Factors regulating cladoceran dynamics in a Venezuelan floodplain lake

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Abstract. Five cladoceran zooplankton species in a Venezuelan floodplain lake, Laguna la Orsinera, were analyzed to identify factors controlling their dynamics over a period encompassing isolation, inundation by the Orinoco River and drainage. The abundance of each species increased rapidly to a maximum associated with flooding of the lake by the Orinoco River. We calculated birth, death and population growth rates, and developed a method for estimating uncertainty in these parameters, in order to interpret observed cladoceran abundance patterns. Rapid increases in population sizes resulted both from high birth rates associated with decreasing turbidity following inundation and from the hatching of resting eggs. Birth rates remained high throughout the study, but high death rates restricted each population to a brief maximum and then maintained small population sizes throughout the remainder of the study. Our demographic analyses suggest that high mortality resulted from intense predation by fish and by *Chaoborus* larvae, rather than from resource limitation, and that this mortality was the major factor regulating cladoceran abundance during inundation and drainage in this tropical floodplain lake.

Introduction

Floodplains and their associated lakes form an integral part of unregulated tropical river systems (Welcomme, 1979). Production within floodplain lakes can be high, contributing biomass to rivers at specific times of the year (Schmidt, 1970: Fisher and Parsley, 1979; Hamilton and Lewis, 1987; Lewis, 1987). In turn, physical and biological cycles within floodplain lakes are governed by the annual rise and fall of the main river (Fisher, 1979: Hamilton and Lewis, 1987).

Although physical and nutrient cycles have been described for several floodplain lakes (e.g. Marlier, 1967: Schmidt, 1972, 1973a: MacIntyre and Melack, 1984; Tundisi *et al.*, 1984; Hamilton and Lewis, 1987), we know little about the dynamics or production of their plankton populations. This lack of understanding results, in part, from the difficulty of quantifying population processes in lakes, such as floodplain lakes, that experience large fluctuations in volume. In these circumstances, a population can increase in size while declining in density due to seasonal increases in lake volume; and population density is a poor measure of total abundance (Twombly and Lewis, 1987). Changes in lake volume have seldom been considered in quantitative studies of floodplain zooplankton, yet they are essential to accurate descriptions of plankton dynamics. Thus, reports that zooplankton in some floodplain lakes reach peak densities during low water (e.g. Holden and Green, 1960; Schmidt, 1973b; Fittkau *et al.*, 1975; Brandorff and deAndrade 1978; Vasquez and Sanchez, 1984) yield little information about actual population size, and plankton dynamics in these lakes remain poorly known.

In a previous paper, we described changes in zooplankton species composition and abundance in Laguna La Orsinera, a floodplain lake of the Orinoco River (Twombly and Lewis, 1987), using estimates of total population size to correct for large seasonal changes in lake volume. Cladoceran abundance patterns were particularly distinctive: population maxima developed rapidly as the lake filled with water from the Orinoco River, after which time cladoceran abundance was low. Here, we use demographic analyses of changes in total population size to identify the factors regulating cladoceran dynamics in Laguna La Orsinera, and to separate these factors from the effects of changes in lake volume.

Methods

Study site

Laguna La Orsinera is a small, permanent lake laying on the floodplain north of the Orinoco River, at 8°10′N, 63°30′W (Figure 1). The lake fills a dish-shaped depression that is deepest at its western edge. During the dry season in 1984 (December–April) the lake was <2 m deep, very turbid (Figure 2), isothermal and well-mixed. Inundation began in late July 1984, and lasted for ~3 months. During this time the lake volume increased 9-fold, transparency (measured by
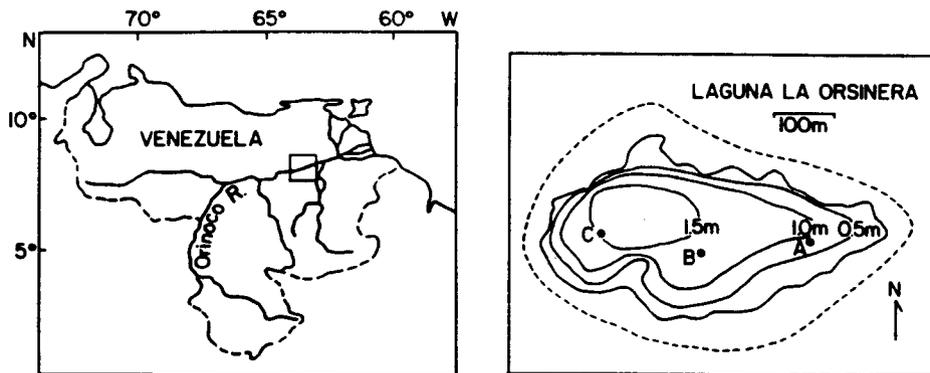

