VI.4g. The Amphipoda

CLAUDE DEJOUX

Despite the abundance and species richness of the Amphipoda in Lake Titicaca, there have been very few studies devoted to this group of animals, with the exception of the work of Faxon (1876), resulting from the collections brought back by Alexander Agassiz, that of Chevreux (1904), based on the collections from the Crequi-Montfort and Sénéchal de la Grange expedition in 1903, and the record of one species by Weckel in 1909. This species, which had originally been described by Bate (1862), had been redescribed by Weckel himself in 1907.

These publications served as the basis for identifying the amphipods collected during our extensive study of the benthic fauna of the Bolivian part of the lake, leading us to distinguish 11 different taxa, based frequently on macroscopic characters; that is one additional species (?) compared to those already recorded. In his 1876 study, Faxon described 7 new species belonging to the genus *Allochertes* (now *Hyalella*) coming from Lake Titicaca and recorded the presence of a species already known from North America: *Allochertes inermis* Smith, 1874.

Thirty years later, Chevreux recorded the occurrence of 4 of these species in the material available to him and discovered a new species: *Hyalella neveu-lemairei*. Since that time, as far as we know, taxonomic knowledge has not progressed.

Brief description of the known species

They all belong to the family Orchestidae.

Hyalella armata (Faxon, 1876) (Plate 1, Fig. 1)

This is a species measuring 8 to 9 mm from head to telson, with a rounded body without dorsal spines. The main distinguishing morphological character is the presence of lateral spines on the first four thoracic segments, increasing

