

Zooplankton abundance and evidence for its reduction by macrophyte mats in two Orinoco floodplain lakes

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Abstract. Zooplankton populations were sampled over one annual cycle in two floodplain lakes of the Orinoco River, Venezuela, in an attempt to establish the relationship between abundance patterns and the hydrology and morphometry of the lakes. One of the lakes (Tineo) is relatively large with a gently sloping basin; the other one (Aguilera) is smaller and channel-shaped. The hydraulic residence time of Lake Aguilera during inundation by the river is shorter (<1 day) than the minimum generation times of crustacean (4–12 days) and rotiferan (2.5 days) zooplankton. For Lake Tineo, residence time during inundation (7 days) is longer than generation times for all taxa except copepods. Although Lake Aguilera receives water from Lake Tineo during inundation, zooplankton densities were greatly reduced during passage through a large bed of the floating aquatic grass *Paspalum repens* located near the outlet of Lake Tineo. This retention was not size-selective and affected phytoplankton as well as zooplankton. In the Orinoco floodplain zooplankton densities are affected not only by hydraulic residence times but also by passage of water between lakes, which exposes populations to large losses within macrophyte beds. Retention of plankton by floating macrophyte beds is potentially important to the trophic ecology of tropical floodplain lakes because it results in the concentration of planktonic production in epiphytic and benthic habitats, where it can readily support food webs consisting of macroinvertebrates and fishes. Export of plankton from floodplain waterbodies to the river is also reduced by this mechanism.

Introduction

The lakes, channels and seasonally inundated land commonly found on the floodplains of large rivers comprise an important type of aquatic habitat in the tropics. Welcomme (1985) estimates that in South America alone >300 000 km² is inundated seasonally along large rivers. Tropical floodplains are typically highly productive, and this production may show strong seasonal patterns that are related to the annual riverine inundation (Junk, 1984). Pronounced seasonality in the physical and chemical characteristics of floodplain waterbodies appears to be a key factor regulating the biota in these habitats.

Seasonal patterns of zooplankton abundance have been studied in floodplain waterbodies of the Amazon River near Manaus (Robertson and Hardy, 1984). In Amazonian lakes the highest densities of zooplankton generally occur during the low-water period, when there is little or no exchange of water between the lakes and the river. When the floodplains are inundated by the rising river, zooplankton densities often decline rapidly and remain low throughout inundation. Although dilution is a major cause of this seasonal pattern, other factors may also be involved.

Similar seasonal patterns in zooplankton density have been reported in the Orinoco River floodplain in Venezuela. Vásquez and Sánchez (1986) found that the highest densities of zooplankton in a large Orinoco floodplain lake (Mamo) occurred mainly at low water; densities decreased during periods of elevated turbidity. Twombly and Lewis (1987, 1989) examined zooplankton abundances in a small Orinoco floodplain lake (Orsinera) over a 6-month period encompassing inundation. By calculating zooplankton population sizes from densities and lake volumes, Twombly and Lewis showed that many zooplankton populations actually increased in total population size during inundation, despite a decline in density caused by the rapid increase in lake volume. Twombly and Lewis also present evidence for effects of turbidity, food quality and predation on zooplankton abundance and species composition.

These studies have suggested that hydrologic factors, e.g. dilution and residence time, are of exceptional importance to zooplankton in floodplain lakes, in which variable flow patterns, changing lake volumes and seasonally high flushing rates are characteristic features. The present study addresses these factors in greater detail through the analysis of seasonal changes in zooplankton abundance in two Orinoco floodplain lakes that represent contrasting morphometric and hydrologic conditions. We use hydrologic data for the two lakes to account for dilution of zooplankton by river water, and to evaluate the effect of flushing on zooplankton abundance. Flow between the two lakes during inundation permits us to examine the fate of zooplankton carried into flowing waters on the floodplain. We present evidence for substantial losses of zooplankton during passage of lake water through a macrophyte bed between the two lakes, and discuss the ecological implications of this phenomenon.

Materials and methods

Study site

The Orinoco River, which drains 1000 000 km² in Venezuela and Colombia (Figure 1), has a well-developed fringing floodplain of ~7000 km² that contains >2300 permanent waterbodies (unpublished data). Seasonal variation in rainfall in the Orinoco drainage results in a pronounced annual cycle of discharge in the river. As the river rises 10–15 m each year, water from the main channel inundates the fringing floodplain. The lakes, channels and forests on the floodplain are often covered during inundation by a continuous body of water, in which there is commonly substantial flow. When the river level falls, permanent and ephemeral waterbodies of variable morphometry remain on the floodplain, usually isolated from the river. The waterbodies may steadily decrease in size during the period of isolation, when evaporation exceeds rainfall (Hamilton and Lewis, 1987), and some may become completely dry.

Four hydrological phases can be distinguished in Orinoco floodplain lakes (Hamilton and Lewis, 1987): (i) the filling phase, when water from the river first contacts the lake and rapidly fills the basin; (ii) the through-flow phase, when inflow and outflow of river water occur simultaneously; (iii) the drainage phase, when inflow ceases but outflow continues; and (iv) the isolation phase, when the

lakes are not connected to each other or to the river. The filling and through-flow phases will be collectively referred to here as the inundation period. The Orinoco River usually begins to rise in April, and first inundates much of the fringing floodplain in May and June. Between July and October, river water flows through most floodplain areas. Through-flow peaks at the time of maximum river level in late August or early September. As the river level falls during November and December, water on the floodplain drains into the river.

