Zooplankton abundance and species composition in Laguna la Orsinera, a Venezuelan floodplain lake

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With 9 figures and 1 table in the text

Abstract

Laguna la Orsinera, a lake lying in the floodplain of the lower Orinoco River, was sampled four days per week between late June and late December of 1984. Over the same interval, measurements were made of temperature, oxygen, transparency, and lake volume. During June, while the lake was shallow, turbid, and still isolated from the Orinoco River, the densities of all zooplankton species were extremely low. Increases in the abundance of selected populations, probably involving resting stages, began three weeks prior to inundation of the lake by the Orinoco River in late July. An extended sequence of species replacements extended through December, six weeks after the drainage of the lake into the river. Cladocerans, which reached substantial densities (mean, 45/liter), were almost entirely restricted to the first two months of this sequence. Important genera included *Moina, Bosmina, Diaphanosoma,* and *Ceriodaphnia.* Declines in populations of cladocerans coincided with high densities of *Chaoborus,* a zooplankton predator. Populations of three copepod species (two diaptomids, one cyclopoid) expanded just after inundation of the lake, but reached their peak abundances more slowly, and persisted in abundance until December. Rotifers were also abundant *(Filinia, Hexarthra, Polyarthra, Brachionus, Keratella, Asplanchna).* The peaks in abundance of rotifer species were spread from early July to December, and suggest differential responses to changing abundance and composition of phytoplankton foods. Comparisons with two tropical lakes not occupying floodplains indicate that, on an annual basis, Laguna la Orsinera has a higher species diversity and a greater degree of equitability among species than would be expected for non-floodplain lakes. This is consistent with the hypothesis that externally-driven physical and chemical changes in the lake induce a greater range of environmental conditions in floodplain lakes. The greater range of conditions leads to a more extensive sequence of species replacements and allows a greater number of species to reach significant abundance.

Introduction

Tropical floodplain lakes, which are abundant along many unregulated tropical rivers (Welcomme 1979), experience distinct seasonal cycles that are governed by the annual rise and fall of river discharge. During the period of low discharge, these lakes often decrease greatly in size and depth. Some of the lakes dry

completely, while others are permanent. Because they are shallow during the dry season, permanent floodplain lakes are likely to mix frequently (often daily), and to have relatively uniform temperature and oxygen concentrations throughout the water column (MacINTYRE & MELACK 1984, SETARO & MELACK 1984, TUNDISI et al. 1984, TUNDISI & MATSUMURA-TUNDISI 1984, HAMILTON & LEWIS 1987. At the same time, transparency is often very low and nutrient concentrations can be high because bottom sediments are frequently resuspended (MARLIER 1967, SCHMIDT 1972, 1973 a, b).

At high discharge, rivers inundate shallow floodplain lakes. Depth, area, and volume increase, which may cause some lakes to extend far into forested areas. As their depth increases, floodplain lakes may stratify (MacINTYRE & MELACK 1984). If so, bottom waters are likely to become anoxic, and transparency is likely to increase because sediments are not resuspended (FITTKAU et al. 1975). Vertical nutrient exchange may also be restricted (SCHMIDT 1972). Incoming river water usually differs substantially from lake water and can have large effects on nutrient dynamics (FISHER & PARSLEY 1979, FURCH 1984, HAMILTON & LEWIS 1987). Many floodplain lakes begin to drain back into the main river soon after they reach maximum depth. As a result, physical conditions are stable for only a short period of time during inundation.

Floodplain lakes can be very productive, particularly in relation to their associated rivers (SIOLI 1975, WELCOMME 1979). Nutrients from the river stimulate production, part of which passes as biomass to the river. Floodplain contributions of zooplankton to the main river channel depend partly upon the degree of synchronization of production and transport between the floodplain and the river. Maximum densities of phytoplankton and zooplankton in many lakes occur during low water (HOLDEN & GREEN 1960, SCHMIDT 1973 b, BRANDORFF & de ANDRADE 1978, CORRALES 1979, RODRIQUES 1980, VASQUEZ & SANCHEZ 1984, MATSUMURA-TUNDISI & OKANO 1983), suggesting that production is highest when floodplain lakes have little or no exchange with the river. This impression may be misleading, however, in that population sizes can rise even as densities decline if inundation increases the size of the lake. Changes in lake volume have seldom been taken into account quantitatively in studies of zooplankton in tropical floodplain lakes. Partly because of complications caused by large changes in water volume, the dynamics of phytoplankton and zooplankton in floodplain lakes are still poorly known.

We give here the results of a study of zooplankton in Laguna la Orsinera, a floodplain lake of the Orinoco River, Venezuela. Our purpose is to quantify zooplankton abundance and species composition, and to evaluate the influence of inundation on total zooplankton population size.

The study site

Laguna la Orsinera is a permanent lake lying on the floodplain north of the Orinoco River at 8° 10′ N, 63° 30′ W near Ciudad Bolivar (Fig. 1). The floodplain that borders this portion of the Orinoco is narrow, and lakes occupy discrete, shallow basins. Laguna la Orsinera fills a dish-shaped basin that is deepest at its western side (Fig. 1). The lake is surrounded by tropical deciduous forest and is
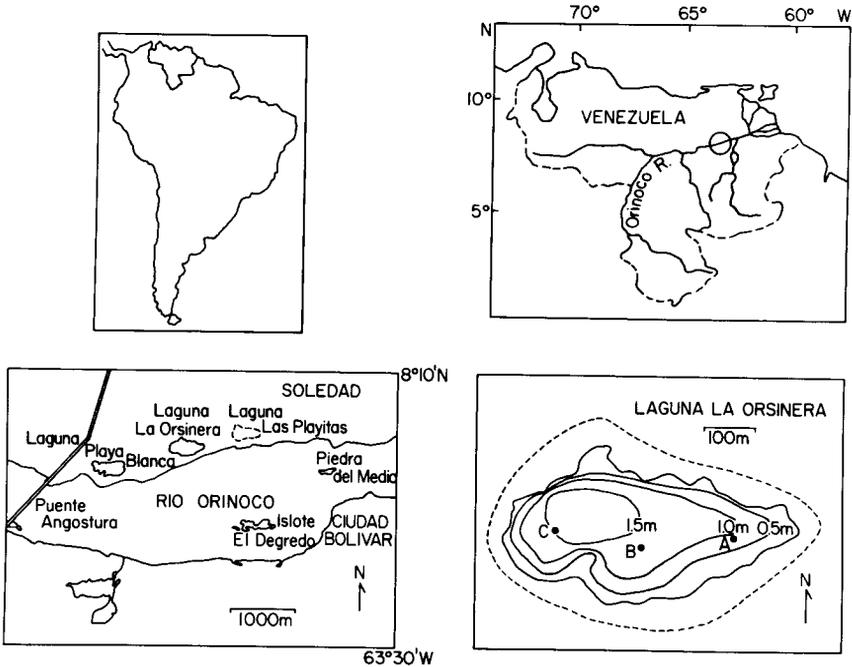

Fig. 1. The Orinoco River near Laguna la Orsinera and a bathymetric map of the lake. The dashed line indicates the approximate extent of flooding.

ringed throughout the year by macrophytes (mainly *Eichhornia crassipes* and *Paspalum repens*). Although macrophytes grow during inundation, most of the lake surface remains free of macrophytes throughout the year. During the dry season, the lake is completely separated from the river by a high levee; a narrow break in this levee forms the primary connection with the river during the rainy season. Floodplain lakes in this area receive some watershed runoff and some flowthrough from connections with other lakes. However, the major features in their water budgets are loss by evaporation during the dry season and extensive flooding by the river during the rainy season (HAMILTON 1985). The major human influence on La Orsinera is likely to be fishing, which is concentrated during the dry season, when the lake is shallow and fish densities are high.