C. Dejoux and A. Iltis (eds.), Lake Titicaca, 346–356.

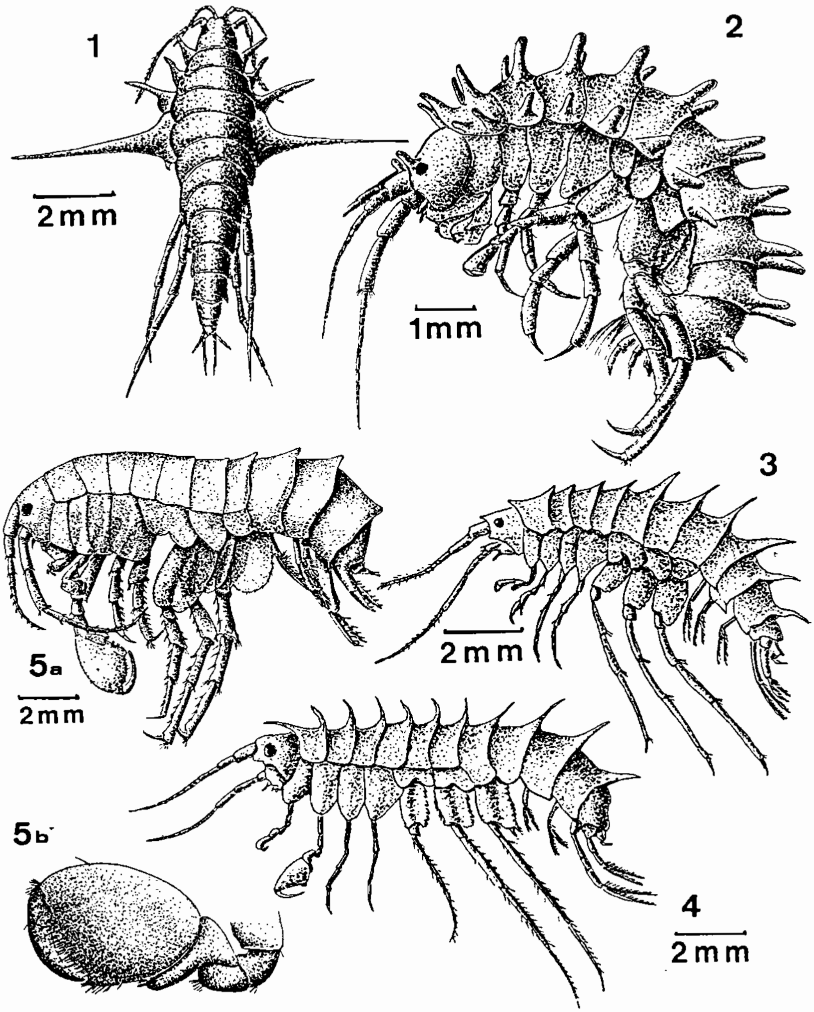

Plate 1. 1: *Hyalella armata*; 2: *Hyalella echina*; 3: *Hyalella longipes*; 4: *Hyalella lucifugax*; 5a: *Hyalella latimana*; 5b: male gnathopod.

in size posteriorly. The first three pairs of spines are directed forwards and downwards whereas the fourth pair are almost at right angles to the body axis. The second pair of antennae is much longer than the first and the second pair of thoracic legs is particularly broad in males. The flagellum of the first pair of antennae has 12 segments and that of the second 13 segments.

The size of the lateral spines is variable and is usually greater in individuals inhabiting deeper water, in which the fourth pair can reach a span of 10 mm from tip to tip.

Hyalella echina (Faxon, 1876) (Plate 1, Fig. 2)

This species is even more characteristic. The body is very arched and decorated with spines giving it the appearance of a hedgehog. A row of 8 spines runs along the mid-lateral line and two parallel rows of 11 spines along the length of the body either side of the mid-dorsal line. The eyes are slightly protuberant. The flagellum of the first pair of antennae has 6 to 8 segments and that of the second pair 9. The total body length can reach 10 mm.

Hyalella longipes (Faxon, 1876) (Plate 1, Fig. 3)

Eleven spines are arranged all along the mid-dorsal line. The first thoracic segment has two spines, one small and situated at the front of the segment and the other slightly longer at the rear. All the other spines start at the rear of the segment and increase in size posteriorly, as far as the 9th segment. The eyes are protuberant. The first 4 epimera are triangular, and pointed ventrally; the telson is entire. The flagellum of the first pair of antennae has 13 segments and that of the second 14. The 6th and 7th pairs of legs are very long.

Hyalella lucifugax (Faxon, 1876) (Plate 1, Fig. 4)

Again this species is easy to identify because of the row of 11 spines running along the mid-dorsal line, arising from the rear of each segment, except the first spine which arises from the anterior part of the first segment. The first 6 or 7 spines are curved forwards whereas the others are at right angles to the body axis.

The antennae are of about equal length and the abdominal legs are very long. The body measures about 11 mm.

Hyalella latimana (Faxon, 1876) (Plate 1, Fig. 5a and b)

This thick-bodied species reaching up to 12 to 13 mm in length, is much less distinctive in shape than the previous species, although 4 or 5 more or less flattened dorsal spines can still be distinguished. These are more in form of projections from the dorsal part of the segments than true spines as in the previous species.

The first pair of antennae is clearly shorter than the second and when extended, its peduncle scarcely reaches the centre of the peduncle of the second pair. The flagellae of both pairs of antennae have 11 segments. The base of the male gnathopod is very angular (Fig. 5b).