Two lakes, Tineo and Aguilera, were sampled weekly from July 1984 to January 1985 and three times per month from January to June 1985. The two lakes are located on the north bank of the Orinoco River ($8^{\circ}12'N$, $63^{\circ}28'W$), 8 km east of Ciudad Bolívar (Figure 1). Lake Tineo is a relatively large floodplain lake lying in a basin of gentle and regular slope. The area of the lake varies seasonally from 1.8 to 7.7 km² (Figure 1). Most of the seasonally inundated land around the lake is forested. During the study, the grass *Paspalum repens* Berg was the only abundant macrophyte in Lake Tineo. This grass grew in floating mats along the forest edge at high water, and covered ~5% of the maximum lake area. Hamilton and Lewis (1987) report the physical and chemical conditions of Lake Tineo during the period of this study. Lake Aguilera is a smaller (0.6–2.1 km²), slightly deeper, channel-shaped lake that forms part of a connection between Lake Tineo and Lake Piña during inundation (Figure 1). Lake Aguilera also

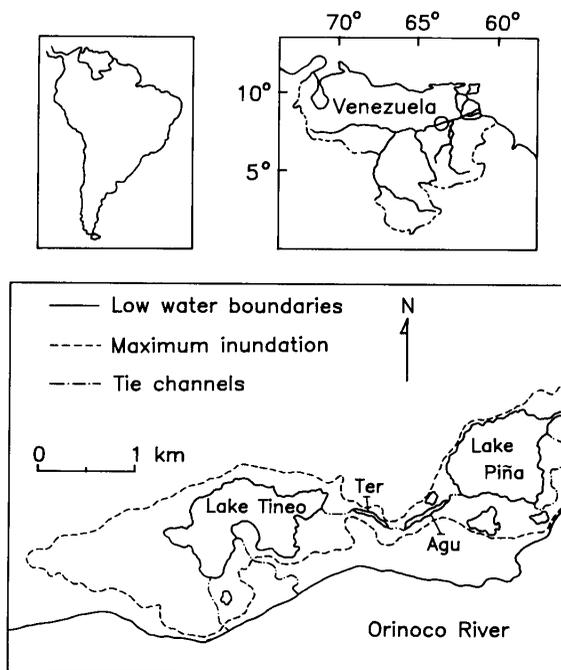


Fig. 1. Map of the study site. The upper right panel shows the Orinoco River system in Venezuela, with the study site circled. In the lower panel Ter = Lake Terecaya and Agu = Lake Aguilera.

extends into the forest at high water, but for a shorter period than Lake Tineo. Macrophytes were not present in Lake Aguilera during the study.

Methods

Samples for water chemistry and plankton were collected during the afternoon at the center of each lake. On each sampling date, light penetration (PAR) was measured with a photometer and a spherical quantum sensor. Vertical profiles of dissolved oxygen and temperature were measured at 0.5 m intervals with a dissolved oxygen meter and thermistor. An integrated sample of the water column was collected with a flexible plastic tube for chemical analysis. During the through-flow phases of both lakes, the water sample for chemical analysis was collected from the upper 1–2 m of the water column; the entire water column was sampled during the remainder of the annual cycle. The partial sampling of the water column during through-flow should not bias the chemistry data. Hamilton (1985) showed that the water column of Lake Tineo was chemically uniform (analyses included particulates, major ions and nutrients) during through-flow, despite the existence of thermal and dissolved oxygen gradients (see Results). In Lake Aguilera, current during through-flow precluded chemical layering, as verified by sampling at discrete depths on several dates (unpublished data). Samples were filtered on the day of collection with tared Whatman (GF/C) glass-fiber filters (effective pore size 0.7 μm ; Sheldon, 1972). The particulate material retained on the filter was measured gravimetrically after it had been dried at 65°C. Particulate carbon on the same filter was measured with a Carlo Erba elemental analyzer; replicate analyses ($n = 31$) showed a coefficient of variation of 3.3%.

Zooplankton was sampled with a flexible plastic tube of 10 cm diameter (Unger and Lewis, 1983; Twombly and Lewis, 1987), which was used to collect an integrated sample of the water column from the surface to within 0.5 m of the bottom. Calibration of the tube allowed for calculation of sample volumes from the sampling depths. The sample, which varied from 15 to 50 l depending on the depth of the water column, was immediately filtered through a 37 μm net, and the concentrated sample was preserved in the field with a solution of 4% formalin and 0.15 M sucrose (Haney and Hall, 1973).

Zooplankton was counted in subsamples until at least 100 of the most common species or developmental stage had been counted. Additional subsamples were counted (up to eight) if the subsample counts for the most common species were not within 10% of their mean. In two cases, rotifer species could not be routinely distinguished, and counts were combined under the name of the predominant species: *Keratella americana* includes some individuals of *K.cochlearis*, and *Filinia pejeri* includes some *F.longiseta*.

Zooplankton densities were converted to whole-lake population sizes using data on lake volume so that the interpretation of zooplankton population dynamics would not be complicated by the influence of the changing lake volume on organism densities (Twombly and Lewis, 1987). The areas of the lakes were determined from aerial photographs (Venezuelan Dirección de

Cartografía Nacional). Water level was read from a permanent staff gauge at each lake. A bathymetric map was prepared for each lake from echo-sounding data collected at high water and lake volume was calculated from data on bathymetry and water level by the method of frustum volumes (Hakanson, 1981). The maximum 'area error' of the bathymetric maps is estimated at <10% using the technique of Hakanson (1981), and water level was determined to an accuracy of 1–3%. The uncertainty in the zooplankton population estimates is therefore likely to be determined largely by that of the original density data, which are subject to sampling error resulting principally from spatial heterogeneity in zooplankton across the lakes.

Results

Morphometry and hydrology

Seasonal patterns in volume and depth of Lake Tineo are presented in Figure 2. During the filling phase (June 17 to July 30) the lake expanded into the surrounding forest as water entered from the river and from Lake Piña. On July 30 flow in the channel from Lake Piña reversed, establishing an outflow and beginning the through-flow phase, during which water continued to enter Lake Tineo directly from the river. The falling river level caused flow in the channels between the lake and the river to reverse around November 4, thus beginning the drainage phase. Outflow decreased gradually throughout the drainage phase until it ceased on December 30. During the ensuing isolation phase, which lasted through June 1985, the lake volume decreased by evaporation (Hamilton and Lewis, 1987).

