

## Composition and seasonality of the zooplankton community of Lake Valencia, Venezuela

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**Abstract.** The composition and temporal abundance patterns of planktonic herbivores in Lake Valencia, Venezuela, were studied over a 5-year period. The herbivore community was typically composed of only 9 or 10 species, of which four (*Notodiaptomus deevevorus*, *Mesocyclops decipiens*, *Brachionus calyciflorus*, *Ceriodaphnia cornuta*) accounted for more than 90% of community biomass ( $67 \mu\text{g l}^{-1}$ , mean dry mass). Annual average biomass varied by a factor of three over the 5-year study and this is comparable to interannual variation observed in lakes of the temperate zone. Lake Valencia has a pronounced seasonal cycle based on an annual mixing period and an annual stratification period. Herbivores were usually more abundant during the mixing season than the stratification season. Proximate control of herbivore abundance patterns could be ascribed largely to predation by *Chaoborus*. Predation pressure was diminished during the circulation season because the *Chaoborus* population was reduced by two mortality mechanisms: catastrophic losses due to chemical changes at overturn, and increased predation by fish coincident with loss of the hypolimnetic refuge. *Chaoborus* fed on all herbivore species in Lake Valencia, but electivities for specific herbivores varied greatly. The early developmental stages of both copepod species experienced low predation pressure; *Notodiaptomus* nauplii escaped predation entirely. Adult copepods, on the other hand, were highly vulnerable to predation. A statistical analysis of temporal patterns of abundance and production for the major herbivore species suggests that closely related species responded differently to growth control mechanisms; the two species with similar responses (*M. decipiens* and *B. calyciflorus*) also had coincident abundance patterns. Despite statistical differences in responses to growth control mechanisms, there was remarkable dietary similarity among the species. There was no obvious dietary specialization and no statistical evidence of strong selectivity for or aversion to particular algal species. Zooplankton species composition is very simple in Lake Valencia in contrast to the high species richness of many other kinds of tropical communities. Herbivore community abundance is highly seasonal in Lake Valencia; the amplitudes of abundance fluctuation exceed those of other large tropical lakes and are comparable to those in lakes of the temperate zone. Herbivore production in Lake Valencia, and in tropical lakes in general, is not necessarily higher than that in temperate lakes, but production per unit biomass probably is higher.

### Introduction

Early studies of tropical zooplankton communities were based mainly on samples collected by expeditions, and thus provided little information on seasonality or community dynamics (e.g. de Beauchamp, 1932, 1939; Kiefer, 1933; Lowndes, 1933; Ruttner, 1952; Harding, 1955). In the last 20 years, however, more effort has been devoted to quantitative ecological investigations of individual lakes (e.g. Burgis, 1971, 1974, 1978; Burgis *et al.*, 1973; Widmer *et al.*, 1975; Burgis and Dunn, 1978; Kalk, 1979; Lewis, 1979; Carmouze *et al.*, 1983; Saint-Jean, 1983; Twombly, 1983; Vareschi and Jacobs, 1984; Vareschi and Vareschi, 1984). Quantitative data now exist on the abundance or production of zooplankton in a number of large tropical lakes from various parts of the world, and some general characteristics of tropical zooplankton communities are beginning to emerge (Nilssen, 1984).

The high temperatures in waters of the lowland tropics set high potential rates for biological processes. Despite low seasonal variation in temperature, however, at least some tropical zooplankton populations demonstrate conspicuous seasonality (Lewis, 1979; Twombly, 1983; Nilssen, 1984); zooplankton in large tropical lakes sometimes show seasonal fluctuations that approach those observed in lakes at higher latitude (cf. Morgan *et al.*, 1980). The explanation for seasonality of tropical zooplankton populations lies in a strong and pervasive tendency for seasonality in the mixing regimes of tropical lakes (Lewis, 1987).

Perhaps more surprising than the seasonality of tropical zooplankton is the simplicity of community composition. Data for species richness in communities of most terrestrial plants and animals show that tropical communities typically contain more species than do those of the temperate zone (Pianka, 1966). A similar trend has been documented for fish (Lowe-McConnell, 1969); however, a rigorous test of this trend would need to account for the complicating effects of river basin size, and this has not yet been done (Lewis, 1987). Phytoplankton communities are no more diverse at low than at high latitudes (Lewis, 1978, 1987), and tropical zooplankton communities appear to be even less diverse than those of the temperate zone (Fernando, 1980). Detailed studies of individual lakes may help demonstrate why the latitudinal trends characteristic of terrestrial communities are not observed for the freshwater plankton.

We have analyzed the productivity of the herbivore community of Lake Valencia, Venezuela, and the mechanisms that regulate the dynamics of its zooplankton herbivores (Saunders and Lewis, 1988), but with minimal attention to community composition and temporal patterns of abundance for individual species. We focus here on the composition and species abundance patterns of planktonic herbivores in Lake Valencia on an annual and seasonal basis for a five-year period of study. The duration of this study is long in comparison to other published works on tropical lakes and will thus help establish some perspective on interannual variation.

### Site description

Lake Valencia lies in the Aragua Valley of north-central Venezuela and historically was part of the Orinoco River drainage basin (Figure 1). The lake level has been falling for at least 250 years (Bockh, 1972) and the present lake level is well below the outflow. The lake has been completely dry at least once, in an episode that ended about 10,000 years ago (Schubert, 1979; Bradbury *et al.*, 1981; Lewis and Weibezahn, 1981). One consequence of the present desiccation episode is the gradual concentration of solutes in the water column: specific conductance is presently above  $2100 \mu\text{S cm}^{-1}$ .

The morphometric characteristics of Lake Valencia vary somewhat over time with changes in water level (Lewis, 1983a). At the time of study (1977–1981) the lake had a maximum depth of 37 m, a mean depth of 18 m and a surface area of  $350 \text{ km}^2$ , which ranks Lake Valencia as the second largest natural lake in South America. A summary of major physical and chemical features is given in Lewis and Weibezahn (1976).

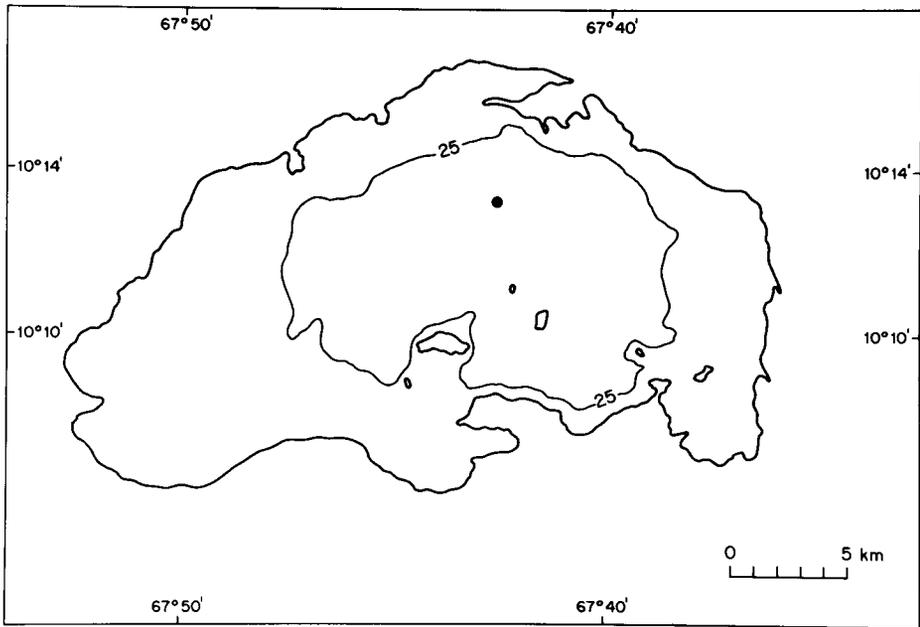


Fig. 1. Map of Lake Valencia showing the primary sampling site.

