VI.1c. Phytoplankton: Quantitative aspects and populations

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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 l^{-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 l^{-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 μm^3, medium forms of 350–3500 μm^3, large forms of 3500–10,000 μm^3, and the largest forms of greater than 10,000 μm^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 μm^3 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 μm^3, 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-*

Table 1. Average percentages of major algal groups in the Bolivian side of the lake. These percentages were calculated according to cellular biovolumes rather than number of individuals.

	April 1985	June 1985	December 1985	April 1986	October 1986	February 1987	Mean
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.

Table 2. Average values of the Shannon diversity index during six cruises made in the Bolivian side of Lake Titicaca.

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

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 phyto-plankton 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 mg C 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).

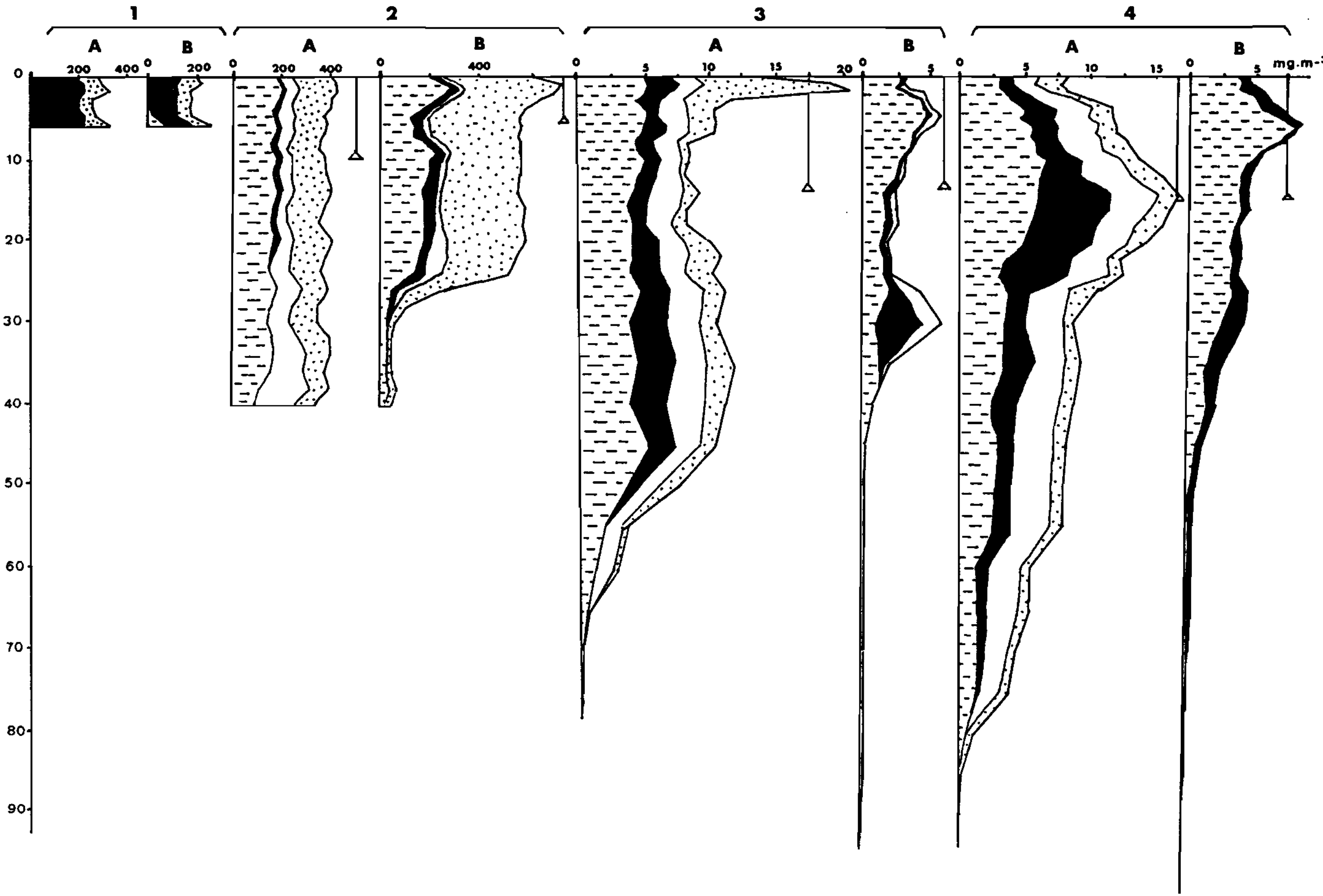

Figure 1. Vertical algal biomass distribution in Lago Menor (left) and in Lago Mayor (right). 1: shallow zone of Lago Menor, 2: Chua Depression, 3: Lago Mayor close to Island of Moon, 4: close to Island of Sun; A: during mixing (13–15 July 1988), B: during stratification (14–16 December 1988). To the right of each profile is the Secchi depth reading (except the first station, where it was not possible). Dashes-cyanophytes; black-pyrrhophytes; white-