Changes in volume and depth of Lake Aguilera are shown in Figure 2. The volume of Lake Aguilera is ~2% that of Lake Tineo. Between June 24 and July 1 water from Lake Piña filled the basin of Lake Aguilera, and on July 1 through-flow toward Lake Tineo was just beginning. The filling phase of Lake Aguilera was shorter than that of Lake Tineo because of the smaller lake volume. During inundation, Lake Aguilera formed part of the channel that carried water between Lake Piña and Lake Tineo (Figure 1). On July 30 the direction of through-flow reversed and water from Lake Tineo began to flow through the basin. The forest along the lake was inundated only during September; this period of extended lake area caused the brief decrease in mean depth shown in Figure 2. Through-flow decreased gradually until December 23. The drainage phase of the lake occurred between December 23 and 30, and the lake was subsequently isolated through the end of the study.

Turbidity, light and phytoplankton

Lake Tineo was very turbid before inundation because sediments were resuspended while the lake was very shallow (Figure 2; Hamilton and Lewis, 1987). The depth of the euphotic zone in Lake Tineo (Figure 2), as defined by the depth of 1% subsurface irradiance, gradually increased as particulate material sedimented during the filling and through-flow phases. The increased

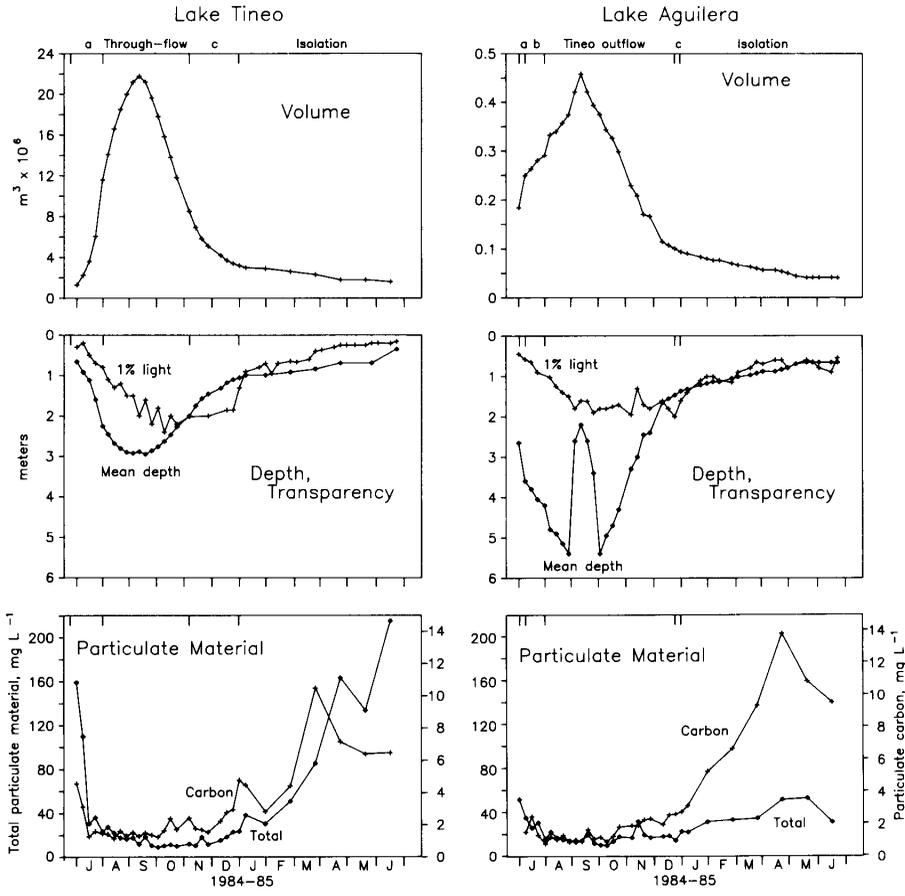


Fig. 2. Volume, mean depth, transparency (as depth of 1% subsurface irradiance) and concentration of particulate material in the two lakes. Hydrological phases are shown along the top: a = filling phase; b = flow of water from Lake Piña through Lake Aguilera; c = drainage phase.

depth of the lake resulted in sedimentation of particulate material, despite the continual inflow of turbid river water. Light penetration was highest during the late through-flow and drainage phases, when inflow of river water ceased and the lake was still relatively deep. Throughout the isolation phase, light penetration decreased, at first because of light attenuation by high phytoplankton densities, then later because inorganic sediments were resuspended as the depth of the lake decreased. The concentration of total particulate material peaked during the late isolation phase (Figure 2). The concentration of particulate carbon, which during peaks reflects the biomass of phytoplankton in Lake Tineo (Hamilton and Lewis, 1987), was highest during the drainage and isolation phases (Figure 2). Blue-green algae dominated the phytoplankton in Lake Tineo during most of the year (Hamilton and Lewis, 1987).

Lake Aguilera was less turbid than Lake Tineo before inundation (Figure 2).

The turbidity of Lake Aguilera decreased during the through-flow phase, reflecting the low turbidity of Lake Tineo during inundation. Most of the water column was euphotic throughout the isolation phase. There was much less resuspension of inorganic sediments in Lake Aguilera than in Lake Tineo because Aguilera was less exposed to wind. The increase in concentration of particulate material during the late isolation phase in Lake Aguilera is accounted for largely by organic matter (Figure 2). The concentration of particulate carbon in Lake Aguilera was much higher during isolation than during inundation, as in Lake Tineo, reflecting the higher concentration of phytoplankton biomass during the isolation phase (Figure 2).

Mixing regimes

Thermal stratification was observed in Lake Tineo during the filling, through-flow, and early drainage phases, but water near the bottom always contained oxygen (Figure 3). Influent river water, which was cooler and more turbid than the lake water, flowed to the bottom of the basin (unpublished data), while the shallower outflow channel drained the surface water of the lake. This pattern of flushing during through-flow maintained oxygen in the bottom waters of the lake and effected continuous vertical mixing of the water column despite the presence of thermal and dissolved oxygen gradients, resulting in uniform vertical profiles for particulates and major solutes (Hamilton, 1985). During the drainage and isolation phases, uniform profiles of temperature and dissolved oxygen indicate that the water column was usually mixed daily by wind or nocturnal convection. The water was almost always supersaturated with dissolved oxygen during the drainage and isolation phases.