Two large cities, Valencia and Maracay, are located on the shores of Lake Valencia. Most domestic and industrial wastes from these cities go into the lake and account for a relatively high nutrient load— $3.3 \text{ g m}^{-2} \text{ year}^{-1}$  for phosphorus and  $10.3 \text{ g m}^{-2} \text{ year}^{-1}$  for nitrogen (Lewis and Weibezahn, 1983). In response to the high nutrient load, the phytoplankton community is highly productive ( $2 \text{ g C m}^{-2} \text{ day}^{-1}$ ; unpublished data) and is nitrogen-limited (Lewis, 1983b).

Lake Valencia can be classified on the basis of the annual mixing regime as a warm monomictic lake (Lewis, 1983c). Seasonal changes in the stability of the water column cause pronounced seasonal variation in chemical and biological conditions. The period of circulation, which corresponds to the dry season in Venezuela, typically extends from November through April. Isothermal mixing does not occur continuously during the circulation season, however; it may be interrupted by temporary stratification for periods of up to a few weeks. The period of stratification, which corresponds to the rainy season, usually begins in April. The water column below 20 m is usually anoxic throughout the period of stratification. Stratification usually ends abruptly in late November or December; the onset of complete mixing at this time may cause mortality in the zooplankton (Infante *et al.*, 1979a).

In addition to the predictable alternation of seasons, important unpredictable abiotic events occur during the period of stratification. The thickness of the mixed layer is quite variable over time in response to short-term changes in weather (Figure 2). A period of clear, calm weather allows for the formation of a

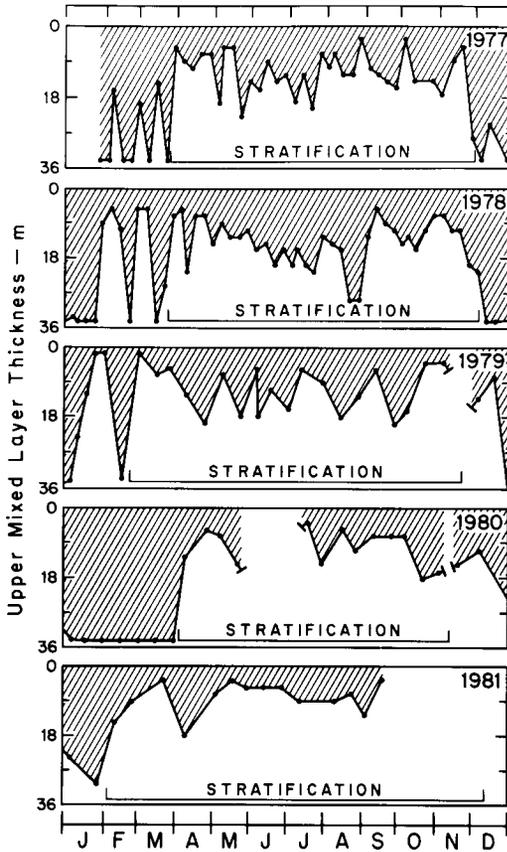


Fig. 2. Thickness of the upper mixed layer in Lake Valencia over the sampling period. Gaps in 1979 and 1980 indicate intervals lacking temperature data.

secondary thermocline that bounds a relatively thin mixed layer. Below the temporary thermocline, oxygen is depleted rapidly and nutrients are released through decomposition. Thus, vertical dimensions of the pelagic environment may change greatly from month to month. Cool weather or a storm may remove the secondary thermocline and thus abruptly extend the thickness of the mixed layer (Lewis, 1973). Such unpredictable alterations in abiotic conditions have great influence on the plankton. For example, the return of mineralized nutrients to the mixed layer may release phytoplankton from nutrient control that would otherwise persist until the beginning of the period of circulation.

**Materials and methods**

*Routine collections*

Zooplankton were sampled from the entire water column at a site over the deepest part of the lake. Studies of horizontal spatial heterogeneity have demonstrated that this site is representative of the central lake area (Cressa,

1985; Saunders and Lewis, 1988). For the first 2 years of the study seven vertically contiguous samples, each consisting of a 5-m segment of the water column, were taken with a flexible integrating sampler (40 l each; Lewis and Saunders, 1979). For the remaining 3 years of the study a flexible integrating sampler 35 m long was used to obtain two replicate samples of 160 l each. Samples were usually collected between 07.00 and 08.00 hours. The water was filtered through a net of 55  $\mu\text{m}$  mesh, and the organisms were preserved in Lugol's solution. Species and stages were enumerated until 10 or more individuals of the most common rotifer and crustacean taxa had been counted, or until the entire sample had been examined. All *Chaoborus* larvae were counted in each sample. Biomass was estimated for each developmental stage of each herbivore species on the basis of calculated volume (Bottrell *et al.*, 1976), and with the assumption that the density of the organism is approximately the same as that of water. *Chaoborus* biomass was based on the length-mass relationship determined by Cressa and Lewis (1984). Dry mass is assumed to be 11% of wet body mass (Sitaramaiah, 1967), and carbon is assumed to comprise 44% of dry mass.

#### *Herbivore production*

Production methodology is described in detail in Saunders and Lewis (1988); a summary is given here. Standard values of production for rotifers and cladocerans were based on the product of population biomass and growth rate (Kimmerer, 1987). Birth rate, determined by the equation of Paloheimo (1974), was assumed to closely approximate growth rate. Standard production rates for copepods were determined by the incremental summation method (Rigler and Downing, 1984; Kimmerer, 1987) in which development times are assumed constant over time. Copepod development times were estimated from examination of mean pulse times for each of the various life history stages in several different cohorts (Rigler and Cooley, 1974; Lewis, 1979; Saunders and Lewis, 1988). Application of these development rates in modelling population dynamics produced loss rate estimates in excess of estimated predation mortality. We have interpreted the unexplained loss as an estimate of growth suppression. On each date, nominal growth rates were reduced by the amount of growth suppression to give actual growth rates. Revised production rates were calculated for all taxa as the product of biomass and actual growth rate. Only the revised production data are presented here.

#### *Chaoborus* crop analysis

*Chaoborus* larvae intended for crop analysis were preserved in Lugol's solution to prevent crop eversion that occurs commonly when larvae are preserved in formalin (Kajak and Ranke-Rybicka, 1970; Lewis, 1975). Crops were dissected by the method of Swift and Fedorenko (1973) and were examined at  $\times 50$ – $100$  so that small food items would not be overlooked. Loricated rotifers and even the smallest crustaceans were readily identified at this magnification, but illoricate rotifers in advanced stages of digestion might not have been recognizable. Crops

were occasionally examined at higher magnification for trophi or other indigestible remains of illoricate rotifers, but these were never found.

## Results

### *Community composition and standing stock*

The average number of zooplankton species (excluding *Chaoborus*) appearing in the samples collected from Lake Valencia on a given date was 9–10 (range 5–14). Thirteen species of limnetic rotifers were found, and most of the species have broad geographic ranges (Table I). Five of the limnetic species, including the three most common ones, are from the family Brachionidae, the species of which often live in hard waters. The *Anuraeopsis* found in Lake Valencia was originally described as an endemic species (Berzins, 1962), but has since been placed in synonymy with *A.navicula* by Koste (1978). *Hexarthra intermedia brasiliensis*, which was not common in Lake Valencia, appears to be restricted in distribution to the neotropics (Koste, 1978). *Lilliferotrocha subtilis*, an unusually small rotifer, had been reported previously only from Europe and Asia. Although it occasionally reached high abundances, *Lilliferotrocha* was present only sporadically in Lake Valencia. *Asplanchna*, one of two carnivorous invertebrate taxa, was present in only a few of the samples.