The region of Venezuela near Laguna la Orsinera experiences pronounced wet and dry seasons. Annual air temperature averages 27.7°C, and monthly averages range from 26.6 to 28.8°C. Annual precipitation averages 983 mm, 85–90% of which falls between May through November (Vasquez & Sanchez 1984). In 1984, air temperatures were slightly lower than normal, the dry season was unusually long, and inundation of the floodplain was delayed by approximately 1 month.

Methods

Three sampling stations were established along the east-west axis of the lake (Fig. 1). Depth was measured at each station on each sampling date with a calibrated line. In addition, changes in depth following inundation were measured with a calibrated staff located on shore at the edge of the lake. Temperature and oxygen profiles were taken weekly with a thermister and oxygen probe at station B at intervals of 0.5 m from the surface to within 0.5 m of the bottom. Water transparency was also measured weekly with a Secchi disc (diameter, 15 cm).

The bathymetric map shown in Figure 1 is based on echosounding data collected at high water along 3 east-west transects across the lake. This map, together with aerial photographs showing the extent of inundation at high water (provided by the Venezuelan Direccion de Cartografia Nacional), was used to calculate the lake volume and area for each sampling date.

We sampled zooplankton with a flexible tube sampler that was 10 cm in diameter (Lewis & Saunders 1979). This tube was fitted at one end with a nylon-coated tafetta collar attached to a heavy metal ring (Unger & Lewis 1983). The metal ring weighted the sampling end of the tube so that it rapidly sampled the entire water column to within 0.5 m of the bottom. When retrieved, this ring also collapsed the water-proof tafetta collar against the opening of the sampler, and thus closed the tube to further water collection. The tube was calibrated so that we could calculate the volume of water collected in vertical samples of varying depth. The volume of all samples was greater than 10 l and was usually greater than 20 l. The contents of the tube were filtered through a net of 37-μm mesh and preserved in 4% formalin and 0.15 M sucrose (Haney & Hall 1973).

Three samples were collected at each of the three sampling stations. Replicates were then combined across stations to create three composite samples; each was a mixture of one sample from station A, one sample from station B, and one sample from station C. From June through mid-September, zooplankton were sampled on Monday, Wednesday, Friday, and Saturday of every week. From mid-September through December, samples were taken on Monday, Tuesday, Wednesday, and Thursday of each week. All zooplankton samples were collected between 0900 and 1200 hours. We also sampled zooplankton in the channel connecting the lake to the river. This was done weekly during flooding, until flow was negligible and the channel became obstructed with macrophytes. Subsamples of each composite sample were counted with a stereomicroscope at 25 X. Subsample size was chosen in such a way that at least 100 individuals of *Diaptomus negrensis* were counted. Because this species was never the most abundant in the lake, far more than 100 individuals of most species were counted in each subsample. Nauplii of the predominant cyclopoid, *Oithona amazonica*, were not distinguished during counting from the nauplii of 2 or 3 other species of cyclopoids that occurred rarely as copepodites and adults in the plankton. *Diaphanosoma brevireme* and *D. birgei* were identified as one species in samples collected during the first 3 months of the study. For this reason, counts of these two species were combined throughout the sampling period. *Diaphanosoma birgei* was secondary in abundance to *D. brevireme*

until October, when it became the more abundant of the two. For samples taken in November and December, all species were enumerated only in samples taken on Monday and Thursday of each week, but all of the samples were counted for the two diaptomid copepods. Means, ranges, and standard deviations were calculated for the three replicate samples for a given date. From the organism densities and lake volume, numbers of individuals in the entire lake were calculated for each sampling date.

Results

Physical characteristics of the lake

In 1984, Laguna la Orsinera remained separate from the Orinoco River until 27 July. The maximum depth of the lake before inundation was as low as 1.2 m (Fig. 2). On 27 July the Orinoco filled the narrow channel connecting it with La
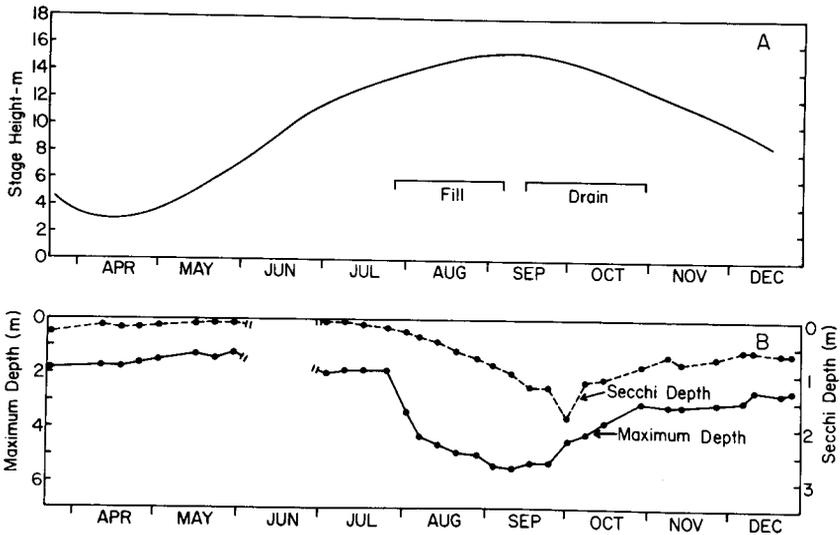

Fig. 2. A: Stage height of the Orinoco River, showing periods when floodplain lakes fill and drain. B: Maximum lake depth and secchi depth between March and December, 1984.

Orsinera. For 8 days, the flow through this channel into the lake was swift (0.44 to 0.80 m/sec). By 3 August, river and lake levels had equilibrated; the two then continued to rise in synchrony. The lake reached its maximum depth (5.5 m) in early September, six weeks after initial inundation. During this period, the volume of the lake increased approximately 9-fold (Fig. 3). The rapid rise in water level was followed by approximately one week during which there was no change in depth. Water level then gradually decreased from mid-September until 29 October, when the connection between the river and the lake closed. During the drainage period,
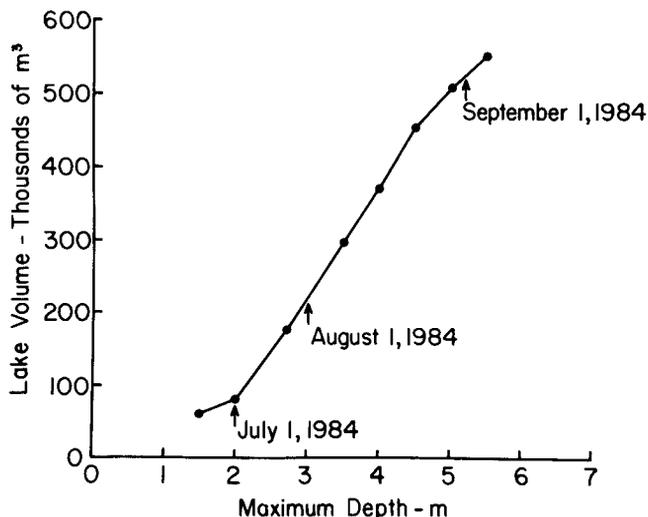
Fig. 3. Relationship of volume and maximum depth in Laguna la Orsinera.

it was not possible to measure the flow in the channel connecting the lake with the river because the channel was inaccessible. Following separation of the lake from the river, depth decreased at a slower rate, due to evaporation.

