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DYNAMICS AND CONTROL MECHANISMS IN A TROPICAL ZOOPLANKTON COMMUNITY (LAKE VALENCIA, VENEZUELA)¹

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Abstract. The dynamics of zooplankton herbivores in Lake Valencia, Venezuela, were studied over a 5-yr interval. Lake Valencia is a large, warm-monomictic, eutrophic lake. Copepods were the dominant group; rotifers were more abundant than the cladocerans, which were not present in all years. Variation between years in herbivore biomass bore no statistical relationship to patterns in algal biomass. The average annual dry mass production of the herbivores was high ($7.0 \mu\text{g} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$), but less than expected given the high primary productivity of the lake. The annual ratios of production to biomass for individual species were well below the maxima expected for steady growth, and thus imply growth suppression.

Feeding capacity of *Chaoborus*, the principal primary carnivore, exceeded herbivore production for 66% of the sampling dates. Annual overturn broke the coupling between predator and prey by causing extensive mortality in both herbivores and carnivores; herbivores recovered from this suppression more rapidly than carnivores.

Herbivores followed three basic strategies for coexistence with their predators in Lake Valencia: (1) two *Brachionus* species were able to match predation losses by reproductive output; (2) the copepods, which experienced intense predation pressure as adults, were able to sustain the high losses because the adult stage was subsidized by recruitment from earlier, less vulnerable developmental stages; (3) *Keratella* and the cladocerans were opportunistic in that they became abundant only in response to a decline in the predator population. The opportunistic species were most abundant during the mixing season, which was the period of minimum abundance for *Chaoborus*.

Predation strongly influenced the herbivore populations, but population data indicate that inadequate food resources also played a role. Growth suppression was the result of qualitative rather than quantitative inadequacy in the algal food base. The intensity of control by the two factors was strongly affected by abiotic factors associated with mixing events. Partial mixing provided brief respite from growth suppression for certain species (typically rotifers), but did not alter predation pressure. Annual overturn resulted in improvement of food quality, but because mortality of herbivores coincided with relaxation of predation, the herbivores were delayed in exploiting qualitative improvements in the food resources. Periods of simultaneous release from growth suppression and predation were infrequent and brief. Herbivores were thus controlled simultaneously by predation and quality of food resource.

Key words: aquatic productivity; community structure; Lake Valencia; predation; tropical limnology; zooplankton; zooplankton nutrition.

INTRODUCTION

Zooplankton herbivores in lakes may be controlled by nutrition or by predation. Food resources, which can be inadequate in quantity or in quality, have seemed to be the primary control on herbivores in some lakes (e.g., Nauwerck 1963, Burgis et al. 1973, Horn 1981). For other lakes, predation has appeared to be of greatest importance in suppressing and thus controlling herbivore populations (e.g., Hall 1964, Wright 1965, Cummins et al. 1969, Dodson 1972, Fedorenko 1975, Kajak and Rybak 1979, Zaret 1980, Greene 1983). Different conclusions about the identity of the major

control mechanisms may partly reflect true differences among lakes. There is a tendency, however, for interpretations to emphasize the control factors that can be best quantified, and for nutrition and predation to be studied at different times by different investigators.

Food and predation need not operate dichotomously; they may control planktonic herbivores simultaneously or alternately (e.g., Herzig et al. 1980, Tessier 1986). In fact, it is possible to view plankton systems as having two distinct sets of control pathways that converge on the herbivores (Lewis 1979). The first set of control pathways originates with the abiotic factors that cause seasonal and nonseasonal changes in water column stability and mixing. Mixing and stability affect the phytoplankton, which in turn control herbivore

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populations through changes in food quality or quantity. A second set of control pathways originates at the top trophic levels, which determine the mortality and thus the composition and density of zooplankton herbivores through selective predation. The herbivore trophic level absorbs and integrates these two sets of influences originating above and below it on the trophic pyramid. A similar concept has been elaborated by McQueen et al. (1986) to describe the regulation of biomass at different trophic levels in freshwater pelagic ecosystems. Applied to planktonic herbivores, their model predicts that maximum biomass is regulated by food availability, and that realized biomass is inversely related to planktivore biomass. Variations in zooplankton herbivore abundance would thus typically be difficult to explain from the viewpoint of food or predation alone.