Six widely distributed cladoceran species were collected during the study, but the three chydorid species were never abundant in open water. Males of *Alona davidi*, indicating induction of a sexual reproductive phase in these normally

**Table I.** Zooplankton species occurring in the limnetic zone of Lake Valencia, 1977–1981

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#### Rotifera

- Brachionus plicatilis* (O.F.Muller)
- B.calyciflorus* Pallas
- B.havanaensis* O.F.Muller
- Epiphanes macrouras* (Barrois and Daday)
- Keratella americana* Carlin
- Anuraeopsis navicula* Rousselet (= *A.racensis* Berzins)
- Trichocerca pusilla* (Lauterborn)
- T.stylata* (Gosse)
- Asplanchna? sieboldi* (Leydig)
- Polyarthra vulgaris* Carlin
- Hexarthra intermedia brasiliensis* (Hauer)
- Lilliferotrocha subtilis* (Rodewald)

#### Cladocera

- Moina micrura* Kurz
- Diaphanosoma birgei* Korinek
- Ceriodaphnia cornuta* Sars
- Leydigia acanthocercoides* (Fisher)
- Alona cambouei* Guerne and Richard
- A.davidi* Richard

#### Copepoda

- Mesocyclops decipiens* (Fischer)
  - M.venezolanus* Dussart (= *M.meridianus*)
  - Notodiaptomus deeveyorus* (Bowman)
-

parthenogenetic animals, appeared shortly after one of the seasonal mixing events, and at that time constituted almost 15% of the *Alona* population. Males of other cladocerans were not encountered. There were three species of Copepoda, but only two, *Mesocyclops decipiens* and *Notodiaptomus deeveyorus*, were common. Kiefer's (1956) taxonomic study implied that *Mesocyclops venezolanus* (listed by him as *M. brasilianus*) was the common cyclopoid, yet it was rare during our study. Further details of the taxonomy of copepods in the lake are given elsewhere (Infante *et al.*, 1979b; Dussart, 1984; Dussart, 1987). The only other invertebrate of importance in open water was the predaceous dipteran *Chaoborus brasiliensis* (Theobald) (Saether, 1976), which was a significant source of mortality for other species of zooplankton in Lake Valencia (Saunders and Lewis, 1988).

Dry masses, lengths and average standing stocks of the more abundant taxa of zooplankton herbivores are given in Table II. The Cladocera of Lake Valencia were relatively unimportant, both numerically and as biomass (Table III). Rotifers accounted for  $\frac{2}{3}$  of total herbivore numbers, but less than 20% of standing stock. Of the three planktonic copepods, one species (*Mesocyclops venezolanus*) accounted for less than 1% of copepod biomass over the 5 years. The other two species were, in terms of biomass, the two most important herbivores in Lake Valencia.

Biomass in each group was dominated by very few species. For example, although we found 13 limnetic rotifer species in Lake Valencia, three species accounted for more than 95% of rotifer biomass. Similarly, the Cladocera of Lake Valencia were dominated by three species, and the single most important species comprised 75% of the biomass for the group. On average, 90% of the biomass of the herbivore community of Lake Valencia consisted of one calanoid species, one cyclopoid species, one rotifer species and one cladoceran species. If another cladoceran and two more rotifers are added, it would account for 98% of herbivore biomass.

Although the number of species that made significant contributions to biomass and numbers in Lake Valencia is very small, the two important copepod

**Table II.** Size and biomass per individual of the major herbivore species

Species	Stage	Length ( $\mu\text{m}$ )	Biomass [ $\mu\text{g}$ (dry)]
Copepoda			
<i>Notodiaptomus deeveyorus</i>	adult female	1259	5.145
	adult male	1206	4.617
	C5	1035	3.141
	C4	840	1.857
	C3	684	1.107
	C2	550	0.639
	C1	435	0.354
	N6	345	—
	N5	300	—
	N4	262	0.180 <sup>a</sup>
	N3	237	—
	N2	214	—
	N1	189	—
	egg	135	0.130

Table II. Continued

Species	Stage	Length ( $\mu\text{m}$ )	Biomass [ $\mu\text{g}$ (dry)]
<i>Mesocyclops decipiens</i>	adult female	759	1.048
	adult male	546	0.398
	C5	590	0.559
	C4	507	0.398
	C3	436	0.277
	C2	369	0.186
	C1	308	0.121
	N6	194	—
	N5	170	—
	N4	143	0.036 <sup>a</sup>
	N3	120	—
	N2	103	—
N1	93	—	
egg	73	0.020	
<i>Mesocyclops venezolanus</i>	adult female	1006	4.685
	adult male	638	0.779
	C5	717	1.085
	C4	617	0.711
	C3	522	0.441
	C2	446	0.284
	C1	378	0.177
	N6	254	—
	N5	222	—
	N4	188	0.085 <sup>a</sup>
	N3	157	—
	N2	132	—
N1	110	—	
egg	90	0.040	
Cladocera			
<i>Moina micrura</i>	adult female	500	0.600
	egg	130	0.138
<i>Diaphanosoma birgei</i>	adult female	580	0.800
	egg	125	0.110
<i>Ceriodaphnia cornuta</i>	adult female	450	0.500
	egg	115	0.052
Rotifera			
<i>Keratella americana</i>	adult female	160	0.008
	egg	62	0.007
<i>Brachionus calyciflorus</i>	adult female	245	0.279
	egg	119	0.070
<i>Brachionus havanaensis</i>	adult female	220	0.056
	egg	80	0.050
<i>Polyarthra vulgaris</i>	adult female	120	0.034
	egg	80	0.030
<i>Hexarthra intermedia</i>	adult female	115	0.029
	egg	75	0.025

<sup>a</sup> Average for stages N1–N6.

Table III. A 5-year average of herbivore abundance

Species/stage	Biomass			Numbers (indiv. l <sup>-1</sup> )	
	$\mu\text{g l}^{-1}$ , dry mass	Within species %	Within group %		
<i>Notodiaptomus deeevorus</i>					
Female	13.94	36.5	28.0	20.7	2.71
Male	11.82	30.9	23.7	17.6	2.56
C5	5.10	13.3	10.2	7.6	1.62
C4	2.44	6.4	4.9	3.6	1.31
C3	1.35	3.5	2.7	2.0	1.22
C2	0.74	1.9	1.5	1.1	1.16
C1	0.43	1.1	0.9	0.6	1.20
Nauplii	1.39	3.6	2.8	2.1	7.71
Eggs	1.04	2.7	2.1	1.5	7.97
Total	38.24	—	76.7	56.8	27.47
<i>Mesocyclops decipiens</i>					
Female	2.26	20.0	4.5	3.4	2.16
Male	1.74	15.4	3.5	2.6	4.37
C5	1.61	14.2	3.2	2.4	2.87
C4	1.65	14.6	3.3	2.5	4.14
C3	0.98	8.7	2.0	1.5	3.53
C2	0.77	6.8	1.5	1.1	4.14
C1	0.85	7.5	1.7	1.3	7.00
Nauplii	1.28	11.3	2.6	1.9	35.51
Eggs	0.18	1.6	0.4	0.3	9.11
Total	11.31	—	22.7	16.8	72.81
<i>M. venezolanus</i>	0.32	—	0.6	0.5	3.07
Total Copepoda	49.86	—	—	74.1	103.35
<i>Moina</i>	1.23	—	19.5	1.8	2.73
<i>Diaphanosoma</i>	0.29	—	4.6	0.4	0.44
<i>Ceriodaphnia</i>	4.78	—	75.9	7.1	12.26
Other Cladocera	<0.01	—	<0.1	—	0.01
Total Cladocera	6.30	—	—	9.4	15.43
Total Crustacea	56.16	—	—	83.4	118.78
<i>Keratella</i>	0.96	—	8.6	1.4	122.22
<i>Brachionus calyciflorus</i>	8.26	—	73.9	12.3	36.84
<i>B. havanaensis</i>	1.53	—	13.7	2.3	28.04
<i>Polyarthra</i>	0.09	—	0.8	0.1	2.72
<i>Hexarthra</i>	0.02	—	0.2	—	0.62
Other Rotifera	0.32 <sup>a</sup>	—	2.9	0.5	11.00
Total Rotifera	11.17	—	—	16.6	201.45
Total herbivores	67.33	—	—	—	320.22

Values reported for Cladocera and Rotifera include eggs.