During through-flow, Lake Aguilera was well mixed by advective currents, which were noticeable when sampling equipment was lowered into the lake. Such currents were not observed in Lake Tineo. Heat accumulation was often observed in the upper meter of the water column of Lake Aguilera, however (Figure 3). Concentrations of dissolved oxygen were usually only slightly lower in bottom waters than at the surface during through-flow (Figure 3), indicating that the thermal layering that was observed in the upper meter was probably a diel phenomenon (Melack and Fisher, 1983). Between 1.0 m and the bottom, profiles of temperature and dissolved oxygen were generally uniform during periods of substantial through-flow. During the isolation phase there were often vertical gradients of temperature and dissolved oxygen (Figure 3), although anoxia never developed and changes in bottom water temperature indicate that mixing occurred occasionally. Lake Aguilera did not mix as frequently as Lake Tineo during the isolation phase. Lake Aguilera is smaller and slightly deeper than Lake Tineo, and is therefore less affected by wind. The surface water in Lake Aguilera, as in Lake Tineo, was almost always undersaturated with oxygen during the through-flow phase and supersaturated during the isolation phase. Water near the bottom of Lake Aguilera was generally undersaturated with oxygen during the isolation phase; the better mixing maintained higher oxygen concentrations near the bottom of Lake Tineo.

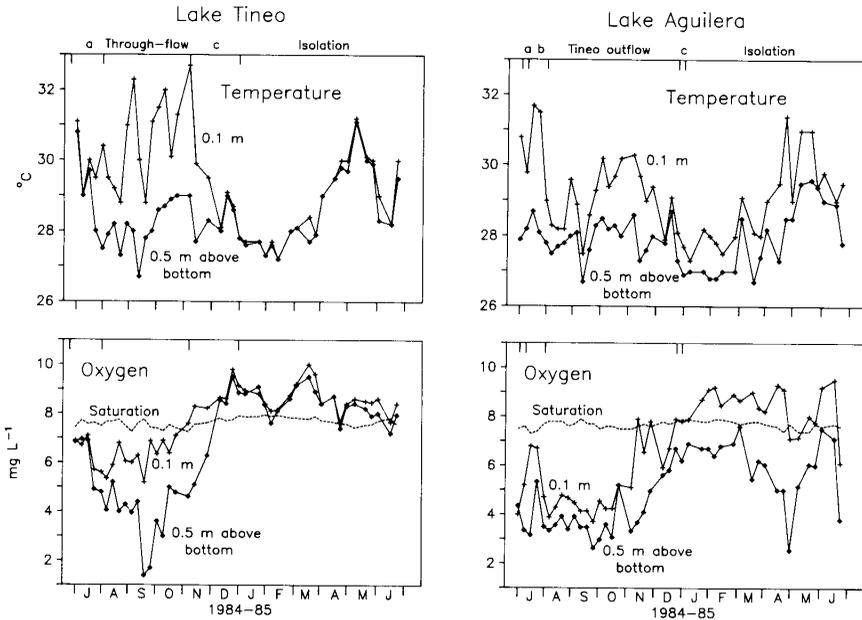


Fig. 3. Temperature and concentration of dissolved oxygen in the two lakes. Hydrological phases are shown along the top: a = filling phase; b = flow of water from Lake Piña through Lake Aguilera; c = drainage phase. Dashed lines show the concentration of dissolved oxygen at saturation, determined from the *in situ* temperatures (0.1 m).

Zooplankton

Mean densities of zooplankton during each hydrologic phase are presented in Table I for Lake Tineo and in Table II for Lake Aguilera. The tables give total densities for each group as well as densities for the most important species or genera in each group. Totals include all developmental stages except eggs.

Asplanchna and *Chaoborus* larvae are included in the tables not because of their numerical dominance but because of their potential ecological importance as predators of other zooplankton. *Asplanchna* was found in Lake Tineo occasionally during both inundation and isolation (Table I), but was found in Lake Aguilera on only a few dates (Table II). *Chaoborus* was occasionally found in Lake Tineo during inundation and in Lake Aguilera during late through-flow and isolation (Tables I and II). The daytime sampling in this study could have underestimated *Chaoborus* abundance, however, because the larvae sometimes remain in or very near to the sediments during the day (LaRow, 1969; Parma, 1971).

Rotifer density and population size in the two lakes are shown in Figure 4. For convenience, the term 'population' is used here to refer to groups that may include more than one species. The differences between density and population size are greatest during the filling, through-flow and drainage phases, when the lake volumes change most rapidly. During the isolation phase, abundance more

Table I. Mean densities of zooplankton in Lake Tineo

	Mean density (individual l ⁻¹)				
	Filling	Through-flow	Drainage	Isolation	Annual
Rotifera: total	315	925	2116	4387	2540
1. <i>Polyarthra vulgaris</i>	257	576	935	816	701
2. <i>Lecane prolecta</i>	0.5	9	70	914	409
3. <i>Brachionus mirus</i>	18	66	138	799	389
4. <i>Keratella americana</i>	11	19	279	472	255
5. <i>Filinia pejleri</i>	11	80	170	405	227
6. <i>Trichocerca</i>	3	31	153	438	223
7. <i>Brachionus angularis</i>	0	0	17	181	81
8. <i>Anuraeopsis fissa</i>	0.3	9	99	69	48
9. <i>Brachionus dolobratus</i>	0.3	48	96	23	39
10. Asplanchna	0.8	0.6	0	6	3
Cladocera: total	27	16	16	155	77
1. <i>Moina</i>	20	5	1	70	34
2. <i>Bosmina</i>	2	0.8	15	74	35
3. <i>Bosminopsis</i>	0	10	0.4	0	3
4. <i>Diaphanosoma</i>	4	0.4	0	1	1
Copepoda: total	177	104	448	688	419
1. Cyclopoids					
Eggs	3	3	18	11	9
Nauplii	138	79	386	611	364
Copepodites	22	20	49	57	40
Adult males	2	0.4	2	4	2
Adult females	4	1	9	5	4
2. Calanoids					
Eggs	0	0	0	0	0
Nauplii	8	2	1	10	6
Copepodites	2	0.5	0.5	2	1
Adult males	0.4	0.01	0.06	0.06	0.08
Adult females	0.3	0.06	0.06	0.2	0.1
<i>Chaoborus</i>	0.4	0.4	0.2	0.02	0.2

closely follows density. Because the relationship of density to population size varies little across species, additional time-series data for zooplankton will be presented as abundances.

