VI.4j. The benthic populations: Distribution and seasonal variations

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As has been shown in the previous chapters, the macro-invertebrates of Lake Titicaca are for the most part only partially known, this knowledge generally being limited to a simple, often incomplete, species list. Until the last few years, no attempt had been made to study the benthic fauna as a community of organisms and it is only for the mollusca, which were collected in abundance in the past, that information exists on the major features of their depth distribution.

The setting and limits of recent studies

Two studies on the benthic populations of Lake Titicaca have been undertaken so far. The first was carried out in Puno Bay as part of the hydrobiological works directed by the University of Puno and the IMARPE (Instituto del Mar del Perú), in order to assess the degree of eutrophication in the bay (Medina, 1983; Morales *et al.*, 1989). We ourselves carried out the second study in the Bolivian part of the lake, in order to evaluate the importance of this component of the fauna in the overall ecology of the lacustrine environment and to demonstrate the type of populations present and their seasonal cycles.

These two works are certainly insufficient for a thorough understanding of the benthic fauna of such a vast water body as Lake Titicaca. The main biotopes present such as shallow bays, large areas covered with charophytes or other macrophytes and areas of medium or great depth, have however been studied at least once.

The various locations for which information on the composition of the macro-invertebrate populations is available are shown in Fig. 1. This information is usually based on quantitative sampling made with an Ekman grab, or qualitative samples taken with a net or by scrubbing and sieving submerged substrates.

Some of these stations (those underlined) have been the subject of regular sampling aimed at determining the temporal patterns of change in the fauna.

C. Dejoux and A. Iltis (eds.), Lake Titicaca, 383–404.

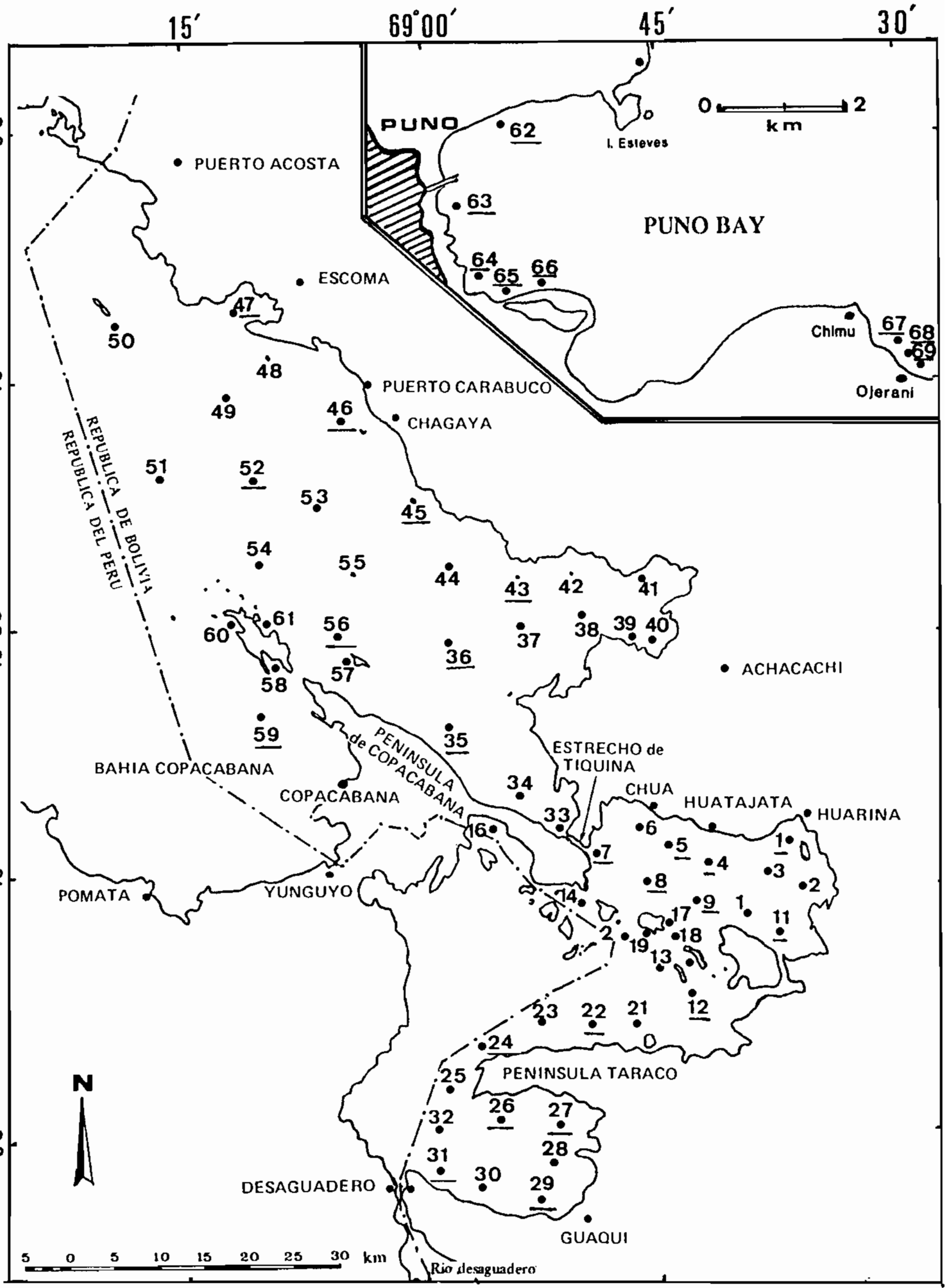

Figure 1. Location of benthic fauna sampling stations in Bolivian part of Lake Titicaca and in Puno Bay.