<sup>a</sup>Approximate due to partial loss of two very small genera (*Anuraeopsis* and *Lilliferotrocha*).

species increased the functional diversity of herbivores to a considerable degree because of their numerous developmental stages. Individuals and biomass were distributed very differently among stages for the two species (Figure 3). For *Notodiaptomus*, adults accounted for  $\sim\frac{2}{3}$  and the five copepodid stages accounted for  $\sim\frac{1}{4}$  of the biomass. In contrast, for *Mesocyclops decipiens*  $\sim\frac{1}{3}$  of the biomass was found in the adult stage and  $\sim\frac{1}{2}$  was found in the five copepodid stages. The most conspicuous differences between the two species was the relative abundance of the naupliar stages. In the *Mesocyclops* population these six stages accounted for  $\sim 50\%$  of all individuals, as might be expected if development were approximately isochronal. For *Notodiaptomus*, on the other hand, the naupliar stages were no more abundant than the egg stage and represented  $<30\%$  of all individuals.

The difference in distribution of individuals among stages suggests important differences in the way population growth was regulated over the developmental stages of the two copepod species. We have shown elsewhere (Saunders and Lewis, 1988) that growth suppression had a significant impact on both

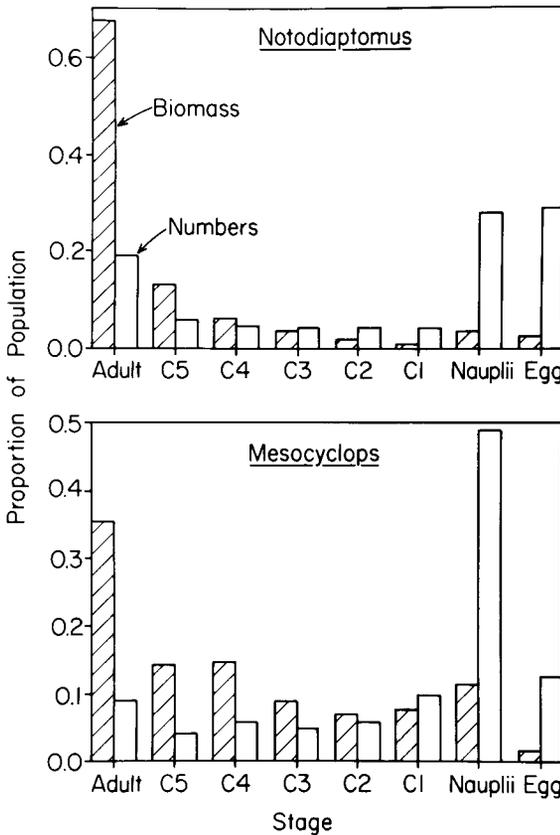


Fig. 3. Distribution of biomass and individuals among the developmental stages of *Notodiaptomus deevoyorus* and *Mesocyclops decipiens*.

populations. Growth suppression was most extreme in the *Notodiptomus* population, where the naupliar stages grew poorly and probably faced starvation. The effects of growth suppression are evident in the distribution of production over the developmental stages and in the turnover of biomass in each stage (Figure 4). For the *Notodiptomus* population the naupliar stages appear to have constituted a severe bottleneck.

Biomass turnover rates were also very low for the adults of both populations (Figure 4). The production of eggs was relatively inefficient and was essentially subsidized by high P/B ratios in earlier stages (cf. Lewis, 1979). In part, this inefficiency can be attributed to predation mortality, which greatly restricted adult lifespan. Interspecific differences in reproduction illustrate the differences in strategies (Table IV). The calanoid produced a large egg, but the difference in egg size between species was not nearly so great when expressed as a percentage of body mass. For both species the mass of a single egg was ~2% of adult female body mass. The eggs of *Mesocyclops* were slightly smaller as a percentage of adult female body mass, but this was more than offset by the larger clutch size in the cyclopoid.

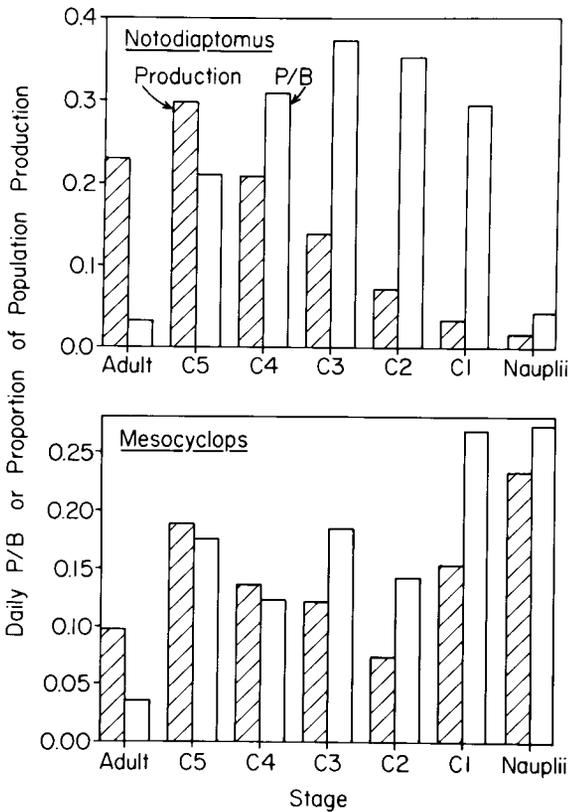


Fig. 4. Distribution of production among the developmental stages and daily biomass turnover rates for each stage of the two common copepod species in Lake Valencia.

**Table IV.** Reproductive output of female copepods from Lake Valencia

Species	Single egg		All eggs		Lifetime statistics				
	Mass [ $\mu\text{g}$ (dry)]	% body mass	Modal no. of eggs	% body mass	Biomass [ $\mu\text{g}$ (dry)]	% body mass	Female output [ $\mu\text{g}$ (dry)]	Female output (%)	No. of young
<i>Notodiaptomus deevyorus</i>	0.13	2.5	6	15.2	0.78	15.2	3.12	60.6	24
<i>Mesocyclops decipiens</i>	0.02	1.9	16	30.5	0.32	30.5	0.16	15.3	8

Output of females is based on the finite birth rate and estimated longevity of females.

The average lifetime output for a female differed much more drastically between the two copepod species than one might suppose from the general similarities in egg development time and birth rate (Table IV). The critical difference was in the average female lifespan as estimated from the assumption that density ratios are determined mainly by relative durations of the developmental stages. The average lifespan of adult *Mesocyclops decipiens* was only a few days, whereas that of *Notodiaptomus deveyorus* was 11 days. Thus the average cyclopoid female produced no more than one full clutch, while the calanoid produced about four smaller clutches.

The distribution of individuals across stages was controlled differently for the two copepod populations. Growth suppression caused by poor nutrition limited recruitment for *Notodiaptomus* and high reproductive output was needed to sustain the population. Despite its higher fecundity, *Mesocyclops* was held in check by a high adult mortality rate.

#### *Temporal variation in zooplankton biomass*

The data in Figure 5 suggest that variation in the zooplankton populations of Lake Valencia over a span of years may be comparable to that of temperate lakes (Morgan *et al.*, 1980). Both rotifers and copepods showed two- to threefold variations in annual average standing stock over the 5-year period. Variation in the zooplankton populations is probably explained by the great variation in physical and chemical conditions that can occur between years in Lake Valencia (Lewis, 1984, 1986).

The two major seasons in Lake Valencia (mixing, stratification) can be identified easily on a physical basis, but the biological implications of seasonal change are not easy to predict. In most monomictic lakes of the temperate zone lower light availability and lower temperature during the mixing season are associated with a suppression of both phytoplankton and zooplankton biomass because growth rates of both algae and zooplankton are suppressed. However, the mixing season in Lake Valencia is not accompanied by any major decline in water temperature, and the mixing is interrupted with sufficient frequency to relieve the light deprivation of the algae. Thus there was no assurance that the seasonal events would have the same consequences for the biota as they might in a temperate lake. In fact, the herbivores in Lake Valencia were almost always more abundant during the mixing season than during the stratification season (Figure 5). This is a major contrast with most temperate monomictic lakes.