Control mechanisms affecting herbivore populations can be demonstrated by intensive studies of individual lakes. Such studies should extend over at least a year, because control mechanisms may alternate seasonally or irregularly. Our study of Lake Valencia, Venezuela, draws on a 5-yr data base for zooplankton and for variables related to the regulation of the zooplankton community. Given that the influences of food and predation can be resolved from the data, the 5-yr span will provide a reasonable time interval over which to measure the relative importance of these two factors. Furthermore, because it is tropical, Lake Valencia may offer some special advantages in causal analysis of zooplankton abundance patterns; the organisms are not so much affected by seasonal abiotic factors of the type underlying annual cycles in lakes of the temperate zone. Although the emphasis here is on general questions related to the regulation of zooplankton herbivores, documentation of zooplankton dynamics is also of interest in view of the relatively poor background of information on tropical lakes.

DESCRIPTION OF LAKE VALENCIA

Lake Valencia occupies a graben in the Aragua Valley of north-central Venezuela ($10^{\circ}10' N$, $68^{\circ}8' W$). The lake is probably $>100,000$ yr old, although it has been partially or completely dry several times. The most recent desiccation episode ended $\approx 10,000$ BP (Schubert 1979, Bradbury et al. 1981, Lewis and Weibezahn 1981). Lake Valencia is presently endorheic; there has not been an outflow since the early 18th century (Bockh 1972).

Major physical and chemical features of Lake Valencia have been summarized by Lewis and Weibezahn (1976). During the study period (1977–1981), the lake had a maximum depth of 37 m, a mean depth of 18 m, and a surface area of 350 km². These morphometric features change slightly from year to year and season to season due to fluctuations in water level (Lewis 1983a).

Lake Valencia was probably mesotrophic in its nat-

ural condition (Lewis and Weibezahn 1983). For some time, and especially over the last two decades, Lake Valencia has experienced considerable eutrophication under the influence of sewage effluents entering the lake from the cities in the watershed. In 1977 and 1978, phosphorus loading averaged $2.4 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, and, due to increased sewage diversion, loading increased in 1979–1981 to an average of $3.3 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. The nitrogen loadings for the same two time intervals were 11.2 and $10.3 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, respectively. Studies of nutrient chemistry and enrichment experiments with the phytoplankton have established that the phytoplankton community is strongly limited by nitrogen (Lewis 1983b).

Lake Valencia, like most tropical lakes, shows pronounced seasonal cycles in physical, chemical, and biological variables. Seasonal cycles are principally explained by changes in the stability of the water column. The year is divided into a circulation season and a stratification season, and Lake Valencia thus can be classified as warm monomictic (Lewis 1983c). Circulation spans the dry season (typically November through April), when wind strength is greatest and nocturnal air temperatures are lowest (Lewis 1983d, 1984). Over the course of the circulation season, the water temperature declines from a maximum of $\approx 27.3^{\circ}$ to a minimum of $\approx 24.9^{\circ}\text{C}$. The water column does not mix continuously; it can be stratified for periods of one or more wk during the circulation season. Stable stratification of the water column begins typically in April, and complete mixing of the water column does not occur again until the onset of the next mixing season in November or December. The onset of complete mixing can be a very striking event during which fish and zooplankton are killed by anoxia or by chemically reduced solutes from deep water (Infante et al. 1979). The lake is typically anoxic below 20 m during the stratification season.

