, whereas in shallow lakes it is limited by the depth of the water body itself. So, at the same latitude, deeper lakes have a greater degree of thermal regulation. The intensity of vertical mixing is a function of a large number of factors including the morphology of the site, the wind speed and fetch, the horizontal circulation of water, Coriolis force and the resistance to mixing when there is a vertical density gradient (thermal or chemical stratification). These factors will not be analysed here, but in order to determine the reasons for the uniqueness of Lake Titicaca, it is interesting to demonstrate the fact that a high altitude tropical lake has a greater heat regulation than that of a low-altitude tropical lake under the same conditions. In fact, if one considers the density gradients created by temperature gradients, it takes twice as much mechanical energy to mix two masses of water, one at 24°C and the other at 26°C (water temperatures typical of low-altitude tropical lakes) than to mix two water masses at 11.5°C and 13.5°C (water temperatures in Lake Titicaca). In other words, all things being equal, the resistance to thermal diffusion created by the penetration of the temperature front is half as great in Lake Titicaca than it would be at sea level at the same latitude, the thermal regulation is thus increased and the micro-climate created by the lake is reinforced.

Conclusions

The analysis of the various terms of Lake Titicaca's energy balance has enabled the following points to be elucidated:

- the high altitude has the effect of increasing the solar radiation by 10 to 15% by inducing decreases in atmospheric transparency, scattering by gas molecules and in the thickness of condensable water vapour traversed. Because of this, the radiation emitted by the atmosphere is reduced, increasing the losses of long wavelength radiation by 30 to 35%. The sum of these opposing effects is that the energy balance, or the energy available at the lake's surface is of the same order of magnitude as for other lakes at the same latitude, but at low altitudes (1400 to 1450 J cm⁻² d⁻¹).
- on an annual basis, the heat exchanges between the lake and the atmosphere by convection and evaporation are approximately equal to the energy balance. As a result, they have about the same value as those recorded at sea level at the same latitude (mean values: evaporation = $1160 \text{ J cm}^{-2} \text{ d}^{-1}$, thermal convection = $248 \text{ J cm}^{-2} \text{ d}^{-1}$). Because of the altitude, a decrease in evaporation losses might have been expected, because for the same quantity of water vapour, the deficit in the partial pressure of water vapour (to which evaporation is directly proportional) decreases with increasing air and water temperatures. A decrease in losses

by convection may also have been expected since these are directly proportional to atmospheric pressure. In practice, because of a major difference between the air and water temperatures (4 to 5°C), which maintains the local atmospheric circulation for most of the year (dominance of cold winds coming from the Western Cordillera), the thermal exchanges over a year are comparable with those recorded at sea level at the same latitude.

- changes over the course of the year in the heat content of Lake Titicaca, which result from seasonal disequilibria between the inputs and losses of energy within the water body, are very pronounced. As we have seen this is due to its great depth (100 m average) and the low water temperatures for a tropical lake (11-14°C).

The heat gains reach a maximum in October and November (378 and $349 \text{ J cm}^{-2} \text{ d}^{-1}$, respectively) whereas the losses are greatest in June $(-667 \text{ J cm}^{-2} \text{ d}^{-1})$. Taking into account its size (8448 km^2), the lake releases $16.9 \times 10^{17} \text{ J}$ of energy during the cooling period in the month of June alone and absorbs $18.7 \times 1017 \text{ J}$ during the warming period between October and November. These figures give some idea of the heat regulation of Lake Titicaca and of the major thermoregulatory role that it has on the surrounding environment (Boulangé and Aquize Jaen, 1981). These workers showed that the mean annual temperature of the air and the maximum and minimum temperature values become lower the further from the lake shore. As an example, the mean annual temperature at Puno on the lake shore is 8.5° C compared to 6.5° C at Chuquibambilla 60 km to the north-west and the annual temperature range is 12° C at Puno compared to 18° C at Chuquibambilla.

V.6. Nutrients and nutrient limitation of phytoplankton

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Although physical factors and grazing can affect growth of phytoplankton populations in aquatic systems, algal production is often limited by the supply of nutrients (Paerl, 1982). This conclusion is supported by many studies showing the close correlation between the total amount of phosphorus or nitrogen in lakes, and the amount of algal production (Smith, 1983). Good correlations are also found between the supply rate of nutrients to lakes (loading) and the abundance of phytoplankton in those systems (Vollenweider, 1976). Additional support for the hypothesis that nutrients control primary productivity in lakes comes from laboratory and field experiments showing that algal production is increased when nutrients are added to the water.

Understanding factors that control algal growth allows us to predict how environmental changes will change lake productivity. For example, the nutrient loading model of Vollenweider (1976) has been used extensively to understand and control cultural eutrophication when excessive nutrients are introduced into a lake. Similarly, if we hope to understand seasonal and interannual changes in primary productivity in a lake (see Chapter VI 1, this volume), we must understand how nutrients and other factors control the growth of phytoplankton.

Phosphorus is often cited as the most important nutrient controlling phytoplankton in lakes. This conclusion, however, is derived largely from studies from glaciated regions of North America and Europe. Despite conflicting evidence from even this geographical area (Elser *et al.*, 1990), an oversimplified view has emerged that algal growth is limited by phosphorus in most natural lakes. Because the supply of nutrients in a lake will be affected by the bioegeochemistry of the drainage basin, by river-borne and atmospheric pollutants, and by lacustrine processes, it is unrealistic to expect that all lakes will be limited by the same nutrient. In fact, some results suggest that lakes in the tropics are more frequently limited by nitrogen than by phosphorus (see Vincent *et al.*, 1984).

Here we review the evidence for nutrient control of algal production in Lake Titicaca, a high-altitude tropical lake in South America. We first exam-

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Table 1. Nutrient loading by river inputs and precipitation (Vincent *et al.*, unpublished) and by nitrogen fixation (Wurtsbaugh *et al.*, unpublished) on Lake Titicaca. The estimates are for total nitrogen and phosphorus in 10^3 tonnes per annum.

	Nitrogen	Phosphorus
Rivers	3.70	1.22
Precipitation	1.81	0.07
Total external	5.51	$\overline{1.27}$
N ₂ fixation	12.91	

ine the nutrient characteristics of the lake, with emphasis on the sources, forms and distribution of nitrogen. We then examine the influence of nutrients on phytoplankton growth in Lake Titicaca. In the early 1980s several types of bioassays were applied to assess nutrient limitation in this system. The majority of the analyses were done from water collected: (1) near the centre of Puno Bay, (2) 20 km east of the Capachica Peninsula in Lago Grande, and (3) at several stations in Lago Pequeño (Lago Huiñaimarca). These results suggest that supplies of nitrogen, rather than phosphorus, control algal growth in this lake.

Results

Nutrient sources and sinks

Five of the major inflows to Lake Titicaca (Ramis, Coata, Ilave, Huancane and Suches, accounting for 68% of the total river input) and precipitation at a mid-lake site (Rocas Misteriosas) were each sampled and analysed for nitrogen and phosphorus on 7 to 15 occasions over 1981/82. These analyses allowed a first order estimate of the external N and P load on the lake (Table 1). More than twice the total N, and 16 times the total P entered the lake through the river inputs than by direct precipitation on the lake. The overall external loading ratio of N:P was 4.3:1 (by weight) – well below the typical phytoplankton growth requirements of about 10:1. The rainfall and river data also emphasised the strong seasonal pattern in nutrient input to Lake Titicaca. More than 50% of the rainfall and its nutrients fall on the lake over the 3 month period December, Janaury, February. Similarly, 75% of the total nitrogen and 85% of the total phosphorus that enter the lake each year via the rivers do so during the period of peak discharge, January – March.

The low nitrogen input to the lake from external sources may be substantially augmented by nitrogen fixation. Although N₂-fixing cyanobacteria rarely account for more than 20% of the total phytoplankton biomass, our acetylene-reduction assays suggest that much larger quantities of nitrogen can potentially be fixed by these organisms than enters the lake via other mechanisms (Table 1). However, the magnitude of fixation varies enormously between years as well as season, and in Puno Bay probably caused the bulk of the variation in phytoplankton biomass and photosynthesis over the 1981-82 period (Vincent et al., 1986). Denitrification is likely to be an important nitrogen loss process in Lake Titicaca, and like N2-fixation, it varies substantially with season and between years (Vincent et al., 1985). The magnitude of nitrate loss from Lago Grande by this mechanism appears to be highly dependent upon the extent of hypolimnetic anoxia, which in turn varies from year to year. In 1981 a relatively thick stratum of water in the deep hypolimnion (200-275 m) was anoxic and devoid of detectable nitrate. The denitrifier utilization of nitrate associated with this event was calculated to be of the same order as the annual input of nitrogen from all sources, including nitrogen fixation. This anoxic zone was substantially eroded during deep mixing in August 1981, and in 1982 winter mixing brought oxygenated water to the bottom of the lake. Denitrification was probably much less important as a net sink for water column nitrogen during these periods.

Nutrient concentrations

Concentrations of dissolved inorganic nitrogen (DIN = $NO_3^- + NO_2^- + NH_4^+$) are often low in Lake Titicaca relative to the amounts of soluble reactive phosphorus (SRP) available for phytoplankton growth. Nitrate and ammonia in the surface waters of Lago Grande and Puno Bay were usually below the limits of detection (3.5 and 2.5 µg N l⁻¹, respectively) except during or shortly after mixing periods (Fig. 1A). Concentrations of SRP, however, ranged from near $3 µg P l^{-1}$ during stratified periods to near $24 µg P l^{-1}$ in Lago Grande during deep mixing (Vincent *et al.*, 1984). In Puno Bay SRP remained between 1.5 and $6 µg l^{-1}$ through most of 1981/82, but with peaks up to $11 µg l^{-1}$ (Vincent *et al.*, 1986).

The ratio of DIN to SRP can provide a useful indication of algal nutrient deficiency, and in Lake Titicaca this value was usually well below 10:1, and strongly suggestive of nitrogen limitation. Ratios of DIN:SRP in the mixed layer of Lago Grande during 1982 were always less than 3:1 (Vincent *et al.*, 1984). DIN:SRP ratios in deep hypolimnetic water where mineralization was presumably complete were also low, averaging about 5:1 (Authors' unpublished data; Vincent *et al.*, 1985). Analysis of data reported by Lazzaro (1981,1985) for eight stations in Lago Pequeño indicates that mean seasonal concentrations of SRP ranged from $2-4 \ \mu g \ l^{-1}$, while NO_3^- levels ranged from $4-8 \ \mu g \ N \ l^{-1}$, giving NO_3^- :SRP ratios always less than 1.3:1.

The ratio of total nitrogen to total phosphorus also provides an index of the relative shortage of these two nutrients, however, the ratio is affected by the large contribution of dissolved organic nitrogen (DON) much of which may be biologically unavailable (Pick and Lean, 1987). In Lake Titicaca DON contributed 65 to 100% of the total dissolved nitrogen (TDN) pool, and



Figure 1. Seasonal changes in mixing depth, available nutrients and algal nitrogen deficiency in Lake Titicaca during 1982. A. Temporal variation in soluble reactive phosphorus (SRP) and NO_3^- in the surface water of Lago Grande. B. Changes in the depth of the mixed layer (Z_m), and nitrogen deficiency of the phytoplankton in the surface waters (NH_4^+). Nitrogen deficiency was assayed by adding NH_4^+ to water samples, and measuring the relative increase over controls in the dark uptake of ¹⁴C during 4–hr incubations. Ammonium enhancement of dark carbon uptake occurs only when phytoplankton are nitrogen deficient. Adapted from Vincent *et al.* (1985).

in the inflowing rivers this fraction amounted to 79–90% of TDN (Vincent *et al.*, unpublished). The mean TN/TP ratio for the surface waters of Lake Titicaca was 11.4:1 (Table 2) which is low by comparison with many phosphorus-limited lakes in the north temperate zone (e.g. Pick and Lean, 1987).

In Lake Titicaca concentrations of soluble reactive silicon, a nutrient that can limit the growth of diatoms or other siliceous algae, sometimes declined to levels that approached limiting concentrations (400–800 μ g Si(OH₄) l⁻¹;

Site	n	TN/TP	CV(%)
Lago grande ^a	5	11.4	40.4
Precipitation ^b	6	40.9	73.1
Rivers ^c :			
Ilave	7	4.7	84.8
Ramis	13	12.1	96.4
Coata	10	6.6	69.8

Table 2. Mean TN/TP ratios (by weight) in waters of Lake Titicaca basin. n = number of sampling times, cv = coefficient of variation.

^a O m samples, June 24 to November 11, 1982.

^b Samples collected September 15–December 6, 1982, Rocas Misteriosas

^c These three rivers contribute 58 % of the Lake Titicaca inflows (Carmouze and Aquize Jaen, 1981). Samples collected from February 18, 1981 to November 18, 1982.

Reynolds, 1984). Reported concentrations in Lago Grande and Puno Bay ranged from 200 to $1000 \ \mu g \ l^{-1}$ (Vincent *et al.*, 1984; Vincent *et al.*, 1986; Wurtsbaugh *et al.*, 1985). In Lago Pequeño, mean concentrations among stations ranged from 375 to 550 $\ \mu g \ l^{-1}$ during different seasons (Lazzaro, 1981).

Bioassay experiments

Additional support for the hypothesis of nitrogen limitation in Lake Titicaca has come from bioassay experiments in which various nutrients were added to cultures of lake algae. Carney (1984) measured how the addition of nitrogen, phosphorus, silica or a mixture of micronutrients affected the growth of phytoplankton in four semi-continuous laboratory experiments. In all four experiments – two with water from Puno Bay and two with water from Lago Grande – NH_4^+ significantly increased chlorophyll production, while PO_4^- additions did not (Fig. 2). When NH_4^+ and PO_4^- were added together, however, chlorophyll was stimulated even more than when NH_4^+ was added alone. Thus if algae could obtain sufficient nitrogen, phosphorus then became limiting.

Nitrogen was also found to be the dominant limiting nutrient in bioassays conducted by Wurtsburgh *et al.* (1985), during 1981. In their experiments, water from Lago Grande or Puno Bay was incubated *in situ* in large polythene bags. In six experiments, nitrogen significantly stimulated carbon fixation four times (Fig. 3) and chlorophyll production five times. In contrast, phosphorus additions stimulated carbon fixation only one time. The bioassay results indicated that silica concentrations did not limit algal production in Lake Titicaca. In the ten experiments in which it was tested, silica did not stimulate



Figure 2. Effects of nutrient additions on algal growth in a culture of natural plankton from Puno Bay (29 October-12 November 1982). Algal growth was monitored by measuring chlorophyll fluorescence. Error bars show ± 2 standard errors of four replicate flasks in each treatment. Nutrient additions were: NH₄⁺, 25 µg N l⁻¹ d⁻¹; PO₄⁻, 7 µg P l⁻¹ d⁻¹; and a micronutrient mixture of Cu (0.3 µg l⁻¹), Mn (2.2 µg l⁻¹), Mo (1.9 µg l⁻¹), Zn (1.3 µg l⁻¹), Co (58.9 µg l⁻¹), and 8 µg-atom EDTA. Additions of N, N + P, and micronutrients all significantly (Analysis of variance; p < 0.05) enhanced chlorophyll concentrations over control cultures (C). Adapted from Carney (1984).

either photosynthesis or carbon fixation (Fig. 3; Wurtsbaugh et al., 1985; Carney, 1984).

Micronutrients may also limit phytoplankton growth at certain times in Lake Titicaca. Carney (1984) found that a micronutrient mixture stimulated chlorophyll production of Puno Bay water (Fig. 2), but not in water from



Figure 3. Relative response of algal photosynthesis (¹⁴C uptake) to additions of NH_4^+ or NO_3^- , 70 µg N $I^{-1} d^{-1}$; PO₄ 62 µg P $I^{-1} d^{-1}$; Si, 280 µg Si $I^{-1} d^{-1}$; FeCl₂, 112 µg Fe $I^{-1} d^{-1}$; and a micronutrient mixture of Cu, Mn, Mo, Zn and Co. Cultures were assayed after 5–6 day incubations and their response calculated relative to control cultures. * indicates treatments significantly different from controls (p < 0.05; ANOVA followed by Dunnett's test to compare each treatment against controls). L = Lago Grande; B = Puno Bay. Histograms, from left to right, show experiments conducted on 19 March, 9 June, 17 Sept., 26 Nov., 19 May and 2 Oct., 1981. Five experiments conducted in 1982 did not show significant results because of high variance among replicates, and are not shown here. Adapted from Wurtsbaugh *et al.* (1985).


Figure 4. Luxury uptake of nitrogen and phosphorus by seston in Lago Grande during four periods of the mixing cycle during 1982. Plankton were incubated for two hours in the laboratory with additions of NH_4^+ and PO_4^- . The amount of N and P in the cells was then compared with controls that did not have nutrients added. Late mixing, 5 August; early stratification, 15 October; midstratification, 18 February; late stratification, 11 April. Statistical analysis, F-test of orthogonal comparisons from ANOVA, ** p < 0.005, * p < .05. Adapted from Vincent *et al.* (1985).

Lago Grande. Wurtsburgh *et al.* (1985), indicated that iron stimulated photosynthesis of Lago Grande in one experiment, but not in seven others (Fig. 3). A micronutrient mixture without iron never enhanced photosynthesis.

Temporal changes in nutrient limitation: physiological assays

Although the bioassays described above indicate that nitrogen is an important limiting nutrient in Lake Titicaca, frequent physiological assays of phytoplankton provide us with a better view of temporal changes in the factors controlling algal growth. In Lago Grande ammonium enhancement experiments demonstrated that phytoplankton were nitrogen deficient during much of the year, but particularly near the end of thermal stratification (Fig. 1B). With the onset of winter mixing in May, nitrate was brought into the photic zone (Fig. 1A), and nitrogen deficiency dropped to near zero. It remained low until after stratification began and nitrate in the surface water was nearly exhausted (October). The phytoplankton in Lago Grande thus appeared to be limited by nitrogen during most of the stratified period, but not during periods of deep mixing. In Puno Bay, however, the ammonium enhancement assays indicated a persistent nitrogen deficiency in the phytoplankton throughout 1982 (Vincent *et al.*, 1985).

The luxury uptake of added inorganic nitrogen and phosphorus by the natural plankton assemblages also varied seasonally. When the lake was mixing, or shortly after stratification, the plankton did not accumulate significant amounts of added NH_4^+ or PO_4^- (Fig. 4). In contrast, during midand late-stratification, nitrogen, and to a lesser extent phosphorus, was rap-

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Table 3. ${}^{32}PO_4$ uptake rates, turnover time (T/O), and soluble reactive phosphorus concentrations (SRP) of Lago Grande and Puno Bay surface waters during 1982. Uptake rates were measured by injecting ${}^{32}PO_4$ into lake water samples and measuring its accumulation in the seston after 2, 4, 8, 16, 30 and 60 minute periods. Rates were calculated from the natural log regressions of the uptake data over the time period. Turnover time is the time period necessary for PO₄ to be completely replaced in the media. Adapted from Vincent *et al.* (1985).

	Lago G	rande		Puno Bar						
	Uptake (%/min.)	T/O (min.)	SRP (µg/L)	Uptake (%/min.)	T/O (min.)	SRP (µg/l)				
20 Feb.	0.017	5.9×10^{3}	4.0	1.667	6.0×10^{1}	_				
18 Mar.	0.036	2.8×10^{3}	5.9	0.108	9.3×10^{2}	11.2				
20 May	0.011	8.9×10^{-3}	9.0	0.077	1.3×10^{3}	8.4				
17 Jul.	0.001	8.7×10^{4}	13.6	0.008	1.2×10^{4}	_				
25 Sep.	<.001	$>10^{5}$	19.5	<.001	$>10^{5}$	17.1				
7 Dec.	<.001	$> 10^{5}$	14.6	0.001	$8.2 imes 10^4$	-				

idly absorbed and stored by the plankton, indicating nutrient deficiency at these times.

Assays of ³²PO₄ uptake rates demonstrated that there were seasonal changes in phosphorus reserves of lake phytoplankton, but that this nutrient was unlikely to be limiting (Table 3). During winter mixing, or shortly thereafter when SRP concentrations were high in the surface waters of both Lago Grande and Puno Bay, phosphorus turnover rates were always less than 0.008% min⁻¹. During stratified periods when soluble reactive phosphorus concentrations dropped below 9 μ g P l⁻¹ turnover rates increased to between 0.01 and 1.7% min⁻¹. These faster turnover rates, however, still suggest that the algae were relatively replete with phosphorus, as rates of 3–10% min⁻¹ are characteristic of P-starved phytoplankton (Wetzel, 1983).

Discussion

The dissolved nutrient data, physiological assays and bioassay results reviewed here indicate that phytoplankton in Lake Titicaca were usually nutrient deficient, except during periods of mixing. The bioassay results did suggest that phosphorus would often limit algal production if the nitrogen deficiency were overcome. Temporal variations in availability and demand for different nutrients may, however, have allowed nutrients other than nitrogen to become limiting. For example, when phosphorus levels in Lake Titicaca dropped to very low levels after prolonged thermal stratification in 1981, phosphorus was the principal element limiting algal photosynthesis (Fig. 3; Wurtsbaugh *et al.*, 1985). Micronutrients such as iron or molybdenum may have also limited productivity at times (Figs 2 and 3). Nevertheless,



Figure 5. Effects of nutrient additions on nitrogen fixation rates of cyanobacteria (blue-green algae) in Lake Titicaca. Natural lake assemblages were incubated for 5–6 days in batch culture experiments and then assayed with the acetylene reduction technique to measure fixation rates. A micronutrient addition significantly depressed fixation during one experiment, while silicate had no significant effect (not shown). Added nutrient concentrations are the same as indicated in Fig. 2. Each set of histograms, from left to right, indicates the following experiments: Lago Grande; 26 Nov. 1981, 4 Feb. 1982, 19 Feb. 1982; Puno Bay; 19 May 1981, 2 Oct. 1981, 26 Jan. 1982. Statistical analysis – ANOVA followed by Dunnett's test; * p < 0.05, ** p < 0.01.

nitrogen appeared to limit production over most of the year, at least during the two years for which we have adequate data.

In some lakes, nitrogen deficiency is reduced when cyanobacteria become abundant and fix atmospheric N₂ gas (Schindler, 1977; Hecky and Kilham, 1988). Although green algae and diatoms dominated the plankton assemblage in Lake Titicaca, cyanobacteria were also common (Carney *et al.*, 1987; Lazzaro, 1981, 1985). Nitrogen fixation in the lake was also important, with annual rates ranging from 2–4 g N m² in Lago Grande (Wurtsbaugh *et al.*, unpublished data). Nevertheless, the experimentally measured persistence of nitrogen limitation suggests that nitrogen fixation was unable to entirely overcome the deficiency.

Consequently, we may ask what factors limited nitrogen fixation in the lake? Results of bioassays of Lago Grande and Puno Bay water indicated that both phosphorus and iron additions stimulated nitrogen fixation (Fig. 5; Wurtsbaugh *et al.*, 1985). Both of these nutrients have been shown to limit nitrogen fixation in other lakes (see Hecky and Kilham, 1988; Wurtsbaugh and Horne, 1983). The SRP levels in Lake Titicaca (Fig. 1) fluctuated near the $10 \,\mu \, I^{-1}$ level that some authors suggest is necessary for nitrogen-fixing bacteria to prosper (Pick and Lean, 1987). Consequently, although phosphorus levels may have allowed some nitrogen fixation to occur, it may have limited cyanobacteria so that they could not completely surmount the nitrogen deficiency. Additional loading of phosphorus (or iron) might increase populations of nitrogen-fixing cyanobacteria, and thus increase Lake Titicaca's overall productivity. The moderate total N:P ratio of lake water

(11.4) also suggests that phosphorus may limit production in Lake Titicaca. In addition to phosphorus, other factors, such as water column stability, temperature and the previously mentioned iron limitation could also regulate cyanobacterial abundance and nitrogen fixation in the system (Vincent, 1989). More work is needed in Lake Titicaca and elsewhere, to fully understand factors limiting N₂-fixation by cyanobacteria and how this leads to nitrogen deficiencies in aquatic systems.

Several biogeochemical factors may foster nitrogen limitation in Lake Titicaca. First, hypolimnetic denitrification may strip large amounts of NO₃ from the system during periods of hypolimnetic anoxia and thus lower the available N:P ratio (Vincent *et al.*, 1985). Secondly, the high erosion rate of phosphorus-rich marine sedimentary rocks in the watershed may cause relatively high P loading (Wurtsbaugh *et al.*, 1985). Additionally, Wurtsbaugh *et al.* (1985) argued that nitrogen fixation may be low in the arid terrestrial environment surrounding Titicaca and this may contribute to the relatively low levels of nitrate of river waters draining into the lake. Finally, levels of anthropogenic NO₃ and NH₄⁺ in the airshed may be low in relation to industrialized regions of the world where acid rain may elevate nitrogen loading (Heil *et al.*, 1988).

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References of chapter V

- BAXTER (R.M.), PROSSER (M.V.), TALLING (J.F.), WOOD (R.R.), 1965. Stratification in tropical African lakes at moderate altitudes (1,500 to 2,000 m). *Limnol. Oceanogr.*, 10: 510–520.
- BAZOBERRY (Q.), 1968. Balance hídrico del Lago Titicaca. Dir. de Irrig. Min. Fom., Lima.
- BOULANGE (B.), AQUIZE JAEN (E.), 1981. Morphologie, hydrographie et climatologie du lac Titicaca et de son bassin versant. *Revue Hydrobiol. trop.*, 14 (4): 269–287.
- BOULANGE (B.), VARGAS (C.), RODRIGO (L.A.), 1981. La sédimentation actuelle dans le lac Titicaca. *Rev. Hydrobiol. trop.*, 14 (4): 299–309.
- CARMOUZE (J.P.), AQUIZE JAEN (E.), 1981. La régulation hydrique du lac Titicaca et l'hydrologie de ses tributaires. *Rev. Hydrobiol. trop.*, 14 (4): 311-328.
- CARMOUZE (J.P.), MIRANDA (I.), 1978. Estudio de los factores de control de los carbonatos disueltos en las aguas del lago Titicaca. Proceso de precipitación de calcita. *Rev. Boliviana de Química*, 2 (1): 57–67.
- CARMOUZE (J.P.), ARZE (C.), QUINTANILLA (J.), 1977. Circulación de materia (agua, sales disueltas) a través del sistema fluvio-lacustre del Altiplano. *Cah. ORSTOM., sér. Géol.*, 10 (1): 49–68.
- CARMOUZE (J.P.), ARZE (C.), QUINTANILLA (J.), 1977. La régulation hydrique des lacs Titicaca et Poopó. *Cah. ORSTOM.*, *sér. Hydrobiol.*, 11 (1): 269–283.
- CARMOUZE (J.P.), ARZE (C.), QUINTANILLA (J.), 1981. Régulation hydrochimique du lac Titicaca et l'hydrochimie de ses tributaires. *Rev. Hydrobiol. trop.*, 14 (4): 329–348.
- CARMOUZE (J.P.), ARZE (C.), QUINTANILLA (J.), 1984. Le lac Titicaca: stratification physique et métabolisme associé. *Rev. Hydrobiol. trop.*, 17 (1): 3–12.
- CARMOUZE (J.P.), AQUIZE JAEN (E.), ARZE (C.), QUINTANILLA (J.), 1983. Le bilan énergétique du lac Titicaca. *Rev. Hydrobiol. trop.*, 16 (2): 135-144.
- CARNEY (H.J.), 1984. Productivity, population growth and physiological responses to nutrient enrichments by phytoplankton of Lake Titicaca, Peru-Bolivia. *Verh. Internat.Verein. Limnol.*, 22: 1253–1257.
- CARNEY (H.J.), RICHERSON (P.J.), ELORANTA (P.), 1987. Lake Titicaca (Peru/Bolivia) phytoplankton: Species composition and structural comparison with other tropical and temperate lakes. *Arch. Hydrobiol.*, 110: 365–385.
- CHURUTA SALLUgA (J.), MAMANI HUANCA (L.A.), 1977. Hidrología de la cuenca del río Ramis. Tesis Ing. Agron. UNTA, Puno: 173 p.
- CSANADY (G.T.), 1973. Turbulent diffusion in the environment. Reidel, Dordrecht, 248 p.
- DERKOSCH (I.), LÖFFLER (H.), 1960. Spektrochemische Spurenanalyse Südamerikanischer Binnengewässer. Ark. Geofysik, 3: 337–345.
- DUSSART (B.), 1966. Limnologie. L'étude des eaux continentales. Gauthiers-Villars, Paris, 677 p.
- ELSER (J.J.), MARZOLF (E.R.), GOLDMAN (C.R.), 1990. Phosphorus and nitrogen limitation of phytoplankton growth in freshwaters of North America: a review and critique of experimental enrichments. *Can. J. Fish and Aquat. Sci.*, 47: 1468–1477.
- GILSON (H.C.), 1939-40. The Percy Sladen Trust Expedition to Lake Titicaca in 1937. *Trans. Linn. Soc. London*, ser. 3, 1: 1-357.
- GILSON (H.C.), 1964. Lake Titicaca. Verh. Internat. Verein Limnol., 15: 112-127.
- GOLDMAN (C.R.), 1981. Lake Tahoe: two decades of change in a nitrogen deficient oligotrophic lake. Verh. Internat. Verein. Limnol., 21: 45-70.
- GOLDMAN (C.R.), JASSBY (A.), POWELL (T.), 1989. Interannual fluctuations in primary production: meteorological forcing at two subalpine lakes. *Limnol. Oceanogr.*, 34: 310–323.
- GOLTERMAN (H.L.), 1975. Physiological limnology. Elsevier Scientific, Amsterdam, 489 p. GUYOT (J.L.), BOURGES (J.), HOORELBECKE (R.), ROCHE (M.A.), CALLE (H.),
 - CORTES (J.), BARRAGAN (M.C.), 1988. Exportation de matières en suspension des Andes vers l'Amazonie par le Rio Béni, Bolivie. Proc. Porto Alegre Symposium, December 1988. IAHS, n° 174: 443-451.

- GUYOT (J.L.), CALLE (H.), CORTES (J.), PEREIRA (M.), 1990. Transport de matières dissoutes et particulaires des Andes vers le Rio de La Plata par les tributaires boliviens (rios Pilcomayo et Bermejo) du Rio Paraguay. J. Sci. Hydrol., 35 (6): 653–665.
- GUYOT (J.L.), ROCHE (M.A.), NORIEGA (L.), CALLE (H.), QUINTANILLA (J.), 1990. Salinities and sediment loads on the Bolivian Highlands. J. Hydrol., 113: 147-162.
- GUYOT (J.L.), BOURGES (J.), Calle (H.), CORTES (J.), HOORELBECKE (R.), ROCHE (M.A.), 1991. Transport of suspended sediments to the Amazon by an andean river: the River Mamore, Bolivia. Fourth Internat. Symposium on River Sedimentation, Beijing, November 1989 (in press).
- HECKY (R.E.), KILHAM (P.), 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. *Limnol. Oceanogr.*, 33: 796–822.
- HEGEWALD (E.), ALDAVE (A.), HAKULI (T.), 1976. Investigations on the lakes of Peru and their phytoplankton. 1: Review of literature, description of the investigated waters and chemical data. *Arch. Hydrobiol.*, 78 (4): 494–506.
- HEGEWALD (E.), RUNKEL (K.H.), 1981. Investigations on the lakes of Peru and their phytoplankton. 6: Additionnal chemical analyses. *Arch. Hydrobiol.*, 92 (1): 31–43.
- HEIL (G.W.), WERGER (M.J.A.), de MOL (W.), van DAM (D.), HEIJNE (B.), 1988. Capture of atmospheric ammonium by grassland canopies. *Science*, 239: 764–765.
- HOWE (M.R.), TAIT (R.I.), 1969. Some observations of the diurnal heat wave in the ocean. Limnol. Oceanogr., 14: 16–22.
- HUTCHINSON (G.E.), 1957. A treatise on Limnology. I. Geography, Physics, and Chemistry. John Wiley & Sons, New York, 1015 p.
- HUTCHINSON (G.E.), LÖFFLER (H.), 1956. The thermal classification of lakes. Proc. Nat. Acad. Sci. USA, 42: 84–86.
- ILTIS (A.), 1987. Datos sobre la temperatura, el pH, la conductibilidad eléctrica y la transparencia de las aguas de superficie del lago Titicaca boliviano (1985–1986). UMSA-ORSTOM, La Paz, Informe 3: 19 p., multigr.
- IVANOFF (A.), 1975. Introduction à l'Océanographie. Tome II. Vuibert. Paris, 340 p.
- JACOBS (W.C.), 1951. The energy exchange between sea and atmosphere and some of its consequences. Bull. Scrips Inst. of Oceanogr. Tech. Ser. Univ. of Calif., 6: 27-122.
- KESSLER (A.), 1970. Über den Jahresgang des potentiellen Verdunstung im Titicaca-Becken. Arch. Met. Geoph. Biokl., Ser. B, 18: 239–252.
- KESSLER (A.), MONHEIM (F.), 1968. Der Wasserhaushalt Titicacasees nach neueren Messergebnissen. Erdkunde, Arch. für Wissenschaft. Geogr., Bonn, 22 (4): 275–283.
- KITTEL (T.), RICHERSON (P.J.), 1978. The heat budget of a large tropical lake, Lake Titicaca (Perú-Bolivia). Verh. Internat. Verein. Limnol., 20: 1203–1209.
- LAZZARO (X.), 1981. Biomasses, peuplements phytoplanctoniques et production primaire du lac Titicaca. *Rev. Hydrobiol. trop.*, 14: 349–380.
- LAZZARO (X.), 1985. Poblaciones, biomasas y producciones fitoplanctónicas del Lago Titicaca. *Rev. Inst. Ecol.*, La Paz, 7: 23–64.
- LEWIS (M.W., Jr.), 1973. The thermal regime of Lake Lanao (Philippines) and its theoretical implications for tropical lakes. *Limnol. Oceanogr.*, 18: 200–217.
- LEWIS (M. W., Jr.), 1983. Temperature, heat and mixing in Lake Valencia, Venezuela. *Limnol. Oceanogr.*, 28: 273–286.
- LÖFFLER (H.), 1960. Limnologische Untersuchungen an Chilenischen und Peruanischen Binnengewassern. Ark. Geofysik, 3: 155–254.
- MEYBECK (M.), 1979. Concentrations des eaux fluviales en éléments majeurs et apports en solution aux océans. *Rev. Géol. Dynam. et Géogr. Phys.*, 21 (3): 215–216.
- MONHEIM (F.), 1956. Beiträge zur Klimatologie und Hydrologie des Titicacabeckens. Selbstverl. d. Geograph. Heidelberg: 152 p.
- MONTGOMERY (H.A.C.), THOM (N.S.), COKBURN (A.), 1964. Determination of dissolved oxygen by the Winkler method and the solubility of oxygen in pure water and sea water. J. Appl. Chem., 14: 280-296.

- NEALE (P.J.), RICHERSON (P.J.), 1987. Photoinhibition and the diurnal variation of phytoplankton photosynthesis – I. Development of a photosynthesis-irradiance model from studies of *in situ* responses. J. Plank. Res., 9: 167–193.
- NEVEU-LEMAIRE (M.), 1906. Les lacs des hauts-plateaux de l'Amérique du Sud. Imprimerie nationale, Paris, 197 p.
- PAERL (H.W.), 1982. Factors limiting productivity of freshwater ecosystems. In: Advances in microbial ecology, Marshall ed.; Plenum Press, New York, 6:75–110.
- PERRIN de BRICHAMBAUT (C.), LAMBOLEY (G.), 1968. Le rayonnement solaire au sol et ses mesures. Cahiers de l'AFEDES: 111 p.
- PICK (F.), LEAN (D.R.S.), 1987. The role of macronutrients (C, N, P) in controlling cyanobacterial dominance in temperate lakes. New Zeal. J. Mar. Freshw. Res., 21: 425–434.
- POSNANSKY (A.), 1911. El clima del Altiplano y la extensión del Lago Titicaca con relación a Tihuanacu en épocas prehistóricas. Tipografía comercial de Ismael Argote, La Paz, 29 p.
- POWELL (T.), KIRKISH (M.H.), NEALE (P.J.), RICHERSON (P.J.), 1984. The diurnal cycle of stratification in Lake Titicaca: eddy diffusion. *Verh. Internat. Verein. Limnol.*, 22: 1237–1242.
- QUINTANILLA (J.), CALLICONDE (M.), CRESPO (P.), 1987. La química del lago Titicaca y su relación con el plancton. Documento de pesca 004, Oldepesca, Lima, 321 p., multigr.
- QUISPE ZAPARA (L.L.), AMAN UI (A.A.), 1978. Caracterización hidrológica de la cuenca del río Coata. Tesis Ing. Agron. UNTA, Puno: 143 p.
- REYNOLDS (C.S.), 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge, 384 p.
- RICHERSON (P.J.), WIDMER (C.), KITTEL (T.), 1977. The limnology of lake Titicaca (Peru-Bolivia). Univ. California, Davis. Inst. Ecology, 14, 78 p., multigr.
- RICHERSON (P.J.), WIDMER (C.), KITTEL (T.), LANDA (A.), 1975. A survey of the physical and chemical limnology of lake Titicaca. Verh. Internat. Verein. Limnol., 19: 1498– 1503.
- RICHERSON (P.J.), NEALE (P.J.), WURTSBAUGH (W.A.), ALFARO TAPIA (R.), VINCENT (W.F.), 1986. Patterns of temporal variation in Lake Titicaca, a high altitude tropical lake. 1: Background, physical and chemical processes and primary production. *Hydrobiologia*, 138: 205-220.
- SCHINDLER (D.W.), 1977. The evolution of phosphorus limitation in lakes. *Science*, 195: 260–262.
- SMITH (V.H.), 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: an empirical and theoretical analysis. *Limnol. Oceanogr.*, 27: 1101–1112.
- SMITH (V.H.), 1983. Nutrient dependence of primary productivity in lakes. *Limnol. Oceanogr.*, 28: 1051–1064.
- S.N.D.C. G.T.Z., 1981. Programa de irrigación Altiplano/valles. Estudio de factibilidad Huarina. Salzgitter Consult GmbH, La Paz, multigr.
- TALLING (J.F.), 1969. The incidence of vertical mixing and some biological and chemical consequences in tropical African lakes. *Verh. Internat. Verein. Limnol.*, 17: 998–1012.
- TALLING (J.F.), 1969. The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). *Internat. Rev. ges. Hydrobiol.*, 51: 545–621.
- TAYLOR (M.), AQUIZE JAEN (E.), 1984. A climatological energy budget of Lake Titicaca (Peru/Bolivia). Verh. Internat. Verein. Limnol., 22: 1246-1251.
- TEJADA CARI (A.), 1977. Caracterización hidrológica de la cuenca del río Ilave. Tesis Ing. Agron. UNTA, Puno, 104 p.
- VALLENTYNE (J.R.), 1957. Principles of modern limnology. American Scientist, 45 (3): 218– 244.
- VINCENT (W.F.), 1989. Cyanobacterial growth and dominance in two eutrophic lakes: review and synthesis. Arch. Hydrobiol., 32: 239–254.
- VINCENT (W.F.), WURTSBAUGH (W.A.), VINCENT (C.L.), RICHERSON (P.J.), 1984. Seasonal dynamics of nutrient limitation in a tropical high-altitude lake (Lake Titicaca, Peru-Bolivia): application of physiological bioassays. *Limnol. Oceanogr.*, 29: 540–552.

- VINCENT (W.F.), VINCENT (C.L.), DOWNES (M.T.), RICHERSON (P.J.), 1985. Nitrate cycling in Lake Titicaca (Peru-Bolivia): the effects of high-altitude and tropicality. *Freshw. Biol.*, 15: 31–42.
- VINCENT (W.F.), WURTSBAUGH (W.A.), NEALE (P.J.), RICHERSON (P.J.), 1986. Polymixis and algal production: latitudinal effects on the seasonality of photosynthesis. *Freshw. Biol.*, 16: 781–803.
- VOLLENWEIDER (R.A.), 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol., 33: 53-83.
- WASSON (J.G.), GUYOT (J.L.), SANEJOUAND (H.), 1991. Premières données concernant le carbone organique transporté par le Rio Desaguadero (Altiplano bolivien). *Rev. Fr. Sci. Eau* (in press).
- WASSON (J.G.), MARIN (R.), 1988. Tipología y potencialidades biológicas de los ríos de altura en la región de La Paz (Bolivia). Congreso Iberoamericano y del Caribe sobre la Pesca y la Acuicultura, Isla Margarita, Venezuela, 8–14 Mayo 1988: p. 120, multigr.
- WETZEL (R.G.), 1983. Limnology. Saunders College Publishing, Philadelphia, 767 p.
- WIDMER (C.), KITTEL (T.), RICHERSON (P.J.), 1975. A survey of the biological limnology of Lake Titicaca. Verh. Internat. Verein. Limnol., 19: 1501–1510.
- WURTSBAUGH (W.A.), HORNE (A.J.), 1983. Iron in eutrophic Clear Lake, California: its importance for algal nitrogen fixation and growth. *Can. J. Fish. Aquat. Sci.*, 40: 1419–1429.
- WURTSBAUGH (W.A.), VINCENT (W.F.), ALFARO TAPIA (R.), VINCENT (C.L.), RICHERSON (P.J.), 1985. Nutrient limitation of algal growth and nitrogen fixation in a tropical alpine lake, Lake Titicaca (Peru/Bolivia). *Freshwat. Biol.*, 15: 185–195.

B. BIOLOGICAL COMMUNITIES

VI.1. PHYTOPLANCTON VI.1a. The diatoms

SIMONE SERVANT-VILDARY

Introduction

The diatoms of Lake Titicaca are known solely on the basis of studies of Frenguelli (1939), Richerson *et al.* (1977, 1986), Theriot *et al.* (1985) and Carney *et al.* (1987) in the Peruvian side of the lake, and by Liberman and Miranda (1987) in the Bolivian part.

The flora described here was established from samples taken at eleven stations in the Bolivian part of the lake. This work however, like the others mentioned above, still gives a very limited picture in both time and space of this component of the flora. The physical and chemical conditions vary at hourly and daily time scales, in part due to the high altitude of the lake, and the response of the flora to these changes may be correspondingly rapid. For this reason it is difficult, without regular sampling and measurements during the day and at larger time scales, to establish a representative and exhaustive inventory of the total diatom flora in this environment.

Methods

The diatoms studied were fixed in formol and first observed without additional preparation of the samples. They were then treated and cleaned in order to eliminate the organic material and better observe the frustules with an optical microscope.

The days and hours of collection are indicated in lines 2 and 4 of Table 1, for 11 stations indicated in Fig. 1. Diatons were collected with plankton nets in the surface waters; only sample 10 consists of washed epiphytes from Characaea macrophytes at stations 1 and 10. Also listed in Table 1 are certain physical and chemical parameters measured at the time of collection, or calculated from about fifty measurements made in Lago Pequeno or Lago Grande during the same months as the sampling (Iltis, 1987).

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Figure 1. Sampling locations in the Bolivian part of Lake Titicaca.

The diatom flora

As has been previously discussed by the above mentioned authors, the pelagic diatom flora does not appear to be species rich. We have found 101 species, and only 38 are abundant. This may appear relatively few for such an extensive system. The number of truly planktonic species is quite low in relation to the number of taxa at shallow stations which include benthic, epiphytic and facultative planktonic species (see Table 2). The most species-rich genera are *Navicula*, *Nitzschia*, *Fragilaria* and *Cyclotella*, and the most abundant are *Cyclotella* and *Fragilaria*. Frenguelli (1939) identified 118 species at 7 stations, but he considered that only 38 species really were present in the lake water. Carney *et al.* (1987) list 50 species found in the lake, 25 of which are abundant.

The analysis of our samples allows us to distinguish six groups based on the species composition:

1. (Stations 44 and 48). This group is dominated by the planktonic stelligeroid *Cyclotella*. Station 44, distinguished by its more turbid waters, is characterised by greater species richness which is especially due to epiphytes such as *Achnanthes delicatula* and *Amphora pediculus*. Table 1. Physical and chemical characteristics of the stations studied. 1) Stations; 2) Dates of sampling and measurements of temperature, pH, transparency and conductivity; 3) Dates which were used for calculations of averages: 3a) days, 3b) months and years; 4) Hours of sampling; 5) Depth (m) of water column at sampling location; 6) Transparency at time of sampling; 7) Average transparency; 8) Temperature in °C at time of sampling; 9) Average of temperatures; 10) pH of surface water at time of sampling; 11) Average pH; 12) Conductivity in S cm⁻¹ at 25°C at time of sampling; 13) Average conductivity. Average values are based on fifty measurements made on the dates listed in line 3a.

		Lago Mayor (east)		Lago Menor (south)			Characea			
1)	48	51	39	44	27	6	5	4	9	1	10
2)	17/10/86	17/12/86	27/6/85	17/10/86	9/12/85	24/4/86	14/12/88	11/12/85	9/12/86	27/6/85	24/2/87
3a) 3b)	14-18/ 10/86	9-11/ 12/86	26-29/ 6/85	14-18/ 10/86	-	21-23/ 4/86	:	12/85	9-11/ 12/86	26-29/ 6/85	-
4)	9.25	12.40	17.25	7.25	12.12	16.55	14,45	7	7.30	9	10.50
5)	140	150	80	8	3	25	40	10	6	3.5	3
6)	11.5	13	10.5	5	3	5.5	5.5	-	4.5	3.5	3
7)	12.39	11.94	11.77	12.39	-	5.63	-	4	4.45	4.66	-
8)	12.1	13.5	12.8	12.3	16.3	14.6	15.1	-	14.5	8.9	15
9)	12.8	13.7	12.6	12.8	-	14.7	-	14.1	15.3	10.7	-
10)	-	8.22	-	-	9	8.28	8.42	-	8.4	-	8.4
11)	8.31	8.48	-	8.31	-	8.40	-	8.31	8.68	-	-
12)	1500	1500	1700	1450	960	1450	1500	-	1525	1610	1400
13)	-	1501	-	1490	-	1368	-	1500	1521	-	-

- 2. (Station 27). This is distinguished from all the others by the abundance of *Cocconeis*, including *C. titicacaensis*, and also *Nitzschia admissoides* and *Fragilaria capucina*. This flora may depend on the low conductivity measured at this station, or it may simply represent a shallow environment colonized by aquatic plants which are a preferred substrate for *Cocconeis*.
- 3. (Stations 1 and 39). This community is distinguished by the almost exclusive presence of *Cyclotella andina*. These two stations are quite different in depth (80 and 3.5 m) and temperature (12.6 and 8.9°C); the only common factor is that they were both sampled in June 1985. Theriot et al. (1985) also indicated that densities of *C. andina* increased at two stations which were quite different in depth (147 m and 14 m) between May and August in the Peruvian Lago Grande. According to these authors, thermal stratification was disrupted during this period and limiting nutrients increased as a result of mixing from bottom waters. Thus the abundance of this species in June 1985 could be explained by this factor.
- 4. (Stations 5, 6 and 51). This group is characterised by a predominance of *Fragilaria crotonensis*, while *C. andina* is rare. These are deep-water stations, at 25, 40, and 150 m, respectively. *F. crotonensis*, which is present in large chains (Figs. 22, 23), is clearly planktonic here. Another species, *Entomoneis palludosa* var. *salina*, has been found only at station 5. Its presence cannot be explained since its preferred ecological habitats are meso- to euhaline.

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Table 2. Diatoms found at the eleven stations examined. Semi-quantitative evaluation of the abundance of each species: 6 - very abundant; 5 - abundant; 4 - frequent; 3 - rare; 2 - very rare; 1 - present; 0 - absent.

	44	48	39	51	6	4	1	9	27	5	10
Achnanthes delicatula Kützing	3	1									
Achnanthes hungarica Grunow		:				1					
Achnanthes lanceolata Brebisson	4									:	
Achnanthes minutissima Grunow	-				-	2		-			
Achnanthes saccula Carter	i										
Amphora inariensis Krammer	:		•	•		1		•			
Amphora lybica Ehrenberg	1								1		
Amphora pediculus (Kütz.)Grunow	à					1			:		
Amphora veneta Kützing	č					i					1
Anomoeoneis serians (Breb.)Cleve	•					:					i
Caloneis bacillum (Grun.)Cleve	1	1		•						1	:
Caloneis molaris (Grun.)Krammer	:	:	•	•	•	1	•	•	•	:	
Cocconeis placentula Ehrenberg	2	1				ż			2		1
Cocconeis titicacaensis Frenguelli	-				•				4		ż
Cyclotella andina Theriot Carney & Richerson	3	1	6		1	1	6			2	•
Cyclotella atomus Hustedt	-	1								-	
Cyclotella iris Brun & Heribaud		÷									
Cyclotella kützingiana Thwaites	1	5				÷					
Cyclotella meneghiniana Kützing		~			1	2				4	
Cyclotella stelligera Cleve & Grunow	6	6	4		5	5			÷	+	:
Cyclotella s. var. glomerata (Bach,)Haworth & Hurley	1	ğ			2	-			÷	!	
Cyclotella s. var. pseudostelligera (Hust.)Haworth & Hurley	4	3									
Cymatopleura solea (Breb.)W.Smith	1	-							1		
Cymbella cistula (Ehr.) Kirchner	!					÷			÷		-
Cymbella c. var. maculata (Kütz.)Van Heurck	:	:	:	:	:		:	•	4	•	!
Cymbella cymbiformis Agardh			•	•	•	•	•	•	5	•	•
Cymbella falaisiensis (Grun,)Krammer & Lange-Bertalot	•		•	•	•	•	•	÷	~	•	;
Cymbella gracilis (Ehr.) Kützing				•		•	•		÷	•	~
Cymbella microceobala Grunow				•	•	•	•	;		•	· ·
Cymbella minuta Hilse					•	~	•	-	•	•	4
Cymbella pusilla Grunow	•	•	•	•	•	•	•	•	•	•	5
Denticula elegans Kützing	•	•	•	•	•	:	•	•	•	•	4
Entomoneis paludosa var. subsalina (Cl.)Krammer	•	•	•	•	•		•	•	•	5	•
Epithemia sorex Kützing	•	•	•	•	•	÷	•	•		3	•
Epithemia zebra (Ebr.)Kützing	i	÷	•	•	•	+	•	•		÷	
Fragilaria brevistriata Grunow	•	'	•	•	•	-	•	•	•	•	-
Franjlarja capucina Desmatières	•	•	•	•	•		•	•	:	•	-
Franjlaria o van vaucheriae Lance-Rentalot	;	•	•	•	•	4	•	•	2	•	
Fragilaria construent (Fbn)Grunow	~	•	•	•	•	;	•	•	ю	•	•
Fragilaria o subrotuodata Mayor	:	•	•	•	•	4	•	•	•	•	•
Enacilania contononcio Kitton		:	•		:	•	•	•	•	:	:
Fragilaria famolica Lango-Pontalot	•	1	•	1	D	•	•	•	•	σ	1
	•	•	•	•	•	:	•	•	1	•	•
Fragilaria iapponica orunow	•	•	•	•	•	2	•	•	•	:	•
Fragilaria pinnaca chrenberg	•	•	•	•	1	3	•	•	•	1	•
Fragilaria p. var. lancettula (Schum.)husteut	:	•	•	•	1	•	•	•	•	•	•
Fragilaria tabulata Lange-Bertalot	1	•	•	•	•	:	•	•	•	•	:
Fragilaria ulha Lange-bertalot	•	•	•	•	•	2	•	•	•	•	3
Constants any instanties	1	:	•	•	•	•	•	•	•	•	•
Compromena acuminatum var. coronata (cnr.)m.Smith	•	1	•	•	•	•	•	•	:	•	•
Compromenta angustatum (Kütz.) Käterios	•	•	•	•	•	•	•	•	1	•	•
Complement unlentinics Nik	•	•	•	•	•	1	•	•	2	•	
Compromense valentinica mik	•	•	•	٠	•	•	•	•	1	•	1
byrosiyma acuminatum (NUTZ.)Kadennorst Vastachia achievus (Eba)Gruesu	1	•	•	•	•	1	•	•	:	•	•
nanizsinia amphioxys (cnr.jorUNOW	•	•	•	•	•	•	•	•	1	•	:
Nosloyila alacamae nusleol	•	•	•	•	•	:	•	•	•	•	1
Mastugila smithii inwaites	:	:	•	•	•	2	•	•	•	•	6
Rovieula daglica Ralls			•	•	•	•	•	•	•	•	•
תמיונטים שמוטצופונגוג (טרטה,)טרטהטא	1	•	•	•	•	•	•	•	•	•	•

Table 2. Continued.

	44	48	39	51	6	4	1	9	27	5	10
Navicula capitata var. hungarica (Grun.)Ross						1					
Navicula c. var. capitata Ehrenberg	1					•	•	•	•		•
Navicula cohnii (Hil.)Lange-Bertalot	•		•			1			•		•
Navicula cryptotenella Lange-Bertalot	•	•	•	•	•	2		2		•	3
Navicula cuspidata (Kütz.)Kützing		•	•	•		1		•	•	•	
Navicula halophila (Grun.)Cleve			•	•	•	1	•	•		•	1
Navicula kotschyi Grunow	1		•		•	•	•	•	•		•
Navicula margalithii Lange-Bertalot	•	•	•	•	•	1	•	1	•	•	•
Navicula minuscula var. muralis (Grun.)Lange-Bertalot	1	•	•	•	•	•	•	•	•	•	•
Navicula mutica Kützing	•	•	•	•	•	1	•	1	•	٠	•
Navicula pseudoanglica Lange-Bertalot	1		•	•	•	•	•	•	•	•	•
Navicula pseudolanceolata var. denselineolata Lange-Bertalot	•	•	•	•	•	•	•	6	•	•	1
Navicula pupula yar. pupula Kützing	•	•	•	•	•	1	•	•	•	•	•
Navicula radiosa Kützing	•	•	•	•	•	3	•	2	•	•	1
Navicula rhynchocephala Kützing	•	•	•	•	•	•	٠	•	•	1	•
Navicula subrotundata Hustedt	1	4	•	•	•	•	•	٠	•	•	•
Navicula tenera Hustedt	2	٠	•	•	•	•	•	٠	•	•	•
Navicula tripunctata (O.Mull.)Bory	•	•	•	•	•	•	•	٠	•	1	•
Navicula viridula (Kütz.)Ehrenberg	1	•	•	•	•	•	•	•	•	•	•
Navicula vulpina Kützing	•	•	٠	•	•	1	•	•	•	•	•
Nitzschia acidoclinata Lange-Bertalot	٠	•	•	•	•	6	•	1	•	•	1
Nitzschia admissoides Cholnoky	•	•	•	•	•	•	•	•	6	•	•
Nitzschia amphibia Grunow	1	•	•	•	•	1	•	•	3	•	÷
Nitzschia denticula Grunow	•	•	•	•	•	•	•	•	2	•	5
Nitzschia dissipata (Kütz.)Grunow	1	•	•	•	•	•	•	•	•	•	•
Nitzschia eglei Lange-Bertalot	•	•	•	•	•	1	•	•	•	•	•
Nitzschia frustulum Kützing	٠	•	•	•	•	1	•	1	•	•	•
Nitzschia gracilis Hantzsch	•	•	•	•	•	1	٠	•	•	•	•
Nitzschia hantzschiana Rabenhorst	1	٠	•	•	•	4	•	•	•	2	•
Nitzschia hungarica Grunow	1	٠	•	٠	•	1	•	•	•	•	•
Nitzschia intermedia Hantzsch	2	•	٠	•	•	٠	•	٠	•	•	•
Nitzschia mediocris Hustedt	1	•	•	•	•	1	•	•	•	•	•
Nitzschia microcephala Grunow	1	•	•	•	•	1	•	•	•	•	•
Nitzschia palea (Kütz.) W.Smith	•	٠	•	•	•	1	•	٠	•	•	•
Nitzschia p. var. debilis (Kütz.)Grunow	1	٠	•	•	•	5	•	•.	•	•	•
Nitzschia recta Hantzsch	2	•	•	•	1	•	•	:	•	•	:
Nitzschia sp.	•	•	•	•	•	•	•	2	•	•	2
Nitzschia valdestriata Aleem & Hustedt	1	•	•	•	•	1	•	•	•	•	•
Pinnularia borealis Ehrenberg	•	•	•	•	•	1	•	•	•	٠	•
Pinnularia divergentissima (Grun.)Cleve	1	•	•	٠	•	•	•	•	•	•	•
Rhoicosphenia abbreviata (Ag.)Lange-Bertalot	1	•	•	•	•	1	•	•	•	•	•
Stephanodiscus dubius (Fr.)Hustedt	•	1	•	•	٠	•	•	•	•	•	•
Stephanodiscus hantzschii Grunow	2	•	•	•	•	•	•	•	•	•	•

- 5. (Stations 4 and 10, considered as one station). These communities have in common *Fragilaria ulna*, *Mastogloia smithii* and *M. atacamae* which are not present, or only quite rarely, at other stations. Also in these associations are other species such as *Nitzschia denticula* and *Nitzschia palea debilis* which can, like the above two species, adapt to waters relatively high in salts (Servant-Vildary and Roux, 1990).
- 6. (Station 9). This final group is similar to the previous, but is distinguished by the abundance of *Navicula pseudolanceolata*. The growth of this species at only this station cannot be explained, since stations 4, 9 and 10 are located quite close to each other in them Lago Pequeño.



Plate 1.



Plate 2.



Plate 3.

Morphological observations on certain taxa

We consider here only abundant or characteristic species; the complete list of species found is given in Table 2.

Amphora pediculus (Kütz.) Grunow

This species is abundant at station 44 and rare at station 4. Despite its small size, it is easy to observe the punctae on the striae. The predominant form is identical to that described by Krammer (1980, Plate 6, Fig. 42). Larger and longer forms, in which the punctae on the striae are finer, are rarer. This species lives in well oxygenated running waters, so its presence at station 44 can be explained by the proximity to the outflow of Suches river. At station 4 some larger forms with less rudimentary pores may be *A. inariensis*. Krammer (1980) indicates this species is found in lightly acid (pH = 6.8) freshwaters. Here it is found at a more elevated pH. This is a typically northern alpine species, but it is rare.

Cocconeis titicacaensis Frenguelli

Found by Frenguelli in Lake Titicaca, it does not appear to have been found by others to date and thus may be one of the rare endemic species. Frenguelli indicated that it was very abundant near the port of Guaqui and rare in Lago Grande. In our samples, it is also quite abundant at station 27 near Guaqui, and it is also present as epiphytes washed from Characeae at stations 1 and 10 in northern Lago Pequeno. We observe, as Frenguelli, that the smaller forms are round and the strial density of the hypotheca is high (close to 30 in 10 μ m – Fig. 20). The larger forms are more oval and the strial density is much lower (between 20 and 24). The hyaline space of the hypotheca, which is located midway between the raphe and the marginal border, may continue, according to Frenguelli, beyond the terminal pores of the raphe to a linear space to the apices. This character could not be seen clearly despite the large numbers of individuals observed (Fig. 21). On the contrary, we have noted small ridges irregularly arranged around the inferior valve in the interstrial spaces.

Cyclotella andina Theriot, Carney & Richerson

Many specimens observed from the Bolivian part of Lake Titicaca are morphologically quite similar to those described by Theriot *et al.*, 1985. We insist on only three differences: 1) there is not a ring of silica (Fig. 9) at the base of the ribs on the inside (Theriot *et al.*, Fig. 13); 2) the labiate process

is effectively on the same rib as the strutted process, but it does not have the same form; according to Theriot *et al.* (Fig. 14) it is an elongate tube, somewhat separate from the strutted process, while it is round and appears attached to the rib by some type of "spokes" (Fig. 8); 3) the cingulum (Theriot *et al.*, Fig. 11) consists of several copulae (Figs. 1 to 3), but in some individuals this could be covered by a thick leaf of silica with 8 peduncles; only 4 can be seen in Fig. 5. This structure is unknown, and we are uncertain whether it is some specialization of the mantle, a modification of the cingulum, or some structure underneath the cingulum and thus invisible most of the time.

As indicated by Theriot *et al.* (1985), the dimensions of this species are quite variable, but in station 1 where this taxon can represent 100% of the diatom flora, the larger forms are more frequent.

The stelligeroid Cyclotella group. Haworth, 1986

The genus *Cyclotella* is the most varied and abundant in the pelagic flora of Lake Titicaca. The stelligeroid group being particularly well represented in at stations 44 and 48.

We are in agreement with Haworth (1986) that there exists continuous variation within this group. We thus follow this author who proposes combining these taxa within the species *stelligera*, maintaining the following varieties in order not to lose ecological information: *C. stelligera* var. *stelligera*, *C. stelligera* var. *glomerata*, *C. stelligera* var. *pseudostelligera*. All these varieties pertain to type 1 defined by Servant-Vildary (1986) and are characterised by simple chambers (*C.s.* var. *stelligera*) or alveolar depressions (*C.s.* var. *pseudostelligera*) widely opened toward the inside.

These varieties are present together at stations 44 and 48, though C. s. stelligera (Fig. 10) predominates. According to Haworth (1986), this form grows best in waters of high silica content, while C.s. pseudostelligera grows better in more silica-poor waters.

Cymbella cistula var. maculata (Kutz.) H. van Heurck

First noted by Frenguelli (1939) in Lake Titicaca, it was later found by Manguin (1964) in bogs of highland Peru and by Pierre (1986) in highland lakes of Bolivia. Based on Fig. 11 of this last author, this variety belongs to the group of *Cymbella cistula* without papillae (Lange-Bertalot, 1986). But as this author has observed, separation of this variety solely on the basis of the absence of the stigma is very tenuous. Still, the Bolivian forms present a rather special morphology. Much shorter than the type species, they are also much more arched (with sub-rostrated extremities) than the varieties depicted by Hustedt (1930) and Van Landingham (1964). It may be useful

to record these differences, at least for Andean forms, since they may reflect particular ecological adaptations such as to temperature conditions.

Entomoneis paludosa var. subsalina Cleve

This species name has been chosen over *E. alata* because of the high number of striae per 10 μ m. The striae of the wings and the cell are equally punctuated by a line of simple pores, which are not altered by the line of union between the wing and cell; this line is lightly sinuous (Figs 13–15).

At station 5 this species is second in abundance after *Fragilaria crotonensis* (Fig. 15). It has not been found at another station. Presented here is a particularly fragile skeleton which is somewhat fragmented. Given its frequency, it does not appear to be transported. The species is cosmopolitan in waters of moderate conductivity; the subsalina variety is in waters of higher dissolved salts. Its presence in only station 5 is inexplicable.

The genus Fragilaria Lyngbye

This genus is both abundant and species rich in Lake Titicaca. We adopt the nomenclature of Lange-Bertalot (1980) which groups the species and varieties of this genus with those of *Synedra*. The list of synomyms is provided here to demonstrate the variety of forms which are found in the lake; we refer to the figures published by Lange-Bertalot (1980) listed after the taxa to provide fuller information:

- 1) Fragilaria capucina vaucheriae includes: Fragilaria intermedia (L-B, Figs 35–38), Exilaria vaucheriae (L-B, Fig. 31), at station 27.
- Fragilaria capucina includes: Synedra sumpens var. familiaris (L-B, Fig. 50) at station 44. Synedra rumpens rumpens (L-B, Figs 61-62) at station 27. Synedra vaucheriae (L-B, Figs 121-116 (?)) and Synedra rumpens (L-B, Fig. 42) at station 4.
- 3) Fragilaria tabulata includes: Fragilaria fonticola (L-B, Fig. 157), Synedra tabulata (L-B, Figs 160, 167, 168, 173) at station 44.
- 4) Fragilaria ulna includes: Synedra acus angustissima (L-B, Fig. 194) at station 4; Fragilaria construens oregona (L-B, Fig. 193) at stations 4 and 10.

Fragilaria capucina Desm

We note (Figs 24–25) the presence of a saw-like structure on the internal border of the valvocopula. This structure is similar to those described by Kobayasi (1979) for *F. pseudogaillonii* (Fig. 9), in the genus *Diploneis* at Charaña by Servant-Vildary and Blanco (1984) (Plate 1, Fig. 9, and Plate 5,

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Figs 2 & 3), and by Idei and Kobayasi (1986), (Fig. 19). The internal thickening located at the extreme of the valve can be discerned over the central specimen of Fig. 24. This could be related to the "ligula" described by Idei and Kobayasi (1968) for *Diploneis parma*. More detailed studies are needed to describe this structure which to date has been little noticed in the genus *Fragilaria*.

Fragilaria crotonensis Kitton

There is no particular morphological character which distinguishes the morphotype here from the forms in the other parts of the world. This species is present in large chains (Fig. 15). Enlarged at the center in valve view, cells are connnected only at these points (Fig. 22) thanks to the adaptation of the teeth. These expand and take the form of blades at the center of the frustule, while they are much smaller toward the extremes of the frustules (Fig. 23) where there is paper-like cohesion between individuals.

This taxon is extremely abundant at stations 5 and 6 near the Chua Depression. It can live in shallow areas, close to aquatic macrophytes, and can be transported to areas of greater depth and float near the surface because of its colonial morphology.

Gomphonema cf. valentinica Nik

This species is very small, elongate and sharp, almost isopolar in valve view, and with very rudimentary striae. It attaches to plants with a particularly resistant mucilagenous tube; this firm attachment provides protection against predators. Its presence in sample 10 indicates that it lives attached to Characeae. The study of this form deserves more study since some individuals do not have the rectangular hyaline area which characterises this species.

Mastogloia atacamae Hustedt

This is rare in the Characeae epiphyte samples (stations 1 and 10), and is associated with *Mastogloia smithii* which predominates (Figs 16 to 19).

This species belongs to the group of M. elliptica, but is distinguished by a higher strial density of rather oblique striae and a larger central area, characterised by alternatively large and short striae, and by a number of more elevated chambers.

It has been found in the fossil state (Servant-Vildary, 1984) in the Charana formation of presumed late Pliocene age, in a highly saline paleoenvironment. Hustedt (1927) described it from the Loa formation, where it was associated with many species typical of environments with high salt concen-

trations. The presence of this species in relatively fresh waters indicates that, like many species of the genus *Mastogloia*, it can adapt to a wide range of salinities.

Conclusions

In addition to the relatively low species diversity indicated above, the diatom flora composition appears highly cosmopolitan. With the exception of three species (*Cocconeis titicacaensis*, *Cyclotella andina*, *Mastogloia atacamae*) which can currently be considered as endemic, all the other taxa appear to have extensive geographical distributions. We cannot at present compare this flora with those of other aquatic systems in Bolivia. The principal studies realized to date in this country have concerned superficial or quaternary sediments of small mountain bogs or saline lakes of the southern Altiplano. These systems are generally quite shallow and favor benthic pennate diatoms over pelagic species. Still, cores taken by Pierre and Wirrmann (1986) from deep high- altitude lakes of the Bolivian Cordillera have demonstrated that during the recent Quaternary in these lakes there existed a flora which alternated between *Cyclotella stelligera* and *Fragilaria construens* plus *F. pinnata*, the two most abundant genera today in Lake Titicaca.

The incomplete observations of this study also make clear the substantial spatial variability in species composition of the diatoms. The few available data on environmental factors such as pH, temperature, conductivity and other chemical variables still do not allow interpretations in terms of these factors. However, it is possible to hypothesize that water depth, the presence or absence of rooted aquatic vegetation, and the water transparency in relation to proximity to the river outflows are some of the more important factors which influence diatom community composition.

VI.1b. Algae: General floristic study

ANDRÉ ILTIS

The first studies on the algal flora of Lake Titicaca were carried out by Frenguelli (1939) on diatoms of the littoral zone and by Tutin (1940) on the algae collected during the Percy Sladen Expedition of 1937. Later, various authors made partial observations on the phytoplankton, particularly Thomasson, 1956; Gilson, 1964; Ueno, 1967; Hegewald et al., 1976; Revssac and Dao, 1977. In 1977, Richerson et al. provided a list of 33 taxa with information on their abundance. Later came the studies of Acosta and Ponce (1979) and Lazzaro (1981), followed by the inventories of Iltis (1984) who listed 58 taxa in the lake and 69 in the lakes of the mountain range located above Lake Titicaca (diatoms were not included in this study). In 1985, Theriot et al. described a new centric diatom from the Peruvian side of Lago Mayor. In 1987, the Latin American Organization of Fisheries Development published an illustrated inventory of 62 phytoplankton species of the lake (Liberman and Miranda, 1987) in addition to a repertoire of 168 taxa found in the lake by various authors; in the same year Carney et al. (1987) published a list of 172 taxa, and made comparisons with other tropical and temperate lakes. Finally, for this book, we make an inventory complementary to that of 1984, and Servant-Vildary (Chapter VI 1a) provides a list of the diatoms present. The combined total of 259 taxa is based on the samples collected between 1985 and 1989 in the Bolivian part of the lake.

Composition of the flora

For this analysis of the characteristics of the flora, only three of the published species lists (Frenguelli, 1939; Tutin, 1940; Carney *et al.*, 1987) are included plus those of Servant-Vildary (Chapter VI 1a) and Iltis (1991) because of their relative completeness (Fig. 1 and Table 1).

What stands out from these data is that three groups comprise about 90% of the flora: cyanophytes, chlorophytes and diatoms. The euglenophytes, pyrrhophytes, xanthophytes and chrysophytes supply in all the lists only a limited number of taxa. The percentages observed are quite consistent given

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Figure 1. Graphical representation of the proportions of different algal groups in the algal flora of Lake Titicaca. A: after Frenguelli (1939) and Tutin (1940); B: after Carney *et al.* (1987); C: after Servant-Vildary and Iltis. Horizontal dashes, cyanophytes; Dots, chlorophytes (E, euchlorophytes; U, Ulotrichales; D, desmids); Blank, bacillariophytes (diatoms); Black, pyrrhophytes; Horizontal lines, cuglenophytes; Vertical dashes, xanthophytes and chrysophytes.

the diversity of authors, times and sampling locations. The cyanophytes constitute approximately 10–12% of the flora, diatoms 27–39% and chlorophytes 43–57%. In this last group, there is a high proportion of euchlorophytes, the Chlorococcales generally comprising the most abundant group at the species level: 48% in the most recent list, and 58% in the list of Carney *et al.* Only the inventory of Tutin (1940) gives a relatively low proportion for this group, the filamentous algae (Ulotrichales, Chaetophorales, Oedogoniales, Zygnemataceae) being analyzed in more detail by this author. The desmids represent about 10–20 % of the total taxa of the flora.

Within the diatoms, the Centrales:Pennales ratio is 0.05 in the list of Frenguelli (*op. cit.*), 0.19 in that of Carney *et al.* (*op. cit.*), and 0.08 in that of Servant-Vildary (*op. cit.*).

	FREN	GUELLI, 1939 I, 1940	CARNEY	, RICHERSON, TA, 1987	SERVANT-VILDARY ILTIS (in press)		
	N taxa	%	N taxa	%	N taxa	%	
Cyanophyceae	17	12.5	19	11.0	26	10.0	
Chlorophyceae - Euchlorophyceae	78	57.3 22.8	86 60	50.0 34.9	112 58	43.3	
- Desmidiae	45	2.9	18	10.5	45	17.4	
Pyrrophytes	1	0.8	14	8.1	7	2.7	
Xani. + Chrys.	2	1.5	4	2.3	4	1.5	
Diatoms	38	27.9	47	27.4	101	39.0	
	136	100	172	100	259	100	

Table 1. Number of taxa and proportions of the major groups of algae in the flora of Lake Titicaca.

Considering the tropical location of Lake Titicaca, the proportion of pantropical and subtropical taxa in relation to cosmopolitan forms is low; it is not higher than 5% in the above inventories, even though there is some imprecision due to the fact that certain sterile forms, principally filamentous ones, could only be identified to genus level. The same is the case for the American forms which represent a maximum of 4.5% of the taxa listed.

Considering the desmids as good indicators of geographical distributions, the empirical indices proposed by Bourrelly (1957) presenting percentages, first of *Pleurotaenium* species plus filamentous desmids divided by the total of desmids, and second of *Pleurotaenium* and *Euastrum* species plus filamentous desmids divided by total desmids, are calculated here for the two most recent lists. These percentages are 5.5 and 11.1% for Carney *et al.* (*op. cit.*) and 25.5 and 31.9% for Iltis. The higher proportions in the latter list are due to the presence of eleven taxa of filamentous desmids; the lower values of Carney *et al.* may be due to the fact that they concentrated on the deeperwater plankton. These indices are not calculated for the study of Tutin (*op. cit.*) because this author indicated that his analysis of desmids was not complete.

Comparison with other floras

There is little known about the algal flora of lakes and other inland waters in South America, so it is at present difficult to confidently determine similarities and differences between them. Carney *et al.* (*op. cit.*) used a method developed by Lewis (1978) to determine affinities between floras. This method provides an estimate of percent similarity between two lists based on the genera in common. In this way the generic list of algae for Lake Titicaca were compared with the lists of 35 other lakes throughout the world. Carney *et al.* found that the Lake Titicaca flora was somewhat different from those of 18 other tropical lakes (on average 53% of genera in common) and even more distinct from those of 13 temperate lakes (only 50% of genera in common). By contrast, there was a much greater affinity with floras of four lakes of the Andes mountains (on average 67.5% genera in common).

The comparisons made here are between the recent Lake Titicaca lists and, on the one hand, tropical waters such as the Bolivian Amazon (Therezien, 1985, 1986a, 1986b, 1987, 1989), and, on the other hand, mountain lakes, some Peruvian located at 3600 m a.s.l. in the department of Cuzco (Hegewald *et al.*, 1980), some alpine in the Vanoise region of France (Martinot and Rivet, 1985), some Bolivian (lakes of Hichu Kkota between 4300 and 4900 m) in the Eastern Cordillera (Iltis, 1984). The percentages of the major algal groups have been calculated without taking into account the diatoms (Table 2 and Fig. 2).



Figure 2. Graphical representations of proportions of major algal groups (excluding diatoms) from lists of algal floras. A: in Bolivian Amazon (Therezien), B: in Peruvian lakes (Hegewald *et al.*), C: in alpine lakes of the Vanoise (Martinot and Rivet), D: in high-altitude lakes of the La Paz, Bolivia, region (Iltis), E and F: Lake Titicaca (Carney *et al.*) and (Iltis), respectively. Horizontal dashes, cyanophytes; Dots, chlorophytes (E, euchlorophytes; U, Ulotrichales; D, desmids); Black, pyrrhophytes; Horizontal lines, euglenophytes; Blank, xanthophytes and chrysophytes.

The percentage of cyanophycean taxa is higher in the Andean lakes of Peru (close to 25%) and Bolivia (14 to 16%) than in north temperate alpine lakes or in waters of the Bolivian Amazon (3 to 4%). The chlorophytes are always present in high proportions, the largest component being the Euchlorophyceae in Lake Titicaca and the lakes studied in Peru, and the desmids in high-altitude Andean and alpine lakes, and in warmer waters of the Bolivian Amazon. The pyrrhophytes, euglenophytes, chrysophytes and xanthophytes are always found in relatively low abundances, though the proportion of pyrrhophytes is generally somewhat higher in mountain lakes, and euglenophytes are somewhat higher in lowland tropical waters. The taxa which have been classified until now as characteristic of the tropics reach 7% in the Bolivian Amazon, only slightly above 4% in Lake Titicaca, and they are absent in the mountain lakes of the Andes and other regions. Bourrelly's (1957) indices of tropicality have quite variable values: zero in lakes of Peru, 4 and 12% in alpine lakes, 7.5 and 12.5% in high-elevation lakes, 13 and 23% in the plains of Bolivia, and for Titicaca 5 and 11% (1987 list) and 27 and 31% (1991 list). The percentage of genera in common with

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	Bolivian Amazone (Thérézien)	Peruvian lakes (Hegewald <i>et al.</i>)	Alpine lakes (Martinot and Rivet)	Andean lakes (Ittis)	Lake Titicaca (Carney <i>et al.</i>)	Lake Titicaca (ilüs)	
Number of taxa	642	65	199	69	125	158	
Relative composition in %							
Cyanophyceae	3.1	24.6	3.5	14.3	15.2	16.4	
Chlorophyceae	76.0	64.6	87.4	81.4	68.8	70.9	
Euchlorophyceae	15.6	44.6	21.6	13.1	48.0	36.7	
Ulotrichophyceae	5.3	4.6	0.5	10.1	6.4	5.7	
Desmidiae	55.1	15.4	65.3	58.2	14.4	28.5	
Pyrrhophytes	1.5	6.2	7.5	1.4	11.2	4.5	
Euglenophytes	15.4	3.1	0.0	0.0	1.6	5.7	
% Xant. Chrys.	4.0	1.5	1.6	2.9	3.2	2.5	
% of pantropical forms	6.7	0.0	0.0	0.0	2.4	4.4	
Pleurot.+desm.filam.							
Total desm.	13,3	0	3.8	7.5	5.5	26.7	
Pleurot.+Euasir.+D.filam.							
Total desm.	23.4	D	12.3	12.5	11.1	31.1	
% of genus common							
with Lake Titlcaca							
Cyanophyceae	26.3	62.5	11.1	50.0	-	-	
Chlorophyceae	42.6	29.9	31.0	35.9	-	-	
Total (except diatoms)	36.1	36.1	24.2	33.3	-	-	

Table 2. Proportions of major algal groups in the flora of Lake Titicaca and, by comparison, with other recently studied systems. Diatoms are not included in this analysis.

the most recent algal list for Lake Titicaca is highest for the mountain lakes of Peru and Bolivia, slightly lower for the Bolivian Amazon, and relatively low for temperate alpine lakes.

Combining these analyses, we find that the Lake Titicaca algal flora is most similar to that of Peruvian lakes of similar altitude (3600 metres). The flora of high-altitude Bolivian lakes is distinguished by a higher percentage of desmids, as in the Amazon, and in alpine lakes, where, in addition, the percentage of cyanophytes is particularly low.

Conclusions

Although the study of the Lake Titicaca algal flora cannot in its present state be considered exhaustive, it is possible to determine some major characteristics from the work completed to date.

Firstly, the number of algal species appears to be relatively limited. Even though the pelagic zones appear to have been investigated more than the shallower littoral areas (Totora wetlands, for example) and the periphyton, none of the inventories to date exceed 260 species. This is a relatively small number of taxa for such an extensive ecosystem which includes a great variety of habitats.

Secondly, there is a clear predominance of chlorophytes, with the Chlorococcales generally being the best represented order in the samples. This latter feature distinguishes the flora of Titicaca, on the one hand from the floras of tropical regions, where desmids constitute the most important group, and on the other hand from the floras of Bolivian Andean lakes between 4300– 4900 metres (Iltis, 1984) and of alpine lakes (Martinot and Rivet, 1985) where desmids also predominate.

One should also appreciate the cosmopolitan character of the algal flora: the percent of tropical forms is only slightly less than 5%. The number of species which can be considered endemic are quite low. The only ones found so far have been: four species of diatoms (Frenguelli, 1939), seven species described by Tutin (1940) which have not been found by others, one species of *Peridiniopsis* (Iltis and Coute, 1984) and a species of *Cyclotella* (Theriot *et al.*, 1985). The endorheic basin of the Altiplano and the unique ecological conditions of Lake Titicaca thus do not appear to manifest in a strongly endemic algal flora, as is the case for certain animal groups.

Finally, the comparisons made above with floras from various regions (temperate as well as tropical, mountains as well as lowland plains) lead us to conclude that Lake Titicaca contains an algal flora which has few similarities with most lowland or mountain lakes of temperate regions; it has a greater affinity with floras of tropical South America, for example the Bolivian Amazon. Carney *et al.* (*op. cit.*), following their analysis of genus-level similarity between Lake Titicaca and four smaller lakes in Peru and Ecuador (Hegewald *et al.*, 1978, 1980; Steinitz-Kannan *et al.*, 1982), suggest the possible existence of a biogeographical region in the central Andes. The characterization and geographical delineation of such a zone will require additional algal inventories in the lakes prospected up to now, and detailed studies in many other Andean lakes of which we have as yet very little or no knowledge.

VI.1c. Phytoplankton: Quantitative aspects and populations

ANDRÉ ILTIS

The first quantitative estimates of Lake Titicaca phytoplankton were made by Tutin (1940) with samples obtained in different parts of the lake by the Percy Sladen expedition in 1937. The numbers of organisms per litre collected with nets were given for dominant taxa, with the exception of *Botryococcus braunii* which existed in large quantities that were difficult to estimate.

In 1977, Richerson *et al.* provided estimates of biomass expressed as milligrams carbon per cubic metre during the course of 1973, based on the number of cells and volumes of each dominant species. Reyssac and Dao (1977) indicated algal densities as cells per litre, at eight different points throughout the lake, during the first part of December 1976. Lazzaro (1981) studied seasonal variations of algal biomass expressed as wet weight, total chlorophyll and carbon, for different stations in Lago Menor in 1979–1980. Carney *et al.* (1987) provided the extreme values of biomass in the Peruvian part of Lago Mayor for 1981–1982 in terms of wet weight per cubic metre. Iltis (1988) indicated the distribution of algal biomass in wet weight during six different periods between March 1985 and February 1987 in both parts of the Bolivian side of the lake.

Recorded algal biomasses and densities

After partial estimates given by different authors (especially Richerson *et al.* 1977 in Lago Mayor) for a certain number of dominant taxa, the first values of total phytoplankton density and biomass in Lago Huiñaimarca were given by Lazzaro (1981): the extreme values then were 300,000-1,600,000 cells 1^{-1} for the whole of Lago Menor, except at Chua, the deepest point of Huiñaimarca, where the density fluctuated between 200,000 and 8 millions cells 1^{-1} . The biomass in wet weight thus ranged from 250 to 800 mg m⁻³ within Lago Menor. The phytoplankton carbon content varied between 60-180 mg C m⁻³ in the former station and 30-90 mg C m⁻³ in the latter, while chlorophyll content varied from 0.5 mg chl m⁻³ in winter to slightly more than 4 mg chl m⁻³ in autumn.

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Later, Richerson *et al.* (1986) indicated an average chlorophyll concentration of 1.5 mg m⁻³ for Lago Mayor, and Carney *et al.* (1987) noted that algal wet weight during 1981 and 1982 varied between 122 and 1310 mg m⁻³, with an average of 511 mg m⁻³; chlorophyll *a* varied at the surface between 0.6– 5.9 mg m⁻³, with an average of 2.6 for 22 measurements. Finally, Iltis (1988) observed, in surfaces waters, wet weights ranging from 28 mg m⁻³ (close to the outflow of Tiwanaku river) to 4054 mg m⁻³ in Lago Menor, with an average of 1071 for six series of samples taken between 1985 and 1987. In the Bolivian part of Lago Mayor, values ranged from 3 mg m⁻³ (close to the outflow of Suchez river) to 263 mg m⁻³, with an average of 60.

Biomass composition

Composition by size

The organisms have been classified into four size ranges, according to the total volume of colonies, coenobia and filaments: small forms of less than $350 \ \mu m^3$, medium forms of $350-3500 \ \mu m^3$, large forms of $3500-10,000 \ \mu m^3$, and the largest forms of greater than $10,000 \ \mu m^3$.

According to observations made on six occasions during 1985–1987 at 28 stations in the Bolivian sector of Lago Menor and 19 in Lago Mayor, forms smaller than 350 μ m³ are rarely abundant in the surface plankton of Titicaca. The medium and large forms generally constitute the majority of the population in Lago Menor at all stations. In Lago Mayor, these medium and large forms represent 50–70% of biomass at only certain stations. Organisms of greater than 10,000 μ m³, which virtually never dominate in Lago Menor, constituted more than 70% of biomass in almost all of Lago Mayor from March 1985 until the middle of 1986.

In conclusion, we note that in 155 samples examined from Lago Menor, medium forms dominated in 60% of cases, large forms in 26%, small forms in 8% and the largest forms in 6%. In Lago Mayor, in 107 samples considered, the largest forms dominated in 51% of cases, large forms in 36%, medium forms in 12% and small forms in 1% of the total.

Composition by algal groups

The great majority of the phytoplankton biomass is distributed among five groups: chlorophytes, pyrrhophytes, cyanophytes, diatoms and euglenophytes, the last group being the least abundant. The importance of each of these groups seems to have varied only slightly since the first observations. In 1937, Tutin (1940) noted a plankton clearly dominated by chlorophytes; pyrrhophytes were fairly abundant while diatoms and cyanophytes were relatively rare. In the last group, the author indicated that the genus *Nodu*-

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Table	1.	Average	percentages	of major	· algal	groups in	the	Bolivian	side	of	the	lake.	These
percei	ntag	ges were o	calculated acc	cording to	cellula	ar biovolur	nes i	rather tha	n nui	mbe	r of	indiv	iduals.

	April 1985	June 1985	December 1985	April 1986	October 1986	February 1987	Məan
Lago Menor north	%	%	%	%	%	%	%
Cyanophyceae	1.3	36.3	29.1	61.1	60.5	30.3	36.4
Chlorophyceae	94.8	34.5	33.3	31.4	30.0	63.7	48.0
Pyrrhophytes	3.9	13.5	24.5	6.4	6.9	4.0	9.9
Diatomophyceae	0.0	15.7	12.9	1.1	2.5	2.2	6.0
Lago Menor south							
Cyanophyceae	1.3	14.0	9.0	15.6	19.5	11.6	11.8
Chlorophyceae	94.8	63.1	67.0	63.7	45.8	55.2	64.9
Pyrrhophytes	3.9	19.5	20.0	19.8	30.0	31.8	20.8
Diatomophyceae	0.0	3.4	4.0	0.9	4.7	1.3	2.4
Lago Mayor							
Cyanophyceae	41.4	30.1	83.2	64.8	20.6	78.3	53.1
Chlorophyceae	57.1	48.4	15.3	30.2	60.1	20.1	38.5
Pyrrhophytes	1.0	2.4	1.3	0.2	11.9	1.6	3.1
Diatomophyceae	0.5	19.4	0.1	4.7	7.2	0.0	5.3

laria was "fairly frequent" but mistakenly stated that blue-greens were totally absent. Richerson *et al.* (1977) indicated there were four major groups which comprised the biomass during 1973: chlorophytes, pyrrhophytes, cyanophytes, and diatoms. This was confirmed for 1976 also by Reyssac and Dao (1977). Lazzaro, studying stations in Lago Menor during 1979–1980, founds that the proportion of chlorophytes was greatest, followed by Dinophyceae and diatoms, and finally by a relatively low percentage of cyanophytes.

Iltis (1988) indicated the average proportions observed in different parts of the Bolivian sector of the lake between 1985 and 1987 (Table 1). There were three major zones: Lago Menor north (16 stations), Lago Menor south (12 stations) and Lago Mayor (19 stations).

Euglenophytes were found in appreciable quantities in only six samples. The maximum percent was 4% in Lago Mayor, close to Escoma Bay in October 1986.

The chlorophytes and cyanophytes were two groups which predominated alternatively according to seasonal fluctuations of algal biomass in Lago Mayor and northern Lago Menor. In southern Huiñaimarca, chlorophytes predominated during all periods studied. Pyrrhophytes were never biomass dominants; they reached greatest proportions (up to 31.8%) in southern Lago Menor, principally in zones close to river outflows. Diatoms were generally present in low proportions. They rarely represented over 10% in samples except during winter, for example in June 1985 when they reached

more than 15% in northern Lago Menor and 19% in Lago Mayor. This can be attributed to the enrichment of silica in the water column through aestival thermal destratification and mixing. Exceptionally massive and localized growths of *Cyclotella* sp. may occur during brief periods, as was observed at a northeastern station of Lago Menor in December of 1985 (over 53% diatoms). However, this phenomenon occurred only once during our observations.

Species composition

The first observations on phytoplankton (Tutin, loc. cit.) indicated a predominance of Botryococcus braunii Kützing in association in Lago Mayor with Dictyosphaerium ehrenbergianum Nägeli, Staurastrum paradoxum Meyen, Ankistrodesmus longissimus (Lemmerm.) Wille, Ulothrix subtilissima Rabenhorst and Peridinium sp.. Richerson et al. (1977) noted that the dominants during 1973 were Lyngbya vacuolifera Skuja, Anabaena sphaerica var. attenuata Bharadwaja, Ulothrix subtilissima Rabenhorst, Oocystis borgei Snow, Mougeotia cf viridis (Kütz.) Wittrock and Stephanodiscus astraea var. minutula (Kütz.) Grunow (now identified as Cyclotella andina (Theriot, Carney & Richerson)). Lazzaro (1981) found the following dominant species in Lago Menor: Monoraphidium sp., Cosmarium phaseolus Brebisson, Closterium kuetzingii Brebisson, Mougeotia sp. and Peridinium sp.. During 1981-1982, Richerson et al. (1986) listed as dominants Anabaena spiroides Klebahn, A. affinis Lemmerm., Planctonema lauterbornii Schmidle, Gloeotilopsis planctonica Iyengar & Philip, Oocystis spp., Staurastrum manfeldtii Delponte, Cryptomonas ovata Ehrenberg and Cyclotella andina Theriot et al..

During 1985–1987, the chlorophytes represented the greatest number of species among biomass dominants. In a given sample, this group generally is represented by 7 to 10 species while the other groups are usually represented by only one or two. The following species are most commonly found in the Bolivian part of the lake: *Oocystis* sp., *Sphaerocystis schroeteri* Chodat, *Dictyosphaerium pulchellum* Wood, *Botryococcus braunii* Kutzing, *Chlorhormidium subtile* (Kützing) Fott, *Mougeotia* sp., *Closterium aciculare* T. West, *Staurastrum gracile* Ralfs. The cyanophycean biomass dominants are *Gomphosphaeria pusilla* (Van Goor) Komarek and *Nodularia harveyana* var. *sphaerocarpa* (Bornet & Flahault) Elenkin. Within the pyrrhophytes are *Cryptomonas* sp., *Gymnodinium* sp. and *Peridinium willei* Huitfeld-Kaas. Finally, *Synedra ulna* (Nitzch) Ehr., *Fragilaria crotonensis* Kitton and especially *Cyclotella andina* Theriot *et al.* are the most abundant diatoms.

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Samples mean	March April 1985	June 1985	December 1985	April 1986	October 1986	February 1987	Total mean
Lago Menor north	0.524	2.648	2.628	1.844	1.710	1.774	1.855
Lago Menor south	1.437	2.233	2.003	2.261	2.177	2.291	2.067
Lago Mayor	1.707	2.142	0.815	1.523	2.524	1.122	1.639

Table 2. Average values of the Shannon diversity index during six cruises made in the Bolivian side of Lake Titicaca.

Species Diversity

The first data on species diversity estimated for 1973 using the Shannon index (Richerson *et al.*, 1977) varied during the course of the year between 2-3.5 bits for biovolumes and 1.2-3.7 bits for cell numbers. Diversity was relatively high and stable during autumn and winter (April to November), and declined during the summer (December to March). During 1979–1980 the diversity index varied between 1.5-3.5 bits per cell in two stations of Lago Menor (Lazzaro, 1981); there was one peak in March, and another from October to December.

During 1985–1987 in Lago Menor the minimum observed was 0.251 bits per mg in April 1985, while the maximum was 3.075 bits in December 1985. In Lago Mayor, the minimum was 0.222 bits in December 1985 and the maximum was 3.094 bits in October 1986. Combining all the measurements made (Table 2), one can observe that the phytoplankton of Lago Mayor was less diverse than that of Lago Menor, except during March–April 1985, and February of 1987. The present state of knowledge on species diversity and its fluctuations does not allow us to determine whether cyclical changes occur in the algal biocenosis of the lake.

General distribution of phytoplankton

Vertical distribution

The first studies made by Tutin (1940) indicated a homogeneous composition of the plankton from the surface to 50 metres depth. Later, Richerson *et al.* (1977) provided information on the distribution of phytoplankton biomass expressed as milligrams of carbon during 1973 in Lago Mayor. The phytoplankton zone, much deeper than the theoretical euphotic zone, reached 100 metres depth, principally during the periods of mixing.

Lazzaro (1981) presented a number of 25 metres profiles which show the vertical distribution of phytoplankton biomass expressed as carbon at the deepest point of Lago Menor. During the stratified period (February–March)

the major part of the biomass was concentrated in the upper fifteen metres. As temperatures declined in May there was greater mixing of the water column and high biomass levels (greater than $150 \text{ mg C} \text{ m}^{-3}$) occurred at depths down to 20 m. The low winter biomass levels are characterized by relatively rectilinear profiles.

In 1988, profiles of wet weight biomass were made at two stations of Lago Menor (Station 12: Sukuta, and Station 5: Chua) and two in Lago Mayor (close to the Island of the Moon and offshore of the Island of the Sun), during mixing (July 1988) and during stratification (December 1988).

Observed algal biomasses are presented graphically in Fig. 1. Distributions appear relatively uniform throughout the water column at all the shallow stations. Such is the case for the shallowest station studied (6 m depth), which is probably representative of the entire Lago Menor at depths less than 20 metres. In the Chua depression, the only point in Lago Menor where the bottom reaches 40 metres, the phytoplankton declines sharply between 22 and 30 metres during stratification (December). Within 4 to 5 metres, the algal biomass volume declines fivefold. In July, phytoplankton is distributed throughout all the water column.

In Lago Mayor, the vertical profile of biomass distribution is different. During stratification, the biomass maximum is located between 5-8 metres; during mixing the maximum appears between 12-18 metres at the station close to Island of the Sun, while it is only at 1-2 metres near the Island of the Moon. As demonstrated by Vincent et al. (1984), the form of the distribution curve of biomass in the epilimnion is a function of the mixing within this surface zone; the sampling near the Island of the Moon was during a very calm period, while the three other profiles were sampled during higher winds and waves. The phenomenon of surface inhibition thus appears in four cases in Lago Mayor, but more or less modified by surface mixing. Thus, in a series of samples taken during February 1987 throughout the Bolivian part of the lake both at the surface and at four metres depth, there was an average increase in biomass at 4 m of 11.6% for 28 Lago Menor stations, and of 21.8% for 19 Lago Mayor stations. The thermocline at 20-30 metres was not marked by a decline in the algal biomass, in contrast to the deepest zone of Lago Menor; there was even an important localized growth of pyrrhophytes at about 30 m at the station next to Island of the Moon in December. High algal populations do seem to extend more deeply during the mixing period than during thermal stratification.

The depth of the phytoplankton zone is of the order of 5 to 5.5 times that of the Secchi depth measured at the same point. Therefore, it appears that the sharp decline of phytoplankton biomass at the deepest part of Lago Menor between 22 and 30 metres, corresponds to the lower limit of the real euphotic zone. Consequently, the disappearance of algae below this depth is due more to the lack of light ("self-shading effect") than to the presence of the thermocline (which in Lago Mayor is not marked by a decline in biomass).



Figure 1. Vertical algal biomass distribution in Lago Menor (left) and in Lago Mayor (right). 1: shallow zone of Lago Menor, 2: Chua Depression, 3: Lago Mayor close to Island of Moon, 4: close to Island of Sun; A: during mixing (13–15 July 1988), B: during stratification (14–16 December 1988). To the right of each profile is the Secchi depth reading (except the first station, where it was not possible). Dashes-cyanophytes; black-pyrrhophytes; white


Figure 2. Grouping of stations at the Bolivian part of the lake according to cluster analysis (index of similarity indicated at top). To the left dry season (June 1985), A: northern Lago Menor, B: southern Lago Menor, C: Lago Mayor. Stations 26 and 27 are located close to the outflow of Tiwanaku river. To the right rainy season (February 1987), A: northern Lago Menor, C: Lago Mayor. In addition, four stations of Guaqui Bay (22, 24, 25, 28) in southern Lago Menor appear relatively similar.

Horizontal distribution

This has been studied only in the Bolivian part of the lake. Phytoplankton populations inventoried at 28 stations of Lago Menor and 19 stations of Lago Mayor were compared with each other to determine the affinities between stations. Two periods were chosen: June 1985 and February 1987, as periods representative of southern hemisphere winter and summer, respectively. Correlations were calculated between samples with the help of a distance matrix in order to group stations with the same types of populations and delimit zones where the plankton was relatively homogeneous (Fig. 2).

In June 1985, three stations appeared unrelated to the other populations of the Bolivian part of the lake; they were stations 26 and 27 located at the outflow of Tiwanaku river and station 46 in Lago Mayor where at this period there was a very important and localized growth of *Botryococcus*. The rest

of the other stations divided into two groups: the Lago Mayor stations with relatively high correlation values (stations 30 to 52), and the Lago Menor stations (stations 1 to 25, and 28). The latter clearly subdivided into two associations. The first (stations 1 to 15) included all of northern Lago Menor and the central stations 14, 15 and 19. The second consisted of the stations of southern Lago Menor (with the exception of the Tiwanaku river outflow) and the stations in the extreme southeast (17, 18 and 20); station 10 in the north was also placed anomalously in this group.