Herbivore taxa differed considerably in their seasonal patterns of abundance (Figures 6 and 7). *Notodiaptomus* and *Brachionus havanaensis* did not produce annual maxima according to any kind of seasonal pattern. *Mesocyclops* and *B. calyciflorus*, on the other hand, appeared favored by the conditions of the mixing season. The Cladocera were even more extreme in their dependence on the mixing season. In years when measurable populations were produced, Cladocera were much more abundant during the mixing season than during stratification. In 3 of the 5 years, populations of the rotifer *Keratella* were much more abundant during the mixing season; abundances were relatively constant over seasons in the last 2 years.

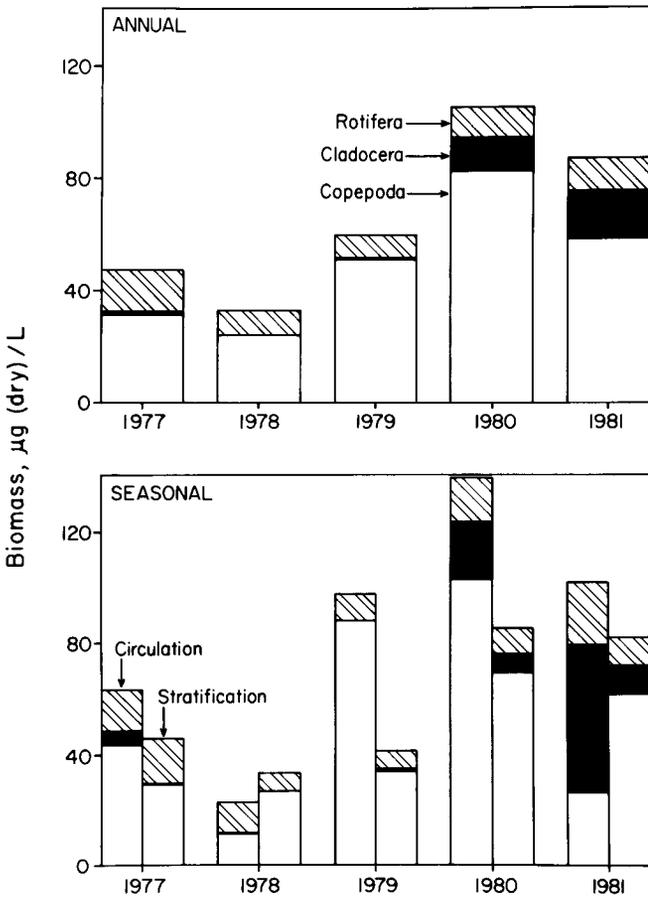


Fig. 5. Annual mean biomass for herbivores over the 5-year study interval (upper panel), and mean standing stock of herbivores during the mixing season and the stratification season in each of the 5 years (lower panel). Rotifers, cladocerans and copepods are shown separately in the stacked bar graphs.

*Statistical analysis of herbivore similarities*

Common or contrasting trends in abundance or production of herbivore species can be detected by correlation analysis and can be used to make inferences about ecological similarities (Lewis, 1979). The density and production data for Lake Valencia were used in preparing four correlation matrices: abundance (N matrix), change in abundance ( $\Delta N$  matrix), production (P matrix) and change in production ( $\Delta P$  matrix). The data were first tested for autocorrelation with the Durbin-Watson statistic. Because significant autocorrelation was present for most variables, all variables were transformed as described by Chou (1975) to eliminate first-order serial correlation. Production data are from Saunders and Lewis (1988).

The N matrix incorporates an historical component whose magnitude varies

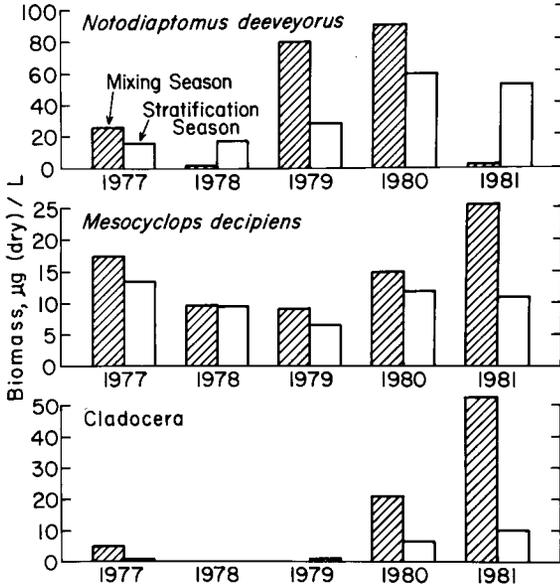


Fig. 6. Mean standing stock of the major crustacean species in Lake Valencia during the mixing season and stratification season over the 5 years.

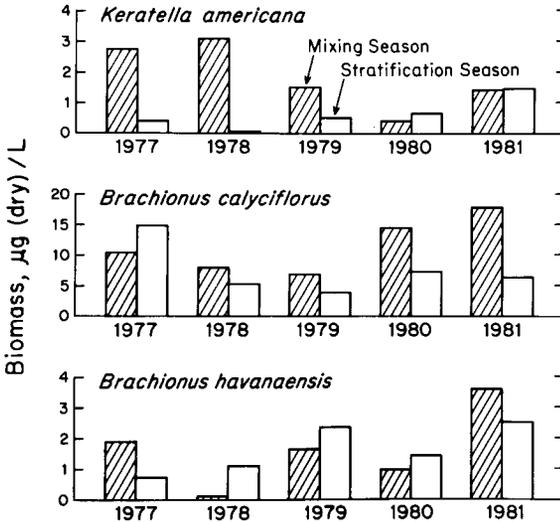


Fig. 7. Mean standing stock of the major rotifer species in Lake Valencia during the mixing season and stratification season over the 5 years.

with the generation time of the species. Consequently the **N** matrix is mainly useful in providing information on patterns of community composition and coexistence of species through time. The **P** matrix, which has an historical component similar to that of the **N** matrix, can be used to identify similarities in

growth patterns and demand on resources. The  $\Delta N$  matrix indicates the similarities in population response and thus can be used as a general measure of ecological similarity. Unlike the  $N$  matrix, it has a minimal historical component. The  $\Delta P$  matrix is based on the rate of change of growth and, since growth is a rate of change, the  $\Delta P$  matrix is fundamentally a second derivative of abundance. Within the herbivore community  $\Delta P$  will indicate ecological similarities, but, unlike the  $\Delta N$  matrix, it is sensitive mostly to growth control mechanisms. Although  $\Delta P$  and  $P$  both provide information on growth control mechanisms, the  $\Delta P$  matrix will indicate general ecological similarities based on growth control mechanisms, whereas the  $P$  matrix will indicate similarities in demands on food resources.

Twenty-five of the 66 paired comparisons for the  $N$  matrix were statistically significant ( $P \leq 0.05$ ) and all of these were positive (Table V). As expected from the historical component of the  $N$  matrix, there were clusters of positive correlations showing linkage between the developmental stages within each copepod species. Half of the significant positive correlations were accounted for in this way. The general rarity of interspecific correlations demonstrates the independence of the timing of growth and decline for individual species. A few significant interspecific correlations are worthy of note, however. The copepodid and adult stages of *Mesocyclops* were correlated in abundance with the three most common rotifer species. The only other cluster of interspecific correlations was between rotifer species. The pattern of relationships for the  $P$  matrix was similar to that of the  $N$  matrix because abundance exerts a powerful influence on production.

The herbivore community can be divided into three groups on the basis of the  $N$  and  $P$  matrices. The trends of *Notodiaptomus*, the most abundant herbivore in terms of biomass, did not coincide with those of the other species. Also, *Notodiaptomus* was one of two common species that lacked discernible seasonal abundance patterns. The cladocerans made up group 2. The virtual disappearance of cladocerans for nearly 2 years, while significant, does not affect this conclusion because densities below the detection limit were excluded from the correlation analysis; even when cladocerans were present, their abundances did not correspond to abundances of other crustaceans. The third group of herbivores (*Mesocyclops* and the rotifers) included nearly 80% of the organisms in the community. Species in this group had predictable seasonal patterns of abundance.