As is typical of tropical, warm-monomictic lakes (Lewis 1983c), the upper mixed layer of Lake Valencia is quite variable in thickness. These variations in thickness, which are controlled by changes in weather during the stratification season, have important consequences for the plankton. A combination of calm weather and clear skies persisting for days or weeks often leads to net heat gain. Heat gain under these conditions is likely to be poorly distributed through the mixed layer for three reasons: (1) the mixed layer is often thicker than it would be in a temperate lake, (2) the stability that results from small heat gain is especially high at the high temperatures in tropical lakes, and (3) in calm weather, the energy causing vertical mixing is minimal. Thus a temporary thermocline forms nearer to the surface than the previous thermocline. Oxygen depletion and other chemical evidence of decomposition then occur below the new thermocline. With the onset of windy weather and cloudy skies, this upper temporary thermocline is disrupted and the mixed layer is thus

thickened. Such a thickening of the mixed layer that does not lead to complete mixing has been referred to as "atelmixis" (Lewis 1973). Atelmixis relieves nutrient depletion in phytoplankton populations because it allows return of sedimented nutrients to the upper mixed layer prior to the end of the stratification season (Lewis 1974).

Alternation of calm, sunny weather with cloudy, windy weather causes frequent changes of thickness in the mixed layer of Lake Valencia. The primary producers respond to repeated incidents of enrichment followed by nutrient depletion of uncertain duration. The seasonal cycle produces predictable changes of importance to the herbivores, but nonseasonal weather patterns also produce significant, unpredictable changes.

METHODS

Routine collections

Plankton were sampled weekly (1977–1978) or bi-weekly (1979–1981) at a station located over the deepest part of the lake. During the first 2 yr, zooplankton samples were taken with a flexible integrating sampler 5 m long and 10 cm in diameter (40 L; Lewis and Saunders 1979) from the entire water column in a series of seven vertically contiguous segments. For the remainder of the study, two zooplankton samples were taken on each date with a flexible integrating sampler 7.5 cm in diameter that extended over the entire water column (≈ 160 L; Unger 1985). Each sampler had a capture efficiency of essentially 100%, even for large, fast-swimming zooplankton (Lewis and Saunders 1979). Each sample was filtered through a net of 55- μ m mesh and the contents were preserved in Lugol's solution. All quantitative samples were taken within a span of 30–45 min, usually prior to 0800. A concurrent vertical series of seven samples was taken with a 5-m rigid sampler (Lewis and Saunders 1979) for phytoplankton and water chemistry.

In the laboratory, the zooplankton subsamples were typically counted until 100 or more individuals of the most common species or developmental stage had been enumerated, or until the entire sample had been examined. Abundance and production estimates are based on averages for the vertical series of seven samples or the two samples spanning the entire water column. Details of the phytoplankton counting methods are given elsewhere (Lewis 1986).

Counting effort differed slightly for rotifers and crustaceans, and for the two different sampling protocols. Given the expected conformance of replicate counts to a Poisson distribution, a coefficient of variation (cv: $100 s/\bar{X}$) of 10% is reached with a density of 10.6 organisms/L for rotifers and 7.6 organisms/L for crustaceans; a 20% cv applies to densities of 2.7 organisms/L for rotifers and 1.9 organisms/L for crustaceans. For the six most common species, the average density (summing over all life history stages) is suffi-

cient to place the coefficient of variation well below 10% for individual abundance estimates.

Mean densities for annual and for seasonal time spans were based on 5 to 51 sampling dates. The standard error (s/\sqrt{n}) for annual mean abundances was $<5\%$ of the mean for all stages of the seven most common species. The same was true for mean abundances over the stratification season except for *Notodiaptomus* C1–C4, for which the standard errors were between 5 and 10% of the mean. For mean abundances during circulation seasons, the standard error was between 5 and 10% of the mean for *Notodiaptomus* C1–C6 and for *Mesocyclops* C5 and adult females; for all other stages of the seven most common species, the standard error was $<5\%$ of the mean. All *Chaoborus brasiliensis* larvae were counted in each sample to eliminate variation due to subsampling.