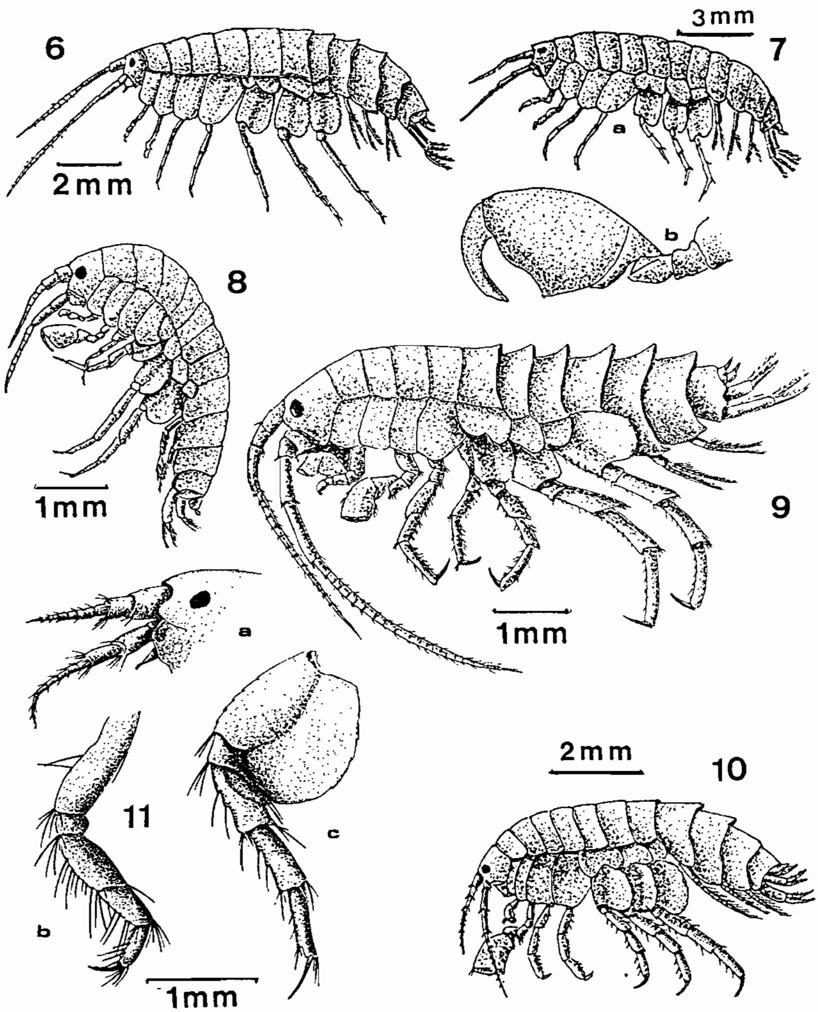

Plate 2. 6: *Hyalella longipalma*; 7a: *Hyalella cuprea*; 7b: male gnathopod; 8: *Hyalella dentata* var. *inermis*; 9: *Hyalella neveu-lemairei*; 10: *Hyalella knickerbrockeri*; 11: *Hyalella* sp.; a: head, b: thoracic leg, c: abdominal leg.

Hyalella longipalma (Faxon, 1876) (Plate 2, Fig. 6)

This also large-sized species (10 to 13 mm) only has 3 dorsal spines situated on the 5th thoracic segment and the first two abdominal segments. The spines vary in the extent to which they project, depending on the individual, and may even curve forward slightly. The posterior ventral angle of the first 3 abdominal segments is pointed towards the rear; the telson is entire. The flagellum of the first pair of antennae has 15 segments, the same as on the second pair which is however longer. The carpus of the male gnathopod is oval in shape, without a basal point as in the previous species. The integument of the carapace is covered with sparse short setae forming scattered cross-shaped patterns.

Hyalella cuprea (Faxon, 1876) (Plate 2, Fig. 7)

No spines or teeth are present on this species and the posterior ventral angles of the first 3 abdominal segments are scarcely pointed. The flagellum of the first pair of antennae has about 10 segments, the second pair being considerably longer than the first and being equal to about a third of the total body length.

The 5th, 6th and 7th pairs of thoracic legs are short but have broad basopodites; the 5th pair is shorter than the others. The total body length is about 9 to 11 mm and the integument has brassy reflections over the entire body.

Hyalella dentata var. *inermis* Smith, 1874 (Plate 2, Fig. 8)

The specimens examined by Faxon and identified under this name only differ from the species described from the United States by Smith (1874) by the firmer and less transparent appearance of the integument. It is a small form without spines, 5 mm long, with an extremely undistinctive morphology. Being rather similar to the previous species, small specimens are not easy to identify.