In February 1987, stations within Lago Mayor were relatively similar (stations 30 to 52) with the exception of stations 41 and 50. Ten stations of northern Lago Menor had strong affinities, but the points in the extreme southeast (2, 10, 11 and 12) were not included in this group. The other stations of Lago Menor (central, southern and southeast limit) did not group well. Stations 22, 24, 25 and 28 of Guaqui Bay were the only ones which appear to have high similarities. The algal populations in these central and southeastern parts of Lago Menor are thus quite heterogeneous during the rainy season; the outflows of the rivers Tiwanaku, Catari, Keka, and Batalla Chica entering this zone, where the depth varies between tens of centimeters to ten metres, inhibit the formation of stable and homogeneous populations here, while they have much less effect on the phytoplankton in deeper zones.

Using the affinities of algal communities, it is possible to divide the Bolivian part of the lake into three major ecological zones (Fig. 3). The first is the northern part of Lago Menor, delimited approximately by stations 1 to 15, with the exception of station 7 close to the Tiquina strait and station 13 close to the outflow of Catari river. Phytoplankton populations here are characterized by relatively high biomasses; it is here that the highest densities per unit volume are observed. The dominant groups are either chlorophytes (April and December of 1985, February of 1987) or cyanophytes (June 1985, April and October of 1986). The percentage of diatoms is generally low, but can reach an average for all stations of 15.7% in June 1985 and 12.9% in December of the same year. The proportions of pyrrhophytes are generally 4-7%; they can reach an average of 13.5% (June 1985) or even 24.5% (December 1985) for all stations.

The second zone consists of the central and southern parts of Lago Menor (stations 19 to 28), with the exception of stations 26 and 27 near the outflow of Tiwanaku river. Biomass levels are somewhat lower than in the first zone. Chlorophytes still dominate, followed by cyanophytes and pyrrhophytes; the diatoms are always relatively low (on average 4-5 % for all stations). During the rainy season this zone has a particularly heterogeneous phytoplankton.

Finally, the third zone consists of the entire Bolivian part of Lago Mayor with the exception of the mouth of the Suchez river. Here biomass levels are much lower (12 to 135 mg m^{-3} on average) than in the other two zones. Chlorophytes dominated during April and June 1985, and October 1986. Cyanophytes dominated December 1985, April 1986 and February 1987 (the summer stratified season). Pyrrhophytes were always quite low (1–3% on



Figure 3. Ecological zonation of the Bolivian part of Lake Titicaca according to phytoplankton. A: northern Lago Menor, B: southern Lago Menor, C: Lago Mayor. In dots, the transition region between the two major basins; vertical lines, perideltaic regions; in white along the shore, border zones.

average), except in October 1986 when the average percentage of this group was 12%. Diatoms become important only when the thermocline disappears and the water column mixes (on average 19.4 % during June 1985).

To these three major zones should be added much smaller areas with particular characteristics that are located in the aforementioned zones. These areas include:

- A region of transition between Lago Menor and Lago Mayor located in

the vicinity of Tiquina Strait. Algal biomass levels are intermediate between the two basins this region joins.

- Perideltaic regions of southeastern shores of Lago Menor where there are outflows of several rivers (Batallas, Keka, Catari, Tiwanaku), and in Lago Mayor at the mouth of Suchez river. Generally in these regions there is less phytoplankton than in neighbouring areas during the growth season, but during the dry season a richer plankton. The proportions of the principal algal groups are different, with the proportion of pyrrhophytes generally higher than in adjacent zones (this group may even dominate at certain times).

- The coastal wetlands, primarily of Totora, that occupy extensive surface areas of Lago Menor, and certain bays of Lago Mayor. The plankton, and especially the periphyton, are still little known and particularly need study.

Seasonal variations

In principle, in tropical waters where the depth is sufficient for thermal stratification, and where there is sufficient volume so that the effect of inflowing rivers is relatively low during the wet season, seasonal variations are much less marked than in temperate zones, the solar insolation being relatively constant throughout the year. Richerson *et al.* (1986) provide an analysis of these different types of variations and propose the term "almost seasonal" to indicate fluctuations which are not in rhythm with the annual cycle, in contrast to variations tightly coupled to wet and dry seasons as in Lake Chad (Carmouze *et al.* 1983), or to seasonal temperature and light cycles as in temperate lakes.

In Lake Titicaca it is advisable to distinguish Lago Menor and Lago Mayor. The former is characterized by shallow depth, absence of a thermocline, presence of abundant emergent macrophytes, reduced transparency, and greater amplitude in the thermal gradient and in the variation of dissolved salts (Iltis, 1987). Lazzaro (1981) noted phytoplankton maxima during April-May in 1979 and, to a lesser extent, in November-December, with winter (July to September) having lower values (Fig. 4). According to observations made the following years (Iltis, 1988), clear maxima appeared at the beginning of April 1985 and in February 1987, in agreement with previous observations. However, April of 1986 was characterized by quite low algal biomass which was probably related to the unusually high lake level of that year.

In Lago Mayor, for which there are fewer data, there is in the Bolivian part a maximum due to diatom growth (up to 41% of total cellular biomass in one central station) during the disappearance of the thermocline (June). This phenomenon has been attributed to "a sharp increase in the level of dissolved silica coming from the bottom when thermal stratification disappears" (Carmouze *et al.*, 1984). Median biomass is then 2.5–12 times higher



Figure 4. Total phytoplankton biomass, divided according to major classes, at a depth of 5 metres at Chua of Lago Menor. Din-Dinophyceae; Chl-chlorophytes; Dia-diatoms; Cya-cyanophytes (Lazzaro, 1981).

than in other parts of the year except December. A second less marked maximum appears during this month due to growth of cyanophytes, *Gomphosphaeria pusilla* in particular, (up to 97% of cellular biomass in a central station) during the period of maximum solar insolation and stratification.

What stands out from these fragmentary observations is that the phytoplankton of relatively shallow regions (Puno Bay, Lago Menor) have different temporal patterns from those of Lago Mayor. For example, the winter period is a biomass minimum in Lago Menor, but a maximum in Lago Mayor. At this point, long-term studies which can determine seasonality and interannual variability are still lacking. These will be needed to test the hypothesis of Richerson *et al.* (1977, 1986) that interannual variability here is greater than seasonal variability.

Conclusions

The following remarks can be made on the features of the phytoplankton as they are now known:

- The composition of phytoplankton is characterized by the predominance of chlorophytes and cyanophytes during the late 1980s. The increasing percentage of the latter group since the first observations made at this point should be underlined. Tutin (1940) noted an absence of this group in samples collected during 1937. Lazzaro (1981) encountered only very low proportions in Lago Menor during 1979–80, with the chlorophytes as clear dominants and the pyrrhophytes as the second most important group. By contrast, during six series of observations of 1985 to 1987, cyanophytes dominated or codominated in Lago Mayor and the entire northern half of Huiñaimarca. Thus observations in the future should determine whether this cyanophyte increase is part of normal phytoplankton fluctuations, or whether it marks the beginning of eutrophication which could extend to the entire lake.

- A clear seasonal cycle cannot be found. It is probable that the seasonality varies in amplitude and modality for the different ecological zones which have been considered.

– Light appears to be the principal factor which controls the vertical distribution of phytoplankton, though the role of nutrients, and particularly nitrogen, should not be omitted (Wurtsbaugh *et al.* 1985). The phenomenon of surface inhibition, caused by elevated solar radiation due to the altitude and tropical location, appears quite clear. In Lago Mayor, algal populations are present to depths of 80–100 metres, or about 5–6 times the Secchi depth. The influence of the thermocline appears relatively weak due to the small shift within it (2–3°C) and its limited duration in the annual cycle. This conforms with the conclusions on primary production of Brylinski and Mann (1973) that light has a greater effect on primary production than nutrient distributions in relation to the presence of the thermocline.

- The analysis of horizontal phytoplankton distributions, according to information for the Bolivian side of the lake, indicates the differences between Lago Menor and Lago Mayor and, by analogy, between the large shallow bays and the main basin. While the species present in these environments are the same, the biomass levels and proportions of the major groups are quite different. For example, biomass levels during 1985-1987 were 5 to 36 times higher in Lago Menor than in Lago Mayor; the minimum difference was observed in June 1985 during which a maximum in Lago Mayor and a minimum in Lago Menor coincided. Pyrrhophytes generally have a higher percentage in the latter. Analysis of algal populations also indicate a greater heterogeneity, both qualitative and quantitative, in shallow regions. It is probable that in Lago Menor and in shallow bays, the proximity to the bottom and the permanent instability of the heat structure favour circulation of mineralized organic matter near the bottom and localized growths of algae there (Lazzaro, loc. cit.), more especially as light is available throughout all the water column due to the shallow depth. Finally, the influence of river outflows is much less buffered in these areas.

According to the results in Lago Menor (Lazzaro, *loc. cit.*) and in Lago Mayor (Richerson *et al.*, 1977), and the classification of Rodhe (1960) based on annual primary production per surface area, Lago Menor can be classified as oligotrophic while Lago Mayor can be considered moderately eutrophic. However, this classification based on primary production has been criticized and judged inadequate in certain cases. Vollenweider (1968) proposed, followed by others including Munawar and Munawar (1976, 1982), using the level of biomass to compare lakes or parts of lakes. According to their

scheme for trophic states, Lago Mayor can be classified as ultraoligotrophic and Lago Menor as mesotrophic. This second classification, with opposite results to the first, seems more correct, especially considering in addition that the biomass and production of periphyton, phytobenthos and macrophytes which are particularly abundant in Lago Menor yet almost absent or limited to a very narrow shoreline zone of Lago Mayor, were not taken into account. Thus, a more comprehensive estimation of biomass and productivity which includes all these elements would probably indicate that productivity in Lago Menor is substantially higher than in Lago Mayor and thus in the eutrophic range. Given our present level of knowledge, this remains a hypothesis proposed by Lazzaro (*loc. cit.*) which will have to be confirmed by future studies.

VI.1d. Patterns of planktonic primary production and algal biomass

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Both physical and biological processes are important in controlling mean levels and fluctuations of primary production and algal biomass. Climatic factors drive production variation directly (e.g. through fluctuations in light) or indirectly through the regime of stratification (Richerson, this volume). Biotic processes, such as grazing and competition, affect biomass, the species composition of the biomass, and potentially overall rates of primary production. Biotic effects have a special opportunity to affect overall rates of production in a nitrogen limited system like Lake Titicaca (Wurtsbaugh et al., this volume; Vincent et al., this volume) if they affect the potential of N-fixing cyanobacteria to flourish. The relative importance of physical and biotic controls on phytoplankton primary production and biomass has recently been discussed extensively under the rubric of "top down" (biotic) versus "bottom up" (physical/chemical) hypotheses (Carpenter and Kitchell, 1984; Harris, 1986). Tropical lakes should show at least relatively more effects of "top down" control than higher latitude lakes because the muted seasonal cycle of the tropics reduces the variation in important physical drivers of phytoplankton variation, including light, temperature, and strength of stratification.

Description of studies and methods

Three studies of primary production and phytoplankton biomass of a year or more in duration have been conducted in the various basins of Lake Titicaca. Richerson *et al.* (1977), working in Lago Grande in 1973, conducted the first such study. This programme was maintained for another year for phytoplankton production and still longer for other parameters by the staff of the Instituto del Mar del Perú. Lazzaro (1981, 1982) conducted a similar study in Lago Pequeño (Huiñaimarca) in 1979–80. In 1981–82, Richerson *et al.* (1986) and Vincent *et al.* (1986) conducted parallel studies of production and biomass variation in Lago Grande and shallow, polymictic Puno Bay. All studies estimated phytoplankton biomass carbon by applying the regression

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equation of Mullin *et al.* (1966) to cell volume estimates (from enumerations) and used the *in situ* ¹⁴C method to measure primary production. Except for deficient estimates of nitrogen and phosphorus in 1973, these three studies also measured a relatively complete suite of physical and chemical factors using standard methods. Details can be found in the original papers.

Thus, our understanding of patterns of variation in phytoplanktonic production processes in Lake Titicaca is restricted to four years for Lago Grande and even less for Puno Bay and Lago Pequeño. Some additional data exists for Lago Grande for the years 1984–5 (Alfaro Tapia and Roncal, personal communication) and 1985–8 (Iltis, this volume).

Lago Grande

Figure 1 shows profiles of primary production from 1973. Table 1 gives the basic statistics describing photosynthesis in Lago Grande for 1973 (annual means; for more detailed data see Richerson *et al.*, 1977). Figure 2 shows the pattern of primary production for 1973–5 and 1981–2.

The productivity of Lago Grande was moderately high in these years, averaging a little above $1 \text{ g C m}^{-2} \text{ d}^{-1}$. Because the epilimnion of this large lake is deeper than the euphotic zone, the phytoplankton crop is diluted into a large volume of water. Thus production per unit volume of water is relatively low $(5-30 \text{ mg C m}^{-3} \text{ h}^{-1})$ and the depth of maximum photosynthesis is rather deep (3-10 m).

The variation of production during the year is modest compared to temperate lakes but the pattern of variation of production during the year is highly variable (see below for a statistical analysis). Given the highly regular pattern of variation in stratification and fairly regular variation in chemical parameters visible in Fig. 2, one might expect a more predictable seasonal pattern of primary production. We believe that there are several reasons for the irregular variations within years. First, the variation in insolation is quite modest, so this variable cannot impose a strong seasonal signal. Second, photosynthesis is usually nitrogen limited (Vincent et al., 1984; Wurtsbaugh et al., 1985; Carney, 1984; Wurtsbaugh et al., this volume). This limitation leads to a highly variable incidence of nitrogen fixing cyanobacteria during the stratified season, resulting in unpredictable peaks of production, as in December 1973. At other times, less intense cyanobacterial fixation has resulted in broad plateaux of production, as in the February-May period of 1982. When N-fixing populations are not present, the stratified season often shows pronounced production minima, as in October 1973, January and February 1981, and the last 5 months of 1982. We have no explanation for these variations in cyanobacterial populations; they are often absent for prolonged periods even when nitrogen limitation is intense (Wurtsbaugh et al., this volume). Episodes of intense denitrification, such as we observed in 1981 (Vincent et al., 1984), might also impose considerable variation in



Figure 1. Vertical profiles of daily net 14 C (light minus dark bottle) uptake estimates of photosynthesis in Lago Grande in 1973. Bar shows the range of duplicate light bottles (Richerson *et al.*, 1977).

Table 1. Statistics describing primary production in Lake Titicaca. Θ is the rate of photosynthesis at Z_{opt} (averaging over the three maximum depths). Z_{mix} is the depth to the top of the main thermocline. Z_{cu} is the last depth at which light ¹⁴C uptake exceeds that in the dark. Biomass was computed from algal counts using the method of Mullin *et al.* (1966). R was measured with a Belfort pyrheliometer at Lago Grande, but with a PAR sensor (n = 8 only) at Lago Pequeño. P_{cal} was computed assuming 10 kcal g C⁻¹.

ANNUAL MEANS											
Production (P) gC m ⁻² day ⁻¹	Biomass (B) C m ⁻²	P/B day ⁻¹	⊖ hr ⁻¹	Incident Radiation(R) kcal m ⁻² day ⁻¹	P/B/R X10 ⁻³ m ² kcal ⁻¹	P _{cal} /R %	z _{opt}	z _{mix}	Z _{eu} m		
Lago Grande (197	73)										
1.45	2.97	0.51	0.13	5086	0.10	0.29	6	50	17.7		
Lago Pequeño (1	979-80)										
0.56	2.52	0.22			0.19		5.3	24	25.2		

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Figure 2. Monthly averaged series of basic limnological data from Lake Titicaca. \triangle temp. is the difference between the temperature at 10 m and the deep hypoliminion temperatures at 150 m (Richerson *et al.*, 1986).



Figure 3. Profiles of estimated photosynthesis, as in Figure 1, for the Fosa de Chúa station in Lago Pequeño (Lazzaro, 1981). Vertical scale is mg c m^{-3} hr⁻¹.

production when mixing during isothermy is incomplete. Third, the impact of the deepening of the thermocline and isothermy during the dry season has only a modest and variable influence on production rates. Production peaks do generally occur in this period, but the effects of added nutrients tend to be offset by the deteriorating light climate caused by deep mixing of the phytoplankton crop.

Lago Pequeño

Figure 3 shows vertical profiles of primary production for the 40 m deep Fosa de Chúa station, and Figure 4 a similar plot for the 6 m deep Sukuta station. Figure 5 shows the pattern of variation at these two stations for production and related variables over the course of the study. Table 1 lists average statistics describing production at the Fosa de Chúa station.

There are interesting contrasts between the Lago Grande and Lago Pequeño data (Table 1). Mean primary production is much lower in Lago Pequeño, averaging just $0.56 \text{ g C m}^{-2} \text{ d}^{-1}$ in the most comparable relatively deep Chúa station, although the biomass (average 2.52 g C m⁻²) differs little



Figure 4. Vertical profiles of estimated photosynthesis at the shallow Sukuta station in Lago Pequeño. Dark bottle uptake is shown in black (Lazzaro, 1981).



Figure 5. Temporal variation of important limnological variables at the Chúa and Sukuta stations in Lago Pequeño. Chl. is chlorophyll determined spectrophotometrically. Z_s is transparency as measured by the Secchi disk (Lazzaro, 1981).

from Lago Grande. As a result the P/B ratio at Chúa is less than half of that of Lago Grande (0.22 d^{-1}). Production was even lower in the shallow Sukuta station, but the P/B ratio was rather similar, indicating generally similar conditions for phytoplankton growth. The shape of the vertical profiles of primary production are very similar in Lago Grande and Lago Pequeño.

A number of hypotheses might explain the relatively low production in Lago Pequeño. Large areas of this shallow sub-basin are covered with macrophytes (Collot, this volume), which might compete with phytoplankton for nutrients. The sub-basin might receive less nutrient loading, due to its water budget being dominated by nutrient-depleted inflows of surface water from Lago Grande (Carmouze, this volume). However, the comparable phytoplankton biomass in the two sub-basins indicates roughly similar levels of total nutrients. The lack of nitrogen fixing cyanobacteria during the period of study, despite relatively low N:P in the hypolimnion of the Fosa de Chúa station, perhaps only means that the 1979-80 period studied by Lazzaro was one of unusually low production. Our limited knowledge of the variation in Lago Grande (see below) suggests that years with production as low as half of the mean reported in Table 3 do occur there. Finally, the shallow, well illuminated water column that characterizes so much of Lago Pequeño may deny grazing zooplankton a refuge from diurnal predation that is available to vertically migrating plankters in Lago Grande. Lower grazing rates in Lago Pequeño might therefore result in a lower turnover of biomass, and thus lower P/B. Further work is clearly required to solve this problem.

Lazzaro (1982) analysed the relationship between various measures of photosynthesis and physical parameters in Lago Pequeño. Table 2 summarises his results. These data can be used to test the validity of Talling's (1957) model of production in a vertically well mixed system. In this model, Z_i should estimate the depth at which production is half of Z_{opt} . The mean and 95% confidence interval for this relationship is 1.07 ± 0.27 , indicating a good fit. Assuming that the model fits, I_k , the initial slope of the photosynthesis-irradiance curve, could be estimated. Because surface irradiance data (photosynthetically active portion of the spectrum) are available for only 4 dates, the 95% confidence interval for I_k is rather wide $(1.59 \le I_k \le 5.48 \text{ J cm}^{-2} \text{ h}^{-1})$.

Bahía de Puno

Figure 6 shows the pattern of production observed in Bahía de Puno in 1981– 2. Mean production for the two-year period was $0.82 \text{ g C m}^{-2} \text{ d}^{-1}$, similar to the 1.02 g C m⁻² d⁻¹ recorded for the same period in Lago Grande. Vertical profiles of primary production closely resemble those for Fosa de Chúa and Lago Grande, with surface inhibition always present, a maximum at moderate depths (3–7 m), and increasingly severe light limitation below Z_{opt}. As shown in Figure 6, photosynthetic rates near the bottom of the 25 m





deep station varied from zero to 40% of the maximum, depending upon transparency. Bahía de Puno is polymictic (Richerson, this volume) and is sometimes stratified within the euphotic zone. Vincent *et al.* (1986) showed that stratification sometimes led to the formation of a deep chlorophyll maximum in and below the stratified layer, and to higher production in the light-limited region than under unstratified conditions. On some dates in late 1982, the production curve was bimodal. These relatively clear-water conditions are reflected in Fig. 6 in the high production at 24 m from September through to November, 1982.

Vincent *et al.* (1986) examined nutrient and light controls on photosynthesis in Bahía de Puno. N:P ratios were below 10:1 during the period of the study, and, as in the main lake, nutrient bioassay experiments (Wurtsbaugh *et al.*, 1985; Carney, 1984) and physiological measures of nutrient limitation (Vincent *et al.*,1984a) generally showed nitrogen limitation of photosynthesis (see also Wurtsburgh *et al.* this volume). Consistent with this experimental evidence, the maximum and areal total photosynthesis responded quite strongly to an episode of nitrogen fixation (December 1981–June 1982). During this period, production approximately doubled relative to background values measured throughout most of 1981 and the latter half of 1982. As Fig. 6 indicates, areal production was closely correlated with surface light intensity in 1981 (r = +0.85, p < .01, one month lag), but the relationship is not significant in 1982 due to the N-fixation supported peak. There is no



Figure 6. Photosynthesis and other important limnological variables in Bahía de Puno. (a) Daily production (closed circles), temperature at 4 m (open circles) and monthly average incoming radiation (thin line). (b) Maximum photosynthetic rate (Z_{max} , closed circles) and photosynthesis at 24 m as a percentage of Z_{max} (open circles). The horizontal line is drawn at 10% of Z_{max} (Vincent *et al.*, 1986).

indication in either year that the dry season circulation of Lago Grande had any effect on production in Bahía de Puno.

Comparative analysis of patterns of variation in production and related variables

The three sub-basins of the lake exhibit a good deal of independence of behaviour. Lago Pequeño is only connected to Lago Grande via the narrow Estrecho de Tiquina, and has somewhat different major ion composition from the main lake (Lazzaro, 1981; Carmouze, this volume). The connection between Lago Grande and Bahía de Puno is quite broad, and there are no marked differences in water chemistry. Nonetheless, patterns of production in the latter two systems at 0, 1, and 2 month lags are uncorrelated (Vincent *et al.*, 1986). The 1982 peak of production due to the presence of cyanobacter-

ial N-fixation was present in both lakes, but with somewhat different timing. Production in Lago Grande appears to respond to deep circulation in that basin in many years, but Bahía de Puno did not apparently receive enough nutrients by advection or diffusion from the main basin to stimulate production in 1981 or 1982.

Richerson et al. (1986), Richerson and Carney, (1988) and Vincent et al. (1986) examined the seasonal and interannual patterns of variation in primary production and other variables in Lago Grande and Bahía de Puno with several different statistical approaches. These studies compared patterns of variation in Titicaca with those of other temperate and tropical lakes. Vincent et al. (1986) examined the relationship between variation in light intensity and variation in primary production in 12 tropical and 11 temperate systems. The tropical systems had a much higher variance in production relative to variation in light than did temperate lakes. Many, but not all, tropical lakes, including both Bahía de Puno and Lago Grande, had a variance in primary production several to many times higher than that for incident solar radiation (averaging 14.44). Temperate lakes showed a narrower range, this ratio averaging 1.8. Moreover, the overall correlation between monthly incident solar radiation and monthly primary production (scaled by the annual mean in each lake) for all temperate lakes was large and significant (n = 160, =0.57, p < 0.01), whereas it was small and insignificant for tropical systems (n = 150, r = +0.11, p > 0.05). A more detailed look at the data confirmed this overall result. For 13 years of tropical data, 5 years showed significant lags (p < 0.05) at 0, 1 or 2 months lag. However, in only two of these years (including Bahía de Puno in 1981, as already mentioned) were the correlations positive. By contrast, 11 of 14 temperate lake years showed significant correlations for at least one lag, and only one of these was negative. In most temperate lakes, primary production is strongly entrained in the seasonal cycle of insolation, but as the amplitude of this cycle diminishes in the tropics, this effect appears to vanish.

Richerson *et al.* (1986) and Richerson and Carney (1988) tested the weak seasonality hypothesis with the multi-year time series of physical, chemical and biological data from Lago Grande (Fig. 2). Multi-year data sets were assembled for four comparison sets of data from other temperate and tropical lakes (lakes George, Leven, Washington and Tahoe). Monthly mean data were analysed using two-way Analysis of Variance to estimate variance due to fixed monthly (seasonality) and between-year effects. Richerson and coworkers also estimated autocorrelation functions for these time series. The results are quite striking. In the ANOVA analysis (see Table 3) Lago Grande showed a strongly seasonal pattern of physical variation, with months effects dominating the pattern. By contrast, chemical and biological variables (with the exception of diatom biomass) varied much less seasonally and usually not significantly. However, variation between years is large for such variables (again excepting diatom biomass). Richerson and Carney (1988) extended this analysis to biomass, diversity and measures of succession rate. Patterns

LAKE	Latitude	N	df		Variance		k/X		Grand	
			Months	Years	% Years	% months	Total	Years	Months	mean
George	0°									
1) Chlorophyll a		36	11	3	14	40	9581	0.09	0.15	411.5 mg Chl a m ⁻²
Titicaca	16°S									
1) Radiation		41	11	3	13**	76**	1101	0.05	0.10	251.8 watts m-2
2) Difference of temperature		62	11	5	3	92**	0.131	0.11	0.67	1.55°C
Silicate in epilimnion		54	11	4	39**	8	45.8	0.43	0.20	9.69 µg–at I-1
4) Silicate in hypolimnion		54	11	4	31**	19	78.9	0.27	0.21	18.14 µg-at I-1
5) Oxygen in epilimnion		60	11	5	39**	13	0.300	0.06	0.03	6.38 mg I-1
6) Oxygen in hypolimnion		60	11	5	26**	31*	0.97	0.11	0.12	4.62 mg I-1
7) Primary production		49	11	5	29**	26	0.182	0.20	0.19	1.13 g C m-2 d-1
8) Diatom biomass		25	11	2	17*	49*	0.101	0.41	0.82	0.256 ml m-3
Tahoe	39°N									
1) Primary production		116	11	9	49**	22**	0.0046	0.24	0.16	0.196 g C m-2 d-1
Washington	48°N									
1) Radiation		102	11	8	4	73**	7057	0.11	0.56	128 watts m^{-2}
2) Chlorophyll a		102	11	8	23**	47**	109.5	0.41	0.59	12.2 µg l-1
3) Primary production		102	11	8	18**	63**	2.77	0.34	0.64	2.07 g C m-2 d-1
Leven	56°N									
1) Primary production		43	11	3	、 9*	66**	13.48	0.28	0.76	4.82 g O ² m ⁻²

Table 3. Results of analysis of variance of data series from Lago Grande and some comparison with temperate and tropical lakes. One asterisk indicates a treatment effect significant at the .05 level, two asterisks at the .01 level. k/X is the coefficient of variation of treatment means (Richerson *et al.*, 1986).

were similar; all variables showed large and significant variation between years. Only diversity showed a significant fixed 12-month effect, as a result of a tendency to low diversity during the middle of the stratified period in the three years of record. Richerson (unpublished data) has also examined the other major groups of algae, and diatoms are the only one to show significant months effect in the ANOVA. The biological data from comparison temperate lakes (Table 3) show highly significant monthly effects, which are higher than between years effects except for Tahoe, where cultural eutrophication and relatively sunny winters reduce the effect of seasonality.

The autocorrelation analyses confirm these results (Fig. 7). In highly seasonal time series, the autocorrelation function is significantly negative at 6 months lag (winter and summer are very different), while there is a significant positive peak at 12 months lag (one year is much like another). Physical variables in Lago Grande show the highly seasonal pattern, as do biological variables in classical temperate lakes like Loch Leven. By contrast, production in Lago Grande and chlorophyll in Lake George show no statistically significant sign of a seasonal pattern, although there is a hint of a 6 month cycle in both systems. For Lago Grande, a 6 month cycle is consistent with the weak tendency of production to peak either during maximum stratification (due to N-fixation occurring during this season), or during the period of minimum stratification (due to cycling of nutrients from the hypolimnion).

Figure 8 shows a similar general pattern for major algal groups. All groups except cryptophytes exhibit some patterning with significant positive autocorrelations for up to 3 months lag (Fig. 8b), reflecting the major episodes of abundance clearly visible in Fig. 8a. For Cyanophyceae and Chlorophyceae the autocorrelation function becomes significantly negative slightly after six months and then increases. This indicates moderate seasonality; there are fairly consistent patterns with mixing and stratification. No group, however, has a pattern of regular seasonality that repeats in subsequent years, as would be indicated by a distinct minimum autocorrelation at 6 months and maximum at 12 months.

An analysis of variance with biomass data of the major groups also indicates that interannual variability is quite significant, while regular seasonal variation within years is more modest. Variance between years is significant at p < 0.01 for all major groups (Cyanophyceae, Chlorophyceae, Bacillariophyceae, Dinophyceae), while the months effect is only significant for Bacillariophyceae.

Dominant phytoplankton species show generally similar patterns to the major groups (Fig. 9). The filamentous blue-green *Nodularia spumigena* shows one of the strongest seasonal signals we have detected among biological measures. This species regularly peaks during the stratified period and reaches minima during mixing. The filamentous green *Gloeotilopsis planctonica* and the centric diatom *Cyclotella andina* are more typical. They show significant lags, but virtually no hint of truly regular seasonality. Even though species like *C. andina* have only occurred during the cool season, the exact



Figure 7. Autocorrelation functions for data series from Lago Grande and some comparison with tropical and temperate lakes. The vertical axis gives the value of the autocorrelation (r) as a function of months of lag on the horizontal axis. The near-horizontal dashed lines delimit the envelope in which 95% of the autocorrelations from a random series of the length of each data series should fall (Richerson *et al.*, 1986).

timing and magnitude of their maxima and minima is so variable as to fail to indicate a statistically significant seasonal cycle.

Principal components analysis is a useful technique to summarize the "seasonal" succession pattern of the whole community (Allen *et al.*, 1977).



Figure 8. Biomass of the major algal groups for the three years of record (A). Autocorrelations for the major groups (B).

Figure 10 shows how the Lake Titicaca community changes during the three years; each point represents the composition of the community during a given month. The abundance of the 15 commonest species defines the axes of the multidimensional space of possible communities in this analysis. A large change in the community from one date to another is reflected by a



Figure 9. Autocorrelation functions for three species of algae.

large shift in position. A strong and regular seasonality would be indicated by a large circle or oval for a yearly trajectory. Each year would come close to mapping out the same trajectory of species composition as every other. Clearly, the Lake Titicaca phytoplankton do not exhibit this behaviour. During the three years for which we have data, the Titicaca community wanders about in a rather irregular pattern without any apparent tendency to form closed 12 month polygons (Fig. 10). These very irregular intra-year patterns, and substantial changes between years, are in sharp contrast to PCA results for north temperate lakes (Allen *et al.*, 1977).



Figure 10. Plot of the first two principal components of monthly average phytoplankton biomass in Lake Titicaca.

In Lago Grande, a rather large proportion of the variation in many biological and chemical variables is unexplained by either months or years effects in the ANOVA, and shows up as significant autocorrelations at one or two months lags. In the two most typical temperate lakes in Richerson *et al.*'s comparison, seasonal plus between years effects accounts for a very large proportion of the variation in all series. This reflects the tendency of biological and physical variation. In any one year, this looks something like the familiar seasonal cycles of the temperate zone, but the patterns are not repeated in subsequent years.

We wish to end this section with a note of caution. It is clear from less complete and unpublished data from other years that Lake Titicaca varies outside the bounds of the data analysed above. Alfaro Tapia and Roncal (personal communication) and Iltis (personal communication) have observed a long episode of very low production and biomass, and high transparency, in Lago Grande during the years 1984–8. Both groups report large numbers of secchi depths exceeding 10 m with maxima of almost 20 m, whereas in earlier studies secchi depths exceeding 10 m were unusual. Both production and phytoplankton biomass were only a fraction of the averages based on the data shown in this paper. Our understanding of the interannual variability of both temperate and tropical lakes is still very incomplete. Longer and more complete time series of data are urgently required from lakes like Titicaca both to help in the management of local resources, and to understand basic questions regarding the effects of climate change and similar phenomena.

Surface inhibition of photosynthesis

As shown by the profiles in previous sections, primary production in all sub-basins of Lake Titicaca is usually characterized by surface inhibition, a maximum of production around 5 m, and an exponential decline below that depth. One problem posed by profiles with this shape is the significance and reality of the surface inhibition above Z_{max} . This effect is a result of high light intensities, and is termed photoinhibition. Photoinhibition takes some time to develop, and in experiments with moving bottles designed to mimic mixing in the epilimnion of lakes eliminate or greatly reduce the photoinhibition effect (Jewson and Wood, 1975; Marra, 1978). On the other hand, as described by Richerson (this volume), diurnal stratification in the top few metres of the water column, due to the same high light intensities that cause photoinhibition in fixed bottle experiments, also reduces mixing at shallow depths during daylight hours.

Vincent *et al.* (1984b) and Neale and Richerson (1987) used the poison DCMU, which blocks the reoxidation of Photosystem II intermediates, as a physiological measure of state of algal cells. When DCMU is administered,



Figure 11. Diel cycle of temperature and fluorescence depression, 21-22 July, 1982, in Lago Grande. a) 16:30 21 July; b-f) 22 July; b) 05:30 h; c) 07:30 h; d) 09:30 h; e) 11:30 h; f) 13:30 h. Open box, $F_{aft}-F_{bcf}$; solid circle, temperature (Vincent *et al.*, 1984b).

light cannot be used to produce electrons in the reaction centre and is instead lost by chlorophyll fluorescence. Thus DCMU generally enhances the fluorescence of living cells. However, when the PS II reaction centre is inactivated by photoinhibition, electrons are no longer produced, and DCMU ceases to increase fluorescence emission. In Lake Titicaca, there is minimal increase of *in vivo* fluorescence in near-surface algal populations upon addition of DCMU, but populations near Z_{max} show maximal DCMU enhancement. Thus, at the surface, DCMU does not increase fluorescence very much because photoinhibition has already resulted in the inactivation of Photosystem II. Figure 11 shows an example of the daily cycle of inhibition and recovery, measured by the difference between fluorescence before (F_{bef}) and after (F_{aft}) the administration of DCMU. Neale and Richerson conducted a series of experiments to quantify the dynamics of inhibition and recovery during the diurnal cycle in Lago Grande. On 8 different experimental days, short-term experimental incubations were conducted in which algae from shallow (3-5 cm) and deep (15-20 cm) in the euphotic zone were incubated at several different light intensities. These experiments showed that the inhibition of ¹⁴C uptake closely parallels the decline in DCMU enhanced fluorescence. The inhibition process is quite rapid, with a time scale of a few minutes, whereas recovery is slow, requiring hours. Hence, the photosynthetic capacity of an algal cell declines to a level set by the highest light intensity to which it is exposed during the daily cycle, and does not significantly recover until after dark.

These results show that diurnal stratification, at least in Lake Titicaca, but probably in many other systems under bright light conditions, is easily strong enough to subject shallow phytoplankton populations to inhibiting light intensities. The traditional fixed bottle experiment is thus not misleading about the effects of photoinhibition. One might expect algal populations to adapt to high light intensities and eliminate the photoinhibition effect. However, the deep mixed layer of Lake Titicaca means that most cells experience suboptimal light on any given day. Nocturnal mixing (Richerson, this volume) prevents the community from segregating into high and low light adapted forms, as is possible with the sun and shade leaves of terrestrial plants. Thus, the photoinhibition of the plankton is perhaps an inevitable tradeoff caused by the need to adapt to the low average light conditions of planktonic environments.

Conclusion

Lake Titicaca exhibits a level and pattern of primary production that is basically tropical, although modified by its altitude. Brylinski and Mann (1973) estimated regression equations describing patterns of global production in lakes. Their simplest equation based only on latitude and altitude predicts ($r^2 = 0.49$; n = 93) that Titicaca production should be 0.90 g C m⁻² d^{-1} . A second equation based on latitude, altitude, visible incident radiation, day length range, air temperature and precipitation ($r^2 = 0.58$; n = 84) predicts 1.26 g C m⁻² d⁻¹. Measured values from Lago Grande (1.13 g C m⁻² d^{-1} , 4 year average from Table 3), Lago Pequeño (0.56 g C m⁻² d⁻¹), and Bahía de Puno $(0.82 \text{ g C m}^{-2} \text{ d}^{-1})$ are rather close to these predictions. Even the Lago Pequeño value is not so far off considering the inevitable noise inherent in such a broad comparison. The lake might be described as moderately eutrophic based on its total annual production compared to lakes on a worldwide basis. On the other hand, its position near the regression line given its physical situation (especially the long tropical growing season) suggests that the designation "mesotrophic" is more appropriate.

The pattern of temporal variation in Lake Titicaca is fascinating, especially if it turns out to be typical of large, deep tropical lakes. Despite the seasonal pattern of variation of physical factors, the low amplitude of physical vari-

ation appears to result in a failure to entrain biological processes in the seasonal cycle. Unlike the case in higher altitude lakes, seasonality in the sense of a regular 12 month cycle is essentially absent. Total variation is reduced somewhat, interannual variation is comparable, and the amount of variation unexplained by the factors analysed in this study is substantially higher, compared to temperate lakes. Two hypotheses seem worth pursuing in future studies. (1) Subtler physical and chemical mechanisms may control the variation in production and other biotic factors. (2) Biological interactions, such as predator-prey and competitive processes, may generate endogenous variation, perhaps of the chaotic sort. These ideas are closely related to the "top down" (biotic) versus "bottom up" (physical) hypotheses about the most important factors regulating processes in the plankton currently being actively investigated by temperate zone limnologists (Carpenter et al., 1985; Harris, 1986). Richerson and Carney (1988) hypothesize that complex dynamics (e.g. chaos) may be responsible for a significant amount of the acyclical within-years and interannual variation in Lake Titicaca. Titicaca is an excellent place to study such effects. It has the three contrasting basins for comparison, and its mean temperatures are much like those of the better studied temperate lakes. It has easily detected physical forcing effects, but apparently not such a strong seasonal signal as to dominate biological and chemical processes. If biotic processes have free-running dynamics that generate their own patterns of variation, these might be convincingly separated from physical controls in such a lake. Workers are encouraged to develop the long-term data that would be so valuable from such a system to test these and similar ideas.

Understanding the causes of variation is, of course, also important for applied purposes in Lake Titicaca. The present evidence from Titicaca suggests that it is less variable than temperate lakes only in having little predictable seasonality. There is every reason to expect that year-to-year variation will be important to management of the lake's biotic resources. Our data only sample a few years and do not reflect the longer term variation that might be induced by lake-level changes and the like. We know some years have values of transparency, production and phytoplankton biomass outside the range of the data analysed here.

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References of chapter VI.1

- ACOSTA POLO (J.), PONCE HERRERA (A.), 1979. Las algas superficiales del Lago Titicaca (Departamento de Puno, Perú). Univ. Nac. Federico Villarreal. Centro Invest. Pesq. Lima, 1: 5-40.
- ALLEN (T.H.F.), BARTELL (S.M.) and KOONCE (J.F.), 1977. Multiple stable configurations in ordination of phytoplankton community change rates. *Ecology* 58: 1075-84.
- BOURRELLY (P.), 1957. Algues d'eau douce du Soudan français, région du Macina (A.O.F.). Bull. IFAN, sér. A, 19 (4): 1047–1102, 21 lám.
- BOURRELLY (P.), 1970–1972–1980. Les algues d'eau douce. I. Algues vertes, II. Algues jaunes et brunes, III. Algues bleues et rouges. Boubée, Paris, 572 p., 517 p. y 512 p.
- BRYLINSKY (M.), MANN (K.H.), 1973. An analysis of factors governing productivity in lakes and reservoirs. *Limnol. Oceanogr.*, 18: 1–14.
- CARMOUZE (J.P.), AQUIZE JAEN (E.), 1981. La régulation hydrique du lac Titicaca et l'hydrologie de ses tributaires. *Rev. Hydrobiol. trop.*, 14 (4): 311-328.
- CARMOUZE (J.P.), DURAND (J.R.), LEVEQUE (C.), 1983. Lake Chad. Monographiae biologicae n° 53, Junk. The Hague, 575 p.
- CARMOUZE (J.P.), AQUIZE JAEN (E.), ARZE (C.), QUINTANILLA (J.), 1983. Le bilan énergétique du lac Titicaca. *Rev. Hydrobiol. trop.*, 16 (2): 135-144.
- CARMOUZE (J.P.), ARZE (C.), QUINTANILLA (J.), 1984. Le lac Titicaca: stratification physique et métabolisme associé. *Rev. Hydrobiol. trop.*, 17 (1): 3–12.
- CARNEY (H.J.), 1984. Productivity, population growth and physiological responses to nutrient enrichments by phytoplankton of Lake Titicaca. *Verh. Internat. Verein. Limnol.*, 22: 1253–1257.
- CARNEY (H.J.), RICHERSON (P.J.), ELORANTA (P.), 1987. Lake Titicaca (Peru/Bolivia) phytoplankton: Species composition and structural comparison with other tropical and temperate lakes. *Arch. Hydrobiol.*, 110 (3): 365–385.
- CARPENTER (S.R.), KITCHELL (J.F.), 1984. Plankton community structure and limnetic primary production. *Amer. Nat.*, 124: 159–172.
- CARPENTER (S.R.), KITCHELL (J.F.), HODGSON (J.R.), 1985. Cascading trophic interactions and lake productivity. *Bioscience*, 35: 634–639.
- COMPERE (P.), ILTIS (A.), 1983. The phytoplankton. In: Lake Tchad. Carmouze, Durand, Lévêque eds., Monographiae Biologicae n° 53, Junk. The Hague: 145–197.
- COUTE (A.), THEREZIEN (Y.), 1985. Première contribution à l'étude des *Trachelomonas* (Algae, Euglénophyta) de l'Amazonie bolivienne. *Rev. Hydrobiol. trop.*, 18 (2): 111-131.
- COUTE (A.), ILTIS (A.), 1988. Etude en microscopie électronique à balayage de quelques Desmidiacées (Algae, Chlorophyta, Zygophyceae) des lacs andins boliviens. *Cryptogamie*, *Algologie*, 9 (1): 13–26.
- FRENGUELLI (J.), 1939. Diatomeas del Lago Titicaca. Notas Mus. La Plata, 4: 175-196.
- GERMAIN (H.), 1981. Flore des diatomées. Faunes et flores actuelles, Boubée, Paris, 444 p.
- GILSON (H.C.), 1939. The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1 (1): 1–116.
- GILSON (H.C.), 1964. Lake Titicaca. Verh. Internat. Verein. Limnol., 15: 112-127.
- GUERLESQUIN (M.), 1984. Contribution à la connaissance des Characées d'Amérique du Sud (Bolivie, Equateur, Guyane française). *Rev. Hydrobiol. trop.*, 14 (4): 381-404.
- HARRIS (G.P.), 1986. Phytoplankton ecology: structure, function, and fluctuation. Chapterman and Hall, London, 384 p.
- HAWORTH (E.Y.), Hurley (M.A.), 1986. Comparison of the Stelligeroid taxa of the Centric diatom Genus Cyclotella. In: Proceedings of the Eighth International Diatom Symposium, 1984, Ricard ed.; Koeltz, Koenigstein: 43–58.
- HEGEWALD (E.), ALDAVE (A.), HAKULI (T.), 1976. Investigations on the lakes of Peru and their phytoplankton. 1. Review of literature, description of the investigated waters and chemical data. *Arch. Hydrobiol.*, 78 (4): 494–506.

- HEGEWALD (E.), SCHNEPF (E.), ALDAVE (A.), 1978. Investigations on the lakes of Peru and their phytoplankton 4: The algae of Laguna Paca with special reference to *Chodatella* subsalsa and Scenedesmus ellipticus. Arch. Hydrobiol., suppl. 51 (Algological Studies 21): 384-392.
- HEGEWALD (E.), SCHNEPF (E.), ALDAVE (A.), 1980. Investigations on the lakes of Peru and their phytoplankton. 5: The algae of Laguna Piuray and Laguna Huaypo, Cuzco, with special reference to *Franceia*, *Oocystis* and *Scenedesmus*. Arch. Hydrobiol., suppl. 56 (Algological Studies 25): 387-420.
- HUSTEDT (F.), 1927. Fossile Bacillariaceen aus dem Loa-Becken in der Atacama-Wüste, Chile. Archiv. Hydrobiol., 18: 224–251.
- HUSTEDT (F.), 1930. Die Süsswasser-Flora Mitteleuropas. 10: Bacillariophyta (Diatomeae). Fischer, Jena, 466 p.
- HUTCHINSON (G.E.), 1967. A treatise on Limnology. 2: Introduction to lake biology and the limnoplankton. John Wileys and Sons, New York, 1115 p.
- IDEI (M.), KOBAYASI (H.), 1986. Observations on the valve structure of freshwater Diploneis (Bacillariophyceae), D. oculata (Breb.) Cleve and D. minuta Petersen. Sörui, Jap. J. Phycol., 34 (2): 87–93.
- IDEI (M.), KOBAYASI (H.), 1988. Examination of the Type Specimens of *Diploneis parma* Cl. In: Proceedings of the Ninth International Diatom Symposium, 1986, Round ed: 397– 403.
- ILTIS (A.), 1984. Algues du lac Titicaca et des lacs de la vallée d'Hichu Kkota (Bolivie). *Cryptogamie, Algologie*, 5 (2-3): 85-108.
- ILTIS (A.), 1987. Datos sobre la temperatura, el pH, la conductibilidad eléctrica y la transparencia de las aguas de superficie del lago Titicaca boliviano (1985–1986). UMSA.ORSTOM, La Paz, Informe 3: 19 p., multigr.
- ILTIS (A.), 1988. Biomasas fitoplanctónicas del lago Titicaca boliviano. UMSA.ORSTOM, La Paz, Informe 10: 30 p., multigr.
- ILTIS (A.), 1988. Datos sobre las lagunas de altura de la región de La Paz (Bolivia). UMSA.OR-STOM, La Paz, Informe 14: 50 p., multigr.
- ILTIS (A.), 1991. Algues du lac Titicaca bolivien. Cryptogamie, Algologie, I2 (3): 1-18.
- ILTIS (A.), COUTE (A.), 1984. Péridiniales (Algae, Pyrrhophyta) de Bolivie. Rev. Hydrobiol. trop., 17 (4): 279-286.
- ILTIS (A.), RISACHER (F.), SERVANT-VILDARY (S.), 1984. Contribution à l'étude hydrobiologique des lacs salés du sud de l'Altiplano bolivien. *Rev. Hydrobiol. trop.*, 17 (3): 259– 273.
- JEWSON (D.H.), WOOD (R.B.), 1975. Some effects on integral photosynthesis of artificial circulation of phytoplankton through light gradients. Verh. Internat. Verein. Limnol., 19: 1037–1044.
- KITTEL (T.), RICHERSON (P.J.), 1978. The heat budget of a large tropical lake, Lake Titicaca (Peru-Bolivia). Vehr. Internat. Verein. Limnol., 20: 1203-1209.
- KOBAYASI (H.), IDEI (M.), 1979. Fragilaria pseudogaillonii sp. nov., a freshwater pennate diatom from Japanese river. Sörui, Jap. J. Phycol., 26 (4): 193-199.
- KRAMMER (K.), 1980. Morphologic and taxonomic investigations of some freshwater species of the diatom Genus *Amphora* Ehr. *Bacillaria*, 3: 197–225.
- KRAMMER (K.), LANGE-BERTALOT (H.), 1986. Süsswasserflora von Mitteleuropa. Bacillariophyceae. 1. Naviculaceae. Fischer, Jena, 876 p.
- LANGE-BERTALOT (H.), 1980. Zur systematischen Bewertung der bandförmigen Kolonien bei Navicula und Fragilaria. Nova Hedwigia, 33: 723-788.
- LANGE-BERTALOT (H.), KRAMMER (K.), 1987. Bacillariaceae. Epithemiaceae. Surirellaceae. *Bibliotheca diatomologica*, 15, 289 p.
- LAZZARO (X.), 1981. Biomasses, peuplements phytoplanctoniques et production primaire du lac Titicaca. *Rev. Hydrobiol. trop.*, 14 (4): 349–380.
- LAZZARO (X.), 1982. Biomasses, peuplements phytoplanctoniques et production primaire du lac Titicaca. *Rev. Hydrobiol. trop.*, 14: 349–380.

- LEWIS (W.M. Jr.), 1978. A compositional phytogeographical and elementary structural analysis of the phytoplankton in a tropical lake. J. Ecol., 66: 213–226.
- LIBERMAN (M.), MIRANDA (C.), 1987. Contribución al conocimiento del fitoplancton del Lago Titicaca. Documento de pesca 003, Oldepesca, Lima, 82 p., multigr.
- LÖFFLER (H.), 1960. Limnologische Untersuchungen an Chilenischen und Peruanischen Binnengewässern. Ark. Geofysik, 3: 155-254.
- LÖFFLER (H.), 1964. The limnology of tropical high-mountain lakes. Verh. Internat. Verein. Limnol., 15: 176-193.
- LOWE-McCONNELL (R.H.), 1987. Ecological studies in tropical fish communities. Cambridge University Press, Cambridge, 382 p.
- MANGUIN (E.), 1964. Contribution à la connaissance des diatomées des Andes du Pérou. Mem. Mus. Nat. Hist. nat., nouvelle série, B, 12 (2): 4–98.
- MARGALEF (R.), 1983. Limnología. Omega, Barcelona, 1010 p.
- MARRA (J.), 1978. Phytoplankton photosynthetic response to vertical movement in a mixed layer. *Mar. Biol.*, 46: 203–208.
- MARTINOT (J.P.), RIVET (A.), 1985. Typologie écologique des lacs de haute altitude du parc national de la Vanoise en vue de leur gestion. Parc National de la Vanoise. Min. Environn., 78 p., multigr.
- MEDLIN (L.K.), 1981. Effects of grazers in epiphytic diatom communities. *In* : Proceedings of the Sixth Symposium on recent and fossil Diatoms 1980, Ross ed., Koeltz, Koenigstein: 399–412.
- MONHEIM (F.), 1956. Beiträge zur Klimatologie und Hydrologie des Titicaca beckens. Selbstverl. d. Geograph. Heidelberg, 1: 1–152.
- MULLIN (M.M.), SLOAN (P.R.), EPPLEY (R.W.), 1966. Relationship between carbon content, cell volume and area in phytoplankton. *Limnol. Oceanogr.*, 11: 307–311.
- MUNAWAR (M.), MUNAWAR (I.F.), 1976. A lakewide study of phytoplankton biomass and its species composition in Lake Erie, April-December 1970. J. Fish. Res. Bd. Can., 33 (3): 581–600.
- MUNAWAR (M.), MUNAWAR (I.F.), 1982. Phycological studies in Lake Ontario, Erie, Huron and Superior. Can. J. Bot., 60: 1837–1858.
- NEALE (P.J.), RICHERSON (P.J.), 1987. Photoinhibition and the diurnal variation of phytoplankton photosynthesis – I. Development of a photosynthesis-irradiance model from studies of *in situ* responses. J. Plank. Res., 9: 167–193.
- OSADA (K.), KOBAYASI (H.), 1985. Fine structure of the brackish water pennate diatom Entomoneis alata (Ehr.) Ehr. var. japonica (Cl.) comb. nov. Sörui, Jap. J. Phycol., 33 (3): 215-224.
- PADDOCK (T.B.B.), SIMS (P.A.), 1981. A morphological study of keels of various raphebearing diatoms. *Bacillaria*, 3: 177-222.
- PATRICK (R.), REIMER (C.W.), 1975. The diatoms of the United States. Monogr. Acad. Nat. Sci. Philadelphia, 13, 2 (1): 213 p.
- PIERRE (J.F.), WIRRMANN (D.), 1986. Diatomées et sédiments holocènes du lac Khara Kkota (Bolivie). Géodynamique, 1 (2): 135-145.
- REYSSAC (J.), DAO (N.T.), 1977. Sur quelques pêches de phytoplancton effectuées dans le lac Titicaca (Bolivie-Pérou) en décembre 1976. Cah. ORSTOM, sér. Hydrobiol., 11 (4): 285–289.
- RICHERSON (P.J.), CARNEY (H.J.), 1988. Patterns of temporal variation in Lake Titicaca, a high altitude tropical lake. 2. Succession rate and diversity of the phytoplankton. Verh. Internat. Verein. Limnol., 23: 734–738.
- RICHERSON (P.J.), WIDMER (C.), KITTEL (T.), 1977. The limnology of Lake Titicaca (Peru-Bolivia), a large high altitude tropical lake. Univ. California, Davis, Inst. Ecology, 14: 78 p., multigr.
- RICHERSON (P.J.), WIDMER (C.), KITTEL (T.), LANDA (A.), 1975. A survey of the physical and chemical limnology of Lake Titicaca. Verh. Internat. Verein. Limnol., 19: 1498– 1503.
- RICHERSON (P.J.), NEALE (P.J.), WURSTBAUGH (W.A.), ALFARO TAPIA (R.),

VINCENT (W.F.), 1986. Patterns of temporal variation in Lake Titicaca. A high altitude tropical lake. I. Background, physical and chemical processes, and primary production. *Hydrobiologia*, 138: 205–220.

- RODHE (W.), 1958. Primärproduktion und Seetypen. Verh. Internat. Verein. Limnol., 10: 377-386.
- RODHE (W.), 1969. Crystallisation of eutrophication concepts in Northern Europe. In: Eutrophication: Causes, consequences, correctives. An international symposium on eutrophication; University of Wisconsin, Madison, 1967, National Academy of Sciences, Washington: 50-64.
- ROUX (M.), SERVANT-VILDARY (S.), SERVANT (M.), 1991. Inferred ionic composition and salinity of a Bolivian Quaternary lake, as estimated from fossil diatoms in the sediments. *Hydrobiologia*, 210: 3–18.
- SCHOEMAN (F.R.), ARCHIBALD (R.E.M.), 1976. The diatom flora of southern Africa. CSIR, Wat 50, Pretoria.
- SERVANT-VILDARY (S.), 1978. Les Diatomées des dépôts lacustres quaternaires de l'Altiplano bolivien. Cah. ORSTOM, sér. Géol., 11 (1): 25–35.
- SERVANT-VILDARY (S.), 1984. Les Diatomées des lacs sursalés boliviens. Cah. ORSTOM, sér. Géol., 14 (1): 35-53.
- SERVANT-VILDARY (S.), 1986. Les Diatomées actuelles des Andes de Bolivie (Taxinomie, écologie). Cah. de Micropaléontologie, 1 (3-4): 99-124, 14 pl.
- SERVANT-VILDARY (S.), 1986. Fossil Cyclotella Species from Miocene lacustrine deposit of Spain. In: Proceedings of the Eighth International Diatom Symposium, 1984, Ricard ed., Koeltz, Koenigstein: 495–512.
- SERVANT-VILDARY (S.), BLANCO (M.), 1984. Les Diatomées fluvio-lacustres plio-pléistocènes de la Formation Charaña (Cordillère occidentale des Andes, Bolivie). Cah. OR-STOM, sér. Géol., 14 (1): 55-102.
- SERVANT-VILDARY (S.), ROUX (M.), 1990. Multivariate analysis of diatoms and water chemistry in Bolivian saline lakes. *Hydrobiologia*, 197: 267–290.
- STEINITZ-KANNAN (M.), NIENABER (M.), RIEDINGER (M.), PETTY-HARELL (L.), MILLER (M.), 1982. Estudios limnológicos en la Laguna de San Marcos con descripciones de las especies principales de Diatomeas. Publ. Mus. Ecuat. Ci. Nat., 3 (3): 39–65.
- TALLING (J.F.), 1957. Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation. *New Phytol.*, 56: 29–50.
- THEREZIEN (Y.), 1985. Contribution à l'étude des algues d'eau douce de la Bolivie. Les Desmidiales. Nova Hedwigia, 41: 505-576, 22 pl.
- THEREZIEN (Y.), 1986. Nouvelle contribution à l'étude des algues d'eau douce de la partie amazonienne de la Bolivie. 1^{ère} partie: Chlorophycées (sauf Desmidiales). *Rev. Hydrobiol. trop.*, 19 (3-4): 177-188, 4 pl.
- THEREZIEN (Y.), 1986. Nouvelle contribution à l'étude des algues d'eau douce de la partie amazonienne de la Bolivie. 2^{ème} Partie: Desmidiales. *Rev. Hydrobiol. trop.*, 19 (3–4): 189– 205.
- THEREZIEN (Y.), 1987. Contribution à l'étude des algues d'eau douce de la partie amazonienne de la Bolivie: Xanthophycées. *Cryptogamie*, *Algologie*, 8 (2): 143–152.
- THEREZIEN (Y.), 1989. Algues d'eau douce de la partie amazonienne de la Bolivie. 1: Cyanophycées, Euglénophycées, Chrysophycées, Xanthophycées, Dinophycées. 2: Chlorophytes: troisième contribution. Bibliotheca phycologica, 82: 124 p.
- THERIOT (E.), CARNEY (H.J.), RICHERSON (P.J.), 1985. Morphology, ecology and systematics of *Cyclotella andina* sp. nov. (Bacillariophyceae) from Lake Titicaca, Peru-Bolivia. *Phycologia*, 24 (4): 381–387.
- THOMASSON (K.), 1956. Reflections on arctic and alpine lakes. Oikos, 7 (1): 117-143.
- TUTIN (T.G.), 1940. The Algae. In: Reports of the Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1 (11): 191–202.
- UENO (M.), 1967. Zooplankton of Lake Titicaca on the Bolivian side. *Hydrobiologia*, 29: 547–568.

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- VAN LANDINGHAM (S.L.), 1964. Miocene non-marine diatoms from the Yakima region in south central Washington. Nova Hedwigia, 14: 78 p.
- VINCENT (W.F.), NEALE (P.J.), RICHERSON (P.J.), 1984. Photoinhibition: algal responses to bright light during dial stratification and mixing in a tropical alpine lake. J. Phycol., 20: 201–211.
- VINCENT (W.F.), VINCENT (C.L.), DOWNES (M.T.), RICHERSON (P.J.), 1985. Nitrate cycling in Lake Titicaca (Peru-Bolivia): the effects of high altitude and tropicality. *Freshw. Biol.*, 15: 31–42.
- VINCENT (W.F.), WURTSBAUGH (W.A.), NEALE (P.J.), RICHERSON (P.J.), 1986. Polymixis and algal production in a tropical lake: latitudinal effects on the seasonality of photosynthesis. *Freshw. Biol.*, 16: 781–803.
- VINCENT (W.F.), WURSTBAUGH (W.A.), VINCENT (C.L.), RICHERSON (P.J.), 1984a. Seasonal dynamics of nutrient limitation in a tropical high-altitude lake (Lake Titicaca, Peru-Bolivia): application of physiological bioassays. *Limnol. Oceanogr.*, 29: 540–552.
- VOLLENWEIDER (R.A.), 1968, 1970, 1971. Les bases scientifiques de l'eutrophisation des lacs et des eaux courantes sous l'aspect particulier du phosphore et de l'azote comme facteurs d'eutrophisation. O.C.D.E. Paris: 182 p.
- WIDMER (C.), KITTEL (T.), RICHERSON (P.J.), 1975. A survey of the biological limnology of Lake Titicaca. Verh. Internat. Verein. Limnol., 19: 1504–1510.
- WURTSBAUGH (W.A.), VINCENT (W.F.), ALFARO (R.), VINCENT (C.L.), RICHER-SON (P.J.), 1985. Nutrient limitation of algal growth and nitrogen fixation in a tropical alpine lake, Lake Titicaca (Peru-Bolivia). *Freshw. Biol.*, 15: 185–195.

VI.2. MACROPHYTES VI.2a. The higher plants

ALINE RAYNAL-ROQUES

The higher plants are represented by a very small number of species in the waters of Lake Titicaca; this poverty is particularly evident if the flora is compared with the much more diverse flora of the small lakes lying in the Cordillera above Lake Titicaca. The higher plants are distributed all around the margins of the lake in the littoral zone that they colonise down to depths of 8 to 10 m.

Life forms

The first impression of the vegetation is of a band of tall totoras (*Schoenoplectus tatora*) emerging from the water and situated at some distance from the shoreline; this species of Cyperaceae grows in water depths of about 2 to 4.50 m.

Between the shoreline and the band of totora, the water, which is never deeper than 2 to 2.50 m, is populated by a submerged flora with here and there an overlying stratum of floating species. Near the shoreline, in the very shallow temporarily flooded areas where the water is, discontinuous populations of small, partly emergent herbs occur, as well as shoreline grass-land communities that are only flooded exceptionally for short periods.

Beyond the totora belt is a zone of submerged vegetation rooted in the substrate, that the transparency of the water allows to grow down to depths of more than ten metres.

These submerged species produce long branching stems which fill the water column; the leaves, regularly spaced on the branches, are always submerged and their metabolism takes place entirely in the aquatic environment. Flowering is the only biological function that takes place out of the water. Depending on the genus, either only the flower emerges, floating on the surface (*Elodea*) or the tip of a stalk emerges bearing leaves (various submerged species) in the axils of which are the flowers (*Myriophyllum*). Certain genera (*Potamogeton*) only produce flowering spikes when the water

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is not too deep; in deep water they do not flower or rarely produce submerged flowers.

The floating species are free-living with no anchorage, floating on the surface; the water depth does not affect them directly. However, their passively mobile life-habit exposes them to the risk of being destroyed by wave action in the deeper areas, so they are only found in the shallow margins, where they are sheltered by the totora band.

Despite occurring in a relatively shallow zone, *Schoenoplectus tatora* is only submerged in its juvenile stages. As soon as its growth allows, its tall erect stems emerge; most of them do not bear flowers and flowering is not related to emergence. Although it grows in 2 to 4 m of water, the metabolism of this species is essentially aerial.

All of this vegetation provides the shore-dwelling human inhabitants with natural resources of great importance (see Chapter VII.1d).

Taxonomic review

The taxa making up the aquatic vegetation belong to systematically diverse groups.

The Pteridophyta, or ferns in the wider sense, are vascular plants whose reproduction implies alternating diploid and haploid individuals.

The family **Azollaceae** only contains one genus (*Azolla*) with 6 species. These are small aquatic ferns whose floating branches bear minute green scale-like leaves in pairs at each node, appressed to the upper surface of the branch. Roots (derived from the embryonic leaf tissue) hang down from the lower surface into the water. They are never rooted in the sediment, except in the event of drying out of the biotope, and then only just before the plants die.

The plant lives in symbiosis with a blue-green alga (Procaryota, Cyanophycaea), *Anabaena azollae* which is capable of fixing ammonia from atmospheric nitrogen: the association is rich in nitrogenous compounds.

The spores are contained in sporocarps hanging from the submerged underside of the thallus. Some produce floating female prothalli and others clusters of male prothalli surrounded by hooked hairs. The male prothalli attach to the female ones and together they sink to the bottom where fertilisation takes place.

The Angiospermae (true flowering plants) comprises about 250,000 species spread over 380 families, of which aquatic plants only make up a tiny minority. The organisation of aquatic plants implies very special anatomical and morphological adaptations, so that frequently they do not correspond to the general description given to the group to which they belong; they are therefore exceptions.

The Dicotyledons make up the largest and most diversified group of the


Figures 1-15. 1. Ranunculus trichophyllus: submerged leaf and emergent axillary flower. 2. Myriophyllum elatinoides: whorl of submerged leaves. 3. Hydrocotyle ranunculoides: leaf. 4. Lemna gibba: floating thalli. 5. Lilaeopsis andina: submerged flowering plant. 6. Elodea potamogeton: flowering stem, submerged except for the flower. 7. Ditto: male flower. 8. Ditto: female flower, front and side view. 9. Azolla filiculoides: whole floating plant. 10. Potamogeton strictus: insertion of leaf onto submerged stem. 11. Ditto: emergent flower spike. 12. Zannichellia palustris: insertion of leaf onto submerged stem. 13. Ditto: submerged fruits. 14. Ruppia maritima: base of submerged leaves. 15. Ditto: cluster of submerged fruits. Notes (Figs 10 to 14): The leaf of Zannichellia does not widen to form a sheath at the base; the leaf sheath of Potamogeton is prolonged into a sharply pointed ligule; that of Ruppia ends in 2 small rounded transluscent auricles.

The scale unit is 1 mm unless otherwise indicated.

Angiospermae, with about 315 families of which only 3 are represented in Lake Titicaca.

The **Ranunculaceae** contains about 1750 species, all toxic and mostly nonaquatic, grouped into 58 genera. The floral organs are distributed over an elongated receptacle, the gynoecium is formed of numerous free carpels which become achenes. The genus *Ranunculus* (250 species) is made up of herbs with regular flowers of 5 sepals and 5 petals, but with an indeterminate number of stamens and carpels inserted in a spiral pattern. The aquatic *Ranunculus* species with white flowers make up the sub-genus *Batrachium* to which belongs the only species present in the lake.

The **Haloragaceae**, a family with 9 genera and 120 species, includes a large proportion of aquatic plants. The minute polypetalous flowers have a small inferior ovary. The 40 all-aquatic species in the genus *Myriophyllum* have finely divided pinnate leaves; the flowers, grouped on an erect emergent spike, are accompanied by small leaves, less divided than the submerged ones. The pollen, produced by stamens with a long flexible filament, is transported by the wind.

The **Umbelliferae**, with more than 3000 species in 420 genera, only includes a few small groups of aquatic plants whose members differ profoundly from the rest of the family. The Umbelliferae normally have finely divided leaves with a well-developed leaf sheath, but this is not the case with species described here. The characteristic inflorescence in the form of an umbel is very reduced and difficult to recognise in these species, but the small hermaphroditic pentamerous flowers, with a schizocarpous inferior ovary are clearly evident in the two genera in question. The two carpels of the fruit, joined together along one face, separate at maturity.

Hydrocotyle spp. (about 75 species) are all aquatic herbs or plants living in damp environments. Their slender creeping stems bear alternate leaves with a rounded peltate blade and long erect petiole. In the species occurring in Lake Titicaca, the flowers are borne on a pedicel which is shorter than the petioles of the leaves, so that flowering takes place at the water surface. The genus *Lilaeopsis* (about 15 species) is typically aquatic. A thick, fleshy and aerenchymatous white rhizome bears rosettes of small upright submerged cylindrical leaves, tapering to a point. These hollow, air-filled and somewhat swollen leaves have some transverse septa at which point they are slightly constricted. The minute inflorescences only contain a few flowers, borne on a filiform flexible pedicel, longer than the leaves, which reaches to the water surface to flower.

The Monocotyledons only contain a total of 64 families, but they are better represented that the Dicotyledons in aquatic environments.

The approximately 100 species included in the family **Hydrocharitaceae** are entirely aquatic, most of them living submerged and some of them being marine. The small, fragile and short-lived flowers are the only part to break the water surface. The 12 species in the genus *Elodea* are submerged herbs with long stems covered with small linear leaves and with intense powers of

vegetative multiplication. The plants are dioecious; the minute single-sex flowers are borne on thread-like flexible pedicels which carry them to the water surface at the time of fertilisation.

The **Potamogetonaceae** comprises about 90 species, all of them aquatic, with well-developed vascular subterranean organs. The leaves are of two types: either filiform or translucent and submerged, or broadly oval, coriaceous and floating on the water surface. The species with floating leaves pass through a juvenile stage with linear submerged leaves. The small, hermaphrodite tetramerous flowers are densely clustered on a more or less swollen spike, emerging from the water. Apart from *Potamogeton*, the family only includes one other monospecific genus.

The **Ruppiaceae**, closely related to the previous family, are distinguished by the absence of vascularisation in the roots. The inflorescence only contains two simplified flowers reduced to 2 stamens and 4 carpels. The fruits are generally borne by a pedicel that elongates in the form of a spiral after fertilisation. Flowering and fertilisation often take place under water. The only genus in the family, *Ruppia*, occurs in brackish and saline waters. Some workers have distinguished up to 7 species of *Ruppia*, but we, along with many other workers, consider it to be monospecific.

The Zannichelliaceae, with its 7 species grouped into 4 genera, are again entirely submerged aquatic herbs; the vascularisation of their rhizomes does not contain lignified vessels. As with the two previous families the leaves, borne in non-elongated spikes, often appear clustered into lateral bunches of 2, 3 or 4 leaves. The minute flowers have a very simplified structure; the flowers are single sexed, the two sexes being situated side by side on the same sessile inflorescence inserted in the leaf axils. The monospecific genus Zannichellia occurs in fresh and brackish water. The carpels bear a delicate stigma in the form of a funnel; fertilisation takes place under water. The fruit is a small elongated achene bearing denticulations along its dorsal margin.

The Lemnaceae (about 30 species in 6 genera) are unique among the flowering plants in the remarkable reduction of the vegetative structures. The plant is made up of a thallus, without recognisable stems or leaves, sometimes bearing one or more roots on its lower surface; buds are included in two lateral pouches. The extremely small flowers only appear rarely, they are clustered (one female and 2 or 3 male flowers) in an inflorescence contained in one of the pouches. The male flower is reduced to a stamen and the female to a carpel. The Lemnaceae are all capable of very efficient vegetative multiplication by budding from the marginal pouches, the daughter thalli eventually breaking free from the parent. Most of the species in the genus *Lemna* float on the water surface in fresh waters. They form flattened or gibbous lens-shaped structures less than a few millimetres in diameter, shiny on the upper (emergent) surface and bearing a single root inserted at the middle of the lower surface.

The large family of the Cyperaceae, with its 115 genera and more than

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3600 species, is in the majority composed of terrestrial species. These are scabrous herbs (because they are incrusted with silica crystals) whose leaves, arranged in three vertical rows, form a closed sheath at the base enclosing the stem. The very reduced flowers are surrounded by scarious scales (glumes), and grouped into complex inflorescences made up of spikelets arranged in various ways. The fruits are small achenes, often triangular in cross-section. *Schoenoplectus* spp.(often included in the genus *Scirpus*) are aquatic or marsh plants with upright rush-like stems, having a photosynthetic role. At the summit they bear a branched inflorescence, offset to one side by the development of a stiff upright bract extending beyond the tip of the stem. Frequently, no inflorescence develops on the stem, which then only fulfils an assimilatory role. The leaves are reduced to short reddish sheaths originating from the rhizome and surrounding the stem base (fully developed green leaves only occur during the brief juvenile stage). The inflorescence branches bear more or less elongated oval spikes.

Identification key

1. 1'.	Herbs rooted in the substrate; plants of large size, never measuring less than a few centimetres and usually much larger
2.	Stems submerged, elongated, upright or trailing in the water, bearing regularly spaced leaves
2'.	Cylindrical upright organs (stems or leaves, but with similar appearance), without green appendages resembling leaves, in tufts coming from a rootstock
3.	Leaf blade often emergent, rounded, deeply 5-lobed, the lobes them- selves crenate at the margins. Leaves with long petioles coming from a white stem rooted in the bottom; plant of shallow water
3'.	Leaf with parallel margins, either entire or divided (in this case the segments always have parallel margins), flat or filiform. Leaves petiolate or not, arising from a more or less green stem floating in the water
4.	Leaves sessile with a flat, entire, vivid transluscent green blade, reaching 20 mm long and 4 mm wide, in whorls of 3 (rarely 4). Flowers very small, pinkish white (5 mm diameter), of a single sex, floating at the end of a long thread-like flexible pedicel. The species is dioecious, each individual only bearing one sex <i>Elodea potamogeton</i> (Bert.) Espin.

4'. Leaves petiolate or not, with a filiform blade (width never exceeding 2

- 9. Tall cylindrical stems, coming from a thick hard robust rhizome spreading in the underwater soil. Stems pithy inside, can exceed 3 m in height from the lake bottom (the emergent part reaching 1 to 2 m above water level). No fully developed leaves, only a few stiff bracts at the tip of the stem. The flowering stems end in a panicle of brown, ovate, shortly pedicillate, spikes, offset to the side by the first bract, extending beyond the stem

9'.	tip
10.	Plants made up of tiny branching stems, covered in minute triangular, reddish green leaves (sometimes blood red), which float in layers on the surface. They bear bunches of black roots hanging down into the water
10'.	Tiny, oval, light green fronds, floating on the surface, budding. Each bears a small, white, unbranched root inserted into the middle of the underside
11.	Fronds very swollen on the upper side, height almost as great as di- ameter. Some fronds are much less swollen; upper side very shiny, waxy looking
11′.	Fronds hardly swollen, in the form of a flattened disc; upper surface

less shiny Lemna cf. aequinoctialis

Biogeography

The flora of Lake Titicaca is a combination of species of very diverse geographical distribution. Although some species (*Schoenoplectus tatora*, *Elodea potamogeton*, *Myriophyllum elatinoides* and *Lilaeopsis andina*) are endemic to the high plateaux of the Andes, a number of others have, in contrast, a very wide distribution. *Lemna gibba*, *Ruppia maritima*, *Zannichellia palustris*, *Ranunculus trichophyllus* and *Hydrocotyle ranunculoides* are cosmopolitan, whereas *Azolla filiculoides*, a plant originating in the warm regions of the American continent, is now distributed in all continents, except in the coldest areas.

The lake therefore has a large contingent of species with a wide world distribution, and its vegetation could seem a commonplace, one if the *Schoenoplectus*, *Elodea* and *Myriophyllum*, by their very abundance, did not give the vegetation communities their characteristic appearance.

Conclusion

Up to the present, only a dozen aquatic plant species have been recorded in Lake Titicaca, a very low number considering the extent of the lake. More intensive surveys around its margins could probably add a few more species

to the list, but the floristic homogeneity of the biotopes studied, together with the slight ecological variations recorded in each of them, makes it very likely that any species still to be discovered will be uncommon.

Despite this floristic poverty, it must be admitted that the plants are still insufficiently known in terms of their intraspecific variablity, their ecological and geographical distribution and their biology. Certain species are only known from a small number of phenologically poor samples and their identification is likely to be changed following future, more representative, sampling (*Lilaeopsis*, *Lemna*, *Potamogeton*). It is also worth noting that these taxa belong to groups in which the systematics are insufficiently studied and for which new revisions are needed to redefine the species and provide better identification criteria.

The aquatic flora of the high valleys of the Andes includes a fair number of species (e.g. *Ranunculus mandonianus* and *Isoetes herzogii*) that are probably absent from the Altiplano and therefore from the lake, but the aquatic flora of the ponds, pools and rivulets of the Altiplano is also richer than that of the lake (*Callitriche, Crassula, Eleocharis, Rorippa*, etc. occur here). The floristic population of the lake seems to be impoverished in species by the exclusion of the species of the higher altitude valleys and of those living in calm and shallow waters around the lake. Although only species capable of withstanding the ecological conditions of a vast water body occur in the lake, they form dense and well-structured communities, which make it even more unlikely that the small plants of the calm rivulets of the Altiplano could exist here and there close to the lake shores. As has generally been observed in large lakes, in which the general features are similar to those of the marine environment, the phanerogamic vegetation is poor in species, but remarkably well distributed and organised.

VI.2b. Charophytes

MICHELINE GUERLESQUIN

The three major and complementary publications on the macrophytes of Lake Titicaca (Tutin, 1940; Allen, 1940; Collot *et al.*, 1983) reveal the overwhelming importance of Characeae populations in the emergent and submerged plant communities.

Collot *et al.*(1983) estimated the areas covered by Characeae to be 436 km^2 in Lago Huiñaimarca, or over 60% of the area covered by vegetation, and at 198 km^2 in just Puno Bay, in the Lago Grande, i.e. one-third of the vegetated surface area. A transect between Cojata Island and Taraco Point covers a line of over 40 km where the bottom is vegetated by *Chara* (Fig. 1). The Characeae therefore constitute the most abundant plant group in Lake Titicaca, where the three dominant *Chara* species are found either in monospecific or in mixed communities.

Because of the enormous size of the lake basin of Lake Titicaca, we can only sketch an outline description of the submerged vegetation rather than provide a detailed study.

Characeae zones

Generally speaking, these are the gently shelving shorelines liable to flooding, the sandy beaches and beaches with scattered pebbles. The organo-detritic calcareous sediments on gently shelving bottoms between 10 and 20 m in depth in Lago Huiñaimarca and the calcareous deposits at depths of 4 to 10 m in Lago Grande (Puno and Achacachi Bays) are also favourable for an abundant cover of calcium-fixing Characeae (Boulangé *et al.*, 1981). Characean oospores are found in the medium-grained sand fraction.

According to Allen (1940), the Charophyta form the dominant group of plants in two areas of Lake Titicaca: Puno Bay in the west and Lago Huiñaimarca, where the salt concentration is slightly higher.

Because of the rise in lake level during the last few decades, the descriptions of the vegetative zonation published in 1940 (Tutin, Allen) and those made in 1983 (Collot *et al.*) are somewhat different (Table 1). As well as the nature of the substrate, Tutin (1940) also stressed the importance of

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Figure 1. Geographical and bathymetric map of Lake Titicaca (depth contours in m) showing known localities of Charophytes.

light intensity in explaining variations in populations of Characeae whose development zone is usually situated between the shallower *Myriophyllum* and *Elodea* association, and the deeper water *Scariomium* association. *Chara* spp. can also establish immediately after the totoras have been cut or where the reed density is low.

Brief systematic study

Information to date from the literature and from collections confirms the existence of eleven taxa of Characeae in Lake Titicaca and its flood zone.

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Table 1. Bio-ecological data on Characeae species recorded from Lake Titicaca. A) Lago Grande B) Lago Huiñaimarca.

Sites and localization on the map	Type of exposition	Depth of areas with Characeae	Species	Authors (litterature, herbarium	
A) Lago Mayor					
Perú , Península de Capachica			Chara denudata	ALLEN	
Perú , Tamán	quiet	1.50 - 9 - (12) m 1 50 m 1.70 m	Chara papillosa Chara denudata Chara globularis	ALLEN,TUTIN ALLEN ALLEN	
Perú . Uruni bay	little exposed	10 - 12 m	-	ALLEN, TUTIN	
Perú: Outer Sucune bay	more exposed	10 – 14 m	-	ALLEN, TUTIN	
Perú – Sucuné bay	more shellered	2.90 m 5 m 11.80 m	Chara papillosa Chara globularis Chara denudata	ALLEN ALLEN, GRIFFIN ALLEN	
Perú : Campanaria de Ceotos island, coast on the continent side	sheltered	0.70 – 1.30 m	Chara papiliosa	ALLEN, TUTIN	
Perú : Puno bay	well sheltered	common or dominant in deep water		ALLEN, TUTIN	
Perú : Puno bay		(0.50) - 4.50 - 7.50 - 15 m	Chara sp. pl.	COLLOT et al.	
Perú : Puno bay (D)* second channel		the shallowest zone	Nitella clavata	COLLOT et al., GRIFFIN	
Perù : Capachica channel			Nitella clavata	ALLEN	
Bolivia : around Achacachi ciose to Pocoata			Chara baltica var. andina	MANDON	
B) Lago Menor	more sheltered	shallow water	Chara denudata Chara papillosa	ALLEN	
Bolivia : Huatajata (A)*		3 – 9.50 m	Chara sp. pl. Chara globularis	COLLOT <i>et al.</i> RAYNAL	
Bolivia : Huacultu (B)*		3 m	Chara sp. pl.	COLLOT et al.	
Bolivia : Guaqui (C)*		3 m	Chara sp. pl.	COLLOT et al.	
Bolivia : Guaqui bay		2.10 - 2.50 m	Chara papillosa	ALLEN	
Bollvia : Punta de Taraco		3.30 m - 8.60 m	Chara papillosa	ALLEN	
Bolivia : Tiwanaku			Chara contraria Chara gymnophylla Tolypella sp.	RAYNAL RAYNAL RAYNAL	
Bollvia : Copacabana (F)*		0.30 m	Chara contraria	GRELON	
Bolivia : site 4 (E)*		10 m	Tolypella sp. Lamprothamnium succinctum	LAUZANNE LAUZANNE	

* See the map (fig. 1).

In addition, the following species have been quoted without precision : Chara contraria, Lake Titicaca, Perú, TUTIN; Chara vulgaris, without collector name nor date and place of collection. Chara fibrosa, wells close to Lake Triticaca, Bolivia, BECK, 1973; Chara batica, Chara papillosa, Chara vulgaris L. advina, COLLOT.

An identification key to these various species is given in Table 2 and their chief morphological characteristics are described below¹.

1. Chara fibrosa Ag. ex Bruz. (Pl. 1, Figs 1 and 2).

An incrusted species with diplostichous cortication on the axis but not on the branchlets. A single whorl of well-developed stipulodes, two at the base

¹For synonyms and descriptions, see Wood & Imahori (1964, 1965), Corillion (1975), Guerlesquin (1981).

Table 2. Identification key for Lake Titicaca Characeae

la.	Vegetative organs without cortication
b.	Vegetative organs (axis and branchlets) at least partly corticate
2a.	Stipulodes in a single whorl Chara fibrosa
b.	Stipulodes in 2 superimposed whorls
3a.	Axial cortex normally diplostichous
b.	Axial cortex rudimentarily diplostichous or absent
c.	Axial cortex triplostichous Chara globularis
4a.	Spine cells single or double, well developed.
	Stipulodes as long or longer than the axial diameter
b.	Spine cells single or rarely double, often very small and sparse
	Stipulodes shorter than the axial diameter
5a.	Posterior bract-cells well developed. Specimens not, or only slightly incrusted
	Chara baltica var. andina
b.	Posterior bract-cells reduced. Specimens encrusted Chara papillosa
6a.	Axial cortex isostichous or aulacanthous
b.	Axial cortex often heavily tylacanthous Chara contraria
7a.	Axis regularly corticate. branchlets not corticate Chara gymnophylla
b.	Axis and branchlets with rudimentary or no cortication Chara denudata
8a.	Branchlets simple with more than 3 segments forming bract cells at the nodes.
	Antheridia above or beside the oogonia Lamprothamnium succinctum
b.	Branchlets branching one or many times.
	Oogonium coronula small, formed of 2 stages
	of 5 superposed cells
9a.	Antheridia terminal and 1-3 lateral oogonia at the point of branching of the branchlets.
	Oospore laterally compressed Nitella clavata
b.	Lateral antheridium surrounded by 2-5 oogonia at the 1st branchlet node.
	Oospore almost globular,
	not flattened

of each branchlet. Rudimentary and sparse spine cells. A tropical species collected by St. Beck in a well near the lake (1979).

2. Chara globularis Thuill. (Pl. 1, Figs 3 and 4).

Axial cortication triplostichous and isostichous. Stipulodes and spine cells very small. Branchlets entirely corticated except 1–2 terminal cells. A monoecious species with gametangia conjoined at the 1–3–(4) lowest branchlet nodes. A cosmopolitan species recorded from Peru: Taman (Allen, depth 1.70 m on 9.06.1937) and in Sucuné Bay (Allen, depth 5 m, 13.07.1937; Griffin, 1968). Bolivia: Near Huatajata in a sparse *Schoenoplectus tatora* stand (Raynal, at 1.5 m depth, 14.08 1979).

3. Chara baltica Bruz. var. andina A. Br. (Pl. 1, Figs 5, 6, 7, 8).

A species not or only slightly incrusted. Axial cortication diplostichous. A double whorl of well-developed stipulodes. Spine cells long, single or double. A monoecious species with male and female gametangia conjoined on 1-3 lowest branchlet nodes. Bolivia: in the Achacachi area near Pocoata, Omasuyos province (Mandon, 3.06.1859; Collot, DC28).



Plate 1. Chara fibrosa Ag. ex Bruz.

Figure 1. Axial node, a whorl of stipulodes, diplostichous axis with small acute spine cells. *Figure 2.* Branchlets with an oogonium. (After Wood and Imahori, 1964).

Chara globularis Thuill.

Figure 3. Axial node, double whorl of stipulodes, triplostichous axial cortication, small spine cells and triplostichous basal segment of a branchlet with conjoined male and female gametangia. *Figure 4.* Apex of a branchlet (after Wood and Imahori, 1964).

Chara baltica Bruz. var. andina A. Br.

Figure 5. Axis with- diplostichous cortication bearing long simple spine cells, node with a double whorl of well-developed stipulodes.

Figure 6. Sterile corticated branchlet with two pairs of stipulodes at the base.

Figure 7. Bicellular apex of the branchlet.

Figure 8. Bifid spine cell. Original.

Chara vulgaris L.

Figure 9. Axial node, double whorl of stipulodes, diplostichous axis with small isolated spine cells.

Figure 10. Branchlet composed of 5 segments, long anterior bract-cells and bracteoles, reduced posterior bract-cells, two-celled end segment and conjoined male and female gametangia (after Wood and Imahori, 1964).

4. Chara papillosa Kütz.

A large, very variable plant resembling *C. contraria* and *C. baltica*, characterised by diplostichous, tylacanthous cortication, long spine cells single or in groups of 2–3, the posterior bract-cells visible. A heavily incrusted species and the commonest in Lake Titicaca in Allen's (1940) view, who recorded it from several parts of the lake, Peru: Isla Campanaria de Ceotos at 1.30 m depth (8.07.1937), Taman at 1.50 to 9 m depth (8.07.1937), Sucuné Bay at 2.90 m (13.07.1937), Taraco Point between 3.30 and 8.60 m (29.07.1937), and in Bolivia: Guaqui Bay between 2.10 m and 2.50 m (29.07.1937).

This physically large and very polymorphic taxon is like *Chara contraria* in that the single spine cells and the posterior bract-cells remain rudimentary or poorly developed. It is also like *C. polyacantha* A.Br, which has numerous bundles of spine cells on the axis and long posterior bract-cells. The main feature distinguishing it from *C. baltica* is the major incrustation of the vegetative parts.

Another difficulty is brought about by the interpretation of Wood and Imahori (1965), who place in the binomial, C. *vulgaris* f. *andina*, two of Mandon's specimens (sub C. *baltica* var. *andina*) and one of Tutin's (Isla Campanaria de Ceotos, at 1.30 m depth, 9.07.1937 sub C. *papillosa*). These authors add that Allen gives a list of 8 samples from Lake Titicaca, but that no figures had been published.

A re-examination is therefore needed of herbarium specimens of diplostichous *Chara* with a "spiny appearance" due to the development of spine cells, stipulodes or bract-cells, or of new specimens collected from different areas of the lake (fresh or fluid preserved).

5. Chara vulgaris L. (Pl. 1, Figs 9 and 10).

A cosmopolitan species with a very variable vegetative structure. The herbarium specimens give no details of locality, date or collector's name.

6. Chara contraria A. Br. ex Kütz. (Pl. 1, Figs 11, 12, 13).

Differs from the previous species by reason of its diplostichous tylacanthous axial cortication (primary cortical rows wider than the secondary), longer stipulodes and less black mature oospores. A cosmopolitan species recorded from the Peruvian part of the lake by Tutin (1940) without details and collected by Grelon in Bolivia, near Copacabana, next to the landing-stage at the strait at 0.30 depth (July 1988).

Chara contraria A. Br. ex Kütz.

Figure 11. Axial node with double whorl of well-developed stipulodes, diplostichous axis with solitary spine cells.

Figure 12. Branchlet with 4 corticated segments and two-celled apex.

Figure 13. Fertile node with conjoined male and female gametangia (after Wood and Imahori, 1964).



Plate 2. Chara gymnophylla A. Br.

Figure 1. Axial node with double whorl of stipulodes, isolated globular spine cells and diplostichous axis;

Figure 2. Branchlet with 3 uncorticated segments and conjoined gametangia at the lower nodes (after Wood and Imahori, 1964).

Chara denudata A. Br.

Figure 3. Axial node with double whorl of small stipulodes, rudimentary diplostichous axial and branchlet cortication (after Wood and Imahori, 1964).

Lamprothamnium succinctum (A. Br. in Asch.) R.D.W.

Figure 4. Sterile branchlet.

Figure 5. Axis and base of a whorl of branchlets showing 4 well-developed stipulodes

Figure 6. Branchlet with 2 fertile nodes and male and female gametangia at its base. Original. *Nitella clavata* Kütz.

Figure 7. Axis (a) without cortication. Whorl of branchlets composed of simple accessory branchlets (c) alternating with furcate branchlets (b)

7. Chara gymnophylla A. Br. (Pl. 2, Figs 1 and 2).

This taxon, closely related to C. vulgaris differs mainly by the absence of cortication on the segments of the branchlets, only the lowermost, isolated 1-2 segments can be corticated. The male and female gametangia are borne on the nodes of the corticated or bare segments, and are sometimes separated.

Collected by Raynal (18.08.1979) in Bolivia from a stream running into the lake at 0.20 m depth near Tiwanaku (altitude 3900 m).

8. Chara denudata A. Br. (Pl. 2, Fig. 3).

Characterised by a very variable cortication of the axis and branchlets, always however rudimentary or incomplete. Allen (1940) noted that *C. denudata* was always found at great depth, which no doubt is partly the cause of its "undeveloped" character. Collected in Sucuné Bay at a depth of 11.80 m and at Taman at 1.50 m depth in Peru. Tutin (1940) considered that the Characean community was composed of thick swards of *C. papillosa* and *C. denudata*, the two species alternating in distinct patches and thus dominating locally. There would not seem to be a clear predominance of either species.

9. Lamprothamnium succinctum A. Br. in Asch. (Pl. 2, Figs 4, 5, 6).

A species without cortication with stipulodes in a single irregular whorl underneath each branchlet. Male and female gametangia at the nodes and at the base of the branchlets. Antheridium above or at the side of the oogonium.

This tropical species, previously unknown from the American continent, was collected by Lauzanne (8.12.1976) in a part of the lake with a high concentration of dissolved salts.

10. Nitella clavata Kütz. (Pl. 2, Figs 7 to 10).

A species with acute single-celled end segments (terminal cells of the branchlets). The branchlets are arranged in two rows at the axial nodes, the upper ones branching alternating with simple lower ones. Allen (1940) recorded that specimens were all found in the lake and in canals in the north-west (Peru): in the higher part of Capachica channel dried-out in winter, in Puno Bay (Griffin, 1968) and in the shallower part of the second canal in Puno Bay (Collot *et al.*, 1983).

Figure 9. Branchlet node with geminate oogonia.

Figure 10. Coronula of oogonium (after Wood and Imahori, 1964).

Tolypella nidifica (O.Müll.) A. Br.

Figure 8. Branchlet node with one antheridium.

Figure 11. Fertile branchlet composed of 5 segments. Basal node of the branchlet bearing 3 lateral multicellular branchlets (2 sterile and 1 fertile)

Figure 12. Fertile branchlet bearing 1 oogonium and 2 sterile lateral branchlets at the basal node (after Wood and Imahori, 1964).

11. *Tolypella nidific*a group (O.Müll.) A. Br. (Pl. 2, Figs 11 and 12). A small slender plant with the long, narrow apical cell on the branchlets bluntly rounded at the end and shorter than the penultimate segment.

Collected by Lauzanne at around ten metres' depth in water with a high conductivity (1200 μ S cm⁻¹)at 10–15°C (8.12.1976). Low temperature and great depth are unusual for *Tolypella* spp., an uncommon genus in Latin America.

Among the macrophytes, the Characeae, a family with few genera (six) and species (around 440) on a world scale, is the most abundant plant group in Lake Titicaca: a third of the bottom is colonised by *Chara* spp. They constitute a large part of the total biomass (more than 60% in Lago Huiñaimarca, 35% in Puno Bay). Their productivity is also highest: 60% of the production in Lago Huiñaimarca, 47% in Puno Bay (Collot *et al.*, 1983).

Finally, three rare species are found in Lake Titicaca: *Nitella clavata*, *Lamprothamnium succinctum* and the *Tolypella* sp., which deserves more detailed study.

VI.2c. Higher plants: Distribution and biomass

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The first observations on the aquatic vegetation were made by the Percy Sladen Trust expedition in 1937 (Tutin, 1940; Allen, 1940; Gilson, 1964). At that time, six phanerogams, one bryophyte and two charophytes were identified and grouped into four associations.

Several decades later, from 1978 to 1980, Collot (1980, 1982a, 1982b, 1983) described the state of the aquatic vegetation as it was then. The main results of his study form the basis of this chapter. Extensive beds of aquatic vegetation occur in Ramis, Huancané and Achacachi bays and especially in Puno Bay and in Lago Pequeño; distribution maps have been drawn for these last two areas and estimates of the standing crop biomass have been made.

Occasional observations carried out in recent years have provided information on temporal changes in the plant populations following recent variations in lake level.

Distribution of the species

The areas occupied in these two areas of the lake by the most important species were estimated from observations made on a large number of transects (Table 1). In Lago Pequeño nearly a third of the bottom was colonised by *Chara* spp. The genus *Potamogeton* was well represented, occupying 23% of the bottom. In Puno Bay, *Potamogeton* covered nearly 50% of the bottom and *Myriophyllum* and *Schoenoplectus* 38 to 39% (Fig. 1). Six plant associations were defined, occurring at different water depths and distances from the shoreline:

Littoral Lilaeopsis + *Hydrocotyle community* (0–0.2 metres)

A small species of Umbelliferae, *Lilaeopsis*, occurred in sheltered areas on gently sloping shorelines, on sandy and clayey substrates. Occurring together

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Species	Surfaces (km ²)	% of the surface with vegetation	% of water surface		
Elodea	222	29	16		
Myriophyllum	222	29	16		
Potamogeton	308	41	23		
Near the shore	172	23	13		
In depth	136	18	10		
Schoenoplectus	185	24	13		
Scarce	116	15	8		
Very abundant	69	9	5		
Chara	436	58	32		
Surface with					
vegetation	758	-	56		
Superficie without					
vegetation	607	-	44		
B. Puno bay	-				
Elodea	185	39	31		
Myriophyllum	227	48	38		
Potamogeton	281	59	47		
Near the shore	269	57	46		
In depth	12	2	1		
Schoenoplectus	238	50	39		
Scarce	69	14	13		
Very abundant	169	36	26		
Chara	196	41	33		
Nitella	2	0,5	0,3		
Surface with					
vegetation	476	-	79		
Surface without					
vegetation	126	-	21		

Table 1. Areas occupied by the main species (Collot et al., 1983).

with this species or alone over large areas along the shoreline was another Umbelliferae, Hydrocotyle. Ranunculus could be found sporadically within this zone. This community was absent where the shoreline was rocky or stony.



Figure 1. Vegetation distribution maps of Lago Huiñaimarca (A, B and C) and Puno Bay (D, E and F). (From Collot *et al.*, 1983).

$Myriophyllum + Elodea \ community \ (0.2-2.5 \ metres)$

This developed particularly in areas sheltered by *Schoenoplectus*. In Puno Bay, *Myriophyllum* occupied large areas from the shoreline as far as the inner edge of the totora stands, and in a less dense manner as far as the outer limits of this zone and in Chucuito Bay. In Lago Pequeño *Myriophyllum* also developed between the shoreline and the totoras and sometimes within the totora stands. The ideal depth for its growth would appear to be between 1 and 2 metres, but this species also colonises recently flooded shallower areas.

Elodea occurred as an understorey beneath the *Myriophyllum* and occupied almost the same areas in the Lago Pequeño and Puno Bay, although in the latter its distribution was more restricted near Chucuito. *Elodea* grew close to the bottom and only the flowers reached the surface on the end of a long fragile peduncle.

In addition to these two species, four other plants were frequently encountered: *Potamogeton*, *Zannichellia*, *Ruppia* and *Sciaromium*. The first occurred abundantly, in dispersed clumps among the *Myriophyllum* and *Elodea*, and only produced flowers where the depth was less than 1.5 metres, the reproduction being entirely vegetative beyond this depth. *Zannichellia* and *Ruppia*, two genera similar in appearance to *Potamogeton*, also occurred together with the latter or in isolated clumps. Finally, a moss of the genus Sciaromium was occasionally found in small quantities mixed in with the other plants; it was particularly abundant at the entrance to Puno Bay.

Schoenoplectus tatora community (2.5-4.5 metres)

This member of the Cyperaceae, known as "totora." occupied half of the area covered by macrophytes in Puno Bay and nearly 30% of that of Lago Pequeño. It is found in depths down to 5.5 metres, but is never very abundant beyond 3 metres. It commonly reaches 4 metres in height and examples of more than 6 metres in height have been recorded. It used to be particularly abundant in the north-west part of Puno Bay where the outer edge running from south-west to north-east was almost impenetrable. In Lago Pequeño totoras were particularly well developed along the eastern side, and were at their densest some way from the shore.