Coincidence in time does not necessarily imply overall ecological similarity because the operation of control mechanisms may be obscured by historical trends in abundance. We focus on control mechanisms through the  $\Delta N$  matrix (Table V), which shows that the rotifer species and the later stages of *Mesocyclops* responded similarly to control mechanisms. *Notodiaptomus* was distinct from this group of herbivores, as were the cladocerans.

The  $\Delta P$  matrix, which emphasizes the role of growth control factors, shows that the three rotifer species that were coincident in time differed with respect to growth control mechanisms, and this may have facilitated their coexistence (Table V). Intraspecific correlations for *Notodiaptomus* were restricted to

**Table V.** Pairwise comparisons among the herbivore taxa for abundance (above diagonal) and production (below diagonal) in upper panel, and change in abundance (above diagonal) and change in production (below diagonal) in lower panel

	Notodiaptomus			M. decipiens			Nauplii	Moina	Ceriodaphnia	Keratella	B. calyciflorus	B. havanaensis
	Adult	C4-C5	C1-C3	Adult	C4-C5	C1-C3						
<i>Notodiaptomus</i>												
adult												
C4-C5	+											
C1-C3	+	+										
nauplii	+	+	+									
<i>M. decipiens</i>												
adult												
C4-C5				+								
C1-C3				+	+							
nauplii				+	+	+						
<i>Moina</i>												
<i>Ceriodaphnia</i>												
<i>Keratella</i>												
<i>Brachionus calyciflorus</i>												
<i>B. havanaensis</i>												
<i>Notodiaptomus</i>												
adult												
C4-C5	+											
C1-C3	+	+										
nauplii	+	+	+									
<i>M. decipiens</i>												
adult												
C4-C5				+								
C1-C3				+	+							
nauplii				+	+	+						
<i>Moina</i>												
<i>Ceriodaphnia</i>												
<i>Keratella</i>												
<i>Brachionus calyciflorus</i>												
<i>B. havanaensis</i>												

**Table VI.** Ecological associations within the herbivore community

	Response to growth control mechanisms	
	Similar	Dissimilar
Abundance through time		
Similar	<i>Mesocyclops</i> and <i>B.calyciflorus</i>	rotifers
Dissimilar		cladocerans and copepods

adjacent groups of juvenile stages in a manner that suggests changes in growth control factors during the course of development. Although the three rotifer species and *Mesocyclops* responded similarly to control mechanisms in general, only *Mesocyclops* and *B.calyciflorus* responded alike to growth control mechanisms.

*Notodiaptomus* and *Mesocyclops* differed in their temporal distributions and ecological affinities. Moreover, their intraspecific affinities differed. Nearly all stages of *Mesocyclops* responded alike to growth control mechanisms, whereas few of the *Notodiaptomus* stages did. The fragmentation of affinities within the calanoid life history probably reflects growth suppression in the naupliar stages, which was not characteristic of the cyclopoid (Saunders and Lewis, 1988).

The herbivores were separated in time and by differential response to growth control mechanisms (Table VI). *Mesocyclops* and the three rotifer species were coincident in time, but only *Mesocyclops* and *B.calyciflorus* were similar in their response to growth control mechanisms. Abundance patterns for *Notodiaptomus* and the cladocerans differed from one another and from those of *Mesocyclops* and the rotifers. Moreover, the two copepod species were separated both ecologically and in time, as were the two cladoceran species. There were no species with common growth control mechanisms that were not also coincident in time. Species with common growth control mechanisms differed taxonomically at the class level or higher; the more closely related species were separated by response to growth control mechanisms.

*Predation*

Most of the mortality of herbivores in Lake Valencia was attributable to predation by *Chaoborus* (Saunders and Lewis, 1988). The *Chaoborus* population in Lake Valencia was very abundant; it had an average biomass [67 µg (dry) l<sup>-1</sup>] equal to that of the herbivores and an average density of 0.8 l<sup>-1</sup>. Instar-specific feeding electivities of *Chaoborus* were estimated for all major herbivores (Table VII), based on dissection of the crops of more than 1000 *Chaoborus* larvae from 10 sampling dates. Electivities were computed as  $r_i/p_i$ , where  $r_i$  is the proportion of item  $i$  in the diet and  $p_i$  is the proportion of item  $i$  in the lake. Median electivities are reported unless there were too many tie scores, in which case the average electivity was used. For a given instar dates were excluded where <5 crops were examined, and electivity values were excluded where  $p_i < 0.005$  for a particular prey item.

The *Chaoborus* population consumed all common planktonic herbivore

Table VII. Prey electivities for each instar of *Chaoborus* based on numerical abundance

Prey	<i>Chaoborus</i> instar			
	I	II	III	IV
<i>Keratella</i>	2.12	1.41	1.08	0.83
<i>Brachionus calyciflorus</i>	0.20	2.06	1.20	0.47
<i>B. havanaensis</i>		0.74	0.06	0.05
<i>Moina</i>			2.31 <sup>a</sup>	1.12 <sup>a</sup>
<i>Ceriodaphnia</i>			1.37	1.22
<i>Diaphanosoma</i>			0.54	2.06 <sup>a</sup>
<i>Mesocyclops decipiens</i>				
Female			3.13	4.60
Male			0.70	0.55
C4-C5			1.89	4.11
C1-C3			0.40	0.50
Nauplius			0.43	0.55
<i>Notodiaptomus deveyorum</i>				
Female				1.38
Male				2.62
C4-C5				0.59
C1-C3				0.37
Nauplius				

<sup>a</sup>Single value.

species in Lake Valencia. Thus prey size provided no refuge from predation. Electivities changed as the instars grew, but electivities were not related consistently to the size of the prey. The smallest *Chaoborus* larvae could not consume the largest herbivores, but all instars of *Chaoborus* fed on the smallest prey. Electivities for small prey declined as the larvae grew. Electivities for large stages of copepods were about the same as electivities for cladocerans. This is surprising because electivities for cladocerans other than *Daphnia* are usually higher than for copepods when the two are available concurrently as food to *Chaoborus* (Lewis, 1977). However, the cladocerans were so often absent during the study that the electivities could easily be underestimated, especially if *Chaoborus* were capable of behavioral focusing on abundant prey.

Vulnerabilities of the developmental stages differed for the two species of copepods. Electivities for *Mesocyclops* nauplii were very low and *Notodiaptomus* nauplii were not consumed at all (cf. Lewis, 1977, 1979). For later stages of *Mesocyclops* vulnerability increased with size, while the vulnerability of *Notodiaptomus* remained low until the adult stage.

Herbivores for which *Chaoborus* had a low electivity essentially escaped predation. In this category were the subadult stages of *Notodiaptomus*, the naupliar stages of *Mesocyclops*, and *Diaphanosoma*. The low vulnerability of the early copepod stages must be related to their ability to escape detection because they fall within the size range of prey taken by *Chaoborus* and because they coexisted in abundance with *Chaoborus*. *Chaoborus* detects prey by mechanoreceptors (Horridge, 1966). The size, shape and swimming speed of an organism

determine the nature of its hydrodynamic signal (Strickler and Twombly, 1975). Cyclopoid nauplii, and probably calanoid nauplii as well, avoid detection by moving infrequently over short distances (Gerritsen, 1978). Furthermore, the swimming speed of cyclopoid copepodites and adults increases with size (Gerritsen, 1978). Thus if *Chaoborus* is 'Reynolds number selective', the larger copepods will be preferred prey (Gerritsen, 1978). Our data for *Mesocyclops* support this expectation.