In the most favourable conditions, quantitative samples have been taken, but it is certain that the manipulation of an Ekman grab without anchoring the boat and in depths exceeding 50 metres, does not always provide samples covering the same area and depth of penetration. Similarly, the use of this equipment on bottom sediments carpeted with macrophytes is often difficult. In this latter case, we have expressed the densities of invertebrates collected in terms of the number of organisms per unit dry weight of plant material collected (unit = 10 g after drying at 60°C, to constant weight), rather than per unit area (m^{-2}), as was the case on soft sediments devoid of vegetation. All the samples were sieved through a mesh of 250 μm, before preservation and sorting.
Because of the taxonomic complexity of some groups of organisms, or even the impossibility of identifying certain of them precisely, especially in the larval stages, we frequently only took into account taxonomic levels such as the family or even order.

The benthic fauna of a highly eutrophicated environment: Puno Bay

The inner part of Puno Bay, rather isolated from the rest of Lago Grande and receiving virtually all the urban effluent from the town of Puno (nearly 100,000 inhabitants) and several other small shoreline communities, is highly eutrophicated (Northcote *et al.*, 1989 and Chapter VII.4 of this book). This eutrophication, which manifests itself by the presence of extremely abundant aquatic vegetation and heavy decomposition of organic matter leading to local or periodic anoxia, results in the occurrence in this area of animal populations differing significantly from those in the rest of the Lago Grande. The outer part of the bay is also affected by this eutrophication, but to a lesser extent, because of easier exchanges with the open water outsisde the bay.

The quantitative and qualitative studies of the benthos of these various zones reported by Medina (1983) and Morales *et al.* (1989), based on transects running from the innermost part of the bay to the outside, have provided the following results.

- The inner part of the bay has a much less diverse and much less dense fauna than the outer part, this difference being more pronounced the deeper the water (Fig. 2).
- No macro-benthic organisms were collected in the inner bay beyond depths of 6 metres for a period of several months.
- Although the populations showed seasonal changes in density in the outer bay, with a maximum in the dry season or slightly before, they remained almost identical and at low densities throughout the year in shallow parts of the inner bay.
- The faunal associations of the inner bay only included 4 taxonomic groups (oligochaetes, leeches, amphipods and chironomids), which can all with-

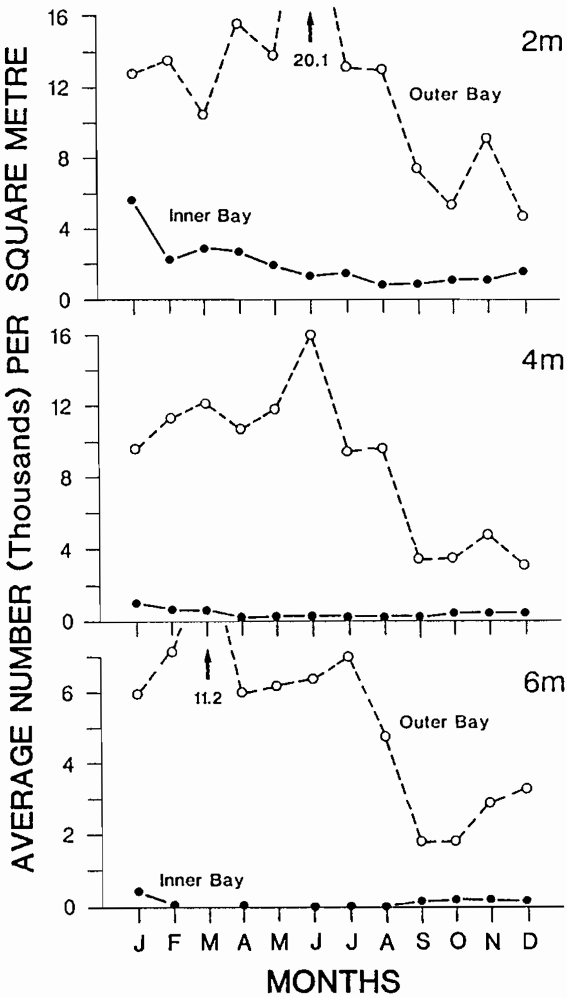

Figure 2. Monthly average abundance of total zoobenthic organisms at three depth zones in inner and outer Puno Bay, 1982. Averages based on 3 samples at each depth on each date. (From Morales *et al.*, 1989)

stand low oxygen concentrations, whereas 16 groups occur outside the bay.

On a more general level, the studies carried out by the authors cited above provide some information on the seasonal changes in relative densities of the main taxonomic groups in the shallow zone of the outer part of Puno Bay, the part least subject to the disrupting effects of eutrophication (Fig. 3). As the study only lasted one year, it is however impossible to know whether the recorded changes occur every year with each of the groups.

At 2 metres depth, the most abundant organisms in order were molluscs, amphipods and sponges, the same situation occurring at 4 metres, but at about 6 metres the situation changed as the sponge populations became very