Depending on the density of totoras, two types of community were distinguished. Where they were close together (more than 50 stems per square metre), *Potamogeton* could develop thanks to its upright filiform leaves. A few *Elodea* plants and some tufts of *Sciaromium* were also present, but at low densities. When the totoras were less dense, Characeae formed a lower stratum. In areas where the totoras were heavily exploited, *Chara* took over and the totora regrowth was poor or even non-existent. In Puno Bay it was noted that very heavily exploited areas were colonised by *Chara*, which formed almost pure stands, even though the depth would have normally allowed other species to develop.

Pleustophyte community: Lemna + Azolla

These plants occurred in all three of the preceding communities and were found along the shorelines in well-sheltered areas, particularly in the port of Puno. They were also found in very dense stands of totora. In ideally sheltered conditions, they could form a stratified layer 0.5 to 1 cm thick. More frequently these species occurred in a single layer, sometimes mixed, sometimes alone.

Characeae community (4.50–7.50 metres)

Chara spp. occurred from the inner margin of the totoras, or even from the shoreline where the totoras were sparse or absent, or sometimes from the outer margin of the totoras, down to a maximum of 15 metres depth. The zone of maximum development was between 4.5 and 7.5 metres, where they covered immense areas on their own. The Characeae were therefore the most abundant community in Lake Titicaca. In Puno Bay they covered the



Figure 2. Diagram of the various plant associations in the littoral of Lake Titicaca (Collot et al., 1983).

areas where totora stands were absent. In Lago Pequeño they covered about 436 km^2 , or more than 60% of the area covered by vegetation.

Deep water Potamogeton community (7.5–9.5 metres)

In Puno Bay and in Lago Pequeño, there was usually a zone at a depth of 7.5 to 9.5 metres occupied by the same species of *Potamogeton* as close to the shore. This species was sometimes, as in the northern part of Lago Pequeño, associated with *Zannichellia*. *Potamogeton* never flowered at this depth and only reproduced vegetatively, whereas *Zannichellia* was found flowering and fruiting.

The succession of plant communities from the shoreline to the open water can be summarised in the form of a diagram (Fig. 2). If the shore had a gentle slope (grassland down to water's edge), it was colonised by *Lilaeopsis* or *Hydrocotyle*. If the site was particularly well sheltered, *Lemna* and *Azolla* also occurred. If the shoreline was rocky or more steeply shelving the first community was *Myriophyllum-Elodea*. As a general rule, this latter community occurred from the shoreline as far as the inner margin of the *Schoenoplectus tatora* belt at a depth of about 2.5 metres, with *Potamogeton*, *Ruppia*, *Zannichellia* and *Sciaromium* as accompanying plants. In the totora belt either *Chara* or *Potamogeton* occurred, depending on density of rushes. From the outer margin of the *Schoenoplectus*, *Chara* colonised the bottom down to depths of 7.5 metres and then if the gradient was slight *Potamogeton* occurred again sometimes together with *Zannichellia* down to a depth of 9 metres. Beyond this depth no vegetation was recorded.

Biomass

This was estimated by harvesting at regular intervals in the three vegetation zones representative of Lake Titicaca: the *Myriophyllum-Elodea* community, *Schoenoplectus* and *Chara*. The technique used was to harvest all the plants, roots included, present in a quadrat of known area (0.5 m^2) and then to determine the fresh weight (FW), dry weight (DW) ash weight (AW) and organic weight (OW).

Chara

These were measured as a whole, without distinguishing individual species. During the study period the dry weight per unit area could be considered as relatively constant $(1031 \pm 83 \text{ g DW m}^{-2})$ and the variability recorded was probably due to sampling variation.

Chara had a high proportion of ash due to the presence of calcium compounds and only contained 36.4% OW. Given that the area occupied by *Chara* was of the order of 436 km^2 in Lago Pequeño and 196 km^2 in Puno Bay, the approximate total biomass in each of these areas was therefore $450\ 000$ and $202\ 000$ tonnes DW, respectively (Table 2).

Myriophyllum-Elodea

The mean biomass of this association was estimated at $470 \pm 134 \text{ g DW m}^{-2}$, equally distributed among the two species. The total biomass of *Myriophyllum* was therefore about 52 200 tonnes DW in Lago Pequeño and 53 300 tonnes in Puno Bay; that of *Elodea* was practically identical in Lago Pequeño and 43 300 in Puno Bay.

Potamogeton, Azolla and Ruppia

These plants were dispersed in the various communities and the biomass per square metre was very variable.

Plants	Lago Menor	Puno bay
Chara	450 000	202 000
Schoenoplectus		
Very dense area	105 000	260 000
Light cover area	6 700	15 900
Total	131 700	275 900
Mvriophvllum	52 200	53 300
Elodea	52 200	43 300
Association	104 400	96 800
Potamogeton		
0.00 - 2.50	4 600	7 300
7.50 – 9.00 m	36 300	3 200
Total	40 900	10 500
Total	727 000	585 200

Table 2. Estimates of the dry weight biomass of plants in Lago Pequeño and in Puno Bay in tonnes (Collot et al., 1983).

Schoenoplectus

At the station studied, a mean value of $1522 \pm 636 \text{ g DW m}^{-2}$ with 165 ± 29 stems m⁻² was obtained as representative of areas of dense totoras. In less dense areas (25 ± 20 stems per square metre) the mean biomass was estimated at $230 \pm 96 \text{ g DW m}^{-2}$. On the basis of these figure the total biomass was estimated at about 131 700 tonnes DW in Lago Pequeño and 275 900 in Puno Bay.

The biomass of *Potamogeton* associated with totora was of the order of 27 g DW m^{-2} . When occurring on its own in certain of the deeper parts of Lago Pequeño the density was at least ten times higher, on average 267 g DW m^{-2} . The total biomass taking into account these differences in density and the area colonised was estimated at about 40 900 tonnes DW in the Lago Pequeño and 10 500 tonnes in Puno Bay.

As an indication, the biomasses of *Azolla* and *Ruppia* were 56 and 267 g DW m⁻² respectively when they occupied an area on their own; this was therefore the maximum value of biomass that these species could reach.

In conclusion, comparison of the overall biomasses in Lago Pequeño and Puno Bay demonstrated the important contribution of *Chara* to the total biomass: 62% in Lago Pequeño and 35% in Puno Bay, the area of bottom

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PLANTS	К	Na	Ca	Mg	SiO2	s	Р	с	N	Fe	Cu	Ma	Zn	В
Chara	0.76	0.28	25.67	0.70	0.83	0.42	0.10	21.3	0.84	925	7.0	32	10.0	210
Schoenoplectus	5.85	2.50	0.90	0.19	1.07	0.77	0.20	39.7	1.88	950	5.5	97	14.5	160
Myriophyllum	1.77	1.03	16.25	0.50	1.02	0.35	0.20	31.3	1.46	940	6.0	170	20.0	345
Elodea	3.15	0.71	15.40	0.48	2.94	0.71	0.20	29.5	1.53	3290	7.5	422	17.0	370
Potamogeton	5.20	0.81	2.80	0.33	0.54	1.11	0.20	40.5	1.83	350	3.5	62	10.0	1225
Ruppia	1.98	0.41	13.68	0.54	1.32	0.28	0.14	32.8	1.39	658	5.0	282	15.0	560

Table 3. Chemical composition of plants from Lake Titicaca; for the nine elements on the left in percentage of dry matter; for the five elements on the right, in p.p.m. dry matter (from Collot, 1980).

suitable for colonisation of *Chara* (between 4.5 and 7.5 metres) being less in the latter. The biomass of *Schoenoplectus* was greater in Puno Bay: 47% against 18% in Lago Pequeño. These two communities in both cases accounted for more than 80% of the total biomass. The *Myriophyllum-Elodea* community was in third position with approximately equal biomasses for each of the two species.

Potamogeton had a large distribution range, but its density being lower its proportion of the overall biomass was low (6% in Lago Pequeño and 2% in Puno Bay).

Storage and consumption of mineral salts

Samples of dried plants were analysed to measure the quantities of mineral salts contained in the vegetation (Table 3). These analyses demonstrated:

- the abundance of calcium in Chara (25.7% of DW). Myriophyllum, Elodea and Ruppia frequently also had high contents of this element since their leaves were encrusted with calcite.
- *Elodea* appeared to be the plant richest in other mineral elements (silica, phosphorus, iron, copper, manganese, zinc).
- in terms of their Na, K, Ca and Mg concentrations, three groups of plants could be distinguished: the first with very abundant calcium (*Chara*); the second with very abundant potassium (*Schoenoplectus* and *Potamogeton*) and the third with very abundant calcium and abundant potassium (*Myriophyllum*, *Elodea* and *Ruppia*).
- the relative proportions of cations in the plants were different from those in the water; the ranking was generally as follows: K > Ca > Mg > Na except for *Schoenoplectus* where the ranking was slightly different (inversion of Na and Mg).

From the results of the analyses and the overall biomass estimated for each plant, the quantities of mineral salts stored in the macrophytes in Lago Pequeño and Puno Bay were estimated. It appeared that calcium was the element stored in the greatest quantity (more than 200 000 tonnes for the

						LAGO	MENOR							
PLANTS	c	N	P	s	Ca	Na	К	Mg	SiO ₂	Fe	Cu	Mn	Zu	В
Chara	95 850	3 780	450	1 890	115 515	1 260	3 420	3 150	3 735	416	3	14	42	95
Schoenoplectus	52 285	2 476	263	1 015	1 185	3 293	7 705	251	1 410	125	1	13	2	21
Myriophyllum	16 339	762	104	183	8 483	538	924	261	532	49	0.3	9	1	18
Elodea	15 399	799	104	371	6 995	371	1 644	251	1 535	172	0.1	22	1	19
Potamogeton	16 765	748	82	454	1 145	331	2 127	135	221	15	0.1	2	0.4	50
Total	196 638	8 565	1 003	3 913	133 325	5 793	15 820	4 048	7 433	777	4.5	60	46.4	203
						PUNO	BAY							
Chara	43 026	1 697	202	848	51 853	566	1 535	1 414	1 677	187	1	6	2	42
Schoenoplectus	109 532	5 187	552	2 124	2 483	6 898	16 140	524	2 952	262	1	27	4	45
Myriophyllum	16 683	778	107	187	8 661	549	943	267	544	50	0.3	9	1	20
Elodea	12 833	666	87	309	5 829	309	1 370	209	1 279	143	0.3	18	1	53
Potamogeton	4 253	193	21	117	294	85	546	35	56	4	0.0	1	0.1	13
Total	186 327	8 521	969	3 585	69 120	8 407	20 534	2 449	6 508	646	2.6	61	8.1	175
Daily uptake :								ł						[
Lago Menor	2 4 4 1	109	12	55	1651	48	197	52	118	13	0.1	1	0.1	4
Puno bay	1 743	80	10	40	883	38	167	30	85	9	0.0	1	0.1	4

Table 4. Daily storage and consumption of various mineral elements by macrophytes in Lake Titicaca (Lago Pequeño and Puno Bay), expressed in tonnes (from Collot, 1980).

whole of Lago Huiñaimarca and Puno Bay). Next came potassium with more than 35 000 tonnes, sodium and silica with about 14 000 tonnes and sulphur and magnesium with about 7000 tonnes (Table 4).

By using an estimate of the production of plant matter by each species, Collot (1980) made an approximate evaluation of the daily consumption of mineral salts (Table 4). As an example, the daily requirement in Lago Pequeño and Puno Bay was of the order of 2500 tonnes for calcium, 360 tonnes for potassium, 200 tonnes for silica and 80 tonnes for sodium and magnesium.

Changes in the plant populations between 1986 and 1989

Between 1983 and 1986, the mean level of Lake Titicaca rose by about 3.50 metres and nearly 85 000 hectares were thus flooded. After this period the level once more fell. It therefore seemed interesting to examine the effects of these changes on the behaviour and development of the various plant forms. Observations made in 1986 (maximum water level) and in 1989 (falling water level) underline the multiplicity of responses by the various plant communities studied (Table 5).

- The Myriophyllum-Elodea community developed a opportunistic strategy,

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s	ITUATIO	ON IN THE	E LAGO	MENOR		SITUATI IN THE LAGO GR	ON ANDE	
Year 1980		Ycar 1986		Year 1989		Year 1989		
Alt. 3808.	50 m	Alt. 3810.75	5 m	Alt. 3809.75	m	Alt. 3809.75	m	
Hydrocotyl	c 0.2 m	Hydrocotyle	0.2 m	Hydrocotyle	0.2 m	Hydrocotyle	0.2 m	
Elodea	2.5 m	Elodca	2.5 m	Elodea	0.9 m	Elodea	1.3 m	
Totoras	4.5 m	Totoras	4.5 m	Totoras	2.0 m	Totoras	2.5 m	
				Elodea	3.5 m	Elodea	5.75 m	
Chara	7.5 m	Chara	7.5 m	Chara	7.5 m	Chara	14.5 m	
Potamoget	on 9 m	?		?			?	
Bryophytes		Bryophyt	cs	Bryophytes		Bryophytes		
?			?		12 m		30 m	
	•••••	••••••	•••••	••••••		•••••	•••••	
		LIMITI	E OF F	IXED VEGET	ATION			
						_		

Table 5. Changes in plant populations during the rise and subsequent fall in water level between 1980 and 1989. Depth ranges of the main species.

very quickly colonising the newly flooded areas or those left vacant by other species, in particular the totoras.

- In 1986 the Schoenoplectus tatora community occupied water depths of from 2.5 to 4.5 metres, corresponding to its preferred range. In 1989, the totora stands were in 0.8 to 2.5 metres depth. It appeared that these were the same plants as in 1986 which had resisted the drop in water level and therefore found themselves in an abnormal position compared to their preferred range. In some areas (near Huatajata and Achacachi), they were even found in less than 40 cm of water, but this situation was a reflection of human activity rather than of natural change, as the peasants carried out transplantation of young shoots in this area.
- With the great rise in water level, the *Chara* community did not persist beyond 7.5 metres depth in Lago Pequeño. In April 1986, at the maximum water level, large areas populated with *Chara* were seen to start decomposing, a phenomenon which reached its maximum intensity at the end of the year. In the Lago Grande in contrast, it seems that the deep water macrophyte beds persisted in 1986. The lower water turbidity and therefore better light penetration in this part of the lake certainly explain this difference between the two basins.
- The deep water *Potamogeton* community seems to have completely disappeared at present and we have been unable to find any trace. Collot (1980)

had even suggested that during a rise in water level, this vegetation stand could disappear.

The diagram of the macrophyte distribution drawn up by Collot (1980) and Collot *et al.* (1983) and reproduced here (Figs 1 to 3), therefore only gives a picture of the situation occurring during a period of water level stability. It does not take into account the natural changes that the plant populations undergo under the influence of interannual variations in the physico-chemical conditions of the water body. Increases in water salinity can for example play the role of a limiting factor, as was the case during the severe drought in 1943, which probably favoured the growth of species such as *Ruppia*. Conversely, the rapid rise in water level led to heavy plant mortality, especially in Lago Huiñaimarca where plants were living at their lower depth limit. This mortality, followed by decomposition, itself led to more or less severe local anoxia with repercussions on the survival of benthic organisms.

Conclusions

The aquatic macrophyte communities of Lake Titicaca are typified by their density and extent; they occupy all the shallow water areas, that is most of Lago Pequeño and the shallow bays of the Lago Grande. In contrast, the number of species present is rather low when the extent of the area of vegetation is considered. This relative poverty is perhaps related to the frequent changes in lake level, both on the seasonal (during normal periods the annual range is about 0.70 m) and on a long-term scale; these latter variations in certain periods being much greater (more than 3 metres between 1983 and 1986). Because of this, the relative areas covered by the various plant associations change, the communities colonising new areas depending on the preferences of the dominant species, the light available for growth at first sight seeming to be the main factor involved in this dynamic situation. Certain associations can even disappear completely when the water depth becomes too great and limits penetration of solar radiation. Human activities, whether they be massive harvesting of certain useful species or their transplantation to maintain sufficient production, also intervene and modify the natural equilibrium of the existing populations.

The production is in any case extremely high. According to the estimates made by Collot *et al.* (1983) between 1978 and 1980 using the method of successive harvesting, *Chara* has a mean production of the order of $11.6 \text{ g DW m}^{-2} \text{ day}^{-1}$, which at that period represented about 5000 tonnes of dry matter in Lago Pequeño and 2200 in Puno Bay. The production of totoras varied between 0.2 and $1.5 \text{ g DW m}^{-2} \text{ day}^{-1}$, depending on their density, from which the total daily production was estimated at 120 tonnes in Lago Pequeño and 265 in Puno Bay. The *Myriophyllum-Elodea* community with production values of 0.8 and 10 g DW m⁻² day⁻¹ repectively

had total a production of 175 tonnes for the first species and 2200 tonnes for the second in Lago Pequeño and 180 and 1850 tonnes in Puno Bay. Finally, for *Potamogeton*, with 5 g DW m⁻² day⁻¹, the total daily dry weight production was 770 tonnes in Lago Huiñaimarca and 200 tonnes in Puno Bay.

Even though the author of these estimates considered that, because of the method used, they were probably overestimates, these approximations demonstrate the high plant production of this ecosystem. It can therefore be concluded that the ecological conditions controlling the vegetation in Lake Titicaca are not particularly unfavourable, despite the low temperatures and the oxygen deficit due to the high altitude.

Finally, mention should be of the importance of *Chara* spp. in the lacustrine ecosystems in the Titicaca basin: this is the most abundant genus in terms of biomass in the lake itself and also very clearly the most productive; they invade for example all the areas left clear by totora exploitation. They form the marginal vegetation in many lakes situated at higher altitudes in the Cordillera. They are capable of adapting to fairly high salinities and carpet vast areas on the bottom of Lake Poopo, which receives the overflow from Lake Titicaca and where the salinity is currently 10 to 12 g l⁻¹.

References of chapter VI.2

- ACLETO OSORIO (C.), ZUÑIGA (R.), MONTOYA (H.), MORON (S.), SAMAMEZ (I.), TAVARA (C.), 1978. Algas continentales del Perú. 1. Bibliografía y lista de géneros y especies. Univ. Nac. Mayor S. Marcos, Museo Hist. Nat. "Javier Prado." depart. Bot., Lima, ser. divulgación 9: 53-54.
- ALLEN (G.O.), 1938. The Charophyte collecting tours of Thomas Bates Blow. Jour. Bot., 76: 295–298.
- ALLEN (G.O.), 1940. 9. Charophyta. In: The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1(2): 155–160.
- ASPLUND (E.), 1926. Contribution to the flora of the Bolivian Andes. I. Pteridophyta. Gymnospermae. Helobiae. Ark Bot., 20 A (7): 1-38.
- BOULANGE (B.), AQUIZE JAEN (E.), 1981. Morphologie, hydrographie et climatologie du lac Titicaca et de son bassin versant. *Rev. Hydrobiol. trop.*, 14 (4): 269–287.
- BRAUN (A.), 1882. Fragmente einer Monographie der Characeen. Nach den hinterlassen Manuscripten A. Braun's, herausgegeben von Dr O. Nordstedt. Abh. Kön. Ak. Wiss. Berlin aus dem J: 211 p.
- COLLOT (D.), 1980. Les macrophytes de quelques lacs andins (lac Titicaca, lac Poopo, lacs des vallées d'Hichu Kkota et d'Ovejhuyo). ORSTOM, La Paz: 115 p., multigr.
- COLLOT (D.), 1982 a. Vegetación acuática del lago Poopó. Rev. Inst. Ecol., La Paz, 1: 47– 55.
- COLLOT (D.), 1982 b. Mapa de vegetación de la Bahía de Puno. Rev. Inst. Ecol., La Paz, 2: 49-65.
- COLLOT (D.), KORIYAMA (F.), GARCIA (E.), 1983. Répartitions, biomasses et productions des macrophytes du lac Titicaca. *Rev. Hydrobiol. trop.*, 16 (3): 241–261.
- COOK (C.D.K.), 1966. A monographic study of *Ranunculus* subgen. *Batrachium* (DC.) A. Gray, *Mitt. Bot. Staatssamml. München*, 6: 47–237.
- COOK (C.D.K.), GUT (B.J.), RIX (E.M.), SCHNELLER (J.), SEITZ (M.), 1974. Water plants of the world. Junk, The Hague: 561 p.
- CORILLION (R.), 1975. Flore des Charophytes (Characées) du Massif armoricain et des contrées voisines d'Europe occidentale. *In* : Flore et végétation du massif armoricain. Jouve. Paris, 4: 214 p.
- FOSTER (R.C.), 1958. A catalogue of the ferns and flowering plants of Bolivia. Contr. Gray Herb., Harv., 184: 223 p.
- GILSON (H.C.), 1939. 1. Description of the expedition. In: The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1: 1–20.
- GILSON (H.C.), 1964. Lake Titicaca. Verh. Internat. Verein. Limnol., 15: 112-127.
- GRIFFIN (D.), 1988. Sumario de nuestro conocimiento de las *Charophyta* del Perú. Publ. Museo Hist. Nat. "Javier Prado." Univ. Nac. Mayor S. Marcos, ser. B, Bot., Lima, 22: 1– 32.
- GUERLESQUIN (M.), 1981. Contribution à la connaissance des Characées d'Amérique du Sud (Bolivie, Equateur, Guyane française). *Rev. Hydrobiol. trop.*, 14 (4): 381-404.
- HILL (A.W.), 1927. Lilaeopsis (Umbelliferae). J. Linn. Soc., London, Bot., 47: 525-551.
- HORN af RANTZIEN (H.), 1950. Charophyta reported from Latin America. Arkiv Bot., 1 (8): 355-411.
- LANDOLT (E.), 1986. Biosystematic investigations in the family of duckweeds (Lemnaceae),
 2. Veroff. Geobot. Inst. ETH Stiftung Rübel, Zürich, 71, 566 p.
- OSTRIA (C.), 1987. Phytoécologie et paléoécologie de la vallée alto-andine de Hichu Kkota (Cordillère orientale, Bolivie). Thèse Univ. Paris 6, 180 p.
- SHELDON (R.B.), BOYLEN (C.W.), 1978. An underwater survey for estimating submerged macrophyte population density and biomass. *Aquatic Botany*, 4: 65–72.
- TUTIN (M.A.), 1940. 10. The macrophytic vegetation of the Lake Titicaca. In : The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, Bot., ser. 3, 1 (2): 161–189.
- WOOD (R.D.), IMAHORI (K.), 1964–1965. A revision of the Characeae. 1: Monograph, 1965, 904 p.; 2: Iconograph, 1964, 394 pl.; Cramer, Weinheim.

VI.3. ZOOPLANKTON VI.3a. The Cladocera

JEANNE REY

Data currently available of the Cladocera population of Lake Titicaca have been provided by the works of Moniez (1889), Brehm (1936, 1957), Harding (1955), Ueno (1967) and more recently by Valdivia-Villar (1988).

Analysis of 14 samples collected in 1985–1986 in the Bolivian part of the lake (3 stations located in Lago Grande: Nos. 39, 40 and 44, and 9 in Lago Huiñaimarca: Nos. 9, 10, 16, 17, 18, 19, 23, 24 and 27 cf. Chapter VI.1.c, Fig. 3) provide additional information on the Cladocera fauna of this habitat.

Faunistic and taxonomic aspects

The list of species recorded in Lake Titicaca up to the present includes 31 taxa (Table 1). This list combines data in the literature and those resulting from this study.

Taxonomic remarks on the species recorded during this study

Bosmina huaronensis (Delachaux) (Figs 1 and 2). Species present in all the samples analysed.

Material: parthenogenetic non-ovigerous and ovigerous females; 280 to 450 μ m.

Described from Lake Huaron (Peruvian Andes) by Delachaux (1918) as a new variety of *Bosmina longispina*, this taxon was recently elevated to the rank of species by Paggi (1979). Recorded in Titicaca by Harding (1955) under the name of *Bosmina coregoni obtusirostris* and Ueno (1967) as *B*. cf. *hagmanni* (synonymy established in Paggi *op.cit.*), *B. huaronensis* was recently mentioned again from this locality by Valdivia-Villar (1988).

Abundant and recorded regularly in all the samples analysed, this species forms one of the components of the pelagic Cladocera community in Lake Titicaca. All the individuals examined possess the specific characters rede-

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Table 1.	List	of Cla	locera	species	recorded	l from	Lake	Titicaca	to the	presei	nt day.	(1): Mo	niez
(1889);	(2): 1	Brehm	(1936)	; (3):	Harding	(1955)	; (4):	Brehm	(1957)	; (5):	Ueno	(1967);	(6):
Valdivia	-Villa	ar (1988	3); (7):	this st	udy.								

BOSMINIDAE	
Bosmina huaronensis (Delachaux, 1918) (3) (5) (6) (7)	CHYDORINAE
DAPHNIIOAE <u>Ceriodaphnia quadrangula</u> O.F. Müller, 1785 (1) a (7) <u>Ceriodaphnia dubia</u> Richard, 1894 (7) <u>Daphnia pulex</u> Leydig, 1860 (3) (5) (6) (7) <u>Daphnia peruviana</u> Harding, 1955 (6) <u>Simocephalus vetulus</u> O.F. Müller, 1776 (1) (2) (3) (4) (6) <u>Scapholeberis spinifera</u> (Nicolet, 1849) (6)	Pleuroxus aduncus Jurine, 1820 (3) (4) (6) (7) Pleuroxus trigoneilus (0.F. Müller, 1785) (6) Pseudochydorus globosus (8 aird, 1850) (7) <u>Dunhevedia crassa</u> King, 1853 (7) <u>Dunhevedia odontoplax</u> Sars, 1901 (6) <u>Ephemeroporus acanthodes</u> Frey, 1982 (3 7) (7) <u>Ephemeroporus poppei</u> (Richard, 1897) (6) <u>Chydorus sphaericus</u> 0.f. Müller, 1776 (1) (3) (6)
MACROTHRICIDAE <u>Echinisca palearis</u> (Harding, 1955) (3) (4) (6) <u>Macrothrix montana</u> Birge, 1904 (6) <u>Macrothrix hirsuticornis</u> Norman et Brady, 1B67 (6)	<u>Chydorus eurynotus</u> Sars, 1901 (3) (7) <u>Chydorus brevilabris</u> Frey, 1980 (7) ALONINAE <u>Leydigia ciliata</u> (Gauthier, 1939) (3) (6) <u>Alonopsis titi</u> Harding, 1955 (6)
CHYDORIDAE CHYDORINAE <u>Alonella nana</u> (Baird, 1843) (4) <u>Pleuroxus caca</u> Harding, 1955 (6) <u>Pleuroxus piger</u> (Sars, 1862) (4) <u>Pleuroxus similis</u> Yavra, 1900 (7)	<u>Camptocercus aioniceps</u> Ekman, 1900 (/) <u>Alona poppei</u> Richard, 1897 (6) <u>Alona diaphana</u> King, 1853 (3) (4) (7) <u>Alona cambouei</u> Guerne et Richard, 1893 (3) (4) (6) (7) <u>Alona</u> cf. <u>fasciculata</u> Daday, 1905 (6)

fined by Paggi (1979), in particular the rostrum and antennule forming an almost continuous arc, the median frontal cephalic pore situated between the rostral bristles, and the smooth mucrons without any trace of indentation.

A species endemic to South America, the distribution range of *B. huaronensis* covers Argentina and extends as far as Peru.

Ceriodaphnia dubia Richard (Fig. 6). Species present in all the samples analysed.

Material: parthenogenetic non-ovigerous and ovigerous females; 450 to $675 \ \mu m$.

The identity of *C. dubia* Richard 1894 and of *Ceriodaphnia affinis* Lilljeborg 1900, both characterised by the presence of a comb on the postabdominal claw with teeth that are longer and and more robust than the rest of the bristles, is generally accepted by authors.

C. dubia has been recorded in all samples, together with *Ceriodaphnia quadrangula* (Fig. 7 and 8) from which it differs mainly by the proximal comb, absent on the terminal claw of *C. quadrangula*. This comb, which is more or less pronounced in the various populations of this cosmopolitan species (cf. Harding, 1955), has also been shown to be variable within the Lake Titicaca population. *C. dubia* was not recorded in Titicaca (Harding *op.cit.* mentioned the species from a region neighbouring the lake). It does, however, appear to be well installed in this habitat since numerous examples were regularly found in all the samples studied.

C. dubia, a species considered to be cosmopolitan, is known in South America (under various synonyms) from Patagonia (Ekman, 1900), Brazil



Plate 1. (Figs 1 to 13): Figs 1–2. *Bosmina huaronensis.* 1: parthenogenetic female; 2: frontal cephalic pore and rostral bristles. – Fig. 3 *Echinisca palearis*: parthenogenetic female. – Fig. 4. *Macrothrix montana*: head and cervical sinus. – Fig. 5. *Scapholeberis spinifera*: parthenogenetic female. – Fig. 6. *Ceriodaphnia dubia*: terminal postabdominal claw. – Figs 7–8. *Ceriodaphnia quadrangula*.7: parthenogenetic female; 8: postabdominal claw. – Fig. 9. *Simocephalus vetulus*: parthenogenetic female – Figs 10 to 12. *Daphnia pulex*. 10: parthenogenetic female; 11: abdominal process and postabdomer; 12: terminal claw. – Fig.13. *Daphnia peruviana*: head and rostrum. (Scales in mm).(Figs 3 and 13, after Harding, 1955; Fig. 4, after Pennak, 1989; Fig. 5, after Richard, 1897).

(Sars, 1901), Paraguay (Daday, 1905), Colombia (Stingelin, 1913), Peru (Delachaux, 1918; Harding, 1955), Guatemala (Brehm, 1939) and Bolivia (this study).

Daphnia pulex Leydig (Figs 10 to 12). Species present in all the samples analysed.

Material: Parthenogenetic non-ovigerous and ovigerous females; 600 to $1250 \,\mu\text{m}$ (length from the anterior border of the head to the base of the carapace spine).

Previously reported by Harding (1955) Ueno (1967) and Valdivia-Villar (1988) and regularly recorded in this study, *D. pulex*, together with *Bosmina huaronensis*, *Ceriodaphnia quadrangula* and *C. dubia*, form the pelagic Cladocera community of Lake Titicaca.

The characters of the head area of the individuals examined (head slightly raised, with rounded anterior border and concave ventral edge; optic vesicle, eye and ocellus well developed; A1 not inserted on a protuberance), of the carapace valves (absence of a row of bristles on the median area of the ventral internal edge of the valves) and of the postabdominal claw (proximal comb of 5 to 7 short fine teeth, median comb of 4 to 6 teeth increasing in size distally), comply with those of *D. pulex* in the sense of Scourfield (1942) and Brooks (1957). The only discordance concerns the abdominal processes which are clearly much shorter than in the typical form, an observation agreeing with that made by Ueno (1967: p. 552, Figs 4, 5 and 6) on populations from the same locality.

D. pulex, a Holarctic, Afro-tropical and Oriental species, had previously been recorded from South America in Argentina (Wierzejski, 1893) and Guatemala (Birge, 1908) (*in* Harding, 1955).

Pleuroxus similis Vavra (Fig. 17 to 21).

Material: parthenogenetic non-ovigerous and ovigerous females; 425 to $600 \,\mu m$ (St. 27).

Among the specimens of *Pleuroxus* examined, many individuals could be ascribed to *Pleuroxus similis* described from Chile by Vavra (1900) and redescribed and figured from Argentina by Sars (1901).

It is characterised by its short thick antennules, without a basal peg, the eye much larger than the ocellus and a relatively long and narrow postabdomen, truncated distally and armed with numerous long marginal teeth. The only difference observed concerned the postero-ventral angle of the valves, which were spineless on the Titicaca individuals, whereas these had one or two teeth on the specimens studied by Sars and Vavra. This is, however, a character whose variability has been frequently recorded for other species of the genus and particularly by Harding (1955) for examples from Lake Titicaca.



Plate 2. (Figs 14 to 25). Fig. 14. *Pleuroxus caca:* parthenogenetic female. – Figs 15–16. *Pleuroxus piger.* 15: parthenogenetic female; 16: postabdomen. – Figs 17 to 21. *Pleuroxus similis.* 17: parthenogenetic female; 18: anterior head region; 19: posterior region of head shield; 20: postero-ventral angle, left valve inner face; 21: postabdomen. – Figs 22 to 25. *Pleuroxus aduncus.* 22: anterior head region; 23: posterior margin of head shield; 24: postero-ventral angle, right valve innner face; 25: postabdomen. (Scales in mm). (Figs 14 to 16, after Harding, 1955).

P. similis occurs in Australia, the Caucasus and the Tashkent area (in Smirnov, 1971). In South America, the species has been recorded from Chile (Vavra, 1900), Argentina (Sars, 1901), Colombia (Stingelin, 1913: var. *fuhrmanni*), Peru (Delachaux, 1918 var. *fuhrmanni*) and Bolivia (this study).

Pleuroxus aduncus Jurine (Figs 22 to 25).

Material: parthenogenetic non-ovigerous and ovigerous females; 350 to $500 \,\mu m$ (St. 27).

All the specimens identified in this work as *P. aduncus* have a characteristic peg at the base of the antennules, which are thin and elongated, almost reaching the end of the rostrum.

The short and distally rounded postabdomen is armed with marginal spines arranged in groups. The number of teeth at the postero-ventral angle of the valves varies from 1 to 2 according to the specimen, but also from one valve to another on the same individual. In addition to these typical individuals, various phenotypes intermediate between *P. aduncus* and *P. similis* (labrum more or less pointed and elongate, postabdomen more or less long and sinuate, marginal spines more or less numerous and developed) have been observed, perhaps representing interspecific hybridisation.

P. aduncus is considered as a cosmopolitan species and is known in South America from Patagonia (Ekman, 1900: *P. scopuliferus*; Daday, 1902: *P. scopulifer*), Peru (Delachaux, 1919: *P. inermis*; Harding, 1955) and Bolivia (this study).

Pseudochydorus globosus (Baird) (Figs 26 and 27)

Material: 1 parthenogenetic non-ovigerous female; 530 µm (St. 27).

The characteristics of the carapace of this single example, the setation of the valves, the characteristics of the head (long ventrally incurved rostrum, labrum without flattened anterior process) and of the postabdomen (long, narrow, of uniform width, armed with 25 marginal spines and short lateral bristles), are in no way special compared to the typical form.

P. globosus, a Holarctic species, known from the Afro-tropical, Indo-Malaysian and Australian regions (in Smirnov, 1971), is recorded for the first time in South America.

Dunhevedia crassa King (Fig. 28)

Material: 2 parthenogenetic non-ovigerous females; 425 and 450 µm (St. 27).

The individuals examined showed the labrum with a smooth anterior margin, without indentations, characteristic of D. crassa. This characteristic separates at a glance this species from the others in the genus, which is represented in South America mainly by the neotropical species D. odonto-plax



Plate 3. (Figs 26 to 39): Figs. 26–27. *Pseudochydorus globosus.* 26: parthenogenetic female; 27: Postabdomen. – Fig. 28. *Dunhevedia crassa*: parthenogenetic female. – Figs 29 to 32. *Ephemeroporus acanthodes.* 29: labrum; 30: postabdomen; 31: antero-ventral angle of left valve; 32: postero-ventral angle of right valve, inner face. – Figs 33 to 35. *Chydorus eurynotus.* 33: parthenogenetic female; 34: postabdomen; 35: terminal claw. – Figs 36 to 39. *Chydorus brevilabris.* 36: parthenogenetic female; 37: rostrum and labrum; 38: posterior region of head shield; 39: postero-ventral part of right valve inner face (Scales in mm).
D. crassa, a Holarctic species, has also been recorded from the Afrotropical, Indo-Malaysian and Australian regions and has recently been reported for the first time in South America (Venezuela: Rey and Vasquez, 1986). Its presence in the Bolivian Andes confirms the distribution of the species in the South American continent.

Ephemeroporus acanthodes Frey (Figs 29 to 32)

Material: 1 parthenogenetic non-ovigerous female; 365 µm (St. 19).

The anterior margin of the labrum with a single well-developed tooth, the postero-ventral angle of the carapace without indentations, the ventral bristles on the valves followed by spiniform bristles inserted submarginally, the 8 parallel incurving striations at the anterior margin of the valves with indistinct reticulations in between and the equally-sized postabdominal spines in the distal group, all ascribe this single specimen of Chydoridae to *Ephemeroporus acanthodes*, a genus and species created by Frey (1982) in a study of the members of the *barroisi* complex. The only difference between the Titicaca specimen and those studied by Frey is the size (365 μ m, compared to 200–340 μ m).

Recently *E. acanthodes* has been reported from various Peruvian lagoons in the Puno area (Valdivia-Villar, 1988). The specimens of *Chydorus poppei* studied and figured by Harding (1955: p. 351, Fig. 99), coming from various sites in the Titicaca region, apparently belong to this taxon.

E. acanthodes, which has a distribution ranging from Louisiana, Texas, Oklahoma, California, Cuba and Guatemala (Frey, 1982), is therefore now known from South America: Peru (Valdivia-Villar, 1988; Harding, 1955), Bolivia (this study).

Chydorus eurynotus Sars (Figs 33-35)

Material: parthenogenetic non-ovigerous and ovigerous females; 430 to $595 \,\mu\text{m}$.

Recorded by Harding (1955) from the littoral waters of Titicaca, C. eurynotus was rediscovered in 3 samples from station 27.

The relatively enlarged distal postabdomen of the individuals examined, the presence of a double emargination on the ventral edge of the valves along the distal fold and its continuation as a narrow band parallel to the free posterior margin of the valves, ascribe these individuals to the subspecies *strictomarginatus* defined by Paggi (1972). They differ however by the lower number of teeth on the terminal claw (6 to 8 teeth instead of the 9 to 11 generally present in this subspecies).

C. eurynotus is a species widely distributed in the Afro-tropical, Indo-Malaysian and Australian regions. In South America it is known from Bolivia, Brazil, Colombia, Guatemala, Paraguay, Peru, Uruguay and Venezuela (cf. Paggi, 1972).

Chydorus brevilabris Frey (Figs 36 to 39).

Material: parthenogenetic non-ovigerous and ovigerous females; 300 to $400 \,\mu m$ (St. 27).

In these individuals the characters of the head shield (broad and terminated by a rather short emarginated rostrum, the post-pore distance slightly greater than the inter-pore distance), of the labrum (relatively short with a blunt apex), of the ocellus (nearly as large as the eye) and of the carapace reticulation (reaching the ventral and postero-ventral margins of the valves), have led us to ascribe these individuals to *Chydorus brevilabris*, described by Frey (1980) from Montana.

C. brevilabris had not been mentioned in the South American Cladocera fauna. However, as this taxon is morphologically very close to *Chydorus sphaericus* (cf Frey op. cit.), it is possible that *C. brevirostris* was formerly attributed to this species.

Distribution: Montana, Guatemala, Philippines, Congo (in Frey, 1980), Bolivia (this study).

Camptocercus aloniceps Ekman (Figs 44 and 45).

Material: parthenogenetic non-ovigerous and ovigerous females; 500 to $815 \,\mu m$ (St. 27).

The oval, very laterally compressed body form, the spineless posteroventral angle of the valves, the head without a keel, the rounded apex of the labrum, the long postabdomen armed with marginal spines and spinules, the narrow terminal claw with a basal spine and a row of bristles decreasing in length distally, all comply with the original description and figures of Ueno (1967).

C. aloniceps is known from South Africa where it was reported by Brady (1913) and from South America: Patagonia, where it was first described (Ekman, 1900), Peru (Delachaux, 1918: C. naticochensis), Bolivia (Ueno, 1967; this study).

Alona diaphana King (Figs 46 and 47).

Material: parthenogenetic non-ovigerous females; 400 to 475 µm (St. 27).

A. diaphana had been previously recorded from water bodies neighbouring Lake Titicaca by Brehm (1936) and Harding (1955). The taxonomic status of these species, which has frequently been considered as a synonym of *Alona davidi* Richard 1895 and *Alona punctata* Daday 1898, is still being questioned.

The general body form of the Lake Titicaca specimens, the characters of



Plate 4. (Figs 40 to 49): Figs 40–41. Leydigia ciliata. 40: parthenogenetic female; 41: postabdomen. – Figs 42–43. Alonopsis titi. 42: parthenogenetic female; 43: postabdomen. – Figs 44–45. Camptocercus aloniceps. 44: parthenogenetic female; 45: postabdomen. – Figs 46–47. Alona diaphana. 46: parthenogenetic female; 47: postabdomen. – Figs 48–49. Alona cambouei. 48: parthenogenetic female; 49: postabdomen. (Scales in mm). (Figs 40 to 43, after Harding, 1955).

the rostrum, labrum and carapace are in no way special. The postabdomen on the other hand appears shorter and broader than is usually figured (cf. for example the Argentine individuals figured by Sars (1901: Pl.X, Figs 3 and 3a). The terminal claw bears a group of 2 spinules beyond the basal spine, as observed by Harding (1955).

In South America A. diaphana has been recorded from Argentina (Sars, 1901; Biraben, 1939: Alonella diaphana), Paraguay (Daday, 1905: Alonella punctata), the Lake Titicaca basin (Brehm, 1957; Harding, 1955; this study).

Alona cambouei Guerne and Richard (Figs 48 and 49).

Material: parthenogenetic non-ovigerous and ovigerous females; 300 to $450 \,\mu\text{m}$ (St. 27).

Widely distributed in tropical and subtropical areas of the world, A. *cambouei* has been recorded from the Lake Titicaca basin in many previous works.

The variability of the more or less abrupt dorso-distal angle of the postabdomen was also underlined by Harding (1955). The number of lateral bristle bundles is also variable and can be as high as 10 groups of bristles.

A. cambouei is known in South America from Chile (Richard, 1897), Argentina (Richard, 1897), Patagonia (Ekman, 1900) Paraguay (Daday, 1905), Peru (Delachaux, 1918; Harding, 1955; Brehm, 1957; Valdivia-Villar, 1988) and Bolivia (Ueno, 1967; this study).

Conclusions

From a faunistic point of view, of the 14 species of Cladocera identified in this study, 8 species belong to taxa not previously recorded in the plankton of Lake Titicaca, and two (*Chydorus brevilabris*, *Pseudochydorus globosus*) had not previously been recorded on the South American continent. When added to data from the literature, these observations bring the total number of species currently known in this locality to 31.

As a far as the structure of the population is concerned, the planktonic Cladocera community uniformly consists of the association of *Bosmina huaronensis*, *Daphnia pulex*, *Ceriodaphnia quadrangula* and *Ceriodaphnia dubia*. This population is found both in Lago Grande and Lago Pequeño, with the exception of station 27 in the latter, where the population is relatively diversified and where in addition to the pelagic community mentioned above, numerous species of Chydoridae were also found.

From the biogeographical point of view, the Cladocera fauna of Lake Titicaca would appear to be a mixture of roughly equal proportions of temperate or very widely distributed species and of species distributed in the tropical and subtropical regions of the world (in total about 70 % of the population). The rest of the population is represented by species only occur-

ring on the American continent (Macrothrix montana and Ephemeroporus acanthodes) among which are 8 species endemic to South America (Daphnia peruviana, Scapholeberis spinifera, Bosmina huaronensis, Echinisca palearis, Pleuroxus caca, Alonopsis titi, Alona cf. fasciculata, Camptocercus aloniceps).

Key to the Cladocera species recorded to the present day from Lake Titicaca

1.	Dorsal branch of the antennae with 4 segments, ventral branch with 3
	segments
	Dorsal and ventral branches with 3 segments
2.	Antennules large, prolonging the rostrum in a sort of proboscis. Fornix
	(lateral fold of the head carapace) not connected to the rostrum. Dorsal
	margin of the head and the antennules forming an almost continuous
	arc Bosmina huaronensis (Fig.1)
	Antennules small. Fornix connected to rostrum, forming a sort of beak
	more or less covering the antennules Chydoridae 11
	3. Antennules long, moveable, inserted on the antero-ventral part of the
	head Macrothricidae 4
	Antennules short, not moveable, not inserted onto the antero-ventral part
	of the head Daphniidae 6
4.	Antennules slender. Ventral margin of head and labrum forming a sort
	of double chin
	Antennules more or less enlarged distally Macrothrix 5
5.	Dorsal margin of carapace with folds at the level of the cervical
	sinus
	Dorsal margin of carapace without folds
6.	Ventral margin of the carapace straight, prolonged posteriorly by a
	mucron. Head and valve armed with rows of spines. Rostrum rounded
_	Ventral margin of carapace convex
7.	Head without rostrum Ceriodaphnia (Fig.7) 8
	Head with rostrum
8.	Postabdominal terminal claw with basal comb
	Ceriodaphnia dubia (Fig.6)
	lerminal claw without basal comb
0	Ceriodaphnia quadrangua (Fig.8)
9.	Rostrum and nead small. Carapace without posterior spine. Occilus
	Postrum more or less devialened. Used rother lerge Correspondence realized
	kus more or less developed. Head rainer large. Carapace prolonged
	by a more or less long posteriorspine
	10. Rostrum ciongated. Sensory nairs on antennules covered by ros-

	trum
	Rostrum short and blunt. Sensory hairs of antennules projecting beyond
	rostrum Daphnia peruviana (Fig.13)
11.	Posterior free margin of valves short. Terminal claw usually with 2 basal
	spines (sometimes 1). Exopodite of P4 with 7 bristles. 2 separate median
	cephalic pores and secondary lateral pores
	Posterior free margin of valves long. Terminal claw with one basal spine
	(sometimes minute or absent). Exopodite of P4 with six bristles. 2 or 3
	median cephalic pores and secondary lateral pores
	Aloninae 25
12.	Valves with bristles inserted over all the ventral margin
	Valves with bristles on the anterior half of the ventral margin, and on
	the internal face of the ventral margin in the posterior half
13.	Length of free margin of valves about 1/2 the maximum height.
	Rostrum short. Valves with longitudinal postero-ventral striae. Post-
	abdomen short. Pre-anal angle prominent. 0.20 to 0.30 mm
	Length of posterior free margin of valves about 1/3 of maximum height.
14	Rostrum snort
14.	Body sub-spherical
15	Coronace with characteristic strong ribbing
15.	(Fig 14)
	Carapace valves with broad antero-ventral striae. Postabdomen broad
	and short, narrowed distally, 7 to 8 marginal teeth with numerous spin-
	ules of decreasing size proximally
16.	Distal part of postabdomen truncated. 14 to 16 marginal teeth decreasing
	in size proximally Pleuroxus similis (Fig.21)
	Distal part of postabdomen rounded17
17.	Marginal teeth fine and small, distributed in groups
	Pleuroxus aduncus (Fig.25)
	Marginal teeth robust, uniformly distributed Pleuroxus trigonellus
18.	Postabdomen long and narrow Pseudochydorus globosus (Fig.27)
	Postabdomen more or less short
19.	Body spherical. Postero-ventral angle of valves with or without spines.
	Postabdomen more or less rectangular. Claw with 2 basal spines. Anal
	sinus half way between abdominal bristles and terminal
	claw
	Body oval. Postero-ventral angle of valves with one large tooth. Post-
	abdomen ovoid, very broad. Terminal claw with one basal spine. Anal
20	Antonior margin of labrum with one tooth or on independent
20.	Amenor margin of labrum with one tooth or an indentation

..... Dunhevedia odontoplax Anterior margin of labrum without tooth . Dunhevedia crassa (Fig.28) 21. Cephalic pores absent in adults. The proximal 2 to 3 anal teeth finer and longer than in distal group Ephemeroporus 22 Cephalic pores present in adults. Marginal teeth sub-equal or decreasing in size proximally Chydorus 23 22. Labrum smooth, without teeth or crenulations Ephemeroporus poppei Labrum with a tooth on the anterior 23. Labrum short, apex rounded. Terminal claw armed with short teeth at its base Chydorus eurynotus (Fig.35) Labrum longer. Terminal claw ciliated, without teeth. 24 24. Polygonal reticulation on valves not reaching the posterior or posteroventral margin. Labrum elongated, apex more or less pointed. Post-pore distance much greater than inter-pore distance....Chydorus sphaericus Polygonal reticulation on valves reaching the posterior or postero-lateral margin. Labrum relatively short, apex blunt. Post-pore distance only slightly greater than inter-pore distance.. Chydorus brevilabris (Fig. 37) 25. Lateral bristles on postabdomen very long. Post-anal region long, broadening distally. Marginal teeth very small. Terminal claw without basal spine or with a minute spine. Ocellus triangular and larger than eye. Labrum pubescent anteriorly Levdigia ciliata (Fig.40) 27. Postabdomen relatively long with dorsal and ventral margins almost parallel Alonopsis titi (Fig.42) Postabdomen very long and narrow, thinning distally Camptocercus aloniceps (Fig.44) 29. Large distal bristle in lateral bundles long, reaching beyond the dorsal margin of the postabdomen in its distal part Alona poppei Lateral bristle bundles short, not reaching beyond the dorsal margin of the postabdomen Alona diaphana (Fig.47) 30. Lateral bristle bundles well developed. Usually 10 or more marginal teeth Alona cambouei (Fig.49) Lateral bristle bundles short. Usually less than 10 marginal teeth Alona cf fasciculata

VI.3b. Zooplankton distribution in the Bolivian part of the lake

JULIO PINTO

The first studies on the lake's zooplankton were carried out by researchers working on material collected by visiting expeditions. In 1939, De Beauchamp thus identified six taxa of Rotifera and in 1955 Harding produced a study of the Cladocera and Copepoda, based on samples collected by the Percy Sladen Expedition in 1937.

Later, Kiefer (1957) carried out a more detailed revision of the Copepoda, with a description of new subspecies, and in 1967 Ueno produced a general work on the zooplankton of the Bolivian part of Lago Huiñaimarca, taking into account the Copepoda, Cladocera and Rotifera. The taxonomic characters and geographical distribution of some species were described. Richerson *et al.* (1977) for the first time in a study of Lago Grande dealt with the biomass aspect of both the zooplankton and phytoplankton and determined the quantitative seasonal variations of some species. Pawley (1982, 1983) analysed the distribution of the zooplankton in Lago Grande in relation to nutrient concentrations. Moreno (1983) carried out a quantitative study of the animal plankton in the pelagic zone of Lago Grande and measured the abundance of microcrustacea and Rotifera on a transect carried out across Puno bay.

Haney and Trout (1985) carried out *in situ* and laboratory experiments on the feeding habits of Copepoda and Cladocera using selected seston particles and *Chlorella* labelled with Carbon 14.

In 1987 and 1988, Repelin *et al.* measured the spatio-temporal abundance of Copepoda, Cladocera and nauplius larvae in the Bolivian part of the lake, produced distribution maps for both Lago Grande and Lago Pequeño and analysed the diel vertical migration of some groups in Lago Pegueño (Huiñaimarca).

Population composition

The cladoceran fauna has already been described in the previous paper so only the Copepoda and Rotifera species currently known from the lake are given below.

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Figure 1. Some Copepoda occurring in Lake Titicaca: A) Boeckella titicacae. B) Boeckella occidentalis. C) Metacyclops leptopus.

COPEPODA (Fig.1)

- Calanoida
 Boeckellidae
 Boeckella titicacae Harding
 Boeckella occidentalis Marsh
- Cyclopoida
 Cyclopidae
 Eucyclops neumani (Pesta)
 Metacyclops leptopus Kiefer
 Tropocyclops prasinus meridionalis Kiefer
 Mesocyclops annulatus (Wierzejski)
 Microcyclops anceps (Richard)

ROTIFERA (Fig. 2)

 Ploima Brachionidae Brachionus angularis Gosse Keratella quadrata (Muller) Testudinellidae Filinia longiseta (Ehrenberg) Pompholyx sp. Asplanchnidae Asplanchna sp. Synchaetidae Polyarthra sp. Gastropidae Ascomorpha sp.



Figure 2. Some Rotifera occurring in Lake Titicaca: a) *Keratella quadrata*, b) *Asplanchna* sp., c) *Filinia longiseta*, d) *Pompholyx* sp., e) *Ascomorpha* sp., f) *Polyarthra* sp., g) *Brachionus* sp.

Spatio-temporal distribution of Copepoda and Cladocera

During the course of a study of the zooplankton of the Bolivian part of the lake carried out at the start of the 1980s (Fig. 3), the overall population of microcrustacea (Rotifera were not taken into account) observed in Lago Huiñaimarca consisted of 42% adult Copepoda, 31% nauplius larvae and only 27% Cladocera.

The distribution of these microcrustacea varied greatly with time: for example, the mean concentrations fluctuated between a minimum of 24 000 organisms m^{-3} in August 1981 to maximum values of around 58 000 organisms m^{-3} in March 1981 and more than 90 000 and 80 000 organisms m^{-3}



Figure 3. Map showing location of sampling stations.



Figure 4. Average temporal distribution of zooplankton in the Bolivian part of the lake; A. in Lago grande (1984–85); 1 = Plankton total; 2 = Copepoda; 3 = Cladocera; 4 = Nauplius; B. in Lago Huiñaimarca (1981–82).

in January and February 1982, respectively. The highest densities occurred during the summer rainy season (Fig. 4).

When considered separately, the Copepoda showed two periods of maximum abundance (March 1981 and January-February 1982) with densities varying from 24 000 and 30 000 individuals m^{-3} . The nauplius larvae and Cladocera showed similar types of quantitative variations, but the peak of abundance in 1981 was much less clearly marked (Fig. 4).

During a study carried out in the Lago Grande in 1984–85, Copepoda represented 63% of the population. Nauplius larvae at 31% made up the same proportion as in the Lago Pequeño in 1981–82, but Cladocera on the other hand only made up 6% of the total population of planktonic microcrustacea.

Although only four series of samples coming from the area of the lake have been studied in detail, it would appear that there was a significant



Figure 5. Zooplankton distribution in the Huiñaimarca; left: Copepoda (January 1982); right: Cladocera (January 1981). As in the following figure, the numbers in the different areas of the lake are Frontier (1974) indices of abundance.

variation in total zooplankton concentration with time, with a clear maximum in August 1984 (more than $66\,000$ org.m⁻³). The maximum tailed off at the end of the year after the winter period and reappeared the following year, although less distinctly (Fig. 4). This cycle mainly depends on variations in the density of adult Copepoda, the nauplius larvae and Cladocera having rather different fluctuations.

Moreno (1983), studied a transect running from Puno bay to the northeast shore of the lake over a whole year and demonstrated a maximum of total plankton in April, a transition period corresponding to autumn.

In terms of the spatial distribution of zooplankton in Lago Pequeño, Copepoda dominate on average over the year at station 19, situated to the north of the Taraco Peninsula (more than 39 000 ind.m⁻³). Their maximum concentration was recorded in the same region of the lake at station 17 (175 000 ind.m⁻³) in January 1982. At the same data minimum densities were observed off of Puerto Perez.

The highest mean abundance of Cladocera over the year also occurred to the north of the Taraco Peninsula (more than 19 000 ind.m⁻³), with a maximum density of nearly 69 000 ind.m⁻³ recorded in January 1981 at station 21 (Fig. 5). In the same month minimum densities were found between the islands of Paco and Cohani and off Puerto Perez, as in the case of Copepoda.

The highest mean annual concentrations of Copepoda over the period 1984–85 in the Lago Grande were found in the area between the Tiquina



Figure 6. Zooplankton distribution in Lago Grande: left: Copepoda (August 1984); right: Cladocera (December 1984).

Strait (Estrecho de Tiquina) and Sun Island (Isla del Sol). Here, the mean annual density was nearly 60 000 ind.m⁻³, with a maximum density of over 119 000 ind.m⁻³ at station 52 in August 1984. In contrast, the minimal densities at the same period were found off the mouth of the Río Suchez.

The much less abundant Cladocera had maximum values of mean annual density in the area situated to the west of Santiago de Huata, and near the Tiquina Strait. A maximum abundance of more than 17 000 ind.m⁻³ was recorded from station 35 in December 1984 (Fig. 6).

Relationship with the fish population

According to Leblond (1983), the populations of *Orestias ispi* have an influence on the distribution of the zooplankton population. This fish, which is mainly pelagic in Lake Titicaca, is very abundant and its diet is mainly composed of zooplankton. It feeds by day by actively hunting its prey. Examination of stomach contents shows that the most frequently captured prey are Cladocera, which have poorer powers of escape than Copepoda. In second place come female cyclopoids, whose powers of escape are probably less than those of males when they are carrying egg sacs. Small forms such as Rotifera, Copepoda nauplii and the copepodite stages of Bocekellidae are only very infrequently captured.

According to the study of Vaux et al. (1988) carried out at the mouth of

Puno Bay, *O. ispi* captured at the surface or at a depth of 25 m were feeding almost equally on Cladocera (*Daphnia pulex*) and Copepoda (*Boeckella titicacae*), though diet composition varied considerably between individuals.

Other specise of Orestidae such as *Orestias forgeti* and *O. pentlandii* must also be considered as as zooplanktivores (Loubens, 1989). They are however much less abundant than *Orestias ispi* and their impact on the lake's zooplankton is relatively limited.

Some other species of fish at certain stages of their development (fry and young stages) also have a diet in which zooplankton prey make up a considerable proportion. For example young 'pejerreys' (*Basilichthys bonariensis*) with a standard length of 5 to 27 cm feed on Amphipoda, but also on Copepoda and Cladocera to a major extent (Loubens, 1988; Vaux *et al.*, 1988). This type of food has also been found in the stomachs of young rainbow trout (*Salmo gairdneri*) from the lake.

Conclusions

Other than a species list for certain groups and information on their distribution in part of the lake, it would appear that knowledge of the zooplankton in Titicaca is still very limited, especially concerning the biology and ecology of the species occurring.

As a general rule Copepoda are largely dominant in the population compared to Cladocera and their reproduction would appear to continue throughout the year. There is very little information on the Rotifera populations, a group that would however appear to be well represented in the zooplankton.

At the present state of knowledge on the composition of the animal plankton, no endemism has been observed and the species recorded have been found in many lacustrine environments in the region and neighbouring countries.

VI.3c. Temporal and spatial variation of zooplankton in Lago Grande

ANITRA L. PAWLEY and PETER J. RICHERSON

Knowledge of the distribution of zooplankton populations in tropical lakes is still limited, and information on high altitude tropical lakes is extremely meagre (Nilsson, 1984). Because such lakes have mean temperatures similar to temperate zone lakes but seasonal regimes like the lowland tropics, they are important cases for advancing our knowledge of the processes controlling community structure and variability through time.

Zooplankton in tropical systems breed continuously (e.g. Gras *et al.*, 1967; Hart, 1981) which has led temperate limnologists to interpret tropical lakes as aseasonal. However, it is becoming increasingly apparent that tropical zooplankton populations are variable (Infante, 1982), and that these variations include both short term unpredictable changes (Lewis, 1979; Richerson *et al.*, 1977) and repeatable annual variation (Twombly, 1983). Lake Titicaca, with its low mean annual temperatures (ca. 12.5°C), presumably lower rates of population turnover, and low species diversity lends itself well to describing and understanding these processes.

This paper presents a description of "seasonal" (repeatable annual) and "aseasonal" (intra-annual) zooplankton variation in the pelagic zone of Lago Grande, Lake Titicaca. Because seasonal variation of limnetic tropical systems is generally muted, changes observed at one location are often explained as being ephemeral in nature. It is easy to imagine that relatively small changes in time measured at one station are confounded with spatial patchiness. Therefore, as a means of establishing the importance of spatial, relative to temporal variation, we also evaluated spatial variation on four dates during the study.

Methods

Lago Grande, the main basin of Lake Titicaca, was sampled for a variety of limnological parameters on a biweekly basis during 1981 and 1982 (see Chapters V.4 and VI.1d for more details). During this period, zooplankton were collected with a 12.2 cm diameter Clark Bumpus sampler hauled vert-

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ically from a depth of 150 metres to the surface. The sampler was initially equipped with a 41 μ m and later an 80 μ m mesh net. A comparison of the two methods indicated that there was no difference in the sampling efficiency of the two nets. Generally two or three subsamples from each of three replicate tows were counted at 30x magnification for each date. During the joint UCD-IMARPE study, transects were performed on four separate dates spanning the "seasons" to determine zooplankton spatial heterogeneity. On each date, six stations were sampled during the night on a transect from Conima to Capachica.

Results

Zooplankton composition

A complete species list of the pelagic zooplankton of Lake Titicaca is presented in Chapter VI.3a and b. As is apparent from this short species list, Lake Titicaca is low in species diversity. In fact the zooplankton community is even less diverse than in many temperate lake systems (e.g. Nauwerck, 1963); however many species lists of temperate systems include littoral species which makes comparison difficult (Lewis, 1979). In addition, the number of species present at any instant in time is rarely less than the number yielded by a composite list of species for the entire year, which emphasizes the limited seasonal variation of zooplankton.

Spatial versus temporal variation in zooplankton abundance

A two way ANOVA was performed on the entire data set (4 dates \times 6 stations) to evaluate the relative importance of spatial and temporal variation of copepod nauplii. These organisms were always present and were consequently the most conservative estimate of the relative importance of temporal variability. In this analysis, the date effect is interpreted as temporal variation, the station effect as the fixed variation between stations, and the interaction term (date × station), a measure of ephemeral patchiness (Lewis, 1978). The results (Table 1) indicate that for both species the seasonal (date) effect and the station effect are significant; however, the date effect outweighs the station effect in magnitude. This clearly indicates that temporal variation is more pronounced than both the fixed and ephemeral components of spatial variation. This is especially apparent for Boeckella titicacae nauplii; however, for Metacyclops leptopus nauplii, the station effect and interaction effect are fairly large (Table 1). In summary, seasonal varaiation contributed most to the total variation, suggesting that the seasonal variation observed from date to date was real and not an artifact of spatial patchiness. (Additional graphs

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Species & stage	Source of Variation	DF	MS	F	Significance Level (p)
<i>Boeckella titicacae</i> nauplii	Station	5	3.71	4.22	< 0.005
	Date	3	27.44	31.29	< 0.001
	Sta x Date	15	1.36	1.55	
	Error	48	0.88		
Metacyclops					
leptopus nauplii	Station	5	56.44	14.47	< 0.001
	Date	3	120.07	30.79	< 0.001
	Sta x date	15	49.83	12.78	< 0.001
	Error	48	3.90		

Table 1. Spatial heterogeneity study: Two Way Analysis of Variance for all triplicate zooplankton tows (n = 72). Replicates form the error term.

and results apart from this analysis are presented in more detail by Moreno (1983)).

Patterns of temporal variation

A previous study performed in 1973 (Richerson *et al.*, 1977) using a 300 μ m mesh net, documented the quantitative variations of the largest macrozooplankton. The calanoid and cyclopoid copepods were the most numerous and least varying aspect of the plankton; whereas the cladocerans and rotifers were intermittently present. *Boeckella titicacae* (Fig. 1) exhibited a well defined peak in egg production in July, followed by a peak in copepodids in October, which led Richerson and his collaborators to propose a generation length of 6 months. Their data also suggested that *Metacyclops leptopus* (Fig. 2) might have generations of a similar length. Copepod egg production, though variable for both species, was clearly continuous, so any changes were not a question of presence or absence but one of magnitude.

During the 1981–82 study, copepods were again the most consistently present and abundant part of the zooplankton community (Figs 4 and 5). *Boeckella titicacae* was found in similar numbers; however *Metacyclops leptopus* was even more abundant than in 1973. *Boeckella occidentalis*, the largest calanoid copepod present, was generally rare during all three years (Fig. 6). The copepods were again found to reproduce continuously which made it difficult to estimate lifespan duration. However there was a sustained peak of *B. titicacae* nauplii (Fig. 4) from August through October of 1981, followed by a peak in copepodids from October 1981 to February 1982. As in the 1973 study, this suggests that the lifespan duration is approximately six



Figures 1 and 2. Seasonal variation in the abundance of the life history stages of *Boeckella titicacae* and *Metacyclops leptopus* in 1973. Standard deviation of counts (replicate counts on a single sample) are as follows: *B. titicacae* adults, 3000 m⁻²; copepodids, 9250 m⁻²; eggs, 1700 m⁻²; *M. leptopus* adults + copepodids, 1300 m⁻²; eggs, 2000 m⁻². (reprinted from Richerson *et al.*, 1977).

months. The patterns observed in 1982 are not nearly as distinct. Following a sharp peak in *B. titicacae* egg production and nauplii in June, the copepodids showed only a broad increase in density during the latter half of the year. It is also interesting to note that the timing of the peak in *B. titicacae* nauplii is fairly consistent with egg production in 1973 (Fig. 1), which suggests a certain level of seasonality.

As in the 1973 study, the pattern of cyclopoid reproduction and develop-



Figure 3. Seasonal variation of zooplankton biomass in 1973. Boec. occ. is *Boeckella occidentalis*, Bos. h. is *Bosmina hagmanni*, D.p. is *Daphnia pulex*, C.q. is *Ceriodaphnia quadrangula* and Aspl. is *Asplanchna* sp. Note log scale. Biomass is given as wet weight. (reprinted from Richerson *et al.*, 1977).

ment was less distinguishable. *M. leptopus* nauplii (Fig. 5) peaked in February and November of 1981 to January of 1982 and again during the following April and November. *M. leptopus* copepodids (Fig. 5) peaked in February of 1982 and again in May to June. This also suggests a generation length of slightly less than six months and perhaps a degree of seasonality.

In 1973 and 1981, peak reproduction of the dominant calanoid, *B. titica-cae*, is consistent with the period of deepest mixing. Mixing increases nutrient availability and phytoplankton biomass. So the variation observed in copepod abundance may be directly linked to the availability of its food source. *M. leptopus* displays a different pattern, with nauplii generally more abundant during the stratified period.

The distribution of cladocerans throughout the 1981–82 study demonstrated a high degree of variability and unpredictability. *Daphnia* were nearly absent during 1981, but were prevalent in 1982 from early August through October (Fig. 7). Heavy *Daphnia* grazing apparently had major impacts on phytoplankton abundance during this period (Vincent *et al.*, 1984). This hypothesis is supported by the decrease in diatom biomass observed in September (Richerson, unpublished data), as well as by the decline of ultraplankton from mid-May to August. Lake Titicaca *Daphnia* are known to feed preferentially on ultraplankton (Haney and Trout, 1985), so this result is not particularly surprising.

The cause of the large fluctuations in the *Daphnia* population is unknown; however, it may be due to the presence of strong predation pressure (Brooks



Figure 4. Variation of the abundance of the life history stages of *Boeckella titicacae*. Values are the means of 3 replicate tows collected biweekly in Lago Grande.

and Dodson, 1965). In the tropics, *Daphnia* predominates in areas of low fish predation (Nilssen, 1984). Vaux *et al.* (1988) have demonstrated a preference for *Daphnia* by the two principal pelagic fish species in Lake Titicaca. The less variable occurrence of the smaller cladoceran species, *Bosmina* (Fig. 7) also supports this explanation.

In 1981 and 1982, the rotifer populations displayed strong irregular fluctuations in abundance, often being virtually absent from the population and then exploding in numbers (Fig. 8). The peaks are rarely coincident in time, suggesting that the different rotifer species react to different environmental cues. During 1981, *Filinia* increased dramatically in February, followed by a peak in *Polyarthra* in May, *Keratella* in August and *Brachionus* in December. During the following year, the pattern was similar for *Filinia*, suggesting a possible repeatable seasonal pattern for this species. However for the remaining rotifer species the pattern in 1982 differs substantially from the pattern



Figure 5. Variation of the abundance of the life history stages of *Metacyclops leptopus*. Values are the means of 3 replicates.



Figure 6. Variation in the abundance of the largest calanoid copepod, *Boeckella occidentalis.* Values are the means of 3 replicates.



Figure 7. Variation in the abundance of the two most prevalent cladoceran species, *Daphnia* sp; and *Bosmina hagmannii*. Values are the means of 3 replicates.



Figure 8. Variation of Rotifer abundance in Lake Titicaca (Lago Grande) during 1981 and 1982. Values are the means of 3 replicates.

in 1981, indicating that for rotifers there is little in the way of repeatable seasonal patterns.

Conclusions

This study underlines the fact that the assessment of one year of data in tropical systems cannot adequately describe the distribution and ecology of plankton. The comparison of data for three years shows that Lago Grande exhibits both intra-annual variation and variations between years. Few species appear to have repeated seasonal cycles. The more r-selected species, cladocerans and rotifers, are strikingly variable in abundance. Richerson et al. (1987) stress the importance of irregular "within year" variation in the phytoplankton population at Lake Titicaca. The zooplankton follow a somewhat similar pattern. Yet, despite these variations, certain species are consistently dominant. As Richerson et al. (1977) suggested, the K-selected character of copepod life histories does appear to give these species a competitive edge in relatively aseasonal tropical lakes. It remains to be demonstrated whether the largely irregular fluctuations in the zooplankton population in 1973 and 1981 to 1982 are more closely related to minor physical variations or to biotic processes such as competition and predation. As with the phytoplankton, the lack of a close correlation with major physical variables like the stratification cycle suggests that complex biotic interactions are more important than physical controls in determining zooplankton community structure.

VI.3d. Note on the feeding behaviour of zooplankton

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Some knowledge of selective feeding behaviour is essential if utilization of food and competitive interactions of zooplankton are to be understood. Although it is appealing and convenient to consider herbivorous zooplankton as passive filters, there is now considerable evidence indicating that the complexity of feeding behaviour of copepods may include multiple feeding modes that can be switched on and off, an ability to adjust feeding according to biomass peaks and chemosensory selection of food particles. Cladocerans also appear to be selective grazers. Unfortunately, there is inadequate information to permit general predictions of the selective behaviour of zooplankton grazers in the complexity of natural waters.

J. F. Haney and M. A. Trout, in a study headed "Size selective grazing by zooplankton in Lake Titicaca" (*Arch. Hydrobiol.*, 1985, 21:147–160) gave some precisions on the major trophic pathways for zooplankton grazers in Lake Titicaca, examined feeding activities on large (>10 μ m) and small (<10 μ m) fractions of seston. We report here the abstract published with their results.

"Feeding experiments were conducted in the laboratory and *in situ* using ¹⁴carbon labeled natural seston and ¹⁴carbon labeled *Chlorella*. Boeckella *iticacae*, Daphnia pulex, and Ceriodaphnia quadrangula graze selectively on small seston <10 μ m in Lake Titicaca. Bosmina coregoni and Boeckella occidentalis females and large copepodids preferred large seston >10 μ m, whereas male *B. occidentalis* and small copepodids showed negative electivities for the large seston fraction. Microcyclops in Puno Bay ingest a greater portion of the >10 μ m seston and in Lago Grande prefer particles <10 μ m. Its very low collection rates suggest it is more omnivorous than the other species. At natural seston concentrations, Daphnia and Ceriodaphnia ingest a greater portion of their body weight per day than Boeckella. Food addition experiments indicate both Boeckella species would benefit more than cladocerans by a dramatic increase in small particulate, with *B. occidentalis* gaining the most."

References of chapter VI.3

- BEAUCHAMP (P. de), 1939. 5: Rotifères et Turbellariés. In: The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1 (1): 52–79.
- BIRABEN (M.), 1939. Microfauna de Río Santiago (La Plata). Los Cladóceros de la familia Chydoridae. *Physis*, 18: 651–671.
- BRADY (G.S.), 1913. On freshwater Entomostraca from various parts of South Africa. Ann. Natal. Mus., 2: 459–474.
- BREHM (V.), 1936. Uber die Cladocerenfauna des Titicaca und über einige neue Fundstellen bereits bekannter Copepoden. Zool. Anz., 114 (5/6): 157–159.
- BREHM (V.), 1939. La Fauna microscópica del Lago Peten, Guatemala. Ann. Esc. nac. Cienc. Biol. México, I (2): 173–202.
- BREHM (V.), 1957. Cladoceren und Calanoide, die von Hernando de Macedo in Peru gesammelt wurden. Folia Biol. Andina, Pars 2 - Zoologica. 1: 53–61.
- BROOKS (J.L.), 1957. The systematics of North American Daphnia. Mem. Connecticut Acad. Arts Sc., 13: 1–180.
- BROOKS (J.L.), DODSON (S.I.), 1965. Predation, body size and composition of the plankton. Science, 150: 28–35.
- DADAY (E.), 1902. Mikroskopische Süsswasserthiere aus Patagonien. Termeszet. mus., 25: 201-310.
- DADAY (E.), 1905. Untersuchungen über die Süsswasser-Mikrofauna Paraguays. Zoologica (Stuttgart), 18 (44): 1–374.
- DELACHAUX (T.), 1918. Cladocères des Andes péruviennes. Bull. Soc. Neuchatel. Sc. Nat., 43: 18–38.
- EKMAN (S.), 1900. Cladoceren aus Patagonien gesammelt von der schwedischen Expedition nach Patagonien 1899. Zool. Jb.(Syst.), 14: 62–84.
- FREY (D.G.), 1980. On the plurality of *Chydorus sphaericus* (O.F. Müller) (Cladocera, Chydoridae), and designation of a neotype from Sjaelso, Denmark. *Hydrobiologia*, 69 (1/2): 83– 123.
- FREY (D.G.), 1982. Relocation of *Chydorus barroisi* and related species (Cladocera, Chydoridae) to a new genus and description of two new species. *Hydrobiologia*, 86: 231–269.
- FRONTIER (S.), 1974. Contribution à la connaissance d'un écosystème néritique tropical: étude descriptive et statistique des peuplements zooplanctoniques de la région de Nosy Bé (Madagascar). Thèse Univ. Aix Marseille: 628 p.
- GRAS (R.), ILTIS (A.), LEVEQUE-DUWAT (S.), 1967. Le plancton du bas Chari et de la partie est du Lac Tchad. Cah. ORSTOM, sér. Hydrobiol., 1: 25–100.
- HANEY (J.F.), TROUT (M.A.), 1985. Size selective grazing by zooplankton in Lake Titicaca. *Arch. Hydrobiol.*, 21: 147–160.
- HARDING (J.P.), 1955. 15. Crustacea: Copepoda. In : The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1: 219–247.
- HARDING (J.P.). 1955. 19. Crustacea: Cladocera. In : The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1: 329–354.
- HART (R.C.), 1981. Population dynamics and demography of an estuarine copepod (*Pseudodiaptomus hussei*) in Lake Sibaya, a subtropical freshwater coastal lake. J. Limnol. Soc. S. Afr., 7: 13–23.
- INFANTE (A.), 1982. Annual variations in abundance of zooplankton in Lake Valencia (Venezuela). Arch. Hydrobiol., 93: 194–208.
- KIEFER (F.), 1957. Freilebende Ruderfusskrebse (Crustacea-Copepoda) des Titicacasees. Veroff. Zool. Staatssamm. Munchen, 4: 125–150.
- LEBLOND (R.), 1983. Quelques aspects de l'alimentation et de la sélection des proies chez *Orestias ispi* Lauzanne (Pisces, Cyprinodontidae) du lac Titicaca. ORSTOM, La Paz: 15 p. multigr.
- LEWIS (W.M.), 1978. Comparison of spatial and temporal variation in the zooplankton of a lake by means of variance components. *Ecology*, 59: 666–671.

- LEWIS (W.M.), 1979. Zooplankton community analysis. Studies in a tropical system. Springer Verlag, New York, 163 p.
- LÖFFLER (H.), 1955. Die Boeckelliden Perus. Ergebnis der Expedition Brundin und der anden - kundfahrt unter Prof. Dr. Kinzl, 1953–1954. Österr. Akad. Wiss. Abt. 1, 164 (9): 723–746.
- LOUBENS (G.), 1989. Observations sur les poissons de la partie bolivienne du lac Titicaca. 4. *Orestias* spp., *Salmo gairdneri* et problèmes d'aménagement. *Rev. Hydrobiol. trop.*, 22 (2): 157–177.
- LOUBENS (G.), OSORIO (F.). 1988. Observations sur les poissons de la partie bolivienne du lac Titicaca. 3. Basilichthys bonariensis (Valenciennes. 1835) (Pisces, Atherinidae). Rev. Hydrobiol. trop., 21 (2): 153–177.
- MONIEZ (R.), 1889. Sur quelques Cladocères et sur un Ostracode nouveaux du lac Titicaca. *Rev. Biol. Nord France*, 1: 419–429.
- MORENO (E.), 1983. Estudio cuantitativo del zooplancton de la zona pelágica del Lago Titicaca (Lago Grande). Tesis Univ. S. Agustín, Arequipa: 96 p.
- MURRAY (J.), 1913 a. Notes on the Natural History of Bolivia and Peru. Scottish Oceanogr. Laborat. Edimburgh, 8 vol.
- MURRAY (J.), 1913 b. South American Rotifera. Parts 1 & 2. J. Roy. Micr. Soc., 6: 229–236; 11: 341–362.
- NAUWERCK (A.), 1963. Die Beziehungen zwischen Zooplankton und Phytoplankton im See Erken. Symb. Bot. Upsalienses, 17: 1–163.
- NILSSON (J.P.), 1984. Tropical lakes functional ecology and future development: the need for a process oriented approach. *Hydrobiologia*, 113: 231–242.
- PAGGI (J.C.), 1972. Nota sistemática acerca de algunos Cladóceros del género Chydorus Leach 1843 de la Républica Argentina. Physis, 31 (82): 223–236.
- PAGGI (J.C.). 1979. Revisión de las especies argentinas del género *Bosmina* Baird agrupadas en el subgénero *Neobosmina* Lieder (Crustacea: Cladocera). *Acta Zool. Lilloana*, 35: 137-162.
- PAWLEY (A.), 1982. Ecología del zooplancton en la Bahía de Puno exterior. Univ. California, Davis UNTA.UBC.CIDA. Puno.
- PAWLEY (A.), 1983. Zooplankton in the Lake Titicaca ecosystem: the importance of regenerated nitrogen to phytoplancton productivity. Univ. California, Davis - UNTA.UBC.CIDA. Puno.
- PAWLEY (A.), ALFARO (R.), 1984. Zooplankton in the Lake Titicaca ecosystem: importance of regenerated nitrogen to phytoplankton productivity. *Verh. Internat. Verein. Limnol.*, 22: 1258–1263.
- PENNAK (R.W.), 1989. Freshwater Invertebrates: Protozoa to Mollusca. 3rd ed. John Wiley and Sons, New-York, 628 p.
- REPELIN (R.), VARGAS (M.L.), PINTO (J.), 1987. Distribución geográfica y estacional de la abundancia del zooplancton en la parte boliviana del Lago Grande del Titicaca. *In*: Descripción del lago Titicaca y su cuenca. Parte 2. Documento de Pesca 005, Oldepesca, Lima: 293–325, multigr.
- REPELIN (R.), PINTO (J.), VARGAS (M.L.), 1988. Distribución y migraciones nictimerales del zooplancton en el sector boliviano del lago Titicaca (Lago Pequeño). UMSA.ORSTOM, La Paz, Informe 11: 31 p., multigr.
- REY (J.), VASQUEZ (E.), 1986. Cladocères de quelques corps d'eaux du bassin moyen de l'Orénoque (Vénézuela). Ann. Limnol., 22 (2): 137–168.
- RICHARD (J.), 1897. Entomostracés de l'Amérique du Sud recueillis par MM. U. Deiters, H. von Ihering, G.W. Müller et C.O. Poppe. *Mém. Soc. Zool. Fr.*, 10: 263–301.
- RICHERSON (P.J.), WIDMER (C.), KITTEL (T.), 1977. The limnology of Lake Titicaca (Peru-Bolivia), a large high altitude tropical lake. Univ. California, Davis, Inst. Ecology: 78 p., multigr.
- RICHERSON (P.J.). CARNEY (H.J.), 1987. Patterns of temporal variation in Lake Titicaca, a high altitude tropical lake. II. Succession rate and diversity of the phytoplankton. *Verh. Internat. Verein. Limnol.*, 23: 734–738.

- SARS (G.O.), 1901. Contributions to the knowledge of the fresh-water Entomostraca of South America, as shown by artificial hatching from dried material. Part 1. Cladocera. Arch. Math. Naturv. B., 23: 1–102.
- SCOURFIELD (D.J.), 1942. The "pulex" forms of *Daphnia* and their separation into two distinct series represented by *D. pulex* (de Geer) and *D. obtusa* (Kurz.). *Ann. Mag. Nat. Hist.*, (11), 9: 202–219.
- SMIRNOV (N.N.), 1971. Chydoridae of the world's fauna. Fauna of the USSR, Crustacea, 1 (2), new series, n° 101, Leningrad, 531 p. (in Russian). English transl. A. Mercado, Israel Prog. Sci. Transl., 1974.
- STINGELIN (T.), 1913. Cladoceren aus den Gebirgen von Kolumbien. Mem. Soc. Neuchatel. Sci. Nat., 5: 600-638.
- TWOMBLY (S.), 1983. Seasonal and short term fluctuations in zooplankton abundance in tropical Lake Malawi. *Limnol. Oceanogr.*, 28 (6): 1214–1224.
- UENO (M.), 1967. Zooplankton of Lake Titicaca on the Bolivian side. *Hydrobiologia*, 29: 547–568.
- VALDIVIA-VILLAR (R.S.), 1988. Lista de Cladóceros dulceacuícolas del Perú. Amazoniana, 10 (3): 283–297.
- VAUX (P.), WURTSBAUGH (W.A.), TREVIÑO (H.). MARINO (L.), BUSTAMANTE (E.), TORRES (J.). RICHERSON (P.J.), ALFARO (R.), 1988. Ecology of the pelagic fishes of Lake Titicaca, Peru-Bolivia. *Biotropica*, 20 (3): 220–229.
- VAVRA (W.), 1900. Süsswasser-Cladoceren. Ergebn. Hamburg. Magalh. Sammel., 5: 1-25.
- VINCENT (W.F.), WURTSBAUGH (W.A.), VINCENT (C.L.), RICHERSON (P.J.), 1984. Seasonal dynamics of nutrient limitation in a tropical high-altitude lake (Lake Titicaca, Peru-Bolivia): application of physiological bioassays. *Limnol. Oceanogr.*, 29: 540–552.

VI.4. BENTHIC FAUNA VI.4a. The Bryozoa and Coelenterata

CLAUDE DEJOUX

The Bryozoa

The Bryozoa of Lake Titicaca, a minor component of the benthic fauna of this water body, are only known from the work of Marcus (1953) relating to material collected by the Percy Sladen Expedition of 1937, and which will be frequently cited in this book.

These rather unspectacular and usually small-sized organisms have rarely been collected and are not always capable of being identified. Identification is generally based on the structure of the statoblasts, but these organs are not always present in collected material.

Systematics and distribution

Only two species have been recorded from Lake Titicaca, or rather two subspecies of polyps with a much wider distribution either on a world scale or within South America.

Fredericella australiensis var. browni Rogick, 1945

The material studied by Marcus (1953) was recorded as being abundant and came from the Capachica region, where this species was found in small streams around the shoreline (under stones) as well as in the lake itself under pebbles along the shoreline or on the stems of *Schoenoplectus tatora*. Depending on their stage of growth, their age and type of substrate, the colonies can either form appressed grey-brown incrustations of 2 to 3 cm diameter, or the polyps can be erect and form a rather graceful feathery structure (Plate 1, Fig. 1 to 9).

The polyp tubes have a structure ranging from an elliptical form to a nearly triangular form. The mean size of polyps varies widely, the largest reaching 1.5 to 2.3 mm; the tentacles vary between 0.4 and 0.9 mm in length, and number between 24 and 27 per polyp. Statoblasts are numerous, but

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Figure 1. Known distribution of Bryozoa in Lake Titicaca.

flottoblasts are absent, a characteristic feature of the Fredericellidae. Marcus (*op.cit.*) named these non-floating statoblasts, piptoblasts.

Fredericella australiensis var. *browni* is a taxon very close to *Fredericella sultana*, but differs mainly by the greater diameter of the tubes in which dissepiments are absent, by the larger number of tentacles arranged in an elliptical rather than circular form and by its larger sessoblasts.

Fredericella australiensis is a cosmopolitan species recorded from Australia, Russia, the central Sahara and North America. The variety occurring in Lake Titicaca is distributed widely in the water body and has been recorded under stones or among vegetation on the shore of Lago Huiñaimarca (Huatajata, Taquiri, Suana, Cojata, etc.) and in Lago Grande (Achacachi, Escoma, Copacabana, etc.) (Fig. 1). It should be noted that only isolated individuals



Plate 1. Fredericella australiensis browni; 1. part of a colony growing on algae; 2. centre of an old colony growing on a rock; 3. detached branch of a polypide with erect zooecia; 4. part of a cleared colony showing piptoblast; 5. lateral view of a piptoblast; 6. upper valve of a piptoblast; 7. lower valve of a piptoblast; 8. section of a sessoblast; 9. crown of tentacles from a young polypide. (From Marcus, 1953).

have been collected at these stations, giving the impression that this organism is rare.

Stolella agilis Marcus, 1942

Stolella agilis tica Marcus, 1953

The material collected comes mainly from macrophyte beds of *Elodea*, *Potamogeton* and *Myriophyllum* to which the polyps are attached. The colonies are often found encrusting shells of *Littoridina*. As with previous sub-species it has been recorded from the Capachica region.

The structure of the polyp is much more slender than in *Fredericella* (Plate 2, Figs 1 to 7). The polypides are grouped into clusters of 3 or 4 separated by septa and can break away from their attachment, probably in a stage of extension of the colony towards another substrate.

The tubes of zooecia are not angular but cylindrical with a diameter of 0.6 to 0.8 mm, the zooecia themselves being of very variable size. The ectocyst is thin and transparent with a diameter of 20 to $60 \,\mu\text{m}$ and showing two distinct layers in section (Plate 2, Fig. 6), the outside often being incrusted with debris and fragments of diatoms arranged in concentric lines.

The polyps have a very variable number of tentacles, difficult to count with certainty because of the folded form of the lophophore, but varying from 28 to 43 in the samples studied, with a mode of 35. The colonies contain few statoblasts and no sessoblasts.

The variety *Stolella agilis tica* appears to be a form intermediate between *Stolella agilis agilis* and *Stolella agilis iheringi*, differing in characters of size and shape, especially in the flottoblasts and by internal morphological characters of the endocyst and vestibulum. *Stolella agilis agilis* is a sub-species known only from South America (southern and central regions) whereas the sub-species *Stolella agilis iheringi* is only recorded from northern Brazil. In Lake Titicaca we have only found it once on the stems of *Myriophyllum* near Calahuta Island, which suggests that this subspecies is rarer than the previous one. In the material collected by the Percy Sladen Trust Expedition, the examples of *Stolella agilis tica* were collected in the Lagunilla Lagunilla lake situated to the west of Lake Titicaca, living at depths of between 12 and 24 metres. It is not impossible that these organisms also occur at the same depths in Lake Titicaca, despite the fact that we have never collected them ourselves at more than about 12 metres depth.

The coelenterata

Although very frequent in freshwaters, the South American Coelenterata, including both medusae and hydroids, have only been the subject of very few studies, restricted to taxa from the Amazon Basin (Schlenz, 1981).



Plate 2. Stolella agilis tica; 1. isolated fragment of a colony showing septa; 2. extended part of a budding colony; 3. creeping branch of a polyp incrusted with foreign particles on its surface; 4. general appearance of flottoblasts treated with KOH; 5. lateral view of a flottoblast after KOH treatment; 6. view of upper surface; 7. view of lower surface. (From Marcus, 1953).

It seems highly probable that only one species of Coelenterata belonging to the genus *Hydra* occurs in Lake Titicaca, but it has not been possible to identify this to species level (Fig. 2). It is frequently present in our benthos samples and below we give a brief summary of its distribution in the Bolivian part of the lake.



Figure 2. Polyp of Hydra sp. from Lake Titicaca.

Within this area the highest relative abundance (more than 33% of the benthic fauna in this zone) has been recorded on bare bottom substrates in Lago Huiñaimarca. This organism lives on compact sandy-silt substrates, at depths of thirty metres or more near the entrance to the Tiquina Strait and at lower abundance in the Chua Depression. Its presence in these localities is an argument in favour of the existence of deep-water currents, bringing oxygen and food. These are certainly two factors determining the abundance of *Hydra* that we have also found off the mouth of the Rio Suchez in Lago Grande (depth 8 to 15 m; % of total benthos: 20%).

Hydra sp. is a regular component of the fauna in areas covered with charophytes in Huiñaimarca and Lago Grande, where it represents 5 and 10% of the total macro-invertebrates present, respectively. Absolute densities exceeding 1500 individual per 10 g dry weight of these plants have been encountered on occasion, but densities of 400 to 500 are more frequent.

The *Hydra* sp. occurring in Lake Titicaca is small and of extremely low dry weight and therefore represent a negligible proportion of the biomass, but its nature as filter-feeding organism gives it a certain importance in the processes of organic matter transformation.

VI.4b. The Porifera: Description of a new taxon *Balliviaspongia wirrmanni* n. g., n. sp.

NICOLE BOURY-ESNAULT and CECILIA VOLKMER-RIBEIRO

The sponge fauna of the Bolivian Altiplano has only been studied very superficially up to present. The first collection of sponges from Lake Titicaca was made by the Percy Sladen Expedition in 1937 (Gilson, 1964). The material deposited at the British Museum of Natural History in London was only superficially identified by Burton. From October 1985 to June 1986 detailed faunal surveys were carried out as part of a research programme on Lake Titicaca and these collections provided numerous samples of sponges.

Material and methods

Material was collected by dredging or by pulling up algae using a boat hook or grapnel. After sorting from the algae, the specimens of sponges were photographed and then fixed in formaldehyde. Although this type of fixation did not allow a detailed cytological study, a histological study of a part of the material could be carried out. After dehydration, blocks were embedded in araldite and semi-thin sections were taken and stained with toluidine blue. Preparations of spicules and skeletons for light microscopy follow standard practice (Rützler, 1978). For scanning electron microscopy, preparation of spicules was performed by settlement of a drop of alcohol with dissociated spicules on a stub, followed by evaporation of the alcohol and metallization with gold before observation.

Sampling stations (Map 1)

Lago Pequeño:

1. Offshore of Huataja, 0.1 and 4 m in the totora zone and 16–19 m (30.10.85; 6.11.85; 1.5.86; 14.5.86; 17.6.86); samples N° 853, 854, 8659 and 8661.

2. Taraco Peninsula 4 m (14.5.86); sample N°8658.

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Map 1. Main sampling areas in which specimens were collected.

3. Taraco Peninsula offshore of Santa Rosa, 4 m on algae (14.5.86); sample N° 8657.

- 4. Outflow of the Desaguadero, 3 m on algae (12.5.86); sample N°8656.
- 5. S.E. of Suana Island, 6-7 m on algae (6.11.85); sample N°855.

Lago Grande:

6. Huatapampa Bay on the Copacabana Peninsula, 9 m on algae (29.1.86); sample N°611.


Figure 1. External appearance of paratype 855 of Balliviaspongia wirrmanni nov.gen, nov. sp. from Lago Pequeño, collected 6.11.85.

7. Yunguyo Bay in Copacabana Bay, 3.5 m in the totora zone (11.5.86); samples N°8654 and 8655.

8. Sun Island, N.W. bay, 7.5 and 10 m on algae (10.5.86); samples N°8651b and 8652.

9. Sun Island, Challa Bay, 3.5 m (11.5.86); samples N°612a and 8653.

Description of Balliviaspongia wirrmanni nov. genus species.

Definition: Spongillidae (?) with reticulate skeleton comprising very distinct primary tracts perpendicular to the surface. The only spicules present are acanthoxea. Microscleres and gemmules are absent. Genotype: *Balliviaspongia wirrmanni*.

Derivatio nominis: The generic name is derived from Lake Ballivian, a Pleistocene lake of the Bolivian Altiplano (Lavenu, 1981). The species is dedicated to Denis Wirrmann who collected the samples and made the ecological observations.

The holotype (sample 8656) is deposited at the *Museum national d'Histoire naturelle*. Paris as number MNHN-NBE-CVR-1990-1. The type locality is the outlet of the Desaguadero. Paratypes are deposited at the *Station Marine d'Endoume* and schizoparatypes at the *Museu de Ciencias Naturais da Funda-ção Zoobotanica do Rio Grande do Sul* at Porto Alegre Brazil (Porifera catalogue N°2039-2044). The paratypes were collected in the Bolivian part of Lake Titicaca.

Numerous specimens of this encrusting sponge have been collected from stones or forming a sheath around algae or reeds. The largest specimens are 15 cm long and 3 cm wide, but never exceed a thickness of 1.5 cm. The colour in life is very variable, ranging from bright green to buff; it is soft in consistency (Fig. 1). The surface is very slightly hispid. Specimens collected in November (southern summer) were in the process of reproduction. The embryos measure about 235 to 265 μ m in diameter. The spherical choanocyte

chambers have a diameter of 35 to 45 μ m on the sections, which represents a volume of 22 450 to 48 000 μ m³. By using Rasmont and Rozenfeld's (1981) indirect method of evaluation, the number of choanocytes per chamber can be estimated at between 220 and 360.

The skeleton

The reticulate skeletal framework is made up of parallel primary tracts. The diameter of these tracts varies between 16 and 53 μ m. They are linked together by thinner irregular secondary tracts. The spicules in the tracts are connected by very small amounts of spongin. The ends of the primary bundles protrude beyond the surface which is therefore slightly hispid. The ectosomal skeleton is made up of an irregular network of uni- or bispiculate meshes tangential to the surface.

The spicules (Figs 2 to 7)

The only spicules present are straight or slightly curved acanthoxea. The variable length spines stop at a short distance from the extremities which are smooth. In some specimens, spicules showing malformations in the form of swellings, sharp angles or bifid points, have been recorded. Specimens from shallow water are most often affected by such malformations. Spicule dimensions (10 spicules measured on each of 18 specimens): $153-450/2.6-13 \mu m$, mean 239.9, standard deviation 54.3.

The habitat

This species was collected at depths of between 0.1 and 19 m in the Lago Pequeño and the South of the Lago Grande (Copacabana Bay and around Sun Island). It is most frequently attached to reeds (totoras) on which the largest specimens have been recorded, but also on algae and on stones. The peak abundance is in the totora zone, i.e. down to 4.5-5 m depth. Samples found by dredging at 16-19 m depth were always attached to stones.

We have been able to re-examine a very spicule-rich layer in a core (TD1), taken in the Lago Pequeño south-east of Suana Island and studied by Wirrmann and Almeida (1987). The layer at 153-155 cm in this core has been dated by ¹⁴C dating to 7700 ± 230 years. The spicules come from an even deeper layer (166–167 cm). They are of a single type and identical to those of the sponge living in the lake at present (Figs 5 to 7). This species is known to have been present in Lake Titicaca for more than 7700 years.



Figures 2–7. 2. SEM photomicrograph of acanthoxea; 3. Detail of acanthoxea. Note variations in the sizes of the spines and in the diameter of the acanthoxea in the same sample. SEM photomicrograph: 4. Detail of the extremity of an acanthoxea. SEM photomicrograph; 5. Spicules coming from the 166–167 cm level in core TD1 and including a sand grain. SEM photomicrograph; 6. Spicules from core TD1. SEM photomicrograph; 7. Detail of extremity of an acanthoxea coming from core TD1.

Discussion

In spite of variation in morphology and colour, all the specimens have an identical skeletal framework and the spicules only show slight individual

differences. They therefore belong to the same species, which has persisted in the lake with the present day spicule characteristics for at least 7700 years. It was therefore present before the drying out stage that started about 7000 years BP. This progressive drying out continued as far as the establishment of conditions of evaporite deposition. The water remaining in the central part of the Lago Grande must therefore have become saline. It seems doubtful that *B. wirrmanni* could have survived these conditions. A reintroduction from the rivers which started to refill the lake as from 3650 years BP therefore seems more probable. It would be highly desirable to carry out a study of the distribution of this species on the Altiplano, both at the present time and in sediments from the start of the Holocene.