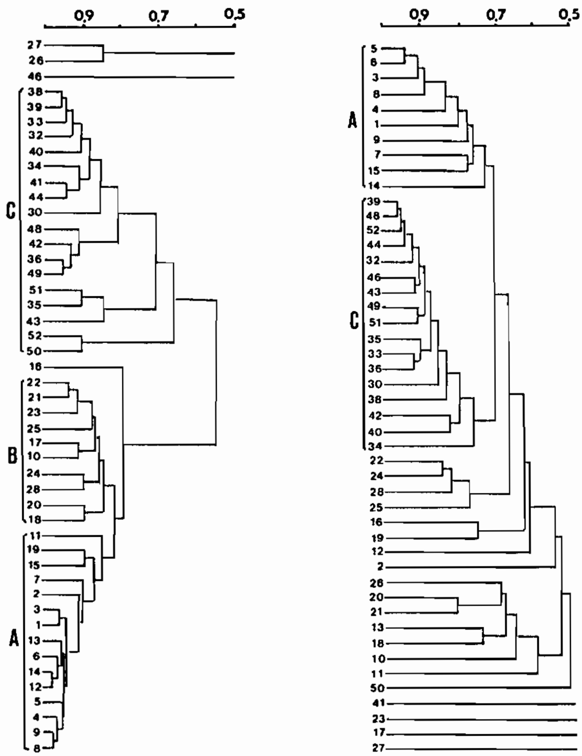

Figure 2. Grouping of stations at the Bolivian part of the lake according to cluster analysis (index of similarity indicated at top). To the left dry season (June 1985), A: northern Lago Menor, B: southern Lago Menor, C: Lago Mayor. Stations 26 and 27 are located close to the outflow of Tiwanaku river. 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

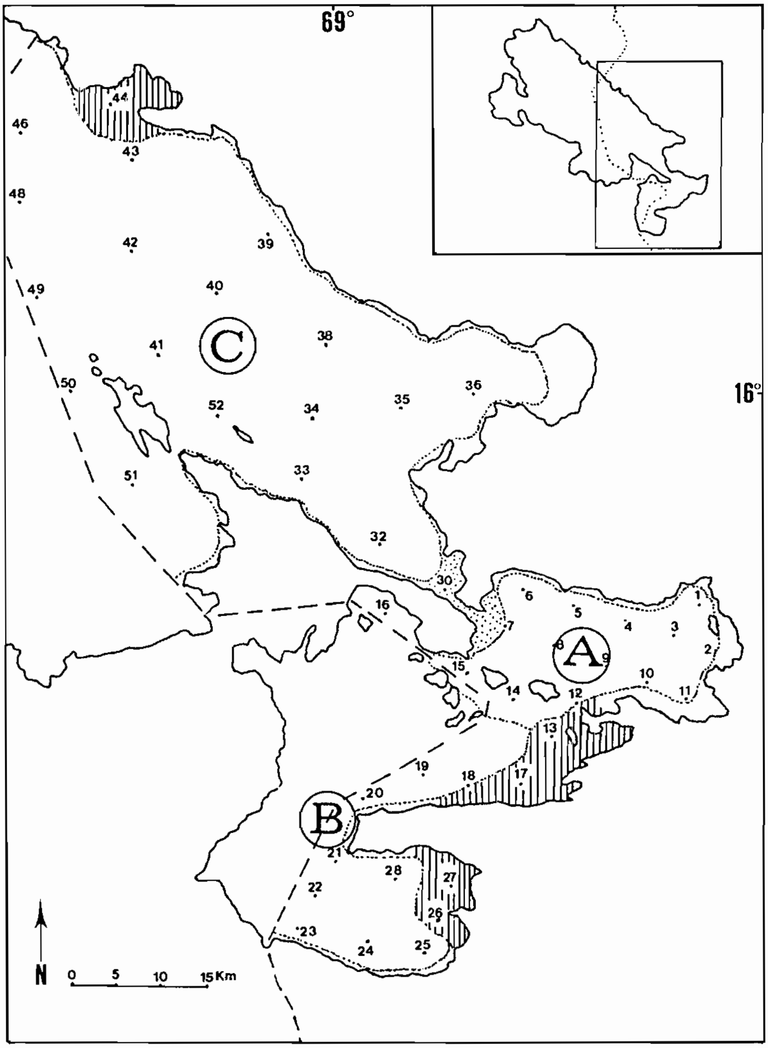

Figure 3. Ecological zonation of the Bolivian part of Lake Titicaca according to phytoplankton. A: northern Lago Menor, B: southern Lago Menor, C: Lago Mayor. In dots, the transition region between the two major basins; vertical lines, perideltaic regions; in white along the shore, border zones.

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

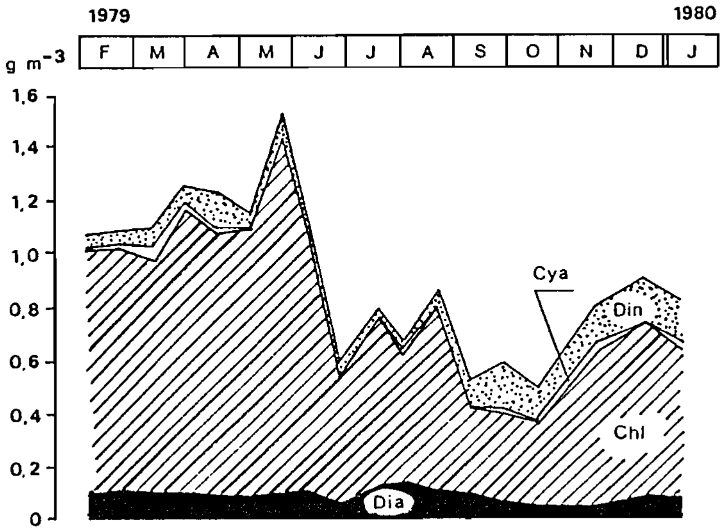

Figure 4. Total phytoplankton biomass, divided according to major classes, at a depth of 5 metres at Chua of Lago Menor. Din-Dinophyceae; Chl-chlorophytes; Dia-diatoms; Cya-cyanophytes (Lazzaro, 1981).

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.

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.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. 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 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 fluvio-lacustres 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 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. 1ère 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. 2ème 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.

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 photosynthcsis. *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.), 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.

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