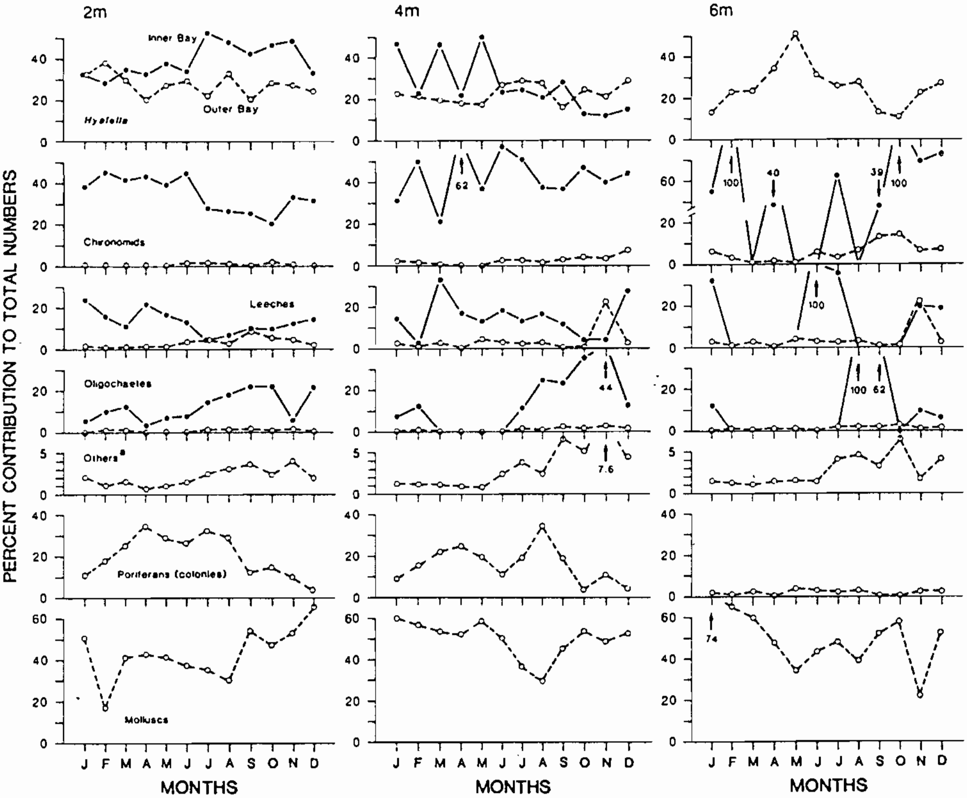

Figure 3. Seasonal changes in percent contribution of major groups to the total zoobenthic abundance in the inner and outer areas (3 depth zones) of Puno Bay, 1982. (from Morales *et al.*, 1989) [a] includes turbellarians, nematodes, ostracods, hydracarinans and hemipterans.

sparse. This situation corresponds partly to what we know from the rest of the lake, although the dominance of sponges in the shallow zone was practically never recorded in for example the Huiñaimarca, where they are generally rather rare.

The populations of the Bolivian part of the lake

Because of the political division of the lake into Peruvian and Bolivian sectors, our sampling was restricted to the latter region. It is therefore not absolutely certain that the results would have been completely identical for the same types of biotopes in the two regions.

Table 1. Relative proportions of the main taxonomic groups of macro-invertebrates in Lake Titicaca, calculated for all biotopes combined, on samples collected between January 1986 and June 1988. Classed in order of decreasing relative frequency and based on 85,000 organisms collected.

TAXONOMICAL GROUPS	Relatives %	Cumulated %
Mollusca	29.51	29.51
Amphipoda	19.32	48.83
Chironomidae	16.86	65.69
Hydracarina	16.24	81.93
Oligochaeta	9.14	91.07
Coelenterata	5.77	96.84
Tricladia	1.31	98.15
Elmidae	1.15	99.30
Hirudinea	0.42	99.72
Trichoptera	0.16	99.88
Diptera others than Chironomidae	0.057	99.937
Hemiptera	0.007	99.944
Hydrophilidae	0.005	99.949
Odonata	0.005	99.954
Bryozoa	0.004	99.958
Dytiscidae	0.001	99.959

General overview of the macrobenthos

The overall picture that we give of the benthic populations in Table 1 represents the mean status for the entire Bolivian part of the lake calculated over a period of slightly more than 2 years.

As with any calculation of this type, in which samples belonging to very different biotopes have been combined, this picture does not necessarily correspond to any particular situation in any given habitat. It is an indication of the mean characteristics of the benthic populations for all biotopes combined at the end of the 1980s, ranking the frequency of occurrence of the main taxonomic groups.

Examination of Table 1 shows that just two groups, Mollusca and Amphipoda, make up nearly 50% of the macro-invertebrates, a feature that can be considered as a biological characteristic of Lake Titicaca. If a further six groups are included, these account for 99.3% of the total population, whereas eight more groups need to be added to make up the total benthic fauna. Among these last eight groups, six are insects, which confirms what was seen in the last Chapter – that this class is on the whole poorly represented in the lake.

When the same analysis is carried out separately on each of the main biotopes present in the lake, very different pictures are obtained, although the major characteristics mentioned above often remain valid.

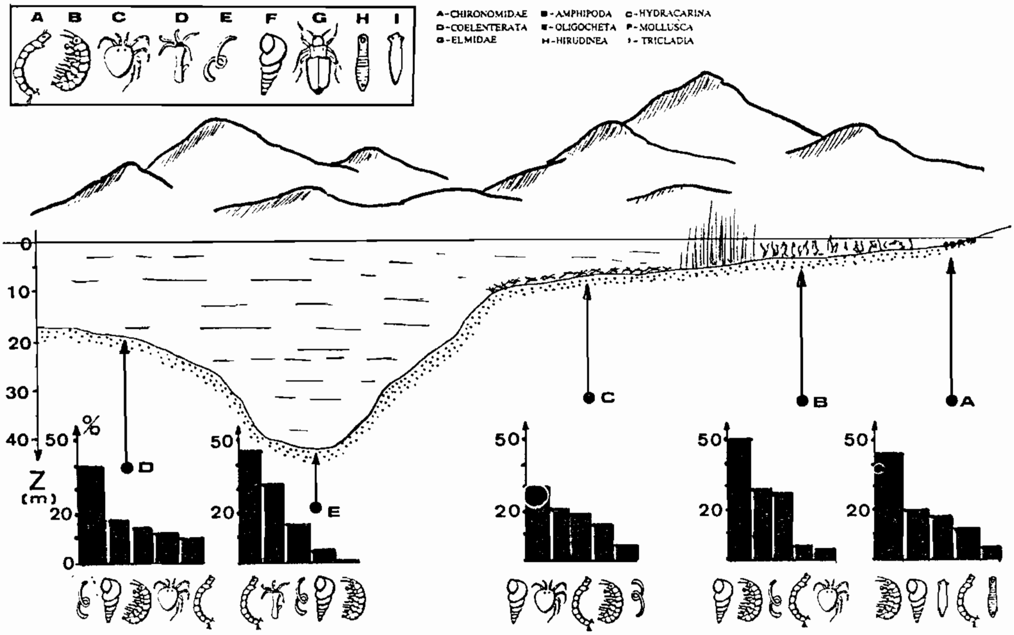

Figure 4. Distributions of the main groups of benthic invertebrates in various biotopes of the Huiñaimarca.