Hyalella neveu-lemairei Chevreux, 1904 (Plate 2, Fig. 9)

This moderate-sized species (ca. 7 mm) has a laterally compressed body with a dorsal row of 6 spines or projections starting at the posterior end of the 5th thoracic segment. These projections, which get progressively longer posteriorly, vary among individuals in the extent to which they stand up away from the body. The flagellum of the first pair of antennae has 16 segments and that of the second pair 18.

Hyalella knickerbrockeri Bate, 1862. (Plate 2, Fig. 10)

This species belongs to the group with dorsal spines. The dorso-posterior spines do however project very little and mostly only occur on the first two abdominal segments. The last thoracic may sometimes have a more or less flattened projection, the total number therefore varying from 2 to 3 de-

Table 1. Relative abundances of various species of amphipod collected in the Bolivian part of Lake Titicaca during 6 sampling campaigns from 1986 to 1988.

N = number of individuals collected per biotope; NT = Total number collected. % = relative percentage of all collections. Types of biotope: A = Bottoms covered by *Chara* spp.; B = Bare sediments (z < 20 m); C = Bare sediments (z > 20 m); D = Bottoms covered by macrophythes other than *Chara* spp.; E = Littoral stones and pebbles; F = Bottoms between 20 and 180 metres depth; G = Bottoms at greater than 180 m depth; H = Areas of the lake near the mouth of the Río Suchez.

	HUIÑAIMARCA					LAGO MAYOR								
	N	N	N	N	N	N	N	N	N	N	N	N	NT	%
Hyalella armata	39	87	-	-	-	-	-	-	-	2	-	-	128	0.84
Hyalella lucifugax	-	-	-	-	-	-	-	-	-	5	-	-	5	0.03
Hyalella dentata	672	126	7	-	37	81	16	-	54	84	-	-	1 077	7.08
Hyalella latimana	1 075	2	-	110	-	-	1	-	11	155	1	-	1 355	8.91
Hyalella Neveu Lemairei	1 099	14	1	37	1	-	15	22	1	65	-	7	1 262	8.30
Hyalelle cuprea	4 938	72	-	580	612		264	301	1 416	611	-	599	9 393	61.80
Hyalella knickerbrokeri	537	37	-	101	-	8	52	12	25	63	-	411	1 248	8.19
Hyalella echina	47	36	-	-	-	-	-	4	-	-	-	-	77	0.50
Hyalella longipalma	357	5	-	72	-	172	16			15		2	639	4.20
Hyalella sp.	16	-	-	-	-	-	-	-	-	-	-	-	18	0.12
TOTAL	8 782	369	8	900	650	261	364	339	1 607	1 000	1	1 019	15 200	
Biotopes	A	B	C	D	E	A	B	D	E	F	G	H		

pending on the individual. In addition the posterior ventral corner of the abdominal segments form an angle of less than 90°.

The antennae are short, the flagellum of the first pair having 7 to 9 segments and that of the second pair, which are very variable in length, can have from 8 to 15. This is a small species measuring 7 to 8 mm.

Hyalella sp. (Plate 2, Fig. 11)

This unidentified taxon was not very frequent in our samples since only 18 specimens have been collected. It is a small species (longest individuals 7 mm long), with a general appearance similar to *H. dentata inermis*, and is characterised by the absence of dorsal spines or dorso-posterior projections on the segments and the presence of abundant setae on the legs and antennae. The legs and antennae are short, giving them a thickset appearance. The flagellum of the first pair of antennae has 8 segments and that of the second, 8 to 9.

Distribution and relative abundance of the species

Details of our collections over several years of Amphipoda in the Bolivian part of the lake have been summarised in Table 1 and details are given below on the distribution of each species identified.

In 1876, Faxon considered *H. armata* as being the most abundant species in the lake, at that time collected from a few metres depth down to depths of 120 metres, as for example off Juli. It was particularly abundant in Achacachi Bay, at about twenty metres depth. In our samples of amphipods from the lake, which include some 15 000 individuals, it only accounts for slightly more than 120 specimens and Chevreux (op. cit.) did not find it at all in the samples he studied. Even though the collections made by Faxon were less extensive than ours, it seems highly likely that a radical change in the species dominance has occurred, a phenomenon that we have also recorded in the case of the Hydracarina (See Chapter VI.4h).