Cladocerans and cyclopoid copepods (Figure 4) were at times abundant in both lakes. The copepods were dominated by cyclopoids throughout the year in Lake Tineo, but in Lake Aguilera, calanoids reached abundances comparable to those of cyclopoids during the isolation phase. Naupliar stages were always more abundant than copepodites and adults (Tables I and II). The predominant cyclopoid in both lakes was *Oithona amazonica*.

Discussion

Similarity of the zooplankton communities in the two lakes on each sampling date was estimated by means of the Bray–Curtis Index (Figure 5). The Bray–Curtis Index, which is also known as Czekanowski's Quantitative Index, incorporates data on species densities and is one of the most accurate and robust

Table II. Mean densities of zooplankton in Lake Aguilera

	Mean density (individual l ⁻¹)			
	Through-flow from		Isolation	Annual
	Lake Piña	Lake Tineo		
Rotifera: total	50	375	1241	732
1. <i>Keratella americana</i>	7	21	470	224
2. <i>Brachionus mirus</i>	14	36	369	185
3. <i>Polyarthra vulgaris</i>	9	197	16	93
4. <i>Filinia opoliensis</i>	0.6	28	95	55
5. <i>Brachionus havanaensis</i>	7	0.2	108	50
6. <i>Trichocerca</i>	0.7	13	83	43
7. <i>Brachionus calyciflorus</i>	0	0	57	26
8. <i>Filinia pejleri</i>	5	36	9	
9. <i>Brachionus zahniseri</i>	0.8	28	0.9	13
10. <i>Asplanchna</i>	0.4	0.9	1	1
Cladocera: total	11	11	180	88
1. <i>Ceriodaphnia cornuta</i>	0	4	65	31
2. <i>Bosmina</i>	3	0.5	54	25
3. <i>Diaphanosoma</i>	5	0.4	60	28
4. <i>Moina</i>	4	4	0.1	2.2
Copepoda: total	47	166	217	176
1. Cyclopoids				
Eggs	7	24	11	16
Nauplii	37	135	135	124
Copepodites	2	20	13	15
Adult males	0.09	1	0.4	0.8
Adult females	3	5	5	5
2. Calanoids				
Eggs	0	0.1	10	4
Nauplii	3	4	24	13
Copepodites	1	0.7	32	15
Adult males	0	0.02	3	1
Adult females	0.2	0.1	5	2
<i>Chaoborus</i>	0	0.7	0.9	0.7

measures of similarity (Bloom, 1981; Faith *et al.*, 1987). The index ranges from 0 (minimum similarity) to 1 (maximum similarity). Density data were standardized by site with a sum-of-squares transformation (Noy-Meir *et al.*, 1975) for calculation of the index. Data for the lowest identified taxonomic levels were used; zooplankton was identified to the same taxonomic levels in the two lakes. Copepods (which were mostly nauplii) were excluded from the calculation of the index because species were not counted separately.

Analysis of isolation-phase patterns

During the isolation phase, the similarity index indicates that the zooplankton communities of Lakes Tineo and Aguilera diverged at first, then became more similar (Figure 5). Based on the similarity index, we can distinguish an initial period of lower similarity (January–March) that is followed by a period of greater similarity (April–June). This pattern contrasts with that of the abiotic