Temperatures at station B ranged between 27 and 30°C over a 10-month period that included March through May of 1984, before routine zooplankton sampling began (Fig. 4). The temperatures were highest in late September and early October, during the drainage phase. Temperature profiles show evidence of thermal stratification during high water, but changes in bottom temperatures indicate that vertical heat flux influenced temperatures near the bottom, even during stratification. A portion of the vertical temperature differences can be attributed to diel heat flux. During high water, however, the vertical differences were too large to be explained entirely by diel heat flux, and thus indicate that the lake was not mixing vertically on a daily basis over this interval.

Oxygen concentrations were high throughout the water column during the isolation phase. Oxygen concentration decreased markedly during inundation and remained well below saturation, even at the surface. In addition, a substantial vertical oxygen gradient persisted during inundation (August–September), and water near the bottom was either anoxic or nearly so over this interval (Fig. 4).

Transparency of La Orsinera was lowest during low water: Secchi disc readings were less than 0.5 m and were sometimes as low as 10 cm (Fig. 2). During inundation, transparency increased gradually to a maximum Secchi disc reading of 1.8 m, which occurred just as the lake began to drain. After this maximum, transparency declined again as the depth of the lake decreased.
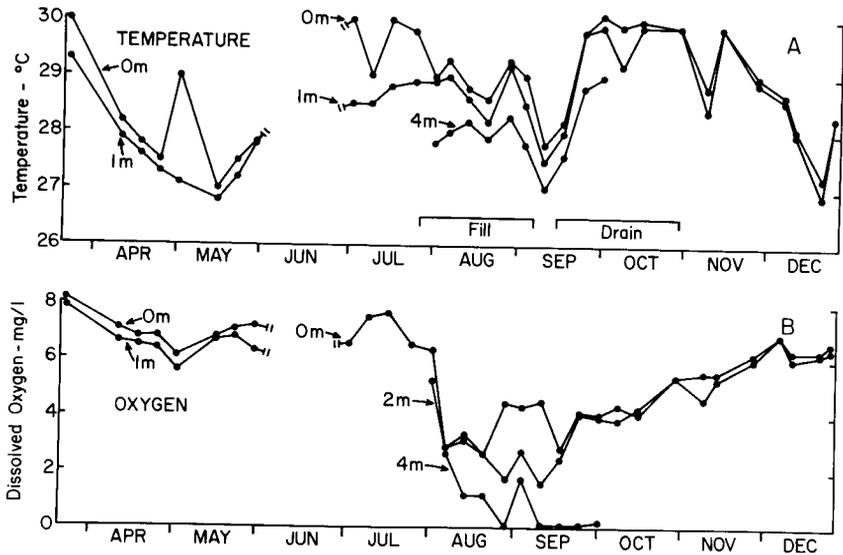
Fig. 4. Temperature and oxygen in Laguna la Orsinera from March through December, 1984.

Zooplankton species composition and abundance

Zooplankton abundance can be expressed either as number of individuals per liter (density) or as total population size. For most lakes, the patterns for these two variables would be essentially indentical. However, because of the large changes in volume of Laguna la Orsinera, variations in density can be substantially different from variations in total number of individuals. This is illustrated in Figure 5 for *Diaptomus negrensis*. In general, the total population size of a species during the period of low water will be far smaller than might be suspected from the densities of organisms. In analyzing the factors that cause the increase and decrease of populations, we emphasize total population size rather than density of organisms. However, Table 1 provides summary statistics for both variables.

Common crustacean zooplankton species in the open water of La Orsinera included the cyclopoid copepod *Oithona amazonica*, two diaptomid copepod species (*Diaptomus negrensis* and *Rhacodiaptomus calatus*), and five cladoceran species (Table 1). *Oithona amazonica* dominated the crustacean zooplankton throughout the study period (Table 1). This species has been found commonly along the Orinoco River (DUSSART 1984). *Diaptomus negrensis* was more common than *R. calatus*. Of the five common cladoceran species, only *Moina minuta* reached mean abundances comparable to those of the copepods. Nine rotifer species were common during the sampling period (Table 1). Of these, *Polyarthra vulgaris* and *Brachionus zahniseri* had the highest mean abundances. Rotifers were never more abundant than copepods.

The two diaptomid species were present in all samples from June through December (Fig. 5). *Diaptomus negrensis* reached a large peak in August, just after inundation began, and a second, smaller peak in late November and early December. *R. calatus*, which is larger, was less abundant than *D. negrensis*. Population size increased slowly in late August and September, rapidly reached a maximum in early October, and decreased in abundance through the end of December. Cyclopoid nauplii increased to a maximum in October and November
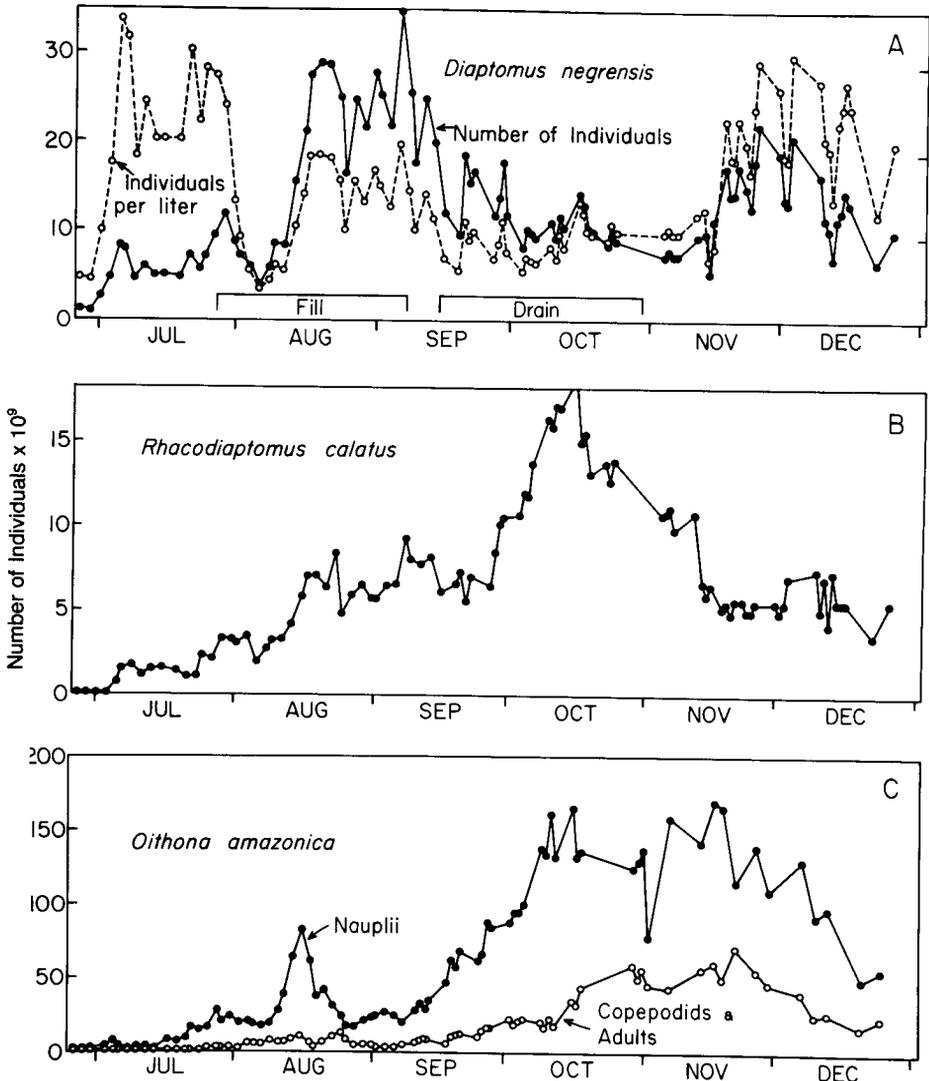

Fig. 5. Population size of copepods in Laguna la Orsinera, June through December, 1984.