The major types of benthic habitats present in the lake

If a sufficiently large scale is taken to ignore the mosaic of tiny habitats which in some cases only extend over a few hundreds of square metres, a map of the major benthic biotopes can be drawn up for the lake and their characteristic invertebrate populations can be defined. In the Huiñaimarca, where the vegetation cover is very extensive, we have made a distinction between bottoms carpeted with *Chara* (which constitutes both large area and an ecological entity), and bottoms covered by other plants, without distinguishing between the species involved.

In the Lago Grande, the morphometry of the basin and the depth are the two main determining factors that have been taken into account.

The Huiñaimarca

The distribution of the major taxonomic groupings of invertebrates is shown diagrammatically in Fig. 4 and the distribution of the principal ecological zones in Fig. 5.

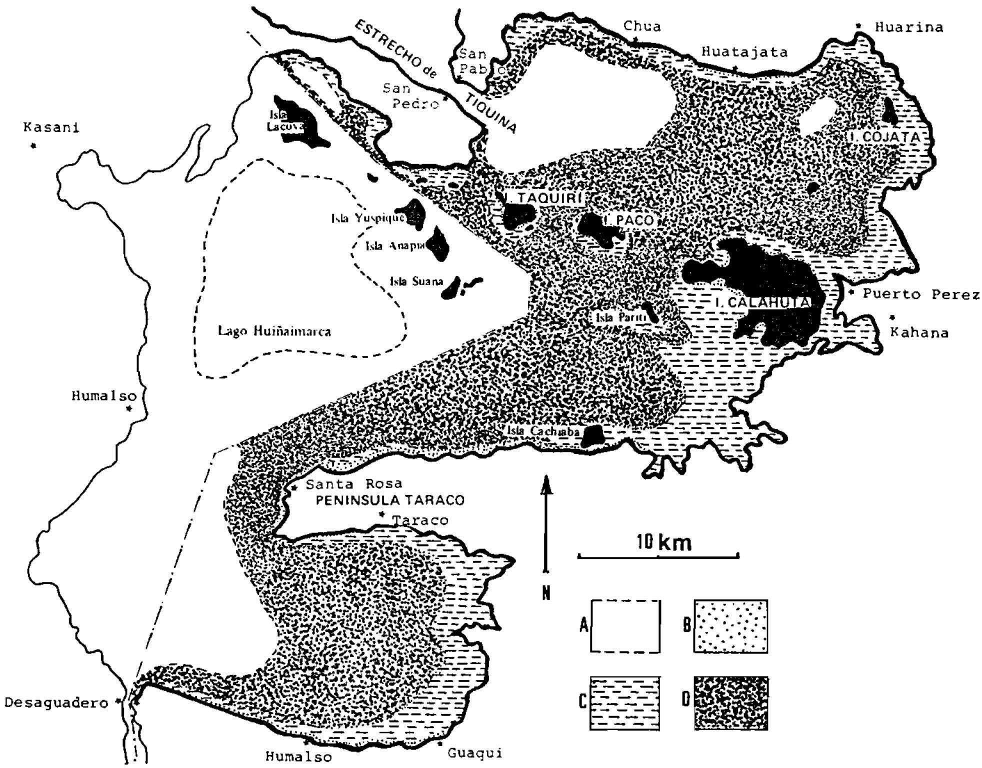

Figure 5. Major ecological zones of the Huiñaimarca (Bolivian part), in relation to the distribution of benthic organisms; A = sediments without vegetation; B = sandy or stony littoral zone; C = bottoms covered by various macrophytes; D = bottoms covered with *Chara* spp.

The littoral fringe

This is rarely muddy, and most frequently composed of accumulations of more or less coarse sand, gravel or worn pebbles. This is a shallow zone (0 to 40 or 50 cm on average), generally under the influence of waves. The animals living here are burrowers or live on the undersides of stones. Nearly 50% of the population of this well-oxygenated biotope is composed of amphipods (*Hyalella* spp.). This is also the preferred habitat for planarians; chironomids belonging to the Tanytarsini can be locally abundant, as can *Taphius* spp. (Planorbidae).

Bottoms covered with macrophytes other than Chara

In this zone we include the populations which inhabit the various types of macrophytes such as *Schoenoplectus tatora*, *Elodea potamogeton*, and *Myriophyllum elatinoides*. Molluscs generally dominate here, making up