Estimates of biomass for individual zooplankton were based on calculations of volume (e.g., Bottrell et al. 1976), and on the assumption that the density of the organism is approximately that of water. Dry mass is assumed to be 11% of the wet body mass (Sitaramaiah 1967). Other conversions are as follows: 0.44 g of carbon = 1.0 g dry mass; 1.0 g of carbon = 40 kJ; 1 g of carbon = 10 kcal. *Chaoborus* mass is based on the length–mass ratios obtained by Cressa and Lewis (1984).

Patchiness as a source of sampling error

A study was made of horizontal spatial variation in the vicinity of the reference station on 28 January 1978. Samples were taken at five stations in addition to the reference station. Stations 1 to 4 were equidistant from one another on the circumference of a circle with a radius of 400 m centered at the reference station. Station 5 was 1 km from the reference station. At each of the six stations, three consecutive vertical tow net samples (0–35 m, 75- μ m mesh, 30 cm mouth diameter) were taken between 2045 and 2345 and preserved in Lugol's solution. Three kinds of organisms were selected for comparison: *Mesocyclops decipiens* males, *Brachionus calyciflorus* adults, and *Chaoborus* larvae. Three subsamples of *Mesocyclops* and *Chaoborus* and four subsamples of *Brachionus* were counted from each sample. For each taxon, a nested analysis of variance (ANOVA) was used to test the hypothesis that there was no significant difference in mean abundance among stations.

The six stations did not differ significantly in abundance for *Brachionus* or *Mesocyclops*. *Chaoborus* was significantly patchy, but the stations still fell within $\pm 30\%$ of the mean. Application of the Least Significant Range procedure showed that, for *Chaoborus*, the stations fell into two groups that were not spatially contiguous; the groups represented random variation between stations rather than discrete patches. The results indicate that the reference station adequately represented the central lake area. Subsequent studies of patchiness have confirmed this (Cressa 1985).

The coefficient of variation due to spatial heterogeneity was 18% for *Mesocyclops*, 45% for *Brachionus*, and 21% for *Chaoborus*. An empirical relationship developed by Downing et al. (1987; Eq. 4), which describes sampling variance as a function of mean organismic density and sample volume, produces variance estimates close to those we measured. Therefore, we used their equation to estimate the patchiness component of variance for seasonal and annual abundance means. Standard errors were computed as described above for subsampling. For the six common species, including the individual copepod stages, the standard error as a percentage of mean density was <6% for annual means, 3–7% for stratification season means, and 5–11% for circulation season means.

Zooplankton development

Problems in estimating zooplankton development times can be caused by variations in temperature (Bottrell et al. 1976, Prepas and Rigler 1978). In Lake Valencia, however, temperature varied so little with depth or with season (25°–28°C) that its effect could be ignored.

Duration of egg development for copepods was determined by the method of Edmondson (1960, 1965), which is based on average rate of decline in an egg population to which no eggs are being added. Because of diel periodicity in egg deposition and eclosion (Saunders 1980), estimation of egg development times for rotifer populations required direct examination of individuals. The Cladocera were not abundant for most of the study; egg development times were therefore approximated from the literature.

Development times of the copepod naupliar stages (N1–N6) were determined in two ways. For *Notodiaptomus*, newly eclosed individuals were maintained in the laboratory with daily changes of lake water until they had reached the first copepodite stage. For *M. decipiens*, individuals of the first two naupliar stages were isolated in clear plastic enclosures (diameter 4 cm, length 5 m) suspended in the lake. Two tubes were removed on each of days 2, 4, and 7 for determination of developmental status of the copepods. Duration of N1 was determined in the laboratory in conjunction with egg development studies.