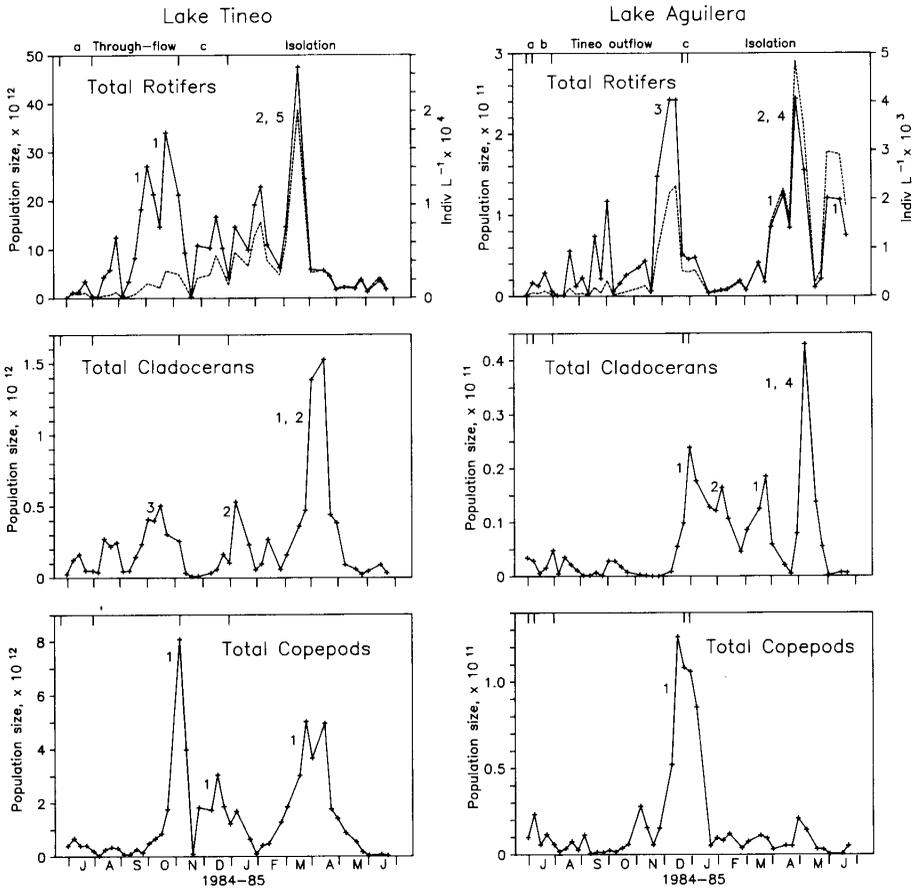


Fig. 4. Population sizes of rotifers, cladocerans and copepods in the two lakes. Densities of rotifers (dashed lines) are also shown for comparison. Hydrological phases are shown along the top: a = filling phase; b = flow of water from Lake Piña through Lake Aguilera; c = drainage phase. Numbers beside peaks refer to Tables I and II and indicate the predominant taxa comprising the peaks.

environments of the two lakes, which were similar early in the isolation phase and diverged later (Figures 2 and 3). The rapid divergence of the zooplankton communities of the two lakes in the isolation phase was therefore more likely to be driven by biotic factors than by changes in the abiotic environments of the lakes.

Turbidity is the greatest contrast between the abiotic environments of the two lakes. In the latter half of the isolation phase, the greater exposure of Lake Tineo to wind resulted in resuspension of sediments and increased inorganic turbidity in the water column. The decreased concentration of particulate carbon suggests that phytoplankton biomass may have decreased in Lake Tineo as turbidity increased (Figure 2), and cell counts show a shift in the dominant phytoplankton from blue-greens to diatoms (Hamilton and Lewis, 1987).

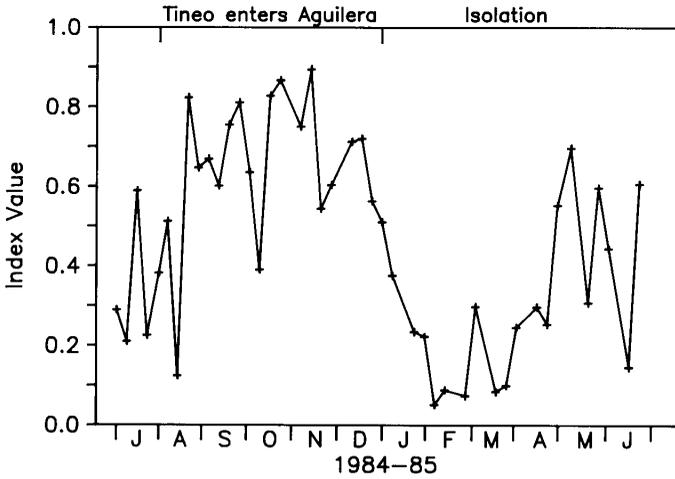


Fig. 5. Comparison of the zooplankton in the two lakes by the Bray-Curtis Index of community similarity, calculated for each sampling date.

Despite these changes that occurred only in Lake Tineo, the similarity index indicates that the zooplankton of the two lakes became more similar during this period. Abundances of all zooplankton taxa were low during the last month of the isolation phase, when turbidity was highest (Figure 4). However, periods of comparably low abundance also occurred at other times during the year when turbidity was not high. A strong role for turbidity as a controlling factor of zooplankton communities, which has been documented in other lakes (Arruda *et al.*, 1983; Geddes, 1984), is therefore not apparent from these data.

Dilution and wash-out during inundation

To interpret zooplankton abundance patterns during inundation we must first determine the importance of advective transport of zooplankton into the lakes by influent water. If transport into the lakes is insignificant, then changes in lake populations must result from recruitment and loss processes within the lake boundaries or from advective transport of zooplankton out of the lake (hydraulic washout: Duncan, 1984; Dirnberger and Threlkeld, 1986; Hawkins, 1988). Zooplankton in the Orinoco River at Ciudad Bolívar was sampled at monthly intervals during the inundation period (Saunders and Lewis, 1989). Densities of the important zooplankton in Lake Tineo during inundation were generally ~100 times higher than densities of these taxa in the river. The contribution of influent river water to patterns in zooplankton abundance in Lake Tineo was therefore negligible. Direct sampling of zooplankton in riverine inflows at another floodplain lake 12 km upriver from Lake Tineo by Twombly and Lewis (1987) led to the same conclusion. During the filling phase of Lake Tineo, ~15% of the total inflow came from Lake Piña, after first passing through Lake Aguilera (Hamilton, 1985). Comparison of zooplankton densities in Lake

Aguilera with densities in Lake Tineo during this period (July) shows that this influent water could have been a significant, albeit not a major, influence on zooplankton abundance during the filling phase in Lake Tineo (Tables I and II).

The situation for Lake Aguilera is more complicated because its inflows always carried water from adjacent lakes that were rich in zooplankton relative to the river. Zooplankton patterns in Lake Aguilera during inundation are largely determined by advective transport from adjacent lakes. This problem will be discussed further below.

Hydraulic washout is likely to be an important loss affecting zooplankton in many floodplain lakes during inundation. Washout rate can be compared with the minimum generation time of the organisms. If the hydraulic residence time for water is shorter than the generation time, then there is insufficient time for a population to increase in abundance, given that (i) inflows are thoroughly mixed into the lake, and (ii) zooplankton do not resist being carried out of the lake in the outflow. The first assumption is probably valid, as indicated in relation to the discussion of mixing regimes. The second assumption is probably valid for rotifers and cladocerans, but possibly not for copepods, which are rheotactic and may be capable of resisting the outflow currents (Brook and Woodward, 1956). However, in Lake Tineo the copepods were dominated by naupliar stages (Table I), which are much less capable of resisting currents than are older stages.