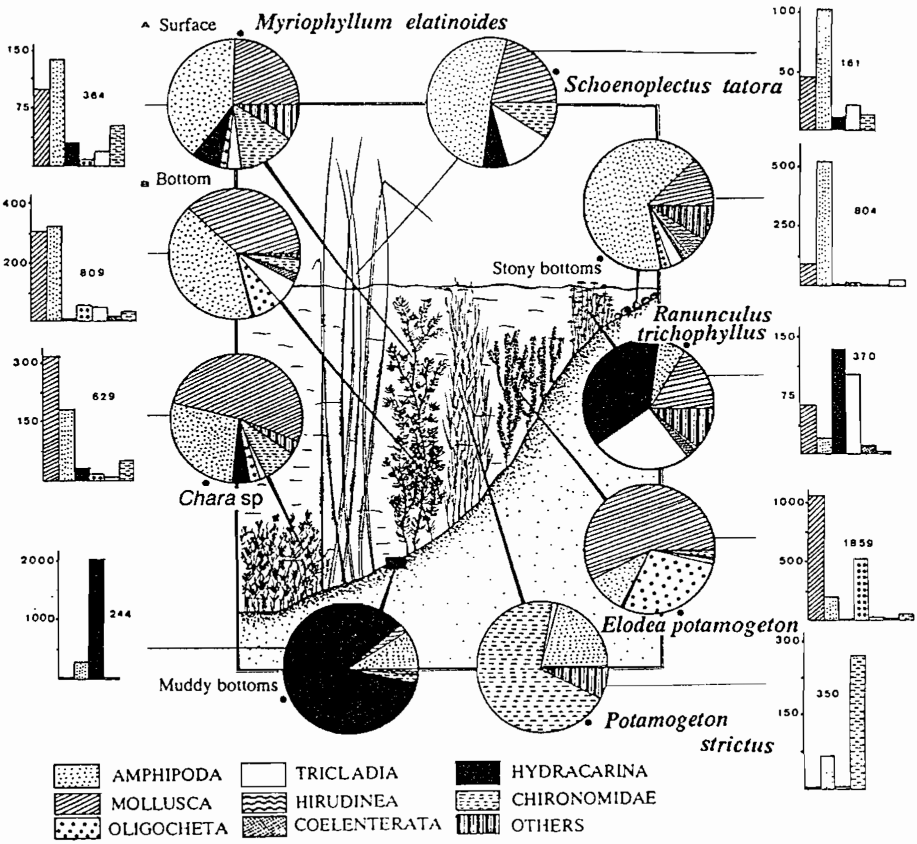

Figure 6. Distribution of the main groups of benthic invertebrates in various types of macrophyte associations and adjacent biotopes.

nearly 50% of the population on average, but amphipods and oligochaetes are also well represented, with percentages for each group close to 20%.

A more detailed analysis of this biotope (Dejoux, 1991) shows that marked differences exist in the composition of the populations occurring among the different species of macrophyte, differences which are essentially related to the morphological structure of the plant substrate. A complex structure together with good oxygenation of the macrophyte stand (situation near the shore or near the surface) being associated with the occurrence of a dense and diversified invertebrate population (Fig. 6).

Bottoms covered with Chara

Molluscs again dominate here, accounting for 30% of the population, but three other groups, the Hydracarina, Chironomidae and Amphipoda constitute 21, 19 and 15% of the mean total population, respectively. This and the previous biotope represent the most diversified habitats in terms of their macro-invertebrate populations. Here, for example, minor groups occur, such as the Corixidae, Ephydridae larvae, occasional Odonata and the majority of the few species of Trichoptera present in Lake Titicaca. These bottoms carpeted with *Chara* cover a very large area of Lago Pequeño (see Chapter VI.2). As they harbour a great biomass of invertebrates, they are of paramount importance for the biological processes of the lake.

Bare sediments in shallow water

Sediments bare of vegetation and occurring at less than 20 metres depth do not cover a very great area within the Huiñaimarca and are mostly situated on the Peruvian side. Another separate biotope could have been distinguished, but is included together in this category of biotope: this consists of areas of bare sediments scattered within the macrophyte beds, at places where there are discontinuities. These areas are usually in shallow water (10 to 12 metres at maximum) and are rich in plant detritus, but still fairly well oxygenated. Amphipods and molluscs dominate here, sometimes together with Chironomidae. Beyond the depth of macrophyte growth, the bare sediments are the site of accumulation of large quantities of plant detritus in the process of decomposition, except in those areas situated near river mouths, where currents can occur, at least occasionally. Oxygen is often lacking in this type of sediment, which is characterised by the formation of black muds, rich in organic matter. Samples of some of these sediments are found to be totally azooic and smelling of H_2S, as a result of prolonged anoxia. In sediments where the oxygen concentration remains sufficient, the benthic populations are nevertheless still dominated by resistant organisms such as oligochaetes (40 to 50% on average), Chironominae and certain molluscs (*Littoridina* sp.) living on the surface. These sediments are however generally poor in invertebrates.

The Chua Depression and Tiquina Strait

These two areas are special because of their great depth (for this part of the lake), and because they have relatively well-oxygenated bottom sediments, probably because of deep water currents. No precise data exist however on the intensity of any such currents, but chemical analysis of the water reveals the existence of exchanges between the two lake basins (see Chapter V), and as the only outflow (Río Desaguadero) from the lake is in the south, outflow by gravity from the northern basin must pass through the Tiquina Strait (see Chapter IV). The presence of compact grey sediments, almost devoid of plant remains, or even of sandy silts difficult for the Ekman grab to penetrate, also seems to indicate that these areas of bottom are at least periodically affected by significant currents.

The areas of softest sediments are colonised by a dense population of *Chironomus* sp. (45% of the population on average); also occurring are Hydra (33%) and oligochaetes (16%), organisms which can withstand temporary oxygen deficits due to the depth (at the time of stratification for example), but which can also benefit from input of particular organic matter, at the time when periodic currents are established.

The Lago Grande

The rocky coastal zone (H)

Rocky and gravelly shores similar to those in the Huiñaimarca also occur in the Lago Grande, but these have been included in with a biotope consisting of large blocks of rock or screes derived from the erosion of usually steeply shelving shores. The shores of the Lago Grande are in fact generally very steep, with a reduced or non-existent macrophyte fringe. Qualitatively, the populations of macro-invertebrates do not differ significantly from those occurring in the same stony habitats in the Huiñaimarca, but amphipods, accounting for nearly 74% of the population, are even more dominant. This is also one of the few biotopes where beetles of the family Elmidae occur in any significant proportion (7%) (Fig. 7).

Shallow bays with macrophytes (F)

Biotopes similar to those found in the Huiñaimarca occur in these areas. Molluscs, with nearly 56% of the total population, are always the dominant group among *Chara* beds (which confirms the homogeneity of this type of habitat). In contrast, chironomids and amphipods dominate among the other macrophytes (43 and 38%, respectively).

With the exception of the very large Achacachi Bay, and those of the Ríos Ramis and Huancané and of Puno Bay that has already been described, these biotopes only represent a very reduced area in the northern basin.