Table 1. Abundances of the common zooplankton species in Laguna la Orsinera and estimates of counting variations.

	Individuals (millions)		Indiv/l	C.V. for
	Mean	Range	Mean	counts, %**
Copepoda				
Oithona amazonica (BURKHARDT)	93973	310–215250	313	10
Diaptomus negrensis (ANDRADE & BRANDORFF)	12824	805– 35000	43	11
Rhacodiaptomus calatus (BRANDORFF)	6973	0– 18500	23	15
Cladocera				
Moina minuta HANSEN	7016	5– 28014	23	25
Bosmina sp.	1521	0– 13723	5.1	25
Diaphanosoma brevireme SARS*	1935	0– 17485	6.5	26
Ceriodaphnia cornuta SARS	2148	0– 16510	7.2	26
Rotifera				
Polyarthra vulgaris CARLIN	28734	0–242446	96	23
Hexarthra intermedia brasiliensis (HAUER)	1474	0– 17662	4.9	30
Brachionus zahniseri AHLSTROM	19621	0–117910	65	34
Keratella americana CARLIN	674	0– 5438	2.2	42
Filinia longiseta (EHRENBERG)	6942	0– 24537	23	17
Asplanchna sieboldi (LEYDIG)	1874	0– 17654	6.2	38
Brachionus mirus DADAY	456	0– 11142	1.5	–
Brachionus dolobratus HARRING	62	0– 4072	0.20	–
Diptera				
Chaoborus sp.	356	0– 2084	1.2	60

* Also includes D. birgei (KORINEK)
** 100 s/x for replicates on a given date

(Fig. 5). Copepodite and adult stages of *O. amazonica* showed much the same pattern.

Moina minuta and *Bosmina* sp. were the only open-water cladocerans in La Orsinera before inundation (Fig. 6). The population size of *Moina* dropped as inundation began, but quickly rose again in early August, while the lake level was still rising. A smaller and more irregular increase in *M. minuta* occurred in November–December. *Bosmina* peaked in population size just as inundation began and remained abundant in the plankton until mid-August. Its maximum abundance occurred between the two successive peaks in *M. minuta*. After August, the abundance of *Bosmina* remained low.

Following inundation, *D. brevireme*, *D. birgei*, and *C. cornuta* appeared. Combined counts of *D. brevireme* and *D. birgei* described a peak in abundance during mid-August coincident with a decrease in abundance of *M. minuta* (Fig. 6). *Ceriodaphnia cornuta* increased rapidly to a peak abundance in late August, soon after this species appeared in the plankton. This peak immediately followed the *Diaphanosoma* maximum. Abundance of *C. cornuta* began to decline in mid-September; from October through December, this species was rare.

Eight of the nine common rotifer species in La Orsinera exhibited rapid increases and declines in population size (Fig. 7). *Filinia longiseta* was the only species that was common for an extended period of time. *Hexarthra intermedia brasiliensis* increased in abundance just before inundation and again in early August, just after inundation began (Fig. 7). Following a decline in *Hexarthra*, *P. vulgaris* was very abundant from late August until early September. The decline in *P. vulgaris* was followed by a rapid but smaller increase in *A. sieboldi* in late September (Fig. 8). *Keratella americana* showed a single, small increase in mid-October and, finally, *B. zahniseri* increased to a large maximum in early November. Abundance of both *K. americana* and *Brachionus* (including *B. mirus* and *B. dolobratus*, which are not shown in the figures) increased again in late December. The progression of dominant rotifer species was similar to the rapid progression of cladoceran population maxima, although cladocerans were restricted to a shorter time period that was coincident with the filling of the lake.