At present this species seems to be restricted to muddy bottoms without vegetation and we have encountered it at depths of between 12.5 and 135 m.

H. echina used to inhabit the same biotopes, but was much less abundant. In terms of abundance it would appear that the situation has hardly changed, since we have only found it sporadically in the Lago Grande and Huiñaimarca (0.5% of all our sampled individuals). This species can be collected at present at depths varying from 4 and 13 m, but Faxon (*op. cit.*) recorded it as being present in the Lago Grande down to depths of 73 metres and classed it among the species preferring deep water.

H. lucifugax is also a deep-water species, the few known individuals having been collected in the Lago Grande at depths of between 70 and 110 metres. It is a remarkable fact that all the deep-water species have a heavy ornamentation of spines, which for any given species seems to increase in extent of development with increasing depth. We have only rarely found this species (5 individuals in total) living at depths of over 100 metres.

On the other hand, we have never collected *H. longipes* that Faxon recorded at several locations in the Lago Grande (Achacachi Bay, Puno Bay, Chucuito), and also off the mouth of the Rio Desaguadero. This absence from our samples does not of course prove that it is extinct.

H. latimana, in contrast is a species that we have encountered at several localities in the lake at depths of between 5 and 22 metres. It accounts for almost 9% of all the amphipods collected and mainly inhabits the aquatic vegetation in the Huiñaimarca, but is little represented in the Lago Grande where we have only found it once in any abundance, at more than 20 metres depth, off the mouth of the Rio Suchez.

H. neveu-lemairei, recorded by Chevreux (1904) as inhabiting water depths of between 2 and 24 metres, seems at present to be a species preferring the aquatic vegetation. We have collected it regularly from bottoms carpeted with *Chara*, but rarely in very great abundance (8.3% of all amphipods). As with the previous species it is found especially in the Huiñaimarca, where it lives at between 4 and 10 metres; it has however been encountered at nearly 20 metres off of Escoma.

H. dentata, accounting for slightly more than 7% of our samples of amphipods, is distributed in numerous biotopes, from a few centimetres depth down to more than 60 metres. We have never found it among macrophytes other than *Chara*, but this absence seems to be due to chance.

Another spineless form, *H. cuprea*, inhabits the same biotopes and is the commonest species in the lake, accounting for nearly 62% of all individuals sampled. It greatly dominates the populations among macrophytes and in the shallow littoral zones.

H. knickerbrockeri is also a ubiquitous species on a lake scale, being found under stones along the shoreline and at depths exceeding 30 metres. It is frequent among macrophytes, but this cannot be said to be its preferred biotope as it is also frequently met with on bare sediments. Accounting for slightly over 8% of the amphipods collected, this species is classed in the group of animals of moderate abundance, but with a wide distribution in all the lake habitats.

Less abundant (4.2% of collected individuals), *H. longipalma* is rare outside of the areas occupied by aquatic vegetation. This species usually occurs in shallow water, although on one occasion 15 individuals were collected at 33 metres depth just off of Sun Island.

It is difficult to say anything precise about the distribution of the 18 individuals of *Hyalella* sp. that we collected from among *Chara* in the Huiñaimarca on two different dates and at two different localities. The small numbers sampled makes it likely that it is a rare species, but it is also possible that it inhabits a very special biotope which is little represented in all of our samples.

Density distribution and temporal changes

The figures given in Table 1 are the total numbers actually collected, either in qualitative or quantitative samples. In order to describe the distribution of abundance of all the samples taken in the Bolivian part of the Huiñaimarca at different times of the year, the data has been related either to a fixed weight of vegetation (10 g dry weight of vegetation for samples taken among macrophytes), or per square metre for samples taken on bare sediments. We have purposefully restricted this analysis to amphipods collected in the Huiñaimarca, because the quantitative sampling coverage is more complete in this part of the lake, both in time and space. The results are summarised in Figures 12 and 13.