The mouths of inflowing rivers (L)

The mouths of the rivers flowing into the lake represent a transitional biotope in which are encountered some faunal components brought down by the biological drift. These components are only present at low densities and are only found in the area of freshwater inputs since they are incapable of maintaining themselves further into the lake environment: this is the case for certain insects for example (see Chapter VI.4i). In general, as a result

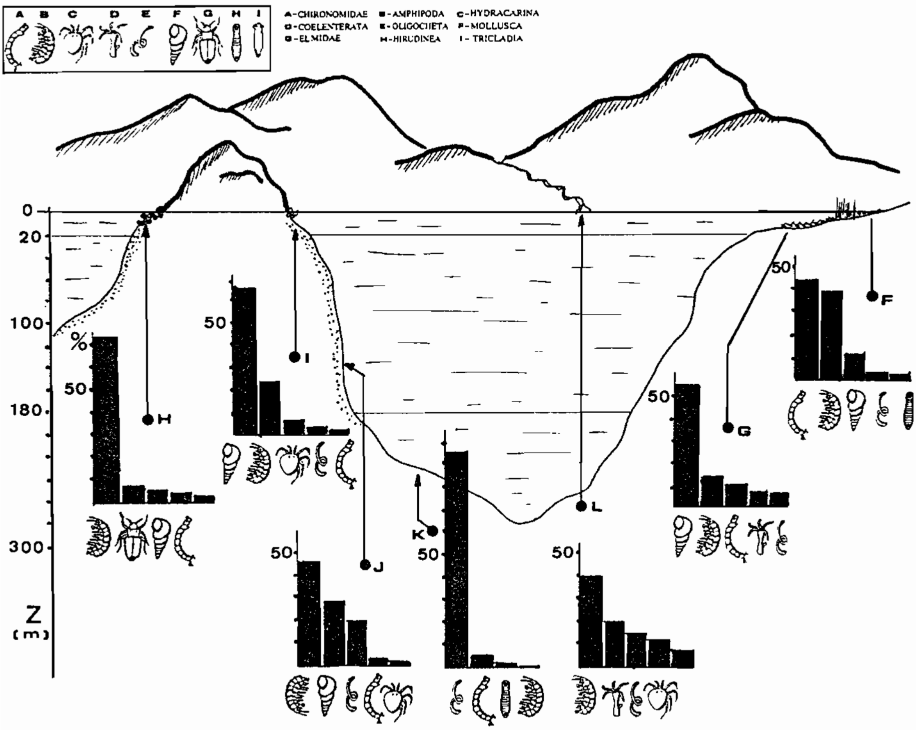

Figure 7. Distribution of the main groups of benthic invertebrates in various biotopes of the Lago Grande.

of the inputs of suspended matter and good oxygenation, amphipods dominate the benthic populations (ca. 50%), followed by *Hydra* (20%).

Bare sediments in less than 20 *metres* (I)

The depth of 20 metres has been arbitrarily chosen for the simple reason that this was the depth adopted in the Huiñaimarca. It would be more correct to speak of bare sediments in shallow water, especially as macrophytes descend to greater depths than in the Huiñaimarca because of the great transparency of the waters of the northern basin. This biotope is therefore composed of muddy sediments more or less rich in plant detritus, generally occurring on rather steep slopes. They receive inputs of organic matter directly from the littoral and are largely dominated by molluscs (more than 65%). It is in these biotopes that this group achieves its highest dominance. Next come the amphipods with nearly 24%. Hydracarina, oligochaetes and chironomids account for almost all the remaining 11%, indicating their low relative abundance.

Bottom sediments between 20 *and* 180 *metres depth* (J)

Although the depths defining the upper and lower limits of this zone should again be considered as approximate, it does have a true ecological reality. This zone is no longer under the direct influence of inputs of macrophyte detritus, but depends more on organic inputs related to the death of the plankton. It is also a zone where the bottom sediments still receive an adequate supply of oxygen, and where the absence of prolonged anoxia allows the survival of diverse benthic populations. On average amphipods dominate, accounting for 45%, then molluscs (nearly 29%). The relative importance of oligochaetes (19%) is also a characteristic of the profound lake zones, this group being one of the best adapted to oxygen deficits.

Bottom sediments in depths of more than 180 *metres* (K)

To be more precise, bottom sediments at more than 180 metres need to be divided into those that are completely azooic and those where benthic populations can still survive. The number of samples taken at these depths was in fact too small to determine the exact limits between these two zones. In the ten samples taken at depths of between 205 and 235 metres (the greatest depth that we were able to sample), we have not found a single living organism. We do not deduce from this however that 205 metres represents the maximum depth for survival of benthic organisms in Lake Titicaca, because of the small number of samples collected in comparison with the area of the lake where the depth exceeds this depth. It is nevertheless reasonable to think that the prolonged periods of anoxia which occur in this zone are a determining factor limiting the colonisation of the sediments. In contrast, we have collected a total of nearly 300 organisms from depths of between 180 and 205 metres. Oligochaetes very largely dominate in this zone, with a relative proportion of 93.7%, but we have also found some *Chironomus* sp. (4.2%) and more unexpectedly Hirudinea (1.8%) and a species of amphipod, *Hyalella echina* (0.3%).

Population densities

The densities of the various groups of macro-invertebrates vary both seasonally at any given locality, as we will see below, and also between sampling sites for any given period of the year. Each faunistic group has its own population dynamics, as we have seen in the case of the amphipods, for example. Such variations in density can have multiple causes; some of these, such as conductivity gradients, variations in light penetration or substrate type from one site to another, can be considered as generalised as they are wide-acting on lake scale. Others are much more local, such as the distribu-