Fig. 1. The Orinoco River near Laguna La Orsinera and a bathymetric map of the lake. The dashed line represents the approximate extent of flooding. A, B and C locate sampling stations.
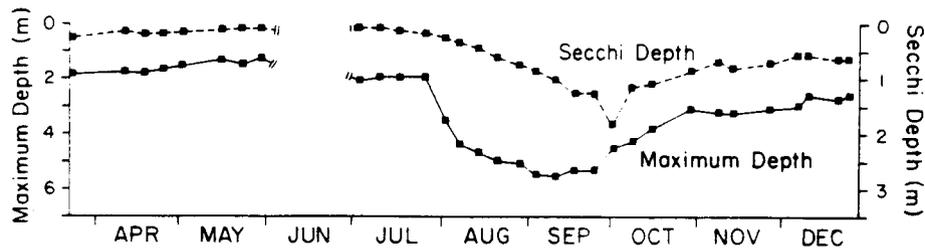

Fig. 2. Changes in lake depth and transparency, April–December 1984.

Secchi depth) increased from 0.1 to 1.8 m. and sufficient thermal layering developed to permit oxygen depletion in the deepest water. By the end of October the water level in both the river and the lake had fallen below the level of the connecting channel. and the lake became separated once again from the Orinoco. A more detailed description of physical characteristics of this lake is given in Twombly and Lewis (1987).

Zooplankton samples

Zooplankton were sampled at three stations (Figure 1) using a flexible tube sampler. 10 cm in diameter. that sampled the entire water column to within 0.5 m of the bottom (Twombly and Lewis. 1987). Triplicate samples were collected at each station. and replicates were combined across stations to create three composite samples. Each sample was filtered through a 37-μm-mesh net and preserved in formalin-sucrose solution (Haney and Hall. 1973).

Zooplankton were sampled from late June to December 1984, a period that encompassed isolation of the lake during low water. filling of the lake. inundation and subsequent drainage. From June to mid-September. zooplankton were sampled on Monday. Wednesday. Friday and Saturday of each week. From mid-September to December. we sampled on Monday. Tuesday. Wednesday and Thursday of each week. All samples were collected between 09.00 and 12.00 h.

Subsamples of each composite replicate were counted with a stereomicroscope at 25×. Subsample size was chosen so that >100 individuals of each of the common cladoceran species present were counted in each sample. Ovigerous females. eggs and non-ovigerous females (including juveniles and adults) were counted for each species; eggs were not staged. Counts of *Diaphanosoma brevireme* and *D.birgei* were combined throughout the sampling period. *Diaphanosoma brevireme* was more abundant until October. when *D.birgei* became predominant. In November and December samples. cladocerans were enumerated only in samples taken on Monday and Thursday of each week.

Means. ranges and standard deviations were calculated from triplicate samples taken on each sampling date. Raw counts were transformed into densities (no. l^{-1}) and then to total population sizes to correct for changes in lake volume.

Demographic parameters

We calculated population birth rate ($b = [\ln(E_t/N_t) + 1]/D_e$) (Paloheimo, 1974). population growth rate [$r = (\ln N_{t2} - \ln N_{t1}/(t_2 - t_1)$] and population death rate ($d = b - r$; Polishchuk and Ghilarov. 1981) for each species (Taylor and Slatkin. 1981). E_t is the number of eggs l^{-1}; the egg development times (D_e) used were those determined for the same species or for congeners. and for tropical populations experiencing temperatures comparable to those in Laguna la Orsinera (Gras and Saint Jean. 1976; Hart. 1985).

We distinguished only three categories in each cladoceran population: eggs. non-ovigerous individuals and ovigerous females. The use of such general

categories, and particularly the combination of non-reproductive juveniles with adults that were not carrying eggs, introduces errors into demographic estimates. Failure to stage eggs (Threlkeld, 1979) requires that we assume constant birth rates, and may also introduce errors. Departures of the stage distribution from stability may contribute a third source of error, although Taylor and Slatkin (1981) have shown that egg ratio estimators, and particularly Paloheimo's formula, are robust when stage or age structure departs from stability. With these potential sources of error in mind, we base our interpretations on temporal trends in birth, death and population growth rates, rather than on values calculated for individual dates.

Statistics

Triplicate counts of total population size and number of eggs were used to calculate triplicate estimates of birth rates, death rates and population growth rates. Replicates from successive pairs of sampling dates were combined randomly to obtain triplicate estimates or r (Keen and Nasser, 1981). From each triplicate series we calculated the mean, standard deviation, standard error (as $S_x/\sqrt{3}$) and coefficient of variation ($100 \cdot S_x$) for each variable. Coefficients of variation (CV) were used as a measure of uncertainty in variable means.

To summarize this uncertainty, CVs for each variable were graphed against total population size on each sampling date. Because total population size reflects counting effort [see Downing et al. (1987): counting effort reaches a plateau above a certain population size], uncertainty in an estimate typically decreased as population size increased and approached a constant value above some threshold population size (Figure 3). This threshold was defined as that value above which regression of CV on total population size was not statistically significant at $P = 0.05$. Above the threshold abundance, coefficients of variation for each variable were averaged to provide a mean uncertainty in each estimate. Dates for which these mean values apply are indicated on graphs for each variable. Uncertainty was usually higher in samples that fell below the threshold population size; for these samples, median uncertainties are reported.