Development times for some groups of stages of *Notodiaptomus* and *M. decipiens* were estimated by the cohort procedure of Lewis (1979), which is based on that of Rigler and Cooley (1974). Hairston and Twombly (1985) have identified errors inherent in the use of this type of cohort analysis. However, over a wide range of conditions, so long as there are no abrupt changes in survivorship from one stage to the next and survival exceeds 0.5, errors in the estimation of development time will remain relatively small ($\pm 10\%$; Saunders and Lewis 1987). Thus for present purposes the method is robust to deviations from underlying assumptions. Moreover, we have validated results of

cohort analyses for most stages with enclosure studies or laboratory work.

Calculation of production

For rotifers and cladocerans, the production rate, PR, can be calculated as the product of population biomass, B , and growth rate, g (Kimmerer 1987). Population biomass included eggs and adults; g was assumed to be constant over an enumerated stage. Our estimates of PR were based on the assumption that g is closely approximated by the birthrate, b , which was determined by the equation of Paloheimo (1974). In the absence of mortality, b will differ from g because average mass per individual will change with changing population structure, but the difference will usually be small.

Because the value of b is very important to the calculation of PR, it must be estimated with the greatest possible degree of certainty. If N_e (egg density) or N_a (adult density) is very small, the uncertainty due to counting, which is compounded in the calculation of b , becomes unacceptably large. Consequently, a screening procedure was used prior to the calculation of b for each sampling date. If for a given date the standard deviation exceeded 20% of the mean for either N_e or N_a , b was assigned an average value based on all dates where the screening criterion was not exceeded.

The methods typically used for estimating rotifer production assume that the deposition of eggs is distributed uniformly over time. In Lake Valencia, this was not the case (Saunders 1980). Because diel patterns of reproduction in rotifers have rarely been documented, little attention has been given to the effect that such patterns have on calculations of production (Magnien and Gilbert 1983). However, if egg deposition does show diel patterns, the proper choice of collection time can eliminate the need for special computations such as those suggested by Dorazio (1986). In Lake Valencia, egg deposition and eclosion occurred for only portions of each day. Sampling did not coincide with deposition or eclosion, when the egg ratio upon which b is based would have been unstable.

For copepods, we used a generalized formula for calculating production (Edmondson and Winberg 1971, Winberg 1971):

$$P_i = N_i W_i / D_i$$

where i = stage of development

P_i = production of dry mass at stage i (in micrograms per litre per day)

N_i = number per litre of stage i

W_i = change in individual dry mass over stage i (micrograms)

D_i = duration of development for stage i (days)

This has been called the incremental summation method (Rigler and Downing 1984, Kimmerer 1987).

Production of stages C4 and C5 for *M. decipiens* is

accounted for entirely by growth of females because males increase in biomass little or not at all beyond C4. Examination of numerous samples showed that the sex ratio in C5 was $\approx 1:1$, and we assumed that the sex ratio in C4 was also 1:1.

Chaoborus crop analysis

The diet of *Chaoborus* was determined by dissection of crops (Swift and Fedorenko 1973). The use of Lugol's solution as a preservative avoided the problem of crop eversion, which is common when formalin is used (Kajak and Ranke-Rybicka 1970, Lewis 1975). Contents were examined at 50–100 \times so that small food items would not be overlooked. Loricated rotifers and the chitinous remains of even the smallest crustaceans were readily identified at this magnification. Occasional searches at higher magnification were made to check for the remains of illoricate rotifers. These remains, which would include trophi, "paddles" (*Polyarthra*), or bristles (*Hexarthra*), were not observed in the crops.

Loss rates

A model similar to that described by Lewis (1979; see also Lynch 1983) was designed for computer estimation of loss rates in the copepods. We designated the output of this model as a loss rate rather than a mortality rate, however, because the model cannot separate suppression of growth rates from true mortality. However, as explained in the Results section, separation of these two types of losses was possible because predation loss could be estimated from predator abundances and feeding electivities.