Data for *Notodiaptomus* suggest very low vulnerability to predation prior to the adult stage, despite the fact that at each developmental stage it was substantially larger than *Mesocyclops*. Mechanisms of locomotion may explain these differences in vulnerability. Unlike cyclopoid copepodids, diaptomid copepodids can move by means of the head appendages involved in feeding, so that the organism can maintain position in the water column or sustain a very slow, even speed (Cannon, 1928; Lowndes, 1935). Diaptomids are not compelled to use the antennae or natatory legs that account for the hopping movement characteristic of cyclopoids. Wright and O'Brien (1984) have shown that intermittent movement makes calanoids less conspicuous to visual predators. Adult calanoids, unlike subadult stages, move rapidly in mate location (Watras, 1983). This behavioral change may explain why the adults were eaten by *Chaoborus*, whereas the subadult stages were not. The poor utilization by *Chaoborus* of subadult calanoids as compared to cyclopoids may provide part of the explanation for the statistical fragmentation of intraspecific affinities shown for calanoids in Table V.

The rotifer *B.havanaensis* is larger than *Keratella* and smaller than *B.calyciflorus*. Its general swimming pattern is not distinctive, yet it was apparently much less vulnerable than *Keratella* or *B.calyciflorus* to predation by *Chaoborus*. It seems unlikely that the spines on the lorica of *B.havanaensis* provide any protection because the organism, even with the spines, is small. This rotifer may have a defensive reaction that is not found in the other rotifers, or may simply create less hydrodynamic disturbance than *Keratella* by swimming more slowly. We have observed that, when placed in crowded conditions where encounters with other organisms were frequent, *B.havanaensis* was soon concentrated at the bottom of the container while the other rotifers showed no such tendency. On this basis, we suspect that the disturbance produced by a *Chaoborus* strike causes *B.havanaensis* to stop moving and thus to sink. The success of such a defense mechanism rests on the assumption that the strike efficiency of *Chaoborus* is <100%, or that *B.havanaensis* senses the presence of *Chaoborus* before it strikes. Moore and Gilbert (1987) have shown that strike efficiencies (probability of ingestion after attack) are considerably less than 100% for *Chaoborus* instars I-III.

### Feeding

Infante's (1978, 1981) detailed investigation of the diets of herbivores in Lake Valencia revealed considerable similarity among the major species, although her method does not provide information on soft-bodied food taxa such as the

cryptomonads. The blue-green algae, which dominated the phytoplankton in Lake Valencia, appeared commonly in the guts of all major herbivores, but for the most part were not digested. The two copepod species showed 74% similarity in diet during the naupliar stages and 98% similarity in later developmental stages. Less detailed comparisons available for diets of the other herbivores show a high degree of similarity in diet (Table VIII). Consequently, differences in nutrition may be explained by differential ability to assimilate common food taxa or by differential use of foods that were not easily detected in gut analysis.

If the herbivores had specific food needs that were often unmet, it should be possible to detect relationships between abundance trends of herbivores and the abundance of their phytoplankton foods. The initial hypothesis is that the change in abundance of herbivore categories over the interval between two sampling dates is influenced by the abundance of important food types at the beginning of the interval. Herbivore categories that we used in testing this proposition were identical to those employed in the  $\Delta N$  matrix.

Phytoplankton food value could be related to taxonomy, size, shape or less easily quantifiable factors. In order to include all reasonable possibilities, we performed six sets of correlation analyses. Phytoplankton species were taken individually and, in addition, in groups defined by taxonomy (division level), growth form within taxonomic groups, greatest axial linear dimension (GALD: Lewis, 1976), second greatest axial linear dimension (SGALD) and GALD  $\times$  SGALD. In no instance did we find more significant correlations than would be expected by chance.

*Chaoborus* abundance might have obscured the relationship between phytoplankton and herbivores. To investigate this possibility we used partial correlation analysis, but again found no more significant relationships than would be expected by chance. Thus true relationships were either masked by an unknown factor or our simple methods for grouping the phytoplankton did not correspond to the basis for food selection by herbivores.

## Discussion

The low species richness of limnetic zooplankton communities at low latitudes contrasts with most latitudinal trends in terrestrial plants and animals (Pianka, 1966). In Lake Valencia the relatively few species that comprised the bulk of the herbivore community were found in virtually all samples. However, instead of zooplankton that are specialists for a particular niche, the major herbivore species in Lake Valencia appear to be eurytopic, as indicated by their broad geographic distributions (Table IX). Absence of specialists would make open-water zooplankton communities different from many tropical communities that contain more species than counterparts in the temperate zone.

The lack of specialization was particularly evident in the diet of the major herbivores in Lake Valencia. Our statistical analysis provided no evidence of strong selectivity for or aversion to particular algal species on the part of any herbivore. Moreover, dietary analyses showed surprising similarity in food items

Table VIII. Ranking of algal species by frequency of occurrence within diet of major herbivore species from Infante (1978)

	<i>Notodiaptomus</i>	<i>Mesocyclops</i>	<i>Ceriodaphnia</i>	<i>Moira</i>	<i>Diaphanosoma</i>	<i>B. calyciflorus</i>
Cyanophyta						
<i>Microcystis</i> sp.	6.5	4.5	5	5		4
<i>Lynghya limnetica</i>	6.5		6.5			
<i>Oscillatoria limnetica</i>						
<i>Anabaena</i> sp.						
<i>Spirulina</i> sp.						
<i>Gomphosphaeria</i> sp.						
<i>Dactylococcopsis</i> sp.						
Chlorophyta						
<i>Oocystis</i> sp.	3	2	1	1	1	3
<i>Tetradron minimum</i>	5	4.5	3	4	3	6.5
<i>Cosmarium</i> sp.	8		8.5			5
<i>Scenedesmus</i> spp.	9		8.5	9	5.5	
<i>Selenastrum gracile</i>						
<i>Treubaria triappendiculata</i>						
<i>Crucigenia rectangularis</i>						
<i>Kirchneriella lunaris</i>						
<i>Coelastrum</i> sp.						
<i>Chodatella ciliata</i>						
<i>Staurastrum</i> sp.						
Bacillariophyta						
<i>Nitzschia amphibia</i>	2	1	2	2	2	2
<i>N.palea</i>	4	7	4	6	5.5	6.5
<i>Cyclotella meneghiniana</i>	1	3	6.5	3	4	1

A rank of 1 is assigned to the species occurring most often in the diet; ranks were not assigned to algal species occurring in <5% of organisms.

**Table IX.** Geographical distribution of major zooplankton herbivore species found in Lake Valencia

Species	Geographical distribution	Source
<i>Notodiaptomus deveyorum</i>	Northern South America	Dussart (1984)
<i>Mesocyclops decipiens</i>	Tropical: Africa and South America	Einsle (1970), Dussart (1984)
<i>Moina micrura</i>	All continents except Antarctica	Goulden (1968)
<i>Diaphanosoma birgei</i>	North and South America	Korinek (1981)
<i>Ceriodaphnia cornuta</i>	Pantropical	Dussart <i>et al.</i> (1984)
<i>Keratella americana</i>	North and South America	Koste (1978)
<i>Brachionus calyciflorus</i>	Cosmopolitan	Koste (1978)
<i>Brachionus havanaensis</i>	North and South America	Ahlstrom (1940), Koste (1978)

among the major herbivores. There was no obvious dietary specialization within the herbivore community of Lake Valencia, even though it could be advantageous given the abundance of algae that are not readily digested (i.e. with gelatinous sheaths; Porter, 1973, 1975). Furthermore, specialization would seem feasible in view of the great abundance and diversity of phytoplankton in Lake Valencia (Lewis and Riehl, 1982; Saunders and Lewis, 1988).

Predation appeared to play a very prominent role in shaping the herbivore community, in part because all common herbivore species in Lake Valencia were subject to predation by *Chaoborus*. In addition, predation by *Chaoborus* was sufficiently intense to remove all herbivore production (Saunders and Lewis, 1988). Three of the more successful herbivores (the two copepod species and *B.havanaensis*) withstood predation by minimizing vulnerability. *Brachionus calyciflorus* was able to offset predation with high reproductive output (Saunders and Lewis, 1988). The other species (*Keratella* and the cladocerans) were only marginally successful in that they became abundant in pulses that occurred when predation pressure was low.