From a systematic point of view, the most important fact is the absence of gemmules and gemmoscleres, at all times of the year. These are also absent in the specimens collected by the Percy Sladen Expedition (BMNH-1938:8:8:10), that we have been able to examine. The absence of microscleres also needs to be underlined. This species is therefore one of the small number of freshwater sponges in which gemmules and microscleres are absent. These mostly belong to monospecific genera and share in common the fact that they live in lakes where they are less subject to climatic stresses such as drying out or cold. For example, the family Lubomirskiidae containing three genera has been described from Lake Baikal, the genus Ochridaspongia Arndt, 1937 from Lake Ochrid (S. Yugoslavia), the genera Cortispongilla Annandale, 1913 and Nudospongilla Annandale, 1913 from Lake Tiberias (Middle East) and the genus Malawispongia Brien, 1972 from Lake Malawi (East Africa). The systematics of freshwater sponges is essentially based on the characteristics of the gemmules and their gemmoscleres and on the microscleres. Therefore, as Brien (1972) stressed, the systematics of the forms in which these are absent is very difficult and it may be necessary to use other criteria such as cytological, biochemical or embryological criteria. Because of the wide geographical separation of the various species without gemmules, authors have preferred to describe them as new genera while waiting for the chance to be able to study their cytological and biochemical characters in detail. Brien (1973) grouped them all in one sub-family, the Globulospongillinae, but it seems to us difficult to define a group solely on the basis of negative characters: absence of microscleres, absence of gemmules and absence of gemmoscleres. This absence of asexual reproduction seems to be related to the ecological conditions (Brien, 1958). These conditions allow species incapable of asexual reproduction to live in large lakes, or in contrast prevent asexual reproduction from manifesting itself in species which possess this ability. To test this hypothesis it would be necessary to look for the possible presence of this sponge and of gemmules in the rivers on the Altiplano.

For all of these reasons the species of sponge from Lake Titicaca is attributed to a new genus *Balliviaspongia*, with *B. wirrmanni* as type species. It should be noted that the skeletal structure corresponds completely with

that of the Haplosclerida (Demospongiae). The volume of the choanocyte chambers and the number of choanocytes per chamber are of the same order of magnitude as that of *Ephydatia fluviatilis* (Rasmont and Rozenfeld, 1981) and the marine Haplosclerida. In spite of the absence of gemmules and microscleres we are including it at present in the Spongillidae, while waiting for a cytological or genetical study (like Solé-Cava *et al.*, 1991) to be carried out to define its affinities with other genera of freshwater sponge.

Acknowledgements

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VI.4c. The benthic oligochaetes

MICHEL LAFONT and JACQUES JUGET

The first lists of aquatic oligochaetes from South America date from the end of the last century, as Gavrilov (1981) notes in a recent bibliographic compilation of papers relating to aquatic oligochaetes of the tropical regions of this continent. Except for the work of Cernosvitov (1939) who described several new taxa coming from Lake Titicaca, the aquatic oligochaetes of this lake have not been the subject of special studies.

The study of material collected by ORSTOM from the Bolivian part of the lake (Dejoux, 1988 and Chapter VI.4 j) is interesting for various reasons:

- it offers the opportunity to compare the oligochaete fauna of this lake with the fauna of other South American habitats, in particular the mountain lakes of Bolivia for which species lists are being prepared (Dejoux and Wasson, in press; Juget and Lafont, in prep.);
- benthos sampling at intervals between depths of 4 and 175 m (Fig. 1) should provide precise information on the role of certain factors, such as oxygen content and water salinity, on the overall structure and depth distribution of oligochaete populations.

List of species collected (Table 1)

At least eleven species have been recorded from the twelve samples examined. Seven belong to a commonplace and cosmopolitan grouping (*Potamothrix hammoniensis*, *P. heuscheri*, *P. bavaricus*, *Tubifex ignotus*, *Limnodrilus hoffmeisteri*, *L. udekemianus*, *Nais pardalis*). Three species belong to the fauna recorded from South America (Gavrilov, 1981): Bothrioneurum americanum, Isochaetides lacustris (= Isochaeta baicalensis sensu Gavrilov, 1981) and Dero sawayai (Plate 1, Figs 1–12).

In the littoral zone at stations 6 and 8 we discovered a *Rhyacodrilus* sp. without hair setae (Plate 1, Figs 13–15). The identification corresponds with a taxon occupying an intermediate position between *R*. *stephensoni* and *R*.

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Table 1. Relative frequencies of oligochaetes recorded from Lake Titicaca at various depths in October 1986; A: species recorded by Gavrilov (1981); B: species recorded by Harman *et al.* (1988); C: species recorded in the littoral zone by Martinez-Ansemil and Giani (1986); (1) samples collected in June 1986.

	LAGO GRANDE					LAGO PEQUEÑO									
Sites :	3	2	4	4 (1)	1	11	6	7	10	5	9	8	A	в	C
Depths (m) :	175	165	153	150	127	65	8	33	11	9,5	7	4,5			
	%	%	%	%	%	%	%	%	%	%	%	%	%		
TUBIFICIDAE															1
Inmature Tubificidae													1		1
with hair setae	64.3	83.3	76.9	93.8	84	70.6	80	70.8	55.6	63.2	69.2	56.2			1
Inmature Tubificidae													J	1	1
without hair setae	-	-	-	-	8	5.9	10	9.2	27.8	21	23.1	20.3			[
Potamothrix hammoniensis	7.1	-	-	6.2	-	-	-	-	-	-	-	-		1	
Potamothrix bavaricus	28.6	13.9	15.4	-	8	17.6	-	8.3	11.1	15.8	7.7	4.7	1		
Potamothrix heuscheri	-	2.8	-	-	-	-	-	-	-	-	-	-		1	
Tubifex ignotus	-	-	-	-	-	-	-	2.5	-	-	-	1.6	1	1	
Limnodrilus udekemianus	-	-	-	-	-	-	-	-	5.5	-	-	1.6			1
Bothrioneurum americanum	-	-	7.7	-	-	-	-	-	-	-	-	-	•		
Isochaetides lacustris	-	-	-	-	-	-	-	-	-	-	-	4.7		1	
Limnodrilus hoffmeisteri	-	-	-	~	-	5.9	-	-	-	-	-	-			
Rhyacodrilus sp.	-	-	-	-	-	-	10	-	-	-	-	4.7	1	1	
NAIDIDAE															1.
Dero obtusa	-	-	-	-	-	-	-	-	-	-	-	-	1		· ·
Dero sawayai	-	-	-	-	-	-	-	7.5	-	-	-	6.2			1
Nais andina	-	-	-	-	-	-	-	-	-	-	-	-		•	· ·
Nais pardalis	-	-	-	-	-	-	-	1.7	-	-	-	-	1	•	
Nais variabilis	-	-	-	-	-	-	-	-	-	~	-	-			•
Pristina leydyi	-	-	-	-	-	-	-	-	-	-	-	-		•	•

komarovi, recently described by Timm (1990) and coming from the River Komarovka (Eastern Siberia).

Ecology and distribution

It is astonishing to note that the list in Table 1 contains only four species previously recorded from Lake Titicaca (Gavrilov, 1981; Harman et al., 1988): B. americanum, I. lacustris, L. hoffmeisteri and N. pardalis. This remark about the fauna leads to some interesting ecological observations. For one, the deep zone of the lake does not seem to have been investigated recently, in contrast to the littoral zone (Martinez-Ansemil and Giani, 1986; Harman et al., 1988). Taxa such as I. lacustris or D. sawayai only occur in samples from the littoral or sublittoral zones (stations 5 to 11, Table 1). Another observation is that the stations sampled in the deep zone below the 100 m isobath are only populated by three common species (P. heuscheri, P. hammoniensis and P. bavaricus) typical of the bottoms of water bodies with a pronounced dissolved oxygen deficit (Milbrink, 1983). The dominance of P. bavaricus, apparently due in part to seasonal factors, should be looked at in relation to the dissolved salt content of the lake water, which is rich in chlorides (Carmouze et al., 1977). This species tolerates high salinities in estuaries (Timm, 1970). At this point, mention might be made of research on the benthic fauna of Lake Chad (Carmouze et al., 1977). This work showed that some oligochaetes, such as the Alluroididae, dissappear as soon



Figure 1. Location of sampling stations.

as the electrical conductivity of the water reaches 420 μ S cm⁻¹, and are replaced by Tubificidae beyond this level of conductivity.

Discussion and conclusion

One of the special features of Lake Titicaca oligochaete fauna is the paradoxical presence of common, cosmopolitan species such as the three species of Tubificidae belonging to the genus *Potamothrix*, which are absent from other mountain lakes in Bolivia (Juget and Lafont, in prep). The absence or rarity in the material studied of typical South American taxa such as *Epirodrilus*



Plate 1. Figs 1–3: *Dero sawayai* Marcus, 1943; 1: Anterior and posterior parts of the animal 2: Detail of posterior branchial cavity 3: Chaetae: A: anterior ventral crotchets (segment IV), B: Dorsal needles, C: Ventral posterior crotchets (segment XII). Figs 4–8: *Isochaetides lacustris* (Cernosvitov, 1939) 4: Anterior end. 5: Anterior crotchets (dorsal and ventral, segment IV) 6: Posterior crotchets (segment XVIII) 7: Spermathecal chaeta (segment X) 8: Male genital pore (segment XI). Figs 9–12 *Bothrioneurum americanum* Beddard, 1894. 9: Anterior end of a sexually mature specimen (first 11 segments) 10: Spermatophore (between segments X and XI) 11: Anterior crotchets (segment IV) 12: Posterior crotchets (segment XX) Figs 13–15 *Rhyacod-rilus* sp. 13: Anterior end of the animal (first 9 segments) 14: Dorsal and ventral crotchets 15: Penial chaetae bundle (segment XI).

antipodum and Bothrioneurum americanum, frequently encountered in the deep zone of other Bolivian lakes, is also worthy of mention. Logically, the low annual temperature range of the surface water of Lake Titicaca (between extremes of 10 and 15°C, Carmouze *et al.*, 1977; Lazzaro, 1985), due to the combined effect of high altitude (3809 m) and tropical latitude (16.5°S), should have provided a climatic context favourable for the homogenisation of the populations of South American mountain lakes.

Two special features related to the physiography and hydrochemistry of Lake Titicaca perhaps provide an explanation for the paradox described above:

- Lake Titicaca is divided into two main water bodies, the Lago Grande with a mean depth of 134 m and maximum depth 285 m, and the Lago Pequeño in which 67% of the water volume occurs at depths of ≤10 m. In contrast to Lago Pequeño, Lago Grande can be classified as a eutrophic lake (Lazzaro, 1985). This eutrophic status is reflected especially in the relationship of dissolved oxygen concentration with depth, with a permanent oxygen deficiency below the depth of 100 m. And, it is precisely at depths of ≥150 metres, where pronounced dissolved oxygen deficits exist, that species of the genus *Potamothrix* occur almost alone.
- The high electrical conductivity of the waters of both the Lago Grande and Lago Pequeño (of the order of 1400 to 1500 μ S cm⁻¹ at 25°C), due mainly to high concentrations of Na⁺ and Cl⁻ ions, is another explanation. This high concentration of NaCl could be the reason for the above-mentioned predominance of Tubificidae and of the species *P. bavaricus*.

Care should be taken in these interpretations however, since the number of samples studied is small considering the size of the lake. Complementary studies taking into account the physico-chemical characteristics of the sediments would undoubtedly be interesting in this context.

VI.4d. The Tricladida and Hirudinea

CLAUDE DEJOUX

The Tricladida

These organisms are extremely abundant in Lake Titicaca, and also in most of the aquatic habitats in the Andes and the Altiplano, a fact already recorded by Beauchamp (1939) in his study of the material collected by the Percy Sladen Expedition.

At first sight one may be led to think that there are several species of triclad in Lake Titicaca, such is their variability in colour and even in shape. In fact there is only one, cosmopolitan species in the lake: *Euplanaria doroto-cephala* Woodworth, 1897, a species very widespread in the United States. According to Beauchamp (*op.cit.*), this was described for the first time from Trinidad by Kennel in 1888.

The diverse appearance of this triclad is the reason for the multiplicity of descriptions under different names, leading to at least ten synonyms. Many descriptions are based on the endemic character of certain forms, for example the individuals described under the name *Dugesia titicana*, by Hyman in 1939.

Brief description of the species

Without giving a complete description of *Euplanaria dorotocephala*, some general characters of its morphology and structure are given here. The mean size of sexually mature individuals is of the order of 8 to 10 mm, but extreme individuals of 5 and 17 mm have been recorded. The general form is elongate, the breadth being about 1/5th of the length (Fig. 1). The mouth is situated about 7/10ths of the way along the body, the genital pore being closer to the mouth than the posterior extremity of the body. The characteristic spearshaped head in the form of an equilateral triangle has two protruding lateral lobes, also triangular in shape. This shape is of course very altered in preserved specimens, but the lobes still remain paler than the rest of the body.

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Figure 1. Euplanaria dorotocephala, a) dorsal view; b) ventral view.

The eyes are placed at the anterior margin of the lobes at the internal margin of an unpigmented patch.

In live specimens the colour ranges from deep black to pale beige, the upper and lower sides being the same colour, or the dorsal side being occasionally darker. On darkest individuals only, there is a colour pattern consisting of two dark bands running from one end of the body to the other and converging anteriorly to enclose a paler central area.

According to the detailed description of the internal anatomy made by Beauchamp (op.cit.), the brain is in the form of an inverted V and the numerous (ca. 35) digestive caecae are irregularly spaced on each lateral branch. The testes can be either dorsal or ventral depending on the individual; the ovaries are situated at the level of the 4th and 5th pair of caecae. The penis is rather short, with a conical, or rarely tapering, free part.

Ecology and distribution

E. dorotocephala is found both in still and running waters. In Lake Titicaca it is particularly abundant under stones and pebbles along the shore where its density can exceed 5000 individuals per square metre. Generally, the light form is more frequent than the dark form, which dominates in running water. Although this species prefers firm, well-oxygenated substrates in the littoral zone, it is also found abundantly among the submerged macrophytes. Here it can account for nearly half of the epiphytic invertebrate population in

terms of number of individuals, as can be seen from the percentages given below from a recent study of macro-invertebrates associated with the aquatic vegetation in the Bolivian part of the lake (Dejoux, in press).

Myriophyllum elatinoides at surface: 3.7%	Myriophyllum at bottom: 6.2%
Elodea potamogeton: 45.6%	Chara spp.: 1.7%
Schoenoplectus tatora: 11.8%	Potamogeton strictus: 1.1%
Ranunculus trichophyllus: 25.5%	Crucifera indet.: 45.4%

E. dorotocephala has been found everywhere in the Bolivian part of the lake, down to a depth of 9.5 m, which seems to be its lower limit. It has been recorded from the Peruvian part of the lake by Medina (1982) and by Morales *et al.* (1989), these latter however noting its absence from the inner part of Puno Bay, the most highly eutrophicated part of the Lago Grande.

Judging from the information given by Beauchamp (op. cit.), who recorded its very frequent occurrence in freshwater habitats in the United States "from the Atlantic to the Pacific and in the Great Lakes," as well as in the Caribbean (Trinidad), *E. dorotocephala* would appear to be a very cosmopolitan species.

The Hirudinea

According to Ringuelet (1978, 1981) the literature on Neotopical Hirudinea is very sparse. These animals are distributed throughout the South American continent in regional taxonomic assemblages corresponding to the major ecological zones related to altitude and latitude. The high Andes constitutes one of these regions.

Four species of leech have been recorded from Lake Titicaca, all belonging to the Glossiphoniiformes and the family Glossiphonidae.

- Gloiobdella michaelseni Blanchard, 1900. This species has been collected at Puno and in the Rio Desaguadero. It is a cosmopolitan species also known from Argentina, Brazil, Chile, Paraguay and Uruguay.
- Helobdella festai Dequal, 1916. Also known from Ecuador, this species has been collected from Juli and Puno bays (Ringuelet, 1981).
- Helobdella simplex Moore, 1911. This species has been recorded from Pomata and from Puno Bay (Ringuelet op cit.); it is also known from Argentina and Uruguay.
- *Helobdella titicacensis* Ringuelet, 1959. This species, known from Puno and Pomata (Ringuelet, 1960), is not endemic to Lake Titicaca since it has also been recorded by this author from water courses and high altitude lakes in Peru.

Distribution of Hirudinea in the Bolivian part of the lake

The records of the above species are all restricted geographically to the Lago Grande since they all refer to Puno Bay and the Pomata and Juli regions. More complete studies would probably show that the Hirudinea have a much wider distribution and perhaps that other species occur in Lake Titicaca. It is known that identification, even to the generic level, frequently requires study of internal organs following special fixation on collection. Not having done either of these in our extensive study of the benthic fauna of the lake, the distribution data given below concern the family Glossosiphoniidae taken as a whole.

The Hirudinea occur in almost all the major biotopes of the lake, from wave-washed shores (under stones and pebbles) to bare sediments in the deepest parts of the lake; the deepest specimen yet recorded was collected in the Lago Grande at a depth of 175 metres.

In relative and also absolute abundance, the greatest density and richness occurs under stones near the shore, where densities of 300 to 400 individuals per square metre are not uncommon. They can account for 3% of the total benthic population in this type of habitat, which is generally very rich in macro-invertebrates (see Chapter VI.4j).

The Hirudinea are a frequent component of the fauna of the submerged macrophyte stands, but generally do not account for more than 2% of the invertebrate population in this habitat. On a more detailed scale, the highest densities occur amongst *Chara* (5% of all invertebrates present and 60 ind. m^{-2}).

On bare sediments at moderate depth, they do not usually account for more than 2% of the benthic population and the maximum densities recorded are barely 20 individuals per square metre.

In conclusion, the Hirudinea, although very widely distributed throughout the lake, can only be considered as a minor group in this ecosystem.

VI.4e. The Mollusca

CLAUDE DEJOUX

As they take up little room and are easy to transport, the terrestrial and freshwater molluscs were frequently collected during expeditions by the great explorers of the last century and in the case of Lake Titicaca they are probably the organisms that occur most frequently in museum collections. Despite this, with the exception of species lists, the malacalogical fauna of this large lake remains poorly known. Subjects such as their biology and ecology have been little or not studied, although these organisms certainly play a very important role in production and in decomposition of organic matter in shallow water areas, particularly in the Huiñaimarca.

History of past studies

Many of the first collections were of a casual nature, taken from near the shore or in shallow water and leading to the first species descriptions. The works of D'Orbigny (1835, 1835–47), Pilsbry and Vanatta (1896), Bavay (1906) and Pilsbry (1924) come into this category. It was not before the works resulting from the Percy Sladen Trust Expedition in 1937 (Gilson, 1939) that more systematic studies were carried out, giving rise to the works of Haas (1955, 1957) in which five new genera and nine new species were described. A few years later Blume (1958) published a supplementary study of the genera *Littoridina* and *Strombopoma*, based on collections made by workers from the Munich Natural History Museum.

After this period, there was then a gap before new data on the molluscs of Lake Titicaca were provided by the studies of Medina (1983 a and b) on the benthos of Puno Bay, and the collections made by Hinz during an expedition to the Andes (Kuiper and Hinz, 1983) and our own works (Dejoux, 1988 and in press) on the benthic fauna of the Huiñaimarca and the Bolivian part of the Lago Grande.

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Taxonomy, endemism and polymorphism

As with other groups of animals (Ostracoda, Amphipoda, Amphibia, etc.), the molluscs of Lake Titicaca show a great variability of form depending on the sampling site, a variability which led the first taxonomists to divide the fauna into multiple species, which later workers have attempted to merge; the most important effort in this field has been carried out by Haas (1955). A list of known species is given below, but for reasons of brevity, synonyms are not given for each species. For these the reader should refer to Haas (*op. cit.*)

GASTROPODA

PLANORBIDAE Tropicorbis (Lateorbis) canonicus Cousin, 1887 Taphius montanus D'Orbigny, 1835

ANCYLIDAE

Anisancylus crequii Bavay, 1904

HYDROBIIDAE

Littoridina stiphra Haas, 1955 Littoridina lacustris Haas, 1955 Littoridina profunda Haas, 1955 Littoridina berryi Pilsbry, 1924 Littoridina andecola D'Orbigny, 1835 L. a. spp. neveui L. a. ssp. andecola L. a. ssp. culminea Littoridina aperta Haas, 1955 Littoridina forsteri Blume, 1958 Strombopoma ortoni Pilsbry, 1924 S. o. ssp ortoni Blume, 1958 S. o. ssp schindleri Blume, 1958 Rhamphopoma magnum Haas, 1955 Rhamphopoma parvum Haas, 1955 Heligmopoma umbilicatum Haas, 1955 Brachypyrgulina carinifera Haas, 1955 Limnothauma crawfordi Haas, 1955 Ecpomastrum mirum Haas, 1957

LAMELLIBRANCHIATA

Sphaerium titicacense Pilsbry, 1924 Sphaerium forbesi Philippi, 1869 Sphaerium lauricochae Philippi, 1869 Pisidium meierbrooki Kuiper and Hinz, 1983

To this list of species already recorded in the literature, must be added two others found in our samples and differing in morphological characters from the species given above. One, belonging to the genus *Rhamphopoma*, has been collected sporadically from various sites in the Bolivian part of the lake and the other, probably belonging to the genus *Littoridina*, is for the moment only known from the littoral zone of Sun Island.

The degree of endemism is high for all the species recorded from Lake Titicaca. Some of them, such as *Ecpomastrum mirum*, *Brachypyrgulina carinifera* and *Limnothauma crawfordi*, have never been collected other than in this water body; others such as *Taphius montanus* are only known from a few other aquatic biotopes close to the lake.

For at least two genera, *Taphius* and *Littoridina*, there is very pronounced polymorphism, whose causes are still far from understood. The most complex case of polymorphism is certainly that presented by the genus *Taphius*. The systematics of this group was not clarified until the works of Haas (1955), and in our opinion the final solution of this problem is yet to be found. Haas proposed an evolutionary morphological phylogeny in two branches starting from an ancestral form *Taphius montanus* D'Orbigny, the least specialised form.

Figure 1 has been drawn up from the explanations of this author, using his drawings in diagrammatical form. One of the branches of the evolutionary line leads directly to the form T. montanus heteropleurus Pilsbry and Vanatta, almost given it the status of a subspecies. The other branch, leading to the form T. montanus andecolus, has several intermediary varieties including one (*Planorbis titicacensis* Clessin, 1884) which is simply mentioned without a drawing, as from the evidence it represents a simple transition form between two extreme forms.

The form *concentratus* has a very compact and angular shell, with a very deep umbilicus, and another variety (T. *montanus concentratus* var.*bakeri*) shows these characters in an exaggerated manner (Plate 1, Figs 3 and 4), an adaptation to living in shallow water under wave influence according to Haas (*op. cit.*). We will discuss this hypothesis later. At the other extreme, the branch leading to the form *heteropleurus* ends in a rather unspecialised planorbid, restricted to deep water zones.

Polymorphism is also very pronounced in *Littoridina* spp., but the relationship between the two extreme forms is more obviously linear; all the intermediates and extreme forms can be present in the same sampling location.

In the genus *Littoridina* the variation also involves the formation of a more or less pronounced keel on the median part of the whorls, compared to an original form with broad round smooth whorls. Three subspecies have been distinguished: *L. andecola culminea* which is considered as the ancestral smooth form, an intermediate subspecies called *L. andecola andecola* and at the other extreme a form *L. andecola neveui* with a very pronounced keel (Fig. 2).



Figure 1. The polymorphism of *Taphius montanus* in Lake Titicaca, relationhips between the forms (from Haas, 1955).

Brief description of the species, distribution and ecological notes

GASTROPODA

PLANORBIDAE

Tropicorbis (Lateorbis) canonicus Cousin, 1887

This species, first described from Ecuador and also recorded from Colombia and Peru, occurs in the rivers and lakes of the Altiplano both on the Atlantic and Pacific slopes (Plate 1, Fig. 5). There is only one record from Lake Titicaca, but this was collected at the mouth of a small stream near Capachica (Haas, 1955; Fig. 3A), making it likely that this species was carried down to the lake in the drift. This species has never been recorded in our own



Plate 1. Fig. 1a, 1b, 1c: ventral lateral and dorsal views of *Taphius montanus montanus*. Fig. 2a and 2b: ventral and dorsal views of *Taphius montanus* var. *heteropleurus*. Fig. 3a, 3b, 3c and 4a, 4b and 4c: dorsal lateral and ventral views of *Taphius montanus* var. *bakeri*. Fig. 5: *Tropicornis canonicus*.

samples, and it is not sure that Lake Titicaca is a favourable habitat for its survival. On the other hand it is recorded from Lake Poopo, so that a relatively high salinity would not appear to be a limiting factor for its occurrence.



Figure 2. Relationships between the various forms of *Littoridina andecola* in Lake Titicaca (from Haas, 1955).

Taphius montanus D'Orbigny, 1835

This species of Planorbidae is endemic to the Lake Titicaca basin and has been recorded in numerous lakes and running waters on the Altiplano (Plate 1, Figs 1–4). It is a large species, with largest specimens reaching 22 mm in diameter and nearly 10 mm high, the shell being wound in $4\frac{1}{2}$ whorls. The distribution of the various described forms within the lake would appear to be less simple than the impression gained from reading Haas (*op. cit.*). This author stated that *T. montanus heteropleurus* was characteristic of deep water (10 to 82 metres depth), but that it could also occur in depths of 3 to 5 metres. In our samples coming from the entire Bolivian part of the lake, this form was found at practically all depths from 2 to 54 metres, but was dominant at a depth of about ten metres (Fig. 3B).

In contrast, it is certain that the subspecies T. montanus and ecolus and its two related forms (concentratus and bakeri) are much more abundant at about 3 to 4 metres depth than at 15 to 20 metres depth, where they occur frequently but at low densities. Living specimens have been found down to 30 metres depth.

An extensive and detailed study would be needed to determine the depth preferenda of each form of the genus *Taphius*, but it is not certain that this is the most important factor in determining the distribution of this mollusc. From the available data it is possible however to draw up the following table showing the possible overlaps in the depth distributions.

	Extreme depths	Most frequent recorded depths
T. montanus montanus	0.20 to 25 m	0.50 to 3 m
T. montanus andecolus	0.10 to 30 m	0.50 to 4 m
T. montanus concentratus	2.70 to 15 m	3 to 6 m
T. montanus bakeri	1 to 6 m	1 to 3 m
T. montanus heteropleurus	3.40 to 82 m	15 to 35 m

The distribution of the various forms of *T. montanus* shown in Fig. 3B, drawn up from data in the literature and from our own sampling, shows that the varieties *montanus* and *andecolus* are by far the most widely distributed in the lake. In contrast the variety *bakeri* is frequent in the Huiñaimarca, but only occurs in isolated spots in the Lago Grande.

ANCYLIDAE

Anisancylus crequii Bavay, 1904

This relatively easy to identify small species has an apex set off to one side and a frequently concave lower margin (Plate 2. Fig. 1a and b). The usual shape of the base of the shell is oval, with a more or less pronounced lateral flattening. Morphological variability in this species involves the shape of the apex and that of the base of the shell which can be almost flat and also broadly oval. Haas (1955) suggested that *A. crequii* could be just an extreme form of *Anisancylus lagunarum*, described from samples found in small lakes near Lake Titicaca (Laguna Tejane, Lagunilla Lagunilla and Lagunilla Saracocha). As we have found some shells in Lake Titicaca very close in shape to typical specimens of *A. lagunarum*, it seems likely that the two forms occur in both the lake itself and in high altitude lakes in the Cordillera, but it is still impossible to say whether these are really two different species.

A. crequii occurs in almost all areas of the lake where the water is shallow or of medium depth. The localities in which it has been recorded are shown in Fig. 3C. Its depth distribution extends as far as the eulittoral where it can be found under stones in only a few centimetres depth to the 5 to 8 metres depth zone, where it reaches it maximum abundance. As some individuals have been collected from a depth of 30 metres its area of distribution can be considered as going beyond that of the strictly littoral zone. This species is also frequent in the aquatic vegetation, among stems of Characeae or on the leaves of *Potamogeton*.



Figure 3. Distribution of various species of mollusc in Lake Titicaca.



Plate 2. Fig. 1a: lateral and dorsal views of *Anisancylus crequii*. Fig. 1b: various forms of the base of the shell. Fig. 2: *Littoridina stiphra*. Fig. 3: *Littoridina lacustris*. Fig. 4: *Littoridina profunda*. Fig. 5a: *Littoridina berryi*; 5b: operculum. Fig. 6a: *Littoridina aperta*; 6b: outer surface of the operculum; 6c: inner surface of the operculum showing the presence of a horny spiral thickening. (Figs 2, 3, 4 and 5 from Haas, 1955).

HYDROBIIDAE

Littoridina stiphra Haas, 1955

The measurements of the type specimen are as follows: height 4.2 mm, breadth 2.8 mm, aperture 1.4×1.1 mm. It is therefore a small, thin, transparent species with a conical shell having $6\frac{1}{2}$ whorls. The upper four whorls are convex, whereas the lower whorls are flattened, the last whorl even being concave towards the aperture (Plate 2, Fig. 2). The operculum is deeply set, thin and horny. Variations in shape affecting this species mainly involve the degree of prominence of the keel. Except for its size, which is relatively smaller, this species is rather similar to certain specimens of *Littoridina andecola neveui*. We have not been able to identify this species in our own samples and for the moment we consider it is a rare species, known only from Molinopampa (Haas, 1955), living at a depth of 3 metres (Fig. 4A).

Littoridina lacustris Haas, 1955

This is also a small species scarcely exceeding 4 mm in height and 3 mm in breadth. Its general shape is therefore strongly conical, the shell being translucent grey, but of solid appearance (Plate 2, Fig. 3). A thin horny operculum closes the shell at a distance about 1/3 of a whorl from the aperture. The number of whorls is reduced to 5–6 at the maximum, a character which distinguishes this species from another of a similar shape: *L. berryi*, but which is much larger and has at least 7 whorls.

From the characteristics of the sampling locations, it seems that L. *lacustris* occurs from the margins to depths of up to 66 metres. Its present known distribution is given in Figure 4B.

Littoridina profunda Haas, 1955

Haas described this species in 1955 from only 7 specimens, collected near Taman at between 56 and 82 metres depth. It is not abundant in our material although it was found regularly in samples taken at depths of between 4.5 and 10 metres in the Huiñaimarca and at 40 m in the Lago Grande off Moon Island. The type specimen, described from a dead shell, is of small size (height 3.5 mm; breadth 2.3 mm; aperture 1.5×1 mm), whereas our largest specimen reaches almost 6 mm, but also has a shell with $6\frac{1}{2}$ whorls. Certain individuals which have dimensions close to those of the type specimen also have $6\frac{1}{2}$ whorls. The main character of the species is that it has a rugous dirty grey periostracum. Another species of *Littoridina* (*L. vestida*) has a similar periostracum but it is smooth and white and this species probably only occurs in the Lagunilla Soracocha and not in Lake Titicaca.



Figure 4. Distribution of various species of mollusc in Lake Titicaca (continued).

Littoridina berryi Pilsbry, 1924

Although recorded as the most frequent species in Lake Titicaca and also the largest (Haas, 1955), this species shows such size variations that distinguishing it from *Littoridina andecola culminea* does not always seem very

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evident to us. Pilsbry in his description of the species describes a shell height varying from 7.5 to 8 mm for adult individuals, with a breadth varying between 3.2 and 4.1 mm (Plate II, Fig. 5). In contrast, Haas (1955) records specimens exceeding 12 mm in height and 5.1 mm in breadth and having 9 to $9\frac{1}{2}$ whorls. In view of the fact that *L. a. culminea* can also have $9\frac{1}{2}$ whorls and measure 10.9×4.5 mm, the only character remaining to distinguish the two species is that the last whorl of *L. berryi* is slightly concave or at most flat at the extremity of the aperture, and never convex as in *L. andecola*: character which is not very evident in our view! As, in addition, the opercula of these two species in samples where they occur together would appear to be a matter of chance.

At the start of the century, L. *berryi* was considered as having a very wide distribution throughout the lake (Fig. 4D), living at depths ranging from 20 cm to more than 30 metres. In our samples we have only identified with certainty 15 individuals belonging to this species, whereas the various forms of L. *andecola* occur almost everywhere. This leads us to think that the relative proportions of certain organisms living in Lake Titicaca have changed greatly, a fact that is also encountered with the Hydracarina.

Littoridina aperta Haas, 1955

This small species (type specimen: height = 3 mm, breadth = 2.2 mm, aperture = $1.4 \times 1.2 \text{ mm}$) was collected by the Percy Sladen Expedition in small numbers at a few locations in the lake at depths ranging from 0.5 to 14.3 metres. The shell has a translucent but solid appearance, with up to 5 whorls, the operculum is terminal and horny, the umbilicus is very open and the general colour is greyish white (Plate 2, Fig. 6). Our sampling in the Bolivian part of the lake provides details of the distribution of this species (Fig. 4E) which is rather infrequent in the study area as a whole, but can be abundant in areas where it lives, reaching densities of more than 6000 individuals per square metre (Sun Island, 22 February 1987, depth 30 metres). The depth at which this sample was taken makes it likely that this species occurs over a wide depth range.

Littoridina forsteri Blume, 1957

This small species, described by Blume (1957), is close in general form to L. *aperta* and L. *lacustris*. It differs from the latter by the presence of an umbilicus and from the former by the less globular shape and different dimensions, all of these characters not being very obvious to recognize, taking into account the morphological variability of most of the species occurring in the lake (Plate 3, Fig. 1).

The shell is robust, almost non-transparent and greyish white in colour. There are $5\frac{1}{2}$ whorls with well-defined sutures. The umbilical aperture is deep and also well pronounced. The surface of the shell has a pitted appearance and the last few whorls have growth striae along the sutures, clearly visible under a binocular microscope. If the pitted appearance of the shell isn't an artefact (erosion ?), it is certainly the most obvious character for distinguishing this species from the two mentioned above. It is however strange that we have never found this species of *Littoridina* in the abundant material that we have collected in the area of the Huiñaimarca from where the type specimen comes (between Huatajata and Patapatani. Fig. 4F). The drawing that we show of this species is very similar to that of *Littoridina aperta* and if we accept the possibility that some special form of erosion occurred to a series of shells at a particular time, it is not impossible that these are in fact the same species.

Littoridina andecola D'Orbigny, 1835

The extreme morphological variability of this species has already been mentioned so only brief descriptions of two of the extreme forms and of the most frequent intermediate form will be given below.

Littoridina andecola culminea

The mean size of this form is 6.5 mm high with a width of about 3 mm; the shell has between 7 and 8 whorls which are slightly convex (Plate 3, Fig. 3a). This is certainly the most frequent form at present, at least in the Huiñaimarca (Fig. 3F).

Littoridina andecola andecola

This form has linear very shallow sutures, the whorls being almost flat, except the last which can be angled at its margin, announcing the transition towards the form *neveui* (Plate 3, Fig. 4a). The operculum is apertural, whereas it is always much deeper in the form *culminea*. The mean size is also different, Haas (1955) giving the following values: H = 7.8 mm; B = 3.6 mm, for a snail with 9 whorls.

Littoridina andecola neveui

This form, which is more abundant than the previous form but less so than the first, is certainly the easiest to identify (Plate 3, Fig. 5). Its general appearance, typified by the presence of a keel which can be very pronounced, resembles the European genus *Pyrgula*. This form has 7.5 to 8 whorls and has mean dimensions of the same order of magnitude as those of *L. a.* andecola.

We have frequently encountered all three forms in the same sample and



Plate 3. Fig. 1: *Littoridina forsteri.* Fig. 2: *Heligmopoma umbilicatum.* Fig. 3a and 3b: *Littoridina andecola andecola* and its operculum. Fig. 4a and 4b: *Littoridina andecola culminea* and its operculum. Fig. 5: *Littoridina andecola neveui.* (Fig. 1 from Blume, 1958; Fig. 2 from Haas, 1955).

the analysis of their distribution in the Bolivian part of the lake, the only part we have surveyed, indicates a very wide distribution (Fig. 3F).

Littoridina (?) sp.

A brief description is given here of three empty shells of a mollusc that we place with uncertainty in the genus *Littoridina*.

One of the three specimens examined still had remains of soft parts inside but no operculum. It is therefore a form still living at present in the lake, but certainly rare or very local, judging by the small number of individuals found.

The shells are transparent, but of a rather robust consistency; the wellmarked columella is very distinctive. The measurements of the three available examples are as follows (in mm):

	Number of whorls	Length	Width at the last whorl	Dimensions of the aperture
1	9.5	4.4	1.3	0.8×1.1
2	9	3.6	1.1	0.7 imes 1.0
3	8.5	3.7	1.0	0.6 imes 0.8

It is therefore a small very elongate species, with a characteristic aperture in which the two outside angles are slightly greater than right angles, the angle along the mid-line of the last whorl is particularly well-marked, giving the impression that the shell is keeled on this whorl. The umbilicus is open but not very well-marked from the exterior, the sutures are linear and the peristome lacks distinctive features. A lamellar periostracum seems to cover the shell (Plate 5, Fig. 4).

Strombopoma ortoni Pilsbry, 1924

This species was originally described under the name *Littoridina* (*Heleobia*) ortoni by Pilsbry (1924), from an example without an operculum, but was placed in the genus *Strombopoma* created by Haas (1955), largely on the basis of the description of the operculum alone. Haas himself seemed however to be rather uncertain of the exact systematic position of this genus. Anatomical studies, which to our knowledge have never been carried out, could confirm whether it really belongs to the tribe of the Littoridinae within the sub-family Hydrobiinae, family Hydrobiidae!

S. ortoni is a very small mollusc (height of the type specimen: 3.1 mm; breadth 1.7 mm; aperture: 0.9×0.8 mm), with a thin, whitish, translucent shell, one of the characteristics of the genus. Growth striae are clearly visible and the whorls $(6\frac{1}{2})$ are convex in the centre and flat near the sutures, which



Plate 4. Fig. 1a: *Rhamphopoma magnum*; 1b: various views of the operculum. Fig. 2a: *Rhamphopoma parvum*; 2b: various views of the operculum. Fig. 3a: *Strombopoma ortoni*; 3b: operculum. Fig. 4a: *Rhamphopoma* sp.; 4b: lateral and outer views of operculum.

are rather shallow (Plate 4, Fig. 3a). The shell is imperforate, but the last whorl is somewhat detached at its base forming an aperture resembling an umbilicus. The peristome is straight and continuous, the aperture being pear-shaped.

The operculum is characteristic (Plate 4, Fig. 3b) and has at least as many

whorls as the shell. It is horny, hollow on its internal face and ornamented with a sinistral spiral lamella having up to 10 whorls. The diameter at the base is less than that of the shell.

The shell is subject to rather great variability in shape and dimensions, reaching 4.5 mm in height and being more or less straight and elongated. This last character led Blume (1958) to propose a division into two subspecies: *S. ortoni ortoni*, the form closest to the type and corresponding to the more elongated individuals, and the subspecies *S. ortoni schindleri*, more robust, globular and with the aperture more detached from the rest of the shell.

Without discussing the validity of such a subdivision, especially as ecological data concerning one or other of these taxa are not available, it is nevertheless worth noting that the same evolutionary tendency will be seen below concerning *Ecpomastrum mirum*. Such variations are perhaps evidence of a particular evolution specific to certain molluscs in Lake Titicaca.

Generally *Strombopoma ortoni* seems to be a rare component of the malacological fauna of the lake. Its present known distribution is restricted to two localities in the Lago Grande (Puno and Ascoma Cove at the mouth of the Rio Suchez) and a few stations in the Huiñaimarca, at between 5 and 13 metres depth, amongst aquatic vegetation (Fig. 5C).

Rhamphopoma magnum Haas, 1955

This moderate-sized species (4.5 to 5.4 mm high), with a relatively translucent shell in young animals becoming whitish opaque in older individuals, is pyramidical in shape, with about 7 whorls, the first five being broader at the margin. The aperture $(2.2 \times 1.5 \text{ mm})$ is oval, but often pointed at the anterior and posterior ends. The border of the columella is hollow and projects slightly over the umbilical slit (Plate 4, Fig. 1a).

The operculum is oblong and has a horny opaque excresence, rolled into a spiral anteriorly and projecting above the opercular plate (Plate 4, Fig. 1b). The spiral is sinistral, the invaginated twisting being particularly clear in young individuals.

Haas (1955) recorded the existence of two forms, one being more elongated and thinner, corresponding to the type. After collecting a rather large amount of material we now think that a full range of intermediate forms exist. The genus *Rhamphopoma* was created by Haas (*op. cit.*) to include two species apparently endemic to Lake Titicaca, since this is the only locality from which they have been recorded up till now. Some uncertainty still exists however as to whether this new genus really belongs to the family Hydrobiidae or at least to its own sub-family, because of the absence of precise anatomical studies.

The present known distribution of this species (Fig. 5A) is restricted to two stations in the Lago Grande and one in the Huiñaimarca, the samples coming from depths of between 0.5 and 11 metres.



Figure 5. Distribution of various species of mollusc in Lake Titicaca (continued).

Rhamphopoma parvum Haas, 1955

This second species, collected by the Percy Sladen Expedition, is smaller than the previous one and is more robust looking (type specimen: height = 3.5 mm; breadth = 1.8 mm; aperture = $1.4 \times 1.0 \text{ mm}$). The shell is whitish

and has a non-perforated umbilicus. The whorls are convex, number $6\frac{1}{2}$ and have a strongly marked suture. The peristome is continuous and the border of the columnella is neither hollow, neither does it project over the umbilicus.

Haas (1955) recorded individual variations in this species which can vary in robustness, width and height. The distinction from the previous species is therefore far from evident, the differences listed making much use of terms such as "less flattened, less pointed and less projected" when talking of the collumellar border – an essential character – which in our view makes precise identification very difficult! The transparency of the shell, especially in large individuals, seems to be a more reliable differentiating character.

This species was only collected by the Percy Sladen Expedition at Molinopampa at depths of between 5.4 and 7.3 m. Our much more abundant samples lead us to think that it has a much wider distribution, especially in the Huiñaimarca (Fig. 5B). It occurs in samples either as a few individuals or in contrast in hundreds and so has a much more clumped distribution than the previous species.

Rhamphopoma sp.

The form of the operculum (Plate 4, Fig. 4b) leaves no doubt that the two series of molluscs that we collected in the Huiñaimarca in February 1987 belong to the genus *Rhamphopoma*. It is even possible that they represent a form of variation of *R. magnum*, although when the two species are put side by side they are very different. A brief description is all that will be given here.

The shell is very elongated, slightly transparent but with a resistant appearance. The largest individuals have $7\frac{1}{2}$ whorls, more or less obtuse in the centre, the last bearing distinct growth striae. The umbilicus is only slightly or not at all evident, the peristome is strong, becoming slightly detached at the base of the aperture. The example chosen as type specimen is 3.7 mm high and 1 mm wide; the largest individual found in our samples (1 empty shell) measures 3.9 mm high and has 8 whorls. The aperture is oval and very pointed at the top, measures 0.9 mm high and 0.6 mm wide. The operculum is identical in shape to that of *R. parvum*.

Heligmopoma umbilicatum Haas, 1955

This is a small species (height of the type specimen 3.3 mm; breadth 2.7 mm, aperture 1.9×1.5 mm), with a strongly conical, whitish translucent shell. The suture separating the $5\frac{1}{2}$ spires is linear, the umbilicus is usually narrow, but can be widely open in some individuals. The peristome is simple, rather broad and is brown coloured in places. The operculum is thick, horny and

usually sunken into the shell. It has three and a half whorls extending in the form of lamellae from the external surface.

The genus comprising a single species was created by Haas (1955) from material coming from a single station (Siripata, Fig. 5D). We have only found this mollusc twice in the Lago Grande, off the mouth of the Rio Suchez, at a depth of 6 metres and further south at a depth of 78 metres.

Limnothauma crawfordi Haas, 1955

A single specimen of the mollusc was collected by the Percy Sladen Expedition, at a depth of one metre, on the shore of Titicaca Island (= Sun Island), but with no further details. It was an animal which had not yet reached full size, but whose very characteristic shape led to it being described as a new genus and species at the time. We have only once found two individuals belonging to this species, despite taking numerous samples in the same region, which confirms its rarity.

It is a small mollusc (height 3.5 mm; breadth 2.8 mm, aperture: $1.8 \times 1.2 \text{ mm}$), with a broadly conical shape. The shell, covered with a brown periostracum has about 5 whorls, marked with two keels. The umbilicus is widely open and invaginated, the aperture is closed by a thin transparent horny operculum, projecting beyond the margin (Plate 5, Figs 2a and b).

Brachypyrgulina carinifera Haas, 1955

This seems to be another rarity, only collected from two stations in the Lago Grande by the Percy Sladen Expedition (Fig. 3D) and that Haas placed in the Hydrobiidae with uncertainty. Again, we have never found this species but we have never had the opportunity of sampling in localities where it was first collected. The very characteristic shaped shell, with two very pronounced keels is somewhat like a compressed form of *Littoridina a. neveui* (Plate 5, Figs 3a and b). Measuring scarcely 4 mm high, with a width of 3.1 mm and an aperture of 2.5×2.4 mm, it has a conical shape, closed umbilicus and is translucent whitish yellow. The operculum is very deeply set in and has a horny structure similar to that of *Littoridina aperta*. This species was collected at depths ranging from between 2.2 and 25 metres.

Ecpomastrum mirum Haas, 1957

This species, with its very characteristic completely unrolled shell, is another endemic species with a very restricted distribution (Fig. 5E). Described from a single empty shell by Haas (1957), we have found numerous living examples living in two regions of the lake, in the area of Sun and Moon islands in the

northern basin and at two sites in the Huiñaimarca (Dejoux and Mourguiart, in prep.). The largest living individuals collected scarcely exceed 3.5 mm in height and 1.4 mm in breadth, the shell having $5\frac{1}{2}$ whorls. The type specimen measures 4.9 mm high and has 6 whorls; it must therefore be concluded that our specimens were of as yet not fully grown individuals or that the type specimen was particularly large. The operculum is very deeply inset into the shell (on preserved specimens) and is typical of a *Strombopoma* operculum in being conical, chitinised and with a membranous lateral extension wound in a sinistral spiral, with the same number of whorls as the shell (Plate 5, Figs 1 a to e). The problem remains as to whether this mollusc really belongs to the new genus *Ecpomastrum* created for it, or whether it belongs to the genus *Strombopoma*.

LAMELLIBRANCHIATA

For a long time only one species of *Pisidium* was known from Lake Titicaca: *P. titicacense* Pilsbry, 1924, described from a single valve collected from Yunguyo Bay! Two other species had also been recorded (*Pisidium forbesi* Philippi, 1869 and *Pisidium chilense* D'Orbigny, 1835, recorded by Bavay in 1904), but their occurrence remained doubtful and it was only after the study of Kuiper and Hinz (1983) that the situation concerning the lamellibranch fauna of Lake Titicaca became clearer. It seems that a single species of *Pisidium (P. meierbrooki)* and three of *Sphaerium (S. forbesi, S. lauricochae* and *S. titicacense*) are present in this water body.

Pisidium meierbrooki Kuiper and Hinz, 1983 (Plate 6, Fig. 2a to e).

P. meierbrooki has an elongate oval, but bulbous form and is distinguished from the other Sphaeriidae in the lake by its very convex, solid, shiny, non-transparent shell with irregular concentric growth rings and a dark line in the centre. The ligament, also dark coloured, is clearly visible from the outside.

The dimensions of the holotype are as follows: L = 4.1 mm, H = 3.3 mm, D = 2.8 mm. The largest individuals rarely exceed 5 mm in length.

According to Kuiper and Hinz (1983), *P. meierbrooki* is more a running water species, living in deep calm waters, but which is also found in Lake Titicaca at depths of down to 20 metres. We have frequently collected it and give its present known distribution in Fig. 5C. This species is frequently associated with *S. forbesi*, and also occurs with *S. lauricochae* and *S. titicacense*.



Plate 5. Fig. 1a: *Ecpomastrum mirum*; 1b: various views of the shell winding: 1c, 1d, and 1 e.: operculum from various angles. Fig. 2a and 2b: *Limnothauma crawfordi*, lateral and ventral views. Fig. 3a: *Brachypyrgulina carinifera*; 3b: operculum. Fig. 4. *Littoridina* (?) sp.

Shaerium forbesi Philippi, 1869 (Plate 6, Fig. 3a to e)

This species which lives at altitudes of between 3200 and 4700 metres frequently occurs in the lakes of the northern Altiplano and the Cordillera, and is also very common in Lake Titicaca (Fig. 5F). The shape of the shell in


Plate 6. Fig. 1: *Sphaerium titicacense*; 1a: lateral view; 1b hinge of left valve; 1c: hinge of right valve; 1d: outline of juvenile; 1e: adult. Fig. 2: *Pisidium meierbrooki*; 2a: lateral view at various stages of growth: 2b hinge of left valve; 2c: hinge of right valve; 2d: outline of juvenile; 2e: adult. Fig. 3: *Sphaerium forbesi*; 3a: lateral view; 3b hinge of left valve; 3c: hinge of right valve; 3d: outline of juvenile; 3e: adult. Fig. 4: *Sphaerium lauricochae*; 4a: lateral views at various stages of growth; 4b hinge of left valve; 4c: hinge of right valve; 4d: outline of juvenile; 4e: adult.

young individuals is characteristic with very rounded margins in profile. In adults, which can exceed a centimetre in length and have a generally globular shape, the first stage of shell growth is clearly distinguishable at the hinge of each valve and separated by a more or less well pronounced ridge, in some cases having the appearance of a cap on each side of the hinge. This extreme form is known as *excessiva*. The general colour of *S. forbesi* is brownish-yellow, the area near the hinge sometimes being bluish-grey.

Sphaerium lauricochae Philippi, 1869 (Plate 6, Fig. 4 a to e)

Kuiper and Hinz (*op. cit.*) did not record this species from Lake Titicaca, but in its near neighbourhood. We give a brief description because we have collected it in the lake itself from the mouth of the river Suchez (Fig. 5F). It is possible however that the individuals found in this locality had been brought down as larvae in the drift of the river (where this species is recorded) and had continued their development in this part of the Lago Grande. The material collected by Philippi seems to have been lost, so a new description of the neotype was given by Kuiper and Hinz, from which we derive the following main characters:

- shell thin, subtransparent and relatively flat,
- periostracum greyish,
- no visible growth rings,
- brownish ligament visible from the exterior,
- hinge long (about 2/3rds of the circumference),
- cardinal tooth small and short, lateral tooth long and straight.

S. lauricochae seems to be a form morphologically intermediate between S. forbesi and S. titicacense and its status as a separate species is not at all certain; it could just be a variety of S. forbesi. The differences in morphology and structure between the two taxa seems to be clearer marked in young individuals, S. forbesi being flat and with a rounded lower profile, whereas S. lauricochae is more globular and pointed in its lower part.

Sphaerium titicacense Pilsbry, 1924 (Plate 6, Fig. 1 a to e)

Originally described from a young individual as belonging to the genus *Pisidium*, it is in fact a *Sphaerium* (Kuiper and Hinz, 1983) and has been rediscovered as abundant in Puno Bay at a depth of 25 metres.

This species resembles *S. lauricochae* but has a thick non-transparent shell. It is also usually a smaller species, which is probably endemic to Lake Titicaca. The ligament is scarcely visible from the exterior and can only be distinguished on large individuals. Kuiper and Hinz (*op. cit.*) recorded a relationship between shell diameter and depth, the maximum size increasing

1	Abundango	
Question	Abundance Semolod number	Porcontago
Species	Sampled number	reicentage
Anysancylus cf. lagunarum	6	0.02
A. crequil	469	1.94
Taphius montanus	2 219	9.17
Sphaerium titicacense	156	0.64
S. lauricochae	41	0.17
S. forbesi	245	1.01
Pisidium melerbrooki	27	0.11
Littoridina andecola culminea	1 337	5.52
L. andecola andecola	7 004	28.96
L. andecola neveul	2 829	11.70
L. berryi	15	0.06
L. lacustris	4 579	18.93
L. aperta	1 845	7.63
L. profunda	1 334	5.51
L. n. sp.	3	0.01
Rhamphopoma magnum	381	1.57
R. parvum	1 223	5.05
R. n. sp.	153	0.63
Strombopoma ortoni	183	0.75
Limnothauma crawfordi	2	0.008
Heligmopoma umbilicatum	21	0.08
Ecpomastrum mirum	111	0.46
Total :	24 183	

Table 1.

from only 5 mm at 40 metres, to 6 mm at 20 metres and 8 mm at 10/11 metres.

Conclusions

The mollusc fauna of Lake Titicaca would appear to be very diversified and rich in species, with nearly thirty described taxa. Their individual numerical importance is however highly variable, as can be judged from the percentages derived from a study of their distribution in the Bolivian part of the lake, a study during which certain taxa previously recorded from this habitat could not be refound (Table 1).

An almost constant component of the littoral benthic fauna, the molluscs also inhabit the entire area of the Huiñaimarca covered with macrophytes and particularly the carpets of Characeae. The sometimes very high densities of Hydrobiidae, reaching 8000 to 10 000 individuals per square metre, makes

them of the highest importance in the primary decomposition of plant material. Practically nothing is known of their biology or their ecology and we have only just started to define their distribution and their prefered biotopes. Although it is known that they are sometimes consumed by fish (see chapters on the fish), their real importance in this respect is not known. It is on the other hand evident that they are "indicators" of ancient lake conditions, but this aspect has been little studied. It is however known that they appear in dense layers at certain levels in sediment cores taken in the Huiñaimarca. This phenomenon could result from massive mortalities occurring for example at periods of sudden rises in lake level, leading to rapid anoxia in depths of 7 to 10 metres, due to decomposition of aquatic vegetation deprived of light. Such a situation has been observed within Guaqui Bay after the major rise in water level in the years 1985/86.

It therefore seems essential that detailed studics of all aspects of this component of the fauna of Lake Titicaca be carried out; even the taxonomy of the species present is not satisfactory. On this subject, in addition to the much needed study of internal anatomical structure, particular attention should be paid to the morphological variations and their causes, as the results are likely to call into question the classification presented in the present inventory.

VI.4f. The Ostracoda

PHILIPPE MOURGUIART

The study of the ostracod fauna living in Lake Titicaca began with the work of Faxon (1876) and of Moniez (1889), but about a century then went by before a new species was described (Lerner-Segeev, 1971) and more information was provided by Vargas' thesis (1982). In 1939, Beauchamp simply wrote of the material collected by the Percy Sladen Trust Expedition (he studied its Rotifera and Turbellaria): "the Protozoa, Cladocera and Ostracoda always predominate", but without any other details.

The only work providing a small amount of information on the systematics and morphology of Andean Ostracoda is that of Delachaux (1928) which deals with the Entomostraca of Lake Huaron in the Huancavelica region of Peru, a long way from Lake Titicaca. Unfortunately, the descriptions of carapace details are not sufficiently precise and because of this, the taxonomy used in this chapter is intentionally left vague so as not to uselessly increase the number of synonyms already very frequent in the literature.

The present fauna

Most of the samples collected in the Lake Titicaca basin reveal at first sight a remarkable number and diversity of species, which is comparable however with other huge ancient lake systems such as Lake Tanganyika.

The majority of species found in Lake Titicaca belong to cosmopolitan genera such as:

Herpetocypris (Family Cyprididae; Baird, 1845), Cyprinotus, Cypridopsis, Potamocypris, Candonopsis (Family Candonidae; Kaufmann, 1900), Ilyocypris (Family Ilyocyprididae; Kaufmann, 1900), Darwinula (Family Darwinulidae; Brady and Norman, 1889), Limnocythere (Family Limnocytheridae; Sars, 1925), Cyprideis (Family Cytherideidae; Sars, 1925).

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Endemic South American genera also present are rare, only the following occur:

Chlamydotheca (Family Cyprididae: Baird, 1845), Amphicypris.

On the other hand, it seems that Lake Titicaca fauna is over 50% endemic at the species level, particularly if one looks at the genus *Limnocythere* (Plate 2). There are however certain convergences with species described by Delachaux from Peru (1928). For example, the species *Neolimnocythere hexaceros* is very close to the species we have called *Limnocythere* sp. A3 and sp. B3, differing only in the angle of the "posterior spine."

The principal species living in Lake Titicaca are shown in Plate 1.

The distribution of communities

In the following section there follows a study of the communities of Ostracoda in relation to the major biotopes found in the lake (Table 1). Nine zones have thus been categorized, each characterized by the density (Table 2), the diversity of the fauna and relative density of each species in the association.

a. The epilittoral zone (ecozone a)

This comprises the streams and rivers that flow into the lake and whose fauna is mainly composed of the genera *Herpetocypris* and *Ilyocypris*, found only in sheltered areas where stands of *Myriophyllum* and/or *Elodea* are usually present. The total density never exceeds 100 individuals per square metre.

b. The supralitoral zone (ecozone b)

This is land liable to flooding where puddles or pools form after the waters have subsided. They harbour an abundant fauna, of up to several hundreds of thousands of individuals. Two very distinct types of populations have been noted:

Type 1 with *Chlamydotheca* and *Herpetocypris* dominant, associated with *Cypridopsis* and *Ilyocypris*.

Type 2 with a more diversified population of *Limnocythere* (2 or 3 species including *L. bradburyi*), *Ilyocypris*, *Cypridopsis*, *Potamocypris* and very large species of *Amphicypris* (> 4 mm).

During periods of flooding, these animals (eggs, larval stages, juveniles



Plate 1. | *Candonopsis* sp. (×150); 2 *Ilyocypris* sp. (×150); 3 *Cyprideis* sp. (×93); 4 *Cyprinotus* sp. (×93); 5 *Cypridopsis* sp. (×143); *Amphicypris* sp. (×31.4); 7 *Chlamydotheca incisa* (×52.3)

and adults) can be swept into the lake and influence the shoreline community patterns.

c. The eulittoral zone (ecozone c; 0–1.10m)

This is a transitional lacustrine zone, its faunal composition being influenced by the presence of species from the epilittoral or supralittoral zones, and/or by typically lacustrine species. The commonest association is that of *Chlamydotheca* and *Herpetocypris*, but *Darwinula*, *Limnocythere* (2 species), *Can*-



Plate 2. Genus Limnocythere. 1 L. sp. A1; 2 L. sp. A2; 3 L. sp. B1; 4 L. sp. B3; 5 L. sp. B4; 6 L. titicaca (×100); 7 L. sp. T2 (×136); 8 L. bradburyi (×157)

donopsis (2 species), Ilyocypris, Cyprinotus and Amphicypris also occur. The densities remain low (< 1000 carapaces /m²) because of the generally coarse substrates.

d. The upper infralittoral zone (ecozone d; 1.10–6.50 m)

Totora occupies the shallower areas (1.10-2.50 m). The populations are as a general rule scanty and of low diversity. Common species are *Limnocythere*



Table 1. Distribution of the ostracod communities in Copacabana Bay (1989)

(several species), *Darwinula* and *Candonopsis*, but *Chlamydotheca* and *Herpetocypris* are also present.

In deeper water (2.50 to 6.50 m) the more or less dense macrophyte stands composed of Characeae, *Myriophyllum* and *Elodea* are inhabited by *Limnocythere* (several species), *Candonopsis*, *Darwinula* and *Cypridopsis* living amongst fragments of decaying totora (< 1000 ind. m⁻²).

e. The middle infralitoral zone (ecozone e; 6.50–15m)

Cypridopsis is always dominant within the stands of Characeae (over 90% of the population), often found in association with *Candonopsis*, *Darwinula* and *Limnocythere* (sp. B4 and *titicaca*). They are all characterized by the fine ornamentation on their shells.

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Table 2. Ostracod density and biomass estimates in relation to habitat type. Macrophytes absent (-); sparse (-+); dense (+); very dense (++).

ECOZONES	MACROPHYTES DENSITY	TYPE OF SUBSTRATE	DENSITY g m ⁻²	MEAN WEIGHT µg	BIOMASS g m-2		
	-	Coarse	0		0		
ŭ	+	Fine	102	100	10-2		
b	+	F	103-105	100	0.1-10		
5	- +	F	104-106	40	0.4-40		
	+	G	0-10	50	0.5-10-4		
Ũ	+ +	F F	10 ² -10 ³	75	75.10-4-75.10-3		
d	+	F	0		0		
<u> </u>	+ +	F	10 ² -5.10 ³	50	5.10 ⁻³ -0.25		
θ	+ +	F	10 ² -3.10 ⁴	25	25.10-4-75.10-2		
f	-	F	104-5.104	50	0.5-2.5		
g	- (bryophyles)	F	105-106	50	5-50		
h	-	F	10 ² -10 ³	40	4.10 ⁻³ -10 ⁻¹		
I	-		0-10 ²	30	0-3.10-3		

f. The lower infralittoral zone (ecozone f; 15–18m)

This is situated at the limit of macrophyte growth. The fauna is diversified and relatively abundant (often > 10,000 ind. m⁻²), composed mainly of *Limnocythere* (several species accounting for 50 to 75% of the population) and *Candonopsis* (20 to 40%), but also of a few *Cyprinotus*, *Cypridopsis* and *Chlamydotheca*, rather typical of shallower waters.

g. The upper sublittoral zone (ecozone g; 18–25m)

Bryophytes are the only plants that grow here. The Entomostraca fauna is very rich (100,000 to 1000,000 individuals per square metre) and very diverse (15 to 18 species) with a majority of *Limnocythere* group A (75 to 90%) and *Candonopsis* (5 to 20%). On the other hand, genera like *Cypridopsis* and *Chlamydotheca* have altogether disappeared.

ECOZONES	LAGO MAYOR	LAGO MENOR				
a						
b	0 m	0 m				
с	1.1 m	0.8 m				
d	2.5 m	2.5 m				
e	6.5 m	3.5 m				
f	15 m	7.5 m				
g	18 m	?				
ĥ	25 m	9 m				
i	40 m	14 m				

Table 3. Comparison of the depth zonation of ecozones in the Lago Grande and Lago Pequeño (1989).

h. The lower sublittoral zone (ecozone h; 25-40m)

This extends down to around 40 m depth. Ostracoda are still numerous but the species diversity has declined. *Limnocythere* gr. A (40 to 60%), *Candonopsis* (30 to 50%), *Darwinula* and *Amphicypris* are found here.

i. The profundal zone (ecozone i; beyond 40m)

Only *Candonopsis* survives here (< 100 ind. m^{-2}) but a few empty shells of *Limnocythere* gp. A and *Darwinula* are present in the sediment, suggesting that these two species can live at this depth during certain seasons or that they arrived there after death.

Ecology

The description of the distribution of Ostracoda communities that has just been described reflects the situation as found in the Lago Grande (Copacabana Bay) during 1989.

It is applicable however to most of the lake, with the exception of gently sloping bays such as Achacachi and almost all of Lago Huiñaimarca. In the latter environments the associations are much the same but their depth zonation is different and ecozones e, f, g, h and i (Table 3) are compressed.

There are however numerous exceptions to the model, resulting from local environmental conditions and from the ecology of these entomostracans. To survive and reproduce they require particular substrate conditions, the presence of shelter, good oxygenation, food and a particular chemical composition of the water – factors that vary spatially over the lake and in time.

The density of these microcrustaceans is related to the presence or absence of vegetation and even its density. For ostracods the proximity of plants means shelter and also food (plant detritus and associated periphyton). Photosynthetic activity by submerged macrophytes also provides conditions of oxygenation in the water ideally suited to secondary consumers. On the other hand, bacterial decomposition of the abundant plant and animal remains leads to an under-saturation of dissolved oxygen at the sediment-water interface and tendency for the pH to become acid, factors unfavourable for benthic life.

As a consequence several types of habitat need to be distinguished to explain the spatial distribution of ostracods:

- very dense macrophyte stands
- open macrophyte stands
- bare sediments.

In the midst of a very dense stand of vegetation, benthic life *sensu stricto* is limited by the lack of oxygen and only a few undemanding species can live. These are mainly *Limnocythere* (sp. A1, sp. B4 and *titicaca*) and *Candonopsis*, with occasional *Darwinula*. On the other hand, free-swimming species not dependent on the substrate are very abundant. In the Characeae these are *Cypridopsis* and in the *Myriophyllum* and *Elodea*, *Chlamydotheca* and *Herpetocypris*.

In a sparse stand of vegetation, life is possible at all levels and benthic and swimming ostracods are fully represented:

- the benthic forms by Limnocythere, Candonopsis, Darwinula and Ilyocypris,
- the swimming forms by *Chlamydotheca* and *Herpetocypris*. *Amphicypris* is also present in this environment as a predator.

Only benthic forms live on bare substrates. This type of environment is found either in the supralittoral zone (temporary pools) or in the "profundal" zone (below 25 m in Lago Grande and 9 m in Lago Huiñaimarca). In the first case, *Ilyocypris* dominates the community; in the second, species such as *Limnocythere* (sp. A1) and *Candonopsis* not requiring high oxygen concentrations.

At first sight it seems that many species occupy the same biotope, but in reality interspecific competition is avoided as much as possible. For example, two periods of maximum biomass have been observed for the swimming forms: December-January and July-August, but with a delay of 2–3 weeks for *Chlamydotheca*. This latter prefers to inhabit the tops of plants whilst *Herpetocypris* stations itself on the lower parts. Of the benthic forms, *Limnocythere* lives in the top few centimetres of liquid sediment whilst *Ilyocypris* moves over the substrate surface. It is also likely that various species, of *Limnocythere* for example, do not seek the same prey, by selecting particular types and sizes of the particles.

The density of microcrustacea is also related to the trophic status of the lake and the annual range of variation in water level. In the supralittoral zone these fluctuations result in changes in chemical composition of the water. The water is oligohaline in periods of high water level, but becomes progressively more concentrated as the water subsides. Genera such as *Chla*-

mydotheca, *Herpetocypris* and *Ilyocypris* are the first to colonise temporarilyflooded habitats. These are then replaced by *Potamocypris*, *Cypridopsis* or *Amphicypris* when the total salinity exceeds $1.5 \text{ g } 1^{-1}$, and then finally by a single species (*Limnocythere bradburyi*), the only one capable of reproducing in waters where the salinity can exceed $30 \text{ g } 1^{-1}$.

Changes in lake level also have repercussions on the entire benthos down to the deepest areas. A period of high water level, by favouring water and detritus circulation leads to a proliferation of benthic organisms, particularly in ecozones f and g. A period of declining lake level would have the opposite effect. This distinction between high and low water levels occurs at the seasonal scale: for example the growth of ostracod populations in ecozones h and i is directly correlated with two factors, firstly the supply of fresh organic material coming from shallower zones, and secondly the dissolved oxygen concentration, factors related to the lake's metabolic cycle and induced by the alternance of wet and dry seasons.

As a general rule, the development of ostracod populations appears to be very dependent on the cycle of plant growth in the macrophyte stands, itself related to hydrological changes in the lake under the influence of meteorological factors. The influence of these abiotic factors is more pronounced in the littoral and supralittoral ecozones, but is still felt in the the profundal zones of the lake ecosystem. An increase in lake volume results in a beneficial effect on the benthic fauna of ecozones f, g, h and even i, whereas falling water level brings about a rapid decrease in the density and diversity of the entomostracan fauna.

Conclusions

The numerous observations made between 1977 and 1989 have provided information on the depth distribution of ostracods, related partly to that of the macrophytes and also to the relationships between these organisms and the hydrological cycles existing in Lake Titicaca at two distinct time scales: annual and long-term. The present day data serve as a reference for a palaeoecological interpretation (see Chapter III.1) providing a reconstitution of changes in lake level in Lake Titicaca over the last 7500 years. This information will also serve as the basis for a statistical analysis (transfer functions between Ostracods/Water Depth and Ostracods/Water Chemistry) which will provide a quantitative assessment of the physico-chemical evolution of the lake in terms of water level and total salinity over the Holocene.

VI.4g. The Amphipoda

CLAUDE DEJOUX

Despite the abundance and species richness of the Amphipoda in Lake Titicaca, there have been very few studies devoted to this group of animals, with the exception of the work of Faxon (1876), resulting from the collections brought back by Alexander Agassiz, that of Chevreux (1904), based on the collections from the Crequi-Montfort and Sénéchal de la Grange expedition in 1903, and the record of one species by Weckel in 1909. This species, which had originally been described by Bate (1862), had been redescribed by Weckel himself in 1907.

These publications served as the basis for identifying the amphipods collected during our extensive study of the benthic fauna of the Bolivian part of the lake, leading us to distinguish 11 different taxa, based frequently on macroscopic characters; that is one additional species (?) compared to those already recorded. In his 1876 study, Faxon described 7 new species belonging to the genus *Allochertes* (now *Hyalella*) coming from Lake Titicaca and recorded the presence of a species already known from North America: *Allochertes inermis* Smith, 1874.

Thirty years later, Chevreux recorded the occurrence of 4 of these species in the material available to him and discovered a new species: *Hyalella neveu-lemairei*. Since that time, as far as we know, taxonomic knowledge has not progressed.

Brief description of the known species

They all belong to the family Orchestidae.

Hyalella armata (Faxon, 1876) (Plate 1, Fig. 1)

This is a species measuring 8 to 9 mm from head to telson, with a rounded body without dorsal spines. The main distinguishing morphological character is the presence of lateral spines on the first four thoracic segments, increasing

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Plate 1. 1: Hyalella armata; 2: Hyalella echina; 3: Hyalella longipes; 4: Hyalella lucifugax; 5a: Hyalella latimana; 5b: male gnathopod.

in size posteriorly. The first three pairs of spines are directed forwards and downwards whereas the fourth pair are almost at right angles to the body axis. The second pair of antennae is much longer than the first and the second pair of thoracic legs is particularly broad in males. The flagellum of the first pair of antennae has 12 segments and that of the second 13 segments.

The size of the lateral spines is variable and is usually greater in individuals inhabiting deeper water, in which the fourth pair can reach a span of 10 mm from tip to tip.

Hyalella echina (Faxon, 1876) (Plate 1, Fig. 2)

This species is even more characteristic. The body is very arched and decorated with spines giving it the appearance of a hedgehog. A row of 8 spines runs along the mid-lateral line and two parallel rows of 11 spines along the length of the body either side of the mid-dorsal line. The eyes are slightly protuberant. The flagellum of the first pair of antennae has 6 to 8 segments and that of the second pair 9. The total body length can reach 10 mm.

Hyalella longipes (Faxon, 1876) (Plate 1, Fig. 3)

Eleven spines are arranged all along the mid-dorsal line. The first thoracic segment has two spines, one small and situated at the front of the segment and the other slightly longer at the rear. All the other spines start at the rear of the segment and increase in size posteriorly, as far as the 9th segment. The eyes are protuberant. The first 4 epimera are triangular, and pointed ventrally; the telson is entire. The flagellum of the first pair of antennae has 13 segments and that of the second 14. The 6th and 7th pairs of legs are very long.

Hyalella lucifugax (Faxon, 1876) (Plate 1, Fig. 4)

Again this species is easy to identify because of the row of 11 spines running along the mid-dorsal line, arising from the rear of each segment, except the first spine which arises from the anterior part of the first segment. The first 6 or 7 spines are curved forwards whereas the others are at right angles to the body axis.

The antennae are of about equal length and the abdominal legs are very long. The body measures about 11 mm.

Hyalella latimana (Faxon, 1876) (Plate 1, Fig. 5a and b)

This thick-bodied species reaching up to 12 to 13 mm in length, is much less distinctive in shape than the previous species, although 4 or 5 more or less flattened dorsal spines can still be distinguished. These are more in form of projections from the dorsal part of the segments than true spines as in the previous species.

The first pair of antennae is clearly shorter than the second and when extended, its peduncle scarcely reaches the centre of the peduncle of the second pair. The flagellae of both pairs of antennae have 11 segments. The base of the male gnathopod is very angular (Fig. 5b).



Plate 2. 6: *Hyalella longipalma*; 7a: *Hyalella cuprea*; 7b: male gnathopod; 8: *Hyalella dentata* var. *inermis*; 9: *Hyalella neveu-lemairei*; 10: *Hyalella knickerbrockeri*; 11: *Hyalella* sp.; a: head, b: thoracic leg. c: abdominal leg.

Hyalella longipalma (Faxon, 1876) (Plate 2, Fig. 6)

This also large-sized species (10 to 13 mm) only has 3 dorsal spines situated on the 5th thoracic segment and the first two abdominal segments. The spines vary in the extent to which they project, depending on the individual, and may even curve forward slightly. The posterior ventral angle of the first 3 abdominal segments is pointed towards the rear; the telson is entire. The flagellum of the first pair of antennae has 15 segments, the same as on the

second pair which is however longer. The carpus of the male gnathopod is oval in shape, without a basal point as in the previous species. The integument of the carapace is covered with sparse short setae forming scattered cross-shaped patterns.

Hyalella cuprea (Faxon, 1876) (Plate 2, Fig. 7)

No spines or teeth are present on this species and the posterior ventral angles of the first 3 abdominal segments are scarcely pointed. The flagellum of the first pair of antennae has about 10 segments, the second pair being considerably longer than the first and being equal to about a third of the total body length.

The 5th, 6th and 7th pairs of thoracic legs are short but have broad basopodites; the 5th pair is shorter than the others. The total body length is about 9 to 11 mm and the integument has brassy reflections over the entire body.

Hyalella dentata var. inermis Smith, 1874 (Plate 2, Fig. 8)

The specimens examined by Faxon and identified under this name only differ from the species described from the United States by Smith (1874) by the firmer and less transparent appearance of the integument. It is a small form without spines, 5 mm long, with an extremely undistinctive morphology. Being rather similar to the previous species, small specimens are not easy to identify.

Hyalella neveu-lemairei Chevreux, 1904 (Plate 2, Fig. 9)

This moderate-sized species (ca. 7 mm) has a laterally compressed body with a dorsal row of 6 spines or projections starting at the posterior end of the 5th thoracic segment. These projections, which get progressively longer posteriorly, vary among individuals in the extent to which they stand up away from the body. The flagellum of the first pair of antennae has 16 segments and that of the second pair 18.

Hyalella knickerbrockeri Bate, 1862. (Plate 2, Fig. 10)

This species belongs to the group with dorsal spines. The dorso-posterior spines do however project very little and mostly only occur on the first two abdominal segments. The last thoracic may sometimes have a more or less flattened projection, the total number therefore varying from 2 to 3 de-

Table 1. Relative abundances of various species of amphipod collected in the Bolivian part of Lake Titicaca during 6 sampling campaigns from 1986 to 1988.

N = number of individuals collected per biotope; NT = Total number collected. % = relative percentage of all collections. Types of biotope: A = Bottoms covered by *Chara* spp.; B = Bare sediments (z < 20 m); C = Bare sediments (z > 20 m); D = Bottoms covered by macrophythes other than *Chara* spp.; E = Littoral stones and pebbles; F = Bottoms between 20 and 180 metres depth; G = Bottoms at greater than 180 m depth; H = Areas of the lake near the mouth of the Río Suchez.

	HUIÑAIMARCA						LAGO MAYOR							
	N	N	N	N	N	N	N	N	N	N	N	N	NT	%
Hyalelia armata	39	87	-		-	-	-			2	-		128	0.84
Hyalella lucifugax	-	-	-	-	-	-	-	-	-	5	-	-	5	0.03
Hyalella dentata	672	126	7	-	37	81	16	-	54	84	-	-	1 077	7.08
Hyalella latimana	1 075	2	-	110	-	-	1	~	11	155	1	-	1 355	8.91
Hyalella Neveu Lemairel	1 099	14	1	37	1	-	15	22	1	65	-	7	1 262	8.30
Hyalelle cuprea	4 938	72	-	580	612		264	301	1 416	611	-	599	9 393	61.80
Hyalella knickerbrokeri	537	37	-	101	-	8	52	12	25	63	-	411	1 248	8.19
Hyalella echina	47	36	-	-	-	-	-	4	-	-	-	-	77	0.50
Hyalella longipalma	357	5	-	72	-	172	16			15		2	639	4.20
Hyalella sp.	16	-	-	-	-	-	-	-	-	-	-	-	18	0.12
TOTAL	8 782	369	8	900	650	261	364	339	1 607	1 000	1	1 019	15 200	
Biotopes	А	Б	с	D	E	A	Б	D	E	F	G	н		

pending on the individual. In addition the posterior ventral corner of the abdominal segments form an angle of less than 90°.

The antennae are short, the flagellum of the first pair having 7 to 9 segments and that of the second pair, which are very variable in length, can have from 8 to 15. This is a small species measuring 7 to 8 mm.

Hyalella sp. (Plate 2, Fig. 11)

This unidentified taxon was not very frequent in our samples since only 18 specimens have been collected. It is a small species (longest individuals 7 mm long), with a general appearance similar to *H. dentata inermis*, and is characterised by the absence of dorsal spines or dorso-posterior projections on the segments and the presence of abundant setae on the legs and antennae. The legs and antennae are short, giving them a thickset appearance. The flagellum of the first pair of antennae has 8 segments and that of the second, 8 to 9.

Distribution and relative abundance of the species

Details of our collections over several years of Amphipoda in the Bolivian part of the lake have been summarised in Table 1 and details are given below on the distribution of each species identified.

In 1876, Faxon considered H. armata as being the most abundant species in the lake, at that time collected from a few metres depth down to depths

of 120 metres, as for example off Juli. It was particularly abundant in Achacachi Bay, at about twenty metres depth. In our samples of amphipods from the lake, which include some 15 000 individuals, it only accounts for slightly more than 120 specimens and Chevreux (op. cit.) did not find it at all in the samples he studied. Even though the collections made by Faxon were less extensive than ours, it seems highly likely that a radical change in the species dominance has occurred, a phenomenon that we have also recorded in the case of the Hydracarina (See Chapter VI.4h).

At present this species seems to be restricted to muddy bottoms without vegetation and we have encountered it at depths of between 12.5 and 135 m.

H. echina used to inhabit the same biotopes, but was much less abundant. In terms of abundance it would appear that the situation has hardly changed, since we have only found it sporadically in the Lago Grande and Huiñaimarca (0.5% of all our sampled individuals). This species can be collected at present at depths varying from 4 and 13 m, but Faxon (*op. cit.*) recorded it as being present in the Lago Grande down to depths of 73 metres and classed it among the species preferring deep water.

H. lucifugax is also a deep-water species, the few known individuals having been collected in the Lago Grande at depths of between 70 and 110 metres. It is a remarkable fact that all the deep-water species have a heavy ornamentation of spines, which for any given species seems to increase in extent of development with increasing depth. We have only rarely found this species (5 individuals in total) living at depths of over 100 metres.

On the other hand, we have never collected *H. longipes* that Faxon recorded at several locations in the Lago Grande (Achacachi Bay, Puno Bay, Chucuito), and also off the mouth of the Rio Desaguadero. This absence from our samples does not of course prove that it is extinct.

H. latimana, in contrast is a species that we have encountered at several localities in the lake at depths of between 5 and 22 metres. It accounts for almost 9% of all the amphipods collected and mainly inhabits the aquatic vegetation in the Huiñaimarca, but is little represented in the Lago Grande where we have only found it once in any abundance, at more than 20 metres depth, off the mouth of the Rio Suchez.

H. neveu-lemairei, recorded by Chevreux (1904) as inhabiting water depths of between 2 and 24 metres, seems at present to be a species preferring the aquatic vegetation. We have collected it regularly from bottoms carpeted with *Chara*, but rarely in very great abundance (8.3% of all amphipods). As with the previous species it is found especially in the Huiñaimarca, where it lives at between 4 and 10 metres; it has however been encountered at nearly 20 metres off of Escoma.

H. dentata, accounting for slightly more than 7% of our samples of amphipods, is distributed in numerous biotopes, from a few centimetres depth down to more than 60 metres. We have never found it among macrophytes other than *Chara*, but this absence seems to be due to chance.

Another spineless form, H. cuprea, inhabits the same biotopes and is the

commonest species in the lake, accounting for nearly 62% of all individuals sampled. It greatly dominates the populations among macrophytes and in the shallow littoral zones.

H. knickerbrockeri is also a ubiquitous species on a lake scale, being found under stones along the shoreline and at depths exceeding 30 metres. It is frequent among macrophytes, but this cannot be said to be its preferred biotope as it is also frequently met with on bare sediments. Accounting for slightly over 8% of the amphipods collected, this species is classed in the group of animals of moderate abundance, but with a wide distribution in all the lake habitats.

Less abundant (4.2% of collected individuals), *H. longipalma* is rare outside of the areas occupied by aquatic vegetation. This species usually occurs in shallow water, although on one occasion 15 individuals were collected at 33 metres depth just off of Sun Island.

It is difficult to say anything precise about the distribution of the 18 individuals of *Hyalella* sp. that we collected from among *Chara* in the Huiñaimarca on two different dates and at two different localities. The small numbers sampled makes it likely that it is a rare species, but it is also possible that it inhabits a very special biotope which is little represented in all of our samples.

Density distribution and temporal changes

The figures given in Table 1 are the total numbers actually collected, either in qualitative or quantitative samples. In order to describe the distribution of abundance of all the samples taken in the Bolivian part of the Huiñaimarca at different times of the year, the data has been related either to a fixed weight of vegetation (10 g dry weight of vegetation for samples taken among macrophytes), or per square metre for samples taken on bare sediments. We have purposefully restricted this analysis to amphipods collected in the Huiñaimarca, because the quantitative sampling coverage is more complete in this part of the lake, both in time and space. The results are summarised in Figures 12 and 13.

On the basis of only four sampling campaigns (1986–1987) at only 28 stations spread over the entire Bolivian part of the Huiñaimarca, it has not been possible to obtain a very detailed picture of the density distributions throughout the year. For this reason the densities have been divided into 6 classes for samples among aquatic vegetation and 4 classes for samples on bare sediments. Examination of Figs 12 and 13 demonstrates the existence of an area of high density of variable extent, lying between Cojata Island and the north of the Taraco Peninsula. This area corresponds to water depths of 6 to 8 metres, where the bottom is carpeted with *Chara*, and where densities of between 50 and 500 amphipods per 10 g of dry weight of macrophytes were recorded. Because of the very great density of Chara in the



Figure 12. Density distributions of Amphipoda in the Huiñaimarca at two dates in 1986, one (April) corresponding to maximum water level.



Figure 13. Density distributions of Amphipoda in the Huiñaimarca at two dates in 1987.

whole of this region, this represents a considerable quantity of animals. In contrast, the coastal areas between Puerto Perez and Huarina and in Guaqui Bay are much less densely populated. The same is generally true of bare sediment substrates, except in June 1987 when high densities were recorded in a deep water area off Chua.

April 1986 was the month of maximum lake level, a level that had not been reached in the lake for many years; the difference in peak annual level between 1985 and 1986 was more than 2 metres. Such an increase in level in a few months had profound repercussions on the entire benthic fauna (see Chapter VI.4j). It led to the sudden death of the *Chara*, which before the rise in water level, populated depths close to their maximum tolerance. It is likely that anoxic conditions developed at many locations, leading to local displacement of the more mobile animal populations. As the amphipods are amongst these, such a phenomenon could explain the greater disparity in density distribution recorded in February 1987, compared to the situation which prevailed before the peak of flooding, in January 1986. This phenomenon was perhaps also responsible for the overall increase in amphipod densities in June 1987 which is clearly evident from the distribution map for this month.

Conclusion

Although the species of amphipod in Lake Titicaca which possess characteristic dorsal spines are easy to identify with certainty, the same is not true for spineless species or those with rudimentary spines, especially as individual variation undoubtedly occurs. A systematic revision is now needed, in order to be able to carry out a detailed ecological study of these very abundant organisms in the lake, which account for about 20% of all the benthic macroinvertebrates. Their role as detritivores or even predators of other small animals (zooplankton, chironomid larvae), gives them a determinant role in the ecosystem dynamics of the lake, a role which deserves special study. In addition, because of the density and biomass that they represent, they constitute a very important component in the lake's biology, serving as food organisms for numerous fish species. Frequently consumed by *Salmo gairdneri* of all sizes (although the largest individuals are mainly piscivorous, they will consume crustaceans when these are abundant), the amphipods are the most important macro-invertebrate group in Lake Titicaca after the molluscs.

VI.4h. The Hydracarina

CLAUDE DEJOUX

The first collections of Hydracarina from Lake Titicaca were made by the Percy Sladen Expedition and were studied by Viets (1955), to whom we owe the greater part if not the totality of the existing information on this group of animals. Previously, the only collections to have been made were those taken from the Andes and which gave rise to the works of Walter (1919) and of Lundblad (1924, 1930 and 1944).

The species present and their distribution

The species currently recorded from Lake Titicaca are shown in Plates 1 and 2, and below a few lines are given on each, indicating their status in this habitat. Former and recent collection sites are given on the map (Fig. 1).

Hydrachna (Scutohydrachna) miliaria Berlese (Plate 1, Fig. 1a-c)

The presence of this large globular species in the lake is uncertain: a single male may have been collected at a depth of 1.2 m at Sucune (Viets, 1955).

Eylais crawfordi Viets, 1953 (Plate 1, Fig. 2a-c)

Known from various lacustrine habitats bordering the lake and in running waters of the Altiplano, this species has been recorded from beds of *My*-*riophyllum* on the shores of Campanario Island. One of the main characters enabling it to be distinguished from other species of the genus is the presence of almost fused ocular capsules.

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Plate 1. Fig. 1. *Hydrachna (Scutohydrachna) miliaria* Berl.: 1a, dorsal view; 1b, right palp; 1c, epimera of the male genital area. 2. *Eylais crawfordi* Viets: 2a, eyes of male; 2b, maxilla; 2c, right palp. 3. *Sperchonopsis pauciscutata* Viets: 3a, ventral view; 3b, dorsal view; 3c, right palp; 3d, left palp. 4. *Limnesia minuscula minuscula* Viets: 4a, ventral view of the female; 4b, right palp; 4c, leg IV. (all figures from Viets, 1955)



Plate 2. Fig. 5. *Limnesia longivalvata* Viets: 5a, ventral view of the female; 5b, right palp; 5c, leg IV. 6. *Neohygrobates puberulus coriaceus* Viets: 6a, dorsal view of the male; 6b, ventral view of the male; 6c, female right palp; 6e, genital area of the female. 7. *Corticacarellus (Tetracorticacarellus) incurvatus* Viets: 7a, ventral view of the female; 7b, dorsal view of the female; 7c, female right palp. 8. *Atractidella porophora* Viets: 8a, dorsal view of the female; 8b, ventral view of the female and genital area; 8c, female right palp. (all figures from Viets, 1955)



Figure 1. Known distribution of the different species of Hydracarina recorded from Lake Titicaca

Sperchonopsis pauciscutata Viets, 1953 (Plate 1, Fig. 3a-d)

Recorded in very shallow water along the shoreline in Taman Bay, this is a medium-sized species (880 μ m long), slightly oval in shape and characterised by the presence of chitinous spines on the anterior part of the back, transformed into rounded papillae on the posterior part. According to Cook (pers. comm.), this species has now been placed in the genus *Notosperchonopsis*.

Limnesia minuscula minuscula Ribaga, 1902 (Plate 1, Fig. 3a-c)

As its name suggests this is a very small species, measuring scarcely more than half a millimetre. It has a wide distribution in South America, being recorded from Peru, Brazil, Paraguay and Venezuela. According to Viets (1955) it used to be common throughout Lake Titicaca, where it occurred at depths of down to 50 metres; it even occurred in the plankton. In contrast, from our recent observations, it has become very rare.

Limnesia longivalvata Viets, 1953 (Plate 2, Fig. 1a-c)

This, the second species of *Limnesia* recorded from the lake, is almost the same size as the previous species, but is more regularly oval in shape. It has short palps with very broad segments and a genital plate very large in comparison with the size of the body. The known specimens come from Sucune, in the Lago Grande.

Neohygrobates puberulus coriaceus Viets, 1953 (Plate 2, Fig. 6a-d)

Males reach almost 1500 μ m in length and 1300 μ m in width and the females are even larger. Again this is a large species frequently encountered in the running waters and lakes of the Altiplano and generally occurring among aquatic vegetation. It has been recorded from Puno Bay, but we have never encountered it in our extensive study of the benthic fauna of the lake.

This brown-coloured species is characterised by the presence of numerous chitinised plates arranged symmetrically on the body surface.

Corticacarellus (Tetracorticacarellus) incurvatus Viets, 1953 (Plate 2, Fig. 7a-c)

This small species, which hardly exceeds half a millimetre in length, is characterised by the presence of four pairs of pitted dorsal plates and one central plate. Only known from Chiffon Bay in the Lago Grande (Viets, 1955), it was collected on a small silurid fish: *Trichomycterus rivulatus*.

Atractidella porophora Viets, 1953 (Plate 2, Fig. 8a-c)

A. porophora is a small globular species about 1 mm in diameter, that has been collected in shallow water amongst vegetation in Puno Bay. Two oblique pitted plates present anteriorly on the back, and spurs on the inner face of the palp segments are the characters that make this species easy to recognize.

Arrenurus (Megaluracarus) hansvietsi Viets, 1953 (Plate 3, Fig. 9a-e)

This species, also recorded from aquatic vegetation in Puno Bay and from aquatic habitats bordering Lake Titicaca, is distinguished by its generally elliptical and unequally flattened shape. The posterior part of the body forms a characteristic sort of flattened tail, lower than the rest of the body. The palps are short and broad.

Hydrozetes sp. (Plate 3, Fig. 10a-g)

This very small hydracarian measuring about $800 \,\mu\text{m}$ belongs to the group Oribatei and does not possess differentiated mouthparts. This is at present the most common species over the whole of Lake Titicaca. It is found almost everywhere down to depths of about 20 metres, inhabiting stony shorelines, all of the aquatic vegetation and bottoms made up of bare sediments. It is dark brown in colour, the legs being short and broad.

Discussion

Viets (1955) only had the collections made by the Percy Sladen Expedition on which to describe the distribution of Hydracarina in Lake Titicaca. These collections did not cover all of both basins, so it was difficult for him to give an exact picture of the populations of these organisms. However it was clearly apparent that these were dominated by *Limnesia minuscula minuscula*, which occurred at 24 different stations, whereas the other species were frequently only represented by a single individual found in a single locality. Only *Arrenurus hansvietsi* and *Sperchonopsis pauciscutata* were found in two different localities.

Given such a type of distribution, the exact status of all the species is therefore questionable. It is known, for example, that the larvae of Hydracarina are capable of being widely disseminated by aquatic insects during their aerial ecophase (Chironomidae are particularly involved in this activity) and that aquatic birds are also a non-negligible means of transport for these small organisms. Hydracarina also constitute a regular and often important component of the biological drift in running waters. All these factors make it likely, that with the exception of *Limnesia minuscula minuscula* at the beginning of the century and of *Hydrozetes* at the present day, the presence of the other species is perhaps simply "accidental", in that they are always rare in all samples collected from Lake Titicaca.

We have almost never found *L. minuscula minuscula* in the numerous benthic fauna samples we have taken in the Bolivian part of the lake, (only 4 individuals have been found out of 13 500 Hydracarina collected, but in contrast *Hydrozetes* sp. has been found practically everywhere. If in addition,





Plate 3. Fig. 9. Arrenurus (Megaluracarus) hansvietsi Viets: 9a, dorsal view of the male; 9b, ventral view; 9c, ventral view of the female and genital area; 9d, male left palp; 9e, dorsal view of the female. (from Viets, 1955) 10. Hydrozetes sp.: 10a,b,c, dorsal, ventral and lateral views; 10d,e,f,g, legs I to IV.

account is taken of the fact that we have only found 2 individuals of *Arrenurus* hansvietsi, a few examples of Sperchonopsis pauciscutata and one as yet unidentified species (2 individuals!), we have a faunal spectrum similar to that described by Viets (op. cit.), with one largely dominant species ubiquitous throughout the lake and a series of rare species, usually restricted to a few sites around the shorelines and always in small numbers. Similar work conducted in other high altitude lakes in the Andes, not far from Lake Titicaca (Dejoux and Wasson, in press) have in contrast shown that the Hydracarina populations in these water bodies are often very dense and especially very diverse, with more than twenty taxa having been recognized, each in sufficient numbers to rule out the possibility of their occurring accidentally. Until more information comes forth, it can therefore be concluded that few species occur at great abundance in Lake Titicaca, and only a few other taxa are encountered there at low densities. At present, no endemic species of Hydracarina are known from Lake Titicaca.

Nothing is known of the biology of *Limnesia minuscula minuscula* and our work only gives a few indications on the ecology of *Hydrozetes* sp. (Dejoux, 1991). The distribution of this species is clumped and its populations are especially dense in the beds of Characeae in the Huiñaimarca where densities of more than 20 000 individuals per square metre have been encountered. Bare bottoms are clearly much less suitable, but it is not rare to find concentrations of several hundreds of individuals per square metre. *Hydrozetes* sp. is a species particularly preferring to live amongst macrophytes, and is more numerous where the vegetation structure is complex and intricated, offering good feeding conditions and shelter. For example over an area of a few tens of square metres off of Calahuta Island, we recorded mean densities of the species which vary from a few individuals per 10 g dry weight of vegetation on the smooth stems of *Schoenoplectus tatora* and *Elodea*, to nearly 500 in *Chara*, with intermediate values of 150 and 270 respectively among the roots of *Ranunculus* and a small species of Cruciferae.

It is evident that these few results are very rudimentary and, as is the case with many other groups of benthic organisms, much work remains to be done, especially on the biology and ecology of the species present.

VI.4i. The insects

CLAUDE DEJOUX

In contrast to the situation generally occurring in tropical lakes, even at high altitudes, aquatic insects only represent a secondary component in the benthic fauna of Lake Titicaca and only certain groups are represented. Of course, it has to be acknowledged that although it is possible to be certain of the presence of an organism in a water body by finding it, its absence from samples is not an absolute proof that it is absent from this biotope, especially if this is as huge as Lake Titicaca. It is however remarkable that out of about 200 samples taken from most of the Huiñaimarca and the Bolivian part of the Lago Grande, we have not collected a single Plecoptera, whereas they are generally common in other lakes of the Cordillera (genus *Claudioperla*), nor any Ephemeroptera.

In samples covering several years and almost all seasons, we have collected and identified more than 84,000 benthic macro-invertebrates. Among these the proportion of insects, represented by the following groups, does not reach 20%:

Diptera Chironomidae	16.9%
Other Diptera	0.06%
Coleoptera	1.16%
Trichoptera	0.16%
Odonata	0.005%

Only chironomid Diptera can therefore be considered as being well represented, the other insects being more or less occasional and usually only occurring in very limited and localised biotopes.

The Odonata

Only two species were recorded by Roback *et al.* (1980), which we have also collected on rare occasions.

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Plate 1. Fig. 1: *Ectemnostegella quechua*; 2: foreleg of male; 3: *Aeschna (Herperaeschna) peralta*; 4: extremity of the abdomen; 5: mask; 6: *Notonecta virescens*; 11: male paramere; 7: *Protallagma titicacae*; 8: mask and head; 9: foreleg; 10: anal gill lamella.

Protallagma titicacae Calvert, 1909 (Plate 1, Figs 7 to 10)

This a zygopteran belonging to the Coenagrionidae, that has been found at various localities in the Andes at between 3000 and 4300 metres altitude, but never in large numbers. The last nymphal stage, described by Balla (1972) measures about 1.5 cm long, excluding the gill lamellae; the body is

elongate and uniform light brown in colour. The abdomen is covered with short spines and ends in elongated gill lamellae about 4 mm long, with spiny borders and a complex tracheal pattern. It was recorded from the lake for the first time by Calvert in 1909 (Puno

It was recorded from the lake for the first time by Calvert in 1909 (Puno and Chililaya). Fraser (1972) refound it near Copacabana and Roback *et al.* (*op. cit.*) recorded it from near the town of Puno. This species is in fact more of an inhabitant of small streams and slow-flowing water courses of the Altiplano, where it lives under stones or among aquatic vegetation. It is most frequent in still water, living among macrophytes which are its preferred habitat.

Despite the fact that Lake Titicaca is very rich in submerged vegetation, it only occurs sporadically in the lake.

Aeschna (Hesperaeschna) peralta Ris, 1918 (Plate 1, Figs 3 to 5)

This species has a very wide distribution in Latin America, from low altitudes up to more than 4000 metres. It is not a large member of the Aeschnidae since the nymph hardly exceeds 3 cm in length. More or less light brown coloured body bears two darker medio-lateral longitudinal lines, formed of a series of spots in the form of exclamation marks, on each segment. In addition, a series of four symmetrical dots occurs along the median line, from the 5th to the 8th abdominal segment. The mask is typical of the family. Collected in the lake near the town of Puno by Roback *et al. (op. cit.)*,

Collected in the lake near the town of Puno by Roback *et al.* (*op. cit.*), we have only found a single specimen among aquatic vegetation from Achacachi Bay. Given that it occurs fairly regularly on the Altiplano in small pools containing macrophytes, we think that its occurrence in the lake is, like that of *Protallagma titicacae*, only accidental.