Chaoborus larvae became abundant in La Orsinera in mid-August, as the depth of the lake was increasing (Fig. 8). Their abundance was highly variable in September and October, and decreased by December. The estimates of *Chaoborus* abundance may be low if some of the individuals were in or very near the sediments, as is often the case during the daytime in shallow lakes.
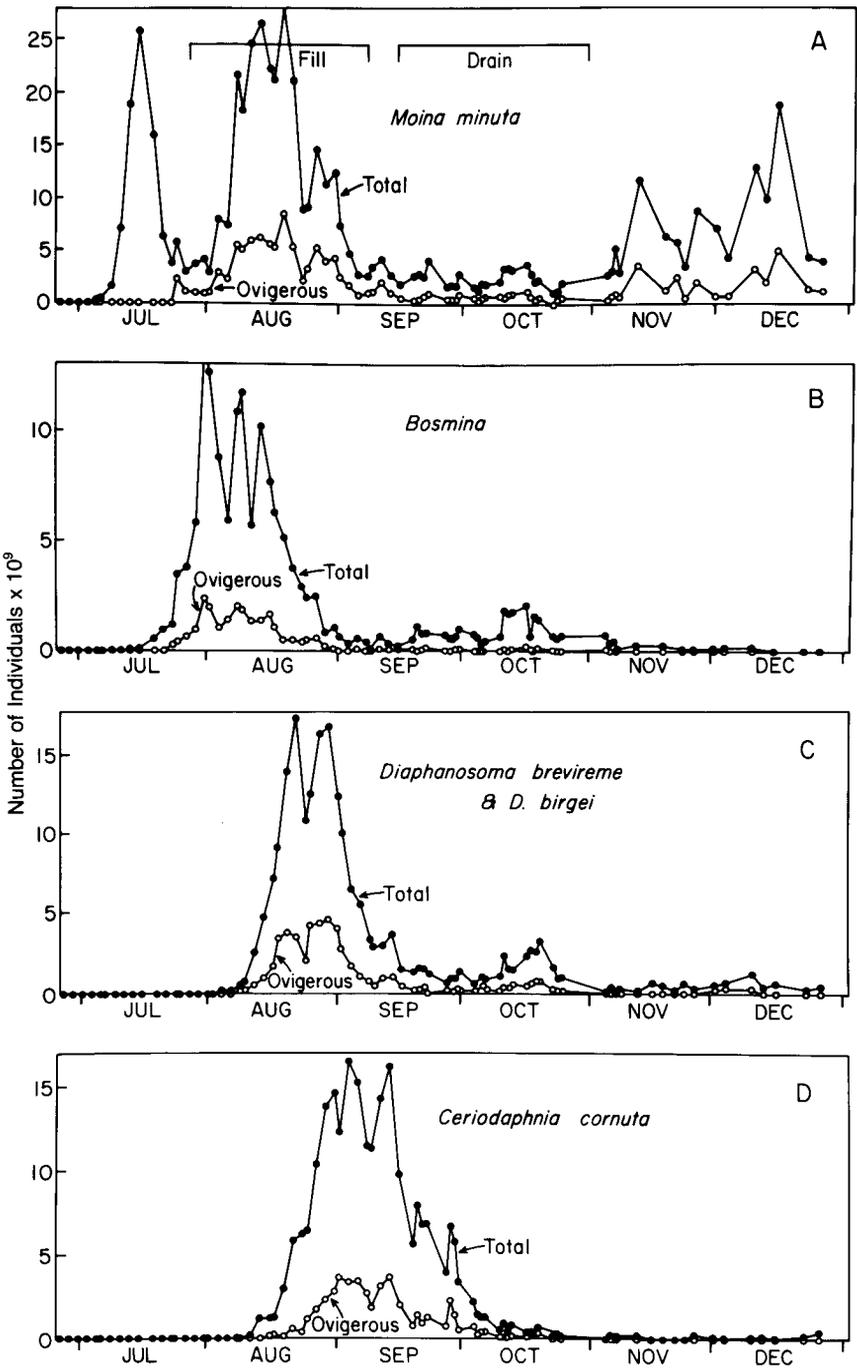
Fig. 6. Population sizes of Cladocera populations in Laguna la Orsinera, June through December, 1984.
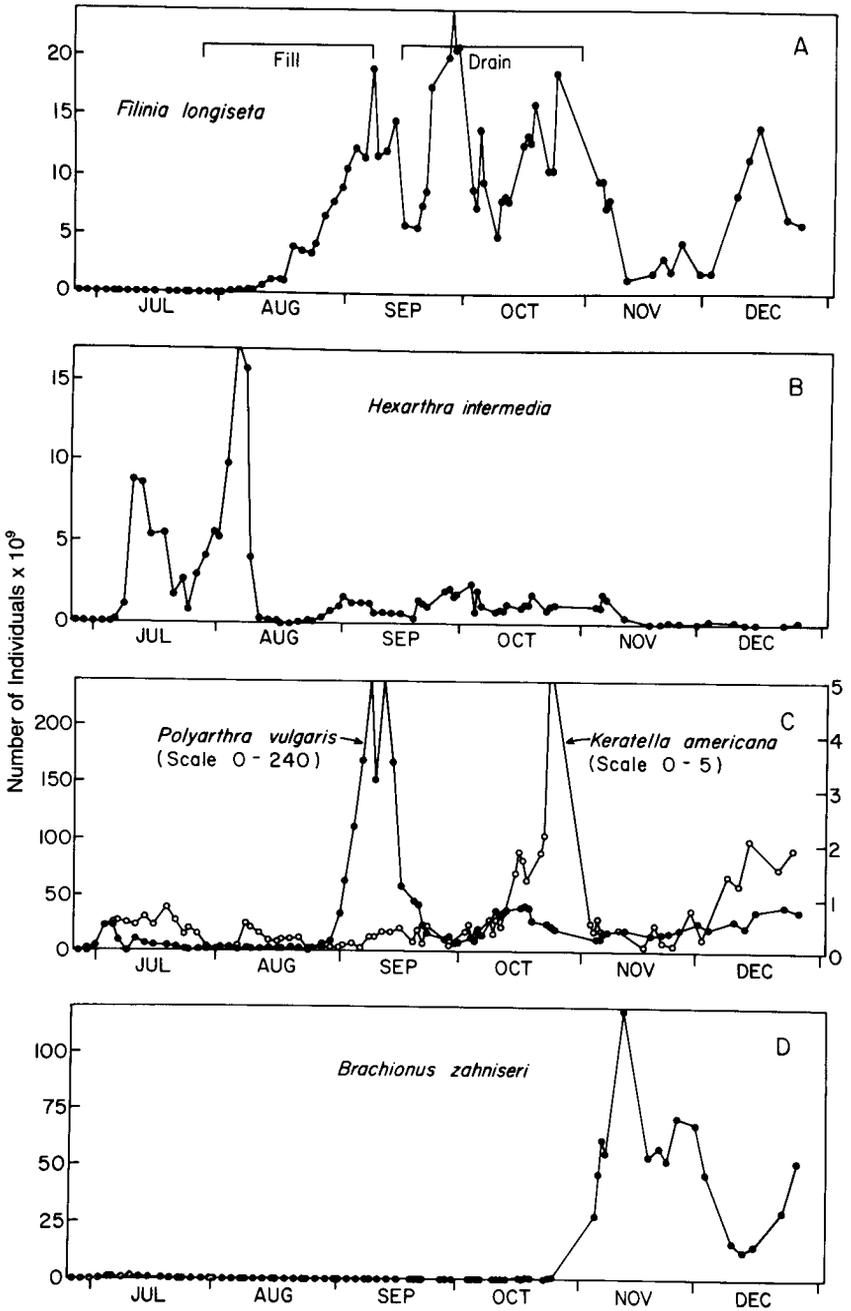
Fig. 7. Population size of rotifers in Laguna la Orsinera, June through December, 1984.
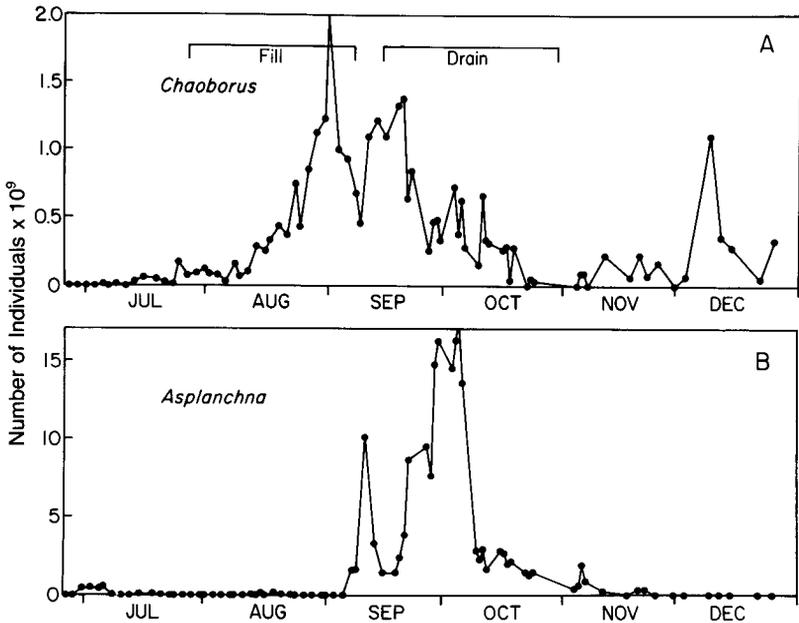
Fig. 8. Population size of *Chaoborus* larvae and *Asplanchna* in Laguna la Orsinera, June through December, 1984.

Discussion

Species abundance patterns

On the basis of abundance patterns, zooplankton species of Laguna la Orsinera generally fall into two groups. The first group consists of species that show steep and rapid increases in population size, followed by a very short interval of persistence at maximum abundance and then an abrupt decline. Typically these species have only one period of increase throughout the entire season, although some show secondary increases in addition to the primary one. To this group belong all the cladocerans and the rotifers except *Filinia*. For both the cladocerans and the rotifers within this group, there was a distinct progression in population maxima. *Filinia* and the three species of copepods belong to a second group that is characterized by more gradual increase in abundance, much less abrupt decline in abundance, and a more sustained interval of maximum abundance.