On the basis of only four sampling campaigns (1986–1987) at only 28 stations spread over the entire Bolivian part of the Huiñaimarca, it has not been possible to obtain a very detailed picture of the density distributions throughout the year. For this reason the densities have been divided into 6 classes for samples among aquatic vegetation and 4 classes for samples on bare sediments. Examination of Figs 12 and 13 demonstrates the existence of an area of high density of variable extent, lying between Cojata Island and the north of the Taraco Peninsula. This area corresponds to water depths of 6 to 8 metres, where the bottom is carpeted with *Chara*, and where densities of between 50 and 500 amphipods per 10 g of dry weight of macrophytes were recorded. Because of the very great density of Chara in the

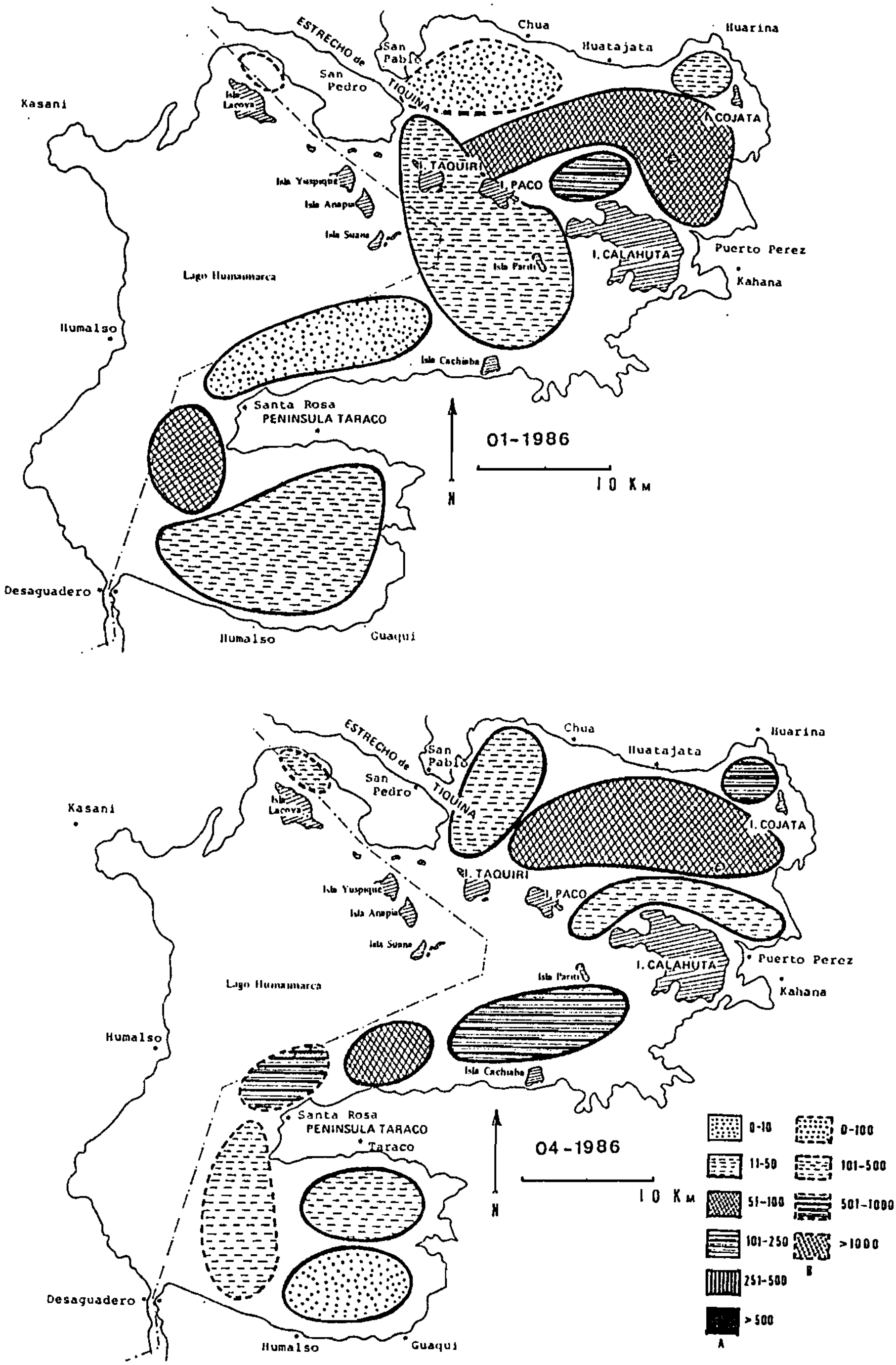

Figure 12. Density distributions of Amphipoda in the Huiñaimarca at two dates in 1986, one (April) corresponding to maximum water level.