The Hemiptera

The only Hemiptera recorded from Lake Titicaca are small Corixidae of the genus *Ectemnostegella*, a genus restricted to the mountainous regions of South America, and a Notonectidae, also known as an inhabitant of the Andes. Their occurrence in the lake is very sporadic, or even rare, whereas the genus *Ectemnostegella* for example occurs abundantly in all the stagnant water pools on the Altiplano and among the vegetation of numerous high altitude lakes. This genus is particularly abundant in the peat bogs of the Cordillera, where the waters are slightly acid. The slight salinity of the waters of Lake Titicaca is perhaps a factor limiting its development in this habitat.

Ectemnostegella quechua Bachmann, 1961 (Plate 1, Figs 1 and 2)

This species, originally described from the Andes in northern Argentina, was rediscovered by the Catherwood expedition among aquatic vegetation from Puno Bay, and in similar biotopes in Copacabana Bay (Roback *et al.*, *op. cit.*). We ourselves have collected it on two occasions in Achacachi Bay, close to the shore.

This small-sized Corixidae (4 to 5 mm at the adult stage) is distinguished from other species in the genus by the last segments of the foreleg of the male being elongated and narrow and by the form of the terminal part of the paramere, which is subparallel (Fig. 11) (Bachmann, 1962).

Ectemnostegella tumidacephala Hungerford, 1948

Also collected from Puno Bay by the Catherwood Expedition, Roback *et al.* (op. cit.) were not absolutely certain of the identification of this species that we ourselves have never found in our samples. Its occurrence in the lake needs confirmation.

Notonecta virescens Blanchard, 1852 (Plate 1, Fig. 6)

Uncommon in stagnant water, but also present in the Andes in Argentina, Chile, Bolivia and Peru, a single record exists for Lake Titicaca (Roback *et al., op. cit.*).

The Coleoptera

These are hardly more diverse than the preceding groups and with the exception of the Elmidae, they are a rare component of the margins of the Lake Titicaca.

Elmidae

This family is no better represented than the following families, but its single representative in the lake *Austrelmis consors* Hinton, 1940, is relatively
abundant in certain biotopes. The larvae and adults of this species (Plate 2, Figs 1–16) are found among submerged aquatic vegetation, mainly among *Elodea* and *Chara*. It is more frequent along the shorelines, inhabiting the undersides of stones. Hinton (1940) recorded it at down to 11 metres depth and we have found it down to 17 metres, but its preferred habitat is between 0.5 and 2 metres depth.

Hydrophilidae

Only three genera are recorded from the Lake Titicaca region: *Berosus*, *Enochrus* and *Tropisternus* (Roback *et al.*, *op. cit.*). The first two are possibly represented in the lake by only one species and the third by two species. This uncertainty is due to the fact that the publications records them from "Puno at Lake Titicaca ", without giving further details of the collection locality. It is therefore possible that these species came from lentic habitats situated at or near Puno, but not in the lake itself, the same being the case for the species they recorded from Huatajata, a small village on the shores of the Huiñaimarca. This is important, since it is possible that, as in the case of other insects, the lake's water is unsuitable for the development of these species, whereas they can find favourable conditions in nearby habitats.

The species recorded are *Berosus chalcocephalus andinus* Mouchamps 1963, *Enochrus (Hugoscottia) peruvianus* d'Orchymont 1941, *Tropisternus setiger* Germar 1824 and *T. lateralis limbatus* Brulle 1837. We ourselves have only ever collected two identical larvae of Hydrophilidae, among aquatic vegetation in the Huiñaimarca, which we are incapable of attributing to one or other of these species (Plate 3, Fig. 1).

Dytiscidae

Only one small species of Hydroporinae, *Liodessus andinus* Guignot 1937, has been recorded from the lake (Puno and Copacabana bays) by Roback *et al.*, 1980. We ourselves have collected two larvae among aquatic vegetation from the bottom of Achacachi Bay, but which we again cannot attribute to this species with certainty (Plate 3, Fig. 2). These rare collections of adults and larvae from Lake Titicaca, contrasting with the more abundant records from neighbouring lentic habitats, again prove that insects do not find the lake a very propitious environment for their development.

The Diptera

No Diptera other than Chironomidae were collected in Lake Titicaca by the Catherwood Expedition. In contrast, our own collections have produced 48



Plate 2. Austrelmis consors. Fig. 1: larva; 2: antenna of larva; 3: mandible; 4: bristle of anterior border of labrum; 5: ventral view of labium; 6: ventral view of right maxilla; 7: ventral view of thorax; 8: ventral view of the operculum; 9: dorsal view of 9th abdominal segment; 10: left opercular claw; 11: pupa; 13: adult; 14: male genitalia; 15: dorsal view of the median lobe; 16: ventral view of paramere. (from Hinton, 1940, except for Figs 1 and 13).



Plate 3. Fig. 1a: Hydrophilidae larva; 1b: ligula; 2: Dytiscidae larva; 3a: Dolichopodidae larva; 3b: extremity of abdomen; 4a: Dolichopodidae larva; 4b: extremity of abdomen; 5a: Ephydridae larva; 5b: ornamentation of the dorsal surface; 5c: extremity of abdomen; 6a: Dolichopodidae larva; 6b: extremity of abdomen.

individuals representing a little less than 0.06% of all the invertebrates examined from the lake. They are therefore rare and, with the exception of the Ephydridae, which were collected from sediments from the shorelines (Plate 3, Fig. 5), all the others come from among aquatic vegetation, either from the Huiñaimarca or from Achacachi bay.

Three species of Dolichopodidae, that we have not been able to identify

any further, have been found; drawings of these are given in Plate 3, Figs 3, 4 and 6.

Chironomidae

This is by far the best represented group of insects in Lake Titicaca.

The first records of chironomids from this habitat appeared in the works of Brundin (1956) and only concerned Puno Bay. He did however compare the specimens collected from this locality with other samples made in neighbouring high latitude lakes and found the Bay to be relatively rich. He recognised 9 species for which he only gave the genera: 2 species of Chironomus, 1 Polypedilum, 1 species from a genus close to Polypedilum, 1 Paratanytarsus, 2 Syncricotopus, 1 species from the Pseudosmittia group and finally 1 Corynoneura. No description of the species collected was given, so that it is difficult to find the correspondence that may exist between these species and certain of the 15 taxa recorded nearly thirty years later by Roback and Coffman (1983) in their study of material brought back from the Bolivian and Peruvian Altiplano by the Catherwood Expedition. These latter in any case only identified the specimens collected incompletely and described them only to the generic level, with the exception of one species of Polypedilum. The material at their disposal was not representative of the entire lake since it came essentially from three regions: Puno Bay and its immediate neighbourhood (Capachica Peninsula) and the areas around Copacabana, together with a few samples made at Huatajata. In addition to Polypedilum (Tripodura) titicacae, they recognised two species of Cricotopus sensu stricto, three species of Cricotopus, probably belonging to the subgenus Isocladius, one species attributed without certainty to the genus Paracladius, a Pseudosmittia, a Corynoneura, two species of the genus Chironomus and finally three Tanytarsini belonging to the genera Tanytarsus, Paratanytarsus and Rheotanytarsus.

Plates 4 to 7 represent the descriptions of the main species recorded by Roback and Coffman (*op. cit.*).

Our samples of the benthic fauna from the Bolivian part of the lake have provided us with numerous chironomid larvae and pupae as well as a few adults, captured along the shore or over the lake itself at emergence. These data have enabled us to define the status of these Diptera within this geographical area.

The proportions of the various species among the more than 14,000 chironomid larvae examined, are given in Table 1. It is immediately evident that during the period of study, 2 genera clearly dominated, one living mainly among aquatic vegetation (*Rheotanytarsus*) and the other in the sediments (*Chironomus*).

Although it is certain that the *Chironomus* species that we have collected is the same as the *Chironomus* sp. 1 recorded by Roback and Coffman, the



Plate 4. Chironomus sp. 1. Fig. 1: antenna of larva and detail of apical segments; 2: mentum teeth; 3: epipharyngeal comb; 4: anterior and posterior epipharyngeal setae; 5: apex of mandible; 6: lateral spur of last abdominal segment of the pupa; 7: cephalic tubercle. *Chironomus* sp. 2. 8: antenna of larva and detail of apical segments; 9: mentum teeth; 10: epipharyngeal comb; 11: apex of mandible. *Polypedilum (Tripodura) titicacae.* 12: last segments of antenna of female; 13: palp: 14: detail of last segments of antenna of larva; 15: premandible; 16: mentum and paralabial plate; 17: lateral spur of last abdominal segment of pupa; 18: ornamentation of tergites III to VI. *Paratanytarsus* sp. 19: apex of mandible; 20: epipharyngeal comb; 21: mentum and paralabial plate; 22: basal segments of the antenna; 23: apex of antenna; 24: respiratory organ of pupa; 25: lateral spur of the last abdominal segment; 26: abdominal tergites. (from Roback and Coffman, 1983).



Plate 5. Tanytarsus sp. Fig. 1: abdominal tergites of pupa; 2: lateral spur of the last abdominal segment; 3: respiratory organ; 4: larval premandible; 5: mandible; 6: epipharyngeal comb; 7: mentum and paralabial plate; 8: segments at the base of the antenna; 9: terminal segments of antenna. *Paratanytarsus* sp.; 10: abdominal tergites of pupa; 11: lateral spur of the last abdominal segment; 12: terminal segments of antenna of larva; 13: epipharyngeal comb; 14: mentum and paralabial plate. (From Roback and Coffman, 1983).

species belonging to the genus *Rheotanytarsus* in contrast is not the same as that described by them. The difference in the larvae is slight although they do have Lauterborn organs on the antennae which are much shorter (about half the length of the last three segments combined). The paralabial plates



Plate 6. Cricotopus (*Cricotopus*) sp. 2. Figs 1 and 2: lateral setae of the last abdominal segment and respiratory organ of the pupa. *Cricotopus* (*Cricotopus*) sp. 3. 3 and 4: mentum and epipharyngeal comb of the larva; 5, 6 and 7: mandible, premandible and antenna; 8 and 9. abdominal tergites and respiratory organ of pupa. *Cricotopus* (*Isocladius*?) sp. 1. 10, 11, 12 and 13: antenna, mandible, epipharyngeal comb and mentum of larva; 14 and 15: abdominal tergites and last abdominal segments of pupa. (from Roback and Coffman, 1983)



Plate 7. Cricotopus (Isocladius?) sp. 2. Figs 1, 2 and 3: antenna, mandible and mentum of larva. with epipharyngeal comb. *Cricotopus (Isocladius?)* sp. 3; 4, 5 and 6: mandible, antenna, mentum and epipharyngeal comb of larva. *Paracladius?* sp. 1; 7, 8, 9, 10 and 11: antenna, mentum, mandible, premandible and structure similar to a ligula, of the larva; 12 and 13: last abdominal segment and respiratory organ of pupa. *Pseudosmittia* sp. 2; 14, 15 and 16: mentum, premandible with epipharyngeal setae and antenna of larva. *Corynonetura* sp. 3; 17 and 18: mentum and basal setae of the parapod of the larva. (from Roback and Coffman, 1983).

Table 1. Main species of Chironomidae collected in the Bolivian part of the lake between 1985 and 1989. Identification refers to the work of Roback and Coffman (1983), or to the collection codes of the author (e.g. sp. CHBF).

Sampled species	Percentages (total number of organisms : 14.282)
Rheotanytarsus sp.	44,5
Polypedilum (Tripodura) titicacae	1,4
Cricotopus (Isocladius) sp. 1, R & C	3,9
Cricotopus (Isocladius) sp. 4, R & C	0,01
Chironomus sp. 1 R & C	42,8
Cricotopus sp. (CHBF)	5,4
Cricotopus sp. (CHBG)	0,6
Corynoneura sp. 3, 4 & C	0,8
Pentaneurini, cf. Pentaneura sp. (CHBI)	0,01
Orthocladiinae sp. (CHBJ)	0,9
Orthocladiinae sp. (CHBK)	0,02

are also long and narrow and the mentum has four teeth on each side of a central monocuspid tooth. The difference is more pronounced in the pupa, which for example has six pairs of chitinous plates on the abdominal tergites of segments III to IV.

Roback and Coffman (*op. cit.*) recorded the occurrence of *Chironomus* sp. 1 down to 120 metres depth in the Lago Grande. In 1986–89 this species was not very frequent in this basin (only present in Achacachi Bay down to about fifteen metres), but it was very abundant in the deep water area of the Huiñaimarca (between 5 and 40 metres), where densities in excess of 2000 individuals per square metre were recorded.

Rheotanytarsus sp. was equally abundant in the Huiñaimarca and in the Lago Grande, inhabiting submerged macrophytes, the larva living in a small tube of irregular shape, generally formed of an agglomeration of mucus and organic debris. Densities reached 700 to 800 larvae per 10 grams dry weight of plant substrate.

The two members of the Orthocladiinae in the genus *Cricotopus* were the third and fourth most abundant species in the Bolivian part of the lake during our study, accounting for 4 and 6% of the individuals collected, respectively. They lived mainly among the aquatic vegetation and on rocky substrates along the shores. *Polypedilum (Tripodura) titicacae*, inhabiting both among macrophytes and in the sediment, seems to be a widespread species in the Andes that we have encountered in other lakes on the Altiplano and in the Cordillera and which occurred regularly in the samples. In contrast, the other species only occurred sporadically in our study.

From our own samples and from previous records, it would appear that about twenty species can be found in the various biotopes in the lake, but among these only 5 or 6 are really abundant. A special study on this group

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would be needed to produce a full description of the taxa present, allowing their identification to the species level.

The Trichoptera

This is also one of the groups of insects rarely collected in the lake, although they can be abundant, but never very diverse in other lacustrine habitats in the Cordillera. We have however found seven species during our study, whereas Roback *et al.* (1980) only recorded one.

Limnophilidae

Anomalocosmoecus blancasi Schmidt, 1957. (Plate 9, Figs 1-3)

This species was recorded for the first time as an adult by Schmidt (1957), from two localities in the Lago Grande (Pomata and Vilquechico); the larvae of this limnephilid belonging to the subfamily Dicosmoecinae were also collected by the Catherwood Expedition in Copacabana Bay in depths of 2 to 5 metres (Roback *et al. op. cit.*; Flint, 1982). Based on what Schmidt *op. cit.* wrote about the genus to which it belongs and in the absence of records from elsewhere, it is likely that this species is endemic to Lake Titicaca. "The genus *Anomalocosmoecus* is very interesting. It is no doubt derived from *Magellomyia* and has acquired the status of a genus to itself by its very marked specialisation. It would appear to be adapted to living on the margins of Lake Titicaca...".

Anomalocosmoecus, nr. argentinicus Flint, 1982. (Plate 9, Fig. 4)

A single individual of this species has been collected from a site off Escoma. Its presence in the lake may be viewed as accidental.

Magellomyia illiesi Marlier. (Plate 8, Figs 8-10)

This species has only been collected three or four times in small numbers in the immediate neighbourhood of the mouths of inflowing rivers (Río Suchez, small seasonal streams near Huatajata and in the Ancoraimes region). As it is very abundant in most of the water courses of the Cordillera, it is almost certain that it entered the lake by the phenomenon of biological drift, and that it continued to grow near the mouths of these water courses in the lake, but did not penetrate any further. As it can complete its life cycle in the



Plate 8. Ochrotrichia (Metrichia) sp. Figs 1, 2 and 3: larva; case and larva in its case. *Oxyethira* sp.; 4, 5 and 6: lateral and front view of case; larva. *Leucotrichia* sp.; 7a: larva; 7b: case. *Magellomyia illiesi*; 8, 9 and 10: general aspect of larva; case, lateral view of front end.

littoral areas of other high altitude lake in the valleys draining into the Altiplano (Dejoux and Wasson, in press), it seems likely that a limiting factor exists in Lake Titicaca preventing its full development away from the areas directly influenced by inflow rivers.



Plate 9. Anomalocosmoecus blancasi. Figs 1, 2 and 3: adult; general view of larva; head. (from Schmidt, 1957 and Flint, 1982). *Anomalocosmoecus* nr. *argentinicus*; 4: dorsal view of head. *Neotrichia* sp.; 5, 6 and 7: general view of the larva; abdominal laws; case.

Hydroptilidae

Four species have been collected sporadically, mainly living among the aquatic vegetation and some under stones along the margins. All these species are of small size.

Oxyethira sp., (Plate 8, Figs. 4-6)

The case in the form of a flattened bottle is characteristic of the genus, the larva itself having a typical morphology, with an abdomen with rounded swollen segments, the posterior pair of legs long and slender and the anterior pair short, broad and prehensile. The case with an average length of 2 mm, is closed at the two ends at pupation. It has a flexible leathery consistency.

We have found about fifty specimens of this species among submerged

macrophytes in the Huiñaimarca and in the same biotopes in the Lago Grande (Achacachi Bay). It seems to be more frequent among plants situated near to the surface and was much more common among a small crucifer growing at the lake margins than on other species of macrophytes.

Ochrotrichia (Metrichia) sp., (Plate 8, Figs 1-3)

This species, in which the last instar larva measures about 2 millimetres, lives in the same biotopes, but is also sometimes found under stones on the shore, especially when these are covered by dense periphyton. The case is also of a leathery consistency and is in the form of a spectacle case; it is often fixed to vegetation by a small mucous ligament situated on the lower side. It is an uncommon species.

Leucotrichia sp., (Plate 8, Figs 7a and b)

We have only rarely encountered this species in its case. It is very small (1.4 mm), and the larva has only ever been found among *Chara* where it is infrequent, only six individuals having been collected. The case is shaped like a grain of wheat.

Neotrichia sp., (Plate 9, Figs 5-7)

A dozen individuals of this small species of Hydroptilidae, occasionally also found in other high altitude lakes, have been collected on two occasions in biotopes of the same type, consisting of angular stones lying on sandy sediments in shallow water. These biotopes, of which one is situated in a bay on the north west of Sun Island and another on the north west of the Taraco Peninsula, are beaten by waves, and therefore well oxygenated. The larva is enclosed in a curved case formed of small sand grains stuck together with mucus. A similar mucus secretion fixes the case to the underside of the stones.

Conclusions

With the exception of chironomid Diptera, the aquatic insects are a minor component of the benthic fauna of Lake Titicaca – a remarkable situation. It is difficult at the moment to know the exact reason; it is only possible to put forward a hypothesis of the existence in this environment of an overall factor unfavourable for insects, which is perhaps the excessive salinity (1000 to 1500 μ s cm⁻¹ depending on locality). The fact that certain species have

only been found in areas close to the mouths of permanent inflowing rivers or along the shorelines, which at certain times of year receive major inputs of freshwater by direct runoff after heavy rainfall, support this hypothesis. It is known that the rivers flowing into Lake Titicaca have a rather high salinity, especially when they flow over the sedimentary formations of the Altiplano (5 to 20 mmol l^{-1} according to Carmouze *et al.*, 1981). Despite this total dissolved salt concentration, the streams support a benthic insect fauna that can be considered as being rich and fairly diverse, when account is taken of the high altitude (Marin, 1989). The biological drift, which is a characteristic feature of every water course should, for those organisms that are not strictly rheophylic, therefore be a factor allowing colonisation of the lake areas near to the river mouths, provided they find suitable ecological conditions there. The fact that only rare individuals of species not found elsewhere in the lake, but present in the water courses, are found in these areas of Lake Titicaca, shows that the phenomenon of arrival in the drift occurs, but that it leads to virtually no colonisation of the lacustrine environment. It therefore seems likely that the salinity threshold allowing normal development of such organisms is quickly surpassed in the lake, or else that they are sensitive to the natural toxins produced by the very abundant charophytes in the lake.

It is remarkable that no Plecoptera have been recorded from the waters of Lake Titicaca, whereas they are very frequent in the other neighbouring lakes of the Cordillera. The same remark cannot be made for the Ephemeroptera since Gilson (1964), without referring to published data, recorded them as present. It is nevertheless strange that in four years of observations we have not encountered a single individual. The chironomid Diptera are in contrast a permanent component of the macro-invertebrate fauna of the lake, and taking into account the altitude, they can be considered as being very diverse. Their occurrence, sometimes in very large quantities in the macrophyte beds or in the sediments, means that they play a considerable role in the secondary production of the lake, comparable in some seasons and some sites to that of the molluscs and amphipods. In the absence of detailed studies of the stomach contents of the fish inhabiting the lake, the position they occupy in the diet of the fish fauna is poorly known. At the times of major emergences of the large Chironomus, it is on the other hand evident that they constitute a real bonanza for many birds, including both gulls and ducks (see Chapter VI.6c).

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VI.4j. The benthic populations: Distribution and seasonal variations

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As has been shown in the previous chapters, the macro-invertebrates of Lake Titicaca are for the most part only partially known, this knowledge generally being limited to a simple, often incomplete, species list. Until the last few years, no attempt had been made to study the benthic fauna as a community of organisms and it is only for the mollusca, which were collected in abundance in the past, that information exists on the major features of their depth distribution.

The setting and limits of recent studies

Two studies on the benthic populations of Lake Titicaca have been undertaken so far. The first was carried out in Puno Bay as part of the hydrobiological works directed by the University of Puno and the IMARPE (Instituto del Mar del Perú), in order to assess the degree of eutrophication in the bay (Medina, 1983; Morales *et al.*, 1989). We ourselves carried out the second study in the Bolivian part of the lake, in order to evaluate the importance of this component of the fauna in the overall ecology of the lacustrine environment and to demonstrate the type of populations present and their seasonal cycles.

These two works are certainly insufficient for a thorough understanding of the benthic fauna of such a vast water body as Lake Titicaca. The main biotopes present such as shallow bays, large areas covered with charophytes or other macrophytes and areas of medium or great depth, have however been studied at least once.

The various locations for which information on the composition of the macro-invertebrate populations is available are shown in Fig. 1. This information is usually based on quantitative sampling made with an Ekman grab, or qualitative samples taken with a net or by scrubbing and sieving submerged substrates.

Some of these stations (those underlined) have been the subject of regular sampling aimed at determining the temporal patterns of change in the fauna.

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Figure 1. Location of benthic fauna sampling stations in Bolivian part of Lake Titicaca and in Puno Bay.

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In the most favourable conditions, quantitative samples have been taken, but it is certain that the manipulation of an Ekman grab without anchoring the boat and in depths exceeding 50 metres, does not always provide samples covering the same area and depth of penetration. Similarly, the use of this equipment on bottom sediments carpeted with macrophytes is often difficult. In this latter case, we have expressed the densities of invertebrates collected in terms of the number of organisms per unit dry weight of plant material collected (unit = 10 g after drying at 60°C, to constant weight), rather than per unit area (m⁻²), as was the case on soft sediments devoid of vegetation. All the samples were sieved through a mesh of 250 μ m, before preservation and sorting.

Because of the taxonomic complexity of some groups of organisms, or even the impossibility of identifying certain of them precisely, especially in the larval stages, we frequently only took into account taxonomic levels such as the family or even order.

The benthic fauna of a highly eutrophicated environment: Puno Bay

The inner part of Puno Bay, rather isolated from the rest of Lago Grande and receiving virtually all the urban effluent from the town of Puno (nearly 100,000 inhabitants) and several other small shoreline communities, is highly eutrophicated (Northcote *et al.*, 1989 and Chapter VII.4 of this book). This eutrophication, which manifests itself by the presence of extremely abundant aquatic vegetation and heavy decomposition of organic matter leading to local or periodic anoxia, results in the occurrence in this area of animal populations differing significantly from those in the rest of the Lago Grande. The outer part of the bay is also affected by this eutrophication, but to a lesser extent, because of easier exchanges with the open water outsisde the bay.

The quantitative and qualitative studies of the benthos of these various zones reported by Medina (1983) and Morales *et al.* (1989), based on transects running from the innermost part of the bay to the outside, have provided the following results.

- The inner part of the bay has a much less diverse and much less dense fauna than the outer part, this difference being more pronounced the deeper the water (Fig. 2).
- No macro-benthic organisms were collected in the inner bay beyond depths of 6 metres for a period of several months.
- Although the populations showed seasonal changes in density in the outer bay, with a maximum in the dry season or slightly before, they remained almost identical and at low densities throughout the year in shallow parts of the inner bay.
- The faunal associations of the inner bay only included 4 taxonomic groups (oligochaetes, leeches, amphipods and chironomids), which can all with-



Figure 2. Monthly average abundance of total zoobenthic organisms at three depth zones in inner and outer Puno Bay, 1982. Averages based on 3 samples at each depth on each date. (From Morales *et al.*, 1989)

stand low oxygen concentrations, whereas 16 groups occur outside the bay.

On a more general level, the studies carried out by the authors cited above provide some information on the seasonal changes in relative densities of the main taxonomic groups in the shallow zone of the outer part of Puno Bay, the part least subject to the disrupting effects of eutrophication (Fig. 3). As the study only lasted one year, it is however impossible to know whether the recorded changes occur every year with each of the groups.

At 2 metres depth, the most abundant organisms in order were molluscs, amphipods and sponges, the same situation occurring at 4 metres, but at about 6 metres the situation changed as the sponge populations became very



Figure 3. Seasonal changes in percent contribution of major groups to the total zoobenthic abundance in the inner and outer areas (3 depth zones) of Puno Bay, 1982. (from Morales *et al.*, 1989) ^a includes turbellarians, nematodes, ostracods, hydracarinans and hemipterans.

sparse. This situation corresponds partly to what we know from the rest of the lake, although the dominance of sponges in the shallow zone was practically never recorded in for example the Huiñaimarca, where they are generally rather rare.

The populations of the Bolivian part of the lake

Because of the political division of the lake into Peruvian and Bolivian sectors, our sampling was restricted to the latter region. It is therefore not absolutely certain that the results would have been completely identical for the same types of biotopes in the two regions.

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Table 1. Relative proportions of the main taxonomic groups of macro-invertebrates in Lake Titicaca, calculated for all biotopes combined, on samples collected between January 1986 and June 1988. Classed in order of decreasing relative frequency and based on 85,000 organisms collected.

TAXONOMICAL GROUPS	Relatives %	Cumulated %
Mollusca	29.51	29.51
Amphipoda	19.32	48.83
Chironomidae	16.86	65.69
Hydracarina	16.24	81.93
Oligochaeta	9.14	91.07
Coelenterata	5.77	96.84
Tricladia	1.31	98.15
Elmidae	1.15	99.30
Hirudinea	0.42	99.72
Trichoptera	0.16	99.88
Diptera others than Chironomidae	0.057	99.937
Hemiptera	0.007	99.944
Hydrophilidae	0.005	99.949
Odonata	0.005	99.954
Bryozoa	0.004	99.958
Dytiscidae	0.001	99.959

General overview of the macrobenthos

The overall picture that we give of the benthic populations in Table 1 represents the mean status for the entire Bolivian part of the lake calculated over a period of slightly more than 2 years.

As with any calculation of this type, in which samples belonging to very different biotopes have been combined, this picture does not necessarily correspond to any particular situation in any given habitat. It is an indication of the mean characteristics of the benthic populations for all biotopes combined at the end of the 1980s, ranking the frequency of occurrence of the main taxonomic groups.

Examination of Table 1 shows that just two groups, Mollusca and Amphipoda, make up nearly 50% of the macro-invertebrates, a feature that can be considered as a biological characteristic of Lake Titicaca. If a further six groups are included, these account for 99.3% of the total population, whereas eight more groups need to be added to make up the total benthic fauna. Among these last eight groups, six are insects, which confirms what was seen in the last Chapter – that this class is on the whole poorly represented in the lake.

When the same analysis is carried out separately on each of the main biotopes present in the lake, very different pictures are obtained, although the major characteristics mentioned above often remain valid.



Figure 4. Distributions of the main groups of benthic invertebrates in various biotopes of the Huiñaimarea.

The major types of benthic habitats present in the lake

If a sufficiently large scale is taken to ignore the mosaic of tiny habitats which in some cases only extend over a few hundreds of square metres, a map of the major benthic biotopes can be drawn up for the lake and their characteristic invertebrate populations can be defined. In the Huiñaimarca, where the vegetation cover is very extensive, we have made a distinction between bottoms carpeted with *Chara* (which constitutes both large area and an ecological entity), and bottoms covered by other plants, without distinguishing between the species involved.

In the Lago Grande, the morphometry of the basin and the depth are the two main determining factors that have been taken into account.

The Huiñaimarca

The distribution of the major taxonomic groupings of invertebrates is shown diagrammatically in Fig. 4 and the distribution of the principal ecological zones in Fig. 5.



Figure 5. Major ecological zones of the Huiñaimarca (Bolivian part), in relation to the distribution of benthic organisms; A = sediments without vegetation; B = sandy or stony littoral zone; C = bottoms covered by various macrophytes; D = bottoms covered with *Chara* spp.

The littoral fringe

This is rarely muddy, and most frequently composed of accumulations of more or less coarse sand, gravel or worn pebbles. This is a shallow zone (0 to 40 or 50 cm on average), generally under the influence of waves. The animals living here are burrowers or live on the undersides of stones. Nearly 50% of the population of this well-oxygenated biotope is composed of amphipods (*Hyalella* spp.). This is also the preferred habitat for planarians; chironomids belonging to the Tanytarsini can be locally abundant, as can *Taphius* spp. (Planorbidae).

Bottoms covered with macrophytes other than Chara

In this zone we include the populations which inhabit the various types of macrophytes such as *Schoenoplectus tatora*, *Elodea potamogeton*, and *Myriophyllum elatinoides*. Molluscs generally dominate here, making up



Elodea potamogeton

Potamogeton

HYDRACARINA

CHIRONOMIDAE

150

strictus

Figure 6. Distribution of the main groups of benthic invertebrates in various types of macrophyte associations and adjacent biotopes.

COELENTERATA THE OTHERS

TRICLADIA

HIRUDINEA

nearly 50% of the population on average, but amphipods and oligochaetes are also well represented, with percentages for each group close to 20%.

A more detailed analysis of this biotope (Dejoux, 1991) shows that marked differences exist in the composition of the populations occurring among the different species of macrophyte, differences which are essentially related to the morphological structure of the plant substrate. A complex structure together with good oxygenation of the macrophyte stand (situation near the shore or near the surface) being associated with the occurrence of a dense and diversified invertebrate population (Fig. 6).

Bottoms covered with Chara

Muddy bottoms

AMPHIPODA

OLIGOCHETA

MOLLUSCA

400

20

1000

Molluscs again dominate here, accounting for 30% of the population, but three other groups, the Hydracarina, Chironomidae and Amphipoda constitute 21, 19 and 15% of the mean total population, respectively. This and the

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previous biotope represent the most diversified habitats in terms of their macro-invertebrate populations. Here, for example, minor groups occur, such as the Corixidae, Ephydridae larvae, occasional Odonata and the majority of the few species of Trichoptera present in Lake Titicaca. These bottoms carpeted with *Chara* cover a very large area of Lago Pequeño (see Chapter VI.2). As they harbour a great biomass of invertebrates, they are of paramount importance for the biological processes of the lake.

Bare sediments in shallow water

Sediments bare of vegetation and occurring at less than 20 metres depth do not cover a very great area within the Huiñaimarca and are mostly situated on the Peruvian side. Another separate biotope could have been distinguished, but is included together in this category of biotope: this consists of areas of bare sediments scattered within the macrophyte beds, at places where there are discontinuities. These areas are usually in shallow water (10 to 12 metres at maximum) and are rich in plant detritus, but still fairly well oxygenated. Amphipods and molluscs dominate here, sometimes together with Chironomidae. Beyond the depth of macrophyte growth, the bare sediments are the site of accumulation of large quantities of plant detritus in the process of decomposition, except in those areas situated near river mouths, where currents can occur, at least occasionally. Oxygen is often lacking in this type of sediment, which is characterised by the formation of black muds, rich in organic matter. Samples of some of these sediments are found to be totally azooic and smelling of H₂S, as a result of prolonged anoxia. In sediments where the oxygen concentration remains sufficient, the benthic populations are nevertheless still dominated by resistant organisms such as oligochaetes (40 to 50% on average), Chironominae and certain molluscs (Littoridina sp.) living on the surface. These sediments are however generally poor in invertebrates.

The Chua Depression and Tiquina Strait

These two areas are special because of their great depth (for this part of the lake), and because they have relatively well-oxygenated bottom sediments, probably because of deep water currents. No precise data exist however on the intensity of any such currents, but chemical analysis of the water reveals the existence of exchanges between the two lake basins (see Chapter V), and as the only outflow (Río Desaguadero) from the lake is in the south, outflow by gravity from the northern basin must pass through the Tiquina Strait (see Chapter IV). The presence of compact grey sediments, almost devoid of plant remains, or even of sandy silts difficult for the Ekman grab

to penetrate, also seems to indicate that these areas of bottom are at least periodically affected by significant currents.

The areas of softest sediments are colonised by a dense population of *Chironomus* sp. (45% of the population on average); also occurring are Hydra (33%) and oligochaetes (16%), organisms which can withstand temporary oxygen deficits due to the depth (at the time of stratification for example), but which can also benefit from input of particular organic matter, at the time when periodic currents are established.

The Lago Grande

The rocky coastal zone (H)

Rocky and gravelly shores similar to those in the Huiñaimarca also occur in the Lago Grande, but these have been included in with a biotope consisting of large blocks of rock or screes derived from the erosion of usually steeply shelving shores. The shores of the Lago Grande are in fact generally very steep, with a reduced or non-existent macrophyte fringe. Qualitatively, the populations of macro-invertebrates do not differ significantly from those occurring in the same stony habitats in the Huiñaimarca, but amphipods, accounting for nearly 74% of the population, are even more dominant. This is also one of the few biotopes where beetles of the family Elmidae occur in any significant proportion (7%) (Fig. 7).

Shallow bays with macrophytes (F)

Biotopes similar to those found in the Huiñaimarca occur in these areas. Molluscs, with nearly 56% of the total population, are always the dominant group among *Chara* beds (which confirms the homogeneity of this type of habitat). In contrast, chironomids and amphipods dominate among the other macrophytes (43 and 38%, respectively).

With the exception of the very large Achacachi Bay, and those of the Ríos Ramis and Huancané and of Puno Bay that has already been described, these biotopes only represent a very reduced area in the northern basin.

The mouths of inflowing rivers (L)

The mouths of the rivers flowing into the lake represent a transitional biotope in which are encountered some faunal components brought down by the biological drift. These components are only present at low densities and are only found in the area of freshwater inputs since they are incapable of maintaining themselves further into the lake environment: this is the case for certain insects for example (see Chapter VI.4i). In general, as a result



Figure 7. Distribution of the main groups of benthic invertebrates in various biotopes of the Lago Grande.

of the inputs of suspended matter and good oxygenation, amphipods dominate the benthic populations (ca. 50%), followed by *Hydra* (20%).

Bare sediments in less than 20 metres (I)

The depth of 20 metres has been arbitrarily chosen for the simple reason that this was the depth adopted in the Huiñaimarca. It would be more correct to speak of bare sediments in shallow water, especially as macrophytes descend to greater depths than in the Huiñaimarca because of the great transparency of the waters of the northern basin. This biotope is therefore composed of muddy sediments more or less rich in plant detritus, generally occurring on rather steep slopes. They receive inputs of organic matter directly from the littoral and are largely dominated by molluscs (more than 65%). It is in these biotopes that this group achieves its highest dominance. Next come the amphipods with nearly 24%. Hydracarina, oligochaetes and chironomids account for almost all the remaining 11%, indicating their low relative abundance.

Bottom sediments between 20 and 180 metres depth (J)

Although the depths defining the upper and lower limits of this zone should again be considered as approximate, it does have a true ecological reality. This zone is no longer under the direct influence of inputs of macrophyte detritus, but depends more on organic inputs related to the death of the plankton. It is also a zone where the bottom sediments still receive an adequate supply of oxygen, and where the absence of prolonged anoxia allows the survival of diverse benthic populations. On average amphipods dominate, accounting for 45%, then molluscs (nearly 29%). The relative importance of oligochaetes (19%) is also a characteristic of the profound lake zones, this group being one of the best adapted to oxygen deficits.

Bottom sediments in depths of more than 180 metres (K)

To be more precise, bottom sediments at more than 180 metres need to be divided into those that are completely azooic and those where benthic populations can still survive. The number of samples taken at these depths was in fact too small to determine the exact limits between these two zones. In the ten samples taken at depths of between 205 and 235 metres (the greatest depth that we were able to sample), we have not found a single living organism. We do not deduce from this however that 205 metres represents the maximum depth for survival of benthic organisms in Lake Titicaca, because of the small number of samples collected in comparison with the area of the lake where the depth exceeds this depth. It is nevertheless reasonable to think that the prolonged periods of anoxia which occur in this zone are a determining factor limiting the colonisation of the sediments. In contrast, we have collected a total of nearly 300 organisms from depths of between 180 and 205 metres. Oligochaetes very largely dominate in this zone, with a relative proportion of 93.7%, but we have also found some Chironomus sp. (4.2%) and more unexpectedly Hirudinea (1.8%) and a species of amphipod, Hyalella echina (0.3%).

Population densities

The densities of the various groups of macro-invertebrates vary both seasonally at any given locality, as we will see below, and also between sampling sites for any given period of the year. Each faunistic group has its own population dynamics, as we have seen in the case of the amphipods, for example. Such variations in density can have multiple causes; some of these, such as conductivity gradients, variations in light penetration or substrate type from one site to another, can be considered as generalised as they are wide-acting on lake scale. Others are much more local, such as the distribu-



Figure 8. Density distributions of the main groups of benthic macro-invertebrates in the Bolivian part of the lake in February 1987.

tion of food or the presence of a current increasing the oxygen concentrations. The detailed picture of the populations obtained from a sampling campaign therefore reflects this situation, frozen at a point in time, even if the campaign takes several days. It nevertheless remains a very imprecise picture because of the vast extent of the usually heterogeneous environments involved. Finally, if we take into account the fact that the majority of the macro-invertebrates have a clumped type of distribution, it will be understandable that the description of the populations that we are capable of giving on a lake wide scale, or at least covering a large part of the lake, must be considered as very approximate.

For these various reasons we will only present a single picture of the density distribution of macro-invertebrates, such as was given by the sampling carried out from the 22 to 25 February 1987. This picture is given in graphic form and only concerns the major faunal groups collected in the Bolivian part of the lake (Fig. 8).

As the diameter of the circles is proportional to the density of the organisms, it is possible to obtain a visual impression of the situation prevailing in February 1987, by associating the size of the circles with their distribution on the various maps. The first impression is the quantitative preponderance of Mollusca over all other groups, with a particular abundance in the northern part of the Huiñaimarca, the areas with lower density or absence (east of the Tiquina Strait) being the deepest sampling stations. Molluscs are also dominant in the Lago Grande along the shorelines of Sun and Moon Islands.

Amphipods are the second most important group in order of abundance and on the whole dominate in the same areas as the molluscs, a situation which was also found to a lesser extent with the Hydracarina. It should be noted however that these latter have a lower occurrence in the stations of the Lago Grande than the previous two groups.

Oligochaetes, chironomids and Hydridae all show distinct distributions. The first are particularly dense in the northern part of the Huiñaimarca, either in deep water or in areas rich in plant detritus. They are also found almost everywhere in the Lago Grande, except in the deepest water in the centre; but even so, they are the group of organisms that live to the greatest depths in the lake. In contrast, for the period in question, the chironomidae and Hydridae had a distribution that was difficult to explain. The north-west part of the Huiñaimarca was for example densely populated with chironomids, whereas these were practically absent or rare from the rest of the lake. In addition, although it was possible to understand the particularly high density of *Hydra* at station 7 (32 metres depth) which received water directly from the Lago Grande, and was therefore well-supplied with oxygen and food, it was difficult to understand why it was also abundant at stations 1 and 16 where these factors played no role.

As a general rule, it would therefore appear that the Huiñaimarca supports considerably higher densities of organisms per unit area than the Lago Grande, mainly because it is shallower. However, areas of the Lago Grande of moderate depth (< ca. 20 metres), situated in non-eutrophicated bays or along the coastlines, also have a rich benthic fauna. Lake Titicaca therefore complies with a general tendency for most high altitude lakes to have a littoral zone that is much richer than the profound. This "ecozone" of the top twenty to twenty-five metres is therefore of paramount importance in the biological functioning of the lake and must be maintained as stable as possible, in order to ensure its role in the secondary production of the entire ecosystem.

Seasonal variations

The demonstration of such variations is based on the density distributions recorded during 5 sampling campaigns made at various seasons from 1986 to 1987. About thirty stations in the Bolivian part of the lake (Fig. 1) were

sampled. The contents of 2 to 4 Ekman grabs were analysed at each station, depending on the sampling campaign.

The overall changes in the benthic populations between sampling campaigns are shown diagrammatically, by using rather wide density classes so that only large changes are evident (Fig. 9). It should be noted that, by chance, the period in question was not entirely typical, since April 1986 was the month with the highest lake level in the last decade. The total range in water level rise being nearly three metres, it is obvious that this phenomenon was likely to interfere greatly with the population dynamics of benthic organisms. Such a rise in water level represented an increase of 20 to 50% in depth in many sites in the Huiñaimarca. The first repercussion to be felt was on the populations of submerged macrophytes and particularly of those parts of the *Chara* beds situated, before the increase in lake level, near their lower limit of depth penetration, at depths of 8 to 10 metres. The decrease in light penetration to this depth, due both to the increase in the height of the overlying water column and also to greater inputs of suspended matter from the inflow rivers and diffuse inputs along the shores, led to their death.

This vegetation quickly decomposed and periods of anoxia were established in the deeper areas, leading to the more or less complete disappearance of the dominant benthic populations (molluscs and amphipods). This was particularly apparent in the southern part of the Huiñaimarca, where the densities of benthic macro-invertebrates decreased from several thousand individuals per square metre or per 10 g dry weight of macrophytes to less than 500, between January and October 1986. This also occurred in the northern part of the Huiñaimarca, where the zone where the density was at least 500 organisms for the same unit area or weight, reached its maximum extent in April 1986. The opposite occurred in the Lago Grande during the same period of water level rise, where because of the greater overall water transparency and the steep gradients of the shorelines, it was not affected to the same extent. The same phenomenon as occurred in the Huiñaimarca only took place at the bottom of Achacachi Bay, where densities also fell below the limit of 500 in October 1986.

Although it is conceivable that the most mobile organisms such as amphipods, for example, may have been able to escape from the areas of anoxia, at least in part, it is certain that this was not the case for mollusca and that very high mortalities occurred in certain areas. This phenomenon is of interest, because it may offer an explanation for the horizons of shells which appear at certain levels in sediment cores from the Huiñaimarca (see Chapter III.1). These could result from mass mortality of molluscs, victims of temporary anoxia following abrupt increases in lake level, or alternatively to periods of temporary drying out.

Another period of deleterious consequences of the rise in lake level of the previous year apparently occurred in February 1987. The lake level had scarcely dropped, and except for the outlet of the Tiquina Strait, the overall densities remained at lower levels than in February 1986 throughout the



Figure 9. Density distributions of benthic macro-invertebrates in the Bolivian part of Lake Titicaca. The maps correspond to the following 5 sampling campaigns: A = January 1986; B = April 1986; C = October 1986; D = February 1987; E = June 1987. Densities expressed in g. 10 g dry weight on bottoms covered with macrophytes and $g \cdot m^{-2}$ on bare bottoms.

Huiñaimarca. In June 1987, in contrast, the situation had greatly improved, particularly in the north of the Huiñaimarca where a hyperdevelopment of the benthic fauna was recorded. Large areas had densities of greater than 5000 individuals per square metre, or per 10 g dry weight in the case of

populations among macrophytes. In the entire region situated offshore of Puerto Perez these densities even exceeded 25,000.

Conclusions

The benthic fauna of Lake Titicaca represents an essential component for the biological functioning of this ecosystem, by playing an important role both in the secondary production (food for the fish fauna), and also in energy transfer (molluscs and amphipods as decomposers).

A very clear contrast exists between the two basins of the lake, the Huiñaimarca being by far the most densely populated over all its area. Only the shallow areas of the Lago Grande have a similar importance, but these areas only represent a very small proportion of the 7000 square kilometres of this basin. Overall more than 95% of the benthic populations occur in the top 15 metres depth in the Huiñaimarca and in the top 25 metres in the Lago Grande. In latter, benthic life does however extend down to great depths, but cannot always be sustained at greater than 200 metres, because of the frequent periods of anoxia that affect this zone.

As a general rule, molluscs and amphipods are the dominant faunistic groups at the scale of the whole lake and over all seasons, both in terms of density and biomass. The former play a primordial role in the decomposition of the enormous biomass of macrophytes that develops and dies in the euphotic zone, the latter being responsible for the transformation of organic matter of animal origin (zooplankton, macro-invertebrates, etc.).

Analysis of fish stomach contents has shown that benthic macro-invertebrates are also the most important prey for many of the endemic species (especially those living among the aquatic vegetation), and also for the young stages of the pelagic predators (*Salmo gairdneri* and *Basilichthys bonariensis*). Some taxonomic groups also represent almost the entire diet of several species of aquatic bird at certain times of year.

Despite the results presented in this chapter, the benthic invertebrates must be considered as being insufficiently studied at the present time. Although more work is still needed on the taxonomy, it is especially studies on the ecology and biology which are lacking, and priority should be given to such studies on the two dominant groups (molluscs and amphipods). Studies on the long and medium-term changes in the populations are also needed in order to demonstrate whether these follow cyclical rhythms, and if this is the case to elucidate the determining factors.

References of chapter VI.4

- ANNANDALE (N.), 1913. An account of the Sponges of the Lake Tiberias with observations on certain genera of Spongillidae. *Journ. proc. Asiatic Soc. Bengal.*, 9: 57–88.
- ARNDT (W.), 1937. Ochridaspongia rotunda n.g., n. sp. Ein neuer Süsswasserschwam aus dem Ochridasee. Arch. Hydrobiol., 31: 636–677.
- BACHMANN (A.O.), 1961. Notas sobre Corixidae (Hemiptera) (2a seria). Neotropica, 7: 19– 24.
- BACHMANN (A.O.), 1962. Clave para determinación de las subfamilias, géneros y especies de las Corixidae de la República de Argentina (Insecta, Hemiptera). *Physis*, 23: 21–25.

BATE (J.), 1862. Allochertes knickerbrockeri. Cat. Amph. Crust. Brit. Mus., p. 136.

- BAVAY (A.), 1904. Mission de Créqui-Montfort et Sénéchal de la Grange en Amérique du Sud. Mollusques terrestres et fluviatiles récoltés par le Dr. Neveu-Lemaire. Bull. Soc. Zool. Fr., 29: 152–156.
- BAVAY (A.), 1906. Mollusques. In: Les lacs des hauts plateaux de l'Amérique du Sud. Neveu-Lemaire. Imprimerie nationale, Paris: 142–147.
- BEAUCHAMP (P. de), 1939. 5. Rotifères et Turbellariés. In: The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1 (1): 44–79.
- BLUME (W.), 1958. Littoridinen aus dem Titicacasee (Mollusca). Op. Zoologica, 25: 1-8.
- BRIEN (P.), 1958. A propos de deux éponges du lac Tanganyika. Mém. Acad. r. Scienc. colon., 8 (1): 1–43.
- BRIEN (P.), 1972. Malawispongia echinoides n.g., n. sp. Eponge Céractinelle Haploscléride africaine du lac Malawi (Formation de la spongine périspiculaire). Rev. Zool. Bot. Afr., 86 (1-2): 65-92.
- BRIEN (P.), 1973. Malawispongia echinoides Brien. Etudes complémentaires. Histologie. Sexualité. Embryologie. Affinités systématiques. Rev. Zool. Bot. Afr., 87 (1): 50–76.
- BRULLE (G.A.), 1837. Insectes de l'Amérique méridionale recueillis par Alcide D'Orbigny. In : Voyage dans l'Amérique méridionale. A. D'Orbigny. Pitois-Levrault et Cie., Paris, 2 (2): 17–56.
- BRUNDIN (L.), 1956. Die bodenfaunistischen Seetypen und ihre Anwendbarkeit auf die Sudhalbkugel. Zugleich ein Theorie der produktionbiologischen Bedeutung der glazialen Erosion. Rep. Inst. Freshw. Res., Drottningholm, 37: 186–235.
- BULLA (L.A.), 1972. La ninfa de Protallagma titicacae (Calvert). Neotropica, 18 (57): 129-135.
- CALVERT (P.P.), 1909. Contribution to the knowledge of the Odonata of the Neotropical region. Ann. Carn. Mus., 6: 73-364.
- CARMOUZE (J.P.), ARZE (C.), QUINTANILLA (J.), 1977. La régulation hydrique des lacs Titicaca et Poopo. *Cah. ORSTOM, sér. Hydrobiol.*, 11 (4): 269–283.
- CARMOUZE (J.P.), ARZE (C.), QUINTANILLA (J.), 1981. Régulation hydrochimique du lac Titicaca et l'hydrochimie de ses tributaires. *Rev. Hydrobiol. trop.*, 14 (4): 329–348.
- CARMOUZE (J.P.), DEJOUX (C.), DURAND (J.R.), GRAS (R.), ILTIS (A.), LAUZ-ANNE (L.), LEMOALLE (J.), LEVEQUE (C.), LOUBENS (G.), SAINT-JEAN (L.), 1972. Grandes zones écologiques du lac Tchad. Cah. ORSTOM, sér. Hydrobiol., 6 (2): 103– 169.
- CERNOSVITOV (L.), 1939. 6. Oligochaeta. In : The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3 (1): 81–116.
- CHEVREUX (E.), 1904. Mission de Créqui-Montfort et Sénéchal de la Grange; note préliminaire sur les Amphipodes recueillis par M. le Dr. Neveu-Lemaire dans le lac Titicaca (juillet 1903). Bull. Soc. Zool. de Fr., 29 (11): 131–134.
- DEJOUX (C.). 1988. Panorama de la fauna béntica del Altiplano boliviano. Congreso Iberoamericano y del Caribe sobre la pesca y la acuicultura, Isla Margarita, Venezuela, 8–14 Mayo 1988: 13 p., multigr.
- DEJOUX (C.), 1991. Les macro-invertébrés associés à la végétation aquatique dans la partie bolivienne du lac Titicaca. *Rev. Hydrobiol. trop.* 24 (2): 91–104.

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- DEJOUX (C.), MOURGUIART (P.), 1991. Ecpomastrum mirum (Mollusque Hydrobiidae) du lac Titicaca: un problème de taxinomie. Bull. Mus. Nat. Hist. Nat. (in press).
- DEJOUX (C.), WASSON (J.G.), 1991. La faune benthique de quelques lacs d'altitude des Andes boliviennes. *Spixiana* (in press).
- DELACHAUX (T.), 1928. Faune invertébrée d'eau douce des hauts plateaux du Pérou (région de Huancavelica, département de Junin). (Calanides, Ostracodes, Rotateurs nouveaux). Trav. Lab. Zool. Univ. Neuchâtel: 45–99.
- D'ORBIGNY (A.), 1835. Synopsis terrestrium et fluviatilium Molluscorum in suo per Amirican meridionalem itinere collectarum. Mag. Zool., 5 (61): 44 p.
- D'ORBIGNY (A.), 1835-47. Mollusques. In: Voyage dans l'Amérique méridionale. A. D'Orbigny. Pitois-Levrault et Cie., Paris, vol. 5.
- D'ORCHYMONT (A.), 1941. Palpicornia (Coleoptera). Notes diverses et espèces nouvelles. Bull. Mus. Roy. Hist. Nat. Belg., 17 (1): 1–23.
- DOS SANTOS (N.D.), 1966. Notas sobre Aeschna (Hesperaeschna) peralta Ris, 1918 e sua ninfa. Actas Soc. Biol. Rio de J., 10 (5): 123-124.
- FAXON (W.), 1876. Exploration of Lake Titicaca by Alexander Agassiz and S.W. Garman. 4. Crustacea. Bull. Mus. Comp. Zool. Cambridge, 3 (16): 361–375.
- FLINT (O.S.), 1982. Studies of neotropical caddisflies, 30: larvae of the genera of South American Limnephilidae (Trichoptera). *Smith. contrib. to zool.*, 355: 30 p.
- FRASER (F.C.), 1957. A revision of the Odonata of Chile. An. Acad. Chil. Cienc. Nat., 21 (2): 153–166.
- GAVRILOV (K.), 1981. Oligochaeta. In: Aquatic biota of Tropical South America, Part 2: Anarthropoda, Hurlbert, Rodríguez & Santos eds., San Diego State University, San Diego, California: 170–190.
- GERMAR (E.F.), 1824. Insectorum species novae aut minus cognitae, descriptionibus illustratae. Halae, 624 p.
- GILSON (H.C.), 1937. 1. Description of the expedition. *In*: The Percy Sladen Trust Expedition to Lake Titicaca in 1937. *Trans. Linn. Soc. London*, ser. 3, 1: 1–20.
- GILSON (H.C.), 1964. Lake Titicaca. Verh. Internat. Verein. Limnol., 15: 112-127.
- GUIGNOT (F.), 1957. Beiträge zur Kenntnis der Insektenfauna Boliviens. Opusc. Zool., 6: 1– 10.
- HAAS (F.), 1955. 17. Mollusca: Gastropoda. In: The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1 (3): 275–308.
- HAAS (F.), 1957. Eine neue endemishe Schnecke aus dem Titicacasee. Arch. Moll., 86 (4/6): 137-139.
- HARMAN (W.J.), BRINKHURST (R.O.), MARCHESE (M.), 1988. A contribution to the taxonomy of the aquatic oligochaeta (Naididae) of South America. *Can. J. Zool.*, 66: 2233–2242.
- HINTON (H.E.), 1940. 7. The Peruvian and Bolivian species of Macrelmis Motsh. (Coleoptera: Elmidae). In : The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London. ser. 3, 1 (1): 117–147.
- HUNGERFORD (H.B.), 1948. The Corixidae of the western hemisphere (Hemiptera). Univ. Kansas Sci. Bull., 32: 4-827.
- HYMAN (L.H.), 1939. New species of flat worms from North, Central and South America. *Proc. U.S. Nat. Mus.*, 86: 419–439.
- KENNEL (J.), 1888. Untersuchungen an neuen Turbellarien. Zool. Jb. (Syst.), 3: p. 444.
- KUIPER (J.G.), HINZ (W.), 1983. Zur Fauna der Kleinmuscheln in den Anden (Bivalvia: Sphaeriidae). Arch. Moll., 114 (4/6): 137–156.
- LAVENU (A.), 1981. Origine et évolution néotectonique du lac Titicaca. Rev. Hydrobiol. trop., 14 (4): 289–297.
- LAZZARO (X.), 1985. Poblaciones, biomasas y producciones fitoplanctónicas del lago Titicaca. *Rev. Inst. Ecol.*, La Paz, 7: 23–64.
- LERNER-SEGEEV (R.), 1971. *Limnocythere titicaca* new species (Ostracoda, Cytheridae) from Lake Titicaca, Bolivia. *Crustaceana*, 25 (1), 88–94.

- LUNDBLAD (O.), 1924. Über einige Hydracarinen aus den peruanischen Anden. Göteborg. VetenskSamh. Handl. (S 4), 27 (10): 1–25.
- LUNDBLAD (O.), 1930. Südamerikanische Hydracarinen. Zool. Bidr. Upsala, 13: 1-86.
- LUNDBLAD (O.), 1944. Einige neue und venid bekannte Hydracarinen aus Südamerica. *Ent. Tidskr.*, 65: 135–162.
- MARCUS (E.), 1942. Sobre Bryozoa do Brasil. II. Bol. Fac. Fil. Ci. Letr. Univ. Sao Paulo. Zool., 6 (1-5): 57-106.
- MARCUS (E.), 1953. Bryozoa from Lake Titicaca. Bol. Fac. Fil. Ci. Letr. Univ. Sao Paulo, Zool., 18: 45-49.
- MARTINEZ-ANSEMIL (E.), GIANI (N.), 1986. Algunos oligoquetos acuáticos de Bolivia. Oecol. aquat., 8: 107-115.
- MEDINA (C.), 1982. Determination of zoobenthos in Puno Bay of Lake Titicaca (Ojerani). *In*: Physical, chemical and biological conditions relating to water quality in Puno Bay, Lake Titicaca; Seminar abstracts, 32 p., multigr.
- MEDINA (C.), 1983a. Determinación de la fauna bentónica en Ojerani. Tesis UNTA, Puno: 116 p.
- MEDINA (C.), 1983b. Fauna bentónica en la bahía de Puno-Ojerani. UNDAP, Puno: 4 p., multigr.
- MILBRINK (G.), 1983. An improved environmental index based on the relative abundance of Oligochaete species. *Hydrobiologia*, 102: 89–97.
- MONIEZ (R.), 1889. Sur quelques Cladocères et sur un Ostracode nouveaux du lac Titicaca. *Rev. Biol. Nord France*, 1: 419–429.
- MORALES (P.), CORNEJO (E.), LEVY (D.A.), CHALLCO (D.), MEDINA (A.C.), NORTHCOTE (T.G.), 1989. Effects of eutrofication on zoobenthos. *In*: Pollution in Lake Titicaca, Peru. Northcote, Morales, Levy, Greaven eds., Westwater Research Centre, Univ. Brit. Columbia, Vancouver: 101–113.
- MOUCHAMPS (R.), 1963. Beiträge zur Kenntnis Insektenfauna Boliviens. 18. Coleoptera, 14. Sur quelques Berosini (Coleoptera-Hydrophilidae) de l'Amérique du Sud. *Mitt. Münchner Ent. Gesell.*, 53: 118–149.
- MOURGUIART (P.), 1987. Les Ostracodes lacustres de l'Altiplano bolivien. Le polymorphisme, son intérêt dans les reconstitutions paléohydrologiques et paléoclimatiques de l'Holocène. Thèse Univ. Bordeaux 1, 263 p.
- NORTHCOTE (T.G.), MORALES (P.S.), LEVY (D.A.), GREAVEN (M.S.), 1989. Pollution in Lake Titicaca, Peru: training, research and management. Westwater Research Centre, Univ. Brit. Columbia, Vancouver, 262 p.
- PHILIPPI (R.A.), 1889. Diagnoses molluscorum terrestrium et fluviatilium peruanorum. Malak. Bl., 16: 32–49.
- PILSBRY (H.A.), 1924. South American land and freshwater mollusks. Notes and descriptions.I. Mollusks of Lake Titicaca. Proc. Acad. Nat. Sci. Philad., 76: 49–51.
- PILSBRY (H.A.), 1925. Lake Titicaca mollusks. Nautilus, 38: 103-104.
- PILSBRY (H.A.), VANATTA (E.G.), 1896. New species of freshwater mollusks from South America. *Proc. Acad. Nat. Sci. Philad.*: 561–565.
- RIBAGA (A.), 1902. Acari sudamericani. Zool. Anz., 25: 502-508.
- RINGUELET (R.A.), 1960. Una colección de hirudíneos del Perú. I. Sanguijuelas del lago Titicaca. *Physis*, 21 (61): 231–239.
- RINGUELET (R.A.), 1978. Nuevos géneros y especies de Glossiphoniidae sudamericanos basados en caracteres ecto y endosomáticos (Hirudinea Glossiphoniiformes). *Limnobios*, 1 (7): 269–276.
- RINGUELET (R.A.), 1981. Hirudinea. In: Aquatic biota of tropical South America. Part 2. Anarthropoda. Hurlbert, Rodríguez and Dos Santos, eds: 191–196.
- ROBACK (S.S.), BERNER (L.), FLINT (O.S.), NIESER (N.), SPRANGLER (P.J.), 1980. Results of the Catherwood Bolivian-Peruvian Altiplano Expedition. Part 1. Aquatic insects except Diptera. Proc. Acad. Nat. Sci. Philadelphia, 132: 176–217.
- ROBACK (S.S.), COFFMAN (W.P.), 1983. Results of the Catherwood Bolivian-Peruvian

Altiplano Expedition. Part 2. Aquatic Diptera including montane Diamesinae and Orthocladiinae (Chironomidae) from Venezuela. *Proc. Acad. Nat. Sci. Philadelphia*, 135: 9–79.

- ROGICK (M.D.), 1945. Studies on freshwater Bryozoa. 16. Fredericella australiensis var. browni, n. var. Biol. Bull., Woods Hole, 89 (3): 215–228.
- RÜTZLER, (K.), 1978. Sponges in coral reefs. *In*: Coral Reefs: Research Methods. Monographs on Oceanographic Methodology, D. R. Stoddart and R. E. Johannes (eds.), UNESCO, 5 (21), pp. 299–313.
- SCHINDLER (O.), 1955. Limnologische Studien im Titicacasee. Arch. Hydrobiol., 51 (1): 42– 53.
- SCHLENZ (E.), 1981. Coelenterata. In: Aquatic biota of tropical South America. Part 2. Anarthropoda. Hurlbert, Rodríguez and Dos Santos, eds., San Diego State Univ., San Diego: 96–97.
- SCHMIDT (F.), 1957. Contribution à l'étude des Trichoptères néotropicaux, II (Trichoptera). Beitr. zur Ent., 7 (3-4): 379-398.

SMITH (J.), 1874. Hyalella inermis. Rep. U.S. Comm. for 1872 and 1873, p. 609.

SOLÉ-CAVA, (A.M.), KLAUTAU, (M.). BOURY-ESNAULT, (N.), BOROJEVIC (R.), and THORPE, (J.P.), 1991. Genetic evidence for cryptic specification in allopatric populations of two cosmopolitan species of the calcareous sponge genus *Clathrina*. *Marine Biology*, 111: 381–386.

TIMM (T.), 1970. On the fauna of the Estonian Oligochaeta. Pedobiologia, 10: 52-78.

- TIMM (T.), 1990. Aquatic Oligochaeta from the farthest South-East of the USSR. Proc. Estonian Acad. Sci. Biol., 39 (1): 55-67.
- VARGAS (C.), 1982. La sédimentation lacustre subactuelle d'un bassin intramontagneux: le lac Titicaca (partie lac Huiñaimarca-Bolivie). Thèse Univ. Bordeaux 1: 91 p.
- VIETS (K.), 1953. Neue Wassermilben aus Peru. Veroff. Ubersee-Mus. Bremen, (A), 2: 129-134.
- VIETS (K.), 1955. 16. Hydrachnellae. In : The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc., London, ser. 3, 1 (3): 249–274.
- WALTER (C.), 1919. Hydracarinen aus der peruanischen Anden und aus Brasilien. Rev. Suisse Zool., 27 (2): 19–59.
- WECKEL (A.L.), 1907. Hyalella knickerbrockeri. Proc. U.S. Nat. Mus., 32, p. 54.
- WECKEL (A.L.), 1909. Freshwater amphipods from Peru. Proc. U.S. Nat. Mus., 38: 623-624.
- WOODWORTH (W.), 1897. On some Turbellaria from Illinois. Bull. Mus. Comp. Zool. Harv., 31: 3-16.
VI.5. FISH FAUNA VI.5a. Native species The *Orestias*

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Apart from Salmo gairdneri Richardson, 1836, introduced in 1941–42 and Basilichthys bonariensis (Valenciennes, 1835), introduced in 1955–56 (Loubens, 1989; Loubens and Osorio, 1988), the fish fauna of Lake Titicaca also includes the genera Trichomycterus and Orestias, both endemic to the Andean Altiplano. The Trichomycteridae family is very widespread in South America, but little is known about the Trichomycterus living in the lake. It is likely that there are only two species: T. rivulatus and T. dispar (Hanek (ed.), 1982).

The genus *Orestias* Valenciennes, 1839 belongs to the Orestiini tribe, of the sub-family Orestinae, family Cyprinodontidae according to Parenti's (1981) classification. These peculiar fish, that have only a single gonad, are also distinguished from other cyprinodonts by the absence of ventral fins, vomer and first postcleithrum (Parenti, 1981).

Systematics (Figs 1 and 2)

Many publications have been devoted to the systematics of this remarkable genus since the early work of Valenciennes (1839). Only the major studies and revisions are mentioned here: Valenciennes *in* Cuvier and Valenciennes (1846); Garman (1895); Eigenmann and Allen (1942); Tchernavin (1944); Lauzanne (1982); Parenti (1984). Tchernavin (1944), working on the extensive collections from the 1937 Percy Sladen Expedition, recorded for the whole Andean Altiplano: 20 species, five subspecies, two hybrids and two new species (sp. 1 and sp. 2) which he did not name. As for Lake Titicaca itself, he mentioned 16 species, three subspecies, the two new species and one hybrid:

O. cuvieri Valenciennes, 1846

- * O. pentlandii Valenciennes, 1846
 - O. agassii tschudii Castelnau, 1855
 - O. agassii pequeni Tchernavin, 1944

C. Dejoux and A. Iltis (eds.), Lake Titicaca, 405–419. © 1992 Kluwer Academic Publishers. Printed in the Netherlands.



Figure 1. The principal Orestias of Lake Titicaca (1: O. pentlandii; 2: O. ispi; 3: O. forgeti; 4: O. agassii).

- * O. jussiei Valenciennes, 1846
 - O. jussiei puni Tchernavin, 1944
- * O. olivaceus Garman, 1895
- * O. luteus Valenciennes, 1846
- * O. albus Valenciennes, 1846
 - O. uruni Tchernavin, 1944



Figure 2. The principal Orestias of Lake Titicaca (5: O. luteus; 6: O. olivaceus sensu Lauzanne, 1982; 7: O. albus juvenile; 8: O. mulleri).

- O. minutus Tchernavin, 1944
- * O. minimus Tchernavin, 1944
- * O. gilsoni Tchernavin, 1944 O. tutini Tchernavin, 1944 O. taquiri Tchernavin, 1944
- * *O. mulleri* Valenciennes, 1846 *O. incae* Garman, 1895
- * O. crawfordi Tchernavin, 1944
- * O. mooni Tchernavin, 1944
 - O. sp. 1
 - O. sp. 2
 - O. cuvieri \times O. pentlandii

From 1978 to 1981 numerous and plentiful collections of Orestias were taken from Lago Pequeño by ichthyologists from UMSA and ORSTOM. These collections allowed Lauzanne (1981) to describe three new species: O. ispi, O. forgeti and O. tchernavini (Tchernavin's sp. 1). The study of the numerous specimens collected and re-examination of previous collections led to a review of Orestias from the Lago Pequeño (Lauzanne, 1982). The species in Tchernavin's list marked with an asterisk were confirmed and redescribed, using numerous biometric and meristic characters taken from very large samples. The great phenotypic variability of the members of the genus Orestias must be stressed, and also that it is imperative to work on very large samples, including age ranges from young to adult, in order to delineate the limits of variation in the characters used to define the species. It was thus, while studying certain biometric and meristic characters used by Tchernavin to characterise the various subspecies of Orestias agassii (especially O. agassii tschudii Castenau, 1855 and O. agassii pequeni Tchernavin, 1944 from Lake Titicaca), that we arrived at the conclusion that they were phenotypic varieties that should be included in the species O. agassii. Nevertheless, we recognise the presence in Lake Titicaca of littoral, pelagic and benthic forms or populations. In the same way, we do not recognise the subspecies O. jussiei puni, Tchernavin, 1944, which we include with O. jussiei Valenciennes, 1846. We also think that O. minutus Tchernavin, 1944, known only from two specimens, is synonymous with O. minimus Tchernavin, 1944.

O. cuvieri Valenciennes, 1846, a large and very characteristic species, was not found by the ORSTOM-UMSA team, despite an intensive search. It would appear that the last captures were made by the Percy Sladen Expedition in 1937 (Loubens, 1989). Many authors have accused Salmo gairdneri for having brought about the disappearance of O. cuvieri (Vellard, 1963; Villwock, 1962 and 1975; Lillelund, 1975; Laba, 1979). Loubens (1989) claimed that this hypothesis could be neither confirmed nor disproved.

We have also not found the following of Tchernavin's (1944) species: O. uruni, O. taquiri and O. tutini nor O. incae of Garman (1895), known only from very few individuals. These are perhaps valid species, but a larger

number of specimens is needed in order to study the variability of the quantitative and qualitative characters which would allow the validity of these taxa to be confirmed or denied.

From the works of Lauzanne (1981, 1982), the following species known to be present with certainty in Lake Titicaca can be added to the species marked with an asterisk in Tchernavin's (1944) list:

O. agassii Valenciennes, 1846

O. jussiei Valenciennes, 1846

O. ispi Lauzanne, 1981

O. forgeti Lauzanne, 1981

O. tchernavini Lauzanne, 1981

To this list should be added the species which were present in Lake Titicaca in 1937 (Percy Sladen Expedition), but which have not been found again by the ORSTOM-UMSA team (1978–1981):

O. cuvieri Valenciennes, 1846

O. uruni Tchernavin, 1944

O. taquiri Tchernavin, 1944

O. tutini Tchernavin, 1944

O. incae Garman, 1895

Orestias cuvieri is, as we have stated, probably extinct. The others, much smaller species have perhaps evaded capture by collectors.

In 1984, Parenti published a revision of all the *Orestias* from the Andean Altiplano, based on the existing type specimens and on a large collection brought together in 1979 by Tom Coon, but without referring to the work of Lauzanne (1982). She recognized 43 species, of which 14 were new, for the Altiplano. For Lake Titicaca, she listed 28 species of which six were new.

Among the 10 species from Lake Titicaca in the Tchernavin list (those marked with an asterisk), she did not recognize, justly, *O. jussiei* of Valenciennes, 1846. This is an error made by Tchernavin, as Valenciennes' specimens (A. 9599) came from the river Guasacona in Peru and not from Lake Titicaca. On the other hand, Parenti considered Tchernavin's subspecies *O. jussiei puni* as a full species, *O. puni* Tchernavin, 1944. We disagree with this proposal because Lauzanne (1982) has shown that these are just large specimens of *O. jussiei* Valenciennes, 1846.

Parenti recognized O. luteus Valenciennes, 1846 and created two new very closely related species, O. rotundipinnis Parenti, 1984 and O. farfani Parenti, 1984, on the basis of a few specimens. Loubens (1989), using convincing arguments, denied the validity of these two species, which are synonymous with O. luteus Valenciennes, 1846.

Parenti recognized O. agassii Valenciennes, 1846 and she reinstated O. frontosus Cope, 1876, on criteria of the shape of the snout and head and the

colour, a taxon that Tchernavin had classified in the subspecies O. agassii tschudii. She included O. agassii pequeni Tchernavin, 1944 in with O. frontosus. She also reinstated O. tschudii Castelnau, 1855 which had been included under the subspecies O. agassii tschudii alongside O. owenii Günther, 1866, O. ortoni Cope, 1876, O. agassizi Garman, 1876, O. agassizi Starks, 1906 and O. agassii Rendahl, 1937. However, Lauzanne (1982) had shown, on the basis of metric and meristic characters, that all these species and subspecies of the O. agassii group were probably only phenotypic variations of the species O. agassii Valenciennes, 1846. Within this very polymorphic complex it seems unreasonable to erect numerous species, because at the extreme it would be possible to create as many species as there are specimens. If O. agassii is in reality an assembly of several species the proof could not be provided by analyses based only on morphological characters, but by using more detailed methods such as the examination of karyotypes, the study of the enzyme polymorphism or breeding experiments in aquaria. In the meantime, it seems advisable to only retain O. agassii, while acknowledging that it is extremely polymorphic.

Parenti also created *O. gracilis* (closely related to *O. mulleri* and *O. imarpe*) *O. robustus* and *O. tomcooni* (related to *O. gilsoni*) on samples of between 10 and 21 specimens. Not having seen this species we can neither confirm nor disprove the validity of the taxa.

She also recognized Tchernavin's O. minimus and O. minutus. As for O. minutus, Lauzanne (1982) considered that this is a synonym of O. minimus.

She considered Tchernavin's O. tutini, O. taquiri and O. uruni and also Garman's O. incae to be valid species. However, as with Lauzanne (1982), she did not collect these, so there is a possibility that these no longer exist.

Loubens (1989) studying the biology of O. olivaceus (sensu Lauzanne, 1982) correctly stated that the species that he was studying was not the O. olivaceus Garman, 1985 as presented by Parenti (1984). "Plusieurs caractères métriques et méristiques (nombre de rayons à la dorsale, nombre d'écailles en série latérale, longueur et largeur de la tête, hauteur du pédicule caudal) ont des valeurs très différentes. Les écailles de la partie antérieure du corps sont épaisses pour Parenti, présentent des stries concentriques et de très fines granulations pour Lauzanne. Les figures (n° 22 chez Lauzanne, 44 chez Parenti) montrent des poissons d'aspect dissemblable. Enfin le principal caractère signalé par Parenti comme permettant de distinguer O. olivaceus de toutes les autres espèces d'Orestias n'existe pas chez O. olivaceus sensu Lauzanne. Il s'agit des orbites qui sont orientées dorsolatéralement de telle sorte que, en vue de dessus, ces deux orbites sont presque entièrement visibles. Il n'est donc pas possible qu'il s'agisse de la même espèce". This error of identification (Lauzanne, 1982) results from the fact that we were unable to compare our specimens with Garman's type (MCZ: 3946), but only with the Tchernavin's very small individuals (BMNH: 1944-6-6: 456-467). We also stated: "qu'un léger doute subsiste quant à l'identification de nos exemplaires". Whatever the case, O. olivaceus sensu Lauzanne, 1982, which is very abundant in the

Lago Pequeño, is almost certainly a good species (close to *O. crawfordi*), which is at the moment unnamed.

Based on the above, we therefore propose the following list of *Orestias* spp. described from Lake Titicaca, grouped into four major complexes according to their phylogenetic affinities (Parenti, 1984). Some of them, marked with an asterisk, have not been found since the Percy Sladen Expedition of 1937:

- O. cuvieri Complex
 - * O. cuvieri Valenciennes, 1846
 - O. pentlandii Valenciennes, 1846
 - O. ispi Lauzanne, 1981
 - O. forgeti Lauzanne, 1981
- O. mulleri Complex
 - O. mulleri Valenciennes, 1846
 - O. gracilis Parenti, 1984
 - O. crawfordi Tchernavin, 1944
 - O. sp. (O. olivaceus sensu Lauzanne, 1982)
 - * O. tutini, Tchernavin, 1944
 - * O. incae, Garman, 1895
- O. gilsoni Complex
 - O. gilsoni Tchernavin, 1944
 - * O. taquiri Tchernavin, 1944
 - O. mooni Tchernavin, 1944
 - * O. uruni Tchernavin, 1944
 - O. minimus Tchernavin, 1944
 - O. tchernavini Lauzanne, 1981
 - O. tomcooni Parenti, 1984
 - O. imarpe Parenti, 1984
 - O. robustus Parenti, 1984
- O. agassii Complex
 - O. agassii Valenciennes, 1846
 - O. jussiei Valenciennes, 1846
 - O. luteus Valenciennes, 1846
 - O. albus Valenciennes, 1846
 - O. olivaceus Garman, 1895

Habitats and communities (Fig. 3)

The main data concerning the habitats of the fish communities come from the American/Peruvian work of the Puno laboratory, and the French/Bolivian work of the UMSA-ORSTOM group (Bustamante and Treviño, 1980; Franc *et al.*, 1979; Collot, 1980; Johannesson *et al.*, 1981; Hanek (ed.), 1982; Lauzanne, 1982; Treviño *et al.*, 1984; Loubens *et al.*, 1984, 1985, 1988; Vaux





Figure 3. The different environments and their characteristic species.

et al., 1988; Loubens, 1989). For reasons of ecological consistency we also include *Salmo gairdneri* and *Basilichthys bonariensis*, the only true piscivores in the lake, in this description of communities.

The lower limit for macrophyte growth, at approximately 10 m depth, separates the lake into two very unequally sized zones: a zone with aquatic vegetation and a non-vegetated zone (about 80% of the total area).

The zone of bare sediments extends from 10 m down to the maximum depth (284 m).

We have some information on the pelagic communities in the most central part of the lake, but the demersal communities, if they exist, are unknown. Only two species are known for certain from pelagic zone, *S. gairdneri* and *O. ispi*, from catches made by local fishermen using surface gill nets. These nets only capture the trout, whose stomachs contain nothing else than *O. ispi*. This observation is corroborated by the results of an echo-location survey carried out in 1979 in the Peruvian part of the lake (Johannesson *et al.*, 1981). This survey revealed a large stock of fish at depths of between 20 and 50 m, which probably consisted of *O. ispi* (Loubens, 1989). It is also likely that *B. bonariensis* makes incursions into this zone.

The populations of the peripheral part of the bare sediment zone are better known, at least down to a depth of about 60 m. Near the bottom, the dominant species is *O. mulleri*, but the benthic form of *O. agassii* is also found (Loubens, 1989). The pelagic zone is much more familiar from commercial and experimental fisheries. The community is comprised of *S. gairdneri*, *B. bonariensis*, *O. agassii* and *O. ispi*, which are very abundant around 25 m depth (Vaux *et al.*, 1988). *O. pentlandii* is a much sought-after species that Bustamante and Treviño (1977, 1980) found in fair abundance in certain parts of Lago Grande (Pusi Bay, the mouth of the Río Ramis) and in the north-western part of Lago Pequeño.

The macrophyte zone extends from the shore, down to a depth of about 10 m. Three different biotopes can be distinguished, depending on the plant associations.

The Chara biotope

This habitat, which extends from a depth of 2 to 3 m down to 10 m, is characterised by the dominance of the genus *Chara* and by the occurrence of the genera *Potamogeton*, *Myriophyllum*, *Elodea*, *Nitella* and *Ruppia*. Its pelagic fish community is qualitatively similar to the preceding one. The demersal, or rather the perimacrophytic community (Loubens *et al.*, 1984) is typified by *O. agassii* and juveniles of *B. bonariensis*. Three other species are present in reasonable abundance: *O. luteus*, *O. olivaceus* (*sensu* Lauzanne, 1982) and *O. ispi*. The sporadic appearance of *O. ispi* is related to reproductive activity, as is the case with *O. pentlandii* in some areas (Bustamante and Treviño, (1980).

The "totora" biotope

This biotope occupies a zone extending from depth of 1 m down to 2-3 m. It is typified by the presence of a species of Cyperaceae, *Schoenoplectus tatora* ("totora"), rooted in the bottom and with a stem emerging to a height of more than a metre above the water surface. The other species of macrophyte are also present in this biotope, and sometimes occupy the entire water column, forming a very dense thicket. The community in this habitat is entirely perimacrophytic, and on the whole is similar to that of the *Chara* biotope.

The littoral biotope

This zone, extending from the "totora" belt and the shore, is a fringe with a very small area in relation to that of the lake, but where small fish, both young and adults, abound.

To this should be added the rocky littoral biotope, with a very steep gradient, which occurs especially in the Lago Grande, but information is lacking on the fish communities occurring there.



Figure 4. Changes in sex ratio in relation to length for some species of Orestias (O. o.: O. olivaceus; O. i.: O. ispi; O. f.: O. forgeti; O. 1.: O. luteus; O. a.: O. agassii; O. p.: O. pentlandii). %M: Percentage of males. L: standard length. (from Loubens and Sarmiento, 1985 and Loubens, 1989).

Biological observations

Certain aspects of the biology of the Orestias are now fairly well-known from the work of Loubens and Sarmiento (1985), Loubens (1989) and Lauzanne and Loubens (in press). Other authors have helped to clear up particular points: (Zuniga, 1941; Treviño, 1974; Bustamante and Treviño, 1980; Leblond, 1983; Treviño et al., 1984; Vaux et al., 1988). The species studied are those with some importance for the commercial fisheries: O. agassii, O. ispi, O. pentlandii, O. luteus, O. olivaceus (sensu Lauzanne, 1982), O. albus and O. forgeti.

Sex ratio

For most species the same change is recorded in the percentage of males with increasing standard length (Fig. 4). Starting from a normal ratio (40–60%), the percentage of males decreases slowly or more sharply to reach very low values, or even zero in large adults. This phenomenon is usually explicable by the different growth rates in males and females. *O. ispi* would appear, however, to be a rather special case. In this species no females are found among the smallest individuals (40 to 45 mm length class), and the percentage of males falls very sharply to around zero in the 70 to 75 mm length class. It would appear to be a case of protandrous hermaphroditism, but this needs to be confirmed by histological examination of the gonads.

Length at sexual maturity (LSM)

The lengths at sexual maturity were estimated by Loubens and Sarmiento (1985) and Loubens (1989). The insufficient numbers of young individuals examined only allowed an upper limit to be given in five cases out of seven, rather than the precise length at sexual maturity:

O. albus	LSM < 100 mm
O. forgeti	LSM < 60 mm
O. ispi	LSM < 55 mm
O. olivaceus	LSM < 45 mm
O. pentlandii	LSM < 125 mm
O. luteus males	LSM = 75 mm
O. luteus females	LSM = 82 mm
O. agassii males	LSM = 60 mm
O. agassii females	LSM = 60 mm

In all studies it has been noted that the LSM values are always much lower than the mean size of fish captured by commercial fishermen, which denotes a rather low exploitation rate.

Breeding season, fecundity, spawning

The changes in the percentage of females ready to spawn (F5) and having spawned (F6), compared to the total number of adult females in the samples for each bimonthly period are given in Table 1 (from Loubens and Sarmiento, 1985 and Loubens, 1989). Changes in the mean gonadosomatic index (GSI) of the females are also given. The percentage of F5 + F6 females is always very high throughout the year, as is the GSI value. This indicates that breeding takes place throughout the year, without major variations. According to Loubens, 1989, the sexual life of the adults is characterised by an uninterrupted succession of $3 \rightarrow 4 \rightarrow 5 \rightarrow 6$ cycles and a return to stages 3 or 4 from maturity till death, the cycles of individual fish not being synchronised.

All species of *Orestias* produce demersal eggs that are heavier than water, adhesive, transluscent and frequently yellow in colour. They vary in size at spawning between 1.3 and 2.3 mm, depending on the species. At each spawning a female lays between 50 and 400 eggs, again depending on the species, but as the number of spawnings per year is unknown, we have no idea of the total fecundity.

As far as spawning behaviour is concerned, Bustamante and Treviño (1980) give some details for *O. ispi* and *O. pentlandii*. These two species approach the shores during the night and lay their eggs on submerged plants. In the case of *O. ispi*, the spawning shoals remain a few hours on the spawning grounds and then disappear until the following night; this lasts for

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MONT	HS	1 + 2	3 + 4	5+6	7 + 8	9 + 10	11 + 12
Orestias agassii	GSI	4.1	5.1	4.2	7.1	7.2	3.5
	% F5 + F6	64	65	64	76	65	44
Orestias albus	GSI % F5 + F6	6.5 100		6.7 80		8.9 80	8.7 64
Orestias forgeti	GSI % F5 + F6	6.8 65	7.7 73	3.9 43		8.8 92	4.4 30
Orestias ispi	GSI % F5 + F6	8.6 100	11.0 100			11.8 100	10.4 86
Orestias luteus	GSI	7.6	6.9	5.2	9.0	8.5	6.7
	% F5 + F6	71	71	50	79	83	67
Orestias	GSI	7.6	6.4	6.0	7.1	6.9	5.6
olivaceus	% F5 + F6	77	77	73	80	93	72
Orestias	GSI	4.6	2.9	4.4	8.1	3.6	4.4
pentlandii	% F5 + F6	77	67	56	80	41	76

Table 1. Breeding seasons for 7 species of *Orestias*. GSI: mean gonadosomatic index. %F5 + F6: percentage of ripe females and females just having spawned.

up to 15 consecutive days. It is almost certain that the other species also spawn in the vegetation belt, given the nature of their eggs and the sites where mature adults have been captured.

Condition

Condition has been studied in three species: *O. agassii* (Loubens and Sarmiento, 1985), *O. luteus* and *O. olivaceus*, *sensu* Lauzanne, 1982 (Loubens, 1989). The condition factor ($K = 10^5 \times P/L^3$) was used in these studies. This factor does not vary with sex and usually remains stable throughout the year in a given region (Fig. 5). From these studies it would seem that this stability is due to the great stability of environmental factors and also to the reproductive strategy (successive spawning spread over the year with absence of synchronisation of individual cycles). A more detailed regional study did, however, reveal small variations in condition factor for any given species. The authors suggest that these variations could be of genetic origin, "Il y aurait, chez ces poissons peu mobiles, panmixie incomplète avec le début de différenciation des stocks géniques".



Figure 5. Monthly changes in condition factor ($K = 10^5 \times P/L^3$) in O. luteus, O. olivaceus and O. agassii in Lago Pequeño. (from Loubens and Sarmiento, 1985 and Loubens, 1989).

Diet

There has been no detailed study of the diet of *Orestias*, but numerous works partly deal with this aspect of their biology. We have largely drawn on Loubens (1989) in attempting to classify the various species according to their dietary affinities.

Pelagic species feeding on zooplankton

These are O. pentlandii, O. ispi and O. forgeti, which feed mainly on entomostracan zooplankton: Copepoda and Cladocera.

Perimacrophytic species

This group comprises *O. luteus*, *O. olivaceus* and *O. jussiei*. These species feed on plants and animals living on and around macrophytes: phytoperiphyton and zooperiphyton, insects, amphipods and molluscs. *O. luteus* and *O. olivaceus* seem to have a marked preference for molluscs.

Demersal species

O. mulleri and O. crawfordi feed on animals such as chironomid larvae, amphipods, ostracods, cladocerans and molluscs living on the bottom. O. crawfordi seems to consume only molluscs.

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O. agassii an ubiquitous species

This fish, as noted before, is capable of colonising various habitats, its diet therefore covers a very wide spectrum, from algae and macrophytes to zooplankton, amphipods, ostracods, insects and insect larvae. Depending on the habitat in which it lives, one or other of these prey items may dominate.

O. albus, mainly piscivorous

This species mainly consumes small *Orestias*, but also a certain quantity of gastropods and lamellibranchs. *O. albus*, therefore seems to be the only piscivorous species of *Orestias*, since the disappearance of *O. cuvieri*.

It should be noted that some major food resources such as the phytoplankton, macrophytes, oligochaetes and organic detritus, are little or not at all exploited. In addition, the terminal piscivorous consumers are only represented among the *Orestias* spp. by *O. albus*, an uncommon species. The introduced species *S. gairdneri* and *B. bonariensis* make up the backbone of this group in Lake Titicaca. *S. gairdneri* feeds mostly on *O. ispi* and *B. bonariensis*, once it has reached a length of about twenty centimetres, eats mostly *O. agassii*, *O. olivaceus* and *O. ispi*.

Parasitism

The Orestias of Lake Titicaca are very often parasitised. The cranial cavity of several species (especially O. olivaceus) is invaded by a Diplostomum sp., but the most remarkable parasite is a platyhelminth (Ligula intestinalis, according to Hanek (ed.) 1982) which lives within the abdominal cavity of several Orestias spp. The parasite is especially abundant in O. forgeti, which led Loubens (1989) to study the host-parasite relationships in this species. About half of the fish are parasitised and the mean number of parasites per host is 2.73. The plerocercoids reach a length of 10 to 20 cm, or twice the length of the host. The maximum length recorded is 420 mm in a female measuring 87 mm. The mean ratio of the weight of the parasite to that of the host varies from 18% for the smaller fish to 42% for the largest. The maximum value recorded is 74.5%. This enormous additional burden hinders the swimming of the fish and leads to greater vulnerability to active fishing gear. In addition, parasitism leads to sterility, to the extent that sometimes

Plate 3. Above: fishing boats catching "pejerreys" with turning gillnets, in the Lake Huiñaimarca; Center: Gillnets catch. A young rainbow trout (above on the picture), 3 "pejerreys" (in the center), 1 *Trychomycterus* (down left) and different species of *Orestias* (down right); Down: Japanese aquaculture Station near the Tiquina strait. *Salmo gairdneri* (rainbow trout) is reared in floating cages. (Photos Claude Dejoux.)



the gonads are so atrophied that it is no longer possible to identify the sex. It is likely that the very pronounced parasitism which affects numerous species has an effect on the health of the *Orestias* populations.

Conclusion

Major progress has been made in our knowledge of the genus *Orestias* over the last decade. The systematics and phylogenetic relationships between the various species are increasingly better understood. The deep water zone in Lake Titicaca has been little surveyed, however, and it is possible that it harbours species not yet described. The biology of the species of direct of commercial value has been studied to varying degrees, but there are still important variables, such as the growth rate, that have not been studied. The relationships between *Orestias* spp. and the introduced predatory species are relatively well known and it does not seem that these latter represent a danger for the survival of *Orestias* populations in Lake Titicaca at the present time.

VI.5b. Introduced species 1. Salmo gairdneri (Rainbow trout)

GÉRARD LOUBENS*

History of introduction and exploitation

Four species of Salmonidae were introduced into Lake Titicaca from 1939 onwards: Salvelinus namaycush, Salvelinus fontinalis, Salmo trutta and Salmo gairdneri. It appears that only small numbers of Salvelinus were released on few occasions. In any event, these species did not adapt to their new environment. Salmo trutta was common in the River Llave in 1970 (Everett, 1973), but at the present time only Salmo gairdneri, which was also successfully introduced into many other Andean lakes, still occurs in Lake Titicaca.

The first rainbow trout were brought to the fish farm at Chucuito near to Puno (Peru) in 1941 or 1942, probably from the United States, although Bustamante and Treviño (1977) say that they originated from the Lautaro fish farm in Chile. 19 million fingerlings were released between 1941 and 1969 (Coutts, 1983). The stocking then continued at a rate of 700 000 per year (Laba, 1979).

Fishing by trolling began from 1948, at first for sport and later commercially, throughout the lake. Specimens of more than 10 kg were captured (Gilson, 1964), the largest individual being 122 cm long and weighing 22.7 kg (Matsui, 1962). Gill-nets came into use as from 1952. The nets quickly replaced trolling, which is now no longer employed.

The trout were at first sold fresh in the regional markets as far away as La Paz, Arequipa and Cuzco. From 1961, canneries were set up and their products exported to the United States and Europe. There were up to 5 plants which processed 500 tonnes of trout in 1965. Very soon after, the production of these plants declined and all were closed by 1970 (Everett, 1973).

Exploitation using surface gill-nets continues at present almost entirely in Peruvian waters. The produce is sent fresh or smoked to the local markets. Annual production in Peru was estimated at 889 tonnes over a one-year

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period 1979 to 1980 (Hanek, 1982). The total production is therefore about 1000 tonnes if the small Bolivian contribution is included.

The most recent period of exploitation shows that the situation is less pessimistic than suggested by the works of Everett which gave a sustainable annual yield of 350 tonnes. This author only studied the fishing effort and production destined for processing plants (as opposed to fishing intended for self consumption or for sale fresh or smoked) as the only data available were from the trips made by lorries collecting trout for the processing plants and the output figures for these plants. His estimate for the annual sustainable yield was therefore founded on partial data, the total production of rainbow trout in the 1960s being unknown. The decline in production of the processing plants and their final closure could have been due to overfishing. Another and perhaps main cause, was a change in the world market for trout, since it was during the 1960s that fish farming of Salmo gairdneri developed enormously. In France, for example, it quadrupled between 1960 and 1970, increasing from 2500 to 10 000 tonnes. In the face of such competition, the processing plants at Lake Titicaca found themselves confronted with a insoluble price problem compared to the fresh product, which is usually preferred by the consumer.

Biology

This summary of the biology of *Salmo gairdneri* in Lake Titicaca is based on the works of Everett (1971, 1973), Bustamante and Treviño (1977) and of Hanek (1982), who reviewed the studies of Peruvian researchers, and on some personal observations made between November 1979 and February 1981 in the Bolivian part of the lake. Additional information comes from Lauzanne and Franc (1980) who studied an isolated population of rainbow trout occurring since 1975 in Lake Khara Kkota in the Eastern Cordillera. On the whole, the biology of the species remains poorly known, especially in quantitative terms. The relationships derived from our results, between the various measurements of length generally used (in mm) and between length and weight (in g) are as follows:

total length = 1.150 standard length + 6.6; r = 1.000fork length = 1.110 standard length + 1.7; r = 1.000log fresh weight = 3.217 log standard length - 5.223; r = 0.995

Salmo gairdneri inhabits all of the Lago Grande and a small part of the Lago Pequeño (Chua and Calata regions). This species of fish occupies coastal areas, except for the totora belt, and all of the pelagic zone. It lives in the surface waters as indicated by the fishing method (fixed or drifting surface gill-nets), but it is not known to what depth it penetrates. The size of individuals taken in the lake is very variable: 166 to 555 mm in our observations and from about 160 to 750 mm in those of Everett (*op. cit.*). The

youngest individuals live in the rivers, where they have frequently been caught, particularly in the Rio Ramis.

Adults or pre-adults start to congregate at the mouths of the major rivers at the start of the rainy season in December. They run up the rivers throughout the rainy season with a maximum seeming to occur in February when the water level is at its highest. The nets are obstructing during this period the areas near the river mouths, as was apparent in the case of the Rio Suchez (Escoma Bay) in 1980. It appears that all the large trout are captured on their passage, because samples taken from the river only contained a total of 12 trout measuring more than 24 cm (Everett, 1973).

Spawning starts in gravelly sites in the middle and upper reaches of the rivers in April, and reaches a peak in June and July. During these two months adults of small size – about 15 cm for the males and 22 for the females – have been seen in the act of spawning. In October, small trout 3 to 4 cm long are caught in the Peruvian rivers. Nothing is known of the proportion of individuals which succeed in reaching the spawning grounds and even less so about the proportion that returns to the lake after breeding.

The cycle of development of the gonads shows that they start to mature in December, followed by a progressive increase in the gonado-somatic index, which reaches a maximum of about 16% for females and 9% for males for mature individuals captured in the littoral zone. The maximum occurs in June in the case of females and in April for males. In contrast, our observations show that individuals taken in the pelagic zone in the Lago Grande from June to November are sexually quiescent, although this is based on few observations (fifteen individuals). The size at sexual maturity is not known with precision. Adults in the advanced stages of maturation occur as from 13 cm in the case of males and from 18 cm for females. The number of mature eggs varies between 1600 and 8000 for females of between 30 and 60 cm length. Lauzanne and Franc (*op. cit.*) gave very similar results for both gonado-somatic index and fecundity.

Growth was estimated by Everett (1973) from catches made with gill-nets (meshes of 38, 50, 63.5 and 76 mm knot-to-knot), using Petersen's method. Rainbow trout reached 342 mm in 2 years, 474 mm in 3 years, 553 mm in 4 years, 613 mm in 5 years and 658 mm in 6 years (standard lengths). These results should be considered as preliminary because of the sampling method (selectivity of gill-nets and small range of meshes used) and the restricted sampling area confined to a band 3 km wide along the shore, whereas trout occupy all of the lake. In addition, the results were obtained from a series of rather indistinct modal lengths, using a method for distinguishing separate age-classes, whose correspondence with reality is unknown. The examinations of scales and otoliths made by Everett did not produce any results.

Lauzanne and Franc (op. cit.) provided a good estimate of growth during the first year for rainbow trout in Lake Khara Kkota. Their captures, made at the height of the spawning season in June and July, demonstrated the existence of a group of young trout of between 8 and 20 cm length (N = 124, mean standard length 14.7 cm) with a mean age of 1 year. The growth of young trout in Lake Titicaca is probably very similar.

It is known that after the first year, the growth of *Salmo gairdneri* can be very rapid in the sea or in large lakes. Laurent (1965) showed by marking that individuals released at a mean length of 16.6 cm grew by more than 18 cm and by more than 500 g in Lake Léman in 7 months. The mean surface water temperature In Lake Léman is 12.5° C, the same value as for Lake Titicaca. Thousands of marked rainbow trout with an average length of 21 cm were introduced into Lake Vättern (Sweden) between 1964 and 1968 and several hundred were recaptured. Their mean size reached 55 cm after two years spent in the lake, despite a long period of no growth in the winter (Grimås *et al.*, 1972a). The *Salmo gairdneri* in Lake Titicaca enjoy excellent living conditions (stable temperature at $11-14^{\circ}$ C, well oxygenated water, abundant food, reduced competition), so their growth should be as rapid as the excellent condition of all the individuals captured would tend to indicate.

As far as food is concerned, rainbow trout living in the rivers feed especially on aquatic insects (62% in volume) and fish (14%). In the Peruvian part of the Lago Grande, individuals of less than 27 cm length (N = 207) fed especially on amphipods (62%), insects (18%) and fish (17%); those measuring beteen 27 and 46 cm (N = 122) mostly on fish (76%) of which a third were Orestias ispi, the rest not having been identified (Hanek, 1982). Our own observations in the Bolivian part of the lake show the same gradual change in diet in relation to two correlated factors: size and habitat. The stomachs of 13 trout measuring 195 to 323 mm taken near the shore, contained 61 O. ispi, 9 Basilichthys bonariensis about 10 cm long, numerous insects and a few amphipods and other crustaceans; in 9 trout measuring 317 to 558 mm taken in open water in depths exceeding 25 m, we found 219 O. ispi of 45 to 70 mm and 3 small B. bonariensis. It should be noted that benthic species of Orestias and those living amongst macrophytes were absent from all these stomach contents, although they are very abundant in or near the vegetation belt. These species of Orestias probably have time to hide among the aquatic vegetation which is too dense for trout to pursue them in.