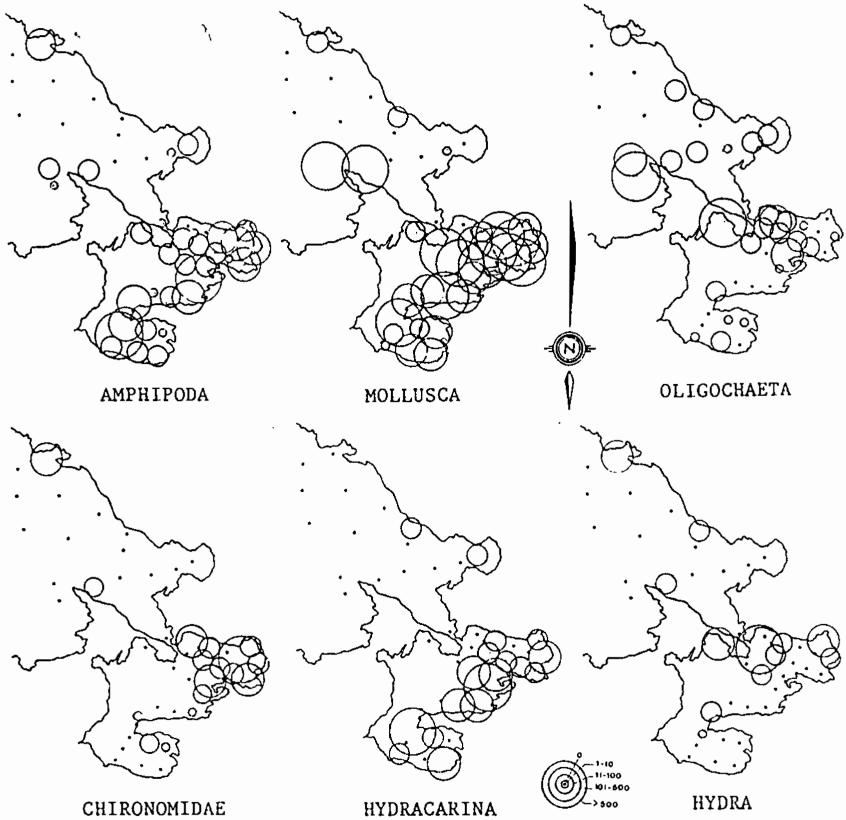

Figure 8. Density distributions of the main groups of benthic macro-invertebrates in the Bolivian part of the lake in February 1987.

tion of food or the presence of a current increasing the oxygen concentrations. The detailed picture of the populations obtained from a sampling campaign therefore reflects this situation, frozen at a point in time, even if the campaign takes several days. It nevertheless remains a very imprecise picture because of the vast extent of the usually heterogeneous environments involved. Finally, if we take into account the fact that the majority of the macro-invertebrates have a clumped type of distribution, it will be understandable that the description of the populations that we are capable of giving on a lake wide scale, or at least covering a large part of the lake, must be considered as very approximate.

For these various reasons we will only present a single picture of the density distribution of macro-invertebrates, such as was given by the sampling carried out from the 22 to 25 February 1987. This picture is given in graphic form and only concerns the major faunal groups collected in the Bolivian part of the lake (Fig. 8).

As the diameter of the circles is proportional to the density of the organisms, it is possible to obtain a visual impression of the situation prevailing in February 1987, by associating the size of the circles with their distribution on the various maps. The first impression is the quantitative preponderance of Mollusca over all other groups, with a particular abundance in the northern part of the Huiñaimarca, the areas with lower density or absence (east of the Tiquina Strait) being the deepest sampling stations. Molluscs are also dominant in the Lago Grande along the shorelines of Sun and Moon Islands.

Amphipods are the second most important group in order of abundance and on the whole dominate in the same areas as the molluscs, a situation which was also found to a lesser extent with the Hydracarina. It should be noted however that these latter have a lower occurrence in the stations of the Lago Grande than the previous two groups.

Oligochaetes, chironomids and Hydridae all show distinct distributions. The first are particularly dense in the northern part of the Huiñaimarca, either in deep water or in areas rich in plant detritus. They are also found almost everywhere in the Lago Grande, except in the deepest water in the centre; but even so, they are the group of organisms that live to the greatest depths in the lake. In contrast, for the period in question, the chironomidae and Hydridae had a distribution that was difficult to explain. The north-west part of the Huiñaimarca was for example densely populated with chironomids, whereas these were practically absent or rare from the rest of the lake. In addition, although it was possible to understand the particularly high density of *Hydra* at station 7 (32 metres depth) which received water directly from the Lago Grande, and was therefore well-supplied with oxygen and food, it was difficult to understand why it was also abundant at stations 1 and 16 where these factors played no role.

As a general rule, it would therefore appear that the Huiñaimarca supports considerably higher densities of organisms per unit area than the Lago Grande, mainly because it is shallower. However, areas of the Lago Grande of moderate depth (< ca. 20 metres), situated in non-eutrophicated bays or along the coastlines, also have a rich benthic fauna. Lake Titicaca therefore complies with a general tendency for most high altitude lakes to have a littoral zone that is much richer than the profound. This "ecozone" of the top twenty to twenty-five metres is therefore of paramount importance in the biological functioning of the lake and must be maintained as stable as possible, in order to ensure its role in the secondary production of the entire ecosystem.

Seasonal variations

The demonstration of such variations is based on the density distributions recorded during 5 sampling campaigns made at various seasons from 1986 to 1987. About thirty stations in the Bolivian part of the lake (Fig. 1) were sampled. The contents of 2 to 4 Ekman grabs were analysed at each station, depending on the sampling campaign.

The overall changes in the benthic populations between sampling campaigns are shown diagrammatically, by using rather wide density classes so that only large changes are evident (Fig. 9). It should be noted that, by chance, the period in question was not entirely typical, since April 1986 was the month with the highest lake level in the last decade. The total range in water level rise being nearly three metres, it is obvious that this phenomenon was likely to interfere greatly with the population dynamics of benthic organisms. Such a rise in water level represented an increase of 20 to 50% in depth in many sites in the Huiñaimarca. The first repercussion to be felt was on the populations of submerged macrophytes and particularly of those parts of the *Chara* beds situated, before the increase in lake level, near their lower limit of depth penetration, at depths of 8 to 10 metres. The decrcase in light penetration to this depth, due both to the increase in the height of the overlying water column and also to greater inputs of suspended matter from the inflow rivers and diffuse inputs along the shores, led to their death.