It is not unusual in lakes for abundances of some zooplankton species to rise and decline abruptly, and these species are more likely to be rotifers or cladocerans than copepods. However, the number of species that rise and decline abruptly seems unusually large in Laguna la Orsinera. As a result, the number of species that reach high abundances in Laguna la Orsinera may be well above average for lakes in general.

Controlling factors

Changes in the major environmental variables coincide with some major changes in zooplankton populations of Laguna la Orsinera. Abundances of all zooplankton were negligible during June, prior to flooding. We conclude that the late isolation period is unfavorable for all categories of zooplankton. High turbidity and possibly the concentration of predators at low water may limit zooplankton at this time, but the extreme nature of the suppression and its extension to virtually all species is surprising, and may not be adequately explained by factors such as turbidity and predation. The range in abundance between the minima of June and the subsequent maxima of the high water period equal or exceed the variations in population abundances between winter and summer periods in lakes of the temperate zone, and plainly demonstrate the alternation of conditions that are extremely favorable with those that are extremely unfavorable for zooplankton growth in Laguna la Orsinera.

The abundance patterns show that the initiation of zooplankton growth occurs in two stages. The first stage anticipates the rise in water that is associated with flooding, and the second stage immediately follows flooding. Species contributing to the first phase of increase include the cladocerans *Moina* and *Bosmina*, the two diaptomid copepod species, and the rotifers *Hexarthra* and *Keratella*. Sharp increases of some of these taxa from small population sizes suggest that resting stages produce the anticipatory peaks, although this has not been verified. This suggestion is strengthened by observations of resting egg production by all cladocerans during their population maxima, and, for *Moina*, by the absence of reproductive individuals during the period of rapid increase in July. Males and sexual females, indicating the possibility for resting eggs, are known in the *Moina* (Paggi & Paggi 1974), as they are for South American *Bosmina* (Lieder 1983, Deevey & Deevey 1971).

Diapause has been studied very little among tropical zooplankton populations. Moghraby (1977) found diapausing stages of rotifers, cladocerans, and copepods in the Blue Nile. Emergence from diapause was prevented in the Blue Nile by large amounts of suspended sediment, but occurred at numerous times throughout the year. Although studies of diapause evidently have not been done on Amazonian lakes, Irmler (1975, 1981) has recorded resting stages of sponges and macro-invertebrates in lakes of the Amazon floodplain. Lasi (M. Lasi, unpublished) has also found resting stages of invertebrates in the sediments of Orinoco floodplain lakes near Laguna la Orsinera.

The trigger for anticipatory increases in abundance is unclear. There appears to have been a slight increase in depth of Laguna la Orsinera during June (Fig. 2), possibly because of small amounts of rain in the watershed, and this may have provided the trigger. Alternatively, some of the populations may, because of physiological adaptation to the floodplain environment, be able to take advantage

of more subtle cues. Such adaptations may be especially well developed in *M. minuta*, which is found only along rivers or lakes opening to the ocean (GOULDEN 1968).

Major increases of abundance coincided with the entry of water into the lake in the last week of July. This phase of increase involved a notable re-stimulation of most species involved in the anticipatory increase. In addition, there was a marked increase in cyclopoid copepods at this time. After a refractory interval of two to four weeks, a number of other species joined the increase. These included the remaining species of Cladocera and *Filinia*. The increase of many species over this interval indicates generally favorable nutritional conditions. This is confirmed by a high ratio of eggs to adults for cladocerans and copepods.

Some significant declines of individual populations began in August and extended into December. For both cladocerans and copepods, decreased abundance coincided with a decrease in the absolute number of ovigerous females, suggesting that increased mortality was partly responsible for observed declines. Furthermore, declines of *Moina, Bosmina, Diaphanosoma*, and *Hexarthra* coincided with a major increase in the abundance of *Chaoborus*. *Chaoborus* is known to be an especially effective predator on cladocerans (LEWIS 1977), and may have contributed to the decline of Cladocera. In addition, it is known that large numbers of larval fish enter the lakes in this vicinity along with the flood waters (M. RODRIGUEZ, unpublished). A steady increase in predation pressure from these larval fish could be expected as they grow and become more effective zooplankton predators. Because small fish often consume cladocerans readily, the growth of larval fish may also have contributed to the general decline of the cladocerans in August and September.

The decline in abundance of *Chaoborus* that began at the end of August and extended gradually into October may be explained by the presence of increasing numbers of fish of sufficient size to capture and consume *Chaoborus*. Steadily increasing transparency of the lake during the interval between early August and late September would also have favored an increasing role for fish predation, both in the control of herbivores and of *Chaoborus*. Copepods are typically more resistant to fish predation, which would explain their continued presence in quantity and their increasing dominance in the community.

Rotifers exhibited population growth phases throughout the study period, despite shifts in potential predation by *Chaoborus* and cyclopoid copepods. Thus, it appears that rotifer populations were predominantly controlled by shifts in food resources that occurred as changes in transparency and chemistry affected the phytoplankton community.

By the end of the sampling interval in December, zooplankton populations had declined to very low levels, but still had not returned to the baseline conditions that prevailed in June when the sampling began. Their return to baseline apparently occurs gradually over the period of isolation. The slow nature of this decline and

its occurrence across all taxa, including those that are relatively resistant to predation, suggest that herbivore nutrition is inadequate over this interval.

Resuspension of sediments and extreme turbidity that characterize the isolation period in Laguna la Orsinera could account for poor nutritional conditions and reduced zooplankton abundance. In nearby Lake Tineo, large increases in turbidity coincide with severe reduction in phytoplankton populations, presumably because of shading of the phytoplankton cells by suspended inorganic materials (HAMILTON & LEWIS 1987). Consequently, the increases in lake level and transparency that occur when the lake level rises can be expected to stimulate phytoplankton growth. A similar increase in phytoplankton growth has been recorded from lakes of the Amazon floodplain (SCHMIDT 1972, 1973 a, b; FITTKAU et al. 1975).

Samples that were taken in the channel connecting the lake with the Orinoco River showed that the numbers of individuals entering the lake from the river were negligible by comparison with the population increases in the lake. Consequently, we attribute no significant role to immigration in producing the increases of population size. The timing of the drainage phase coincided with declines in cladoceran and selected rotifer populations. Although drainage from the lake steadily removed a portion of all zooplankton populations, this removal was small by comparison with the rates of population change.

Community richness and equitability

Laguna la Orsinera produced an extended sequence of zooplankton species. Log-phase increases of the participant species were spread over an exceptionally long interval (July to December). Such an extended series of optima for different species suggests a strong role for allogenic (extrinsic) factors such as flushing, lake depth, and stratification that operate either directly on the zooplankton species or indirectly by forcing changes in the food supply or the intensity of predation. If this is correct, we might expect that the equitability in distribution of individuals across species is greater in La Orsinera, and possibly in other floodplain lakes, than in lakes where the external forcing functions change the environment a minimal amount during the growing season.

To examine this hypothesis, we compare equitability and richness of the zooplankton community of La Orsinera with equitability and richness in two other lakes for which species richness is in the upper range for tropical lakes: Lake Lanao, Philippines (LEWIS 1979) and Lake Valencia, Venezuela (SAUNDERS & LEWIS 1987). We have chosen these two lakes because they were sampled and analyzed by methods similar to those used for La Orsinera, and because we have the raw data necessary for the analysis. The comparison could be extended to other tropical non-floodplain lakes in which the zooplankton community has been studied over an extended period of time.