In Lake Khara Kkota Salmo gairdneri of 15 to 20 cm (N = 35) feed on amphipods (66% by volume) and insects (27%); those of 30 to 45 cm (N = 16) on molluscs (76%), amphipods (14%) and a few fish (6%). In this lake the fish fauna is very poor, only one other species *O. polonorum* being present.

These results show that the rainbow trout feeds on all the organisms available near the bottom or in the water column in which it lives, but that the density of aquatic vegetation prevents it from exploiting the abundant benthic fish fauna.

The only fish species which is a potential predator of the trout is Ba-

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silichthys bonariensis, but no trout have been recorded from the stomach contents of this fish, probably because the *Salmo gairdneri* living in the lake are too large. No cannibalism has been recorded either.

Improvement of the state of stocks

The most sensitive stage in the life cycle of *Salmo gairdneri* is that spent in the river during spawning and growth of the young. Although Lake Titicaca is very large, its five main inflows are of modest size. Four of these are in Peru, The Huancané, Ramis, Coata and Llave. The smallest of the five, the Río Suchez, has its source in Peru but its lower course is in Bolivia. All five flow into the Lago Grande.

The flow regime of these rivers is very irregular (Carmouze and Aquize Jaen, 1981). Although the maximum discharges in February and March range from 19 m³/s for the Rio Suchez to 233 m³/s for the Río Ramis, the dry season flows are very small. In June and July, the period of peak spawning, discharges vary from 3 to 4 m³/s (Suchez) to about 20 m³/s (Ramis). These are the discharges recorded at the river mouths, those of the tributaries making up the middle and upper reaches where the redds are built are obviously much lower. In addition, there are strong variations between years - in August 1965 for example the discharge of the Suchez fell to $0.65 \text{ m}^3/\text{s}$. It can therefore be seen that the available habitat at the time of spawning is very reduced, making capture of fish running up the rivers very easy, whether this be by dynamite, as has been reported by many authors (there are numerous mines established in the region and explosives are easy to come by), or even by hand, as has been recorded by Lauzanne and Franc in the inflow of Lake Khara Kkota. Chemical pollution from washing of mineral ores or clothing in the rivers is also probably occurs. River discharges only start to increase again in December, so that the habitat available to fish fry during their first months of life is very reduced and susceptible to many forms of degradation and pollution.

A proper protection of the main rivers, with in particular the prohibition of all forms of fishing within them, is therefore essential. Large channels to allow the passage of fish should be left permanently free in the areas of the lake near river mouths as long as the periods when fish run up the rivers and when the young descend are not well known. Once these measures have been taken and are respected, detailed monitoring of the fishing is needed. It is possible that the breeding stock is already too low in some rivers and that restocking in some way or other is needed. The best results seem to be obtained by releasing young trout about 20 cm long in the coastal areas of lakes (Grimås *et al.*, 1972b; Laurent, 1972).

Conclusions

There have been several vigorous attacks against the introduction of rainbow trout into Lake Titicaca, accusing it of seriously threatening the fauna of *Orestias* and for having been responsible for the disappearance of *O. cuvieri* (Vellard, 1963; Vilwock, 1962, 1975; Lillelund, 1975; various authors cited by Laba, 1979 and Laba himself). Vellard in particular, declared that: "soon they (the trout) will have brought about the destruction of the entire indigenous fauna of *Orestias* and of *souches*." (local name of *Trichomycterus rivul-atus*).

As we have seen above, this opinion is entirely without foundation as far as the benthic and plant-dwelling species of *Orestias* are concerned, and particularly the main exploited species *O. agassii* (54% of the fishery yield according to Hanek, 1982).

The pelagic species *O. pentlandii* at present lives in the areas where *Salmo* gairdneri is rare or absent. The situation would not appear to have changed much since the observations of Vellard (1963) who wrote: "La boga (*O. pentlandii*) est aussi en voie d'extinction. Devenu à peu près introuvable dans la région de Puno et le Grand Lac, il existe en petites quantités près de Guaqui."

O. cuvieri can be considered as having disappeared since Vellard (1963) and Vilwock (1962) already stated that they had no longer encountered it, and it has not been captured during the numerous fish surveys carried out throughout the lake since the 1970s. From their morphology, the adults of this species were probably piscivorous and were therefore in direct competition with rainbow trout. Nothing is known, however, about the life habits of the young, the preferred habitats, the abundance of the species or even the date of its disappearance. It was seen for the last time with certainty in 1937 (Tchernavin, 1944). The hypothesis of *O. cuvieri* being eliminated by *S. gairdneri* can therefore neither be confirmed nor disproved.

The major problem which needs to be studied in detail at the present day is that of the impact of rainbow trout on populations of O. *ispi*. This species would appear to be very abundant at the moment, but the situation could change quickly with a predator as voracious as S. *gairdneri*, if effective measures for protecting the reproduction of this latter species led to a major increase in recruitment. It would however be fairly easy to redress the unbalance between predator and prey, by starting to fish again in the areas of the lake near to the mouths of the main inflow rivers.

As far as *Salmo gairdneri* and the populations of *Basilichthys bonariensis* are concerned, the two species do not seem to interfere with one another to any great extent and are complementary in terms of their resource utilisation in Lake Titicaca. The rainbow trout breeds and its young stages grow up in the river systems, whereas these stages occur mainly in the vegetation belt in the case of pejerrey. Once they have reached 15-20 cm both species inhabit the lake, but *B. bonariensis* lives much closer to the littoral in more

surface waters than *S. gairdneri*, which occupies the entire lake down to greater depths. The abundance of young pejerreys shows that the predation exerted on them by trout is not too serious under the present conditions.

Two points should however be studied: the relationships between the two species in the lower courses of the inflow rivers, and the methods to be used for stocking with young trout.

In the lower part of the rivers, young trout and small and medium-sized pejerreys occur together. The latter could well feed in part on the former. As regards stocking, the young trout introduced into the lake in the 1940s were not subject to any predation as far as is known. The situation changed however from 1955 when the lake was invaded by *Basilichthys bonariensis*. At the present day, it is possible that any young trout released into the lake would be immediately devoured by pejerreys of a greater size. Rather large trout therefore need to be used to stock the lake, so that they can escape predation from pejerreys, or fertilised eggs could be introduced into the gravel beds of the middle or upper reaches of the inflow rivers.

VI.5b. Introduced species 2. *Basilichthys bonariensis* (The "Pejerrey")

GÉRARD LOUBENS and FRANCISCO OSORIO*

Basilichthys bonariensis (Valenciennes, 1835), locally known as the "pejerrey." is a member of the Atherinidae, originating from estuarine and riverine habitats in Argentina, Uruguay and southern Brazil, from Bahía Blanca in the south as far as the Río da Prata in the north (Lahille, 1929; Fowler, 1954 and Buen, 1959). It penetrates inland several hundred kilometres, since it is one of the main commercial species in the Rosario region, Paraná (Welcomme, 1979, citing Vidal, 1969). Because of its commercial value and its good adaptability it has been introduced in numerous natural and artificial lakes from Argentina to Chile and Brazil (Huet, 1978), and also in Israel and Japan (Bardach et al., 1972). As far as Bolivia is concerned, examples may have been released in 1946 into Lake Poopo by an angling club (Bustamante and Treviño, 1977), but according to Everett (1971), the introduction probably took place a little later into the lake of Oruro. Whichever the case, the pejerrey ascended the Río Desaguadero and entered Lake Titicaca in 1955 or 1956. It invaded the entire lake, including the inflow rivers, where it is at present abundant in all suitable habitats. It is very probably the most important species from an economic point of view in the lake region, as Orestias agassii has a lower market value and Salmo gairdneri (rainbow trout) is now less common after a period of abundance in the 1960s.

According to Bustamante and Treviño (op. cit.) it can attain a fork length of 56 cm and a weight of 2.5 kg. Huet (1978) gave 50 cm and 3 kg. The records in our captures are only 50 cm standard length and 1.65 kg. Individuals of over a kilogram are rare.

Taxonomy

The species *bonariensis* was described for the first time in 1835 by Valenciennes in Cuvier and Valenciennes, *Histoire naturelle des Poissons*, 10, p.

*This chapter has been adapted from Loubens and Osorio (1988) Rev. Hydrobiol. Trop. 21 (2): 153-177.

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469, under the genus Atherina Linné 1758. Nowadays it is generally placed in the genus Basilichthys Girard 1854, but Odontesthes Evermann and Kendall 1906 is still sometimes used, for example by Nion (1977), Huet (1978) and Pinto Paiva and Scheffer (1983). Bertin and Arambourg (1958) and Ringuelet and Aramburú (1961) used the genus Austromenidia Hubbs 1918. The name Odontesthes basilichthys has even been used (Bardach et al., 1972; Pillay and Dill, 1979) ! The latest revision of the Atherinidae seems to be that of Schultz (1948), who placed the species in the genus Odontesthes. However, several characters recorded by us on pejerrey from Lake Titicaca do not correspond with this genus, nor with those of the genera Austromenidia and Basilichthys, according to the key given by this author. Fowler (1954) considered the three genera to be synonyms, but gave no reasons for this decision. The problem as to which genus the Lake Titicaca pejerrey belongs therefore remains unresolved. While waiting for a resolution we retain the most commonly employed name, Basilichthys bonariensis (Valenciennes, 1835).

At the subspecies level, Cabrera (1962) believed he could distinguish between an estuarine population from the Río de la Plata and a riverine population in the Paraná, but the argument proposed – a difference in the length-weight curves, based on a small number of individuals – would appear to be precarious. More recently Freyre *et al.* (1983) designated the pejerrey from a reservoir on the Río Tercero as *B. bonariensis bonariensis*. Finally Linarès (1979) (*non vidi*) named the Peruvian pejerrey as *Basilichthys bonariensis* var. *titicacaensis*. It is then possible that there are several forms.

As far as the pejerrey introduced to the Bolivian Altiplano are concerned, two questions can be posed: firstly, what is the origin of the stock from which they are derived, origin which unfortunately it seems very difficult to retrace; and secondly, what special adaptations have they been able to acquire over the thirty years since they have been isolated from the original stock ? The answer to these questions requires a detailed comparison of the various estuarine and inland populations occurring around the tropic of Capricorn, whether native or introduced.

Age determination and growth

As scale reading, study of the length distribution of fish captured or markrecapture were methods which proved to be too difficult in Lake Titicaca (Loubens and Osorio, 1988), the growth rates of *Basilichthys bonariensis* are only known from works carried out in Chile and Argentina. Burbridge *et al.* (1974) worked on pejerrey in the region of Valparaiso (33°S) using Petersen's method and scale reading. For the first method, the captures made did not appear to be a representative sample of the population. In the case of scale reading, no indication was given of the nature of the rings nor of their chronology of appearance. It is not impossible that they could be used, given that there is a rather pronounced winter at this latitude. The annual growth rate given (total length) was 107 mm for the first year, 111 for the second, 126 for the third, 84 for the fourth and 45 for the fifth. With the exception of the first year these were based on a small number of observations.

Wurtsbaugh *et al.* (in press) report on works carried out in Argentina that we have not been able to consult directly: *Basilichthys bonariensis* reached 20 cm in the first year (Ringuelet and Aramburú, 1961); 28 cm in 1 year and 39 cm in 3 years (Boschi and Fuster, 1959). Lake Lobos near Buenos Aires and a reservoir on the Río Tercero near Córdoba were sampled using beach seines of shallow depth and a few gill nets (Freyre, 1976; Freyre *et al.*, 1983). The recorded size distributions reflected mainly the selectivity of the fishing gear. In the case of the Río Tercero, the standard length was 18.5 cm at one year, 22.3 at 2 years, 25 at 3 years, 27 at 4 years etc. Freyre *et al.* were not able to observe annual rings on the scales, although the latitude was comparable to that of Valparaiso, but report on spawning marks on large individuals.

Sex and reproduction

Sex ratio

We have not recorded any external sexual dimorphism, so the sex and sexual condition was recorded by observation of the gonads, which are recognizable from a body length of about 15 cm.

There are significantly more males than females among young individuals, then as from 18 to 24 cm the sex-ratio is even. The percentage of males then continues to decrease until a minimum of 10%, after which there seems to be a slight rise, although this is not statistically significant, because of the small number of observations. For all pejerrey collected of more than 30 cm there was 1 male for 4 females, for individuals of more than 37 cm there was only one male for 7 females.

The progressive decrease with size in the percentage of males is probably explicable by a slower growth rate, but this could not be proved as the age was unknown.

Wurtsbaugh *et al.* (*op. cit.*) recorded a similar change in sex-ratio with size in their samples from the northern part of the lake.

Stages of sexual maturity and maturation

The development of the ovaries during the life of a female pejerrey can be divided into 6 successive stages, starting with the juvenile stage (stage 1), with a low gonado-somatic index (0.1%) through to individuals which have just spawned in which the gonado-somatic index varies between 1.5 and 4% (stage 6). Each stage is characterised by a particular ovarian morphology. Only three stages have been distinguished in the development of the testes (Loubens and Osorio, 1988).

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	Fei	males			Ma	ales		
L	F	% F.A.	м	M1	M+	M.A1	M.A	% M.A.
135	68	0.0	54	50	4	2	6	11.1
160	134	0.0	174	135	39	19	58	33.3
185	165	0.0	176	98	78	39	117	66.5
210	138	2.2	151	64	87	43	130	86.1
235	112	6.3	109	43	66	33	99	90.8
260	82	22.0	70	26	44	22	66	94.3
285	69	59.4	41	15	26	13	39	95.1
310	62	77.4	26	10	16	8	24	92.3
335	47	87.3	21	7	14	7	21	100.0
360	58	98.3	18	5	13	5	18	100.0
385	68	100.0	8	3	5	3	8	100.0
410	55	100.0	9	2	7	2	9	100.0
> 410	26	100.0	6	3	3	3	6	100.0
L.S.M.: 280 mm Minimum size of maturation :		L.S.M.: 180 mm Minimum size of maturation :						
	201 mn	1			14	in uų		

Table 1. Length at sexual maturity. F, female; M, male; A, adult; +gametogenesis; 1, immature or sexually inactive adult.

Size at sexual maturity

The size at sexual maturity is that at which 50% of individuals are immature and 50% adult. The ability to reproduce, which typifies adults, is considered to have been reached when the gonads are clearly mature.

In the case of females, all individuals of more than 35 cm length show clear signs of more or less active gametogenesis irrespective of the season (% A.F., Table 1). For males, the calculation is a little more complicated because, even among large males, there is a certain proportion of individuals with reduced gonads (M1) which may either be adults or immatures. We have assumed that all the males measuring at least 335 mm are adult, which enables us to calculate a value of 0.50 for the proportion of adult males with resting gonads (M.A1) compared to mature males (M+), which was then applied to size classes of less than 335 mm.

Plots of the percentage adults against length give values for the length at sexual maturity (L.S.M.) of 280 mm for females and 180 mm for males, the minimum length for maturity being 201 mm for females and 140 mm for males. The largest immature female recorded being 344 mm, the range of lengths at sexual maturity is therefore 201–344 mm.

By using the alternative method of the relationship between gonadosomatic index and length, the value of 285 mm for the L.S.M. in females was obtained, a value very close to the first.

Wurtsbaugh et al. gave the following minimum lengths for advanced mat-



Figure 1. Bimonthly changes in GSI and reproductive index, RI.

uration for pejerrey from the north of the lake, based on a small number of observations: 25 cm for females and 17 cm for males. Pinto Paiva and Scheffer (1982), working on *B. bonariensis* in the Río Jacui (Río Grande do Sul State, Brazil, 30° S), were successful in artificial spawning with fish of 25 cm total length and over, or 21 cm standard length. This accords well with our observations. Finally, Burbidge *et al.* (*op. cit.*) found a distinct group of fish among their sample ranging in length between 19 and 30 cm and which were all adults.

Maturation cycle and period of reproduction

Tables 2 and 3 and Fig. 1 give the percentages of males and females in each two-month period at the various stages of gonadal development, and the corresponding mean GSI values. In addition, an index known as the reproductive index RI has been calculated (last column of Table 3), which is intended to represent in a single value all the observations made of the GSI of both males and females. As the GSI of the females is on average 5.5 times greater than that of the males, the RI value is equal to GSI female + 5.5 GSI male. In interpreting this figure it should be noted that if in a particular season all the adults returned to sexual quiescence, the IR would be equal to about 1.5.

The reproductive season covers the entire year, the mean GSI values and reproductive indices being high throughout the year. A slight downturn in March to June is all that can be noted. As with *Orestias agassii*, the cycles of maturation of individual fish are not synchronised, because of the remarkable constancy of the main physico-chemical and biological properties of the lake.

It is interesting to compare these results with those of *Basilichthys bonari*ensis living in their original habitat of estuaries and lowland rivers at between

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		% of the stages						
Months	N	1+2	3+4	5	6	G.S.I.		
1 + 11	96	12	30	20	38	5.7		
lli + i∨	45	4	33	7	56	3.7		
V + VI	125	3	41	13	43	3.0		
VIL + VIII	31		48	19	32	5.4		
IX + X	10		60	30	10	5.1		
XI + XII	6	33	33	33		2.6		
l to XII	313					4.23		

Table 2. Percentage of females at various stages of maturation and seasonal changes in mean GSI for individuals of at least 300 mm

Table 3. Percentage of males at various stages of maturation and seasonal changes in mean GSI and reproductive index RI for individuals of at least 200 mm

		%	of the sta	iges		
Months	N	1	2	3	G.S.I.	R.I.
I + II III + IV V + VI VII + VIII IX + X XI + XII	157 47 136 18 29 57	43 62 25 17 55 40	21 36 30 22 14 16	36 2 35 61 31 44	0.8 0.3 0.7 1.1 0.9 1.1	10.1 5.4 6.9 11.5 10.1 8.7
I to XII	444				0.77	

30°S and 40°S. These habitats show much more pronounced fluctuations in temperature, salinity and in water level. The information that we have been able to find in the literature is, however, brief and contradictory. Buen (1953) indicated that the species spawned in the spring, i.e. from October to December, but according to Boschi and Fuster (1959), sexually mature individuals occur throughout the year in Argentina and especially from September to November. Iwaszkiw and Freyre (1980) considered there to be two periods of reproduction, the first from August to November and the second during the southern autumn. According to Pinto Paiva and Scheffer (1982), spawning takes place from May to July in southern Brazil. These indications need to be made on a solid basis, and in particular providing an insight into how the chronology of maturation has changed after thirty years spent in a stable environment.

The problem of spawning

The pejerrey would appear to experience problems with spawning in Lake Titicaca. We have in fact encountered a significant proportion of mature females at all seasons which appear not to have been able to spawn or not able to complete spawning. Their ovaries contain large quantities of mature eggs beginning to become atretic and sometimes forming enormous hernias from which the eggs could obviously not escape. Some ovaries were also filled with an aqueous liquid.

The main difference in comparison with the original habitat is the water temperature. The slight salinity of Lake Titicaca $(1 g l^{-1})$, its good oxygenation and its abundant vegetation cover are all favourable factors. In contrast, the temperature of the surface 10 m of water in which the pejerrey live, remains at between 10°C and 14°C, with a maximum in December to February (Lazzaro, 1985), whereas the authors cited above all agree that the temperature range favourable for reproduction and egg development is between 15 and 21°C, with an optimum of 17-18°C. The slightly too cold waters of Lake Titicaca probably constitute a major obstacle for the reproduction of this subtropical species, but the fact that reproduction occurs throughout the year enables this obstacle to be overcome. Nevertheless, strong annual variations in recruitment are to be expected, given that the fish are at their lower limit of temperature tolerance. This seems to be confirmed by the remarks of Bustamante and Treviño (op. cit.) on the pejerrey of Lago Pequeño, based on observations made in 1976-1977: "this fish was formerly abundant in Lago Pequeño, but at present it is only rarely captured." After a period of abundance in 1970, the pejerrey became rare in Lago Pequeño and then became abundant again in the period of our observations (October 1979-November 1981).

Are there several cycles of maturation per year for each individual? In mature ovaries, in addition to ripe eggs measuring 1.6 to 1.8 mm, there also occur maturing oocytes of up to 0.7 to 0.8 mm, corresponding to stage 3. A second cycle during the course of a single year would therefore appear to be possible, since the total time taken for maturation from stage 1 to stage 5 is in general of the order of a few months in many species of fish.

The GSI of mature females is very variable, values ranging from 2 and 36%, without any pronounced modal value, which indicates fractional spawning, or perhaps interrupted spawning because of the temperature problem described above.

The number of eggs laid per female in a year is very difficult to estimate. Wurtsbaugh *et al.* recorded a mean of 3570 mature eggs in the ovaries of 6 females of 24 to 28 cm caught in the north of Lake Titicaca. Iwaszkiw and Freyre (1980) working on *B. bonariensis* in a reservoir on the Río Tercero, counted the mature eggs in the ovaries of 80 females of between 20 and 31 cm long, and gave the following relationship between the number of eggs N and the standard length L in mm: $N = 0.0188 L^{2.2955}$. For L = 260 mm, N = 6572, that is much higher than Wurtsbaugh *et al*.

Study of condition

The condition of the pejerrey in the lake was studied using the various factors described by Le Cren (1951) after having overcome several methodological problems described in detail in Loubens and Osorio (1988). This led us to draw up a condition index C, calculated from the means of the condition



Figure 2. Seasonal changes in condition factor of pejerrey of 100 to 249 mm length. A, changes in K for fish of 100 to 149 mm; B, 150 to 199 mm; C, 200 to 249 mm; D, changes in condition index C for fish of 100 to 249 mm length.

factors K calculated for three size classes (100–149, 150–199 and 200–249 mm). The condition factor $K = 10^5 PL^{-3}$, where P is the weight in grams and L is the standard length in mm. For fish of over 250 mm, because of the small sample, the relative condition factor K' was used: $K' = P \times P^{-1}$, where **P** is the weight estimated from the length weight relationship for Lake Titicaca pejerrey.

The most complete results are those for the Lago Pequeño (Fig. 2, Table 4). There is no apparent seasonal cycle in condition, even if some samples have a mean significantly different from those of others. These occasional differences can be attributed to the samples being too small compared to the rather large variance of this variable. The value of the overall index of condition C was particularly stable from October 1979 to December 1980. For large individuals the results are incomplete but do not reveal any major variation. With *Basilichthys bonariensis* the same stability in condition is therefore found as that already demonstrated for another biologically very different species, *Orestias agassii* (Loubens and Sarmiento, 1985). This stability and the reproduction season lasting throughout the entire year are very rare biological characteristics, reflecting the extreme constant environmental conditions, which it would appear have only been found elsewhere in the East African lakes (Loubens and Sarmiento, *op. cit.*).

The results for the Lago Grande are incomplete (Table 5). They do however reveal a tendency for the fish of greater than 150 mm to have a better condition than those in the Lago Pequeño. The difference is significant for large individuals. The large pelagic pejerrey of the Lago Grande have available very abundant prey in the form of shoals of *Orestias ispi*, a small

	100	– 149 mm		150 – 199 mm			200 – 249 mm			
Date	к	v x 10²	n	к	v x 10²	n	к	v x 10²	n	с
30/10/79	1.06	0.59	130	1.15	1.07	72	1.33	2.21	10	1.18
27/11/79	1.08	0.67	169	1.13	0.50	123	1.25	0.87	14	1.15
1/01/80	1,13	0.84	113	1.17	1.04	136	1.17	1.17	21	1.16
17/02/80	1.09	0.65	108	1.15	0.52	126	1.25	2.05	26	1.16
1/04/80	1.07	0.39	11	1.14	0.66	20	1.23	0.57	9	1.15
13/05/80	1.07	0.41	11	1.18	0.63	23	1.28	1.37	40	1.18
19/06/80	0.97	0.20	10	1.27	0.87	11	1.23	0.71	40	1.16
27/09/80	1.04	0.90	300	1.14	1.03	40	1,32	1.35	20	1.17
28/11/80	1.02	0.40	50	1.10	0.63	57				
26/12/80	1.09	0.46	33	1.15	0.74	93	1.15	0.52	13	1.13
1/02/81				1.17	0.72	43	1.25	1.09	70	
12/03/81				1.17	0.35	10				
28/05/81	0.99	0.78	40							
1/10/81	1.05	1.55	14							
12/11/81	1.04	0.71	83	1.04	0.87	10				

Table 4. Seasonal changes in condition factor K and condition index C for pejerrey from the Lago Pequeño; V = variance of K

pelagic species usually living in deep water and therefore rarely present in the southern part of the Lago Pequeño.

It is interesting to compare the pejerrey from Lake Titicaca with those from Argentina and Chile for which there are some publications (Table 6). The condition factor has not however been calculated in these works, but rather the length-weight relationship which can be used when it is really representative of the parent populations. This requires that a wide range of lengths has been taken into account – otherwise the regression lines are biased – and that equal weight has been accorded to the various length classes, which is the case in the works we have selected. The relationships

Table 5. Seasonal changes in condition factor K for pejerrey from the Lago Grande

Length groups				
(mm)	Date	к	v x 10 ²	n
100 - 149	10/05/80	0.95	0.58	12
	22/07/81	1.01	1.10	20
150 - 199	28/03/80	1.15	0.73	15
	10/05/80	1.21	1.24	52
	30/10/80	1.20	0.27	10
	26/02/81	1.21	0.82	22
200 - 249	28/03/80	1.28	0.87	40
	10/05/80	1.29	1.12	65
	25/06/80	1.29	0.89	23
	10/12/80	1.34	2.33	24
	26/02/81	1.25	1.39	49
	23/09/81	1.26	0.84	14

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Parameters	Burbidge <i>et al.</i> , 1974 Peñuelas lake, Valparaíso Chile	Freyre, 1976 De Lobos lake Buenos Aires Argentina	Freyre <i>et al.</i> 1983 Tercero lake Córdoba Argentina	Loubens and Osorio Lake Titicaca Bolivia	
a x 10 ⁶	2.023	3.766	5.046	2.918	
b	3.2525	3.2125	3.1629	3.2669	
Length (mm)		Weig	gth (g)		
200	110	93	96	96	
300	406	342	345	361	
400	1028	861	857	924	

Tuble 0. Length-weight relationships for some peterrey population	Table 6.	Length-weight	relationships	for some	pejerrev	populations
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are regression lines, and reduced major axes would have been preferable for making comparisons, but the correlation coefficients are very high and all the lines very similar for sets of data.

In the case of the Chilean pejerrey, the data are given for the total length which is related to standard length by the relationship LT = 1.177L + 4 (Burbidge *et al.*, 1974). The regressions obtained for the Bolivian and Argentine fish are very similar – the larger Bolivian pejerrey are perhaps slightly heavier – but the difference is probably not significant as the variability in body weight is great among large individuals. In contrast, the Chilean pejerrey are considerably heavier at all lengths. However these results need to be strengthened by additional observations on larger samples, standardised in terms of measurement and analysis.

Transfer of body reserves, gonadal development and condition

Methods

During the life of a fish body reserves can be stored in various organs to be reused at a later date, particularly for the formation of sexual products. These transformations and transfers can provoke sometimes major variations in the relative weights of these organs. In fish, the body reserves are mainly in the form of lipids, glycogen only representing a very low percentage of total weight, at most 0.3% according to Jacquot (1961).

In terms of lipids, two types of fish are traditionally distinguished: the nonoily fish, such as *Gadus*, where the fat reserves are concentrated essentially in the liver (the HSI, hepato-somatic index, is maximum during the early stages of gonad maturation and then decreases as GSI increases), and the oily fish such as the female *Mullus*, in which lipids accumulate in the skin, muscles and peritoneum (the HSI is low, varies little and is not time-lagged with the GSI) (Bougis, 1952; Bertin, 1958 a and b; Hureau, 1970; Lagler *et al.*, 1977, amongst others).

We have attempted to study these transfers in *Basilichthys bonariensis* by measuring 4 ratios or indices of which 3 are well known, the GSI, HSI and condition factor (K for $L \le 300 \text{ mm K'}$ for $L \ge 300 \text{ mm}$), and the fourth must be defined. In numerous species of fish lipids can be deposited in the abdominal cavity, sometimes in large quantities. This is easy to remove by pulling on the peritoneum to which it adheres, this can then be weighed and the PSI calculated, being the ratio between the weight of peritoneal fat to body weight. The weight of the peritoneum itself being very low, this ratio correponds to almost pure adipose tissue. This has been calculated for about 750 pejerrey. The lipids contained in the muscles and skin could not be measured simply. Changes in condition could however, by difference, give an approximate estimate of the quantity of these stored.

Results

The simplest case is that of the males (Table 7, Fig. 3). The HSI varies between 2.0 and 3.1%, being significantly correlated with size and with maturation of the testes. It increases with increasing length up to to the 200–249 mm size class and then remains stable. The influence of sexual maturation is slight but clear, since it leads to a decrease of 0.5 to 0.6% in the HSI, irrespective of size. The PSI is about twice as great as the HSI and undergoes similar, but more pronounced changes, the difference between resting males and maturing males reaching 2.5% of body weight in the largest individuals. K or K' also decreases slightly but significantly in maturing males.

If an attempt is made to draw up a balance for males measuring at least 300 mm, K' equals 1.06 for resting males and 0.99 for others, or a difference in weight of 7%. 3% of this difference corresponds to a decrease in hepatic and peritoneal reserves. The rest of the body therefore loses at least 5%, taking into account the GSI of maturing males, to which must be added the unknown losses due to release of sperm.

Similar results are obtained for females (Table 8, Fig. 3). In immature and pre-adult fish, in which the GSI remains low, the HSI and PSI values increase with length to reach 3.5 and 7.2% respectively. In this stage, growth and accumulation of body reserves predominate. Ovarian development also leads to a decrease in the relative weight of the liver and partial utilisation of the peritoneal fat. In individuals having spawned, the HSI and PSI values are only 2.2 and 3.3%, respectively. As in males the values of K and K' vary little, even in females in the last stage of maturation.

Several remarks can be made on this series of results. In terms of the liver, this certainly plays a lipid storage role, but this is rather limited in

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Individus categori	ies	GSI	HSI	PSI	S	K or K
Prepubescents 140–199 mm GSI < 0.3 %	× v N	~ 0.1	2.56 0.3537 30	3.83 2.0481 20	6.5	1.180 0.0155 30
Young adults	×	1.33	2.03	3.61	7.0	1.190
140~199 mm	v	0.7840	0.2646	2.3032		0.0089
GSI > 0,3 %	N	14	15	9		15
Prepubescents 200–249 mm GSI < 0.3 %	× × × N	0.16 0.0064 39	3.14 0.6353 59	6.04 1.9419 42	9.3	1.292 0.0127 59
Young adults	×	1.38	2.48	4.19	8.1	1.242
200-249 mm	v	0.6175	1.0830	3.2218		0.0161
GSI > 0.3 %	N	75	71	53		74
Adults	×	0.11	3.13	7.14	10.4	1.023
250–299 mm	v	0.0054	0.8272	2.1637		0.0079
GSI < 0.3 %	N	26	34	32		33
Adults	x	1.28	2.54	5.79	9.6	0.965
250-299 mm	v	0.3229	0.6020	6.1196		0.0114
GSI > 0.3 %	N	47	46	42		47
Adults	x	0.11	3.13	7.03	10.3	1.063
300 mm	v	0.0046	1.3400	4.1400		0.0159
GSI < 0.3 %	N	21	27	27		27
Adults	x	1.24	2.60	4.52	8.4	0.991
300 mm	v	0.4332	0.9950	4.5757		0.0099
GSI > 0.3 %	N	42	42	42		42

Table 7. Changes with size and IGS of some variables relating to body reserves in males. S = GSI + HSI + PSI; x = mean; v = variance

terms of the overall balance of energy reserves, most of which come from elsewhere. This tends to lead *Basilichthys bonariensis* being placed among the oily fish, even though the maximum HSI value in any given fish precede that of the GSI. The physiological shock of reproduction would appear to be slight, given that noteworthy quantities of reserves remain and that the condition only drops slightly. In any case this shock is nowhere like as great as that suffered by numerous species of fish, in which the adults are exhausted or die after spawning. Here again the pejerrey is well adapted to its new environment, the only point against it remaining the excessively cold water at the time of spawning.

Finally, the results demonstrate the role played by the peritoneum as a



Figure 3. Changes in HSI and PSI in males (left) and females (right) in relation to length and sexual state. M+ maturing or mature males: M- juvenile or sexually inactive male.

lipid store, a role already known, but rarely measured. This role is very important in the pejerrey since the PSI exceeds 7% before start of gonadal maturation. It would be of value to divide the oily fish species into several types depending on the relative importance of the various lipid storage organs. If, for example, *Basilichthys bonariensis* is compared with *Polydac-tylus quadrifilis*, an amphibious species from the Gulf of Guinea (Loubens, 1966), the combined liver and peritoneal weight accounts for 10% of body weight in pre-adults in the former, so that the concentration of lipids in the muscles is probably rather low and constant. In the latter, the hepatic and peritoneal lipids are of little importance (HSI varies little at around 0.5%, PSI varying between 0.5 to 1.5%), the concentration of lipids in the muscles being undoubtedly higher and more variable. This could have an influence on the market value of fish, depending on local tastes, and in the latter case could lead to seasonal fluctuations in price.

Trophic relations

The diet of *Basilichthys bonariensis* in Lake Titicaca has been studied in detail by Wurtsbaugh *et al.* who examined the stomach contents of several hundred individuals caught in the northern part of the lake in 1973 and 1974. However they only examined a very small number of fish of over 25 cm standard length. For this reason, after a brief report on their main results, we will provide some additional information on the diet of large pejerrey caught in the southern part of the Lago Pequeño.
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Table 8. Changes with size and IGS of some variables relating to body reserves in females. S = GSI + HSI + PSI; x = mean; v = variance

Sexual develop	nent					
Stage and lengt	h (mm)	GSI	HSI	PSI	S	K or K'
	x	~0.1	2.05	2.97	5.1	1.060
120 - 169	v		0.1719	0.6976		0.0054
	Ν		17	18		19
F1	х	0.14	2.35	4.45	6.9	1.214
170-209	v	0.0171	0.2348	1.2212		0.0135
	Ν	23	47	32		59
F1 + F2	x	0.13	2.94	5.81	8.9	1.273
210 + 254	v	0.0099	0.4237	1.8890		0.0128
	Ν	82	95	73		127
F3 + F4 + F5	х	2.65	2.99	5.16	10.8	1.390
210 - 254	v	7.9744	0.8632	3.4398		0.0476
	Ν	14	9	8		14
F1 + F2	x	0.18	3.42	7.18	10.8	1.365
255 - 299	v	0.012	1.0434	2.1736		0.0199
	N	51	63	57		71
F3 + F4	x	2.23	3.26	6.23	11.7	1.346
255 - 299	v	5.5688	1.9660	3.2233		0.0371
	Ν	34	34	34		34
F5	х	7.61	2.53	4.89	15.0	1.407
255-299	v	43.85	0.6981	5.0029		0.0193
	Ν	10	10	10		10
F1 + F2	x	0.28	3.52	7.19	11.0	0.995
300 - 369	v	0.0194	1.408	1.5781		0.0176
	Ν	28	28	28		28
F3 + F4	х	2.42	2.90	5.76	11.1	1.016
300-369	v	5.7410	0.9958	5.4281		0.0271
	Ν	45	45	45		45
F5	x	9.19	2.75	4.03	16.0	1.037
300 - 369	v	53.68	0.8755	2.9656		0.0131
	Ν	23	23	22		22
F6	x	3.12	2.40	3.95	9.5	0.988
300-369	v	5.6248	0.3624	2.4561		0.0188
	Ν	25	25	25		25
F3 + F4	x	4.26	2.80	4.02	11.1	1.054
≥370	v	7.9768	0.5166	3.4701		0.0231
	Ν	41	41	40		42
F5	х	11.60	2.25	3.20	17.0	1.042
≥370	v	41.35	0.4985	5.5121		0.0170
	Ν	25	25	24		25
F6	х	2.80	2.22	3.31	8.3	0.975
≥370	v	4.4640	0.2813	1.8807		0.0171
	N	62	62	62		62

Preys	Standard length sizes (cm) of the predator					
	5-9	9 - 13.5	13.5 – 18	18-27		
Amphipoda	27.5	39.2	31.2	17.9		
Chironomides	39.1	15.2	3.5	2.2		
Copepods	19.7	33.2	25.8	10.3		
Cladocerans	1.5	5.4	7.0	4.1		
Orestias mooni			1.3	32.3		
Other fishes	5.6	2.4	24.7	27.4		

Table 9. Diet of small and medium-sized pejerrey; percentage by volume of the main prey in relation to fish size (from Wurtsbaugh *et al.* in press)

Small individuals less than 9 cm long feed mainly on benthic organisms (Table 9), particularly amphipods and chironomids, as would expected from what is known of their habitat. At a slightly larger size the benthos still remains dominant, but zooplankton represents 39% of the diet in terms of volume. At around 25 cm, the three prey categories, amphipods, zooplankton and fish, are equally important. Finally at around 20–25 cm fish become dominant.

Our results (Table 10) complete the sequence and confirm the increasing predominance of fish in the diet with increasing size of the predator. Zooplankton disappear as from 35 cm, whereas the percentage occurrence of amphipods diminishes to become very low in individuals of more than 40 cm. *Basilichthys bonariensis* therefore exploits all the main groups of animals available in the upper 10 m of water in Lake Titicaca, during the various stages of its development. As a species it can be considered as polyphagous, even though the different stages of development have marked preferences.

As far as the species of prey fish are concerned, Wurtsbaugh *et al.* mainly found a small fish known locally as *ispi* and which they attributed to the species *mooni*. It is very likely that this was *Orestias ispi*, a species described in 1981 by Lauzanne, from numerous specimens of ispi from the Lago Pequeño. In the stomachs of pejerrey from the Lago Pequeño, we have found a few *Orestias olivaceus* and numerous *O. agassii*. In contrast, Vaux *et al.* (*op. cit.*) found no fish in the stomach contents of about forty specimens of 12 to 26 cm long caught in open water at the entrance to Puno Bay, in an area where *O. ispi* were nevertheless abundant. These differences can be explained as follows.

Generally there are few O. *ispi* in the surface water layers, the species being in contrast abundant at a depth of 25–30 m. The pejerrey captured by Vaux *et al.* therefore had to content themselves with zooplankton. If Wurtsbaugh *et al.* found O. *ispi* in the stomach contents of littoral pejerrey this was because the prey species approaches the coast to spawn in the belt of vegetation and then finds itself exposed to the surface water predator, *Basilichthys bonariensis*. Finally, the absence of *O.ispi* in our own results

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Preys		Groups of	standard len	gth (cm) of the	predator
		25-30	30 - 35	35 - 40	> 40
Fish, unidentified Orestias, unidentif Orestias agassii Orestias olivaceus	fied S	47.2 5.6 8.3 5.6	40.0 16.7 13.3	39.3 7.1 42.9	50.0 15.0 30.0
Total fish		69.4	70.0	89.3	95.0
Amphipods Zooplankton Insects		19.4 13.9 2.8	26.7 10.0	10.7	5.0
Number of stomac	hs _	36	30	28	20
Forage fish	L > Z	4.6 0.72 18	6.0 1.52 28	7.0 2.19 26	7.7 2.39 12
Predator	L > N	26.8 0.82 9	32.9 2.76 10	37.5 1.54 16	42.4 2.51 10
L /L'		5.8	5.5	5.4	5.5

Table 10. Diet of large pejerrey: percentage occurrence of the main prey categories and relationship between length of prey fish and that of predators

can be explained by the very sporadic occurrence of this species in the southern part of the Lago Pequeño from where most of our large specimens of pejerrey originate. In its behaviour *B. bonariensis* can therefore be classed as an opportunist, but this opportunism does not go as far as altering its behaviour so that it descends into deep water to take advantage of the abundant prey at 25-30 m.

By measuring the fish found in the stomach contents, a fairly constant relationship is found between the size of the predator and that of its prey, the relationship between the the standard lengths always being close to 5.5. Such a relationship is not usually so clear cut as in this case, where there was only one prey species, *Orestias agassii* and only one habitat, the southern part of the Lago Pequeño.

Finally, it is interesting to note the complete absence of Salmo gairdneri from the prey. It is certain that the data are still incomplete, because Wurtsbaugh *et al.* worked only on *B. bonariensis* less than 30 cm and perhaps only the large pejerrey capture *S. gairdneri*. In our study we obtained about 400 *B. bonariensis* of more than 30 cm, but nearly all came from the Lago Pequeño where the population levels of rainbow trout are very reduced. There are however some indications suggesting that predation by *B. bonariensis* on *S. gairdneri*, if it exists, would not be very important. In contrast, S. gairdneri does feed partly on B. bonariensis: in twenty full stomachs examined, 4 contained young pejerrey of 8 to 12 cm.

In terms of the main species of zooplankton prey, *Daphnia pulex* is most important for pejerrey of less than 20 cm, and the copepod *Boeckella titicacae* in those of 20 to 26 cm (Vaux *et al.*, *op. cit.*). In contrast, according to the results provided by Wurtsbaugh *et al.*, Cladocera are of little importance. This no doubt results from the structure of the zooplankton populations which varies with habitat and season.

Burbidge *et al.* (1974) gave the composition of the stomach contents of 40 young pejerrey of 6 to 9 cm from Lake Peñuelas, Valparaiso, Chile. The diet consisted essentially of zooplankton, with 93% Copepoda and 6% Cladocera. Cabrera (1962) and Cabrera *et al.* (1973) studied the diet of about 300 *B. bonariensis* from the Buenos Aires region. They demonstrated the existence of a very varied diet composed of numerous zooplanktonic and benthic components, but also predominantly fragments of aquatic higher plants. This last item is surprising, since despite the abundance of vegetation in Lake Titicaca, neither Wurtsbaugh *et al.* nor ourselves have ever found the slightest trace of such a component, in spite of the large number of observations. These Chilean and Argentine observations confirm the omnivorous diet of *Basilichthys bonariensis*.

Conclusions

These preliminary results on the biology of *Basilichthys bonariensis* in Lake Titicaca show that this species is very well adapted to conditions of life rather different from those occurring in its original habitat. Coming from a lowland, subtropical riverine environment with fairly marked seasonality, the pejerrey fairly quickly colonised the entire Lake Titicaca basin. The main aspects of their successful acclimatisation are the continuous reproduction, the abundance of young stages in the vast nurseries constituted by the littoral macrophyte beds and of adults in the superficial pelagic zone, the varied diet using the main resources available, the formation of body reserves which always remains considerable and the constancy in body condition.

Considerable gaps remain in the knowledge of the biology of the species. These include: age determination, growth, demographic structure and knowledge of the populations occurring in rivers. On the last point, all that is known from Wurtsbaugh *et al.* is that the pejerrey penetrates fairly far up the inflow rivers in the form of individuals of 10 to 22 cm. It would also be very important to test if the low water temperature is the real cause for the aborted spawnings recorded in many females from Lago Pequeño. More detailed information is also needed on the relationships with native species and *Salmo gairdneri*. Finally, monitoring is required of the impact of fishing on the pejerrey in the lake. Ten years ago captures were of the order of 1700 tonnes for a habitable area (depth zone of less than 50 m) of about

 3000 km^2 , or a yield of 5.7 kg ha⁻¹. This does not seem very great, but the quantity captured at present is unknown, as is the impact of fishing on the various ecophases. It is probable that fishing mainly affects spawning congregations, as we have recorded in Guaqui Bay in 1981, and in this case, in spite of a relatively modest tonnage captured, fishing could be a major factor for the depletion of the stocks of *Basilichthys bonariensis* in Lake Titicaca.

References of chapter VI.5

- BARDACH (J.E.), RYTHER (J.H.), Mc LARNEY (W.O.), 1972. Aquaculture. John Wiley and Sons, New York, 868 p.
- BARRA (C.J.), 1968. Taxonomía del pejerrey del Lago Titicaca y método para su salado y secado. Tesis Univ. Federico Villarreal, Lima.
- BARRA CORDOVA (C.), LA TORRE PEREZ (J.), 1980. Algunos parámetros del crecimiento del pejerrey (*B. bonariensis*) en la represa México, Cochabamba. UMSS. Dep. de Biología, Cochabamba: 14 p.
- BERTIN (L.), 1958 a. Appareil digestif. *In* : Traité de zoologie. Grassé éd., Masson, Paris, 13 (2): 1248–1302.
- BERTIN (L.), 1958 b. Sexualité et fécondation. In: Traité de zoologie. Grassé éd., Masson, Paris, 13 (2): 1584-1652.
- BERTIN (L.), ARAMBOURG (C.), 1958. Super-ordre des Téléostéens. In: Traité de zoologie. Grassé éd., Masson, Paris, 13 (3): 2204–2500.
- BOSCHI (E.E.), FUSTER DE PLAZA (M.L.), 1959. Estudio biológico pesquero del pejerrey del embalse del Río Tercero (*Basilichthys bonariensis*). Depart. Invest. Pesq., Secret. Agric. Ganad., Buenos Aires, 8: 61 p.
- BEVERIDGE (M.C.M.), STAFFORD (E.), COUTTS (R.), 1985. Metal concentrations in the commercially exploited fishes of an endorheic saline lake in the tin silver province of Bolivia. *Aquacult. Fish. Mgmt*, 16 (1): 41–53.
- BOUGIS (P.), 1952. Recherches biométriques sur les rougets (Mullus barbatus L., Mullus surmulatus L.). Arch. Zool. exp. gén., 89: 57-174.
- BUEN (F. de), 1953. Los pejerreyes (Familia Atherinidae) en la fauna uruguaya, con descripción de nuevas especies. *Bol. Inst. Oceanogr.*, Sao Paulo, 4 (1): 3–80.
- BUEN (F. de), 1959. Los peces exóticos en las aguas dulces de Chile. Invest. zool. Chil., 5: 103-137.
- BURBIDGE (R.G.), CARRASCO (M.C.), BROWN (P.A.), 1974. Age, growth, lengthweight relationship, sex ratio and food habits of the Argentine pejerrey, *Basilichthys bonariensis* (Cuv. et Val.), from Lake Peñuelas, Valparaiso, Chile. J. Fish. biol., 6, 2: 299–306.
- BUSTAMANTE (E.), TREVIÑO (H.), 1980. Descripción de las pesquerías en el Lago Titicaca 1975–1979. Inst. Mar Perú, Puno: 73 p.
- CABRERA (S.E.), 1962. La alimentación natural del pejerrey del río de La Plata. Dir. gral. Pesca. Secret. Agric. Ganad., Buenos Aires, 28 p.
- CABRERA (S.E.), 1962. Crecimiento del pejerrey del río de La Plata y algunos datos ecológicos sobre la especie *Basilichthys bonariensis* (Cuv. et Val.). Dir. graI. Pesca, Secret. Agric. Ganad., Buenos Aires, 53 p.
- CABRERA (S.E.), BAIZ (M.), CHRISTIANSEN (H.E.), CANDIA (C.R.), 1973. Algunos aspectos biológicos de las especies de ictiofauna de la zona de Punta Lara (río de La Plata). Alimentación natural del pejerrey (*Basilichthys bonariensis*). Serv. Hidrogr. nav., Buenos Aires, 29 p.
- CARLO (J.M. de), LOPEZ (R.B.), 1957. La válvula intestinal del pejerrey. Notas Mus. La Plata, 19: 161–169.
- CARMOUZE (J.P.), AQUIZE JAEN (E.), 1981. La régulation hydrique du lac Titicaca et l'hydrologie de ses tributaires. *Rev. Hydrobiol. trop.*, 14 (4): 311-328.
- COLLOT (D.), 1980. Les macrophytes de quelques lacs andins (lac Titicaca, lac Poopó, lacs des vallécs d'Hichu Kkota et d'Ovejhuyo). ORSTOM, La Paz, 115 p., multigr.
- COUTTS (R.R.), 1983. Potencial y producción pesquera en Bolivia. 1& Reun. nac. Pesq., La Paz, 13 p., multigr.
- EIGENMANN (C.H.), ALLEN (W.R.), 1942. Subfamily Orestiatinae: 346–381, pl: XVII– XXI. *In* : Fishes of western South America. Univ. Kentucky, USA, 494 p.
- EVERETT (G.V.), 1971. The rainbow trout of Lake Titicaca and the fisheries. UNTA, Puno, 180 p.

- EVERETT (G.V.), 1973. The rainbow trout Salmo gairdneri (Rich.) fishery of Lake Titicaca. J. Fish Biol., 5 (4): 429-440.
- EVERMANN (C.H.), RADCLIFFE (L.), 1909. Notes on a Cyprinodont (Orestias agassizii) from central Peru. Proc. Biol. Soc. Washington, 22: 165–170.
- EVERMANN (C.H.), RADCLIFFE (L.), 1917. The fishes of the west coast of Peru and the Titicaca basin. *Proc. U.S. Nat. Mus.*, 95: 166 p.
- FOWLER (H.W.), 1954. Os peixes de agua doce do Brasil (4e entrega). Arch. Zool. Est. São Paulo, 9, 400 p.
- FRANC (J.), LAUZANNE (L.), ZUNA (F.), 1985. Algunos datos sobre las pesquerías de la parte oriental del lago Titicaca Menor. *Rev. Inst. Ecol.*, La Paz, 7: 1–21.
- FREYRE (L.R.), 1976. La población de pejerrey de la laguna de Lobos. Limnobios, 1 (4): 105-128.
- FREYRE (L.R.), PROTOGINO (L.), IWASZKIW (J.), 1983. Demografía del pejerrey Basilichthys bonariensis bonariensis (Pisces, Atherinidae) en el embalse Río Tercero, Córdoba. Inst. Limnol. ≪Dr R. A. Ringuelet≫, La Plata, 227: 39 p.
- GALLEGOS (P.H.), 1968. Contribución a la biología pesquera del pejerrey (*Basilichthys bonariensis*) del lago Titicaca. Régimen alimentario. Tesis Univ. Federico Villarreal, Lima, 73 p.
- GARMAN (S.W.), 1895. The Cyprinodonts. Mem. Mus. Comp. Zool. Hary. Coll., 19 (1): 179 p.
- GILSON (H.C.), 1964. Lake Titicaca. Verh. Internat. Verein. Limnol., 15: 112-127.
- GODOI (M.P.), 1946. Contribuição a biologia do peixe-rei Odontesthes bonariensis. Rev. bras. Biol., 6 (3): 373-384.
- GONZALEZ (R.J.), MESTRARRIGO (V.), 1954. El pejerrey: acuacultura. Secret. Agric. Ganad., Buenos Aires., 268: 54 p.
- GRIMÅS (U.), NILSSON (N.A.), WENDT (C.), 1972a. Lake Vättern: effects of exploitation, eutrophication and introductions on the salmonid community. J. Fish. Res. Bd. Can., 29 (6): 807–817.
- GRIMÅS (U.), NILSSON (N.A.), TOIVONEN (J.), WENDT (C.), 1972b. The future of salmonid communities in fennoscandian lakes. J. Fish. Res. Bd. Can., 29 (6): 937–940.
- HANEK (G.), 1982. La pesquería en el Lago Titicaca (Perú): Presente y futuro. FAO FI: DP.PER.76.022, Rome, 65 p.
- HUET (M.), 1978. Tratado de piscicultura. Sda. edición. Mundi-Prensa, Madrid, 728 p.
- HUREAU (J.C.), 1970. Biologie comparée de quelques poissons antarctiques (Nototheniidae). Bull. Inst. océanogr. Monaco, 68, 1391: 244 p.
- IWASZKIW (J.M.), FREYRE (L.), 1980. Fecundidad del pejerrey Basilichthys bonariensis bonariensis (Pisces, Atherinidae) del embalse Río Tercero, Córdoba. Limnobios, 2 (1): 36– 49.
- JACQUOT (R.). 1961. Organic constituents of fish and other aquatic animal foods. *In* : Fish as food. Borgstrom ed., Academic Press, New York and London, I: 145–209.
- JOHANNESSON (K.), VILCHEZ (R.), BERTONE (D.), 1981. Acoustic estimation of ichthyomass and its distribution in Lake Titicaca. FAO report: FAO/GCP/RLA/025 (NOR), 65 p., multigr.
- KLEEREKOPER (H.), 1945. O peixe-rei. Min. Agric., Serv. Inform. agric., Rio de Janeiro, 98 p.
- LABA (R.), 1979. Fish, peasants and state bureaucracies: development of Lake Titicaca. Comp. political Stud., 12 (3): 335–361.
- LAGLER (K.S.), BARDACH (J.E.), MILLER (R.R.), PASSINO (D.R.), 1977. Ichthyology. John Wiley and Sons, New York, 506 p.
- LAHILLE (F.), 1929. El pejerrey. Bol. Minist. Agric., Buenos Aires, 28 (3): 261-395.
- LAURENT (P.J.), 1965. Que deviennent les truitelles arc-en-ciel lâchées dans le Léman ? *Pêcheur et chasseur suisses*, sept., 4 p.
- LAURENT (P.J.), 1972. Lac Leman: effects of exploitation, eutrophication and introduction on the salmonid community. J. Fish. Res. Bd. Can., 29 (6): 867-875.

- LAUZANNE (L.), 1981. Description de trois Orestias nouveaux du lac Titicaca, O. ispi n. sp., O. forgeti n. sp. et O. tchernavini n. sp. (Pisces, Cyprinodontidae). Cybium, 5 (3): 71– 91.
- LAUZANNE (L.), 1982. Les Orestias (Pisces, Cyprinodontidae) du Petit lac Titicaca. Rev. Hydrobiol. trop., 15 (1): 39-70.
- LAUZANNE (L.), FRANC (J.), 1980. Las truchas de las lagunas del valle de Hichu-Kkota. UMSA-ORSTOM, Informe 1, La Paz, 21 p., multigr.
- LAZZARO (X.), 1985. Poblaciones, biomasas y producciones fitoplanctónicas del lago Titicaca. *Rev. Inst. Ecol.*, La Paz, 7: 23–64.
- LEBLOND (R.), 1983. Quelques aspects de l'alimentation et de la sélection des proies chez Orestias ispi Lauzanne (Pisces, Cyprinodontidae) du lac Titicaca. ORSTOM, La Paz: 29 p., multigr.
- LE CREN (E.D.), 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol., 20 (2): 201–219.
- LILLELUND (K.), 1975. Pêche et pisciculture. *In*: Le monde animal en 13 volumes, B. Grzimek éd., Stauffacher, Zurich, 4: 63–78.
- LINARES (O.), 1979. Importancia del pejerrey andino (Basilichthys bonariensis var. titicacaensis). Documenta, 8, 70-71: 59-64.
- LOUBENS (G.), 1966. Biologie de Polydactylus quadrifilis dans le bas Ogoué (Gabon). OR-STOM, Paris, 139 p.
- LOUBENS (G.), 1989. Observations sur les poissons de la partie bolivienne du lac Titicaca. IV. Orestias spp., Salmo gairdneri et problèmes d'aménagement. Rev. Hydrobiol. trop., 22 (2): 157-177.
- LOUBENS (G.), OSORIO (F.), 1988. Observations sur les poissons de la partie bolivienne du lac Titicaca. III. Basilichthys bonariensis (Valenciennes, 1835) (Pisces, Atherinidae). Rev. Hydrobiol. trop., 21 (2): 153–177.
- LOUBENS (G.), SARMIENTO (J.), 1985. Observations sur les poissons de la partie bolivienne du lac Titicaca. II. Orestias agassii, Valenciennes, 1846 (Pisces, Cyprinodontidae). Rev. Hydrobiol. trop., 18 (2): 159–171.
- LOUBENS (G.), OSORIO (F.), SARMIENTO (J.), 1984. Observations sur les poissons de la partie bolivienne du lac Titicaca. I. Milieux et peuplements. *Rev. Hydrobiol. trop.*, 17 (2): 153-161.
- MAC DONAGH (E.J.), 1946. Piscicultura del pejerrey en el arrozal de la Facultad de agronomía de La Plata. Rev. Fac. Agron. La Plata, 26: 33–51.
- MATSUI (Y.), 1962. On the rainbow trout in Lake Titicaca. Bull. Jap. Soc. sci. Fish., 28 (5): 497-498.
- NION (H.), 1977. Técnicas para la producción de semillas en cultivo de peces en América latina. FAO, Informe Pesca 159.
- PARENTI (L.R.), 1981. A phylogenetic and biogeographic analysis of Cyprinodontiform fishes (Teleostei, Atherinomorpha). Bull. Am. Mus. Nat. Hist., 168 (4): 334–557.
- PARENTI (L.R.), 1984. A taxonomic revision of the andean killifish genus Orestias (Cyprinodontiformes, Cyprinodontidae). Bull. Am. Mus. Nat. Hist., 178 (2): 107–214.
- PILLAY (T.V.R.), DILL (W.A.), 1979. Advances in aquaculture. Fishing News Books, 653 p.
- PINTO PAIVA (M.), SCHEFFER (A.C.), 1982. Maturidade e reprodução do peixe-rei Odontesthes bonariensis (Valenciennes) na bacia do rio Jacuí (Brasil). Ciênc. Cult., Sao Paulo, 34, 12: 1649–1653.
- QUIROZ (A.), VILLAVERDE (F.), SARAVIA (P.), 1979. Artes y métodos de pesca en las riberas del lago Titicaca. Inst. Mar Perú, Puno, 65: 20 p.
- RINGUELET (R.), 1942. El pejerrey (Odontesthes bonariensis) del embalse Anzalón (La Rioja). Notas Mus. La Plata, 7: 177-200.
- RINGUELET (R.), 1942. Ecología alimenticia del pejerrey (*Odontesthes bonariensis*) con notas limnológicas sobre la laguna de Chascomus. *Rev. Mus. La Plata*, 2: 427-461.
- RINGUELET (R.), 1943. Piscicultura del pejerrey o atherinicultura. Suelo Argentino, Buenos Aires, 162 p.

- RINGUELET (R.), ARAMBURU (R.H.), 1961. Peces argentinos de agua dulce. Minist. Agric. Ganad., Buenos Aires, 7: 98 p.
- RINGUELET (R.), FREYRE (L.R.), 1970. La pesca del pejerrey en la laguna de Chascomus. Publ. municip., Chascomus, Argentina, 12 p.
- SCHULTZ (L.P.), 1948. A revision of six subfamilies of Atherine fishes, with description of new genera and species. Proc. U.S. Nat. Mus., 98: 48 p.
- TCHERNAVIN (V.V.), 1944. A revision of the subfamily Orestiinae. Proc. Zool. Soc. London, 114: 140-233.
- TREVIÑO (H.), 1974. Estudio preliminar sobre análisis de contenido estomacal de la especie Orestias agassii (Carachi blanco), en las localidades de Capachica, Chuiucto, Piata, Conima, en los meses de mayo, junio, julio y agosto. Tesis Univ. S. Agustín Arequipa: 60 p.
- TREVIÑO (H.), TORRES (J.), LEVY (D.A.), NORTHCOTE (T.G.), 1984. Pesca experimental en aguas negras y limpias del litoral de la bahía de Puno, Lago Titicaca, Perú. Bol. Inst. Mar Perú, núm. extraord., 8 (6): 36 p.
- VALENCIENNES (A.), 1839. Rapport sur quelques poissons d'Amérique rapportés par M. Pentland. *L'Institut*, 7: 118.
- VALENCIENNES (A.), 1846. Des Orestias. In: Histoire naturelle des Poissons. Cuvier et Valenciennes, 18, Bertrand, Paris: 221–244.
- VAUX (P.), WURTSBAUGH (W.A.), TREVIÑO (H.), MARIÑO (L.), BUSTAMANTE (E.), TORRES (J.), RICHERSON (P.J.), ALFARO (R.), 1988. Ecology of the pelagic fishes of Lake Titicaca, Peru-Bolivia. *Biotropica*, 20 (3): 220–229.
- VELLARD (J.), 1963. Civilisations des Andes. Gallimard, Paris, 270 p.
- VIDAL (J.C.), 1969. Actividades pesqueras en Rosario. Estac. hydrobiol. Rosario, Argentina, 41 p.
- VILLA (I.), SOTO (D.), 1981. Atherinidae (Pisces) of Rapel reservoir, Chile. Verh. Internat. Verein. Limnol., 21: 1334–1338.
- VILLWOCK (W.), 1962. Die Gattung Orestias (Pisces, Microcyprini) und die Frage der intralakustrischen Speziation im Titicaca Seengebiet. Verh. Zool. Ges. Wien, Zool. Anz. Suppl., 26: 610–624.
- VILLWOCK (W.), 1975. Poissons volants, Cyprinodontes et Athérines. *In*: Le monde animal en 13 volumes, B. Grzimek éd., Stauffacher, Zurich, 4: 402–431.
- WELCOMME (R.L.), 1979. Fisheries ecology of floodplain rivers. Longman, London and New York, 317 p.
- WURTSBAUGH (W.A.), BUSTAMANTE (E.), TREVIÑO (H.), 1991. Biología y pesquería del pejerrey (*Basilichthys bonariensis*) en el Lago Titicaca. *Invest. Desar. soc. Altiplano*, Puno, 34 p. (in press).
- ZUNIGA (E.), 1941. Régimen alimenticio y longitud del tubo digestivo en los peces del género Orestias. Mus. Hist. Nat. Javier Prado, Lima, 16: 79–86.

VI.6. ASSOCIATED ANIMAL COMMUNITIES VI.6a. The Amphibia

JEAN VELLARD

Lake Titicaca and the surrounding areas impose severe living conditions on amphibians. The low water temperatures, the low partial pressure of oxygen, the intense evaporation, the great diurnal range of air temperature and the ultra-violet and infra-red radiation, whose effect on these animals is little known, have only allowed a few groups to cross the altitudinal barrier of 3000 metres. From among the diverse neotropical amphibian fauna, only four genera belonging to three different families have been able to establish themselves in the high altitude areas of Bolivia and central Peru. In Lake Titicaca and its surroundings we therefore find a toad belonging to the genus *Bufo*, the marsupial frog *Gastrotheca* and two genera belonging to the family Leptodactylidae, *Telmatobius* and *Pleurodema*.

This severe selection pressure has been followed by intense diversification. The Andean amphibians, living under limiting biological conditions and therefore very sensitive to slight environmental changes, are distributed among small biotopes, often separated by uninhabitable areas. In these isolated populations, the original forms have undergone numerous changes in their biology and morphology, giving rise to the development of local forms, difficult for taxonomists to classify.

Telmatobius, the most widespread genus in the High Andes, provides remarkable examples of successive evolution. Within the same developmental line the range of forms extends from medium-sized, thick warty-skinned forms living in marshes, to smooth thin-skinned swimming forms living in weedy or torrential streams, ending in giant lake-dwelling forms, spending their life in several metres of water and rarely coming to the surface. Life in these different habitats is accompanied by anatomical changes and modifications of the deep histological structure of the skin which assumes a predominantly respiratory function, as in tadpoles and *Urodela*. Other modifications are also observed. These include: pulmonary reduction, changes in limb morphology and in the position of the eyes and the shape of the head, plus changes in the reproductive cycle and larval development.

These variations are particular to each isolated population, leading to a series of intergrades and causing the taxonomic difficulties so often recorded

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with Andean amphibians (Barbour and Noble, 1920; Parker, 1932, 1940; Vellard, 1951 to 1970). Examination of examples coming from different sites has led to the conclusion that numerous species exist and the study of numerous populations has led to the description of a series of difficult-to-interpret intergrades.

In the Titicaca region, we include not only the lake itself, its shoreline and inflowing streams and river and the outflow, the Desaguadero, but also the neighbouring lakes which were formerly connected to it (Umayo, Arapa) and some high altitude lakes (Lagunillas at 4250 m and Saracocha at 4150 m), about a hundred kilometres away, but dependent faunistically on the great lake and communicating with it via the Rio Coata.

The existence of three very distinct habitats in Lake Titicaca favours the formation of local faunas. Puno Bay, in the north-west, is shallow and rich in macrophytes; the Great Lake in the centre has numerous small rocky islands forming individual biotopes, isolated by deep water that amphibians are unable to cross; and in the south lies Huiñaimarca and its totorales, its reedbeds and beds of *Scirpus*.

A wide variety of small biotopes in the surroundings of lake Titicaca are able support amphibian populations, these include: marshy areas, isolated water holes often of small size, small isolated lakes and ponds, weedy streams or stony torrents and warm springs.

Review of previous studies

The first amphibians were collected from the High Andes by the great scientfic expeditions of the last century. In 1841 Duméril and Bibron described the main forms from Lake Titicaca reported by D'Orbigny and Pentland: *Cycloramphus marmoratus* (now *Telmatobius marmoratus*), *Hyla marmorata* (now *Gastrotheca marmorata*) and *Leiupurus marmoratus* (now *Pleurodema marmorata*). Six years previously, in 1835, Wiegmann studying Meyen's collections coming from the voyage of the German boat, "The Princess Louise." had created the genus *Telmatobius* for a species from the south of Peru (*T. peruvianus*) and redescribed *Bufo spinulosus* which had already been imprecisely described from Chile by Molina in 1782 under the name *Rana arauco*. The journey of Castelnau (1855) did not provide much in the way of novelty for these Andean animals, but in 1845 Tschudi recorded the presence of *Leiupurus viridis* and *Bufo trifolium*.

"Modern" studies started with the voyage of Agassiz and Orton and the publications of Cope and Garman in 1875 and 1877. Then in 1920, Barbour and Noble carried out a first revision of the genus *Telmatobius* and described several new forms. Neveu Lemaire in his voyages to lakes Titicaca and Poopo only collected a few *Telmatobius*, misidentified as *peruvianus*, and *Bufo spinulosus*. With the exception of isolated notes, there is no further information until 1940, when Parker produced his important monograph based

on the specimens collected by the Percy Sladen Expedition to Lake Titicaca, for a critical study of the amphibians of this region. This highlighted the difficulties of such work. From 1950 onwards Vellard carried out studies of Andean amphibians, collecting specimens from the Titicaca region, from the Altiplano, Lake Poopo and the high altitude lakes of the Andes. His observations were published in a series of monographs between 1951 and 1970 and were concerned with describing the taxonomy of the animals and their physiology by studying cutaneous respiration and the role of the skin folds and disc in two species from the Titicaca region: *T. marmoratus* and *T. culeus*. Finally, mention should be made of the very fine film by Cousteau who provided impressive images of colonies of *T. culeus* in several metres of depth in lake Titicaca and the Rohrhirsch's report (1968) on this voyage.

Taxonomy, distribution and ecological information

The genus Telmatobius

Species of *Telmatobius* are the most characteristic representatives of Andean amphibians. They belong to the ancient family Leptodactylidae, of heavy-bodied frogs, related to *Eupsophus* of Chile and already existing in the lower Oligocene in Patagonia, alongside other genera of the same era.

Parker (1940) stressed the difficulties of classifying the various forms in Titicaca into precise taxonomic units. "The status to be accorded to these units is, however, a more difficult problem. The material brought back from the Titicaca Basin is subdivisible into a number of groups, not always clearly defined."

In 1951 we proposed placing *Telmatobius* and the closely related genus from central Peru, *Batracophrynus* into a separate sub-family: the Telmatobinae.

In our publications we have divided *Telmatobius* into major evolutionary lines each presenting numerous varieties, reduced for taxonomic purposes to a few species and subspecies and many simple local varieties. All the varieties in the Titicaca region can thus be placed in *T. marmoratus* D.B., the oldest described species, whereas those of central Peru form a parallel series belonging to *T. jelskii* Peters. The varieties within *T. marmoratus* are themselves divided into two main groups: *marmoratus* living in marshes, streams and the lake margins, and *culeus* containing the purely aquatic lake-dwelling forms, but there are numerous intergrades between all of these forms (Fig. 1).

The first group, *marmoratus*, contains medium-sized forms of about 50 to 60 mm. Duméril and Bibron's type specimen came from Guasacoma, a little to the north of the lake and is distinguished by the following characteristics. Skin not folded, smooth or with a few pustules or warts; occasional presence of very few horny excrescences. Head scarcely wider than long, tympan not



Figure 1. Attempt at classification of the Telmatobius from Lake Titicaca basin.

visible; males with a horny spiny plate on the thumb; no pectoral spines. Back grey with indistinct marbling, belly lightly washed with grey. There are few variations. The form *rugosus* Vellard, from La Paz, has the dorsal parts covered with closely-spaced, often horny, tubercles. The number of tubercles, their extension towards the ventral surface and variations in the webbing of the feet have given rise to the creation of taxa with imprecise limits (*verrucosus* Cope; *hintoni* Parker; from Cochabamba, etc.). The feet are longer in the more aquatic forms (*angustipes* Cope). The presence of thick skin with the hint of a dorsal plate and horny warts on the chest of the males marks the transition (*riparius* Vellard) with the *culeus* group.

Transition towards the lake-dwelling forms takes place via populations restricted to individual bays on Lake Titicaca, living in the totorales or on submerged macrophyte beds at 2 to 3 metres depth. These are all of medium size, with a flattened head narrower than the body and without a pronounced canthus rostralis. Parker placed them all under the name *culeus albiventris*, while at the same time noting the profound differences between them. Almost every bay has a distinct population differing by one or more character. Puno Bay supports a medium-sized form (males 40–60 mm; females 50–65



Figure 2. Distribution of the different forms of the genus Telmatobius (marmoratus and culcus group) in Lake Titicaca and its basin.

mm), coloured a very dark leaden grey dorsally, the belly being light grey. This is the variety *punensis* Vellard of the north of the lake. It is replaced in the south by the type variety of this series *albiventris* Parker, which is slightly larger (males up to 75 mm; females 80 mm) and readily distinguished by the striped thighs and the beautiful bright orange coloured belly, which becomes pure white in preserved specimens, hence the name given by Parker. This variety also shows a slight dorsal disc, more marked in larger individuals. It lives in the Huiñaimarca, the type specimen coming from Taquiri Island. A variety with longer legs, *parkeri* Vellard, lives in Lake Arapa, north of Lake Titicaca; it had already been mentioned by Parker (1940) from the neighbouring Lake Yapupampa, without being given a name. A final form worthy of mention is *globulosus* Vellard from Huiñaimarca (Copani). This is of small size (50 mm), with a short head narrower than the trunk, a short body and long hind feet and is related to certain varieties of the next group.

The large lake-dwelling forms live in deep water (down to 20 metres or

more ?) and occur in two different forms *culeus* of Lake Titicaca and *escomeli* of high altitude lakes above 4000 metres. *T. culeus* is over 130 mm long, with a broad flat head almost as wide as the trunk, the body and legs are enveloped by large floating folds, particularly noticeable on preserved specimens, giving them a scruffy look. The back has a small hard shield. In life these folds are swollen with fluid, doubling the volume of the smooth and rather thin animal.

The second form, *escomeli*, is more or less the same size but is very different on first sight and has its centre of distribution in Lake Lagunillas, situated at 4250 metres altitude. The head is small, narrow and short and half sunken into the dorsal shield. This shield, made of collagen, is hard and as thick as a finger, giving the animal a circular aspect in life, but it softens and decreases in size in preserved specimens. The *culeus* type specimen is greenish grey with a few yellow spots on the back, whereas *T. escomeli* has a grey back, marked with widely spaced whitish spots, which are more abundant on the belly where they sometimes form large marbling patterns. The *culeus* type specimen comes from the Copacabana region.

Other slightly smaller-sized populations with less broad heads occur in various deep parts of the lake, at Ccama, Pomata and Amantani. Those from the Río Ilave have been given the name *fluviatilis* and slightly smaller individuals from neighbouring lakes (Arapa, Azangaro and others) make up the race *lacustris*.

Although at first sight different, culeus and escomeli present a difficultto-resolve taxonomic problem, aggravated by the deformations that appear in liquid preservatives. What are the exact relationships between these two forms?

Several populations of *culeus* show multiple variations linking them with *escomeli*. In addition, mixed colonies occur in which the two forms intermingle, with a series of intermediate types. In the Río Coata, an inflow into Lake Titicaca draining from Lake Lagunillas situated 40 kilometres from the Great Lake, 32 specimens of between 100 and 125 mm in length were collected at the same time. Apart from a few distinct individuals belonging to *culeus* and *escomeli*, the collection was made up of a series of intermediates between the two forms. Was this an autonomous colony or was it made up of individuals of *escomeli* that had descended from Lagunillas and crossed with the local *culeus*? There seem to exist very close affinities between these two forms which are capable of interbreeding. Their specific status remains open and this intermediate population has been given the name *dispar* Vellard.

Small-sized replacement forms occur alongside *escomeli* in streams and water bodies in the neighbourhood. That described by Parker under the name *T. escomeli crawfordi* originated from Lake Saracocha, where we were unable to re-find it, no doubt because of the recent arrival of trout. On the other hand it is abundant in the neighbouring streams. It does not exceed 60 mm in length, the head recalls that of *escomeli*, but the feet are short and a simple thickening of the skin replaces the disk of the latter. A larger form

<i>Table 1.</i> pling-pla	<i>Telmatobius</i> from Lake Titicaca region and principal samces.
TELMAT	OBIUS MARMORATUS Duméril and Bibron, 1841. Guasacoma.
	Form mainly living in swamps and brooks.
۳	rugosus Vellard, 1951. Calacoto (La Paz)
	pustulosus Cope, 1877. Tanta (R. Vilcanota)
	angustipes Cope, 1877. Juliaca
	riparius Vellard, 1953. Juli
TELMAT	OBIUS CULEUS Garman, 1875. Achacachi.
	lacustrine form, also living in deep water bodies.
	albiventris Parker, 1940. Puno bay
"	punensis Vellard, 1951. Amantani island
	parkeri Vellard, 1951. Lake Arapa
м	globulosus Vellard, 1960. Copani
•	lacustris Vellard, 1953. Checavani (Azangaro)
	fluviatilis Vellard, 1953. Checayani (Azangaro)
	dispar Vellard, 1953. Río llave
	escomeli Angel, 1923. Lake Titicaca ? Lagunillas
	crawfordi Parker, 1940. Lake Saracocha
	semipalmatus Vellard, 1953. Lake Chaichora
	exsul Vellard, 1953. Yura (Arequipa)

(*semipalmatus* Vellard) lives in deep pools in the stream situated at the outflow of Lake Chajchora, about twenty kilometres from Saracocha. This is a transition form with an only slightly thickened shield.

From the development viewpoint, there is only a single true species, *marmoratus*, which has colonised the varied habitats of the Titicaca region, reaching up to 5000 metres and undergoing numerous and varied adaptations. In such a multi-formed group with numerous intermediates, it is difficult to establish definite specific and sub-specific divisions. To clarify the taxonomy of *Telmatobius* in Lake Titicaca we propose the recognition of two main taxa, *T. marmoratus* and *T. culeus*, and a certain number of derived forms (Table 1), while at the same time stressing the existence of a series of intergrades between all forms.

The life cycle of the large forms is unknown. They often occur in groups containing large numbers of individuals, almost touching and motionless on the lake bed. Good swimmers, they are nevertheless capable of being drifted over large distances. Their respiration is mainly cutaneous, helped by the numerous skin folds (the "baggings" of Parker) which double their respiratory area. The thin skin is densely vascularised, forming a plexus sending numerous capillaries to the skin where they end in a bulb-shaped infundibulum separated from the exterior by one or two layers of epithelial cells. (Noble, 1928; Vellard, 1951; Macedo, 1960). Angel (1923) attributed an important hydrostatic role to the skin folds, aiding rising to the surface. In contrast, the role of the thickened shield or mantle in *escomeli* has not yet been elucidated; it is perhaps related to sexual activity.

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The genus Pleurodema

Two other small-sized species of Leptodactylidae occur alongside *Telmatobius* in the Lake Titicaca basin: *Pleuroderma cinerea* Cope and *P. marmorata* D.B. Living in damp habitats, they are only really aquatic during the breeding season. During mating the male beats the water with his hindlegs, forming large balls of white foam the size of a fist in which the female lays her eggs and which dissolves when the tadpoles hatch.

These two species are greenish grey with black markings. The larger P. cinerea reaches 46 mm in length and is easily recognisable by the two large shiny black plates in the inguinal region, but these are lacking in the smaller P. marmorata (30 to 35 mm). P. cinerea is a southern species which does not extend further north than Titicaca, whereas P. marmorata is distributed widely in the central Andes of Peru.

The genus Gastrotheca

The presence of Hylidae, an essentially arboricole family, is somewhat unexpected in the High Andes. This family shows an extremely wide range of adaptations, including the marsupial frogs, in which the females incubate their eggs partly or totally in a dorsal brood pouch, making them capable of breeding far from water.

The first Andean marsupial frog was described from Cuzco in 1841 by Duméril and Bibron under the name *Hyla marsupiata*, the type specimen of which is in the Paris Museum. Two years later Fitzinger (1843) created the genus *Gastrotheca* for it.

Numerous species belonging to this genus, whose synonymy is still confused, occur all along the eastern Andes from Bolivia to Ecuador. The Lake Titicaca species, G. boliviana, was named by Steindacher (1892). Of small size (35-40 mm), its head is as wide as long. It is easily recognised by its long hind feet with small digital pads. The back is greenish grey with indistinct ocellated patches and the skin is covered with fine tubercles.

Brooding females have an elongated opening with wrinkled edges at the base of the back, communicating with a large dorsal pouch containing a small number of eggs or tadpoles developing up to the four-legged stage. Although it is not abundant, this species is widely distributed. It favours damp habitats, under stones, but can also be found far from water. It is found all around Lake Titicaca, at Tihuanacu and even very far, as far as Potosi for example. The type specimen comes from Calacoto (La Paz).

Plate 4. Some specimens of the Titicaca toads. Above: *Telmatobius culeus*, form from the Huatajata region (Huiñaimarca). Down Left: *Bufo spinulosus spinulosus*, male; right: female. Forms from Puno (Lago Grande).





The genus Bufo

The only species of toad, *Bufo spinulosus*, was described in 1855 by Wiegmann from specimens from southern Peru. It is a typically Andean species, with a wide geographical distribution from Chile and Argentina to Ecuador, and has been divided into several geographical subspecies. The subspecies at lake Titicaca is the type: *Bufo spinulosus spinulosus*.

There is marked sexual dimorphism. The male (ca. 70 mm) has the back and legs covered with closely-spaced glandular rosettes formed of a large lens-shaped central gland surrounded by a circle of 6 to 7 horny spines which become less distinct outside the breeding season. The colour is greenish grey, the rosettes being surrounded by a black circle. The female (80 mm) has low glandular structures, without horny spines, of greenish grey colour with numerous irregular X or Y-shaped black dorsal patches.

Recently metamorphosed young, about 20 mm long, are black or dark grey with orange ends to the feet. They were described by Weigmann under the name *Phryniscus nigricans*.

The cultural importance of amphibia

Amphibians play an important role amoung the indigineous Aymara and Quechua populations and are never mistreated. The true frogs or Kayra (*Telmatobius* and *Paludicola*) are related to fecundity rites and classed among the cold elements. The large species are used to prepare an infusion used in cases of anaemia, asthenia, tuberculosis and female sterility. A living animal is applied locally in cases of inflammation. Swallowing a small living frog is the recommended remedy for fevers and exanthematic typhus.

They are also used in magical rites. The large T. culeus is a sacred animal and we have often encountered great difficulties in obtaining it. It is associated with rainfall. In time of drought, the indians from Sun Island leave one or two of these frogs in narrow jars placed on the top of a mountain. The frogs "cry" calling the rain which soon arrives, makes the jar overflow and lets them find their way back to the lake. In prolonged drought, the ceremony takes on a community scale. A divine caste, the yatiris, carry a female huankele (T. culeus) to a sacred mountain, Ccapia, to the south of the lake where there is another deep lake. After numerous ceremonies and offerings at the water's edge they make the female frog "cry." a male appears at the water surface and carries her off. The rains will soon come.

The toads (hampatu) are rubbed on the skin for certain skin diseases, but they are especially used to prepare much feared evil potions.

VI.6b. The Ophidians

JEAN VELLARD

Only one small-sized species of snake, *Tachymenis peruviana* Weigmann, inhabits the high altitude areas of Peru and Bolivia. This species was described by this author under its present name from a specimen collected by Meyen in the Andes of southern Peru. It was renamed two years later by Schlegel under the name *Coronella chilensis*, whereas Tschudi referred it to the genus *Ophis* and Yan to the genus *Mesotis*. Several attempts to separate it into varieties and local sub-species have not been adopted.

Description

This is a small colubrid snake not exceeding 40 to 50 cm in length. The tail is short, slightly longer in the male, and rather flat in shape, especially when annoyed. The general colour varies from greenish grey to greenish yellow. A line of large dark grey, sometimes confluent, spots runs along each side, with a second row of similar spots on the flanks. The numerous scales are slightly darker in colour at their tips. The head is marked by two long grey patches on the neck. The underparts are light grey, with more or less distinct grey dots forming two median lines and one lateral line of larger spots. There are 8, or rarely 7, supraorbital scales, 19 lateral scales and the ventral scales vary from 139 to 149. >

It is an opisthoglyphe species in which the back teeth are hollowed out by an open channel, communicating with a supra-labial gland 7.5 mm long and 4.5 mm wide and weighing 55 mg. This arrangement makes it of little danger to man, and besides it is not very aggressive and only bites if picked up.

Distribution and ecology

It has a very wide geographical distribution. It lives at low altitudes in the mountainous regions of southern Chile and Argentina and extends progress-

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Tachymenis peruviana (Photo Jean Vellard)

ively up the high valleys of the Andes. In Bolivia and Peru it occurs at between 3000 and 4000 metres altitude.

It is rarely seen, as it is nocturnal and rather inactive. It is however fairly abundant on the shores of Titicaca in damp areas where it hides under stones, in holes and in the screes bordering the lake.

It feeds especially on small amphibians, such as *Pleurodema* which are very sensitive to its venom. It is a viviparous species bearing 7 to 10 embryos. Fertilisation takes place between October and November, the season of greatest activity for this species in the Titicaca region. In winter, after the month of May, it hides under stones or in holes and becomes difficult to find.

Its venom is rather toxic and very painful. The amphibians *Paludicola* and *Telmatobius* succumb in a few minutes with doses of 1 or 2 mg of gland extract, following rapid paralysis starting posteriorly, without seizures, and ending with loss of reflexes. The heart continues to beat for several minutes after apparent death. The Andean toad is very resistant, but the lizards of the genus *Liolaemus* are fairly sensitive.

In man, the bite provokes a moderately serious effect with local oedema, moderate swelling and fever (Gigoux, pers. comm.).

VI.6c. The avifauna

CLAUDE DEJOUX

There are few publications on the avifauna of Lake Titicaca, but it is possible to give a fairly complete account of the species inhabiting its shore and islands from the works of Niethammer (1953), Aparicio (1957), Adger Smyth (1971), Hughes (1977) and Kempff Mercado (1985), supplementing the existing data in the literature with our own observations carried out on the Bolivian part of the lake.

Lake Titicaca is not an isolated ecosystem with its own special bird fauna. The species occurring here are usually widely distributed, either over the Altiplano or the entire Cordillera. Certain species, in contrast, are frequent in other lacustrine environments in these two regions, but have never (or rarely) been recorded from the lake.

The following list, which should not be considered as exhaustive, gives an overview of the main species inhabiting the lake and also those which live in its immediate surrounds and have been recorded in the literature. Species preceded by an asterisk are those normally inhabiting the lake surroundings, but not closely related to the lake environment. Those preceded by two asterisks are more closely related to aquatic biota, while those with three asterisks are permanent inhabitants of the lake itself. As far as possible we have given the vernacular names and the English names of the species listed.

Following the list we give some ecological observations on the species most characteristic of the lacustrine biotope.

TINAMIFORMES

TINAMIDAE

* Nothura darwinii agassizzi (Bangs). "Codorniz", "inambu chico común", "spotted nothura".

PODICIPEDIFORMES

PODICIPEDIDAE

** Rollandia rolland chilensis (Lesson). "Zambullidor", "maca común", "patito pumpún", "white-tufted grebe".

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*** Rollandia micropterum (Gould). "Ninra", "maca alicorto", "shortwinged grebe".

PELECANIFORMES

PHALACROCORACIDAE

** *Phalacrocorax olivaceous olivaceous* (Humboldt). "Mehke", "olivaceous cormorant".

CICONIIFORMES

THRESKIORNITHIDAE

*** *Plegadis ridgwayi* (Allen). "Rua-rua", "chuwankera", "cuervillo de la puna", "puna ibis".

ARDEIDAE

** Nycticorax nycticorax hoactli (Molina). "Zonzon", "pájaro bobo", "martineta", "night heron".

ANSERIFORMES

ANATIDAE

- * Chloephaga melanoptera (Eyton). "Huallata". "ganso andino", "andean goose".
- *** Anas georgica spinicauda (Vieillot). "Pato del lago", "pato cola aguda", "yellow-billed pintail".
- *** Anas flavirostris oxyptera (Meyen). "Ita", "pato barcino", "pato piojoso", "speckled teal".
- *** Anas versicolor puna (Tschudi). "Kankana", "pato puna", "puna teal".
- *** Anas cyanoptera orinomus (Oberholser). "Junta", "puka", "pato ala azul", "cinnamon teal".
- *** Oxyura jamaicensis ferruginea (Eyton). " Pana", "pato zambullidor", "andean ruddyduck".

FALCONIFORMES

ACCIPITRIDAE

- * *Phalcoboenus megalopterus megalopterus* (Meyen)."Cuervo", "matamico cordillerano", "mountain caracara".
- * *Circus cinereus* (Vieillot). "Aguila", "anka", "cinereous harrier". FALCONIDAE
 - * Falco femoralis pinchinchae (Vieillot). "Cernicalo", "alcón", "aplomado falcón".
 - * Falco sparverius cinnamominus (Cory). "Kilincho", "alconcito colorado", "american kestrel".

GRUIFORMES

RALLIDAE

- *** Rallus sanguinolentus tschudii (Chubb). "Gallineta común", "plumbeous rail".
- *** *Gallinula chloropus garmani* (Allen). "Tika", "gallineta de agua", "moorhen".
- *** Fulica americana ardesiaca (Tschudi). "Ajoya", "gallareta americana", "american coot".

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 - *** Fulicula gigantea (Eydoux and Souleyet). "Choka", "gallareta gigante", "giant coot".

CHARADRIIFORMES

LARIDAE

- *** Larus serranus (Tschudi). " Gaviota andina", "kellwa", "andean gull".
- ** Larus pipixcan (Franklin). "Gaviota menor", "Franklin's gull".

CHARADRIIDAE

- * Vanellus resplendens (Tschudi). "Continela", "tero serrano", "andean lapwing".
- * Charadrius alticola (Berlepsch and Stolzmann). "Chorlito serrano", "puna plover".

SCOLOPACIDAE

- ** Tringa melanoleuca (Gmelin). "Chorlo mayor patiamarillo", "greater yellowlegs".
- ** Tringa solitaria (Wilson). "Chorlito solitario", "solitary sandpiper".
- ** Tringa flavipes (Gmelin). "Chorlo patas amarillas", "lesser yellowlegs".
- ** Gallinago andina andina (Taczanowski). "Sak'a-Sak'a", "Puna snipe".

PHALAROPODIDAE

** Steganopus tricolor (Vieillot). "Falaropo tricolor", "Wilson's phalarope".

RECURVIROSTRIDAE

** Himantopus himantopus mexicanus (Müller). "Ccota-año", "common stilt".

COLUMBIFORMES

COLUMBIDAE

- * Zenaida auriculata hypoleuca (Bonaparte) "Paloma", "eared dove".
- * *Metriopelia melanoptera melanoptera* (Molina). "Tórtola", "palomita moteada", "bare faced ground dove".
- * *Metriopelia ceciliae gymnops* (Chubb). "Palomita ala dorada", "palomita aymara", "black ringed ground dove".

PSITTACIFORMES

PSITTACIDAE

* Bolborhynchus aurifrons orbygnesyus (Souance). "Kitaloro", "catita andina", "mountain parakeet".

APODIFORMES

TROCHILIDAE

* Patagona gigas peruvianus (Boucard). "Picaflor gigante", "giant hummingbird".

PICIFORMES

PICIDAE

* Colaptes rupicola puna (Cabanis). "Pito", "carpintero de las piedras", "andean flicker".

PASSERIFORMES

FURNARIDAE

* Geossita cunicularia titicacae (Philippi and Landbeck). Kiti-kiti", "pampero común", "common miner".

HIRUNDINIDAE

* *Petrochelidon andecola andecola* (Lafresnaye and D'Orbigny). "Golondrina andicola", "andean swallow".

MOTACILLIDAE

* Anthus furcatus brevirostris (Taczanowski). "Bisbitos", "cachirla de una corta", "short-billed pipit".

CINCLIDAE

** Cinclodes fuscus albidiventris (Sclater). "Mirlo acuático", "barwinged cinclodes".

TURDIDAE

* Turdus chiguanco chiguanco (D'Orbigny and Lafresnaye). "Chiguengo", "chiguanco thrush".

TYRANNIDAE

- * Muscisaxicola capistrata (Burmeister). "Dormilona corona castana", "ground tyrant".
- * Lessonia rufa rufa (Sclater and Salvin). "Negrito", "rufous-backed negrito".
- * *Tachuris rubigastra alticol*a (Berlepsch and Stolzmann), "Siete colores", "many-colored rush tyrant".

TROGLODYTIDAE

* *Troglodytes aëdon puna* (Berlepsch and Stolzmann). "Ruiz señor", "chichurico", "tropical house wren".

FRINGILLIDAE

- * Carduelis atrata fasciatus (D'Orbigny and Lafresnaye). "Jilguero", "cabecita negra oscura", "negrillo", "black siskin".
- * Sicalis uropygialis uropygialis (Lafresnaye and D'Orbigny). "Kelluncho", "jilguero cara gris", "bright-rumped yellow finch".
- * Zonotrichia capensis pulacayensis (Manegeaux). "Pichisanka", "rufous collared sparrow".
- * *Phrygilus plebejus plebejus* (Tschudi). "Fringilo plebeyo", "ashbreasted sierra finch".

FURNARIDAE

* Phleocryptes melanops schoenobaenus. "Totorero". "wren-like rushbird".

Ecological observations

Taking into account the fact that this list is, as we have already stated, not exhaustive, it can be seen that the lake and its immediate surroundings are populated by a rather diverse avifauna, with at least 13 orders, 27 families and 50 species being recorded. Despite this, Lake Titicaca cannot be considered as a distinct biogeographical area, as no species is strictly related to this biotope. The concept of a biogeographical area consisting of the Altiplano would be a much more pertinent ecological reality.

Among the 50 species mentioned, 28 (i.e. 56%) are not related to the aquatic environment and occur in numerous localities on the Altiplano when their food is available. It is certain however that the shores of the lake represent a rich environment, with a better developed and more diverse agriculture than on the rest of the Altiplano, which creates an area of attraction for numerous species of bird, enabling them to occur almost permanently in this habitat. Among these species are almost all of the passerines listed (some of them, such as *Phleocryptes melanops* being closely linked with totoras), as well as widespread orders such as the Columbiformes and Falconiformes.

Ten species are restricted to aquatic habitats, but are not permanent or frequent inhabitants on the scale of the lake. They are found occasionally on the islands or around the shoreline. These include the waders such as the Charadriidae and Scolopacidae which at certain seasons are locally abundant when they can find appropriate biotopes (mud flats or shallow water marshes) and abundant food. Large concentrations are rarely observed. One Ciconiiforme (*Plegadis ridgwayi*), which frequents similar habitats within the large shallow bays, does sporadically occur in large flocks searching for aquatic invertebrates among the macrophytes or on bare sediments. This species breeds around the lake margins, building its nests among the totora stems. Other species such as *Cinclodes fuscus* and *Rollandia rolland chilensis* are very uncommon and are only rarely observed.

The remaining dozen species form the basis of the aquatic avifauna of Lake Titicaca. They nearly all belong to families Laridae, Rallidae and Anatidae. The Andean gull (*Larus serranus*) occurs all the year round on the lake, both over and on the open water and along the shorelines. At the time of maximum emergence of the large species of *Chironomus* (October-November), they switch from feeding on fish to become strictly insectivorous, hawking these large dipterans over the Huiñaimarca.

The Rallidae live among the totoras where they nest and find shelter. At present *Fulica americana ardesiaca* is certainly the most abundant species, followed closely by *Gallinula chloropus*. These two species are also abundant on the Altiplano, in all the lacustrine environments rich in macrophytes, which constitute their main food, the totoras only serving as shelter and sometimes nest support. We have never observed *Fulica gigantea* in the Bolivian part of the lake, although it is frequent on the small lakes of the

northern Altiplano and has been recorded from Puno Bay (Aparicio, 1957; Adger Smyth, 1971).

At least five species of duck inhabit the lake. They are rarely abundant at any one locality and are usually met with in pairs or groups of 5 to 10 individuals at maximum. They share the habitat with coots and feed among the submerged aquatic macrophytes at the margins of the totoras. It would seem that they are increasing in numbers at present, probably in relation to the gradual lowering of the water level and the accompanying increase in the area of totora stands submerged macrophytes. They were very rare at the time of maximum lake level in 1986, and at present they are nowhere near as abundant as they were in 1983, when the lake level was a little lower than now.

Finally, mention should be made of two species of aquatic bird that are practically never recorded on the lake or its shores, whereas they can be very abundant elsewhere on the Altiplano. These are the Andean goose (*Chloephaga melanoptera*), which occurs all the year round in the higher valleys of the Cordillera and over the entire Altiplano, and the Chilean flamingo (*Phoenicopterus chilensis*), which is very abundant on Lake Poopo and the shallow salt pans of the southern Altiplano. The former species is very wary and perhaps prefers the solitude of the valleys of the Cordillera, whereas the latter prefers to search for food in waters more saline than those of Lake Titicaca, where the crustaceans that form the basis of its diet abound.

As well as changing over the course of the year with the seasons and with the behaviour of the individual species, the bird population of Lake Titicaca also changes over periods of several years. For example, if the list drawn up by Aparicio in 1957, based on data collected at the start of the 1950s, is compared with later lists, there are many species not mentioned in later publications. It is not impossible that some misidentifications were made when specimens were not collected, but it is also possible that alterations have occurred to the lake ecosytem leading to changes in the bird populations. It is also possible that recent observations have been too limited geographically, or of too short a duration to have found all the species.

The list below gives those species recorded in the work of Aparicio (1957), but which have not been found again in more recent publications.

- Podiceps occipitalis Garnot. Podicipediformes

- Podiceps occipitalis juninensis. Garnot. Podicipediformes

- Egretta thula thula Molina. Ciconiiformes.

- Theresticus caudatus branickii Berlepsch & Stolzmann.

Ciconiiformes

- Plegadis falcinellus (L.). Ciconiiformes.
- Heteronetta atricapilla (Merrem). Anseriformes.
- Anas cyanoptera cyanoptera Vieillot. Anseriformes.
- Anas flavirostris oxyptera Meyer. Anseriformes.
- Anas speculariodes alticola Ménégaux. Anseriformes.
- Anas platalea Vieillot. Anseriformes.

- Merganetta armata leucogenis Tschudi. Anseriformes.
- Fulica leucoptera Vieillot. Gruiformes.
- Laterallus jamaicensis salinasi Phillipi. Gruiformes.
- Rallus limicola antarticus King. Gruiformes.
- Eudromias ruficollis Wagler. Charadriiformes.
- Pluvialis squatarola (L.). Charadriiformes.
- Larus maculipennis Lichtenstein. Charadriiformes.
- Larus dominicanus Lichtenstein. Charadriiformes.

As these 18 species are all strongly related to the aquatic environment, there are finally nearly 40 species which inhabit more or less permanently in close contact with the lake, and find food and shelter here – a number sufficiently high to qualify the avifauna of Lake Titicaca as being quite diverse. The density of individuals, in contrast, is at present rather low.

As is the case with most deep lakes, it is the littoral zone which is the most frequented and which harbours the highest concentrations of birds. The great beds of totora in the Huiñaimarca and in the shallow bays of the Lago Grande (Puno, Ramis and Achacachi) are therefore of prime importance for the avifauna, especially as the submerged vegetation that borders them supports an abundant food supply. As this zone is the most unstable, because it is the most affected by changes in lake level, it is evident that any manipulation of the hydrological balance of the lake leading to a greater stability for the fringing vegetation would be beneficial for the survival of many bird species. It is also certain that too great a stability would bring about a profound change in species succession, and even the local disappearance of some of birds. This would particularly concern those which only inhabit the lake in any numbers under extreme hydrological conditions, either when low water uncovers large mudflats, or when high water levels flood vast areas.