Field data gave the density of each taxon on all sampling dates. Each interval between samples was divided into short time segments (0.1 d) and it was assumed that the changes in density over the sampling interval were linear. The expected change in density was computed over each 0.1-d segment. From the development times for each life history stage, the expected recruitment into each stage and loss by maturation from each stage was determined for each 0.1-d segment. For a given stage, any change in abundance not accounted for by the balance of recruitment and maturation was designated as loss. Loss was summed over all 0.1-d segments within each sampling interval to produce the total loss-rate estimate for the sampling interval.

Because random error is associated with the estimates of abundances, it is possible when the true loss rates are low that the estimated loss rate will be negative. This is expected due to random variation. Negative values were thus averaged with other values to avoid bias in the averages. Under the conditions of this study, the variance due to random error of the total loss rate estimates for copepods, for example, would have been less than three times the variance of the abundance estimates.

Estimation of loss rates for cladocerans and rotifers

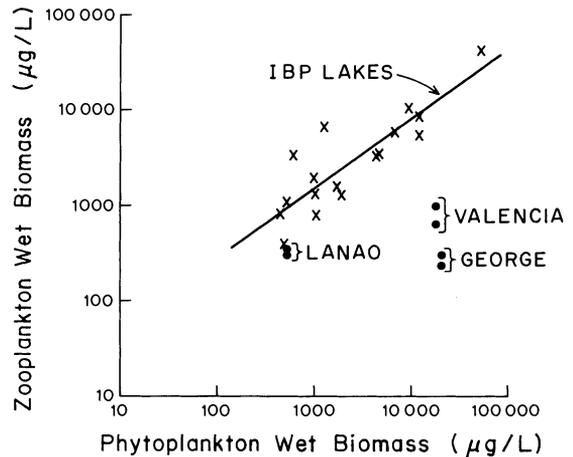


FIG. 1. Relationship of zooplankton to phytoplankton biomass in a selection of Temperate Zone International Biological Program (IBP) lakes (from McCauley and Kalff 1981) as compared with tropical lakes George, Lanao, and Valencia. The upper point for tropical lakes includes carnivorous *Chaoborus*, and the lower point includes only herbivores.

was patterned after the procedure outlined for copepods, except that only two stages were recognized: free-swimming and egg. Recruitment was defined as the hatching rate of eggs, which was calculated from field data according to screening criteria similar to those described for the calculation of production. When densities were very low, recruitment was calculated with an average egg ratio based on all dates where the screening criterion was not exceeded.

Instantaneous loss rates were calculated from the finite loss rates over each 0.1-d segment as follows (Poole 1974):

$$d = \delta r / (\lambda - 1)$$

where d = instantaneous loss rate (d^{-1}), δ = finite loss rate (individuals/d), r = instantaneous rate of increase (d^{-1}), $\lambda = N_{t+1}/N_t$.

RESULTS

Biomass

The total herbivore standing stock was not especially high in comparison to that of other lakes, even though Lake Valencia had high algal standing stock. To illustrate this point, Fig. 1 shows the relationship between phytoplankton and zooplankton biomass in a selection of temperate-zone International Biological Program lakes (from McCauley and Kalff 1981). Lake Valencia falls far below the regression line, as do tropical lakes George (Burgis et al. 1973) and Lanao (Lewis 1979). The zooplankton biomass of Valencia was only slightly greater than that of Lanao, which had a much lower algal biomass.

Total standing stock of zooplankton herbivores was quite variable from year to year, but showed no evident trend or pattern (Fig. 2). The simplest way of explaining variations in herbivore abundance between years would

