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

C. Dejoux and A. Iltis (eds.), Lake Titicaca, 241–253.

Table 1. Areas occupied by the main species (Collot *et al.*, 1983).

A. Lago Menor			
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

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.

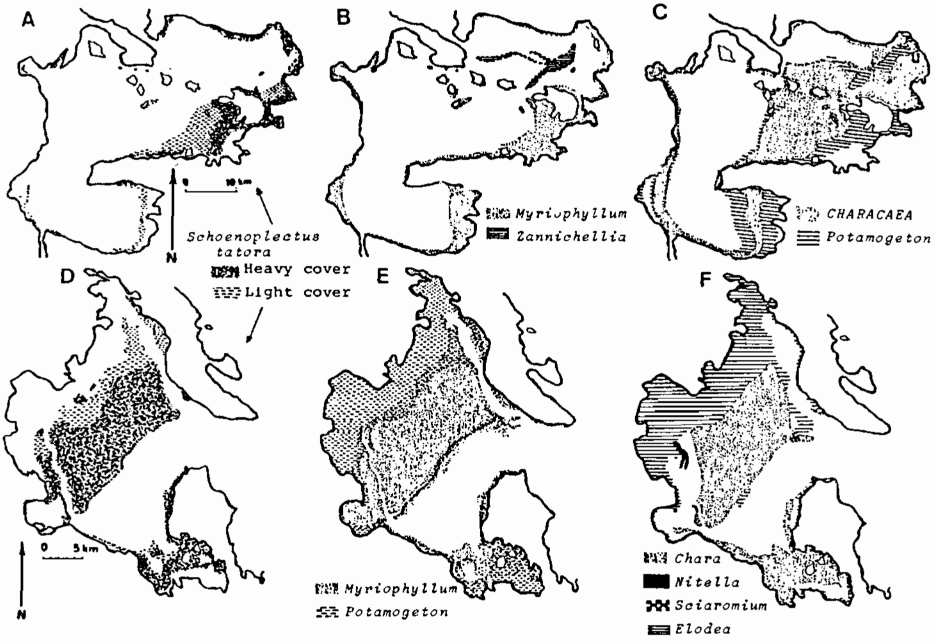

Figure 1. Vegetation distribution maps of Lago Huiñaimarca (A, B and C) and Puno Bay (D, E and F). (From Collot *et al.*, 1983).

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

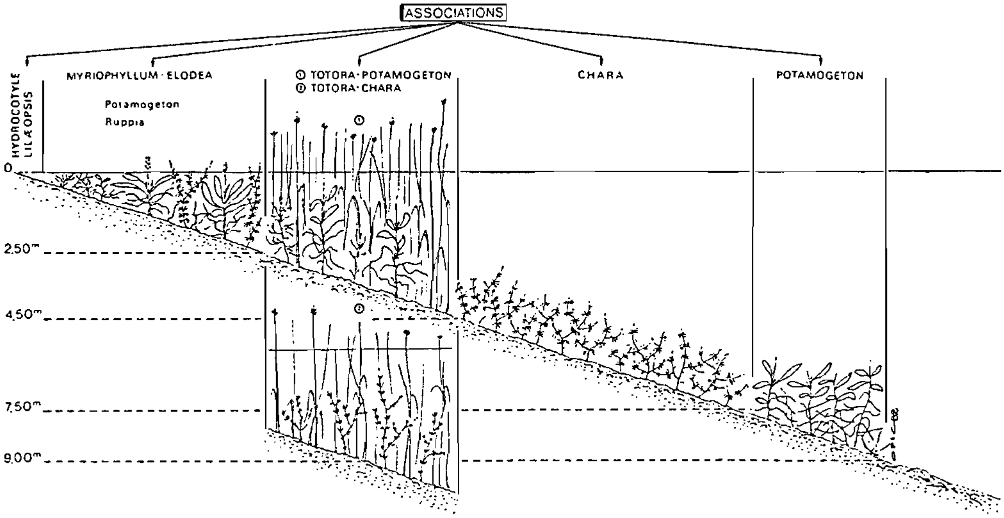

Figure 2. Diagram of the various plant associations in the littoral of Lake Titicaca (Collot *et al.*, 1983).

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 ± 83 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 ± 134 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.

Table 2. Estimates of the dry weight biomass of plants in Lago Pequeño and in Puno Bay in tonnes (Collot *et al.*, 1983).

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
Myriophyllum	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

Schoenoplectus

At the station studied, a mean value of 1522 ± 636 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 ± 96 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

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).

PLANTS	K	Na	Ca	Mg	SiO2	S	P	C	N	Fe	Cu	Mn	Zn	B
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

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

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).

						LAGO MENOR							
PLANTS	C	N	P	S	Ca	Na	K	Mg	SiO_2	Fe	Cu	Mn	Zu	B
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 :														
Lago Menor	2 441	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

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,

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.

SITUATION IN THE LAGO MENOR			SITUATION IN THE LAGO GRANDE
Year 1980 Alt. 3808.50 m	Year 1986 Alt. 3810.75 m	Year 1989 Alt. 3809.75 m	Year 1989 Alt. 3809.75 m
Hydrocotyle 0.2 m	Hydrocotyle 0.2 m	Hydrocotyle 0.2 m	Hydrocotyle 0.2 m
Elodea 2.5 m	Elodea 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
Potamogeton 9 m	?	?	?
Bryophytes ?	Bryophytes ?	Bryophytes 12 m	Bryophytes 30 m

LIMITE OF FIXED VEGETATION

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 g DW m^{-2} 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 g DW m^{-2} 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}.

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