The procedure for summarizing uncertainty is demonstrated in Figure 3. Uncertainty in estimates of Moina minuta population size decreased rapidly with increasing population size (Figure 3a). Above a threshold population size (T) of 4×10^9, there was no significant change in CV with population size. For M.minuta death rates, uncertainty decreased up to a population size of 2×10^9 (Figure 3b). There was no relationship between CV and total population size for Diaphanosoma birth rate (Figure 3c), and coefficients of variation were averaged over all samples.

To identify demographic patterns within and between species, Spearman rank correlations were calculated for total population size, birth, death and population growth rates.

Results

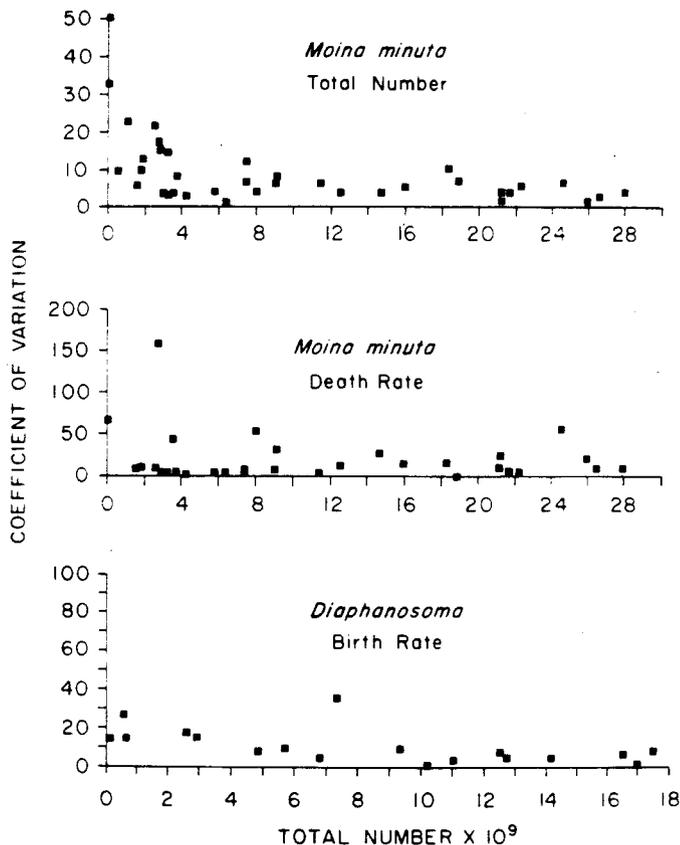Uncertainty estimates for each variable, for each species, are summarized in

Fig. 3. The relationship between uncertainty in a demographic estimate and total population size. (A) *M.minuta* population size. (B) *M.minuta* death rates. (C) *Diaphanosoma* birth rates.

Table I. In two cases (*Bosmina* birth rate and *Diaphanosoma* total eggs), confidence in estimates continued to increase with population size and we report median coefficients of variation. For all other estimates. a threshold was identified; both a mean CV applicable to high abundance and a median CV applicable to low abundances are reported.

Estimates of death rate contained the highest uncertainty. although error in population growth rate estimates for *Bosmina* and *Ceriodaphnia cornuta* also was high. For the remaining variables. including death and population growth rates for *Moina minuta*, coefficients of variation were <20%.

Demography

Population size of *M.minuta* peaked sharply in July 1984. at lowest water (Figure 4a). This peak was followed by a second rapid increase in August. after inundation. By late August population size had declined. and remained low throughout September and October. An irregular and more prolonged increase

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Table I. Uncertainty (CV, %) in demographic estimates, above and below threshold population sizes ($T \times 10^6$)

Species	Abundance			Rates (day^{-1})		
	Adults and juveniles	Eggs	b	d	r	
Moina minuta						
T	4000	4000	2000	2000	2000	
Mean CV above *T*	5.3	9.3	6.5	14.7	17.9	
Median CV below *T*	9.6	9.1	32.0	38.0	23.0	
Bosmina sp.						
T	1000	1000	1500	1000	1000	
Mean CV above *T*	11.6	23.8	19.1	62.6	62.4	
Median CV below *T*	19.3	19.3	22.2	17.1	21.0	
Diaphanosoma						
T	1000	1000	–	–	–	
Mean CV above *T*	9.1	15.3	10.5	48.0	28.0	
Median CV below *T*	33.9	23.3	–	–	–	
Ceriodaphnia cornuta						
T	2000	–	–	–	–	
Mean CV above *T*	9.2	12.9	9.0	64.0	38.0	
Median CV below *T*	30.5	–	–	–	–	

in *M.minuta* abundance occurred in November–December 1984. The initial population peak in July was not associated with reproductive activity (Figure 4b) or with increased birth rates (Figure 4c), suggesting that these individuals hatched from resting eggs. Total egg production increased in August, coincident with the second population maximum. The largest peak in egg production occurred in November–December, although the corresponding increase in population size was smaller than those in July and August.