Figure 6 compares the theoretical residence time of water in the two lakes with estimates of the minimum generation times (egg to egg at 25°C: Allan, 1976) for the three main zooplankton groups. In Lake Tineo, washout during the through-flow phase would preclude abundance increases only for copepods. Examination of the abundance data for Lake Tineo (Figure 4) shows that, while rotifers and cladocerans increased in abundance during the time of maximum flushing of the lake, copepods did not. The data are thus consistent with our hypothesis that washout affected copepods most severely. In Lake Aguilera, washout prevented abundance increases in all three zooplankton groups during through-flow (Figure 6). We conclude that zooplankton abundance patterns in Lake Aguilera during through-flow must have been caused entirely by advective transport from adjacent lakes.

Because of the rapid flushing of Lake Aguilera, zooplankton abundance in Lake Aguilera during through-flow from Lake Tineo is a measure of washout of zooplankton through the outflow from Lake Tineo. The similarity index in Figure 5 indicates that the zooplankton communities of the two lakes were most similar during peak flow (September–October) between Lake Tineo and Lake Aguilera, then diverged as flow decreased in December and January. Despite similarities of zooplankton composition in the two lakes during through-flow, densities of all three zooplankton groups were usually lower in Lake Aguilera than in Lake Tineo (Figure 7). Particulate carbon is included in Figure 7 as an indication of differences in phytoplankton biomass in the two lakes. The uniformity of these differences across all plankton groups is striking. This could be explained by differences between the plankton content of water at the sampling site and that leaving Lake Tineo, or by changes in the plankton content that occur during transit between the two lakes.

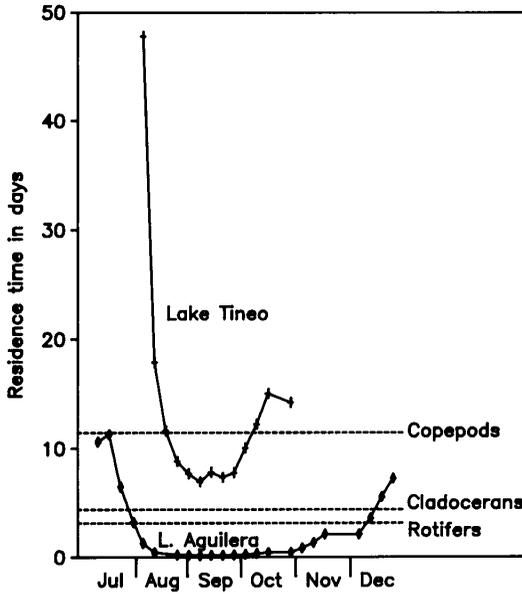


Fig. 6. Hydraulic residence times in the two lakes compared with the estimated minimum generation times (dashed lines) for the three major zooplankton groups.

If influent river water does not mix fully into Lake Tineo before flowing out through Lake Aguilera, plankton densities would perhaps be uniformly lower in outflowing water than at the sampling station in the center of Lake Tineo. The strongest difference in chemistry between influent river water and lake water during inundation is shown by total particulate material (Hamilton and Lewis, 1987). Data on particulate material in the river, Lake Tineo and its outflow (Lake Terecaya) show that the chemistry of outflowing water resembled that of water at the central sampling site and differed strongly from that of river water (Figure 8). In addition, sampling of seven stations across Lake Tineo for analysis of physical and chemical variables on September 16 did not reveal areas where river water was not mixed with the lake water (Hamilton and Lewis, 1987). River water was evidently not shunted to the outflow before mixing fully into the lake.

The apparent change in plankton content of the water during transit between the two lakes merits a more detailed analysis because of its potential ecological importance. The channel between the lakes is 1.6 km long, and the mean transit time of water in the channel, as determined from discharge and volume estimates, is short (1–2 h). At its exit from Lake Tineo, the outflow channel was choked by a large mat of floating grass (*P.repens*). Macrophytes were almost absent between this mat and Lake Aguilera. After the grass mat, the water passed through 0.8 km of flooded forest, beyond which the channel broadened to form a small lake, Lake Terecaya (Figure 1). Beyond Lake Terecaya, the channel passed through 0.4 km of flooded forest before reaching Lake Aguilera.

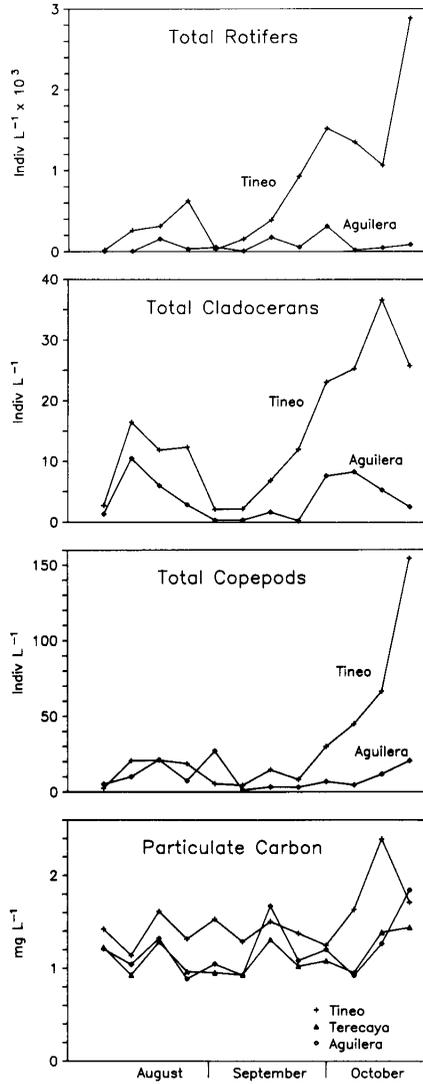


Fig. 7. Zooplankton densities and concentration of particulate carbon in the two lakes during the period of substantial flow from Lake Tineo through Lake Aguilera. Data for particulate carbon in Lake Terecaya are also included as a measure of phytoplankton biomass.