In making the comparisons, we plotted the logarithm of abundance against rank (WHITTAKER 1972, cf. LEWIS & WEIBEZAHN 1974). Curves of this type

typically have an linear mid-section, the slope of which can be determined by least squares. We omit the first value in each series (rank number 1) because of the upward inflection of the points at very low ranks. In general, flat slopes for such regression lines indicate high equitability, and steep slopes indicate low equitability. In addition, communities whose items cut the x axis at higher values of x are richer in species than communities whose curves cut axis at lower values of x.

As shown in Figure 9, the slopes of the lines for Lake Lanao and Lake Valencia are steeper than for the lines representing Laguna la Orsinera. In addition, for a given value of y, the line for La Orsinera cuts the x axis at a higher rank than the lines for the other lakes. This indicates greater species richness as well as greater equitability for La Orsinera. The test results are consistent with our hypothesis that the plankton community of Laguna la Orsinera is more equitable in its distribution of individuals among species across the growing season, and is richer in species than tropical non-floodplain lakes, because of the continuous importance of allogenic factors in driving succession during the growing season.
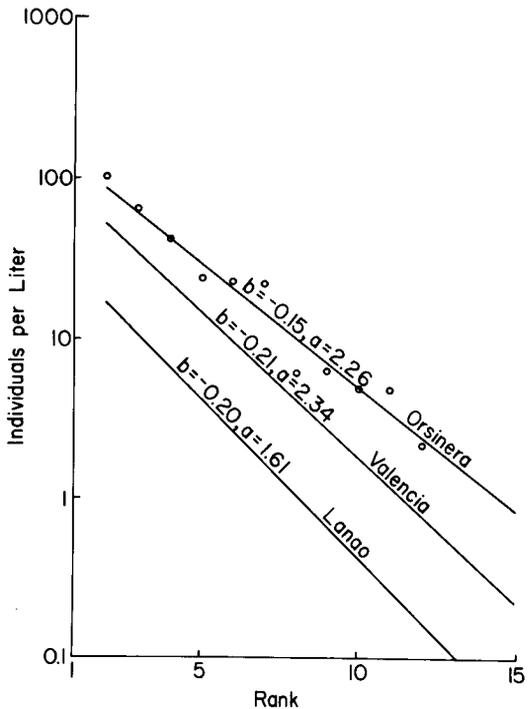

Fig. 9. Relationships between rank and the logarithm of mean abundance for zooplankton species in Laguna la Orsinera and two other tropical lakes.

Comparison with other similar lakes

Because zooplankton dynamics have not been well studied in tropical flood-plain lakes, possibilities for direct comparison of Laguna La Orsinera with other lakes are limited. VASQUEZ (1984) and VASQUEZ & SANCHEZ (1984) sampled zoo-plankton in a number of lakes along the Orinoco River near Ciudad Bolivar. The species composition that they recorded is very similar to the composition of the community that we found in Laguna la Orsinera, although they found communities that were dominated by rotifers. VASQUEZ & SANCHEZ found higher zooplankton abundances at low water than high water. While zooplankton densities in Laguna Orsinera are sometimes high during the period of low water, actual population sizes are largest during the period of high water.

Zooplankton have been better studied in lakes of the Amazon floodplain than along the Orinoco. MARLIER (1967) found no substantial differences in the abundance of zooplankton at high and low water in Lago Redondo. Other studies, however, report maximum densities of zooplankton at low water (BRANDORFF & DE ANDRADE 1978, CORRALLES 1979, RODRIQUES 1980, MATSUMURA-TUNDISI & OKANO 1983). High densities of zooplankton in these lakes do not correspond necessarily to large population sizes, however. Because of the great decrease in lake volume during the dry season, densities may give a misleading impression of population size. Biases introduced by large changes in lake volume may explain why zooplankton densities in Lago Jacaretinga, Brazil, declined despite marked increases in fecundity (BRANDORFF & DE ANDRADE 1978).

Although it is not possible yet to tell how typical Laguna la Orsinera may be of the many floodplain lakes that lie along the middle and lower Orinoco River, it is clear that Laguna la Orsinera is distinct in a number of ways from many tropical non-floodplain lakes. Because of major changes in physical conditions of the lake, the growth of zooplankton is highly seasonal and incorporates intervals of very high and very low abundance. In addition, equitability and richness within the community appear to be higher than might be expected in other kinds of tropical lakes, and this can be explained by the great range of physical conditions that occur over a single year. Finally, regular phasing of predation intensity and of algal abundance under the control of seasonal physical changes in the lake appears to play a large role in the seasonality of the zooplankton community.

Zusammenfassung

Laguna la Orsinera, im Überschwemmungsgebiet des unteren Orinoco, wurde zwischen Ende Juni und Ende Dezember jeweils während vier Tagen pro Woche besammelt. Gleich-zeitig wurden Temperatur, Sauerstoffgehalt, Lichtdurchlässigkeit des Wassers und das See-volumen gemessen.

Im Juni, als der See noch seicht, stark getrübt und noch vom Orinoco getrennt war, waren die Zooplanktondichten extrem gering. Die Abundanzen einzelner Populationen begannen etwa 3 Wochen vor der Überflutung des Sees durch den Orinoco zuzunehmen,

vermutlich aus Dauerstadien. Die Zunahme setzte sich bis Dezember fort, 6 Wochen, nachdem das Überschwemmungsgebiet in den Fluß entwässert hatte. Cladoceren erreichten hohe Besiedlungsdichte (im Mittel 45 Individuen pro Liter) und waren fast ausschließlich auf die ersten beiden Monate der Sukzession beschränkt. Die wichtigsten Gattungen waren *Moina, Bosmina, Diaphanosoma* und *Ceriodaphnia*. Abnehmende Populationsdichten der Cladoceren fielen zeitlich mit hohen Dichten der räuberischen *Chaoborus*-Larven und mit der jahreszeitlich bedingten Zunahme junger planktivorer Fische zusammen. Copepoden-Populationen nahmen unmittelbar nach der Überschwemmung des Sees stark zu, erreichten ihr Maximum aber langsamer und behaupteten sich bis Ende Dezember. Zwei Diaptomiden-arten und eine Cyclopidenart erreichten signifikante Besiedlungsdichten, zeigten aber Anzeichen ernster Beeinträchtigung durch Räuberdruck. Rädertiere waren ebenfalls häufig *(Filinia, Hexarthra, Polyarthra, Brachionus, Keratella, Asplanchna)*. Häufigkeitsmaxima von Rädertierarten traten über den gesamten Untersuchungszeitraum verteilt auf. Sie scheinen durch sich ändernde Ernährungsbedingungen ausgelöst zu werden, die durch ausgeprägte Verschiebungen in der Lichtdurchlässigkeit des Wassers und der Häufigkeit und Arten-zusammensetzung der Zooplanktonnahrung bedingt sind.

Im Vergleich zu tropischen Seen außerhalb von Überschwemmungsgebieten scheint Laguna la Orsinera eine höhere Artenvielfalt sowie einen höheren Äquibilitätsindex zwischen Arten aufzuweisen. Dies stimmt mit der Hypothese überein, daß von äußeren Faktoren beeinflußte physikalische und chemische Veränderungen im See ausgeprägtere Schwankungen in den Umweltbedingungen herbeiführen, die dann ihrerseits eine deutlichere Artenabfolge ermöglichten und einer größeren Zahl von Arten erlaubten, hohe Abundanzen zu erreichen.