Moina minuta birth rates were high throughout the sampling period (Figure 4c), with the exception of a short period in mid-July. In August, high birth rates corresponded with low population growth rates (Figure 4c). Death rates were high but variable during this time (Figure 4d). A similar trend continued throughout the sampling interval: population birth rates were consistently high, but high death rates resulted in low population growth rates. These trends suggest that *M.minuta* population size was regulated by mortality, and that this mortality was not resource-mediated.

Bosmina was abundant only briefly in Laguna la Orsinera. Numbers of individuals and egg production increased just before inundation, in late July, and remained high for ~2 weeks (Figure 5a and b). By mid-August egg production and population size had declined, and birth rates and population growth rates were low (Figure 5c). Death rates increased (Figure 5d) and population size remained very small after mid-August. Birth rates increased again in late August and early September without a corresponding increase in population size, suggesting high death rates. Uncertainty in our estimates of death rates and population growth rates (Table I) prevents detailed analyses of these parameters. However, decreasing birth rates and increasing death rates
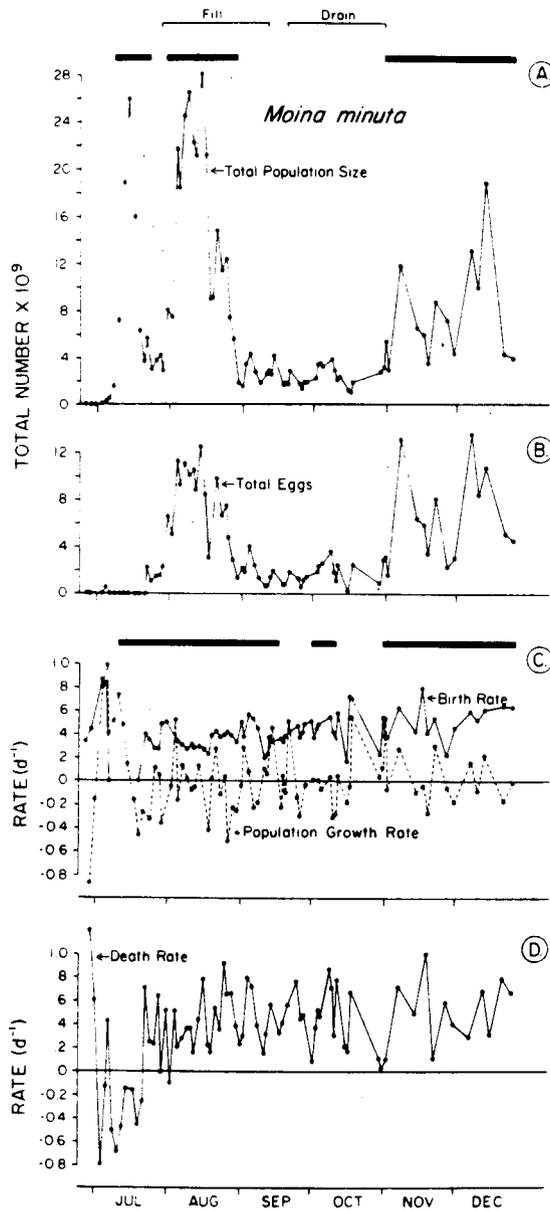
Fig. 4. Demographic analyses for *M.minuta*. Solid bars above each graph indicate samples for which mean uncertainties (Table 1) apply. (A) Total population size. (B) Mean total number of eggs. (C) Mean birth rates and population growth rates. (D) Mean death rates.
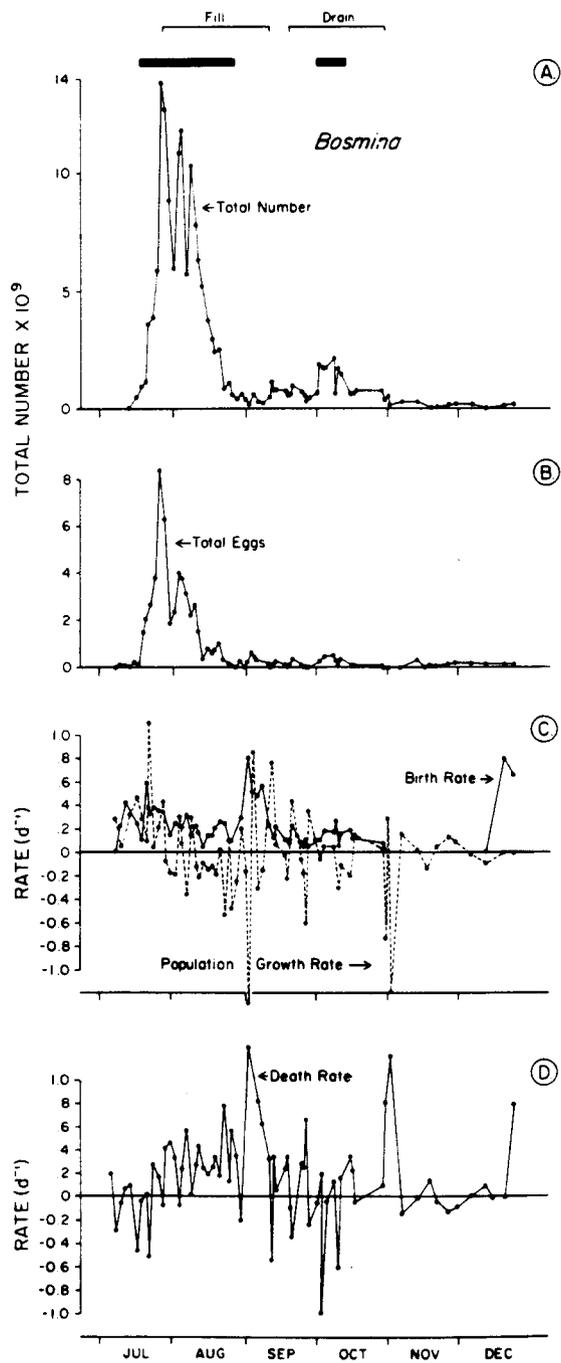
Fig. 5. Demographic analyses for *Bosmina* sp.. as in Figure 4.

