

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; Reyssac 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 (Lieberman 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

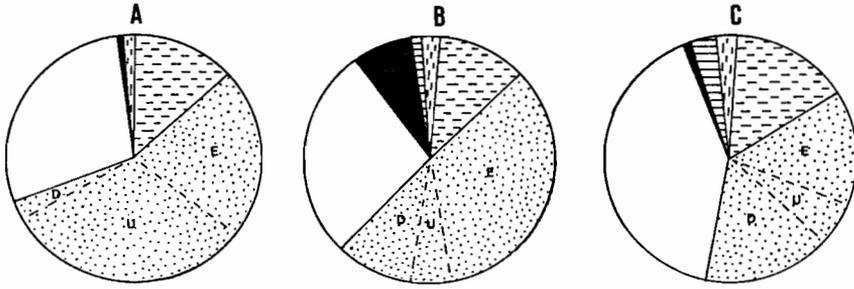


Figure 1. Graphical representation of the proportions of different algal groups in the algal flora of Lake Titicaca. A: after Freguelli (1939) and Tutin (1940); B: after Carney *et al.* (1987); C: after Servant-Vildary and Iltis. Horizontal dashes, cyanophytes; Dots, chlorophytes (E, euclorophytes; U, Ulotrichales; D, desmids); Blank, bacillariophytes (diatoms); Black, pyrrophytes; Horizontal lines, euglenophytes; 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 euclorophytes, 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 Freguelli (*op. cit.*), 0.19 in that of Carney *et al.* (*op. cit.*), and 0.08 in that of Servant-Vildary (*op. cit.*).

Table 1. Number of taxa and proportions of the major groups of algae in the flora of Lake Titicaca.

	FRENGUELLI, 1939 TUTIN, 1940		CARNEY, RICHERSON, ELORANTA, 1987		SERVANT-VILDARY ILTIS (in press)	
	N taxa	%	N taxa	%	N taxa	%
Cyanophyceae	17	12.5	19	11.0	26	10.0
Chlorophyceae	78	57.3	86	50.0	112	43.3
- Euclorophyceae	31	22.8	60	34.9	58	22.4
- Ulotrichophyceae	43	31.6	8	4.6	9	3.5
- Desmidiaceae	4	2.9	18	10.5	45	17.4
Euglenophytes	0	0.0	2	1.2	9	3.5
Pyrrophytes	1	0.8	14	8.1	7	2.7
Xant. + 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

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 deeper-water 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 (Therzien, 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).