The birds inhabiting Lake Titicaca undergo various forms of migration and some are long-distance migrants. This is the case for example of some of the Charadriidae, which either arrive from North America or from the extreme south, flying along the chain of the Andes. For example *Pluvialis squatarola*, which has a holarctic breeding distribution at high latitudes, appears regularly during the austral winter (July -September) on the lake shore but leaves before the northern hemisphere summer. In contrast *Pluvialis dominica dominica*, also arriving from its arctic breeding grounds in October or November, is only a passage migrant, moving on further south to winter as far as Patagonia. *Eudromias ruficollis* migrates in the opposite direction, leaving the lake in October to return to the extreme south of the continent to breed (Aparicio, 1957).

Plate 5. Some bird species occurring along the lake shore. Above left: *Nycticorax nycticorax;* Above right: *Larus serranus;* center: Concentration of the puna ibis *Plegadis ridgwayi,* feeding in the shallow Achacachi Bay (Lago Grande), and a near picture of the same bird. Down: a small Passeriforme feeding adult Chironomids in the totora belt. (Photos Claude Dejoux.)



In addition to these long-distance migrants, other species undergo altitudinal movements, usually controlled by changes in physical environmental factors (temperature and water levels), as well as by the availability of their preferred food. These vertical movements can take birds from sea level up to that of the lake (*Larus dominicanus*) or to much higher altitudes than that of Lake Titicaca as is the case of the American egret (*Egretta alba egretta*), which appears occasionally around the lake at the end of the rainy season, or for *Plegadis rigwayi*, which after having exploited the food reserves of the lake when the level is high, then migrates to lakes at higher latitudes.

A third type of migration is that involving birds which move about within the Altiplano in search of optimal feeding conditions, moving from one water body to another depending on the abundance of their preferred food, whose abundance is itself usually related to the physical characteristics of precise habitats.

There is generally little hunting around the lake, at least by the local population, which certainly explains why most of the species can still be observed at reasonable distances.

Acknowledgements

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References of chapter VI.6

- ADGER SMYTH (J.), 1971. Observaciones ornitológicas en la región del lago Titicaca, Perú-Bolivia. UNTA, Puno, 4: 76–99.
- ALLEN (W.R.), 1922. Notes on the Andean Frog, *Telmatobius culeus* Garman. *Copeia*, 106: 52–54.
- ANGEL (F.), 1923. Sur un batracien nouveau du Pérou appartenant au genre *Telmatobius*. Ann. Sc. Nat. Zool., 6: 107-111.
- Anon., 1974. Observaciones sobre alimentación de anfibios del lago Titicaca en la bahía de Piata. Inst. Mar Perú, Puno, 5 p.
- APARICIO (M.), 1957. Aves del lago Titicaca. UNTA, Puno: 120 p., multigr.
- BARBOUR (T.), NOBLE (G.N.), 1920. Some amphibians from northwestern Peru. Bull. Comp. Zool., 63: 393-421.
- BARBOUR (T.), NOBLE (G.N.), 1921. Amphibians and Reptiles from Southern Peru. Proc. U.S. Nat. Mus., 57: 609-620.
- BARROS (R.), 1958. Citado por TOBAR (R.). Bol. Hosp. Viña del Mar. 14 (4), p. 173.
- BOULENGER (G.A.), 1882. Catalogue of the Batrachia salienta in the collection of the British Museum, London. Ed. 2, 563 p.
- BOULENGER (G.A.), 1894. On the genus *Phryniscus* of Wiegmann. Ann. Mag. Nat. Hist., 14 (6): 374–375.
- BOULENGER (G.A.), 1905. Description of new tailles batracians in the collection of the British Museum. Ann. Mag. Nat. Hist., 16 (7): 180–184.
- CASTELNAU (F. de), 1855. Expédition dans les parties centrales d'Amérique du Sud. 7. Animaux nouveaux ou rares. Paris, 2, 86 p.
- COPE (E.D.), 1874. On some Batrachia brought from the Upper Amazon by professor Orfon. *Proc. Acad. Nat. Sci. Philadelphia*, 26: 120–132.
- D'ORBIGNY (A.), 1835–1847. Voyages dans l'Amérique méridionale. Pitois-Levrault et Cie., Paris, 7 tomes, 11 vol.
- DUMERIL (C.), BIBRON (G.), 1841. Erpétologie générale ou Histoire naturelle complète des Reptiles. 8, 452 p.
- ESCOMEL (E.), 1929. Fauna de Arequipa: obras científicas. Lima, 1, 176 p.; 2, 297 p.
- ESPADA (M. J. de la), 1875. Viaje al Pacífico, Vertebrados, Batracios. J. Ac. Lisboa, 3, 621 p.
- FITZINGER (L.), 1843. Systema Reptilium. 1, 105 p.
- GARMAN (S.W.), 1876. Batracians, Reptiles. In: Exploration of Lake Titicaca. A. Agassiz and S.W. Garman. Bull. Mus. Comp. Zool., 3, 276–278.
- GIGOUX (E.R.), 1940. Los ofidios chilenos. R. Mus. Nac. Hist. Nat., 18, 5.
- HUGHES (R.), 1977. Franklin's gulls *Larus pipixcan* at Lake Titicaca, Peru. *Biotropica*, 9 (1): 52.
- HUTCHINSON (J.), HAINES (H.), ENGBRETSON (G.), 1976. Aquatic life at high altitude. Respiratory adaptations in the Lake Titicaca frog, *Telmatobius culeus*. *Respiration Physiology*, 27 (1): 115–129.
- KEMPF MERCADO (N.), 1985. Aves de Bolivia. Gisbert y Cie., La Paz, 156 p.
- MACEDO (H.), 1960. Vergleichende Untersuchungen an Arten der Gattung Telmatobius. Zeits. Wissensch. Zool., 163 (3/4): 355–396.
- MERTENS (L.), 1952. 3. Amphibien und Reptilien. In: Beiträge zur Fauna Perus. Titschack ed., Ein Zool. Reisber., Iena, 8: 257–266.
- MUÑIZ (N.), 1982. Contenido estomacal de *Telmatobius* (sapo acuático) en Chucuito del lago Titicaca. UNTA, Puno, Bitac. Biol. T. nº 1.
- NEVEU-LEMAIRE (M.), 1906. Les lacs des hauts plateaux de l'Amérique du Sud. Imprimerie nationale, Paris, 197 p.
- NIEDEN (F.), 1933. Das Tierreich 46, Anura I. Berlin und Leipzig, 584 p.
- NIETHAMMER (G.), 1953. Vogelleben am Titicaca See. Natur. V. Volk., 83: 409-416.
- NOBLE (G.K.), 1928. The integumentary pulmonary and vasculary in the Amphibians. *Journ. Morph. Physiol.*, 40: 341–416.
- ORTON (J.), 1873. The Andes and the Amazon. New York, 645 p.

- PARKER (H.W.), 1934. Reptiles and Amphibians from South Ecuador. Ann. Mag. Nat. Hist., 14 (16): 264–274.
- PARKER (H.W.), 1940. 12. Amphibia. In: The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1 (2): 203–216.
- PENTLAND (J.B.), 1848. The Laguna of Titicaca and the valleys of Yukai, Collao and Desaguadero in Peru and Bolivia from geodesic and astronomic observations made in the years of 1827 and 1828, 1837 and 1838. British Admiralty Chart, n° 1268, London.
- PETERS (W.), 1875. Über neue oder wenig bekannte Gattungen und Arten von Batrachien. Monats. D. Akad. Wiss.,: 411-418.
- ROHRHIRSCH (J.), 1968. Expedición Cousteau al Lago Titicaca. Informe del geólogo oceanógrafo Joseph Rohrhirsch, enviado por la Oficina de Investigaciones y Desarrollo de la Marina como observador, 7 p.
- SCHENONE (H.), BERTIN (V.), MANN (G.), 1954. Un nuevo caso de ofidismo. Bol. Chil. Parasitología, 9 (3), p. 88.
- SCHLEGEL (H.), 1937. Essai sur la physionomie des serpents. La Haye, 2, 467 p.
- SCHMIDT (K.P.), 1954. Notes on the frogs of the genus *Telmatobius* with description of two new Peruvian species. *Fieldiana Zool.*, 34 (26):
- SHREVE (B.), 1943. Notes on Ecuadorian and Peruvian reptiles and amphibians. Proc. New England Zool. Club, 18: 71–83.
- STEINDACHNER (F.), 1867. Reise der Österreich Fregata Novara um die Erde. Zool. Theil, Wien, 70 p.
- STEINDACHNER (F.), 1882. Batrachologische Beiträge. Sitzs. Akad. Wien, 85: 188-194.
- STEJNEGER (L.), 1923. Results of the Yale Expedition, Batrachians. Proc. U.S. Nat. Mus., 45: 542 p.
- TERRAZAS (W.), 1980. La rana del lago Titicaca. Rev. Soc. Bol. Hist. Nat., 2 (2): 39-40.
- TITSCHAK (E.), 1951. Beiträge zur Fauna Perus. Ein Zool. Reisber., Iena, I, 403.
- TOBAR (G.R.), 1942. Los ofidios chilenos son capaces de envenenar. Bol. Hosp. Viña del Mar, 3 (2), p. 42.
- TOBAR (G.R.), 1958. Cinco casos de ofidismo. Bol. Hosp. Viña del Mar, 14 (4): 172-184.
- TSCHUDI (J.J. von), 1844. Untersuchungen über die Fauna peruana auf einer Reise in Peru während der Jahre 1838–1842. St. Gallien, Herpetologie, 80 p.
- VELLARD (J.), 1951. Adaptation des Batraciens à la vie à grande hauteur dans les Andes. Tr. Inst. français. Et. andines, Perú-Lima, 3: 88-114.
- VELLARD (J.), 1951. Estudios sobre batracios andinos. 1. El grupo *Telmatobius* y formas afines. Memor. Mus. Hist. Nat. Javier Prado, Lima, 1: 90 p.
- VELLARD (J.), 1953. El grupo marmoratus y formas afines. Memor. Mus. Hist. Nat. Javier Prado, Lima, 2: 53 p.
- VELLARD (J.), 1954. Les Telmatobius du haut plateau interandin. Tr. Inst. fr. Et. andines, Paris-Lima, 4 (1): 1-57.
- VELLARD (J.), 1955. Propriétés venimeuses de Tachymenis peruviana Wiegm. Folia Biol. Andina, 1: 1-14.
- VELLARD (J.), 1957. El grupo Gastrotheca. Folia Biol. Andina, 4: 48 p.
- VELLARD (J.), 1959. Distribución de los Batracios en las altas regiones andinas del Perú y Bolivia. Act. Primer Cong. Sudam. Zoología, La Plata, I: 279–292.
- VELLARD (J.), 1959. El género Bufo. Folia Biol. Andina, 5: 48 p.
- VELLARD (J.), 1960. Notas complementarias sobre Telmatobius. Folia Biol. Andina, 6: 18 p.
- VELLARD (J.), 1966. El género Pleurodema en los Andes. Folia Biol. Andina, 7: 12 p.
- VELLARD (J.), 1970. Contribución al estudio de los Batracios andinos. Rev. Mus. Arg. Ci. Nat., Buenos Aires, 10 (1): 1–21.
- VELLARD (J.), 1975. Les batraciens dans la magie et la médecine des Aymaras. C.R. ler Coll. Ethnozoologie, Paris: 227–230.
- WIEGMANN (J.F.), 1834. In: Reise um die Erde ausgeführt auf dem Kgl. Preuss Seehandlungsschiff Prinzessin Louise 1830–32 von F.. Meyen. Zool. Ber., 3: 512 p.
- WIEGMANN (J.F.), 1835. Amphibien. In: Reise um die Erde ausgeführt auf dem Kgl. Preuss Seehandlungsschiff Prinzessin Louise 1830–32 von F. Meyen. 7° Abhandlungen. N. Acta Leopoldina, 17, 262 p.

C. EXPLOITATION OF THE LAKE RESOURCES SOCIO-ECONOMIC ASPECTS AND CONTAMINATION

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VII.1. ETHNOLOGY AND SOCIO-ECONOMY VII.1a. Past and present human populations

THÉRÈSE BOUYSSE-CASSAGNE

Lake Titicaca has been described by many people who have visited it. This great sheet of water with its capes, islands and encircling mountains was seen by the local people as their *Mare Nostrum*, but 16th century descriptions of its geography, history and myths remain disparate in content, so that it is extremely difficult to find connecting links for these few fragments of information.

It is not possible to write a detailed history of the lake because of the incomplete information we possess, but all the same the attractiveness of the lake, as an object of scientific study in almost all fields, is incontestable.

For social sciences, the origin and history of the lakeside communities, past and present, are always of crucial interest. The discussion was started by the pioneer paper of Rivet and Crequi-Montfort (1905) on the "Uru or Pukina language." which put forward the hypothesis that the Uru group of Titicaca was to be considered as one with the Arawak Amazonians, since they were closely related in language.

Vellard (1954) and Métraux (1967) studied the peoples of Titicaca and the Chipayas of Lake Poopo, adopting the same hypothesis, Vellard distinguishing two dialects spoken by a single group: Pukina and Uruquilla.

The linguist Torero (1970) was the first to consider Pukina as a general language adopted by the Urus in the Tiwanaku era, not to be confused with the vernacular language of this group; this hypothesis remains unproven. Tiwanaku is a village situated about ten kilometres south of Lago Menor, where there are two important pre-Inca sites.

I myself have engaged in this discussion since 1975 and have drawn up the linguistic map of the southern quarter of the Inca empire at the end of the 16th century, using a contemporary document, ("la Copia de Curatos"). In comparing this document with accounts relating to the visit of the viceroy Toledo (1575), I have been able to point out a great diversity of linguistic situations. It proved very difficult to find exact equivalents between language and ethnic group for the oldest groups of the lake after that time, because the linguistic situation and the names of the groups themselves were the result of various processes of domination occurring in the region from at

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least the Tiwanaku era. Recently, Wachtel (1990), in a historical essay going backwards in time, took up the subjects just mentioned and rightly thought that "at the furthermost limit of our sources and our journey back in time . . .- the landscape mists over. The search for origins demands other research techniques."

Ethnological history in the Andes has unfortunately had little occasion of developing alongside the Earth sciences and archaeology, and so it is ethnology – as for example in Wachtel's work – that illuminates our reading of ancient texts, despite the abrupt and sometimes radical impact of the Spanish Conquest. Historians of the Andes have rarely given themselves the opportunity to read 16th century history from "upstream to downstream." We have therefore used disciplines such as geology to try to reconstruct the long time-scale and the many changes that the lake witnessed before the Spanish first set eyes on it. By using the information from such disciplines a reinterpretation can be made of historical, archaeological and mythological material.

Geological data now allow us to date the legend of the "Flood." the birth of the islands and the opening of the Desaguadero. In trying to establish a link uniting the lakeside communities from Pucara, Tiwanaku and Hatuncolla, we should understand why the place of the peoples around the lake cannot be appreciated solely through colonial historical documents, which only give a glimpse of one moment of time and that are silent about some lakeside communities. As a matter of fact, a long time-scale and diachrony reveal the true nature of this world, partly hidden beneath the waters, of which some the 16th century Altiplano peoples were the unknowing descendants.

The Earth sciences (such as climatology and geology) and mythology cover much longer time-scales than History, and enable us to date climatic changes in the region and so understand the ecological upheavals that they have wrought (Tompson *et al.*, 1985 and 1986). Modern agricultural studies also contribute in the same way (Morlon, 1981).

Andean archaeology in which the chronology has been drawn up from the study of horizons, does not help the historian in answering the vital question: what ethnic groups were there before the Spaniards' arrival and up to the 16th century?

As from 1968, certain authors studying the Juliaca Paucarcolla site (Lago Mayor) stressed the importance of irrigation systems and "ados" (ridged fields) and their abandonment, for the understanding of the following cultures in this region (Smith *et al.*, 1968). Twenty years later, this work was echoed in publications of archaeologists on the Cuyo Cuyo (Goland, 1988) and Lukurmata areas at the south-west of Lago Menor (Kolata, 1989). This latter work, on agricultural technology and the organisation of its products in Tiwanaku State, was the first archaeological project to take geological and climatic data into account. The work of Smith *et al.* (1968) and Erikson (1984) on Huata and Umayu areas of the Capachica peninsula, and of Kolata (1985) on the Tiwanaku region are the only ones to refer to changes in lake level, and the particular lakeside farming methods that developed. They are

concerned with the timing of major climatic upheavals. The work of Hyslop (1976) on the Lupaca and of Julien (1983) on Hatuncolla (Lago Menor) are especially concerned with the Late Intermediate Period and the Inca period, or the latest periods. In addition their constant recourse to documented ethnohistory of the 16th century sources implies that this is correct, but the validity of these sources can only be checked by means of other disciplines.

The multidisciplinary, comparative approach leads to the formulation of new hypotheses, without pretending to fill the gaps or to remedy the problems inherent in each discipline. The use of palaeoclimatic and geological data in an examination of archaeological sequences helps to determine the relative importance of climatic events and political change in studying changes in the localisation of sites.

The mythological background

People of the Andes have always had favoured places where they can focus their identity. They have made them sacred, and the background to their legends. The lake is one of these places that gives a meaning to history because of its importance for the organisation of time and space and the way successive peoples of the Altiplano regarded its importance.

The lake, place of origins

To people in the 16th and 17th centuries, the lake was the site of the sun's birth and together with Tiwanaku (in Aymara, Taypicala, "the stone in the middle") the place where certain people originated (pacarina), especially the Incas who venerated the star in the temple on Titicaca Island – the present-day Sun Island. They saw the lake as a *chamaca*, a bottomless body of water that collected rains and rivers and let them drain by way of its interior towards the sea. The Aymara word *chamaca* refers to profound murky waters, and also expresses the mythical series of epochs and the age of the first human beings.

The value to us of these myths is to show that the geography of this inland sea is inseparable from a view of history as a cycle of events, disappearances, the great flood and new creation. The myths describe a first creation during which space is progressively organised: the lake, its islands and the stars, with human life inseparable from the world and in harmony with the long lasting processes of earth and waters. We therefore consider myth as a cosmogony, relating to the various ages in the lake's history.

Several legends put Titicaca and Tiwanaku at the origin of the second creation. When humanity at the time of darkness had been annihilated by the great flood (*pachacuti*), the god Viracocha created the stars, and a prototype of each nation (Bouysse-Cassagne, 1991). He commanded them

to disappear beneath the earth and then made them rise up again through holes or hollows in the earth's crust that are mountain caves, springs and lakes. Lake Titicaca, because it is thought to be bottomless, is seen as a kind of large hole communicating with the enormous ocean (mamacota) on which the Earth floats. It also receives the rain and so becomes a nexus of water flowing in two directions. At the time of the great flood, "when all existing waters united." when the Earth turned upside-down, it helped to reestablish the circulation of the waters again. As for the Desaguadero (Chacamarca), it is seen as a sort of bridge (*chacamarca* = place of the bridge in Aymara) linking Lake Titicaca to Lake Poopo. The Desaguadero is closely linked to myths about the lakes and has its own myth for its origin: a hero from the Collao region, Taguapaca, was an unruly servant of Wiracocha, who "opened the Desaguadero, that hitherto did not exist, with his boat" according to some legends (Bouysse-Cassagne, 1988). The lake and its islands, Titicaca or Sun Island and Coati or Moon Island, were sacred places where the powers of reality became manifest, the sun and the stars pouring forth from Sun Island. In the Andean pantheist cosmic view, the birth of the stars is inextricably linked to these islands.

Ethnogeography

The terms used in the 16th century and sometimes still to designate the lake, bear the stamp of divinities and peoples who lived on its margins and its islands. Each island was named after the idol (*waka*) that it sheltered within. "*Titicaca*" reflects the name of the island where Wiracocha performed his second creation, and is also the name of a god. "*Lake Pukina*" comes from the name of the ancient Pukina ethnic group that once lived in this area. "*Lake Chucuito*" refers to the name of the capital of the Lupacas, an ethnic group speaking mainly Aymara, that seized Sun Island from the Pukina-speaking Collas. The term *Wiñaymarca* or *Huiñaimarca*, which designates the Lesser Lake, means "place of eternity" in Pukina, the word "*wiñai*" meaning "eternal." There are probably historical reasons for the similarity in the place names for the northern and southern extremities of the lake; Pucara/Pucarani, Taraco/Taraco.

The midline axis (*sekhe*) through the waters composed of the Río Azangaro, the lake and the Desaguadero divided the whole world according to a twofold dualist principle. The *Urcosuyu* was the south-western part of the Altiplano and *Umasuyu* extended north-eastwards to the flanks of the Cordillera Real. *Urcosuyu* was the masculine element denoting the high and arid lands suitable for stock rearing (*urco* means male llama in Aymara), the opposite of *umasuyu* signifying the feminine element, also denoting the low fertile valleys and the cultivated land around the lakeshore.



Figure 1. Old Spanish depiction of Lake Titicaca (16th century) in Cieza de Léon – Cronica del Perú.

The succession of ancient civilisations

Geological and palaeoclimatic information

An overview of previous work in these two disciplines reveals several periods in the geological history of Lake Titicaca (Table 1; see also Chapter III.1).

Around 10 000 BC the lake level was about 5 metres higher than it is today. Further south at this time there was an immense lake, Lake Tauca, covering some $43\,000 \text{ km}^2$ and several tens of metres deep over areas currently occupied by lakes Poopo and Uru-Uru and the "salars." In other words, during the entire period preceding the Viscachani culture – the first known inhabitants – a large part of the Altiplano as we know it was under water (c.f. Chapter III. 1).

After 8500 BC a period of progressive drought began, reaching its maximum around 5500 BC. Lake Tauca gradually dried out and further to the north Lago Wiñaymarca was completely empty of water, whilst the Lago

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Table 1. Attempt at classification of the palaeoclimatic, palaeohydrological, archaeological and ethnological sequences in the region of Lake Titicaca from 10,000 BC up to the present day.

	CLIMATE	LAKE PALEOHYDROLOGY	ARCHAEOLOGICAL HORIZONS	CIVILISATIONS	AGRICULTURE ON RIDGED FIELDS
1900 - 1800 - 1700 -	Little • 1860 max. c ice dryne:	PRESENT LEVEL : 3 808 m	3 808 m PRESENT		
1600 - 1500 - 1400 - 1300 - 1200 - 1100 -	Age • 1720 rainy dry • 1160	Increasing lovel cycle (= some meters > present)		INCA LUPACA COLLA	
1000 - 900 - 800 -	+1040 Cold humid	 Ends of bays and Desaguadoro with water 	LATE INTERMEDE	TIWANAKU V	
700 - 600 - 500 -	Hot and humid Dry and hot		MIDDLE HORIZON	TIWANAKU IV	
300 - 200 - 100 -		PRESENT LEVEL		TIWANAKU III TIWANAKU II	
		Final phase of water increase	EARLY INTERMEDE	TIWANAKU I	
10-10 . 2000 .		Level about 10 m < than the present one. Chua depression and NW part of the Lago Menor with where Despanders det	or FORMATIVE	PUCARA CHIRIPA	
30×0 _	Increase of rainfalls	Level 20 to 30 m < than the	(
4000	Wettest period	present one. Chua depressie a with water . Desaguadero dry			
5000	- Extremum of dryness	Level about 60 m < than the present one. Bays and	ERAM .	VISCACHANI	
6000		Desaguadero dry. Saline lake.	L L L L L L L L L L L L L L L L L L L		
7000 . 8000 .		Beginning of water level decrease			
9000 1916	Extremum of rainfalls	Level about 5 m > than the present ono. South Altiplano = Tauca lake (-13 000 km²)	INITIAL PERIOD		

Mayor dropped 50 or 60 metres in level leaving Puno Bay and the northeastern corner of the lake dry. The water turned from fresh to saline.

After this extremely arid period, there was a period of variable hydrological conditions around 5000–2500 BC. The lake levels were higher than in the previous period, but lower than at present. The Lago Mayor lay twenty or thirty metres below today's level. The Lago Menor remained dry except for the Chua depression and another depression immediately to the west of the islands of Lecoya and Suaña. The Desaguadero was waterless.

According to geologists, the beginning of the final phase of the rise in water level in Lake Titicaca can be dated at between 2500 BC and ca. 250 BC. The levels rose to 10 m below the present level; this was due to an increase in rainfall (probably the mythical great flood), with nonetheless a . major, but short-lived drop in level at around 2000 BC. A water level 10 m

below present would mean that most of the Wiñaymarca and a large part of the Lago Mayor was dry. During this phase the Chua Depression and the Lago Mayor communicated once again, and the waters turned fresh again.

According to Binford and Brenner (1989), Lago Wiñaimarca was as deep as present at about 1950 BP. This new dating is more precise than the data of Mourguiart (1987), Servant and Fontes (1975) and Wirrmann (1987), who dated the period of the final rise in the water level of Titicaca (up to its present level and before its rise of a few metres in the "Little Ice Age") at between 250 BC and 1500 AD. This more precise dating helps in understanding land use on the shores at the time of the earliest cultures in the area (Chiripa, Pucara). All this information gives us fresh insight into the history of lakeside cultures which began about 1800 BC.

The archaeological horizons

Since the archaeological works here presented use three distinct time divisions, it would appear necessary to define the notion of the archaeological horizon in the Andes, and to explain in detail the time scales used. They do not concern just the lakeside cultures, but relate their development to other types of cultures in the region.

Three present-day schools of archaeological thought have drawn up diagrams of chronological sequences in the south-central Altiplano. The schemes of Rowe (*in* Willey, 1981) and Lumbreras (1981) cover Peru, whereas that of Ponce-Sangines, recently revised by Kolata (1983), is restricted to Tiwanaku in Bolivia.

The first two authors divide time into "horizons" and base themselves on the expansion of the three great cultures of the Chavin, Tiwanaku-Huari and Incas and create two intermediate periods between each of these: "The Early Intermediate Period" and "The Late Intermediate Period."

The first of these periods was preceded by a "Preceramic Period." followed by an "Initial Period." Lumbreras considered that the Preceramic could be divided into two stages: the "Lithic" and "Archaic" which distinguished between hunter-gatherer and agricultural communities.

He placed the appearance of pottery during the "Late Archaic." Next came the "Formative" period that saw the birth of local cultures on the Altiplano: the Pucara to the north and the Chiripa to the south of the lake. These coincide with the Chavin and Paracas cultures along the Pacific coastal region.

The "Formative" period corresponds to what Willey called "The Early Horizon." This period precedes that of the "Higher Cultures" (Early Intermediate Period) that saw the development of the Moche and Nazca cultures on the Pacific coast and of the Tiwanaku culture (before its expansion) around the lake and on the Altiplano.

In around the 7th and 8th centuries AD, the Tiwanaku-Huari culture

expanded forming the "Middle Horizon." the end of which marked the start of the "Late Intermediate Period" named by Lumbreras as the "Regional States" period and which in turn was followed by the Inca Empire.

Ponce Sangines (*op. cit.*) produced a chronology specific to Tiwanaku, which was taken up by Kolata and coworkers, who divided the Tiwanaku into three major cultural periods, characterised by different types of pottery.

The village period	1580 BC-43 AD	Epochs I and II
The Urban period	133 BC-724 AD	Epochs III and IV
The Imperial period	724 AD-1172 AD	Epoch V

The chronological synthesis of the archaeological data will thus progress from the "Initial Period" (10,000 BC) until the Inca Empire, following some of the horizons given in Table 1.

The cultures involved

From the analysis of the previous data I have attempted to discern the preferred areas of habitation and to define as far as is possible the characteristics of the associated human populations.

During the period preceding the Visachani culture, most of the Altiplano was flooded.

The Viscachani culture existed between 8500 and 2500 BC. The geological data (Servant and Fontes, 1975; Mourguiart, 1987; Wirrmann, 1987) now provide a better understanding of the locations of the associated archaeological sites. All of them without exception are situated on ancient lake terraces and consist of settlements of hunter-gatherers; they include the sites of Viscachani (Sica-Sica Province, La Paz District) and of Laguna Hedionda and Pichalo, identified by Barfield in the south of the Altiplano, and of the Puripica (6000 BC) and Laguna Colorada complexes.

The period of the rise in lake level, to a height varying according to geological estimates to either the present level or about 10 m below the present, occurred between 2500 BC and ca. 250 BC.

Several cultures thrived at this time in the region of the lake and on the Altiplano. These included for example the Wankarani culture of farmers and pastoralists from the north-east of Lake Poopo, dating from 1200 BC and lasting until the 2nd century AD.

In the Titicaca area, two distinct cultures occurred: one to the north of the Lago Mayor (Pucara) and the other to the south of the Lago Menor (Chiripa) from whom the Tiwanaku culture derived. Excavations carried out by Erikson (1984) at Huata (Puno Province) near the Lago Mayor have, according to Willey's (1981) chronology, provided evidence of a first culture associated with pottery of Qalayo (Early Horizon), Wankarani (1200–200 BC) and Chiripa (1800–200 BC).

Traces of these cultures are demonstrated by certain agricultural practices and especially the construction of ridged fields (*ados*) for which the first period of intensive use probably dates from between 1500 and 500 BC. The development and practice of these agricultural techniques were directly related to a better control over water in marshy environments, but also served in the context of irrigated cultivation (Morlon, 1981 and pers. comm.). Their presence was therefore related to the existence of unusual types of agricultural landscapes.

The construction of ridged fields was also developed between 800 and 600 BC, i.e. during the Pucara period. This stage was followed by a long period of abandonment, or reduced use, which probably started at about 300 BC and continued until 500 AD.

If it is accepted, as the works of Binford and Brenner (1989) show, that the lake reached its present level at the start of 1st century AD, the construction of ridged fields would have occurred during the period of rising lake levels and they would have been abandoned after the lake reached its present level.

The existence of the Chiripa culture near the Lago Menor in the Pampa Koani and Lukurmata areas (Kolata, 1983) has been detected by the appearance of traces of agricultural activity at around 500–300 BC. The existence of a well-developed agricultural sector becomes evident as from the Tiwanaku III, with the extension of complex agricultural field patterns at the time of Tiwanaku IV (375–750 AD), i.e. after the rise of lake level to its present height (again according to Binford and Brenner, *op. cit.*). These cultivated lands around the lake were still in production between 750 and 1100 AD, before being abandoned after the Tiwanaku V epoch.

Whatever chronology is attributed to the Pucara culture to the north of the Lago Mayor (1100–100 BC) or to the Chiripa near the Lago Menor (1500–600 BC), the start of agriculture on ados, which appears with these two cultures, coincides with the final phase in the rise of lake level. What is more, certain Chiripa sites are situated on present day islands in the Lago Menor, such as Suriqui, Pariti and Anayutani, which tends to prove that this occupation took place over a much more extensive area than today, since much is now flooded. The remains studied on Anayutani Island and at Pukuru-Uyu on the lakeside show that this was a complex mixed economy, which made great use of the lake's resources, such as fish and birds, of agricultural products such as potatoes and quinoa (a type of buckwheat) and of pastoralism (Browman, 1978).

It is important to note that the dates of the abandonment (or reduced use) of the Huata lands (Lago Mayor) and the putting under intensive cultivation of those situated at the extremity of the Lago Menor (Tiwanaku IV and V), coincide in time. The interpretation given by Erikson (1984) for this upheaval is a political one, related to a change in the centre of power within the Titicaca basin, when the Tiwanaku people replaced the Pucara. This hypothesis can no doubt be confirmed from a study of toponyms, which as has already been stated, are the same at the two ends of the lake and by archaeological evidence: numerous Pucara monoliths and pottery sherds have been found at the Tiwanaku site. These include the two statues that now adorn the porch of the church at Tiwanaku, the "barbado" monolith of the subterranean temple at Tiwanaku, or the "Piedra del Trueno" (thunder stone) of which one half is found at Arapa at the north of the lake and the other at Tiwanaku itself. The architecture at Tiwanaku has also inherited many of the processes already in use at Pucara such as lower patios, Ushaped pyramids and stairways oriented towards the east. Although the Pucara origin of the Tiwanaku culture has been acknowledged for several years (Browman, 1985), thanks to the new chronology, we are now in a position to be able to understand how and at what time the movements between the south and the north of the lake took place.

As far as the Tiwanaku people are concerned, the type of settlement pattern envisaged by Stanish (1989) was a continuous peopling around all the shores, on the model of that of the Taraco Peninsula which was completely refashioned. However, the agricultural systems organised around exploiting raised fields could have predated the Tiwanakus and could have been taken over by them. In the region of Pampa Koani alone, Kolata (op. cit.) estimated that the intensive production from the fields could have fed between 20,000 and 120,000 persons; this implies a dense agricultural population living largely outside the ceremonial centre of Tiwanaku itself (Bouysse-Cassagne, 1991). This author suggested that the key sector for the economy was not restricted to the in-fields surrounding the capital, but was rather a system of administrative centres located near potential arable land and situated all around the lake (Fig. 2). This system was to last from Tiwanaku III to Tiwanaku V. Satellites such as Wankani and Mochachi are situated on the eastern and southern shores of the lake, and there also exist traces in the form of pottery of this occupation further north in the Puno region, on the Lago Mayor. According to the model proposed by Kolata (1985), the reclamation of marshy areas from the lake enabled the State of Tiwanaku to meet its essential requirements.

In the areas occupied by the Colla people, in the region of Juliaca-Paucarolla alone, where the largest number of irrigated fields is found, it has been estimated that the extent of cultivation on ados in the Tiwanaku epoch was more than 56,000 hectares (Smith *et al.*, 1968). These authors were astonished that no Spanish chronicler from the 16th century mentioned this practice. In fact, if Cieza de Leon (1984) in writing about the Collas' region and deploring the general depopulation stated that the Collas "have no irrigation canals." this was because at this time, during the "Little Ice Age." the ridged fields were probably lying a few metres under water. Aerial photographs reveal that more than 83,000 hectares of previously cultivated land were gradually abandoned (Bray, 1990) (Fig. 3). It is to be noted that the irrigated fields are situated *grosso modo* at the two ends of the lake and



Figure 2. Sites of the Tiwanaku culture (epochs III and IV) near Lake Titicaca (from Kolata, 1985).

have their greatest extent in the Colla region which resisted Aymara invaders the longest.

According to Kolata (1985) the original type of human settlement that existed from the northern part of the Lago Mayor to Pampa Koani (Lago Menor) strongly affected the political unity of the lake basin. This important remark throws light on the available historical evidence. When the capital Tiwanaku fell, no doubt under attacks from the Aymaras, and the Colla region took over the intensive cultivation of the land around the shores, but at the other end of the lake, this signifies not only that the Colla should be considered as the last stronghold of the ancient lacustrine cultures derived from the Tiwanaku, but also implies that later battles and alliances they engaged in against the Aymaras and the Incas, were the last death throes of the ancient masters of the lake.

The abandonment of the lands of the Pampa Koani and Lukurmata on the Lago Menor took place between 100 and 1100 AD according to Kolata.



Figure 3. Distribution of ancient ridged field cultivation systems in the Titicaca basin, from aerial photographs and field work by Smith et al. (1968).

However, at the same date cultivation of raised fields and on ados began again to the north of the Lago Mayor at Huata and to the north of Lake Umayo (in the Colla chiefdom whose capital was Hatuncolla) (Smith *et al.*, 1968; Erikson, 1984).

There was therefore a sort of coming and going in the exploitation of the north and south of the lake (in fact between Pucara, Tiwanaku and Hatuncolla), which again cannot be explained entirely by climatological factors. Kolata remarks that flooding could still have had a dramatic influence on agricultural production and could have started the decline of the Tiwanaku State.

The ultimate stage in the exploitation of ridged fields in Colla territory seems to have lasted up until the arrival of the Incas (1445 according to Smith *et al.*, 1968), but it is also possible that the real end may have coincided with the rise in lake level at around the "Little Ice Age." These two hypotheses are not mutually exclusive and both could explain the abandonment of the agricultural practice: so that the cause was the combined effect of rising water level, the invasion of the Aymaras and the wars of the Inca Conquest.

The Collas and the problem of the Pukina language

Direct historical sources are rather silent about what they mean by the label "Colla." and are even confused to the extent that this term is used indifferently for all the people who inhabited the southern quarter of the Inca Empire, and for those who lived in the Colla chiefdom.

Used as an adjective the term "*colla*" was applied both to the Uru and Pukina groups, but never to the Aymaras, but its use as an adjective disappeared in the 16th Century, to become a noun as mentioned above.

Moreover, the meaning of "*colla*" in Pukina and Aymara shows us the semantics involved here. "*Colla*" means "purge, food or drink, or plaster or medicine" and "*collacamana*" therefore signifies doctor. It is also known that the Callawayas (or Collawayas), an old branch of Pukina-speaking people, who outlasted the fall of the original Colla chiefdom, were and still are to this day the most famous herbal healers throughout all the Andes (Bouysse-Cassagne, 1988; Girault, 1984).

"Colla" was also used to designate the chief of the Colla people, just as "Inca" was the name of the chief of a Cuzco people. The chief of the Colla, variously known as Colla Capac (Sarmiento de Gamboa, 1942), i.e. great doctor, Zapana or Capana (Cieza de Léon, 1984), Chuqui Capac or Javilla (Morua, 1590) or even Inca Capac (Sarmiento de Gamboa *op. cit.*), appeared in the records from the 16th century as a man ruling a great territory.

In my view, he represents on the religious and political scale, the inheritor of the Tiwanaku tradition and that of the lake, that is to say the site where Wiracocha created the universe, the stars and above all the sun.

If the extent of Colla territory is described differently according to the

source, this is because these descriptions had to take into account the successive reductions in the area that was constantly being split into smaller units. In addition, the various stories produced for the Spaniards evoke the former glory of the people of the lake and oral tradition has a greater tendency to embellish remembered events when the proof of their very existence is almost shrouded in obscurity (Morua, 1590; Sarmiento de Gamboa, 1942; Cieza de Léon, 1984).

It seems that one linguistic unit can be discerned, covering both the region involved by the rebellions around the lake at the time of seizure of power by the Incas, and the Colla territory itself. In the 16th century, the regions of La Raya, Cuzco and also further south from Ayaviri and Caracollo, and even the Pacific slopes of Arequipa and Arica were all still Pukina-speaking (Barzana, 1954; Bouysse-Cassagne, in press).

As for the Mojos of Bolivian Amazonia, who were also mentioned as a people living at the edges of the Colla kingdom, they have left some of the most spectacular traces of ridged fields, whose importance has been highlighted by the works of Denevan (1963) and Plafker (1963). If future archaeological work manages to demonstrate that a link existed between the hydraulic cultures of Amazonia and those of the Colla region and the lake, we would then be confronted with a vast block, which if it could be shown to have a cultural unity would not be exclusively Andean, but also Amazonian. However, the idea which has been put forward at various times, that the Tiwanaku originated from the forests, has not been supported by sufficient archaeological, linguistic or historical proof.

We now know that the history of this Colla linguistic and cultural unity must be related to the tribulations of the successive cultures that developed around the lake from Pucara and Tiwanaku through to Hatuncolla.

The map of languages spoken in the 16th century from Bouysse-Cassagne (1991) reflects the linguistic transformation in the region. It should be read like a geological map, since there are linguistic layers which overlap or exist side by side: bilingualism (Pukina and Aymara) or trilingualism (Pukina, Aymara and Quechua) are recorded for several regions (Fig. 4). More dense patches of Aymara occur on the Urcusuyu shore, but also occur on the opposite shore and penetrate as far as Chuncho territory.

The maintenance of a Colla presence as shown by the existence of the Pukina language over a vast area, which in addition to the lakeside chiefdom of the Late Intermediate Period, included all the Omasuyu shore and a part of the warm lands dependent on it (Carabaya, Canas and Canchis), the Pacific coast (Arica and Arequipa) and extended as far as Cuzco, can be reinforced by other historical and linguistic proofs (Bouysse-Cassagne, 1991).

The language of the Callawayas, which is still spoken to this day and which uses a Pukina substratum, is the last linguistic trace remaining of the language of the people of the lake.

In the wider sense, the term Colla therefore designated populations distributed over a vast area, corresponding to a Pukina linguistic substratum,



Figure 4. Map of the languages spoken in the 16th century on the Altiplano and in neighbouring Andean areas. A = Aymara; Q = Quechua; P = Pukina; U = Uruquilla (from Bouysse-Cassagne, 1978).

whose origins should be traced back to former cultures of the Late Intermediate Period. But, submerged by successive conquests, they only figure in the form of traces in the historical records. This discussion provides insight on the overall Colla problem, but does not resolve the difficult problem of the differences between the Urus and Pukinas, both of whom were called "Collas." The linguistic map of the 16th century proves that these two groups (a part of the Urus in reality) spoke the Pukina language.

The recent civilisations

The Aymara migration

In the Late Intermediate Period, a new and formidable power, the Lupacas, sprung up between the two extreme ends of the lake formed by Tiwanaku and Hatuncolla (the Colla capital).

The movements of the Aymara-speaking populations over the Altiplano are still poorly known, and historical and linguistic information seem to contradict one another. The chronicles tell us that a Lupaca chief, Cari, seized control of the sacred islands in the lake and the Copacabana Peninsula. Waves of migrants coming from the south settled on the Urcosuyu part of the shoreline. According to Cieza de Léon (1984), Cari the Lupaca came from the Coquimbo valley in Chile and the oral traditions of the Pacajes in the 16th century seem to explain the splitting of the chiefdoms around the lake into two factions by their different origins: one related to the Umasuyu (lake-dwelling people) and the other to the Urcosuyu (pastoralists from the mountains).

The Peruvian linguist Torero (1974) proposed another scheme, according to which the expansion of the Aymara language started from an ancient nucleus situated in Peru in the Cañete or Chincha region and extending as far as Nazca on the Pacific coast, which later moved towards the southern Sierra and the central Sierra. But Bird (1946), in his study of coastal languages based on the work "Art and grammar" by Luis de Valdivia (1606) found no trace of Aymara language in the Coquimbo region from where the Lupaca chief is supposed to have come, but only found the Amazonian language, Arawak, there (Bouysse-Cassagne, 1988).

The struggle of a people

Whereas the time of the Tiwanaku State was marked according to Kolata (1984) by unity around the shores, with the coming of the epoch of the war (*aucaruna*), battles raged from one *pukara* (fortified village) to another. The great Colla nation fragmented and the shores of the lake became shared among several chiefdoms (Fig. 5).

Study of the advance of the Lupacas provide a better understanding of the dismemberment of the lake's unity, and also beyond the shores that of the whole of the Tiwanaku. However, two facts should not be overlooked: the success of the Lupacas was in great part due to their alliance with the Incas; the disintegration of the lakeside communities and the groups allied



Figure 5. Aymara señorios after the decline of Tiwanaku (from Bouysse-Cassagne, 1978).

with Tiwanaku undoubtedly implies some resistance, but also much treachery, as revealed by the history of events.

Cari, the Lupaca chief, thus reached the Urcosuyu shore of the lake, and invaded the islands including Sun Island, then controlled by the Collas. He exterminated the population and then on return to the mainland, founded Chucuito, Ilave, Juli and Pomata on the Urcosuyu shore. He crossed the lake and conquered the Canas. The Collas and the Umasuyu shore were thus cut off (Fig. 5).

At Cuzco, the Inca realised the need for an alliance with Cari and therefore advanced his troops to Collao. After the defeat of their neighbours, the Canchis, the Canas allied themselves to the Inca (Bouysse-Cassagne, 1991). Meanwhile, Cari took the initiative and attacked and killed the Colla chief, Zapana, at Paucarolla. The Inca found himself obliged to make an alliance with the Lupaca in order to ensure the advance of his own troops.

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At this point in time, part of the province of Carabaya (Orurillo, Asillo and Azangaro) allied itself with the Inca chief of Cuzco. This was an area particularly rich in gold-bearing deposits where there were also numerous irrigated fields, as on the shores of the lake.

For the period that followed immediately the historical sources are more confused. Certain sources talk of two rebellions in the Colla region, others only of one. Whatever was the case, it is almost certain that the Colla uprising against the Inca power, which had followed the installation of the Lupacas on the Urcosuyu shore, and against the Inca takeover of part of the western region of Collao, involved all the inhabitants of the lake shores, who even before Tiwanaku and ever since had struggled to master the riches of the lands around the lake by many ingenious improvements. This highly productive agricultural region with a dense population, united in this last fight, henceforth had to share its lands with other peoples.

The land settlement pattern of the Lupacas

Hyslop (1976) distinguished three types of Lupaca site in the Late Intermediate Period:

- hilltop towns with tombs at more than 4000 m;
- towns on flat land with tombs lying between 3812 and 4000 m;
- *chullpa* sites (tombs in the form of a circular tower), which were mainly funerary sites and which represented structures of a new type for the region.

Hyslop suggested that the *chullpas* (attributed variously to the Collas and to the Lupacas), indicating a type of ceremonial enhancement in the relationships with the ancestors, replaced the ceremonial structures of Ti-wanaku (Bouysse-Cassagne, 1991).

A model of land settlement can thus be distinguished for the Lupaca region covering the Middle Horizon and the Late Intermediate Period.

During the Middle Horizon, settlements were usually located in low altitude areas, near the lake. It is likely however, that during the expansion of Tiwanaku in the region south-west of the lake, the population lived on many resources including those from around the lake (agriculture, hunting and fishing) and those from the grazing herds on the high altitude lands, with the establishment of small or seasonal settlements in the puna (pastures near the Cordillera).

During the next period, the Late Intermediate Period, most settlements were situated on high land and were protected by walls or rocky escarpments in areas less favourable for irrigated agriculture, but more adapted to pastoralism. These sites were abandoned during the Inca invasion (around 1450).

The marked changes between the Middle Horizon and the end of the Late Intermediate Period represent, according to Hyslop (*op. cit.*), the time of transition during which the Aymara-speaking populations came to dominate the Pukina-speaking people. This hypothesis needs to be qualified, in my view. Although it is of great interest when applied to the Lupaca territory, it does pose problems when applied to the whole of the area around the lake, as has often been the case. As we have seen, in the territory of the Collas, the last descendants of the lakeside cultures, the shoreline continued to be exploited and inhabited up until the Inca period and therefore well after the Late Intermediate Period.

The end of the ancient masters of the lake

Irrespective of the origin of the migrations of the Aymara and their scale, it is evident that the installation of the Lupacas on the eastern shores of the lake represented a radical social change, affecting the population, land use and the economy.

The Aymara stratum gradually supplanted that of the Collas and all that remained on the lake's margins and on part of the Altiplano of the populations belonging to the ancient cultures. But this replacement, that has been revealed by archaeological remains and by linguistic factors, was not uniform and did not occur at the same time around the entire margin of Lake Titicaca and at all points on the Altiplano.

At the same time as the traces of irrigated fields disappeared and the ancient large religious sanctuaries built on the islands fell into the hands of the invaders, a new society was being built. Like an autumn leaf, the lake culture, for a while still controlled by the Collas, gradually withered away and fell into fragments.

The Inca period

The land settlement pattern

On the whole, the Inca period corresponds to a new model of land occupation which, for the historian, proves to be more complex than the previous uses and makes it even more difficult to identify the ethnic groups who were the inheritors of the ancient lake traditions.

In addition to the climate, which was unfavourable for irrigated cultivation, the whole of this period is characterised by major upheavals in settlement patterns that also corresponds to a period of very high lake levels. A complete infrastructure of roads (which probably used the ancient tracks) was set in place, as well as new religious and administrative centres.

In the Lupaca region, the Copacabana Peninsula and the islands of the Sun and the Moon became sites of imperial pilgrimage, that took over from the ancient sanctuaries of the Urus and Pukinas such as that of Titicaca Island (Bouysse-Cassagne, 1988). Hatuncolla became capital of the province; state trading posts and a temple dedicated to the god of the sun were built.

What is without doubt one of the main findings of this work is that none of the sites dating from this period was situated on hills. All of the population was again on the plains and consequently on the borders of the lake. This change in land occupation has been noticed by several chroniclers, and Cieza de Léon (1954) suggests that it was not only due to the politics of the Incas but also to the peace brought about by their domination. He also notes that the Incas established new frontiers between chiefdoms, which consolidated this peace.

The frontiers also extended over the lake, which received treatment comparable to that of dry land, i.e. in agreement with that of a previous epoch (Bouysse-Cassagne, 1991). The most immediate consequence of these changes in land occupation was without doubt the subjection in certain regions at least of peoples belonging to the Urus and Pukinas, by Aymara populations.

The mixture of ethnic groups

The displacement of settlements towards the regions around the lake led to enforced cohabitation of ethnic groups, which is documented by historical sources from the 16th century, and led to enormous difficulties in understanding. The example of the Pacajes clearly shows this problem. An Uru who spoke Aymara and lived amongst them: was he going to be considered an Aymara, or did he remain an Uru? What were the criteria which in the eyes of the Inca administration, then the Spanish administration, enabled them to be distinguished from one another?

Ethnic labels in the historical documentation, whether they are of Inca or Spanish origin, did not exist to distinguish between cultures – they refer to categories of dependency by tribute. The names given to the ethnic groupings are the products of the dominant groups and the Spanish documents, the only ones we possess, accumulate the various perspectives of various conquering forces: Aymara, Inca, Spanish.

My previous combined study of the linguistic map and of the tribute map of the 16th century (Bouysse-Cassagne, 1987), shows that the assimilation of lakeside communities took place slowly. Confusion between the Pukinas and the Urus became more frequent under the influence of the one economic factor: cohabitation (Morua, 1590).

At Capachica for example, although one part of the inhabitants was classed as Aymara despite the fact that they spoke Pukina, this was because their lifestyle was such that the Spanish visitors had assigned them to the tax category "Aymara." which always signifies a high level of tribute.

This last example clearly shows how and in what context the ethnonyms

were no longer valid from the time of the viceroy Toledo; the criterion of richness was what counted. It also proves that before the Aymaras, at least a part of the Uru groups had been dominated by the Pukinas. If in the list of colonial taxation (tasasiones) both Urus and Pukinas are often listed under the strongly pejorative term of "Uru", this is for various reasons, one of which is now explicable: when the lake rose in level, and later on after the transfer of populations by the Incas, the "lakeside" groups cohabited in a new way. For some it was because the fields they had formerly possessed had disappeared under the waters and they now lived on the lake margins, for others it was because they had been forced to live in areas away from the lake. Finally, it was also because subsequent Aymara and Inca conquerors had every interest in compounding them in order to enforce subjugation.

There were still some ethnic distinctions, however: only the Pukinas possessed llamas (Morua, 1590; Lizzaraga, 1968) and, although those classed under the tribute category as "Uru" were the main group of weavers in the 16th century, they never owned llamas (Bouysse-Cassagne, 1984).

Myths about the lake clearly distinguished between two types of humanity: one, post-diluvian, including the people of Hatuncolla, the inheritors of Tiwanaku and worshippers of Viracocha and the Sun, whilst the Urus were the people from the first time of darkness and the depths of the lake. And did not the Incas forbid them to worship the Sun? (Bouysse-Cassagne, 1988).

Spanish chronicles, the product of domination, describe the Urus as brutish, dirty, lazy – not really men at all. In Bertonio's (1984) Aymara dictionary, they are also designated in pejorative terms. Some documents make reference to the Pacific coastal origin of the Urus (Paredes, 1931), but this origin for the fishermen of the lake and the Desaguadero is not substantiated by any historical proof.

The bilingualism recorded among the Uru group is justified if we assume, as Torero (1974) proposes, that the Uruquilla language was not limited in the 16th century to the southern part of Collao near Lake Poopo and to Zepita in Chucuito province, but was in fact the vernacular language of the group, and that they did not adopt Pukina until after they had been subjugated. This hypothesis assumes an original ethnic and cultural difference between the Urus and Pukinas, that is not disclaimed either by ancient myths or by oral tradition.

Successive waves of conquest, the disappearance of the ridged fields, environmental upheaval and colonial economic practices ended these old differentiations. Incidentally, the chroniclers relate that the Colla lords of Capachica were in ancient times the former occupants of the sacred islands of Inteca, Amantini, the Sun and the Moon (Bouysse-Cassagne, 1988). Their respectful memory endured for a while, along with a few relics. It is said that the lords of the sacred places were the first to wear fine woollen clothes (cumbi) interwoven with metal, purple in colour and decorated with motifs. The last great lacustrine culture is also attributed with the inventions of some of the most sophisticated weaving techniques – the pinnacle of the art. These artistic refinements, which turned the Capachicas into the great Inca weavers and experts in the art of dyeing using aquatic plants, gradually disappeared.

Of the Collas, nothing remains but a name; this refers to the former inhabitants of Collasuyu, of all ethnic groups, and indicates that the Incas had chosen the prestigious name of the last great lake culture for the southern quarter of their empire.

Conclusions

Lake Titicaca only reveals its role as an inland sea when its history is seen from the perspective of a long time-scale. Gradually, an understanding is emerging of how the regional groupings and economic and social structures, built on strips of land reclaimed from the lake, succeeded one another, from the time of Pucara through to Tiwanaku and Hatuncolla, in this ill-defined and tumultuous environment, which nevertheless constitutes a physical entity. Through successive conquests and invasions, the human society that lived largely from the lake was gradually split up and the shores abandoned and covered by the waters. But these migrations, which led to a reconstitution of the human and physical landscape in which townsfolk and people living from the marshes live side by side, can only be comprehended if looked at from a sufficiently long time-scale.

The social and ethnic groups, continually redefined over centuries-long cycles, which involved changes in the lake level, economic changes, migratory movements and conquests, formed a dense and complex world in the documentation of the 16th century. The way in which the Spanish texts are written imposes both its own interpretation of ethnic relationships and gives a static view of the lake, making it difficult to define the social and ethnic status of the various groups present. I have therefore made a re-examination of the 16th century documents, through diachrony and using a long time-scale, while being careful to avoid an ethnocentric viewpoint and an approach linked to an idea of tradition based on the concept of survival.

Acknowledgements

I wish to thank Ph. Bouysse who has been extremely generous with advice and documentation, as with my previous writings, and also J. Perez and R. Gonzales, with whom I have had fruitful discussions. VII.1b. Former lake fisheries and fish fauna of the lake

JEAN VELLARD

During the first half of the century, before the introduction of trout, Lake Titicaca had plentiful fish resources and the fishermen recognised several species of fish.

First of all there were fish with very fine flesh, which formed the basis of trade with the villages and towns of Guaqui, Puno and especially La Paz, where they were served in the best hotels. The two most esteemed fish were *Orestias pentlandi*, the "boga" also known by the Aymaras as "kesi" or simply "chalua" (fish), and *Orestias cuvieri*, the "huminto." Fishing took place especially in winter from June to November. These were pelagic fish and were often exploited by collective fisheries. In these, several boats made of totoras, or "balsas" formed a semi-circle and beat the fish towards a central point, by striking the water with a stone attached to a rope or with gaffes fitted with a ball of rushes. The fish were driven towards a large pouch-shaped net, the "kana" or "kaana" held open by stones and totora floats and with a guide wall that led the fish in.

The fishery was very productive; each "balsa" could bring back one or two alcohol cans (the unit of measurement equivalent to about 20 litres) containing 200 to 300 fish, which at that time (1946) fetched 0.2 sols each. On the Desaguadero and at various points around the lake such as Puno, Puerto Acosta and elsewhere, the fish were driven towards a large V-shaped enclusure of totoras, closed at the apex by a net or "kencha."

The second category of fish, restricted to the native markets, was that of *Orestias* living in the totoras or reedbeds, and lumped together under the name of "karaches." The most abundant species were the black "karache." which corresponded to the different varieties of *Orestias agassii*, followed by the yellow "karache" (*O. luteus*) or "punkhu" and the white "karache" (*O. alba*), which was less frequent and also called "kaño." All these reed-dwelling species were subject to intensive exploitation. During the daytime they were captured by wading or from small "balsas" with hand nets made of cotton ("sakkáña"), or even with the ancient form of hand net made of straw, the heavy "noku" still being used by some groups of fishermen. In shallow water among submerged macrophytes (including *Myriophyllum titicacense*), fish

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Plate 1.

were captured in enclosures, called "pozos" or wells, made with these aquatic plants. These were made by groups of men who advanced in a circle, piling up a wall of the plants reaching from the bottom to the water's surface. When a circle of four to five square metres area was thus enclosed the fish accumulated inside were captured with a landing net.



Plate 2..

The most important fishing took place at night from single "balsas." A lamp fixed to the front attracted the fish that the fisherman caught with a harpoon called a "maxana" "piri" or "yakhaña." Fish were sold fresh at about one boliviano each (1952), or more frequently were opened and dried in the sun on mats and on the roofs of huts or between layers of hot rocks. The fishwives often sold them to the wives of farmers, by silent barter, on the shores of the lake and the islands.

Several small-sized species of *Orestias*, together with the young of other species and grouped under the name "hispi" were subjected to intensive fishing in the open water areas in summer (mainly January), using spherical fish traps ("kulancha") drawn by a "balsa" or with hand nets in the totorales. This fishery was very important.

The siluroids or "suchis" or "mauris" (*Trichomycterus*) formed the fourth category. They preferred to live in the beds of submerged macrophytes and



Photo 1. Large desarmed round net ("tom'kaku") fixed in a totora boat ("balsa").



Photo 2. Half closed fishing system ("kencha") in the mouth of the Desaguadero River.



Photo 3. Fishing technique using a macrophyte assemblage in well form ("pozo"), near Capachica.

especially at the mouths of rivers. They were particularly abundant in the Desaguadero where they were the subject of special expeditions to capture them. The main fishing season lasted two months, at low water level (August to September). Fishermen on the banks of the lake and the Urus descended the Desaguadero as far as Nazakara and Concordia, on "balsas" with two to three men on board, to capture large *Trichomycterus*, especially with spears. The fishermen's children captured small siluroids in the totorales of the lake, with fish traps. The small species (including *T. rivulatus*) were captured in the rivers as well as in nearby high altitude lakes, such as Lake Lagunillas (4250 m).

According to the natives, the hispi disappeared from Puno Bay and the north of the lake as early as 1944–45. In 1950 the fishery ceased to exist. Since this date the "humantos" have become impossible to find and a last collection of this species (*Orestias cuvieri*) was made in 1948 to be sent to the Lima Natural History Museum. Rare individual "bogas" were still captured in the south of the lake in 1952. The "karaches" of the totorales, and especially *Orestias agassii*, have survived better. The most affected by the fishery seems to have been *Orestias albus* ("kano"), but the large siluroid species (*T. dispar* and *T. pictus*) were also no longer captured regularly in the lake after the 1950s.

The photographic plates and figures have been produced from photos by the author and from documents published by Tschopik (1946).

VII.1c. Social and economic aspects of the fisheries

BENJAMIN S. ORLOVE, DOMINIQUE P. LEVIEIL and HUGO P. TREVIÑO

An historical overview

The Lake Titicaca basin has had sizeable human populations for a number of centuries. Archaeological evidence indicates the importance of fishing in the region as far back in the past as 1300–1200 B.C., the earliest phase of the Chiripa culture (Kolata, 1978). Other sources attest to its importance during the periods of major pre-Columbian civilizations, such as Tiahuanaco and Inca, during the period when the basin was incorporated into the Spanish Empire, and in the last two centuries (Leveil, 1987).

In the early decades of this century, lakeshore peasants fished from rafts made of the local totora reed (see Chapter VI.2 of this volume). They used many types of gear, including dragnets (some made of llama wool), dip nets, scoop-nets, basket-traps and spears (Tschopik, 1949). A portion of the fish was eaten fresh, while some was dried and shipped out of the Lake Titicaca basin where it was traded for other foodstuffs.

A number of changes in the last fifty years have altered the fisheries. The rainbow trout (*Salmo gairdneri*) was introduced in 1941; the silverside (*Basilichthys bonariensis*) entered the lake in the 1950s, reportedly after having been introduced into the Río Desaguadero by a Bolivian sport fishing club several years before. The expansion of trout populations led to the establishment of a cannery on the shores of the lake in 1961. In 1965, the peak year, 5 canneries were in operation, with a total catch of 409 tonnes. The trout populations soon declined, due to overfishing, particularly in the mouths of the major rivers, and possibly also due to competition and predation by the silverside (Orlove and Levieil, 1989); by 1970 none of the canneries were still in operation (Everett, 1973).

Although they have closed, the canneries have left their mark on the lake fisheries. The 1960s were a key period of the transition from totora rafts to wooden boats, propelled by sail or by oar; at the beginning of the decade, less than 5% of the craft were boats; by 1970, boats accounted for 33% of the Peruvian craft. This trend continued, with the corresponding figures of 53% for 1976 and 72% for 1980. Although the boats have increased in

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number, they have changed relatively little in design; they are made by local artisans in the Altiplano, and average about 5 meters in length. The percentage of boats, roughly 90%, is even higher on the Bolivian side of the lake. Multifilament nylon gillnets have become the predominant form of fishing gear, and have increased steadily in number (Orlove, 1987). Peruvian, Bolivian and foreign agencies have introduced several fisheries projects, including the raising of trout fingerlings in concrete pens and the cultivation of adult trout in floating cages; these projects have met with very limited success (Orlove and Levieil, 1989). Localised but strong eutrophication has been noted around cage culture projects both in Peru (Acora) and Bolivia (Tiquina).

Spatial characteristics of the Lake Titicaca fisheries

Fairly complete censuses of the Lake Titicaca fishermen are available for 1976 for the Peruvian side of the lake (Bustamante and Trevino, 1976) and for 1980 for Bolivia (Callisaya, 1980). The fishermen are quite dispersed, with nearly all lakeshore villages having at least a few fishermen. The number of villages for which fishermen are reported is 151 in Peru and 199 in Bolivia. The total number of fishermen for those years was estimated at 3040 for Peru and 3216 for Bolivia, though the former figure, collected by a bettertrained team, is probably more accurate than the latter. Fishing is almost exclusively a male activity, although some women occasionally wade into the lake with dipnets, or make short trips to catch fish with gillnets if men are temporarily absent from the household. Resurveys in Peru of 34 communities in 1980 and 38 communities in 1984 indicated a slight possible upward trend in the population of fishermen, since the number of fishermen increased in more communities than it decreased; however, there was considerable variability in the data, so that the 95% confidence interval for the true rate of increase ranged from negative to positive values.

An important aspect of the Lake Titicaca fisheries is the existence of communally-controlled fishing territories. Each lakeshore community systematically excludes individuals who are not members of that community from fishing in the waters adjacent to its lands. In regions where the lake bottom is relatively flat, these territories typically extend several hundred meters beyond the outer edge of the totora beds which may spread several hundreds of meters or even a few kilometers from the shoreline; where the lake bottom is steeper, they reach several kilometers from shore, often up to or beyond the 50-meter isobath (Levieil and Orlove, 1990). Local communities continue to manage these territories despite occasional government opposition (Orlove, 1991).

Organization of fishing activies

Levieil (1979) distinguishes several fisheries in the lake. Firstly, there is a demersal gillnet fishery for native species, which focuses on the black carachi (Orestias agassii), with some other carachi and catfish also being caught. Fishermen set their gillnets with mesh sizes between 38 and 63 mm on the lake bottom, at depths not greater than 30 meters. These fishermen use either rafts or wooden boats. Secondly, there is a pelagic gillnet fishery for trout and silverside, using gillnets of larger mesh (63 to 152 mm), and relying exclusively on wooden boats, some with outboard engines. Thirdly, some fishermen participate simultaneously in both the demersal fishery for native species and the pelagic fishery for introduced species. Finally, there are two small fisheries using other gear; a trawl fishery, also targeting black carachi, operates in the Lago Pequeño, as pairs of boats pull a large trawl behind them, making a number of tows on each fishing trip, and some fishermen harvest ispi (small Orestias) with beach seines or small trawls. In general, fishing trips are of short duration, often only a few hours long and rarely more than overnight (Orlove, 1986). Other than the trawl fishermen, most fishermen operate alone or take along a young male relative as an assistant. Virtually all fishermen also own agricultural fields and livestock, so they coordinate their short trips with their other activities.

Catch

The most complete catch statistics are available from Peru for the twelvemonth period from August 1979 to July 1980. Fifty fishermen, selected randomly from the 1976 census list, kept daily records of their catches. Coverage check surveys conducted by biologists from the Instituto del Mar del Perú provided factors to correct for errors in the self-reported catch data. Using data from the 1976 fishermen census and village surveys in 1980, these data were extended to the entire Peruvian side of the lake.

The estimated total catch for this period is 8160 tonnes. The fishermen average 265 trips per year, and the average catch per trip is almost exactly 10 kg. Analyzing the contribution of different genera to the total catch by weight, it may be noted that *Orestias* alone accounts for just over two-thirds (67.0%). The two introduced genera, each with one species in the lake, are fairly close (*Salmo* at 14.2%, *Basilichthys* at 15.2%), with the remainder made up by the catfish genus *Trichomycterus* at 3.6%. There is relatively little seasonal variation in efforts and yield.

Distribution of fish

The most complete information on distribution of fish is also available for Peru from 1979 and 1980. Most of the catch (83%) is traded in some manner, although a sizeable fraction (17%) is consumed directly by the fishermen, members of their households and their extended networks of kin and friends. This 83% can be divided by the spatial location of the transaction (70% in marketplaces, 13% within villages by door-to-door sale and other forms of nonmarketplace exchange) and by means (67% sold for cash, 16% bartered for foodstuffs). In marketplaces, cash sale predominates (90% of all such distribution, with barter only 10%), but the relative importance is reversed in nonmarketplace exchange (69%, with cash sale 31%). The introduced species are more commonly sold for cash, and the native species more frequently bartered (Orlove, 1986).

Economic returns to fishing

Levieil (1987) provides a detailed account of both the returns to fishing and the costs of fishing, including an analysis of the purchase price, maintenance and depreciation of capital equipment. The average annual net return for fishermen in the 1979-1980 period was S/.311,000, at a time when the conversion rate of the Peruvian sol was S/.250 = US\$1.00. The gillnet fishermen who targeted native species had lower returns, around S/.190,000, and the few who focused exclusively on trout and silverside had much higher returns of S/.675 000. The average hourly return to labor was S/.121, higher than many alternative forms of labor available to lakeshore peasants, such as local wage labor, seasonal wage labor in lowland agriculture, raising cattle, artisanal production and petty commerce. In addition, time-series price data for fish, boats and consumer goods overall suggest that the economic returns to fishing were declining during the 1970s (Orlove, 1986; Levieil, 1987), since the price of Lake Titicaca fish fell relative to the consumer price index while the price of boats rose. Returns by weight to fishing effort probably did not decline, since catch levels appear to be well below the upper limits of sustainability (Levieil, 1987); had these levels been closer to such limits, there might well have been diminishing marginal returns to increases in fishing effort. (The decline in trout in the 1960s seems exceptional, driven both by the incentives from the commercial canneries and by the vulnerability of that introduced species, which concentrates at the mouths of a few major rivers and swims up them prior to spawning). However, the overall contraction of the Peruvian economy led to declines in returns to other forms of labor available to peasants in the lake area, such as commerce (Appleby, 1982) and wage labor (Figueroa, 1984). Fishing has thus remained an attractive form of earning income and obtaining foodstuffs for the inhabitants of the region. This evidence indicates that average hourly returns to labor

remained higher in fishing than in other activities available to shore dwellers throughout the 1970s and early 1980s. It demonstrates that economic overexploitation was constrained during this period (Levieil, 1987).

Granted the higher rates of return of time spent in fishing than in other activities, it is logical to enquire into the reasons that have prevented the expansion of the fisheries. One key factor is the system of the communal fishing territories, which has prevented individuals who are not members of lakeshore communities from fishing. In addition, it is difficult for prospective fishermen to acquire the necessary skills to enter the trade; of a sample of 112 fishermen interviewed in 1981, slightly over 90% were taught to fish by relatives; of this fraction, over 75% learned from their fathers or brothers.

These data suggest that the number of fishermen will grow slowly, if at all, permitting the fishermen to continue to invest in boats and nets and to receive higher returns for their labor than most of the inhabitants of the region. It seems likely that the total catch will remain at levels that are profitable for the fishermen and sustainable for the lake ecosystem (Levieil, 1987).

The one major threat to the fish populations and the fishermen alike would be the development of an urban-based capitalized fishing fleet, which would use larger boats and more complex gear such as seines and large trawls, possibly targeting the smaller *Orestias* species or the silverside. Such a fishery could easily lead to overfishing to recoup initial investment, bringing the "boom and bust" cycle found in numerous other fisheries around the world. It would deplete the ecological resources of the lake and the livelihood of thousands of lakeshore dwellers, as well as reducing an important source of protein and vitamin A in local diets.

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VII.1d. The socio-economic importance of macrophytes

DOMINIQUE P. LEVIEIL and BENJAMIN S. ORLOVE*

Lake Titicaca shoredwellers use aquatic macrophytes as food for their livestock and for themselves, as material for handicrafts, boatbuilding and roofing and as fertilizer for agriculture. Each type of macrophyte, each part of the plant at each age or stage of its development, serves a particular purpose. However, little is known about the socio-economic importance of this resource, or of its various uses and contribution to the local economy.

These macrophytes are found in the lake from the shoreline down to about nine metres depth (Collot 1981), wherever the slope is not excessive and the bottom conditions permit their establishment. However, technical reasons prevent shoredwellers, who are poorly equipped, from harvesting them in waters deeper than five metres.

In this chapter the five major groups of macrophytes that shoredwellers identify are dealt with in turn: 'llachu', 'totora verde' or 'totora tierna' (green or tender totora), 'totora amarilla' or 'totora madura' (yellow or mature totora), 'sacca' or 'siphi' (the roots or rhizome of the totora) and 'chullo' (the white base of the green stalk).

Llachu

The term "llachu" includes several species of macrophytes, the main three being *Elodea potamogeton* ("Yana" or "Chancco llachu"), *Myriophyllum elatinoides* ("Hinojo" or "Waca llachu") and *Potamogeton strictus* ("Huichi huichi" or "Chilka llachu") (Ramirez and Vargas 1974). Llachu is used mainly as livestock fodder and sometimes for handicrafts (e.g. mattress stuffing), or as fuel (e.g. for the kitchen hearths of the Urus).

Livestock graze directly on llachu growing in water less than one metre deep from July to February, when there is no grazing left in the countryside. Shoredwellers also gather the llachu by hand with a sickle or other sharp

*This contribution is dedicated of the memory of Padre Conrado (Konrad Kretz) from Arapa, whose interest for his parish spurred the field research from which this paper results.

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instrument, wading into the water up to their waists. They cut the llachu almost to the bottom and pile up their harvest at the shoreline where the livestock come to feed. The cutting is often performed from a wooden boat or a balsa, (i.e. a reed raft), using a long pole, the "quelina", at the end of which a knife is tied. Although llachu is a heavy, water-logged product, some people carry loads of it to their livestock, up to an hour away from the lakeside.

Llachu harvesting is open to all shoredwellers, since private property or exclusive rights over individual plots of llachu are not customarily recognized. However, the borders between neighbouring shore communities do extend into the lake, thus dividing llachu beds into zones of communal use (Levieil 1987). Selling and bartering, transplanting or sowing of llachu do not seem to be practised, however.

Shoredwellers consider llachu as one of the best fodders for their livestock, which have a marked preference for *Elodea*. Available studies corroborate shoredwellers' assessment of the nutritive value of llachu for meat and dairy production (Ramirez and Vargas 1974, Collot 1981).

The lack of quantitative information on the extraction and consumption of llachu in all the available studies precludes even the crudest evaluation of the total volume extracted. However, emphasis must be put on the contribution of this little-known resource to the economy of shore districts with access rights to large llachu beds, such as those of Huatta and Coata in Puno Bay, which specialize in cheese production (Sanchez 1983).

Totora verde

"Totora verde" or "totora tierna" (green or tender totora) is harvested in much the same way as llachu, except that livestock is never allowed to enter totora beds. An individual harvester is allowed to cut a number of pichus (the quantity of totora which can be carried between the arms and chest), which are then dragged to the livestock. But stalks may not be cut more than 50 cm from the surface and never in the rainy season when the water becomes too turbid, although totora grows all the year round, possibly with less growth during the rainy season. The stalk requires a little more than one year to reach its average height of 3.8 metres. Cutting improves the yield of the plant and promotes an increase in the density of totora beds (Collot 1981).

Once cut, the totora can be piled up in the harvester's craft or simply on the surface of the water (due to its natural buoyancy) in rafts called "tangas" or "marayas". Marayas can attain an impressive size when groups of harvesters come together in search of totora in the Urus or Kapi sector of Puno Bay. Marayas of 400 pichus (about 5 metric tonnes of totora verde) have been observed sailing over distances of more than 20 km. To transport the totora over greater distances (up to 50 km) the people of Socca, Titilaca and Santa Rosa de Yanaque use wooden sailing boats about 10 metres long, able to carry about 150 pichus, and which are faster and easier to handle than the marayas.

When there is still some grazing left for the livestock, shoredwellers keep their animals on the pastures and use their donkeys to bring them totora from the lake shore. A donkey can carry five or six pichus and a man one or two pichus over distances of several kilometres. Farmers often mix the totora which they give their livestock with other feed (llachu, hay, etc.) to introduce some variety in their diets and to maximise food consumption and thus the fattening of their animals. At the end of the dry season (November, December) and in years of prolonged drought, however, llachu and totora verde are the only fodders available. The totora verde thus becomes a critical food source in years of severe drought, not only for the livestock of the lake shore inhabitants, but also for the livestock of the Cooperatives and ranchers of the rest of the Altiplano.

The exploitation of totora, unlike that of llachu, is severely restricted. Most totora plots are privately owned. Each plot of totora has an owner who cares for it as he would a permanent pasture. Cattle can never be allowed to actually enter the totora beds because the plots are not fenced. Totora plots can be sold or exchanged between shoredwellers and divided among inheritors of both sexes. In many cases this process results in the breaking up of totora beds into micro-plots.

Totora can also be bartered or sold by pichu once it is cut. Shoredwellers whose supply of totora is insufficient may also approach those who own abundant totora and propose an arrangement in which the former cut and remove the latters' totora in exchange for a payment of goods (food, coca, alcohol) or cash. This relationship is called rental ("arint'asina" in Aymara, "arindakuy" in Quechua), thus acknowledging the ownership of the totora plots.

The large totora beds of Puno Bay and the Ramis delta in the North Lake are now included in the Titicaca National Reserve. In theory they are administered as a forest resource by the Ministry of Agriculture, which grants licences specifying the quantity that can be harvested and the zone where the harvesting must take place (Orlove, 1991). In practice, however, the exploitation of totora beds is controlled by the inhabitants of the neighbouring communities. Harvesters have to compensate them with food, coca, household implements (spades, stone or clay utensils), or with money for the totora collected.

Elsewhere, shore communities hold assemblies to which all households send representatives in order to determine the specific months of the year and the days in the week on which cutting is allowed. Neighbouring communities coordinate their schedules so that they cut on different days, thus facilitating the surveillance of the totora beds and preventing the incursion of outsiders. Many communities also appoint one or more officials, the "vigilantes del lago", who have the responsibility for overseeing the totora beds during a one-year term.

Although some totora beds may be of natural origin, the majority have

been planted or transplanted by local shoredwellers (Chirapo 1982, Collot, 1981, Hickman, 1963). Methods of sowing totora are adapted to the circumstances and depth of the zones where it is to be planted: a spade in shallow water, a pole further out. Sometimes small stones are tied to clumps of totora with roots, to send them to the bottom. Advantage is also taken of natural seedings. When seeds transported by wind or water reach the shoreline, wave action makes it easier for them to penetrate the earth and mix in with the decaying organic waste. This process requires no human intervention, although cultivation of the land along the shoreline facilitates it.

Totora verde is a good fodder due to its digestibility and protein content (Oyanguren and Tapia 1971), although its high moisture content does not allow the ingestion of nutrients in their most adequate form (Tapia 1971). Shoredwellers consider that totora has less food value than llachu, but that it is easier to harvest and to bring to their cattle.

Collot (1981) estimated the consumption of totora verde per head of cattle at between one and two pichus (or amoros) per day i.e. between 9 and 26 kilos per day. This led him to conclude that actual consumption of llachu and totora verde in Lago Pequeno is considerably smaller than net production would theoretically allow. Applying the same methodology and his data on net production of totora to Puno Bay, we estimated that the net production of totora in Puno Bay would theoretically feed 265 000 head of livestock and that of llachu more than 2 million head. However, this does not take into account the practical feasibility of such a rate of harvest and the limitation on access to totora and llachu beds (Levieil 1987).

Levieil and Goyzueta (1984) estimated the present extraction of totora verde form Puno Bay at five million pichus or 50 000 metric tonnes. To reach these figures they multiplied the average number of head of livestock (cattle, sheep, pigs, cameloids and horses) per shore-dwelling family (according to species), and the total number of shore-dwelling families with access to totora.

A study (Plan Nacional Regional del Dessarolla del Sur del Peru) reported in the late 1950s on the early stages of integration of the Peruvian Altiplano into a livestock market covering much of southern Peru. Calves were brought from the department of Cusco and the higher parts of the department of Puno to the lakeshore region, where they were fattened and sold to buyers from the large cities of Arequipa and Lima. This economy has since expanded. It is thus quite plausible that the demand for green totora has in fact grown considerably in the last 40 years.

Yellow totora

The emergent portions of the totora stalks are subject to the desiccating action of the sun and wind, which causes them to turn yellow. Freezing causes this colour to change to ash grey, indicating the frailty of the stalk. People who harvest totora for handicrafts look for the tall "totora amarilla" or "totora madura" (yellow or mature totora) as it is the most appropriate contruction material for balsas, mattresses or "quesanas", mats or "estera" and for roofing purposes. The artisans from Chimu and Urus-Chulluni who have specialized in the construction and sale of balsas and quesanas go almost weekly to Kapi for their supply of totora amarilla, bringing back marayas of 75 to 100 pichus, weighing about 15 kilos each. The totora is then left to dry and harden in the sun for one or two weeks.

In the past, good totora amarilla was found in many locations, but over the last decades, due possibly to the increased demand for totora verde, balsa and quesana builders have had to go further to provision themselves. Fishermen also complain that due to lack of good quality totora amarilla, the serviceable life of their reed boats or balsas has shortened from a year to less than six months.

The extraction of totora amarilla for handicraft purposes may be crudely estimated, thanks to a number of studies in which the daily production of various artifacts and the quantitative requirements in totora for this production are reported.

Gavancho's (1975) study of quesana production (thick totora mattresses) in the community of Chimu, close to Puno, shows that 128 families produced between 10 and 15 quesanas per day, making three quesanas with each pichu of totora amarilla. This implies a daily extraction of totora of 375 to 624 pichus and, assuming that Chimu families dedicate at most 200 days a year to this activity, an annual extraction of 75 000 to 125 000 pichus.

Calancho (1984) reported that 91.2% of the inhabitants of the Urus Islands dedicate themselves to totora extraction, and 82% to its use for artisanal purposes. He estimated the extraction of totora for the whole community at some 1 360 pichus per month or 16 320 pichus a year.

In 1976 Bustamante and Treviño estimated the number of balsas along the Peruvian shoreline of the lake. Given that the construction of each balsa requires about 30 pichus and that a balsa lasts about six months, 35 000 pichus of totora were used in the construction of fishing balsas in the year 1976.

Given that within Puno Bay, the communities of Chimu and Urus are the major harvesters of totora amarilla for artisanal purposes, we estimate that a minimum of 200 000 pichus of totora amarilla weighing more than 2 000 metric tonnes are extracted annually just from this part of the lake. These are mere indications of the considerable importance of totora amarilla to the local community, to which the extraction for roofing purposes should be added. Although the number of roofs made with totora decreases every year, each one still requires between 200 and 300 pichus.

Totora roots

Lake Titicaca shoredwellers distinguish the tender rhizome or sacca from the mature rhizome or siphi (Gavancho 1975). People eat them both, as well as
the stalk base or chullo (the last 30 to 50 cm), because of their significant carbohydrate content, at the end of the dry season when little is left from the previous harvests (Manrique and Rivera, 1982).

The mixture of mud, rhizomes and decaying organic matter forms the "kille" or "quili", with properties similar to those of a sponge. When it is dry it is very light and floats. The floating islands of the Urus are made of great chunks of kille which the inhabitants have gathered together and to which they continue to add small pieces. Periodically they throw totora amarilla onto the kille so that its surface remains dry. Small killes carried away by the wind are hauled by fishermen to their portion of the shoreline, cut into pieces and used as fertilizer.

Conclusions

To sum up, aquatic macrophytes contribute significantly to the economy of Lake Titicaca shore communities in many different ways. First and foremost, llachu and totora verde are the backbone of milk and meat production on this part of the Altiplano. They also provide a critical back-up during calamitous droughts, such as the one in 1983. Secondly, totora amarilla is one of the few resources that local people may use for useful and original handicraft production. Thirdly, as environments where many fish and wildfowl species can reproduce, totora and llachu beds contribute to the productivity of Lake Titicaca. They provide a substrate and protection for their eggs and later their young, since juvenile fish and birds are much more vulnerable to the rigours of climate and predation in zones without macrophyte growth. Birds, particularly ducks, also consume some species of macrophytes and almost all feed on the arthropods that live in the llachu and totora beds. Just like the macrophytes themselves, the fish and bird fauna contribute to the economy and diet of the shoreline communities. Fourthly, they enhance the ecological and aesthetic value of Lake Titicaca and thus its tourist interest. Finally, they protect fishing boats and the shoreline itself from destructive wave action.

For all these reasons Lake Titicaca macrophytes represent a resource of exceptional economic and social value for the Altiplano of Peru and Bolivia, which must be protected from excessive exploitation and environmental degradation.

Plate 6. Exploitation of aquatic macrophytes in the Lake Titicaca. Above: harvesting of a "totora feld" along the shoreline of the Puno Bay. Center: carriage of numerous totora "pinchus" in the Puno Bay (Lago Grande). (Photos Dominique Levieil.) Down: harvesting of the "Llachu" from a boat in the Achacachi Bay (Lago Grande). Three macrophytes species are the main component of the Llachu: *Myriophyllum elatinoides*, *Elodea potamogeton* and *Potamogeton strictus*. (Photo Claude Dejoux.)





VII.1e. Influence of the lake on littoral agriculture

JEAN VACHER, EMMANUEL BRASIER DE THUY and MAXIMO LIBERMAN

On approaching the shores of Lake Titicaca a marked change in agricultural practices is evident to any visitor. As one approaches the lake, the population density rises (often to more than 100 inhabitants per km² in contrast to 30 further away). Crops grow well and mature 2 to 3 months earlier than on the rest of the Altiplano. Herds of cattle graze in the shallow waters of the lake or on the shore where their diet consists mostly of aquatic plants. This very obvious influence of Lake Titicaca on agricultural activity drove the fathers of the first agricultural tax in Bolivia to divide the altiplano into two zones: one that benefited from the lake's influence, and one that did not. It is easy to prove the existence of two different types of agriculture, but its chapter try to identify the major factors related to the lake which modify the agriculture, and to evaluate their importance, their range of influence and their consequent effects on agriculture.

The study area consists of the Bolivian shore of Huinaimarca. The results that we present are neither exhaustive nor completely generalised, but they will allow, we hope, a better understanding of how agriculture functions on the shores of Lake Titicaca.

The influence of Lake Titicaca on certain important agroecological factors

We have mainly considered the influence of the lake on climate and soil; determining factors for agriculture as well as for the production of macrophyte fodder.

Climate

The major limiting factors for agriculture on the altiplano are incontestably drought and frost (Morlon, 1987; Vacher et al. 1987). The ability to grow maize and other crops for almost ten months a year on the shores of the

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Fig. 1. Map showing localites of meterological stations. Scale 1/1 500 000.

lake testify to the superior climatic conditions in this zone compared to elsewhere on the altiplano. We will now try to analyse the influence of the lake on risks of drought and frost, using meteorological information from the National Service of Meteorology and Hydrology with data obtained at stations at various distances from the lake.

Risks of drought

Four stations were chosen: Copacabana, Huatajata, Huarina and Viacha (Fig. 1). The stations of Copacabana and Huatajata are located on the lake shore, Huarina approximately one kilometre from the lake and Viacha 60 km from the lake. This last station is representative of the agroclimatic zone of the north Altiplano (Vacher and Imaña 1989). We will compare the amount of precipitation at each station, and then, with the help of a simple hydrological balance model, evaluate the risks of drought.

Mean annual precipitation and its distribution over the year for each station are given in Fig. 2 and Table 1; these show that:

- The lake has a very marked influence on the total annual precipitation



Fig. 2. Seasonal distribution of average monthly rainfall at four stations on the Bolivian Altiplano.

(200 mm more for the lake stations) and on its year to year and monthly regularity.

- This influence is very restricted since Huarina, located 1 km from the lake, has the same annual precipitation as Viacha.
- The difference between the stations on the lake and the others occurs essentially during the December-February rainy season; this does not however explain the two months' difference in sowing date between the two areas.

By using a hydrological balance model, taking into account soil behaviour (Lhomme and Eldin 1983, Atteia *et al.* 1988), hydrological deficits for potatoes have been calculated for each ten-day period at each of the four stations (Fig. 3). To make the analysis of the influence of climate easier we have considered only one soil type and one germination date (early December). Evapotranspiration (ETP) was estimated from a Penman type formula, adapted for the altiplano (Vacher *et al.*, 1989). The reduction in the partial hydrological deficit for lake stations for each ten-day period is very great,

Sites	Annual mean (mm)	Coef. var.	Prob. 75 %	Prob.25 %
Copacabana	893	0.20	762	1025
Huatajata	862	0.16	751	937
Huarina	616	0.26	501	683
Viacha	679	0.24	526	788

Table 1. Comparison of total annual rainfall at some stations on the Altiplano

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Fig. 3. Average hydrological deficits at four stations on the Bolivian Altiplano.

particularly in mid-February and early April, during tuber growth, a determining period for final production.

Risk of frost

Total losses of crops due to frost are regularly mentioned in reports ever since Colonial times and are also recalled by peasants. A frost risk study for potato cultivation has shown that the average frost-free period ranges from 100 days on the central altiplano to 140 days on the northern altiplano, thus highlighting the limiting nature of this factor for agriculture (Le Tacon, 1989; Vacher and Imaña, 1989). The probabilities of occurrence of frosts affecting potatoes at Copacabana, Huarina, Viacha and Patacamaya (representative of the central altiplano) are shown in Fig. 4. The probability is very high for Viacha, Huarina and Patacamaya, but is almost non-existent at Copacabana; the average frost-free is 320 days at this station as against 150 days for the other stations, so agriculture is possible almost the whole year round on the shores of the lake. However, this influence is limited to the narrow area of high precipitation. In the future, analysis of satellite images in the infrared band should allow us to localise precisely the influence of the lake on minimum temperatures (for frost risks on the lake shores in Peru, see Morlon 1978, 1979 and 1987).



Fig. 4. Frost risks for potato cultivation at four stations on the Bolivian Altiplano.

Soils

The wide fluctuations in the level of Lake Titicaca (Wirrman, 1987; Mourguiart, 1987) have led to the formation of deep soils. Along the shore of the lake another important factor for the irrigation of crops is the shallowness of the water table (Liberman, 1987). The influence of the lake on the physical, trophic and hydrological features of the soils can be determined from the analysis of the limited information in the literature and the results of experiments carried out during the Program for the Study of the Agroclimate of the Bolivian Altiplano.

The physical, trophic and hydrological features of the soil formed from lacustrine deposit (Belen, located 2.0 km from the lake shore), a typical soil from the northern altiplano (Viacha) and the soil of the central altiplano (Patacamaya) are shown in Table 2. The results refer to the top 30 cm of soil underneath pasture land and demonstrate the higher agricultural value of the alluvial soils. The texture is finer, the organic, total nitrogen and potassium contents are twice as high and assimilable phosphorus is five times higher. The presence of a compact clay horizon at Viacha and of a stone

Sites	Clay (%)	Silt (%)	Sand (%)	pН	ОМ	N tot. (%)	P. ass. (ppm)	K. bot. (meq)
Belén	31	40	29	7.4	3.4	0.16	32	0.53
Viacha	20	29	51	7.2	1.9	0.09	5.3	0.25
Patacamaya	15	26	59	7	1.4	0.06	8.3	0.14

Table 2. Soil characteristics at scientific stations at varying distance from Lake Titicaca

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horizon at Patacamaya at a depth of 35 cm limits root penetration and rising capillary action reducing water availability in the cultivated area (Vacher *et al.*, 1988). In the areas closest to the lake shores (under the 50 m contour), the soil is always wet since the water table lies at a depth of only 30 to 50 cm (Cochrane, 1973; Liberman, 1987). The presence of abundant soil water allows for fast plant growth and germination, even during drought. Occasionally, the water table reaches the surface over extensive areas; agriculture in such areas is carried out by the almost abandoned ditch and hummock system which is in the process of rehabilitation in Peru where it is known as "Waru waru" and in Bolivia where it is called "Suka Kollos" (Erickson, 1987; Garaycochea, 1987; Morlon, 1978, 1979, 1987).

Production of macrophyte forage

The main macrophytes used for cattle feeding are "totora" (Schoenoplectus tatora) "chanco" (Myriophyllum elatinoides) and "hancha" (Elodea potamogeton). Totora is the most widely used forage plant; it is a cyperaceous plant that generally reaches a height of 4 m, two thirds of this being under water. It is usually cut two to three times a year within limited plots that the peasants maintain and resow. The average dry biomass production at Huiñaimarca has been estimated at 132 000 tonnes and the annual production at about 5.5 tonnes per hectare (Collot et al., 1983). However, a great increase in the lake level in 1986 produced a major decline in totora production due to asphyxia and competition with Chara; this had serious consequences for cattle feeding in the lake area. Forage macrophytes from the lake represent a very important food supply for cattle, with a high production per hectare allowing the existence of cattle herds with very little pasture, even by farmers with very little land.

Some general features of agriculture on the shores of Lake Titicaca

We have already described how the present lake reduces the risks of drought, almost removes the risk of frost and provides better agricultural soils and forage production. What are the consequences on agriculture?

Plate 7. Typical land activity along the Lake Titicaca shoreline. Above: Sheep and pigs grazing in felds after harvesting. Cows are mainly feeded with totora or other macrophytes. Agriculture is little mecanized and wood ploughs tracted by oxen are still used. Center: traditional terraces are used everywhere along the shores in shear areas. Agricultural practices respect rotation cycles with potatoes, corn, beans or quinua. Down: corn (wheat, oats, maize) grow very close to the extention limit of water, mainly in the large lowland areas arround the bays. (Photos Claude Dejoux.)



One of the main features of this favoured agricultural area is the greatly increased density of cultivation. The total area per farmer ranges from 0.6 to 3 hectares (Brasier de Thuy, 1989; Liberman, 1987; Urioste, 1977), made up of 12 to 20 plots. This is true for both the Bolivian and Peruvian areas (Montoya *et al.*, 1987). In contrast the cultivated area per farmer varies from 15 to 60 hectares for the rest of the altiplano. This reduction in land holding is a determining factor for cultivation and cattle rearing systems; peasants usually only possess 2 to 3 plots of less than 1000 m^2 area on the shores of Lake Titicaca.

Good edaphic and agroclimatic conditions promote early sowing, the absence of fallow land and higher productivity. The main crops are, as on the rest of the altiplano, potatoes, barley, beans and "quinoa" (a type of buckwheat). The sowing periods are at the end of July for beans and mid-September for potatoes, which provides crops at the beginning of January when selling prices are still high. The most common rotation is potatoes followed by beans, cereals or quinoa, followed by a forage crop, usually barley. There is no fallow stage, whereas on the rest of the altiplano land is usually left fallow for more than 6 years. Cultivation of beans and onions has been increasing for some years now, but according to peasants disease and decreased soil fertility have appeared.

The retention of soil fertility is currently a major agricultural problem on the lake shores. The reduced size of pastures and of aquatic macrophyte plots per farmer, added to the large decrease in totora production since 1986, limits the numbers of livestock. Each family now only owns 2 to 4 cattle (usually cows) and 3 to 8 sheep, which do not provide enough manure or animal traction. The intensity of agricultural exploitation is not accompanied with adequate restitution of organic and mineral nutrients. Chemical fertilizers are scarce and incomes are often too low to purchase sufficient quantities. The lack of draught animals results in farmers renting tractors at a very high cost.

The existence of mimimal climatic risks and good edaphic conditions is reflected in an intensification of agricultural systems on the lake shores, which is aggravated by the division of land holdings into small plots. Peasants benefit from the higher and more consistent agricultural production compared to any other part of the altiplano, although their agriculture is more vulnerable and fragile. In fact, each farmer only has a reduced area of cultivated land and there is no land for cattle grazing nor totora enough to feed a sufficiently large herd to provide good ploughing and restitution of nutrients to the arable land, or to provide a reserve capital during lean years. The recent flood on the lake shore was particularly catastrophic for peasants who saw their most productive land disappear and cattle production drop.

This disaster only emphasises the tendency for multiple activity, and although it would appear paradoxical, farmers in the area where the agricultural conditions are extremely suitable have more diversified activities (education, fishing, handicrafts, etc.) than in other areas.

Conclusions

It is evident that Lake Titicaca has a clear beneficial influence on the agroclimate and local edaphic conditions and also provides a considerable production of "aquatic" forage of about 8 tonnes of dry material per hectare. The influence of the water body and its heat content considerably decreases the risk of droughts and practically eliminates the risk of overnight frost.

Taking into account the further physical and trophic advantages of the soils derived from lacustrine deposits, agricultural conditions are highly favourable along the shores of the lake, but high agricultural productivity is limited to a narrow band. The existence of good edaphic conditions leads however to a great reduction in the size of agricultural holdings and the division into multiple plots. The area useable for cattle rearing is very reduced and the cultivation of arable plots is very intensive. These conditions produce fragile soils, and do not allow for adequate restitution of nutrients and organic matter. In addition, the limited numbers of cattle reduce the possibilities of using natural manure and compels the farmers to resort to a certain level of mechanization, that further reduces their income. All these led to multiple activity, a tendency reinforced by the recent flooding of Lake Titicaca.

References of chapter VII.1

- Anon., 1575. Tasa de la visita general de Francisco de Toledo. Univ. Mayor S. Marcos. Lima, 341 p.
- APPLEBY (G.), 1982. Price policy and peasant production in Peru: regional distribution during inflation. Meetings of the American Association for the Advancement of Science, Washington, 14 p.
- ATTEIA (O.), VACHER (J.), ELDIN (M.), 1988. Analyse des risques de sécheresse à partir d'un modèle simple de bilan hydrique. ORSTOM. La Paz, 13 p., multigr.
- BARZANA (A.), 1594. Vocabulario de la lengua pukina. *In*: La langue Pukina, La Grasserie (R. de) ed., 1884. Paris, Maison neuve, 30 p.
- BERTONIO (L.), 1612–1984. Vocabulario de la lengua aymara. CERES.IFEA.MUSEF, La Paz: 387 p.
- BINFORD (M.W.), BRENNER (M.), 1989. Resultados de Estudios de limnología en los ecosistemas de Tiwanaku. *In*: Primer informe de resultados del proyecto Wilajawira. Ed. Universidad de Chicayo, Instituto nacional de arqueología de Bolivia, La Paz: 213–241.
- BIRD (J.B.), 1946. The historic inhabitants of the North Chilean Coast. In: Handbook of South American Indians, vol. 2. Bur. of Amer. Ethnol. Bull., 143: Smithsonian Institution, Washington, D.C.: 595–597.
- BOUYSSE-CASSAGNE (T.), 1978. L'espace aymara Urco et Uma. Annales F.S.C., 5, 443 p.
- BOUYSSE-CASSAGNE (T.), 1987. La identidad aymara: una aproximación histórica. Hisbol-IFEA, La Paz, 228 p.
- BOUYSSE-CASSAGNE (T.), 1988. Lluvias y cenizas. Dos Pachacuti en la Historia. Hisbol, La Paz, 227 p.
- BOUYSSE-CASSAGNE (T.), 1991. Le lac Titicaca: histoire perdue d'une mer intérieure. *Bull. IFEA* (in press).
- BRASIER de THUY (E.), 1989. Encuentro Achocalla ORSTOM.SEMTA y campesinos. OR-STOM, La Paz, 95 p., multigr.
- BRAY (W.), 1990. Agricultural renascence in the high Andes. Nat., vol. 345, p. 385.
- BROWMAN (D.), 1978a. The temple of Chiripa. 3° Congreso Peruano, El hombre y la cultura andina. Matos ed., Lima, 888 p.
- BROWMAN (D.), 1978b. Towards the development of Tiwanaku State. Advance in Andean Archeology. Mouton ed., La Haye: 327–349.
- BROWMAN (D.), 1985. Cultural primacy of Tiwanaku in the development of later peruvian states. Dial. And., 4: 59-71.
- BUSTAMANTE (E.), TREVIÑO (H.P.), 1976. Descripción de las pesquerías en el Lago Titicaca. Inst. Mar Peru, Puno, 74 p., multigr.
- CALANCHO (E.), 1984. Economía de los Uros del Titicaca. Tesis Ing. UNTA, Puno, 73 p., multigr.
- CALLISAYA (R.), 1980. Informe preliminar del censo de pescadores bolivianos. Proyecto Especial de Estudios Ecológicos y Humanos, La Paz, Bolivia, 44 p.
- CHIRAPO (E.), 1982. Origen y cambios en la producción y consumo en la nacionalidad Aymara: los Yanaques. IIDSA Publ. no. 2, UNTA, Puno, 52 p.
- CIEZA de LEON (P.), 1553-1984. Crónica del Perú. Ed. Historia 16, Madrid, 414 p.
- COCHRANE (T.C.), 1973. El potencial agrícola del uso de la tierra en Bolivia. Ed. Don Bosco. La Paz, 826 p.
- COLLOT (D.), 1981. Les macrophytes de quelques lacs andins (lac Titicaca, lac Poopo, lacs de vallées d'Hichu Kkota et d'Ovejhuyo). ORSTOM. La Paz, 115 p., multigr.
- COLLOT (D.), KORIMAYA (F.), GARCIA (E.), 1983. Répartitions, biomasses et productions des macrophytes du lac Titicaca. *Rev. Hydrobiol. trop.*, 16 (3): 241-262.
- DENEVAN (W.), 1963. Additional comments on the earthworks of Mojos in north-east Bolivia. *Am. Antiq.*, 28: 540–544.
- DENEVAN (W.), 1970. Aboriginal drained field cultivation in the Americas. *Science*, 169: 647-653.