appeared to cause the initial decline in *Bosmina* abundance and to maintain small population sizes after the August maximum.

Neither species of *Diaphanosoma* was present in Laguna la Orsinera before inundation (Figure 6a), when *M.minuta* and *Bosmina* reached peak population sizes. *Diaphanosoma* abundance increased sharply in early August; the individuals responsible for this initial increase could have been transported into
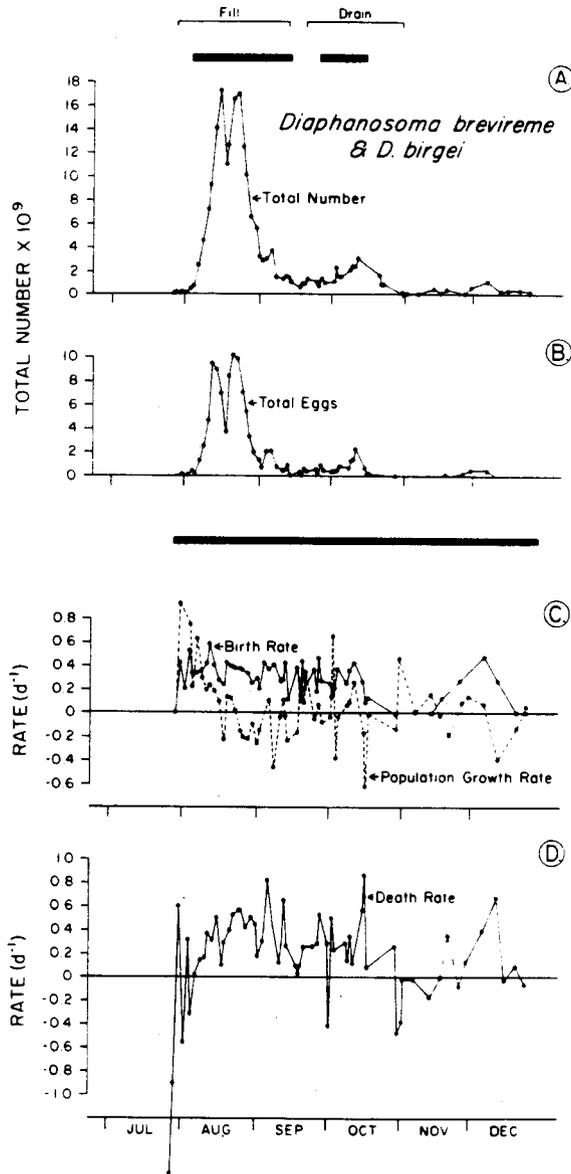

Fig. 6. Demographic analyses for *D.brevireme* and *D.birgei*, as Figure 4.

the lake from the Orinoco or could have hatched from resting eggs. Egg production corresponded with overall abundance patterns (Figure 6b): both total population size and egg production declined by late August and remained low through December. Birth rates were high from August to October (Figure 6c). In late August these high birth rates corresponded with low population growth rates and rapid declines in abundance (Figure 6a and c). This difference between continued high birth rates and low population growth rates suggests that high mortality controlled population size (Figure 6d).

Ceriodaphnia cornuta was the third species (together with D.brevireme and D.birgei) to appear in Laguna la Orsinera following inundation (Figure 7a). after population maxima of each of the other cladocerans. A rapid rise in C.cornuta abundance in mid-August was accompanied by an increase in egg production (Figure 7b). The individuals that initiated this increase likely hatched from resting eggs: population growth rate was very high in early August even though no eggs were produced and birth rates were zero (Figure 7c). Egg production declined in early September, but birth rates remained relatively constant throughout this period. By mid-September population growth rate was negative, but birth rates were still high, suggesting that mortality was responsible for the decline in population size (Figure 7d). Although error in individual estimates of C.cornuta death rates was large (Table I), consistent and reliable estimates of high birth rates together with low abundances indicate that mortality was not resource-mediated. The sporadic presence of C.cornuta in samples taken after October confounds interpretation of demographic trends.