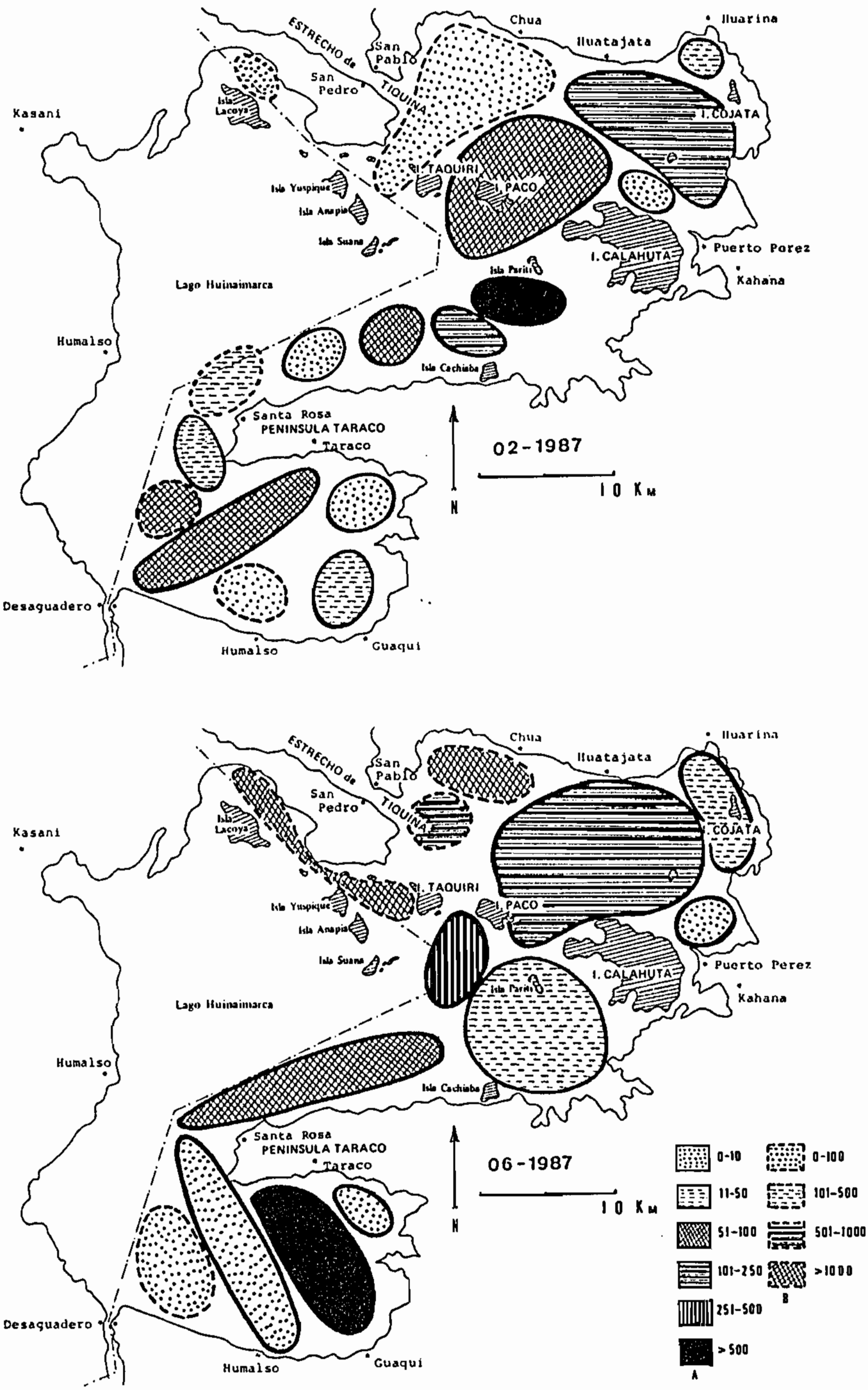

Figure 13. Density distributions of Amphipoda in the Huiñaimarca at two dates in 1987.

whole of this region, this represents a considerable quantity of animals. In contrast, the coastal areas between Puerto Perez and Huarina and in Guaqui Bay are much less densely populated. The same is generally true of bare sediment substrates, except in June 1987 when high densities were recorded in a deep water area off Chua.

April 1986 was the month of maximum lake level, a level that had not been reached in the lake for many years; the difference in peak annual level between 1985 and 1986 was more than 2 metres. Such an increase in level in a few months had profound repercussions on the entire benthic fauna (see Chapter VI.4j). It led to the sudden death of the *Chara*, which before the rise in water level, populated depths close to their maximum tolerance. It is likely that anoxic conditions developed at many locations, leading to local displacement of the more mobile animal populations. As the amphipods are amongst these, such a phenomenon could explain the greater disparity in density distribution recorded in February 1987, compared to the situation which prevailed before the peak of flooding, in January 1986. This phenomenon was perhaps also responsible for the overall increase in amphipod densities in June 1987 which is clearly evident from the distribution map for this month.

Conclusion

Although the species of amphipod in Lake Titicaca which possess characteristic dorsal spines are easy to identify with certainty, the same is not true for spineless species or those with rudimentary spines, especially as individual variation undoubtedly occurs. A systematic revision is now needed, in order to be able to carry out a detailed ecological study of these very abundant organisms