- ERIKSON (C.), 1984. Applications of Prehistoric Andean Technology: Experiments in raised field agriculture. Huata, Lake Titicaca: 1981–1982. Prehistoric Intensive Agriculture in the Tropics, Oxford. I. S. Farrington ed., B.A.R. International Series, no. 232.
- ERICKSON (C.L.), 1987. Modelos prehistóricos para el desarrollo agrícola, los camellones de Illpa, Puno. 5° Congreso Internacional de Sistemas Agropecuarios Andinos. Anales: 317-318.
- EVERETT (G.V.), 1973. The rainbow trout Salmo gairdneri (Rich.) fishery of Lake Titicaca. J. Fish. Biol., (5): 429-440.
- FIGUEROA (A.), 1984. Capitalist development and the peasant economy in Peru. Cambridge University Press, Cambridge. 142 p.
- GARAYCOCHEA (I.), 1987. Los camellones y la recuperación de la frontera agrícola en el Altiplano puneño. 5° Congreso Internacional de Sistemas Agropecuarios Andinos. Anales: 318–319.
- GAVANCHO (M.), 1975. La totora base de la economía de Chimu y su repercusión en la escuela. Tesis Esc. Sup. mixt. Puno, 30 p.
- GIRAULT (L.), 1984. Kallawaya. Guérisseurs itinérants des Andes. Mem. ORSTOM, 106, Paris, 669 p.
- GOLAND (C.), 1988. A preliminary report of the Cuyo Cuyo Archeological Survey. Mus. Anthrop. Michigan, no. 48109, 66 p., multigr.
- HICKMAN (J.M.), 1963. The Aymaras of Chinchera, Peru: persistence and change in a bicultural context. Ph. D. Thesis Cornell Univ.
- HYSLOP (J.), 1976. An archaeological investigation of the Lupaca kingdom and its origins. Thesis Univ. Brit. Columbia, Vancouver, 449 p., multigr.
- JULIEN (K.), 1983. Hatuncolla: a view of Inca rule from the Lake Titicaca. Univ. California Press, Vol. 15: 185-231.
- KOLATA (A.), 1978. The south Andes. In: Ancient South Americans. Jennings ed. Freeman, San Francisco: 241–285.
- KOLATA (A.), 1983. The South Andes. In: Ancient South Americans. J. D. Jennings ed. Freeman and Co., San Francisco: 241–286.
- KOLATA (A.), 1985. El papel de la agricultura intensiva en la economía política del estado de Tiwanaku. *Dial. And.*, 4: 35.
- KOLATA (A.), 1989. La tecnología y organización de la producción agrícola en el estado de Tiwanaku. *In*: Primer informe de resultados del proyecto Wilajawira. Ed. Universidad de Chicayo, Instituto nacional de arqueología de Bolivia, La Paz: 13–40.
- LE TACON (P.), 1989. Manifestation des risques climatiques à l'échelle de l'exploitation agricole, conséquences sur les pratiques paysannes. Cas de l'Altiplano bolivien. Mém. DAA. 130 p., multigr.
- LEVIEIL (D.), 1987. Territorial use-rights in fishing (TURFs) and the management of smallscale fisheries: the case of Lake Titicaca (Peru). Ph. D. Thesis, Univ. Brit. Columbia, Vancouver, 208 p.
- LEVIEIL (D.), GOYZUETA (G.), 1984. Evaluación de la extracción de totora para fines de subsistencia en la Reserva Nacional del Titicaca, sector Puno. CENFOR-Puno, Min. Agrie. Alim. Puno, 24 p., multigr.
- LEVIEIL (D.), ORLOVE (B.S.), 1990. Local control of aquatic resources: community and ecology in Lake Titicaca, Peru. Amer. Anthrop., 92 (2): 18–38.
- LHOMME (J.P.), ELDIN (M.), 1985. Un modèle agroclimatique de simulation du bilan hydrique des cultures. *In*: Les besoins en eau des cultures, CIID.INRA Paris: 841-852.
- LIBERMAN (C.M.), 1987. Uso de la tierra en el Altiplano Norte de Bolivia, como base para la evaluación del impacto ambiental de un proyecto de desarrollo rural. *Rev. Agric. Subtrop. e Trop.*, 81 (1.2): 207–235.
- LIZARRAGA (Fray R. de), 1605–1987. Descripción breve de toda la tierra del Perú, Tucumán, Río de la Plata y Chile. Crónicas de América, Ed. Historia 16, Madrid, 478 p.
- LUMBRERAS (L.G.), 1981. Arqueología de la América andina. Lima, Milla Batres ed., 268 p.

- MANRIQUE (J.), RIVERA (P.), 1982. Análisis bromatológico del "chullo" de totora. Problemática Sur Andina (2): 91-100.
- METRAUX (A.), 1967. Religion et magie indiennes d'Amérique du Sud. Paris, Gallimard ed., 415 p.
- MONTOYA (B.), MORLON (P.), CHANNER (S.), 1986. Los sistemas agropastoriles andinos: un estudio de caso de cinco familias del Altiplano peruano. 5° Congreso Internacional de Sistemas Agropecuarios Andinos. Anales: 450–473.
- MORLON (P.), 1978. Elementos de descripción frecuencial de las heladas. Estudio agroclimatológico de la cuenca del Lago Titicaca. ACDI. Min. Agr. Alim. Puno, 41 p., multigr.
- MORLON (P.), 1979. Apuntes sobre el problema agronómico de las heladas. Estudio agroclimatológico de la cuenca del Lago Titicaca. ACDI. Min. Agric. Alim. Puno, 54 p., multigr.
- MORLON (P.), 1981. Questions sur l'agriculture de l'altiplano péruvien. CNRS-NSF L'homme et son environnement a haute altitude. Paris: 108–113.
- MORLON (P.), 1987. Del clima a la comercialización: un riesgo puede ocultar otro. Ejemplos sobre el Altiplano peruano. Agricultura y Sociedad, 45: 133-182.
- MORUA (Fray M. de), 1590. Historia y origen real de los reyes Incas del Perú. Instit. Gonzalo Fernandez de Oviedo, Madrid, 350 p.
- MOURGUIART (P.), 1987. Les Ostracodes lacustres de l'Altiplano bolivien. Le polymorphisme, son intérêt dans les reconstructions paléohydriques et paléoclimatiques de l'Holocène. Thèse Univ. Bordeaux, 263 p.
- ORLOVE (B.S.), 1986. An examination of barter and cash sale in Lake Titicaca: a test of competing approaches in economic anthropology. *Curr. Anthrop.*, 27 (2): 85–106.
- ORLOVE (B.S.), 1987. Consumption and production perspectives: accounting for the response of Lake Titicaca fishermen to the international debt crisis. Meeting of the Society for Economic Anthropology, Riverside, California, 15 p.
- ORLOVE (B.S.), 1991. Mapping reeds and reading maps. The politics of representation in Lake Titicaca. Amer. Ethnol., 18 (1): 3-38.
- ORLOVE (B.S.), LEVIEIL (D.), 1989. Some doubts about trout: fisheries development projects in Lake Titicaca. In: State, capital and rural society: anthropological perspectives on political economy in Mexico and the Andes. Orlove, Foley, Love, eds., Boulder, Colorado: 211–246.
- OYANGUREN (F.), TAPIA (M.), 1971. Ensayo comparativo de la digestibilidad de ensilaje de avena y de totora en ovinos y alpacas. Rev. UNTA, Puno, 3 (4): 281.
- PAREDES (R.), 1931. Descripción de la provincia de Pacajes. Bol. Soc. Geogr., Lima: 1-21.
- PLAFKER (G.), 1963. Observations on archaeological remains in north-eastern Bolivia. Am. Antiq., 28: 372–378.
- PONCE-SANGINES (C.), 1980. Panorama de la arqueología boliviana. Ed. Juventud, La Paz, 260 p.
- RAMIREZ (S.), VARGAS (C.), 1974. Estudios del llachu en la hoya del Titicaca, Departamento de Puno. Tesis Esc. Sup. Varones, Puno, 60 p.
- RICHERSON (P.J.), WIDMER (C.), KITTEL (T.), 1977. The limnology of Lake Titicaca (Peru-Bolivia). Univ. California, Davis, Inst. Ecology, 14, 78p., multigr.
- RIVET (P.), CREQUI-MONTFORT (G. de), 1905. La langue uru ou puquina. Jour. Soc. Amer., 17: 211-244.
- SANCHEZ (R.), 1983. La promoción campesina en una micro-región del Altiplano. Inf. Coop. tecn. Alemana, Puno, 15 p.
- SARMIENTO de GAMBOA (P.), 1942. Historia de los Incas. EMCE, Buenos Aires, 300 p.
- SERVANT (M.), FONTES (J.C.), 1975. Les lacs quaternaires des hauts plateaux des Andes boliviennes; premières interprétations paléoclimatiques. *Cah. ORSTOM*, sér. Géol., 10 (1): 9–23.
- SMITH (C.T.), DENEVAN (W.M.), HAMILTON (P.), 1968. Ancient ridged fields in the region of Lake Titicaca. Geogr. Journ., 134; 354–367.
- STANISH (C.), 1989. Tamaño y complejidad de los asentamientos nucleares de Tiwanaku. In:

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Primer informe de resultados del proyecto Wilajawira. Ed. Universidad de Chicayo, Instituto nacional de arqueología de Bolivia, La Paz: 41-91.

- TAPIA (M.), 1971. Contribución al estudio de la produccion de ensilaje de avena en comparación con ensilaje de totora en el Altiplano. Rev. UNTA, Puno, 3 (4): 158-165.
- THOMPSON (L.G.), DAVIS (M.E.), THOMPSON (E.M.), LIU (K.B.), 1985. A 1500-year record of tropical precipitation in ice cores from the Quelccaya ice cap, Peru. *Science*, 229, 971–973.
- THOMPSON (L.G.), DAVIS (M.E.), THOMPSON (E.M.), LIU (K.B.), 1986. The little Ice Age as recorded in the stratigraphy of the tropical Quelccaya Ice cap. *Science*, 234: 361–364.
- TICONA (I.), 1980. Determinación del cariotipo de la totora en el lago Titicaca. Tesis UNTA, Puno, 43 p.
- TORERO (A.), 1974. El quechua en la historia andina. Universidad Ricardo Palma, Lima, 240 p.
- TSCHOPIK (H. Jr.), 1946. The Aymara. In: Handbook of South American Indians. Steward ed., Smithsonian Institution, Washington. B.R.E., Bull. 143 (2): 501–574.
- TUTIN (M.A.), 1940. 10. The macrophytic vegetation of the Lake Titicaca. *In*: The Percy Sladen Trust Expedition to Lake Titicaca in 1937. *Trans. Linn. Soc. London, ser.* 3, 1 (2): 161–189.
- URIOSTE (F.M.), 1977. La economía del campesino altiplánico en 1976. Doc. A.C.B. La Paz, 274 p., multigr.
- VACHER (J.J.), ATTEIA (O.), IMAÑA (E.), 1987. Los riesgos climáticos en el Altiplano boliviano. ORSTOM.SENAMHI. La Paz, 12 p., multigr.
- VACHER (J.J.), ATTEIA (O.), IMAÑA (E.), 1988. Consumo de agua, crecimiento y producción de la papa. In: Actas del segundo Simposio de la investigación francesa en Bolivia, La Paz: 143–154, multigr.
- VACHER (J.J.), ATTEIA (O.), IMAÑA (E.), 1989. Net radiation and evapotranspiration on the Bolivian Altiplano. 3° International Conference on Southern Hemisphere Meteorology and Oceanography. American Meteorology Society: 169–172.
- VACHER (J.J.), IMAÑA (E.), 1989. Los riesgos de heladas en el Altiplano boliviano. OR-STOM.SENAMHI. La Paz, 20 p., multigr.
- VALDIVIA (L. de), 1606. Arte y gramática. Cited by Bird. In: Handbook of South American Indians (cf. Bird, 1946).
- VELLARD (J.), 1963. Civilisations des Andes. Gallimard, Paris, 270 p.
- VELLARD (J.), 1963. La pêche. In: Civilisations des Andes. Vellard ed., Gallimard, Paris: 61-67.
- WACHTEL (N.), 1990. Le retour des ancêtres. Les Indiens Urus de Bolivie XXe-XVIe siècle. Essai d'histoire régressive. Gallimard, Paris, 689 p.
- WILLEY (G.), 1971. An introduction to American archeology. Volume II. New Jersey Univ.

WIRRMANN (D.), 1987. El Lago Titicaca: sedimentología y paleohidrología durante el Holoceno (10.000 años BP-Actual). UMSA.ORSTOM. La Paz, Informe 6, 67 p., multigr.

VII.2. HYDROLOGICAL POTENTIAL VII.2a. The water resources

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Lake Titicaca, with its 8500 km² of mirror-like waters during the season of mean water level is one of the largest and highest of the so-called "great lakes" in the world. The water resources of this immense natural reservoir of Lake Titicaca, situated at an altitude of over 3800 m, has aroused the interest of many researchers. No fewer than nine publications have been written on the hydrological balance of its catchment, in addition to numerous projects dealing with the exploitation of its "white gold."

Unfortunately, some of the projects dealing with this natural reservoir, shared between Peru and Bolivia, have been based on incomplete data, very often not supported by verified information, giving rise to an inaccurate interpretation of the true balance, or to theories not in accordance with reality. Moreover, it must be pointed out that these have generally not taken into consideration the impact of this exploitation on the environment as a whole.

In the light of a recent study of the water balance of the lake (Roche and Bourges, 1991), based on up-to-date information, it seems unrealistic to think of taking a discharge of $100 \text{ m}^3 \text{ s}^{-1}$ from the basin and transferring it to another basin, without seriously damaging the environmental balance; this despite the fact that the potential energy that could be generated by taking advantage of a difference of level of 3000 m may be an idea to delight planners, engineers and hydrologists. The practicality of such projects depends not only on technical factors but also on geopolitical factors, since the lake is shared between two countries, and on multi-purpose factors of the applicability of its resources.

The aim of this study is not to propose an alternative project for the exploitation of the resources of Lake Titicaca, but to evaluate the water resources available, in the light of accurate up-to-date information.

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Inventory of resources

The surface water resources of the catchment area

Since Lake Titicaca is a reservoir of water derived from an extensive basin, it is essential to take into account the potential of its catchment area, in order to determine the potential of the lake itself. Studies carried out in recent years have identified favoured areas in terms of availability of water resources:

- To the west of the lake where the main basin is that of the Rio Coata, possessing an exceptional water potential, and to a lesser extent the Rio Ilave. The mean annual specific discharge recorded over a period of 32 years is $71 \text{ s}^{-1} \text{ km}^{-2}$ for the Coata and $51 \text{ s}^{-1} \text{ km}^{-2}$ for the latter.
- To the north of the lake are the basins of the Rio Huancane and Rio Ramis. The mean annual input from these basins is greater than $51 \text{ s}^{-1} \text{ km}^{-2}$ for the former but scarcely reaches $4.61 \text{ s}^{-1} \text{ km}^{-2}$ for the Rio Ramis basin due to its larger area.
- The south and east, mostly in the Bolivian part of the catchment, the specific discharges are lower, at around $41s^{-1}$ km⁻², with the exception of small catchments such as that of the Schuenca (Fig. 1), which benefit from a more favourable situation due to their steep gradients.

It should be pointed out that these mean values for specific discharge do not provide an assessment of the potential inputs from the basins, which are in any case very heterogeneous, but indicate the magnitude of the resources available in the piedmont zone around the lake, and therefore in the zone that is more suitable for agriculture.

In reality, the availability of water in this area depends mainly on two factors:

- firstly the orography, which is related to the influence of air of Amazonian origin descending from the Cordillera;
- secondly the proximity to the lake which provokes heavy precipitation due to nocturnal evaporation (Boulangé, 1981; Roche and Bourges, 1991).

The heaviest and most prolonged rainfall occurs over the lake itself or in its immediate proximity, and on the summits, particularly of some of the mountains in the Western Cordillera.

The estimated available surface water resources in relation to the altitude or the geographical area in question, and the type of environment or time of year, are given in Table 1.

For the zones lying above an altitude of 4500 m, it is useful to divide the basins according to the altitude of their highest point, which can determine whether or not glaciers are present, and therefore whether a different annual flow regime exists. When glaciers are present, a typical catchment would have a dry season discharge from melting snows around 4 to $81 \text{ s}^{-1} \text{ km}^{-2}$, but in the absence of a glacier this would be reduced to about $11 \text{ s}^{-1} \text{ km}^{-2}$.

Quantitative variation in lake inputs over the year follows that of precipi-



Figure 1. Hydrographic map of the Lake Titicaca catchment and location of gauging stations.

tation but with a delay. In general, there is a maximum in February and a minimum in August, but in reality nearly 80% of the annual input of water to the lake from the tributaries occurs between January and April. The dry season lasts for about six months from June to November (Lozada, 1985).

The variability between years in the resources originating from rivers is very great. Over the 20 years for which records are available, the total annual inputs from the network draining into the lake varied by $\pm 70\%$ around the

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Type of area	Dry season (August)	Rainy season (February)	Annual mean
Altitude > 4.500 m Basin with a surface < 100 km ² (presence of glaciers)	3 - 8	30 - 50	8 - 20
Altitude > 4.200 m Basins : 500 < S < 1.000 km²	0.5 – 1.5	20 - 50	6 15
Piedmount area	0.15 - 0.30	6 - 12	2 - 3
Lake shore	0.3 – 0.7	12 - 25	4 - 6

Table 1. Estimation of the water resources in each type of zone $(1s^{-1} \text{ km}^{-2})$.

mean, and in only 10 years out of 20 was it within 20% of the mean value. This irregularity is accentuated by the occurrence of "runs" of years; for example the inflows close to the mean all occurred between 1970 and 1982, whereas during the period 1984–86 the values were all more than 30% greater than the mean.

The utilisation of these resources therefore implies not only rigorous management of the quantities of water taken, but also, depending on the scale of the project, a regulation of discharge at least on an annual basis or even over several years.

The water resources of the lake

Assessment of the resources

The water resources of the lake, as a reservoir, depend directly on those of the catchment. Even though its great volume has the effect of regulating lake levels in the face of variations in input, it is nevertheless very sensitive to meteorological variations.

The overall study of the potential water resources of the lake-catchment system therefore implies the creation of a model taking into account all the variables in the hydrological balance of the reservoir (Roche and Bourges, *op. cit.*), plus a study of the impact of any change in one of the variables on the lake level.

Under a natural regime without any human influence, the lake absorbs any fluctuations in inputs due to weather, by changes in its water volume. In order to manage these resources more efficiently, it is nevertheless possible to control certain of the variables, such as the quantity of water flowing out by the Desaguadero, and therefore influence the lake level.

The theoretical utilisable water resources, available for any given period, can be considered as the algebraic sum of the volume flowing out via the Desaguadero and the change in lake volume compared to its initial volume.



Figure 2. Changes in the theoretical annual cumulative potential water resources from 1956 to 1989 and comparison with the true potential (in billions of m^3). A zero potential was arbitrarily chosen for the level on 1 January 1956, i.e. 3809.65 m altitude. Striped area = available reserve in the case of 43 $m^3 s^{-1}$ option.

To calculate this balance, the outflow discharge needs to be known with an acceptable accuracy that has required a preliminary re-examination of the raw data (Bourges *et al.*, 1991). The real potential only takes into account the lake level.

If the theoretical water resources of the lake are accumulated for each hydrological year running from January to December, over the best documented period (1956–1989), it can be seen that this potential at first fluctuates and then increases greatly from 1973 onwards (Fig. 2).

Because a period of deficit existed between 1956 and 1958, no offtake of water could be envisaged for these years, without leading to an additional lowering of lake level. For the purposes of a simulation, it was therefore necessary to wait until 1959 before starting.

The total offtake of water is the sum of the quantities removed from the tributaries/lake system, whether continuously or discontinuously, and by whatever means: pumping from the lake, evacuation by the Desaguadero or withdrawal from the tributaries.

If, for example, the total annual offtake was fixed, as from 1959, at $315 \times 10^6 \text{ m}^3$, or a discharge of $10 \text{ m}^3 \text{ s}^{-1}$, it appears that such a quantity could be removed from the lake until 1989, without any effect on the lake's resources. It should be noted, however, that by the end of 1970, the lake would have returned to its initial state of 1 January 1959, with a level of

3808.60 m above sea level (Fig. 2). This is in fact what actually was observed, since the lake was 12 cm below this level and the mean discharge of $11 \text{ m}^3 \text{ s}^{-1}$ evacuated by the Desaguadero was very similar to the chosen hypothetical value for offtake. The extreme levels reached between 1959 and 1977 would have been 3808.55 m in December 1970 and 3811.20 in April 1963.

It is evident that after 1970, the total withdrawals, by offtake or by outflow, would have been much greater; if not, the increase in the lake's volume, which was greater than 40×10^9 m³ at the time of the maximum in April 1986, would have led to levels much higher than those recorded during the floods.

If instead of taking $10 \text{ m}^3 \text{ s}^{-1}$, the volume taken as from 1971 was $45 \text{ m}^3 \text{ s}^{-1}$ (equivalent to a volume of $1420 \times 10^6 \text{ m}^3$), with the exception of a slight drop in lake level in 1972, the initial level would have been reached at the end of 1983 (Fig. 2). Under this hypothesis, the lake level from 1971 to 1985 would have fluctuated at between 3808.30 and 3809.90 m altitude and the available resources would have been maintained at about $10 \times 10^9 \text{ m}^3$ for eight years between 1975 and 1982.

Under the same hypothesis, the level reached in April 1986 would have been slightly less than 3812 m, or 60 cm below the maximum recorded, but still excessive in relation to the risks faced.

For the period 1956–1989, it would therefore appear that it would have been possible to ensure an annual volume for withdrawals of 315×10^6 m³, while maintaining a minimum lake level of 3808.55 m, in 31 years out of 34. If this volume were to be increased to 1420×10^6 m³ year⁻¹, it could only have been ensured for 19 years, between 1971 and 1989, and even this would have implied accepting a drop in level to 3808.30 m. In both cases these offtakes would have required additional outflows in 1985 and 1986, to maintain the lake level below the alert threshold.

The hypothetical discharges (10 and 45 $\text{m}^3 \text{s}^{-1}$) correspond to offtake values, which actually could be spread over the year according to real requirements.

Determination of the management criteria

If it were possible to control the discharge evacuated by the Río Desaguadero (creation of artificial spillways, dredging of a channel in the river), it would be possible to fix as objective the maintenance of a minimum lake level of 3808.30 m and a maximum level of 3811.00 m.

Between these two limits, it would be possible in a wet year to use the water resources as from the month of April – which usually corresponds to the peak level – so as to reach at the period of low water level the level of 3809.50 which is the lake's mean level between 1915 and 1989. This would provide two advantages:

- The available reserve above the minimum threshold would represent

 $10 \times 10^9 \text{ m}^3$ which could either provide additional supplies during several successive average years, or lessen the effects of two successive years of deficit (4 × 10⁹ m³) or one exceptionally dry year such as 1983 (8 × 10⁹ m³).

- The lake level could be maintained below the fixed maximum in wet years. Since the annual range in lake level over the 34 years has varied from extremes of 169 cm (in 1984) and 55 cm, with a mean of about a metre, there is a sufficient safety margin.

In contrast in an average or dry year, it is necessary to withdraw from the available reserves and manage the resources so as to try and get back to the level of 3809.50 m.

Simulation of management with upper and lower thresholds. Application to the period 1915–1989

Once the extreme limits of variation in lake level were adopted, a simulation of management was carried out, using the two options already proposed (10 and $45 \text{ m}^3 \text{ s}^{-1}$), and the following results were obtained:

- from 1959 to 1978 inclusive, by taking a hypothetical discharge of $10 \text{ m}^3 \text{ s}^{-1}$, the lake would have fluctuated between 3810.85 m and 3807.35 m. It would have been necessary to release additional discharges in only two years out of twenty, in 1962 and especially 1963 (240 m³ s⁻¹). These volumes of water would not have been available in the dry years from 1967 to 1973 when the lake level would have dropped below the fixed limit of 3808.30 m
- from 1971 to 1989 inclusive, the lake level would have been maintained at between 3811.15 m and 3808.30 m, by taking a hypothetical discharge of 45 m³ s⁻¹. It would have neen necessary to evacuate additional disharges in six years out of nineteen, in particular in 1986 $(210 \text{ m}^3 \text{ s}^{-1})$. The levels fixed would have been complied with, except that the maximum limit would have been slightly exceeded. It should be noted, however, that if the discharge that should have been released in 1986 had been evacuated starting in January, the maximum level would not have exceeded 3811.05 m, or approximately the fixed limit.

It is clearly evident that the period 1959–1989 was a rather wet one compared to the entire period of records (1915–1989), especially after 1973 (Figs 3 and 4) and that care should be taken in extrapolating these results. For example if the overall slope of the curve of cumulative potential resources since 1915 is estimated (Fig. 5), the mean volume of offtake is around $380 \times 10^6 \text{ m}^3$, whereas during the period 1945–1989, this volume would have been $850 \times 10^6 \text{ m}^3$ year⁻¹, i.e. 27 m³ s⁻¹.

A simulation covering the latter period, with an annual adjustment of the dry season level to 3809.50 m, if the level was higher, and an offtake of $315 \times 10^6 \text{ m}^3 \text{ year}^{-1}$, would have made the lake level drop to 3805.30 m in 1943, and the minimum annual level would have been below the limit in 34



Figure 3. Changes in the level of Lake Titicaca from 1914 to 1989. Altitude in metres a.s.l.



Figure 4. Value of the theoretical water potential of Lake Titicaca on the 31 December of each year, compared to its value on the previous 1 January.



Figure 5. Changes in the theoretical annual cumulative potential water resources from 1915 to 1989 and comparison with the true potential. The zero potential corresponds arbitrarily to the level on 1 January 1915, i.e. 3808.81 m altitude., i.e. about $7 \times 10^9 \text{ m}^3$ below the previous reference (Fig. 2).

years out of 75. The maximum of 3911.15 m would have been reached in this case in 1986.

Therefore, over the entire period of observations, from 1915 to 1989, it would appear that it would have been possible to take a hypothetical discharge of $10 \text{ m}^3 \text{ s}^{-1}$ from 1915 to 1936 and then from 1949 to 1972, and from 1973 onwards this could have been increased to $45 \text{ m}^3 \text{ s}^{-1}$, while only just reaching the permissible limits for lake level.

Recommendations

It is evident that the Rio Desaguadero, the natural outflow of the lake and which irrigates all the Bolivian Altiplano, should be accorded a minimum discharge, to prevent salinisation of the water course by its tributaries downstream in the event of drying up of flows coming from the lake.

For a rational management, it should be agreed that the catchment be equipped with a network of remote transmitting rain gauges and river gauging stations, connected to a forecasting model. This arrangement would provide advance information on the quantity of the resources and would warn of natural hazards due to excessive inputs of the catchment and of their consequences on the lake level. For example, the mean monthly input from inflow rivers for February 1971 reached $1700 \text{ m}^3 \text{ s}^{-1}$. By adding the input of direct rainfall on the lake, a total input of $2100 \text{ m}^3 \text{ s}^{-1}$ is reached. More recently

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in March 1986, the mean discharge that it would have been necessary to evacuate in order to avoid a rise in lake level would have been $2000 \text{ m}^3 \text{ s}^{-1}$.

Since the hydraulic properties of the Río Desaguadero limit the discharges that can be evacuated to much lower values, additional outflows have to be looked for. If such a solution is not possible the storage capacity of the lake is incapable of absorbing such inputs and there is no other alternative but to face flooding.

In addition, as Lake Titicaca is part of an endorheic system, account must be taken of the consequences that management of the lake, and the injection or retention of very large volumes of water, could have downstream in Lake Poopo or possibly in the Salar de Coïpasa.

Subterranean water resources

Although quantitatively small the subterranean water resources participate in the hydrological balance of the lake. It is very probable in fact that the lake is fed laterally by the water tables situated around its margins (Gumiel, 1988), and that removal of water from these water tables would decrease inputs to the lake.

Despite the absence of any complete estimate of these subterranean water resources, it is nevertheless on record that on the Peuvian side there are about 12,000 wells or boreholes around the lake (Ministerio de Agricultura, 1986). These are mainly on the plain, near low-lying coastlines and below 4000 m altitude. In this zone the water table is very near the surface, at about 1 to 3 m depth, and therefore always with a positive head with respect to the lake, which supports the hypothesis of subterranean inflows into the lake. Trial pumpings carried out in Peru give average outputs of 20 to 251 s^{-1} .

According to a United Nations study (1973) carried out over only two years, the total recharge available for the Bolivian catchments situated to the south-east of the lake would be around $160 \times 10^6 \text{ m}^3$ per year, mainly concentrated in the Catari catchment (Fig. 1).

Water quality

With a few exceptions (Pallina, Huancané) the surface waters are relatively lightly mineralised. In their lower reaches most of the tributaries have mean concentrations of dissolved salts of between 200 and 300 mg l^{-1} , with the exception of the Río Suches and the rivers running off the Cordillera Real, where they are around 50 mg l^{-1} (Carmouze *et al.*, 1981; Guyot *et al.*, 1990, and see also Chapter V.3).

The underground waters are slightly more mineralised than the surface waters and have salinities around 400 mg l^{-1} (United Nations, 1973).

Because of evaporation, the waters of the lake are more mineralised, their concentration of dissolved salts averaging around 700 mg l^{-1} (Chapter V.1).

The quality of these waters is therefore suitable for all types of usage, although, in the case of the lake water, good drainage is often required if it is to be used for agricultural purposes. For example, Lake Titicaca water has been used for 30 years in the Pirapi irrigation district, situated near Puno (Fig. 1), without any observable soil salinisation.

Use of the water resources

Principles of use

Before dealing with the many possibilities for exploiting these resources, it seems useful to put forward some principles which should govern its use:

- The water used should be exploited as a priority within the catchment area of the lake or of the Desaguadero. Any transfer towards another catchment should only be envisaged as a last resort and be subject to a detailed impact study.
- Priority for use should be given to the areas around the shoreline.
- Since the lake lies in two countries, the use of the resources should benefit both countries in the same manner.

As for the actual use of Lake Titicaca's water, this covers several essential applications such as energy production, agriculture and human requirements.

Energy production

If all transfer outside the catchment is excluded, the only projects that can be envisaged are dams on the tributaries.

In this case the quantities of water lost are rather low since the majority of the water is returned to the water course downstream from the dam. Five moderate-sized projects are planned for the Peruvian side (ElectroPerú, 1981) and a larger project is under study for the Bolivian side on the Río Suches.

Given the very low gradient on the Río Desaguadero, any project for using the outflow from the lake in this water course would seem to be excluded, unless very expensive schemes are carried out.

Agricultural use

Simple forms of irrigation have been practised around the lake for a long time, for crops or more frequently pastures. The non-quantified resulting

water consumption is implicitly taken into account in the estimation of resources and is not therefore included in the present requirements.

As far as irrigation schemes are concerned, the following developments can be noted:

- 18,600 ha in Peru are in the course of being supplied with water, of which 6500 ha already function in an irregular fashion (Ministerio Agricultura Perú, 1986).
- on the Bolivian side, 5000 ha are already functioning near Huarina, irrigated by surface water, and 8800 ha are planned using underground water.

The irrigation period mainly concerns the five or six months of the year from October to March, depending on the crops (cereals, root crops, vegetable gardening). It lasts almost all the year for pasture land.

If the efficiency is assumed to be 50%, the gross water requirements can be evaluated at about 1500 to 2000 m³ ha⁻¹ per month, depending on rainfall. Under this hypothesis, if only surface water is used, the irrigation schemes in the process of being created or already in operation will use the entire resources available under the minimum option envisaged above $(315 \times 10^6 \text{ m}^3 \text{ year}^{-1})$. A small proportion will be returned to the network in the form of drainage. Even if underground resources are also used, it is probable that the inputs into the lake in October of $35 \text{ m}^3 \text{ s}^{-1}$ for the entire catchment, would not guarantee these requirements every year.

Using the same bases for calculation, the entire irrigated area (around 200 000 ha) would require $2 \times 10^9 \text{ m}^3$ in a dry year, of which a part would be returned, but nearly one billion m³ would be used by the plants. In some years this volume would represent a very large withdrawal compared to the inflows to the lake from rivers.

Domestic and industrial water supply

At present these sectors of consumption only involve a negligible proportion of the quantitative balance, especially as in this case the water is usually restored to the network. All the offtake points are situated on the tributaries upstream from the lake.

On the Peruvian side, the industrial requirements include cement works, power stations and food processing. They are probably more of a threat due to possible pollution caused by their effluents than to their water consumption.

On the Bolivian side, in addition to the rural consumption and a few industries (Viacha cement works), mention must be made of the water supply to the city of La Paz, 70% of whose requirements come from the lake's catchment ($32 \times 10^6 \text{ m}^3 \text{ year}^{-1}$), as well as the great quantities pumped from the water table within the catchment ($11 \times 10^6 \text{ m}^3 \text{ year}^{-1}$).

Conclusions

It would appear to be difficult to reconcile an optimal utilisation of the lake's water resources using a regulation between years, with minimal variation in lake level, without creating reservoirs capable of storing the excess volumes of water present in some years, upstream from the lake, on the tributaries. With a total storage capacity of 3 billion m³, discharges would have had to be released (i.e. waste resources) in only two years out of 75, whatever the option chosen from among the two hypotheses presented above. However, other than the fact that the creation and use of reservoirs would lead to an increase in losses, mainly through evaporation, it should be stressed that the volumes to be stored would require the construction of very large engineering schemes, requiring major investment. At present only natural lakes exist, especially in Peru, or artificial reservoirs with a capacity of less than 30 million m³.

Among the potential uses of Lake Titicaca's water resources, it would appear that energy production should not be a priority, since more suitable sites exist in the two countries bordering the lake, in the Amazonian basin. Nevertheless, the construction of hydroelectric reservoirs on the inflows would have the advantage of regulating their discharge without significantly decreasing the resources.

In the hypothesis of a transfer of water out of the catchment area, the maximum discharge could not exceed 30 to 35 m³ s⁻¹, corresponding to an available discharge in the case of the simulated maximum option (45 m³ s⁻¹) and assuming that no other project arrives to create new requirements. Despite the large amount of energy produced (700 MW) because of the considerable head of water that can be used, this discharge would not seem sufficient justification for the investment, which could be very heavy. Even a combined irrigation-hydroelectric scheme, which would be more economically justifiable, could not justify the consequences of transferring these resources out of the basin, unless external inputs could be envisaged, that would at least partially compensate for this removal.

Well-planned agriculture adapted to the existing potential resources would be more beneficial in terms of economic and human benefits for the inhabitants living around the lake or along the Río Desaguadero (maintenance of the rural population). In this case, if the offtakes were limited to a few $m^3 s^{-1}$, the hypothesis of a transfer of water out of the catchment could be envisaged in a different manner.

In any case, if the uses of the lake's water resources are to be planned and coordinated, it is essential above all to draw up a model based on data from an adequate measuring network, which would provide real-time information on the surface and underground resources available. Once the resources are known, optimal use should be made of them by using a management model capable of simulating the various hypotheses complying with the chosen options.

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It is difficult to envisage the extraction of 500 or $1000 \text{ m}^3 \text{ s}^{-1}$ by the only exit from the lake, the Río Desaguadero, since the maximum discharge occurring at the lake outlet with a hundred years recurrence is around 300 and 350 m³ s⁻¹ (Bourges *et al.*, 1991). With the aid of flood forecasting, it would be possible to regulate the volume of the lake's reserves so as to absorb exceptional inputs over 2000 m³ s⁻¹, during one month, with a discharge of only 300 m³ s⁻¹.

Although, *a priori*, a moderate drop in lake level would appear to favour a decrease in evaporative losses and therefore an increase in the potential water resources, a detailed study would be needed to determine the impact of this measure on the hydrological balance, and particularly on the cycle of evaporation and precipitation.

Finally, an overexploitation of the lake's water resources should be avoided as this could lead to an excessive drop in lake level with ecological and human consequences, likely to be negative rather than positive:

- destruction of ecosystems in shallow areas (Puno Bay, Lago Pequeño, etc.) which could lead to a decrease in the fishing potential.
- difficulties in navigation in certain areas.
- progressive decrease in the discharge of the Río Desaguadero, and perhaps drying out of its upper reaches.
- reclaiming of land, with possible, but unproven, agricultural potential.
- lowering of the water tables around the lake and probably of certain parts of the Bolivian Altiplano.
- progressive decrease in evaporation from the lake and therefore of rainfall in the immediate surroundings of the lake and on the lake itself.

Lake Titicaca represents an as yet untouched hydrological system in comparison to many others. In order that man can benefit from its resources he must be able to preserve it from overexploitation. This is the objective that has been fixed by Lake Titicaca Study Project (PELT), financed by the European Community, and at present in the stage of being set up.

Its aim is to draw up an overall binational Management Plan, for controlling, conserving and using the resources of the entire endorheic system as far as the Salars, and especially the water and fishing resources.

- To achieve these aims it will particularly involve itself with:
- studying the problems of draught and flooding
- analysing the various alternatives for regulation using simulation on models
- determining the volumes of water that can be used without inflicting environmental damage
- developing the best solutions by defining the regulatory engineering works and by setting up a binational organisation
- developing a methodology for updating the Management Plan by integrating new data as they become available.¹

¹ According to the terms of reference of the PELT study project.

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References of chapter VII.2

- AMBROGGY (R.), 1965. Cuencas acuíferas del lago Titicaca. *In*: Hidrología del Altiplano de Bolivia, La Paz, Min. Agric: 11 p.
- Anon., 1965. Programa de inventario y evaluación de los recursos naturales del Departamento de Puno. Sector de Prioridad 1. Capítulo 6: Ecología y Agrostología, vol. 4. IN-P.ONERN.CORPUNO, Lima, 35 p.
- Anon., 1967. Solicitud del Gobierno de Bolivia al fondo especial de las Naciones Unidas. Proyecto de aprovechamiento de aguas subterráneas del Altiplano. Secret. Nac. Planif. Coord. La Paz, 38 p.
- Anon., 1971. Proyecto de desarrollo agrícola en la región del lago Titicaca. FAO-BID Washington, D.C: 160 p.
- Anon., 1973. Desarrollo de los recursos de aguas subterráneas en el Altiplano. Proyecto Naciones Unidas 1973: 215 p.
- Anon., 1976. Investigación y desarrollo pesquero. Perú. Resultados y recomendaciones del Proyecto FI:DP.PER.72.008. Informe terminal preparado para el Gobierno del Perú. PNUD-.FAO, Roma.
- Anon., 1977 a. Estudio del potencial hidrobiológico en el Departamento de Puno. DIREPE.-PUNO.
- Anon., 1977 b. Lineamientos de desarrollo a largo plazo, región Puno. Análisis regional. Of. Reg. Planif. 6. INP.ORDEPUNO, Puno, 178 p.
- Anon., 1977 c. Proyecto: Represa Lagunillas (trece planos). Min. Pesq., Of. Reg. Planif. 5, Puno.
- Anon., 1977 d. Perfiles de proyectos de irrigación. Z.A. XII. Puno. DGA. Of. Programación. Min. Agric., Lima, 40 p.
- Anon., 1980. Proyecto a ser considerado para minimizar la problemática de la sequía. Of. Reg. Planif. 5, Puno. DIREPE.ORDEPUNO.
- Anon., 1981 a. Identificación de proyectos específicos de riego, La Paz, Min. Agric. Asunt. Campes., IICA, Bolivia: 1: 517 p.; 2: 660 p.
- Anon., 1981 b. Inventario y evaluación de los recursos hidroeléctricos para centrales entre 1000 y 30000 KW, Electroperú, 163 p.
- Anon., 1981 c. Estudio de la cuenca del río Ilpa. Min. Agric. Puno. DGAS. Proy. Manejo de cuencas. Tomo 1: diagnóstico de la cuenca, 114 p.; Tomo 2: plan de manejo de la cuenca, 102 p.
- Anon., 1986. Principales proyectos de irrigación ejecutados en el departamento de Puno. Plan rehati, Min. Agric., Perú, 45 p.
- Anon., s/f. Programa preliminar de investigación y promoción pesquera en el lago Titicaca. Informe final, Serv. Pesq., Puno, Perú.
- BENITEZ (P.), 1973. Feasibility study of the electrical power requirements for the Lake Titicaca littoral. *In*: Project n° 6, A report of Peru, Min. of Energy & Mines, vol. 1 and 2.
- BOULANGE (B.), AQUIZE JAEN (E.), 1981. Morphologie, hydrographie et climatologie du lac Titicaca et de son bassin versant. *Rev. Hydrobiol. trop.*, 14 (4): 269–287.
- BOURGES (J.), CARRASCO (L.M.), CORTES (J.), 1991. El lago Titicaca: aportes en aguas superficiales y desagüe. PHICAB, La Paz (in press).

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- CARMOUZE (J.P.), AQUIZE JAEN (E.), 1981. La régulation hydrique du lac Titicaca et l'hydrologie de ses tributaires. *Rev. Hydrobiol. trop.*, 14 (4): 311-327.
- CARMOUZE (J.P.), ARZE (C.), QUINTANILLA (J.), 1981. Régulation hydrochimique du lac Titicaca et l'hydrochimie de ses tributaires. *Rev. Hydrobiol. trop.*, 14 (4): 329-348.
- FERNANDEZ JAUREGUI (C.A.), ROCHE (M.A.), ALIAGA (A.), PEÑA (J.), 1987. Los recursos hídricos en Bolivia. PHICAB.CONAPHI, IHH.UMSA, ORTOM, SENAMHI: 20 p., multigr.
- FRISANCHO (I.), 1963. La utilización de las aguas del lago Titicaca. Ed. Los Andes. Puno.
- GARIBALDI (G.), DEL RIO (M.), LEON (A.), VEGA (G.), 1961. Visión futura de la costa peruana. 1: Lago Titicaca. 2: Extracción de las aguas del lago. Tesis UNI, Lima, 170 p.
- GOMEZ (J.), 1972. Estudio del lago Titicaca para aprovechamiento de sus aguas. Tesis Ing. Agríc. UNA – La Molina, Lima, 118 p.
- GUMIEL (D.), 1988. Prospección hidrogeológica del área altiplánica del proyecto de autoayuda campesina, CEE.CORDEPAZ, La Paz. 96 p.
- GUYOT (J.L.), GUMIEL (D.), 1990. Premières données sur l'hydrogéologie et sur l'hydrogéochimie du Nord de l'Altiplano bolivien. Hydrogéologie, 3: 159–164.
- GUYOT (J.L.), CALLE (H.), CORTES (J.), PEREIRA (M.), 1990. Transport de matières dissoutes et particulaires des Andes vers le Rio de La Plata par les tributaires boliviens (rios Pilcomayo et Bermejo) du Rio Paraguay. J. Sci. Hydrol., 35 (6): 653-665.
- GUYOT (J.L.), ROCHE (M.A.), NORIEGA (L.), CALLE (H.), QUINTANILLA (J.), 1990. Salinities and sediment transport in the Bolivian highlands. J. Hydrol., 113: 147–162.
- JIMENEZ (A.), 1967. El plan nacional de agua potable rural en Puno. estudio de fuentes. Tesis UNI, Lima.
- LA FUENTE (I.), 1982. Estudio monográfico del lago Titicaca. Bol. Soc. Geogr., Lima, 1: 263-391.
- LOZADA ENCINAS (G.A.), 1985. Balance hídrico de la cuenca del lago Titicaca. Tesis UMSA, La Paz, 158 p.
- ROCHE (M.A.), FERNANDEZ JAUREGUI (C.A.), 1986. Los balances hídricos de Bolivia. Premier Symposium de la Recherche française en Bolivie, La Paz, Sept. 1986: 44–47. multigr.
- ROCHE (M.A.), ROCHA (N.), 1985. Mapa pluviométrico de Bolivia y regiones vecinas, 1/4.000.000. PHICAB, ORSTOM, SENAMHI. La Paz.
- RONCHAIL (J.), 1985. Situations météorologiques et variations climatologiques en Bolivie (Analyse de séries climatiques, inventaire de saisons exceptionnelles). PHICAB, AASANA, IFEA, ORSTOM, SENAMHI, La Paz, 60 p., multigr.
- SMYTH (J.), COWELL (B.), 1966. Lake Titicaca Resources Study. PASA for US AID Perú, Lima, 19 p.
- VALCARCEL (C.), s/f. Características agrológicas de la provincia de Puno en zonas cultivadas vecinas al lago Titicaca. Tesis UNA – La Molina. Lima. 94 p.

VII.3. ICHTYOLOGICAL POTENTIAL VII.3a. The fishery potential

HUGO TREVIÑO, JULIAN TORRES CALDERON and MARIA RONCAL GUTIERREZ

Small-scale fishing and fish-farming are currently one of the most important sources of human food because almost all countries tend to control natural water resources at a national level and the fishing communities are aware of the economic potential of these activities. At the present time, new bases for the organisation and rational use of fishery resources are being planned, to revise the strategies and policies taking into account previous experience, and planning for the future in relation to production factors such as the boats, fishing methods and gear, training of fishermen and research capacities. Assistance is also being given in terms of fishery planning, organisation and aid for the development of small-scale fishing, aid for fish-farming, for international trade in fish and the promotion of fishing as a solution for the provision of food.

The fishery potential

Lake Titicaca, together with Lake Poopo, is one of the most important water resources for fisheries development on the Peruvian/Bolivian Altiplano.

Fishery activities which have developed around the shores and on the islands, as complements to agricultural activities, contribute to family income, employment and improvement of the diet.

Description of the fish fauna

A detailed description of the fish fauna can be found in Chapter VI.5. There are about 25 endemic Cyprinodontidae belonging to the genus *Orestias* in the lake, 2 species of Bagridae of the genus *Trichomycterus* and 2 introduced

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Table 1. Scientific and local names of the main native fish species in Lake Titicaca

Genus Orestias	
O. agassii (carachi gris)	O. cuvieri (humanto)
O. luteus (carachi amarillo)	O. pentlandii (boga)
O. albus (kello carachi)	O. mullerí (carachi gringo)
O. olivaceus (carachl enano)	<i>O. langui</i> (chiñi chaulla)
	O. ispi
Genus Trichomycterus	
T. rivulatus (suche)	<i>T. dispa</i> r (mauri)

species *Salmo gairdneri* and *Basilichthys bonariensis*. The local and scientific names of the main native species are given in Table 1.

Richerson *et al.* (1977), in their comparison of the native fish fauna with that of other tropical lakes of comparable size and depth (Lake Victoria and Lake Tanganyika for example), concluded that this fauna is much less diverse, probably because of the isolation of the basin and the special physical conditions existing in Lake Titicaca.

Barbour and Brown (1974) produced a regression line, from comparative studies throughout the world, relating the number of native fish species recorded to lake area. They concluded that the number of fish species in Lake Titicaca was far below the line.

The different types of fisheries in the lake

There are no long-term fishery statistics covering the whole of the lake. This makes it difficult to find exact information on the lake's fisheries, their importance and the changes occurring over time.

On the basis of the works of Avila *et al.* (1989) and Franc *et al.* (1985), it is possible however to give a general description of the lake fishery, which is small-scale and of the subsistence type. Four major types of fishery can be distinguished on the basis of their techniques and socio-economic importance:

- a traditional shore fishing for "carachis," usually carried out by women and children using the "sajjana," a small bag net which is pushed through the vegetation. This is not very productive. In 1976, 41% of those fishing in the Peruvian part of the lake still used the "sajjana" (Bustamante and Treviño, 1976).
- fishing for "carachis" with gill-nets. This uses fine mesh nylon nets set for overnight fishing above the vegetation at the edge of the totora beds. For this fishery wooden boats or the traditional balsas made of totora are used.
- a deep water fishery for trout and pejerreys using gill-nets with a mesh of greater than 6.4 cm. This is the most widely practised fishery in the lake, carried out mainly with wooden boats in areas of at least 25 metres depth.



Figure 1. Importance of fishing in the four lake zones of the Peruvian portion of Lake Titicaca in 1981. A. Percentage of total number of fishermen. B. Number of fishermen per km^2 of lake surface. C. Percentage of total population dedicated to fishing.

In 1981, more than 40% of the fishermen in the Peruvian part of the lake practised this type of fishing.

- fishing for "ispis." This activity in fact covers several species of *Orestias*, but with a preponderance of *O. ispi*. Traditionally this fishery was carried out with woven hemispherical baskets, but nowadays small mesh gill-nets or beach seine nets are used. Walls of netting are also used in the pelagic zone.

The importance of each type of fishery varies from year to year depending on several factors and on the dependence of fishery activity on other economic activities such as agriculture.

Catches and fishery statistics

In 1976 Bustamante and Treviño (op. cit.) estimated that there were 3000 fishermen in the Peruvian part of the lake. In 1981, the estimates of Avila *et al.* gave a slightly higher figure. The distribution of fishermen in this part of the lake is shown in Fig. 1.

More than 95% of the captures are made with gill-nets, and the distribution of catches (Table 2) shows that the mean annual catch per fisherman is 2 tonnes.

Franc *et al.* (1985) evaluated the catches obtained by the two types of fishing practised in the Bolivian part of the Huiñaimarca from an enquiry carried out over a period of three months. Their results (Table 3) show that catches of native species were of considerable economic importance at this time.

In the fish catch assessment made by IMARPE in 1979–80, the annual catch in the Peruvian part of the lake was estimated at 6326 tonnes, the same figure for 1984 being 5612 tonnes.



Figure 2. Distribution maps for the total fish fauna and for the most important fisheries species in Lake Titicaca (estimates from echo-integration using four density classes). A. Distribution of total fish biomass and survey transect lines (straight lines) used in 1985. B. Distribution of *Orestias ispi.* C. Distribution of rainbow trout. D. Distribution of pejerrey. (U = integration unit; 1-10 = very dispersed, 11-100 = dispersed, 101-1000 = dense, >1000 = very dense).

In 1980 the native species represented the greater part of the catch, accounting for 70.6%, the genus *Orestias* being the most important and the genus *Trichomycterus* (mauri and suche) only accounting for 2.5%. The introduced species (trout and pejerrey) accounted for about 30% of the total catch. These species have a commercial value, whereas the native species mainly serve for local consumption (Table 4).

The total catch in 1984 was estimated at 5612 t, but fishing activity varies with the seasons, 44% of the catch being made in the rainy season and 56%

ZONE	% catch with gillnets	% catch with native gear	% total catch	Average catch (tonnes/fisher.)
Puno Bay	26.02	1.72	27.74	2.6
Lago Norte	28.57	0.07	28.64	1.9
Lago Sur	27.95	-	27.95	2.3
Lago Pequeño	10.24	5.43	15.67	1.5
Lake Titicaca	92.77	7.22	100.0	2.0

Table 2. Distribution by zones and by type of fishing of annual catches of fish (tonnes) in the Peruvian part of the lake. From Alfaro *et al.*, 1982

Table 3. Evaluation of the monthly catches (tonnes) mainly of Orestias agassii in the eastern part of the Huiñaimarca. From Franc et al., 1985

	Fine meshes gill nets	Trawls
Oct. 1978	6.6	9.8
Nov. 1978	4.5	7.1

Table	4.	Distribution	of	catches	according	to	species	in	Lake	Titicaca	(1980)	and	1984)	and	in
Puno	Bay	y (1990)													

SPECIES	19	80	1984-	-1985	1989-1990		
	(in tons)	%	(in tons)	%	(in tons)	%	
O. agassii	3416.94	54.01	1627.5	29.00	1.50	0.30	
O. luteus	449.50	7.11	448.9	8.00	2.60	0.51	
O. olivaceus	381.89	6.84	84.2	1.50	0.10	0.02	
O. pentlandii	12.59	0.20					
O. mulleri	14.28	0.22	28.1	0.50	0.30	0.06	
O. cuvieri	21.28	0.34					
O. ispi	17.05	0.27			0.01		
Total genus Orestias	4313.53	68.19	2188.7	39.00	4.51	0.90	
T. dispar	142.97	2.26	325.5	5.80	0.30	0.06	
T. rivulatus	12.65	0.20	11.2	0.20			
Total genus Trichomyclerus	155.62	2.46	336.7	6.00	0.30	0.06	
Total native species	4469.15	70.65	2525.4	45.00	9.62	1.91	
Salmo gairdneri	888.50	14.04	168.4	3.0	83.5	16.55	
Basilichthys bonariensis	968.46	15.31	2918.2	52.0	411.3	81.54	
Total Introduced species	1856.96	29.35	3086.6	55.0	494.8	98.09	
Total catches	6326.01	100	5612.0	100	504.42	100	
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SPECIES	1981	1982	1983	1984	1985	1986	1987	1988	1989
Boga	22	425	199	43	14	36	65	52	52
Carachi	344	1874	1900	2029	2003	3270	2974	3367	3000
Ispi	116	629	1445	597	557	1136	1199	276	86
Mauri	25	204	55	155	62	154	202	175	160
Suche	1	18	2	29	16	11	4		
Humanto	13								
Total native species	521	3150	3601	2853	2652	4607	4444	3870	3298
Pejerrey	202	1066	1197	1552	1604	2035	2574	3250	4229
Trout	151	196	85	28	55	55	123	105	46
Total introduced species	353	1262	1282	1580	1659	2090	2697	3355	4275
Total of the catches	874	4412	4883	4433	4311	5697	7141	7225	7573
Fish product									
Trout from aquaculture*	-	-	-	35	13	35	33	118	141
Total fish production									
(fisherles and fish culture)	874	4412	4883	4468	4324	6732	7174	7343	7714

Table 5. Weight of catches of native and introduced species in Puno district

* Farmed production of trout in controlled conditions (floating cages). Source: statistical unit of the Budget and Planning Bureau DIREPE 11–PUNO (figures rounded up to the nearest kilogram).

in the dry season. This estimate shows a decrease in the catch of native species of 25.5% compared to 1980. The best catch index was for the *O. agassii* with 29% of the total catch, followed by that of *O. luteus* (8.0%). There was also an increase in the relative importance of *Trichomycterus* of 4.43% compared to 1980, and in the case of the introduced species an increase of 25% for the pejerrey and a decrease of 11.4% for the trout.

In the experimental fishing operations carried out in the Ojerani community (Puno Bay) for a period of one year (April 1989–April 1990), a dominance of introduced species was recorded, 82.4% being pejerrey and 16.4% trout. The native species represented less than 2% of captures, probably because of alterations in ecological conditions brought about by the changes in lake level which occurred between 1983 and 1986.

Composition of catches in the Puno district

The statistical data of DIREPE-Puno (Production Department) relating to the relative weights of native and introduced species caught between 1981 and 1989, demonstrate a regular growth in total catches between 1982 and 1989, following the great increase that occurred between 1981 and 1982 (Table 5).

The total quantity of native species caught can change greatly from one year to another (e.g. 1985 and 1986), but has been maintained at the same

level overall if 1982 is compared to 1989. "Carachis" are always the most abundantly captured fish because they are in the most demand from the rural and lakeside communities. The catches of Bagridae remain at a rather constant low level.

The relative proportion of native species in the catch was 73.7% (3601 kg), whereas they only accounted for 43.5% in 1989. This phenomenon was due to the strong increase in the catch of pejerrey over the same period. In contrast, catches of trout remained at a very low level, almost certainly because this species does not find ideal environmental conditions in Puno Bay.

Evaluation of the fisheries potential

Taking into account the lake's morphology and its great depth, two distinct ecological zones should be distinguished: the pelagic zone in deep open water and the shallower littoral zone containing the marginal belt of macrophytes and including the vegetated areas of the Huiñaimarca and the large bays.

The pelagic zone

Estimates have been made of the fish biomass and theoretical production in the pelagic zone (Richerson *et al.*, 1977), based on primary production data and coefficients of energy transfer between trophic levels ranging from 10 to 20% (Ryther, 1969). They thus estimated that the maximum sustainable yield (M.S.Y.) would be 50% of the total fish production. By extrapolating these data to the entire pelagic zone, the estimated possible yield of first level predators (ispi) would be 180 to 720×10^3 t year⁻¹ and that of secondary predators (trout and pejerrey) would be 18 to 140×10^3 t year⁻¹.

Studies using echo-integration techniques (Johannesson *et al.*, 1981), have estimated the pelagic biomass at between 80 180 and 87 754 tonnes.

A further assessment of the fisheries potential using the same techniques was carried out in 1985 in the pelagic zone of the lake, as part of the SELA programme. This study concerned three species: trout, pejerrey and *Orestias ispi*. Again this method gave a picture at one instant in time, because it was based on a single echo-location survey. Despite this, the results provided a degree of precision on the distribution of the fish fauna and of its density, which could not be produced by theoretical assessments from production levels. The main results are given in Figure 2. Over the approximately 3000 km² surveyed, the total biomass was estimated at 91,000 tonnes, with the following species distribution: trout 13 000 t (almost entirely in the Lago Grande), pejerrey 20 000 t, *O. ispi* 52,000 t, other species 6000 t (Anon., 1985). 98.5% of the biomass was concentrated in the Lago Grande.

Vaux et al. (1988) studied the distribution of pelagic species in the Lago Grande using gill-nets set at different depths and with trawls operating in 10 m depth. *Basilichthys bonariensis*, *Orestias ispi* and *Orestias mulleri* made

REEDENCES	METHODS	DATAS PER ZONES (t year-1)			
NEPENEIVOES	METHODS	Pelagic	Litoral		
Richerson <i>et al.</i> (1977) Chapman (1968) Johannesson <i>et al.</i> (1981) Larking (1970) Imarpe (1980)	Primary production Biomass production Acoustic method Artisan,fish. Artisan,fish.	180-720 x 10 ³ 110-300 x 10 ³ 80-87 x 10 ³ 0.02 x 10 ³ 1.86 x 10 ³	35-138 x 10 ³ 10 x 10 ³ 4.45 x 10 ³		

Table 6. Table of comparative values for theoretical fishery production

up most of the catch, the first two being the most abundant. *O. ispi* would currently appear to be the most abundant species in terms of biomass in the pelagic zone.

The littoral zone

Richerson *et al.* (1977) assumed that the primary production of the lake littoral was twice that of the pelagic zone. The trophic pathway leading to fish is not direct since part of the primary production passes through the organic detritus stage before moving onto the secondary level. For this reason we consider that fish production in the littoral zone is similar to that of the pelagic zone. This leads to a preliminary calculation of M.S.Y. for the lake littoral of 35 to 138×10^3 t year⁻¹, with a mean of 86.5 tonnes of first stage carnivorous fish.

Because of the technical limits on the use of echo-location methods, which cannot be used in shallow water areas, it is impossible to confirm or disprove these theoretical assessments. The fish biomass in large areas of the Lago Pequeño and the large bays of the Lago Grande cannot therefore be known with certainty. Similarly, nothing is known of the relative importance of the biomass in these parts of the lake compared to the pelagic zone. All that can be noted is that overall the fishery is more productive in the littoral zone than in the pelagic zone.

If these data are compared with the combined values for the small-scale fishery catch in the littoral zone in 1980 (10.7×10^3 t) and in the pelagic zone (0.06×10^3 t, mainly *O*. *ispi*), we arrive at a total yield for the whole of Lake Titicaca of 10.8×10^3 t, which represents approximately 20% of the theoretical capacity (Table 6).

The results given above are too fragmentary, both in time and in space, to provide an exact estimate of the biomass of the main species living in Lake Titicaca at any one point in time, and even less to provide information on year to year changes. It would be very useful to set up a permanent fisheries statistics programme, including both the Peruvian and Bolivian parts of the lake, so as to monitor and direct the exploitation of such an important source of animal protein for the Altiplano.

Fish-farming potential

Fish-farming, aiming at the rational production of fish and including controlling the growth rate and production, is a well-established activity in the Peruvian part of the lake. Alongside with small-scale fishing, intensive pisciculture of rainbow trout (*Salmo gairdneri*) in floating cages is a complementary activity to that of agriculture and provides a good income for the businesses involved.

History of trout farming in the Peruvian part of the lake

Only native species of fish of low fishery value occurred in Lake Titicaca before 1939. In 1935 American experts started the first research and proposed building a joint Peruvian/Bolivian piscicultural station. The project ended up with the formulation of an international plan approved by representatives of Peru and Bolivia. The United States sent a batch of 200,000 partly developed trout eggs, but the results were not at all positive. The Chucuito piscicultural station was founded in 1939–40 and started to rear the following species: rainbow trout (*Salmo gairdneri*), brown trout (*Salmo trutta fario*) and brook trout (*Salvelinus fontinalis*).

Between then and 1952, 69% of all the trout fingerlings (ca. 9 million fish) released in the whole of the Cordillera by the Department of Fisheries and Hunting were released in the Puno district. These releases led to natural recruitment in many of these water bodies.

The results of the first few years were a success and rainbow trout of considerable size were obtained, Lake Titicaca apparently becoming transformed into an enormous basin with exceptional conditions for rearing this introduced species. But, the invasion by this voracious species was to some extent deleterious for the native species.

The motives behind the release of trout fry into the various water bodies in the district were the social goals of providing the rural and urban populations with the opportunity of including this species in their everyday diet and of providing the fishermen living around the lake with a supplementary source of income. In the 1960s, however, uncontrolled exploitation at an industrial scale started for the production of canned fish, with the installation in Puno district of the following five factories: Compañia Pesquera de Puno (1961), Compañia Enlatadora de Trucha (1962), Empresa Pesquera del Titicaca (1963), Compañia Cordero Liebman (1964) and the Enlatadora de Huatajata (Bolivia). These factories decimated the trout stocks by uncontrolled exploitation in the absence of restocking programmes.

The yield of trout from the Peruvian part of Lake Titicaca reached 408.5 t in 1965, a figure which exceeded the production of the 107 fish farms existing in the country at this time, which had a total production of 206 t in 1976. Intensive pond culture of *Salmo gairdneri* started in 1970, reaching its maxi-

mum development in 1975, when there were 12 fish farms in operation in various parts of the Puno district.

The destruction of the trout population in the previous years led to the setting up in 1972 of two organisations, one with scientific aims and the other directed towards the commercial aspects of trout exploitation. A Regional Laboratory of the Instituto del Mar del Perú (IMARPE), was thus set up in Puno with the aim of carrying out research on Lake Titicaca and its catchment, whereas the purpose of the Fisheries Ministry Office was to monitor the hydrobiological resources. Preliminary studies of intensive rearing of *S. gairdneri* in floating cages started in 1977, the first trials being carried out in Huaquina Bay (Juli District), where best results were obtained because of the lower material investment costs compared to the installation of fixed rearing pens of netting.

In 1978 the "Programme of experimental rearing of trout in floating cages" was taken over by DIREPE-PUNO, stimulating the setting up of three businesses: one private and known as Altipesca S.A.; another a mixed economy venture, the Sais Cerro Grande and the third, a binational venture, Pesca-Perú Cordepaz-SELA.

Production in the Puno district

In 1979 the Chucuito hatchery alone produced 2.7×10^6 fertilised eggs and had a hatching success rate of 47.4% (DIREPE-Puno). The original aim was to produce fingerlings for the programme of restocking the various water bodies on the Altiplano, but this aim was then changed to provide fertilised eggs for intensive fish-farming to compensate for the insufficiency of the *S.* gairdneri population in the lake.

In 1980 the production with the floating cage system was 10 t, from an original stock of 80 000 fry released at the start into 11 cages measuring $5 \times 3 \times 1.5$ m, then moved to 3 cages for juveniles of $6 \times 5 \times 4$ m and finally to 4 adult cages, two being $37.5 \times 10 \times 5$ m and the other two $20 \times 10 \times 3$ m.

The "Proyecto Especial Titicaca" was started in 1985 by CORPUNO, with the mission of promoting trout farming in floating cages among the fishing communities along the Peruvian shores of the lake. Up until 1987, 29 cooperatives and companies managed either by the Proyecto Especial Titicaca or by private initiative had come into operation in the Peruvian part of Lake Titicaca.

By December 1990 this number had increased by 46% and had extended to other water bodies in the catchment such as lakes Saracocha, Arapa, Umayo and Lagunilla, where 17% of the total number of existing cooperatives and companies (63) have installed.

Statistical data on the project for production in controlled environments

Years	Kg
1984	35 429
1985	12 894
1986	34 959
1987	33 195
1988	117 641
1989	140 749

Table 7. Production of trout in floating cages in the Puno district

are found in Table 7. In 1989, over 140 000 kg of trout was recorded, with a mean of around 3000 kg per cooperative out of a total of 45.

The rainbow trout requires 9 about months of rearing to reach a commercial length and weight, and its sales price hardly exceeds the production costs. As a general rule, it is sold within the regional market at a low price, but 20% of the sales are carried out outside the Puno District (Lima, Arequipa) and some is exported to Bolivia, which enables the business to reach the level of profitability.

Fish farming attempts with other species

In 1990, IMARPE-Puno carried out a preliminary research programme on artificial spawning in the laboratory of the mauri (*Trichomycterus* sp.) and the yellow carachi (*Orestias luteus*), because of the possibilities of these species becoming extinct and in order to restock the lake.

For artificial spawning of the mauri, the dry fertilisation method was used, after which the fertilised eggs were left to incubate for ten days before they hatched. The larvae are not very mobile and are transparent, without skin pigmentation. At 27 days they already have a well-defined pigmentation and at about 32 days they have resorbed their yolk sac. From this time they start feeding, this being given in the form of living organisms (zooplankton).

Several attempts have also been made to breed the yellow carachi (*Orestias luteus*); fertilised eggs have been obtained, which were incubated at 15.5°C for 20 days with 80% survival.

Fish farming is therefore an important activity in Lake Titicaca, the sales of the fish produced providing good profits. In addition, the rearing method using floating cages is well adapted to the lake conditions and does not require very heavy investment in material. Local manufacture of feeds could also decrease the operational costs of fish rearing.

It would appear that piscicultural activity is less well-developed in the Bolivian part of the lake than in the Peruvian part. Here it is mainly private entreprises, with one or two floating cages enabling a fisherman to have a supply of fish with which he can satisfy the demands of the small restaurants along the shore (at Chua, Huatajata, etc.). A larger, also private exploitation, exists at the outlet of the Tiquina Strait, on the south-west bank of the Lago Grande.

Finally, mention must be made of the important piscicultural station installed in the Lago Pequeño, at the entrance to the Tiquina Strait, by the Japanese International Cooperation Agency (JICA). The piscicultural work carried out since 1977 by this agency on the Altiplano and in the Cordillera has resulted in the construction near San Pablo of a large production unit for producing fry of *Salmo gairdneri* in ponds and rearing them on to adults in floating cages. This centre trains fishermen and peasants interested in trout farming and sells fingerlings for stocking small village fish ponds and high altitude lakes in the Cordillera.

References of chapter VII.3

- ALFARO (R.), BUSTAMANTE (E.), TORRES (J.), TREVIÑO (H.), WURTSBAUGH (W.A.), 1982. La pesca en el lago Titicaca, presente y futuro. Inf. final Proyecto FAO.PER-76.022. Roma, 59 p., multigr.
- Anon., 1985. Resultados de la evaluación de los recursos pesqueros del lago Titicaca. Anexo nº 3. Inf. preliminar. Convenio IMARPE-UMSA. Callao, 53 p., multigr.
- Anon., 1986. Proyecto Evaluación de los recursos pesqueros del lago Titicaca. Informe final IMARPE-UMSA. Callao, 132 p., multigr.
- AVILA (L.), CHARAJA (M.), PAZ (P.), LEVIEIL (D.), 1989. The socio-economic importance of fisheries in Puno Bay. *In*: Pollution in Lake Titicaca, Peru. Northcote, Morales, Levy, Greaven eds., Westwater Research Centre, Univ. Brit. Columbia, Vancouver: 129– 153.
- BUSTAMANTE (E.), TREVIÑO (H.), 1976. Descripción de las pesquerías en el lago Titicaca. Inst. Mar Perú, Puno, 74 p., multigr.
- CHAPTERMAN (D.W.), 1978. Production in fish populations. Ecology of Freshwater Fish production.
- FRANC (J.), LAUZANNE (L.), ZUNA (F.), 1985. Algunos datos sobre las pesquerías de la parte oriental del lago Titicaca Menor. *Rev. Inst. Ecol.*, La Paz, 7: 1–21.
- JOHANNESSON (K.), VILCHEZ (R.), BERTONE (D.), 1981. Acoustic estimation of ichthyomass and its distribution in Lake Titicaca. FAO report: FAO.GCP.RLA.025 (NOR): 65 p., multigr.
- LARKIN (P.A.), 1970. Fisheries managements, an essay for ecologists. Ann. Rev. of Ecol. and System., 9: 57–73.
- RICHERSON (P.J.), WIDMER (C.), KITTEL (T.), 1977. The limnology of Lake Titicaca (Peru-Bolivia), a large, high altitude tropical lake. Inst. Ecol. Publ. no. 14, Univ. of California, Davis: 78 p.
- RYTHER (J.H.), 1969. Photosynthesis and fish production from the sea. Science.
- VAUX (P.), WURTSBAUGH (W.A.), TREVIÑO (H.), MARIÑO (L.), BUSTAMANTE (E.), TORRES (J.), RICHERSON (P.J.), ALFARO (R.), 1988. Ecology of the pelagic fishes of Lake Titicaca, Peru-Bolivia. *Biotropica*, 20 (3): 220–229.
- VERA RIVES PLATA (J.), 1984. Informes nacionales sobre el desarrollo de la acuicultura en América Latina. 13: Breve historia de la acuicultura y su organización en el Perú. FAO report. Inf. pesca 294 (supl.), multigr.

VII.4. CONTAMINATION VII.4a. Eutrophication and pollution problems

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Lakes at low latitude (tropical or sub-tropical) but high altitude (generally over 1000 m) have special features which can make them more vulnerable to eutrophication and pollution problems. Not only do they commonly receive high levels of solar radiation with reduced seasonal fluctuation, but those at intermediate elevations (usually less than 4000 m) and of reasonable size and depth can maintain rather high annual mean temperatures and thereby a relatively long growing season. Both these aspects may lead to higher primary production and biomass. Furthermore at elevations approaching that of Lake Titicaca (over 3800 m) gas solubility in water is considerably reduced, so that fully oxygenated water for example at 10°C contains only 65% of what it would at sea level. This feature can intensify limnological problems associated with anoxic conditions as well as physiological problems of oxygen stress for some of the biota especially those groups of fishes often important for food and recreation. For these reasons alone it would be useful to examine the eutrophication and pollution problems that might occur in a large lake such as Titicaca, lying at approximately 16°S latitude and at an elevation of 3850 m.

But these problems take on an even greater significance when one recalls that Lake Titicaca has been an important centre for a large human population for several thousand years, and one that has relied on its various aquatic resources, some of which at least locally now seem threatened by problems to be considered in this chapter. In addition, because of its isolation and long period of existence spanning about a million years, the lake has developed a rich and unique biota, with many endemic species which have attracted scientific attention since the 1870s.

Understandably most scientific studies on Lake Titicaca have concentrated on the large main and deep basin, dealing with various aspects of its limnology including fishes (see for example Gilson, 1939, 1964; Richerson *et al.*, 1977; Northcote, 1979). Here the waters have often been noted for their great clarity and little evidence of pollution. Some attention has been given to the extinction of a few of its endemic fish species (Villwock, 1972) and to the collapse of an important rainbow trout fishery (Everett, 1973), but these

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apparently have not been related in any direct way to problems of eutrophication or pollution, either in the lake or its watershed. My report to the Food and Agriculture Organization of the United Nations in 1979 did point to the potential problems of eutrophication in one part of the lake (Puno Bay) and to other pollution problems arising largely in its tributaries (Northcote, 1979). Shortly thereafter Dr C. Luna, a professor at Puno (Universidad Nacional del Altiplano), noted that there were several serious forms of pollution in Puno Bay of Lake Titicaca, probabably referring mainly to conditions in inner Puno Bay (Luna, 1981). The first systematic study of water pollution problems in Lake Titicaca began early in 1981 with the start of a training and research programme developed between the universities of British Columbia, Canada (UBC) and Puno, Peru (UNA) under the support of the Canadian International Development Agency (CIDA). Some interim results of this work have already been presented (Morales et al., 1984), its effectiveness reviewed (Dorcey and Northcote, 1988), and most aspects of its first phase now have been assembled in a book on the project (Northcote et al., 1989, 1991). The latter focuses almost entirely on the most severely polluted area of the whole lake - inner Puno Bay - but comparisons are often made with outer Puno Bay and with the main lake.

This chapter will summarize the major findings, relevant to pollution, of the first phase of the UBC/UNA/CIDA study (data collected mainly between 1981 and 1984). In addition other aspects of pollution evident in the main basin of Lake Titicaca will be reviewed and compared to those of Puno Bay that are examined in more detail. Furthermore, reference will be made to conditions in some parts of the lake watershed where human activities have resulted in serious environmental degradation of stream and river habitats with probable effects on the lake itself.

Physical and chemical factors

Location and morphometry

As already noted, the tropical location of Lake Titicaca confers special features on the system that are relevant to pollution problems. In addition to those given previously, it should be noted that ultraviolet radiation levels will be high, as will rates of evaporation, and these will have important effects on the quantity of liquid wastes which make their way to the lake seasonally, as well as on pathogen life spans. Thus one would expect major differences in quantity and virulence of discharges reaching the lake between wet and dry seasons of the year, with higher levels in the former.

The morphometry of the lake watershed and that of the lake basin itself affect the regional location of serious pollution impacts. Nearly three-quarters of Titicaca's watershed enters the northwestern half of the lake via the four major inlet rivers – Ilave, Coata, Ramis, and Suches (Fig. 1). The



Figure 1. Inner Puno Bay showing the 5 m depth contour, location of major totora stands and sewage outfalls from the city of Puno. Left inset shows the drainage basin of Lake Titicaca; right inset shows major tributaries to Puno Bay, location of the two main cities (Puno and Juliaca) and minor lakeshore communities, and location of main totora stands.

southeastern half of the lake including the Lago Pequeño receives only short and small tributaries. Consequently impacts from the greater part of the drainage basin, which is heavily used for agriculture as well as mining, and which contains the two largest population centres (Juliaca and Puno each with over 100,000 inhabitants) have the potential of passing through much of the lake before being flushed out its outlet at the southern end of the Lago Pequeño (Fig. 1).

Another feature of the lake watershed is that of its flat basin containing enormous quantities of fine lacustrine sediments resulting from the large postglacial lake which once occupied much of the adjacent Altiplano at a level some 100 m above that of the present Lake Titicaca. These flats and old lake terraces provide a major source of fine sediment which can be carried into the lake during high runoff periods of the wet season.

Hydraulic mining for placer gold in the headwaters of the Ramis/Huancane system surely must cause severe problems of sediment deposition in the middle reaches of the rivers used by trout for spawning and rearing. Sediment loads carried in runoff from agricultural areas lining the stream and river banks with little or no riparian vegetation must also add to this problem.

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The morphometry of Puno Bay itself makes it highly prone to serious pollution problems. Unlike the large, deep (285 m) and open main lake (Lago Grande), Puno Bay is for the most part cut off from the central lake axis (Fig. 1), and is relatively shallow (maximum depth c. 30 m). Even more critical is the fact that effluents from the only large cities in the watershed of the whole lake, Juliaca and Puno, drain directly into this bay, the latter through an even more constricted inner Puno Bay (Fig. 1). Not surprisingly, inner Puno Bay has the most serious eutrophication and pollution problems to be found anywhere in Lake Titicaca.

Water temperature and transparency

The shallow waters of inner Puno Bay along its western shoreline reach temperatures close to 20°C during the summer wet season (Morales *et al.*, 1989a), values considerably higher than in the limnetic waters of outer Puno Bay or the main lake. Consequently production and decomposition rates should be thermally enhanced in the inner bay region during the wet season but not in the dry season when surface temperatures in nearly all areas except the immediate shoreline are usually close to 11°C.

Water transparency of inner Puno Bay, sometimes less than half a metre, is much lower than that of outer Puno Bay (4-7 m) or the main lake (5-10 m). This is a result of high planktonic algal blooms and at times high suspended sediment levels in the inner bay. Water transparency of inner Puno Bay is usually lowest in the wet season (February to April) and highest in the dry season (Fig. 2), in part responding to seasonal changes in suspended sediment inputs. Similar seasonal fluctuation probably occurs off the mouths of most inlet streams and rivers.

Dissolved oxygen supply and demand

Periodically high supersaturations and marked diel pulses of dissolved oxygen occur near the shore of inner Puno Bay (Miranda *et al.*, 1989), indicative of its high photosynthetic activity in comparison to the slight supersaturations that occasionally occur in outer Puno Bay or Lago Grande (Richerson *et al.*, 1975, 1977, 1986). Highest rates of oxygen demand are recorded close to the western shoreline of inner Puno Bay (Miranda *et al.*, 1989) and reflect the large amounts of organic matter in wastewater entering there as well as decomposition of the littoral vegetation, especially floating forms such as *Lemna* spp. At times, dissolved oxygen concentrations in inner Puno Bay become very low (less than 3 mg.l^{-1} at the surface; 0 at depths below 1 m) and these conditions often coincide with mortalities of fish (*Orestias* spp.).



Figure 2. Upper: monthly precipitation at Puno, October 1981 to December 1982. Lower: seasonal changes in percent areal coverage of inner Puno Bay by two categories of water transparency; maps show spatial distribution of 5 water transparency categories on 2 April and 20 August, 1982 (darkest shading less than 1.0 m, two intermediate shadings = 1.0 to less than 1.5 m and 1.5 to less than 2.0 m respectively, blank = greater than 2.0 m; solid circles = location of minimum transparency; open circles = location of maximum transparency; see Morales *et al.* 1989a, Figs. 3.5 and 3.6 for details).

Dissolved nutrients

Nitrate and ammonium nitrogen concentrations of inner Puno Bay (1982–1983) were usually well above those in outer Puno Bay or the main lake, and on several occasions exceeded the 21 μ g atom.l⁻¹ level conducive to severe eutrophication (Janus and Vollenweider, 1981). Similarly, those for soluble reactive phosphorus at inner bay stations were almost always above the 0.3 μ g atom.l⁻¹ level conducive to severe eutrophication, but were rarely so at outer bay or main lake stations. A very rough estimate of phosphorous

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loading to inner Puno Bay $(3.1 \text{ g.m}^{-2}.\text{yr}^{-1})$ placed it very much above its dangerous level $(0.1 \text{ g.m}^{-2}.\text{yr}^{-1})$ for eutrophication.

Industrial wastes

Effluents from industrial and business activity associated with the cities of Juliaca and Puno no doubt gain entry to Lake Titicaca by river discharge (Rio Coata) or storm and wastewater drainage. The extent and significance of these are largely unknown except perhaps for Puno where they probably are small in comparison to domestic sewage input.

On the eastern shoreline of Lake Titicaca near the mouth of Rio Suches (Fig. 1), effluents and drainage from the Matilde Mine have entered the lake for many years. Dr C. Dejoux has examined effects of this effluent on the benthic invertebrate community (see section 6 under biological effects). Several other old mine sites occur near the shoreline of the lake and leachates from these may find their way into the lake and its biota. Trace metal analyses of four species of fish taken at one such site near Ojerani in Puno Bay showed moderately high levels of arsenic and mercury (Treviño *et al.*, 1989).

Biological effects and consequences

Pathogenic bacteria

The concentration of coliform bacteria (total and faecal) has commonly been used as an indicator of potential pathogenic bacteria in water and acceptable levels have been set for a variety of water uses. Average number of coliforms per 100 ml were measured seasonally in a series of transects over much of inner Puno Bay and also at three near-shore locations in outer Puno bay (Rivera *et al.*, 1989). No coliform bacteria were found at any time or location in the latter area whereas in inner Puno Bay very high counts (some in the order of 100,000 per 100 ml) occurred, with the highest usually being close to shore. Coliform counts at some sites were much above the safe level even for body contact (work or recreation) and at most sites greatly exceeded those for safe use of the raw water for human consumption. Numbers decreased considerably at the outermost station (2 km offshore) at all times of the year.

Parasitic invertebrates

School age children living close to Lake Titicaca have a high incidence of intestinal helminths, many areas being in the 50 to 70% range. Nearly a third of some 159 shore-dwelling families at Puno tested positive for such parasites

(Sánchez *et al.*, 1989). A sampling programme for parasitic helminth eggs, at similar locations to those used for pathogenic bacteria, showed none at outer Puno Bay sites. High numbers, averaging up to 7.5 eggs per litre of water, were found at sites close to the shore of Puno Bay but they decreased sharply 1 km offshore (Sánchez *et al.*, 1989).

Attached and planktonic algae

Highest biomass and growth rates of periphyton were recorded at littoral stations close to the city of Puno, compared to those in outer Puno Bay (Cornejo and Aramayo 1989). Similarly phytoplankton abundance of inner Puno Bay was almost four times that of the outer bay (Cornejo *et al.* 1989), and although chlorophytes accounted for 50 to 60% of the average total abundance in both areas, blue-greens were more prevalent in the inner bay and diatoms were more common in the outer bay.

Macrophytes

The macrophyte community of inner Puno Bay may have changed in response to its severe eutrophication (Cornejo and Aramayo 1989), especially when compared with outer Puno Bay. *Lemna* spp. form very dense floating mats around many parts of the inner bay shoreline but not in the outer bay or main lake. The percent areal coverage of *Chara* spp. for the inner bay is only one fifth that for the outer, and that of *Schoenoplectus tatora* is reduced to nearly a third in the inner compared to the outer bay. *Potamogeton strictus* is the dominant macrophyte of the inner bay, covering 95% of its area, compared to only 47% of the outer bay. Areal coverage of the inner bay by totora (*Schoenoplectus tatora*) may have been as high as 70% in the mid 1930s, but by the early 1980s has been reduced to only about 15%, with most of that classified as sparse stands (Collot 1981).

Zooplankton

Eutrophication of inner Puno Bay waters is clearly indicated by its zooplankton community (Muñiz *et al.*, 1989). Significantly higher average densities occur there (30,000 to nearly a million organisms per m³ during January to June 1982) compared to the outer bay (4000 to less than 20,000 per m³ over the same period) and also to the main lake. Calanoid copepods (*Boeckella* spp.) are always a dominant component of the main lake and outer Puno Bay community, but are rarely so for the inner bay where cyclopoid copepods and rotifers are dominants. The calanoid/cyclopoid + cladoceran ratio, used as an indicator of lake trophic conditions (values usually well above 2 in oligotrophic waters, but as low as 0.2 in very eutrophied systems – see Gannon and Stemberger, 1978), ranged between 0.02 and 0.04 in 1982 for inner Puno Bay and between 0.3 and 0.4 for outer Puno Bay. In the main lake a value of 10.1 was calculated from data in Richerson *et al.*(1977).

Zoobenthos

The zoobenthic community of Lake Titicaca also has responded to the localized effects of severe eutrophication in inner Puno Bay and to mine effluents in the main lake. In the former case several lines of evidence suggest that inner Puno Bay eutrophication has proceeded far beyond the initial phases and is now reaching a state of very severe environmental stress (Morales et al., 1989b). Firstly, the abundance of benthic invertebrates, which may have increased during initial stages of eutrophication, is now much lower in the inner than outer bay littoral areas (2, 4 and 6 m). At times no live benthos was found at 6 m in the inner bay, whereas numbers often exceeded 6000 animals per m^2 at that depth in the outer bay. Secondly, benthic abundance was greatly reduced in areas close to major eutrophication sources along the inner bay shoreline but less so at other locations. There were no marked changes in abundance between sites along the outer bay shoreline. Thirdly, taxa richness was reduced fourfold for the inner bay compared to the outer bay benthic community, but several taxa common at the outer bay (sphaeriids, gastropods) previously did occur at the inner bay transects as evidenced by their empty shells. Finally, the three taxa which can persist at some times of the year in the deeper areas of the inner bay oligochaetes, leeches, and chironomids - are groups containing forms known to be very tolerant of pollution.

Turning to the main lake, there seems to be only one area where severe pollution is obviously reflected in the benthic community. This is off the mouth of the River Suches (Fig. 1) which has received a heavy effluent load from operations of the Matilde Mine. A study made by Dejoux in February 1987 suggests that an area extending out into the lake nearly 1 km with a width up to 0.5 km has been greatly reduced in benthic abundance and taxa richness.

Fish

The fish community of inner Puno Bay has shown a response to the eutrophication of that area. Three species of native cyprinodonts (*Orestias ispi*, *O. luteus*, and *O. olivaceus*) showed greatly reduced catches per unit effort in inner compared to outer Puno Bay whereas that for the introduced 'pejerrey' (*Basilichthys bonariensis*) was much higher in inner Puno Bay (Treviño *et* *al.*, 1989). Shifts in diet and growth rate suggest that the 'pejerrey' are still receiving some beneficial effects from the eutrophication of inner Puno Bay.

Periodic fish kills have occurred in the inner bay, especially when temperature and oxygen conditions would have been severely stressful. Nevertheless, fish kills do occur at times elsewhere in the lake. Wurtsbaugh and Alfaro (1988) record such an event in association with the protozoan parasite, *Icthyophthirius multifiliis*.

Discussion

Eutrophication and pollution problems in Lake Titicaca appear to be restricted to two areas, one in the inner part of Puno Bay and the other at the mouth of the River Suches. The latter, though still severely affected, may gradually show improvement as the mine causing the problem is no longer in operation. Nevertheless effects can continue for many years as contaminants leach out of the affected areas.

The problem at inner Puno Bay seems far more severe, widespread, and likely to intensify as population growth in and around Puno increases sharply. There seems little doubt that the eutrophication and water contamination problems occurring there are caused mainly by the inflow of untreated domestic sewage entering the shoreline from a large number of outfalls. With the rapid increase in the population of Puno (doubling in about 12 years), the economic difficulties faced by the country generally and the community locally, the problems of a poor water supply (both in quantity and quality), and the legacy of a totally inadequate and antiquated sewage collection system, the prospects of effecting a major improvement seem slight in the near future. One positive approach is the cooperative pilot study being conducted jointly by UNA staff with the Instituto de Aguas Alto Andinas under the direction of Professora Elizabeth Cornejo and that of SEDAPUNO (Servicio de Agua Potable y Alcantarillado de Puno) under the direction of sanitary engineer Rosana Berolatti to evaluate use of aquatic macrophytes in lakeshore lagoons as a socio-economically feasible means of interim sewage treatment. This second phase of the work at Puno, funded again in part by CIDA, is showing considerable promise but more time and studies are needed before an appropriate evaluation can be made.

At present the strongly negative effects of severe eutrophication in waters of Lake Titicaca are largely confined to inner Puno Bay, partly as a result of its morphometric characteristics and the restriction of free circulation caused by aquatic macrophyte beds (see Fig.1). But if the latter continue to recede, severely polluted water will surely begin to reach out to the unique floating island communities of the Urus people and eventually extend further into outer Puno Bay.

One should be cautious in assuming from this summary that the pollution problems of Lake Titicaca are indeed confined to only two rather small localities. These in fact are the only areas where detailed studies have been made in the littoral zone and it would not be surprising to find that other areas such as those around the mouth of the Rio Coata and Rio Ramis as well as in the shallows of Lago Pequeño are also subject to some pollutant stress. Furthermore few if any intensive studies have been made on water quality conditions and biological effects in the various parts of the lake's watershed, where impacts of agricultural and mining activity are likely to have been expressed both locally and further downstream. The large area and volume of clear, unpolluted water in Lago Grande should not be taken as a signal that all is well in the Lake Titicaca system!

References of chapter VII.4

- COLLOT (D.), 1981. Les macrophytes de quelques lacs andins (lac Titicaca, lac Poopo, lacs des vallées d'Hichu Kkota et d'Ovejhuyo). ORSTOM. La Paz, 115 p., multigr.
- CORNEJO (E.), ARAMAYO (H.A.N.), 1989. Effects of eutrophication on periphyton and macrophytes. *In*: Pollution in Lake Titicaca, Peru. Northcote, Morales, Levy, Greaven eds., Westwater Research Centre, Univ. Brit. Columbia, Vancouver: 73–79.
- CORNEJO (E.), COMIN (F.), AREVALO (J.Z.), TORRES (M.V.), GREAVEN (M.S.), 1989. Effects of eutrophication on phytoplankton. *In:* Pollution in Lake Titicaca, Peru. Northcote, Morales, Levy, Greaven eds., Westwater Research Centre, Univ. Brit. Columbia, Vancouver: 57–72.
- DORCEY (A.H.J.), NORTHCOTE (T.G.), 1988. Interagency cooperation in training for water resources management: Canadian experiences in the Peruvian Altiplano. Can. Water Res. J., 13: 43-51.
- EVERETT (G.), 1973. The rainbow trout Salmo gairdneri (Rich.) fishery of Lake Titicaca. J. Fish. Biol., 5: 429-440.
- GANNON (J.E.), STEMBERGER (R.S.), 1978. Zooplankton (especially crustaceans and rotifers) as indicators of water quality. *Trans. Amer. Micros. Soc.*, 97: 16–35.
- GILSON (H.C.), 1939. 1. Description of the expedition. In: The Percy Sladen Trust Expedition to Lake Titicaca in 1937. Trans. Linn. Soc. London, ser. 3, 1: 1–20.
- GILSON (H.C.), 1964. Lake Titicaca. Verh. Internat. Verein. Limnol., 15: 112-127.
- JANUS (L.L.), VOLLENWEIDER (R.A.), 1981. The OECD cooperative programme on eutrophication. Canadian contribution. Summary Report Nat. Water Research Inst., Inland Waters Directorate, Canada Centre for Inland Waters, Burlington, Ont., Sci. Series n° 131: parts I to IX with annexes, 325 p.
- LUNA (C.), 1981. Calidad del agua de la bahía de Puno. UNTA, Puno, 17 p., multigr.
- MIRANDA (N.), HALL (K.J.), NORTHCOTE (T.G.), HINOJOSA (A.A.), SARMIENTO (A.), MOLLOCONDO (M.H.), 1989. Effects of eutrophication on chemical conditions. *In:* Pollution in Lake Titicaca, Peru. Northcote, Morales, Levy, Greaven eds., Westwater Research Centre, Univ. Brit. Columbia, Vancouver: 33–56.
- MORALES (P.), NORTHCOTE (T.G.), LEVY (D.A.), 1984. A centre for limnological training and research on Lake Titicaca and the aquatic ecosystems of the Peruvian Altiplano. *Verh. Internat. Verein. Limnol.*, 22: 1335–1339.
- MORALES (P.), NORTHCOTE (T.G.), ZEA (W.), VASQUEZ (M.E.), 1989a. Effects of eutrophication on physical conditions. *In*: Pollution in Lake Titicaca, Peru. Northcote, Morales, Levy, Greaven eds., Westwater Research Centre, Univ. Brit. Columbia, Vancouver: 19-31.
- MORALES (P.), CORNEJO (E.), LEVY (D.A.), CHALLCO (D.), MEDINA (A.C.), NORTHCOTE (T.G.), 1989b. Effects of eutrophication on zoobenthos. *In*: Pollution in

Lake Titicaca, Peru. Northcote, Morales, Levy, Greaven eds., Westwater Research Centre, Univ. Brit. Columbia, Vancouver: 101-113.

- MUÑIZ (B.V.), CHAPTERMAN (M.A.), CHINO (B.), AZURIN (E.), NORTHCOTE (T.G.), 1989. Effects of eutrophication on zooplankton. *In*: Pollution in Lake Titicaca, Peru. Northcote, Morales, Levy, Greaven eds., Westwater Research Centre, Univ. Brit. Columbia, Vancouver, 81–100.
- NORTHCOTE (T.G.), 1979. Investigation and recommendations on the hydrobiological resources of the Lake Titicaca system, Peru. Report FAO.OPER.76.022, 156 p.
- NORTHCOTE (T.G.), MORALES (P.), LEVY (D.A.), GREAVEN (M.A.), 1989. Pollution in Lake Titicaca, Peru: training, research and management. Westwater Research Centre, Univ. Brit. Columbia, Vancouver, 262 p.
- NORTHCOTE (T.G.), MORALES (P.), LEVY (D.A.), GREAVEN (M.S.), 1991. Contaminación en el lago Titicaca, Perú: capacitación, investigaciones y manejo. Westwater Research Centre, Univ. Brit. Columbia, Vancouver. Inst. Aguas Alt. And., UNTA, Puno, 278 p.
- RICHERSON (P.J.), WIDMER (C.), KITTEL (T.), LANDA (A.), 1975. A survey of the physical and chemical limnology of Lake Titicaca. Verh. Internat. Verein. Limnol., 19: 1498– 1503.
- RICHERSON (P.J.), WIDMER (C.), KITTEL (T.), 1977. The limnology of Lake Titicaca (Peru-Bolivia). Univ. California, Davis, Inst. Ecology, 14, 78 p., multigr.
- RICHERSON (P.J.), NEALE (P.J.), WURTSBAUGH (W.A.), ALFARO (R.), VINCENT (W.), 1986. Patterns of temporal variation in Lake Titicaca. A high altitude tropical lake. 1. Background, physical and chemical processes, and primary production. *Hydrobiologia*, 138: 205-220.
- RIVERA (C.), HALL (K.J.), ESCOBEDO (B.E.), ROMERO (M.T.), 1989. Pathogenic bacteria in Puno Bay and Puno well water. *In*: Pollution in Lake Titicaca, Peru. Northcote, Morales, Levy, Greaven eds., Westwater Research Centre, Univ. Brit. Columbia, Vancouver: 177–190.
- SANCHEZ (C.), MORALES (P.), CHURA DELA (M.A.), LUQUE (D.M.), APAZA (C.), 1989. Parasites in Puno Bay and in the population of Puno. *In*: Pollution in Lake Titicaca, Peru. Northcote, Morales, Levy, Greaven eds., Westwater Research Centre, Univ. Brit. Columbia, Vancouver: 191–205.
- TREVIÑO (H.), TORRES (J.), CHOQUEHUANCA (D.J.), LEVY (D.A.), NORTHCOTE (T.G.), 1989. Effects of eutrophication on fish. *In*: Pollution in Lake Titicaca, Peru. Northcote, Morales, Levy, Greaven eds., Westwater Research Centre, Univ. Brit. Columbia, Vancouver: 115–128.
- VILLWOCK (W.), 1972. Gefahren f
 ür die endemische Fishfauna durch Einb
 ürgerungsversuche und Akklimatisation von Fremdfischen am Beispiel des Titicaca-Sees (Peru-Bolivien) und des Lanao-Sees (Mindanao/Philippinen). Verh. Internat. Verein. Limnol., 18: 1227–1234.
- WURTSBAUGH (W.A.), ALFARO (R.), 1988. Mass mortality of fishes in Lake Titicaca (Peru-Bolivia) associated with the protozoan *Ichthyophthirius multifiliis*. *Trans. Am. Fish. Soc.*, 117: 213–217.

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