Some additional evidence that mortality regulated cladoceran dynamics in Laguna la Orsinera is provided by correlation analyses (Table II). Death rates correlated negatively with population growth rates ($P = 0.001$) for all species except M.minuta, but there was no significant relationship between birth and population growth rates. Birth rates and death rates both correlated positively with population sizes ($P = 0.001$), suggesting that the increase in death rates with increasing population size was not the result of density-dependent resource depletion.

Correlations of parameters among species could suggest interspecific interactions, or simultaneous regulation of several populations by one mechanism. Evidence for such interactions was not extensive: Bosmina death rates correlated positively and Bosmina population growth rates correlated negatively with Diaphanosoma abundance; Diaphanosoma death rate correlated positively with C.cornuta birth rates and abundance (Table II). Because birth rates remained high, however, significant correlations between species probably indicate responses to factors other than competition for food.

Discussion

Cladoceran birth rates were high throughout our study, even though population maxima were restricted to brief intervals. The coincidence of high birth rates with small population sizes indicates that mortality controlled cladoceran dynamics in Laguna la Orsinera during much of our study period. The abiotic
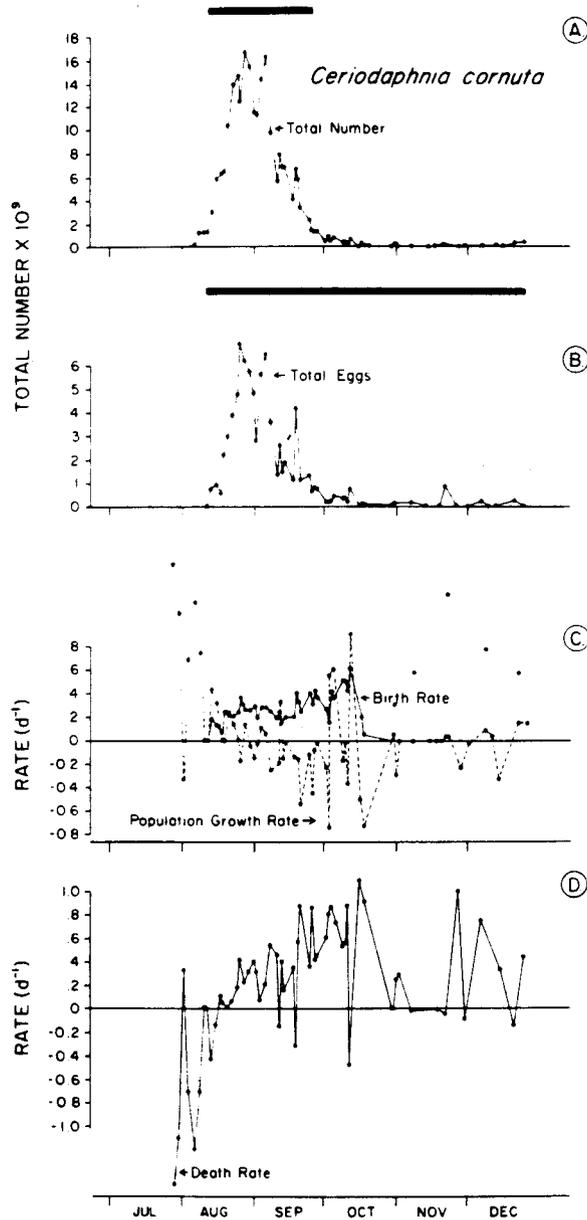
Fig. 7. Demographic analyses for *C. cornuta*, as in Figure 4. Birth rate estimates (**panel C**) in November and December were based on very small population sizes, contain a high degree of uncertainty and are presented as single estimates that are not connected by a solid line with previous, reliable estimates.

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Table II. Spearman Rank correlation coefficients for birth rate (b), death rate (d), population growth rate (r) and total population size (N) within and between all cladoceran species ($n = 79$)

	M.minuta. b	M.minuta. d	M.minuta. r	M.minuta. N	Bosmina. b	Bosmina. d	Bosmina. r	Bosmina. N
M.minuta. b	1.00	0.36*	0.09	−0.21	−0.1?	0.06	−0.19	−0.26*
M.minuta. d		1.00	−0.04	0.06	0.0?	−0.06	0.01	0.03
M.minuta. r			1.00	0.12	−0.0?	−0.29*	0.29*	−0.08
M.minuta. N				1.00	0.1?	0.00	0.08	0.32*
Bosmina. b					1.0?	0.22*	0.05	0.45*
Bosmina. d						1.00	−0.85*	0.10
Bosmina. r							1.00	0.11
Bosmina. N								1.00
Diaphanosoma. b								
Diaphanosoma. d								
Diaphanosoma. r								
Diaphanosoma. N								
C.cornuta. b								
C.cornuta. d								
C.cornuta. r								
C.cornuta. N								

* $P < 0.05$.