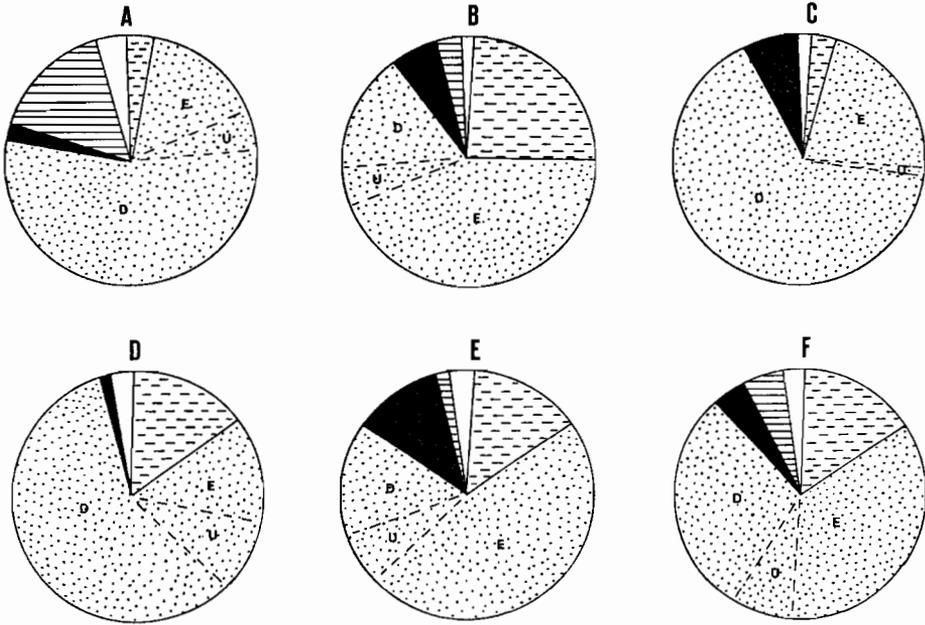


Figure 2. Graphical representations of proportions of major algal groups (excluding diatoms) from lists of algal floras. A: in Bolivian Amazon (Therezien), B: in Peruvian lakes (Hegewald *et al.*), C: in alpine lakes of the Vanoise (Martinot and Rivet), D: in high-altitude lakes of the La Paz, Bolivia, region (Iltis), E and F: Lake Titicaca (Carney *et al.*) and (Iltis), respectively. Horizontal dashes, cyanophytes; Dots, chlorophytes (E, euclorophytes; 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 Euclorophyceae 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

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.

	Bolivian Amazon (Thérózien)	Peruvian lakes (Hegewald <i>et al.</i>)	Alpine lakes (Martinot and Rivet)	Andean lakes (Illis)	Lake Titicaca (Carney <i>et al.</i>)	Lake Titicaca (Illis)
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
Desmidiaceae	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. Chyrs.	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	0	12.3	12.5	11.1	31.1
% of genus common with Lake Titicaca						
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	-	-

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.

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, Zygothryxales) 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. Chapman 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 *Franciaea*, *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. *Söruï, 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. Biomassas 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.ORSTOM, La Paz, Informe 14: 50 p., multigr.
- ILTIS (A.), 1991. Algues du lac Titicaca bolivien. *Cryptogamie, Algologie*, 12 (3): 1–18.
- ILTIS (A.), COUTE (A.), 1984. Péridinales (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. *Söruï, 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 phytoplanktoniques et production primaire du lac Titicaca. *Rev. Hydrobiol. trop.*, 14 (4): 349–380.
- LAZZARO (X.), 1982. Biomasses, peuplements phytoplanktoniques 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 raphe-bearing 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 fluviolacustres plio-pléistocènes de la Formation Charaña (Cordillère occidentale des Andes, Bolivie). *Cah. ORSTOM, 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 Desmidiées. *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 Desmidiées). *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: Desmidiées. *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.

- 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 diel 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.), WURTSBAUGH (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.), RICHERSON (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.

C. DEJOUX and A. ILTIS / Editors

Lake Titicaca

A Synthesis of Limnological Knowledge



Kluwer Academic Publishers

Lake Titicaca

A Synthesis of Limnological Knowledge

Edited by

C. DEJOUX and A. ILTIS



KLUWER ACADEMIC PUBLISHERS

DORDRECHT / BOSTON / LONDON

Library of Congress Cataloging-in-Publication Data

Lake Titicaca : a synthesis of limnological knowledge / edited by C. Dejoux and A. Iltis.

p. cm. -- (Monographiae biologicae ; v. 68)

Includes indexes.

ISBN 0-7923-1663-0 (HB : alk. paper)

1. Limnology--Titicaca Lake (Peru and Bolivia) 2. Aquatic resources--Titicaca Lake (Peru and Bolivia) I. Dejoux, Claude.

II. Iltis, A. III. Series.

QP1.P37 vol. 68

[QH128]

574 s--dc20

[574.5'26322'098412]

92-7958

ISBN 0-7923-1663-0

Published by Kluwer Academic Publishers,
P.O. Box 17, 3300 AA Dordrecht, The Netherlands.

Kluwer Academic Publishers incorporates
the publishing programmes of
D. Reidel, Martinus Nijhoff, Dr W. Junk and MTP Press.

Sold and distributed in the U.S.A. and Canada
by Kluwer Academic Publishers,
101 Philip Drive, Norwell, MA 02061, U.S.A.

In all other countries, sold and distributed
by Kluwer Academic Publishers Group,
P.O. Box 322, 3300 AH Dordrecht, The Netherlands.

Printed on acid-free paper

All Rights Reserved
© 1992 Kluwer Academic Publishers

No part of the material protected by this copyright notice may be reproduced or utilized in any form or by any means, electronic or mechanical, including photocopying, recording or by any information storage and retrieval system, without written permission from the copyright owner.

Printed in the Netherlands