in the lake, which account for about 20% of all the benthic macro-invertebrates. Their role as detritivores or even predators of other small animals (zooplankton, chironomid larvae), gives them a determinant role in the ecosystem dynamics of the lake, a role which deserves special study. In addition, because of the density and biomass that they represent, they constitute a very important component in the lake's biology, serving as food organisms for numerous fish species. Frequently consumed by *Salmo gairdneri* of all sizes (although the largest individuals are mainly piscivorous, they will consume crustaceans when these are abundant), the amphipods are the most important macro-invertebrate group in Lake Titicaca after the molluscs.

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C. DEJOUX and A. ILTIS / Editors

Lake Titicaca

A Synthesis of Limnological Knowledge

Kluwer Academic Publishers

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Edited by

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KLUWER ACADEMIC PUBLISHERS

DORDRECHT / BOSTON / LONDON

Library of Congress Cataloging-in-Publication Data

Lake Titicaca : a synthesis of limnological knowledge / edited by C.
Dejoux and A. Iltis.
p. cm. -- (Monographiae biologicae ; v. 68)
Includes indexes.
ISBN 0-7923-1663-0 (HB : alk. paper)
1. Limnology--Titicaca Lake (Peru and Bolivia) 2. Aquatic
resources--Titicaca Lake (Peru and Bolivia) I. Dejoux, Claude.
II. Iltis, A. III. Series.
QP1.P37 vol. 68
[QH128]
574 s--dc20
[574.5'26322'098412] 92-7958

ISBN 0-7923-1663-0

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

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

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

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

Printed on acid-free paper

Printed in the Netherlands