(e.g. turbidity) or biotic (food limitation. predation) environmental factors that could have accounted for these demographic patterns fluctuated rapidly in the lake over the course of filling. inundation. drainage and isolation from the Orinoco River.

Low water and lake isolation (June and July)

Despite high turbidity and low water levels during this period, population growth rates and population sizes of *Moina* and *Bosmina* increased rapidly. Others have reported severe reductions in phytoplankton growth rates or primary production at low water caused by light limitation and high turbidity (Marlier. 1967; Schmidt, 1973b; Sioli. 1975; Geddes. 1984). High birth rates and large population sizes indicate that primary production and phytoplankton abundance in Laguna la Orsinera were not limiting despite high turbidity.

The sharp increase in *Moina* abundance in July must have resulted from the hatching of resting eggs. There was no reproductive activity associated with this brief maximum, so that birth rates were zero and death rates were negative (suggesting immigration). That hatching of resting eggs could have produced this first *Moina* maximum is substantiated by our observations of sexual females and resting egg production in subsequent field samples. Four of the five cladocerans present (*Bosmina* excepted) were observed producing resting eggs.

Resting stages are not well known in tropical zooplankton populations. Jimenez and Zoppi de Roa (1987) report sexual resting egg production in several cladoceran populations in flooded Venezuelan grasslands. The incidence of sexual females was highest at low water. and species-specific stimuli appeared to regulate hatching from resting eggs. Moghraby (1977) observed hatching of rotifers. cladocerans and copepods from resting stages at several times throughout the year in the Blue Nile. although hatching was inhibited by high turbidity. In Laguna la Orsinera hatching occurred at different times for different species during the cycle of isolation. flooding and inundation (see

Diaphanos... b	Diaphanosoma. d	Diaphanosoma. r	Diaphanosoma. N	C.cornuta. b	C.cornuta d	C.cornuta. r	C.cornuta. N
0.02	0.14	−0.05	0.04	0.40	0.09	0.05	0.09
0.19	0.28	0.01	0.28	0.26	0.06	0.19	0.23
−0.12	−0.05	0.18	−0.15	−0.05	−0.19	0.20	−0.14
0.10	0.02	0.26	0.19	−0.21	−0.28	0.32	−0.01
0.17	0.13	0.08	0.15	−0.05	0.01	0.11	0.18
0.25	0.14	0.02	0.32	0.08	0.07	0.00	0.33
−0.21	−0.16	0.02	−0.29	−0.14	−0.02	0.01	−0.22
0.43	0.14	0.31	0.39	0.01	−0.09	0.16	0.22
1.00	0.56	0.21	0.76	0.39	0.17	0.01	0.66
	1.00	−0.32	0.61	0.42	0.13	0.14	0.61
		1.00	0.08	−0.13	−0.31	0.27	−0.09
			1.00	0.51	0.24	0.10	0.86
				1.00	0.21	−0.03	0.62
					1.00	−0.75	0.32
						1.00	−0.07
							1.00

discussion below for *C.cornuta*) and probably depends upon species-specific cues. The role of resting stages in zooplankton dynamics in floodplain lakes deserves greater attention.

The initial increase in *Moina* abundance lasted only for 8–9 days; reproductive females did not appear until population size had decreased to a small fraction of peak size. However, the initiation of reproductive activity and associated high birth rates for *Moina* in late July provide further evidence that food was not limiting during this period.

Several studies have demonstrated negative effects of high suspended sediment loads on cladoceran dynamics, either through interference with food collection or with locomotion (Arruda *et al.*, 1983; McCabe and O'Brien, 1983; Carvalho, 1984). Such inhibition clearly was not effective in Laguna la Orsinera, at least for *M.minuta* and *Bosmina*. *Moina* abundance declined rapidly in the latter part of July, in part because the onset of reproduction was delayed as individuals emerging from resting eggs matured. However, this delay and the associated decrease in *M.minuta* abundance did not appear to be caused, either directly or indirectly, by high turbidity.

Filling and inundation (August and September)

Bosmina death rates increased just when the lake was first flooded by the Orinoco River; high death rates restricted population size throughout the remainder of the study. Population growth rates and birth rates of *M.minuta*, *Diaphanosoma* and *C.cornuta* increased throughout filling and inundation. Neither *Diaphanosoma* nor *Ceriodaphnia* were present in the lake until after flooding, and both may have been excluded by high turbidity at lowest water. Like *M.minuta*, *C.cornuta* initially appeared in the laguna from hatching of resting eggs: the cues stimulating hatching for these two species must differ. *Ceriodaphnia cornuta* females quickly became reproductive, so that the *Ceriodaphnia* peak in August lasted longer than the July *Moina* peak.