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References

BRANDORFF, G. O. & de ANDRADE, E. R. (1978): The relationship between the water level of the Amazon River and the fate of the zooplankton population in Lago Jacaretinga, a varzea lake in the central Amazon. − Stud. Neotrop. Fauna & Environ. 13: 63−70.

CORRALES, M. A. (1979): Zooplankton of the high Parana River (Argentina and Paraguay). − Ecosur. 6: 185−206.

DEEVEY, E. S. Jr. & DEEVEY, G. V. (1971): The American Species of *Eubosmina* SELIGO (Crustacea, Cladocera). − Limnol. Oceanogr. 16: 201−218.

DUSSART, B. H. (1984): Some Crustacea Copepoda from Venezuela. − Hydrobiol. 113: 25−67.

FISHER, T. R. & PARSLEY, P. E. (1979): Amazon lakes: Water storage and nutrient stripping by algae. − Limnol. Oceanogr. 24: 547−553.

FITTKAU, E. J.; IRMLER, U.; JUNK, W. K.; REISS, R. & SCHMIDT, G. W. (1975): Productivity, biomass and population dynamics in Amazonian water bodies. − [In:] GOLLEY, F. W. & MEDINA, E. (eds.): Tropical Ecological Systems: 289−311; Springer, N.Y.

FURCH, K. (1984): Seasonal variation of the major cation content of the várzea-lake Lago Camaleão, middle Amazon, Brazil, in 1981 and 1982. − Verh. Internat. Verein. Limnol. 22: 1288−1293.

GOULDEN, C. E. (1968): The systematics and evolution of the Moinidae. − Trans. Amer. Phil. Soc. 58: 1−101.

HAMILTON, S. K. (1985): Water chemistry and nutrient mass balance of a floodplain lake along the Orinoco River, Venezuela. − Masters Thesis, Univ. Colorado, Boulder.

HAMILTON, S. K. & LEWIS, W. M. Jr. (1987): Chemistry and nutrient mass balance of a lake on the Orinoco River floodplain, Venezuela. − Limnol. Oceanogr. [in press]

HANEY, J. F. & HALL, D. J. (1973): Sugar-coated *Daphnia:* a preservation technique for Cladocera. − Limnol. Oceanogr. 18: 331−333.

HOLDEN, M. J. & GREEN, J. (1960): The hydrology and plankton of the River Sokoto. − J. Anim. Ecol. 29: 65−84.

IRMLER, U. (1975): Ecological studies of the aquatic soil invertebrates in three inundation forests of Central Amazonia. − Amazoniana 5: 337−409.

− (1981): Überlebensstrategien von Tieren im saisonal überfluteten amazonischen Überschwemmungswald. − Zool. Anz. Jena 206: 26−38.

LEWIS, W. M. Jr. (1977): Feeding selectivity of a tropical *Chaoborus* population. − Freshwat. Biol. 7: 311−325.

− (1979): Zooplankton community analysis. − Springer, N.Y.

LEWIS, W. M. Jr. & SAUNDERS, J. F. III (1979): Two new integrating samplers for zooplankton, phytoplankton, and water chemistry. − Arch. Hydrobiol. 85: 244−249.

LEWIS, W. M. Jr. & WEIBEZAHN, F. H. (1974): Chemistry, energy flow, and community structure in some Venezuelan fresh waters. − Arch. Hydrobiol. Suppl. 50: 145−207.

LIEDER, U. (1983): Revision of the genus *Bosmina*, BAIRD, 1845 (Crustacea, Cladocera). − Int. Revue ges. Hydrobiol. 68: 121−139.

MacINTYRE, S. & MELACK, J. M. (1984): Vertical mixing in Amazon floodplain lakes. − Verh. Internat. Verein. Limnol. 22: 1283−1287.

MARLIER, G. (1967): Ecological studies on some lakes of the Amazon valley. − Amazoniana 1: 91−115.

MATSUMURA-TUNDISI, T. & OKANO, W. Y. (1983): Seasonal fluctuation of the copepod population in lake D. Helvecio (Parque Florestal do Rio Doce, Minas Gerais-Brazil). − Rev. Hydrobiol. Trop. 16: 35−40.

MOGHRABY, A. el. (1977): A study of diapause of zooplankton in a tropical river − the Blue Nile. − Freshwat. Biol. 7: 207−212.

PAGGI, J. C. & PAGGI, S. J. (1974): Primeros estudios sobre el zooplancton de los aguas loticas del Parana medio. − Physis 33: 91−114.

RODRIQUES, E. (1980): Composição do zooplancton en cinco lagos da Amazonia Central. − Acta Amazonica 10: 577−609.

SAUNDERS, J. F. III & LEWIS, W. M. Jr. (1987): Structure, dynamics and control mechanisms in a tropical zooplankton community (Lake Valencia, Venezuela). − Ecol. Monogr. [Submitted]

SCHMIDT, G. W. (1972): Seasonal changes in water chemistry of a tropical lake (Lago do Castanho, Amazonia, South America). − Verh. Internat. Verein. Limnol. 18: 613−621.

− (1973a): Primary production of phytoplankton in the three types of Amazonian waters. II. The limnology of a tropical flood-plain lake in central Amazoniana (Lago do Castanho). − Amazoniana 4: 139−204.

− (1973b): Primary production in the three types of Amazonian waters. III. Primary productivity of phytoplankton in a tropical flood-plain lake of central Amazonia, Lago do Castanho, Amazonas, Brazil. − Amazoniana 4: 379−404.

SETARO, F. V. & MELACK, J. M. (1984): Responses of phytoplankton to experimental nutrient enrichment in an Amazon floodplain lake. − Limnol. Oceanogr. **29:** 972−984.

SIOLI, H. (1975): Tropical river: the Amazon. [In:] WHITTON, B. A. (ed.): River Ecology: 461−488; Blackwell.

TUNDISI, J. G.; FORSBERG, B. R.; DEVOL, A. H.; ZARET, T. M.; TUNDISI, T. M.; Dos SANTOS, A.; RIBEIRO, J. S. & HARDY, E. R. (1984): Mixing patterns in Amazon lakes. − Hydrobiol. **108:** 3−15.

TUNDISI, J. & MATSUMURA-TUNDISI, T. (1984): Comparative limnological studies at 3 lakes in tropical Brazil. − Verh. Internat. Verein. Limnol. **22:** 1310−1314.

UNGER, P. A. & LEWIS, W. M. Jr. (1983): Selective predation with respect to body size in a population of the fish, *Xenomelaniris venezuelae* (Atherinidae). − Ecol. **64:** 1136−1144.

VASQUEZ, E. (1984): Estudio de las comunidades de rotiferos del Orinoco medio, bajo Caroni y algunas lagunas de inundacion (Venezuela). − Mem. Soc. Ciencias Nat. La Salle **44:** 95−108.

VASQUEZ, E. & SANCHEZ, L. (1984): Variacion estacional del plancton en dos sectores del rio Orinoco y una laguna de inundacion adyacente. − Mem. Soc. Ciencias Nat. La Salle **44:** 11−34.

WELCOMME, R. L. (1979): Fisheries ecology of floodplain rivers. − Longman.

WHITTAKER, R. H. (1972): Evolution and measurement of species diversity. − Taxon **21:** 213−251.

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