This vegetation quickly decomposed and periods of anoxia were established in the deeper areas, leading to the more or less complete disappearance of the dominant benthic populations (molluscs and amphipods). This was particularly apparent in the southern part of the Huiñaimarca, where the densities of benthic macro-invertebrates decreased from several thousand individuals per square metre or per 10 g dry weight of macrophytes to less than 500, between January and October 1986. This also occurred in the northern part of the Huiñaimarca, where the zone where the density was at least 500 organisms for the same unit area or weight, reached its maximum extent in April 1986. The opposite occurred in the Lago Grande during the same period of water level rise, where because of the greater overall water transparency and the steep gradients of the shorelines, it was not affected to the same extent. The same phenomenon as occurred in the Huiñaimarca only took place at the bottom of Achacachi Bay, where densities also fell below the limit of 500 in October 1986.

Although it is conceivable that the most mobile organisms such as amphipods, for example, may have been able to escape from the areas of anoxia, at least in part, it is certain that this was not the case for mollusca and that very high mortalities occurred in certain areas. This phenomenon is of interest, because it may offer an explanation for the horizons of shells which appear at certain levels in sediment cores from the Huiñaimarca (see Chapter III.1). These could result from mass mortality of molluscs, victims of temporary anoxia following abrupt increases in lake level, or alternatively to periods of temporary drying out.

Another period of deleterious consequences of the rise in lake level of the previous year apparently occurred in February 1987. The lake level had scarcely dropped, and except for the outlet of the Tiquina Strait, the overall densities remained at lower levels than in February 1986 throughout the

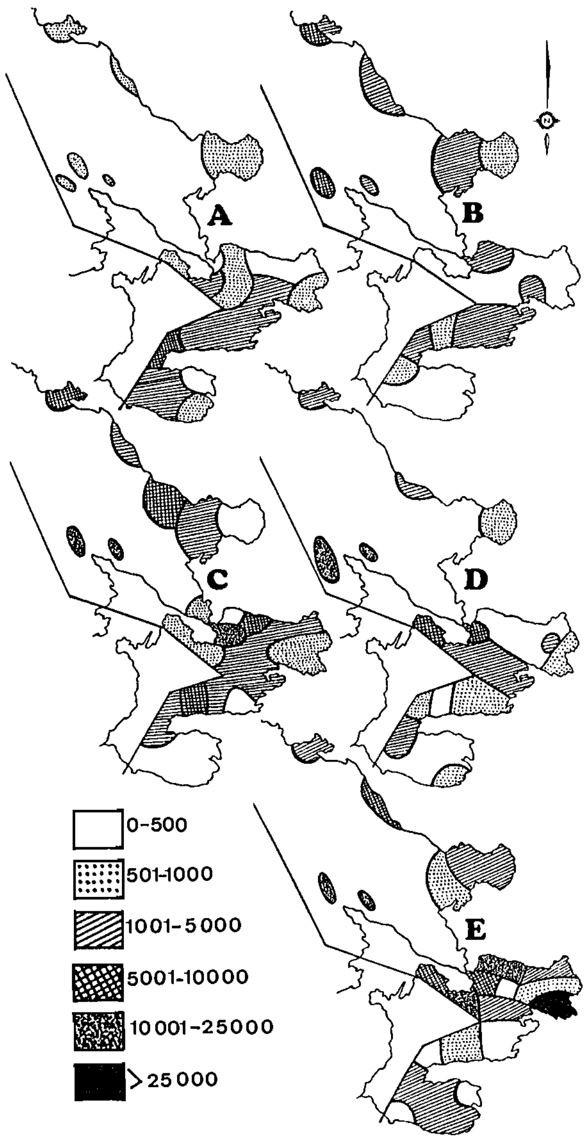

Figure 9. Density distributions of benthic macro-invertebrates in the Bolivian part of Lake Titicaca. The maps correspond to the following 5 sampling campaigns: A = January 1986; B = April 1986; C = October 1986; D = February 1987; E = June 1987. Densities expressed in g. 10 g dry weight on bottoms covered with macrophytes and $g \cdot m^{-2}$ on bare bottoms.

Huiñaimarca. In June 1987, in contrast, the situation had greatly improved, particularly in the north of the Huiñaimarca where a hyperdevelopment of the benthic fauna was recorded. Large areas had densities of greater than 5000 individuals per square metre, or per 10 g dry weight in the case of populations among macrophytes. In the entire region situated offshore of Puerto Perez these densities even exceeded 25,000.

Conclusions

The benthic fauna of Lake Titicaca represents an essential component for the biological functioning of this ecosystem, by playing an important role both in the secondary production (food for the fish fauna), and also in energy transfer (molluscs and amphipods as decomposers).

A very clear contrast exists between the two basins of the lake, the Huiñaimarca being by far the most densely populated over all its area. Only the shallow areas of the Lago Grande have a similar importance, but these areas only represent a very small proportion of the 7000 square kilometres of this basin. Overall more than 95% of the benthic populations occur in the top 15 metres depth in the Huiñaimarca and in the top 25 metres in the Lago Grande. In latter, benthic life does however extend down to great depths, but cannot always be sustained at greater than 200 metres, because of the frequent periods of anoxia that affect this zone.

As a general rule, molluscs and amphipods are the dominant faunistic groups at the scale of the whole lake and over all seasons, both in terms of density and biomass. The former play a primordial role in the decomposition of the enormous biomass of macrophytes that develops and dies in the euphotic zone, the latter being responsible for the transformation of organic matter of animal origin (zooplankton, macro-invertebrates, etc.).

Analysis of fish stomach contents has shown that benthic macro-invertebrates are also the most important prey for many of the endemic species (especially those living among the aquatic vegetation), and also for the young stages of the pelagic predators (*Salmo gairdneri* and *Basilichthys bonariensis*). Some taxonomic groups also represent almost the entire diet of several species of aquatic bird at certain times of year.

Despite the results presented in this chapter, the benthic invertebrates must be considered as being insufficiently studied at the present time. Although more work is still needed on the taxonomy, it is especially studies on the ecology and biology which are lacking, and priority should be given to such studies on the two dominant groups (molluscs and amphipods). Studies on the long and medium-term changes in the populations are also needed in order to demonstrate whether these follow cyclical rhythms, and if this is the case to elucidate the determining factors.

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