The most likely cause of losses in plankton during transit in the channel between lakes is the retention of plankton in the dense mat of grasses. Several investigations of the fate of plankton in streams flowing out of lakes have shown that aquatic macrophytes and aggregations of detrital materials can efficiently retain phytoplankton, rotifers and crustaceans from passing water (Chandler, 1937; Beach, 1960; Hynes, 1970). Although these authors refer to the retention as a straining effect, the observation by Chandler as well as in the present study

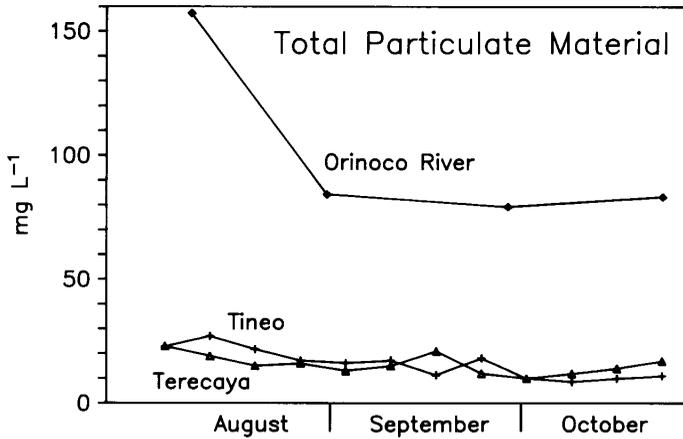


Fig. 8. Comparison of concentrations of total particulate material in the river, Lake Tineo, and the outflow from Tineo (Lake Terecaya) during the period of substantial flow from Lake Tineo through Lake Aguilera.

that a wide size range of zooplankton as well as phytoplankton are affected suggests that the retention is not strongly size-selective, as might be expected if straining were the principal mechanism causing retention of particles. The mechanism of retention may thus involve not only straining but also adhesion to the submersed surfaces and perhaps filter-feeding by organisms within the mat; such mechanisms might retain organic particles while allowing suspended clays to pass through. In the Lake Tineo outflow, densities of both phytoplankton and zooplankton decreased substantially (Figure 7), although inorganic particulates consisting mainly of very fine clays were not removed (Figure 8).

We have data on chemistry but not zooplankton for Lake Terecaya; particulate carbon concentrations in Lake Terecaya mirrored those in Lake Aguilera during through-flow, indicating that the reduction in particulate carbon occurred before the water entered Lake Terecaya. Lake Terecaya is situated at an intermediate point along the flooded forest between Lakes Tineo and Aguilera; it is therefore likely that the retention of lake plankton occurred primarily in the mat of grasses at the outlet from Lake Tineo, rather than in detrital aggregations in the flooded forest.

The total loss of particulate organic material during outflow of water from Lake Tineo was calculated from the discharge of the outflow (Hamilton and Lewis, 1987) and the change in concentration of particulate carbon between Lake Tineo and Lake Aguilera (Figure 7). The total amount of carbon lost during outflow was 37 metric tons (t), which is equivalent to ~74 t of organic matter, most of which was phytoplankton (Hamilton and Lewis, 1987). Chandler (1937) studied the fate of planktonic material retained by macrophytes in streams and found that aggregations built up and eventually sedimented. In the vicinity of the macrophyte mat of the Tineo outflow, currents may have eventually carried much of the sedimented material to Lake Terecaya, where the channel widens and deepens and currents decrease. Consumption of adhered

plankton by grazers as well as decomposition would reduce the quantity of carbon that sedimented from the mats.

Retention of lake plankton by mats of floating macrophytes is potentially important to the trophic ecology of floodplain waterbodies. Dense mats of *Paspalum*, *Eichornia*, *Pistia* and other species of floating macrophytes are widespread and abundant in tropical floodplains (Welcomme, 1985). When macrophyte mats occur at the outflow of a lake, as in the case of Lake Tineo, their retention of plankton from passing water could result in the accumulation of a substantial fraction of the lake's planktonic production in the mats, and would reduce the export of planktonic biomass out of the floodplain to the river. The phenomenon of plankton retention by macrophytes results in the transfer of energy (as biomass) and nutrients from the pelagic zone to the submersed surfaces of the macrophyte mats and the underlying sediments, thereby making a rich food source available to the abundant invertebrate and fish fauna in and around the mats. In floodplain waterbodies, where the combination of flowing water and abundant macrophytes occurs commonly, this could be an important trophic link which has heretofore not been considered.

Wotton (1989) reports extraordinarily high secondary production of blackfly larvae (*Simulium*) feeding on plankton at a shallow lake outflow in England, and attributed this to the unusual combination of a rich particulate food source, flowing water and shelter from predation. A comparable situation may occur in the Lake Tineo outflow. Mats of *P. repens* and other floating macrophytes support an abundant and diverse invertebrate assemblage, which may exceed 100 000 organisms m^{-2} (Junk, 1973; Fittkau *et al.*, 1975). Many of the mat invertebrates are either filter-feeders or grazers adapted to feed on epiphytic material; relatively few species appear to be capable of feeding directly on the vascular plant tissues (personal observations). An hypothesis that emerges from this work is that mat invertebrate assemblages will be more productive in situations where lake water containing plankton flows through the mat, compared with more stagnant areas or areas receiving water directly from the river. However, other factors are also likely to be important to the mat invertebrate assemblage, including the content of nutrients and inorganic particulates in the water, which affects epiphytic algal growth in the mats (Engle and Melack, 1989), and the role of currents in replenishing dissolved oxygen within the mats (Fittkau *et al.*, 1975).

In conclusion, through-flow in floodplain lakes results in hydraulic washout of zooplankton, and will exert increasing control over zooplankton communities as the residence time of lakes decreases. In lakes with short hydraulic residence times, zooplankton reproduction may be precluded, and advective transport controls zooplankton abundance. Hydraulic washout of zooplankton from floodplain lakes is important not only as a loss process, but also because when macrophyte mats are present in the outflow channel, a substantial fraction of the zooplankton passing through the vegetation can be retained. Retention of plankton by vegetation affects trophic relations by making the plankton available as food to epiphytic and benthic organisms, and reduces the export of planktonic carbon from floodplain waterbodies to the river.

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