Seasonality was a conspicuous feature of zooplankton dynamics in Lake Valencia. The extent of seasonal variation for the herbivore community could be characterized simply by the ratio of maximum biomass to minimum biomass, which was 142 for the period of study and ranged from 13 to 99 for individual years. A ratio of <10 has been found in other large tropical lakes (Chad: Saint-Jean, 1983; George: Burgis, 1974; Lanao: Lewis, 1979; Titicaca: Widmer *et al.*, 1975). Higher ratios appear typical of zooplankton communities in the temperate zone; values >10 hold for IBP lakes from the temperate zone (Morgan *et al.*, 1980, Figure 6.2). Reduced seasonality may also be characteristic of arctic and alpine lakes (Morgan *et al.*, 1980).

The amplitude of seasonal fluctuations in biomass in Lake Valencia is extremely high in comparison to that of the few other tropical lakes that have been studied and is also high compared to that of many temperate lakes. The basis for seasonality in Lake Valencia and other tropical lakes may be different than it is for lakes in the temperate zone, however. In temperate lakes, time and temperature are tightly coupled, and temperature can exert a powerful influence on community composition (e.g. Makarewicz and Likens, 1975). Seasonal variation of temperature in Lake Valencia was so slight, however, that there was virtually no potential for direct effects on herbivore community composition.

The abiotic factors showing the greatest seasonal variation in Lake Valencia were associated with vertical structure in the water column, even though temperature variations were relatively small. Chemical conditions differed markedly for the mixing and stratification seasons, especially for nutrients. Seasonal variations in nitrogen concentrations probably had indirect effects on herbivores by regulating the quality of food resources (Saunders and Lewis, 1988).

Another strong seasonal factor affecting the herbivore community was variation over time in the strength of predation by *Chaoborus* (Saunders and Lewis, 1988). Predation pressure by *Chaoborus* on the herbivores was strongest during the stratification season; this explains the seasonal suppression of *Keratella* and the cladocerans. Predation pressure was lower during the circulation season because mortality diminished the *Chaoborus* population by two mechanisms. Chemical conditions associated with overturn may cause catastrophic mortality in the *Chaoborus* population (Infante *et al.*, 1979a), and circulation eliminates the hypolimnetic refuge that protects *Chaoborus* from fish predation (Cressa, 1985).

Rates of biological processes are typically temperature-dependent and thus would be high throughout the year in tropical environments. Productivity is an ecologically useful composite expression of several rates. Brylinsky (1980) found strong correlations between the production of herbivorous zooplankton and phytoplankton production ( $r = 0.69$ ), and between herbivore production and phytoplankton biomass ( $r = 0.46$ ). Either trend would suggest that herbivore production in Lake Valencia should be very high. Furthermore, because primary production is inversely related to latitude (Brylinsky, 1980), secondary production should be higher in the tropics than in the temperate zone. However, this is by no means clear because production has been estimated for so few tropical lakes.

The annual herbivore production of Lake Valencia is about the same as that of Lake Flosek, the most productive of the IBP lakes (tabulated by Morgan *et al.*, 1980; see also Brylinsky, 1980), despite the shorter growing season of temperate lakes (Table X). Daily production of Lake Valencia is lower than that of some of the most productive temperate lakes. Nevertheless, production in Lake Valencia greatly exceeds the median production for IBP lakes of the temperate zone (Table X).

Table X offers a comparison of Lake Valencia with other tropical lakes. Lake George, Uganda, is very shallow (mean depth = 2.1 m) and has very high algal standing stock. Copepods dominate the biomass and production; there is no large rotifer component. Lake Lanao, Philippines, which is deeper than Valencia, is located at almost the same latitude as Valencia and has a very similar zooplankton community. Lake Lanao is considerably less eutrophic than Lake Valencia, and this is reflected in the lower zooplankton herbivore production. Because production in both lakes is concentrated in the copepods, the P/B ratios are nearly equal. Two time periods are presented for Lake Nakuru, Kenya, to illustrate the importance of a major shift in community composition. When a copepod, *Lovenula africana*, dominated herbivore

Table X. Herbivore biomass, production, and the P/B ratio in selected lakes

Lake	Latitude	Mean depth (m)	Biomass (gC m <sup>-2</sup> )	Production (gC m <sup>-2</sup> year <sup>-1</sup> )	P/B annual	Source
George <sup>a</sup>	0'	2.1	0.249	7.2	28.7	Burgis (1974)
Nakuru 1972-1973	0'	2.2	1.592	53.2	33.4	Vareschi and Jacobs (1984)
Nakuru 1975-1976	0'	2.2	1.135	136.0	119.9	Vareschi and Jacobs (1984)
Lanao	8'N	60	0.668	27.3	41.0	Lewis (1979)
Valencia	10'N	18	1.025	39.1	38.1	Saunders and Lewis (1988)
Chad	12-14'N	4.0	0.38	26.5	69.7	Carmouze <i>et al.</i> (1983)
Sibaya <sup>b</sup>	27'S	13	0.033	1.3	40.6	Hart and Allanson (1975)
Flosek (IBP max) <sup>c</sup>	54'N	3.0	1.45	41.9	28.9	Kajak <i>et al.</i> (1972)
Naroch (IBP median) <sup>c</sup>	54'N	9.0	0.340	5.5	16.3	Winberg <i>et al.</i> (1972)

<sup>a</sup> Includes only *Thermocyclops hyalinus*, the main producer.

<sup>b</sup> Includes only *Pseudodiaptomus hessei*, the main producer.

<sup>c</sup> Based on growing season, not entire year.

biomass in 1972–1973 the P/B ratio was similar to that of Lake George, where a copepod also dominated. In 1975–1976 *Lovenula* was absent and rotifers dominated. Despite a slight decline in biomass, production and the resultant P/B ratio in 1975–1976 appear to be the highest ever recorded for a large lake.

Biomass turnover rates (P/B ratios) may be more useful than production as a means of comparing herbivore communities from different latitudes. Brylinsky (1980) found a significant correlation ( $r = -0.37$ ;  $P = 0.05$ ) between the P/B ratio for herbivorous zooplankton and latitude. The least productive tropical lake (George) had a P/B equal to that of the most productive temperate lake (Flosek), and all other tropical lakes had higher P/B ratios. Thus biomass turns over more rapidly in tropical lakes.

## Conclusions

The zooplankton community of Lake Valencia is simple in species composition, highly seasonal and capable of rapid turnover of biomass. Lake Valencia confirms the growing impression that zooplankton communities in tropical lakes contain a relatively small number of species despite the fact that many other types of biological communities tend to be more diverse in the tropics.

Lake Valencia also supports the impression that tropical lakes can be very seasonal in zooplankton composition and abundance. Lake Valencia, which is perhaps the most seasonal of the tropical lakes that have been studied, may offer insights regarding the basis of seasonality. Chemical changes associated with mixing events seem to be of extraordinary importance in Lake Valencia because they may result in catastrophic zooplankton mortality on a seasonal basis.

Tropical lakes are not necessarily more productive than temperate lakes, but the production per unit biomass probably is higher. Absolute rate of production is tied to biomass, which probably does not vary predictably with latitude. The speed of biological events in the tropics is best seen by the rate at which biomass turns over. Consistently high temperatures, which extend the growing season over the entire year, result in a rapid turnover of biomass. From an ecological perspective, tropical zooplankton communities are distinctive in their consistently high capacity for the replacement of biomass. This capacity leads to rapid successional changes and quick responses to environmental change.

## Acknowledgements

The Fundacion Eugenio Mendoza provided valuable logistical support. Financial support was provided by National Science Foundation grants DEB 76-04300, DEB78-05324 and DEB 80-03883 to WML, and by University of Colorado Graduate School Fellowships to JFS.

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Received on December 1, 1987; accepted on May 27, 1988