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Despite high birth rates. all populations experienced only brief maxima before declining rapidly to small population sizes. These data argue against population regulation by resource availability; high mortality during this period was most likely due to predation by fish and by *Chaoborus* larvae. Fish densities are high in floodplain lakes. and the growth of larval fish following flooding could increase vertebrate predation pressure (Novoa. 1982: M.Rodriquez. unpublished results). The impact of these predators on cladoceran zooplankton prey was probably intensified by increasing water transparency during this period (Vinyard and O'Brien. 1976). In late September water transparency reached its maximum value (Secchi disk depth = 1.8 m; Figure 2). At the same time. *Chaoborus* larvae increased in abundance in Laguna la Orsinera (Figure 8). As an effective invertebrate predator on cladocerans (e.g. Fedorenko. 1975: Lewis. 1977: Pastorok. 1980: Hare and Carter. 1987). *Chaoborus* must have contributed to predation pressure on cladocerans in Laguna la Orsinera. By focusing feeding on the most abundant prey. both fish and *Chaoborus* can effect density-dependent regulation of prey population sizes (O'Brien *et al.*, 1976: Lewis. 1977: Pastorok. 1980). In Laguna la Orsinera predator focusing could have caused the rapid and tightly spaced progression of population maxima that we observed.

Drainage and isolation (October–December)

Cladoceran abundances remained low throughout the month of October, as water from the lake drained back into the Orinoco River and turbidity increased. During the early stages of drainage. high birth rates of *M.minuta.* *Diaphanosoma* and *C.cornuta* were balanced by high death rates. resulting in small population sizes. Fish and *Chaoborus* larvae were still plausible sources of mortality. By late October, however, birth rates of *Diaphanosoma* and *Ceriodaphnia* had declined. and death rates were only sporadically high. *Chaoborus* abundance had declined markedly by late October. and increasing turbidity may have limited the intensity of fish predation. Carvalho (1984) accounted for the decline and the maintenance of a small *Daphnia* population in

Fig. 8. Mean abundance of *Chaoborus*.
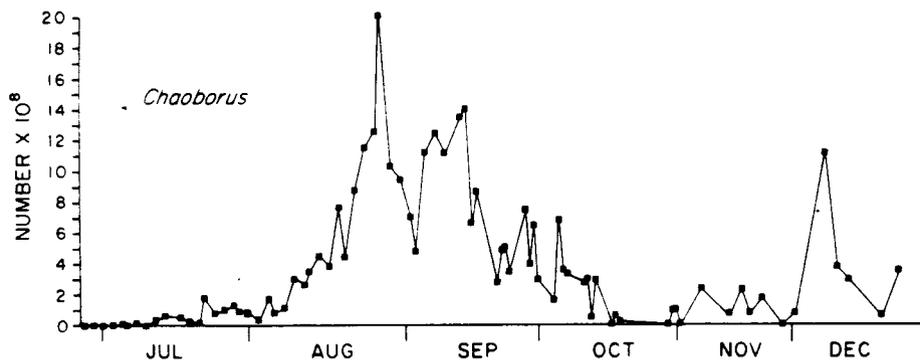
an Amazonian floodplain lake by fish predation, followed by the inhibitory effects of increasing turbidity. A similar situation may describe the dynamics of *Diaphanosoma* and *Ceriodaphnia* in Laguna la Orsinera; neither species was present in the lake until after flooding, suggesting that both may be more sensitive to turbidity than *M.minuta* and *Bosmina* appeared to be.

Moina minuta was the only species to maintain high birth rates during drainage and isolation, resulting in a population increase in November and December. By this time, water transparency was low (secchi disk depth <1.0 m); high birth rates and egg production again demonstrate that turbidity had no direct negative effects on *Moina* dynamics. Turbidity may have had indirect effects on *M.minuta*, however, by providing a refuge from visual predators, and thus facilitating an increase in population size. Despite high birth rates, population peaks in November and December were smaller and less discrete than those in July and August. Reduced population size probably resulted from sporadically high death rates, the causes of which are not clear. We terminated our sampling before this peak in *Moina* had ended, and too early to discover if *Bosmina* also initiated a peak during the early phase of isolation. It is likely that some, if not all, cladoceran populations spend much of the isolation phase (November until June) as resting eggs in the sediment.

This study demonstrates that demographic parameters estimated from intensive sampling of tropical cladoceran populations can be combined with environmental data to target factors controlling population dynamics. During a period that encompassed isolation, filling, inundation and drainage of Laguna la Orsinera, abiotic and biotic environmental conditions changed rapidly. Rapid increases in birth and population growth rates, together with hatching of resting eggs, resulted in increases in the abundance of each species. Differential sensitivity to turbidity and species-specific differences in the hatching of resting eggs affected the timing of population increases; these increases were not simultaneous but exhibited a closely spaced temporal sequence. Birth rates remained generally high throughout the study, but high death rates restricted each population to one (or rarely two) brief maximum, and then maintained small population sizes throughout the remainder of the study. Our demographic analyses indicate that high mortality resulted from intense predation by fish and *Chaoborus*, rather than from resource limitation. This mortality was the major factor regulating cladoceran abundance during inundation and drainage in Laguna la Orsinera.

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