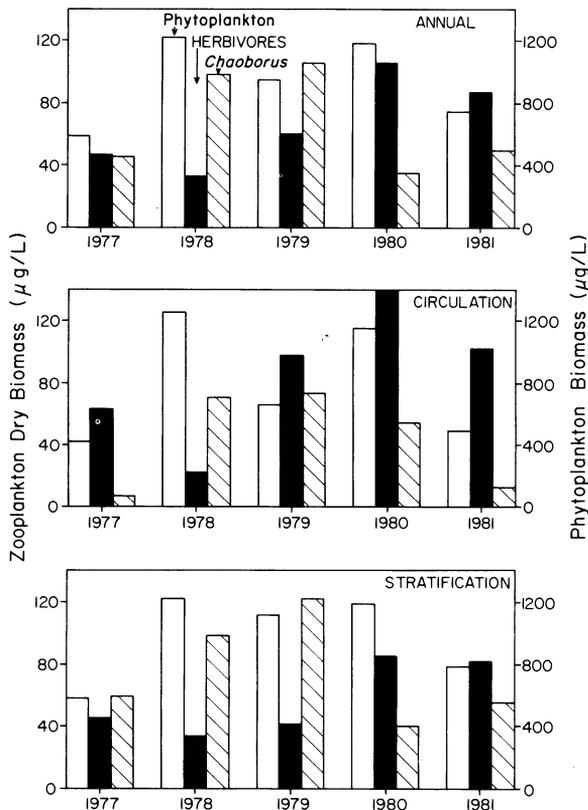


FIG. 2. Mean biomass for herbivores, phytoplankton, and predators (*Chaoborus*) in each of the five years, during circulation (mixing) and stratification seasons and for the whole year. The standard error of the mean associated with random error expressed as a percent of the annual mean was $\approx 2.5\%$ for herbivores, $< 5\%$ for phytoplankton, and $5\text{--}8\%$ for *Chaoborus*. The standard error of the mean associated with random error, expressed as a percent of seasonal mean abundance was $3\text{--}6\%$ for herbivores, $< 5\%$ for phytoplankton, and $7\text{--}27\%$ ($7\text{--}9\%$ for stratification) for *Chaoborus*.

be by association of herbivore abundances with the average abundances of food organisms or of predators. There was no relationship, however, between annual average herbivore abundance and phytoplankton abundance for Lake Valencia ($r = .01$, $P \gg .05$, $n = 5$), nor was total phytoplankton abundance any more variable than total herbivore abundance (Fig. 2). Although the lake received additional phosphorus loading after 1978, this was not reflected in the total phytoplankton standing stock. Therefore any simple explanation that would link nutrient loading to phytoplankton abundance and phytoplankton abundance to zooplankton abundance appears to be without empirical foundation.

Correlations were also determined for the annual abundance of specific herbivore categories (copepods, cladocerans, rotifers) and their foods (total phytoplankton, diatoms, green and blue-green algae), or predators (*Chaoborus*). Only a few relationships between groups of organisms and classes of foods were significant. The

abundance of copepods was correlated positively with abundance of green algae, and rotifer abundance was correlated negatively with total algal standing stock and with standing stock of blue-green algae. It is likely that the relationship of total phytoplankton to rotifers was dictated by the relationship of blue-green algae to rotifers, because the blue-green algae were a major component of phytoplankton standing stock. The Cladocera showed no significant relationships, even though Infante and Riehl (1984) have argued that they are inhibited by blue-green algae in Lake Valencia. There were no significant correlations between the annual abundance of *Chaoborus* and that of any herbivore category.

It is clear from the foregoing comparisons among years that factors controlling the herbivores can only be understood with reference to time scales shorter than 1 yr and by a more comprehensive approach to potential controlling variables. Although causal connections must exist between herbivores and their foods and predators, the interactions were too subtle to be extracted from annual averages.

Changes in abiotic factors clearly separated the mixing season from the stratification season in Lake Valencia. Herbivores were typically (4 of 5 yr) more abundant during the mixing season than during the stratification season (Fig. 2). Phytoplankton biomass in Lake Valencia was not consistently higher or lower during the stratification season than during the mixing season (Fig. 2). It therefore seems unlikely that changes in the quantity of food could explain the seasonal zooplankton patterns, but this leaves open the possibility that changes in phytoplankton species composition between the seasons contributed to the seasonal differences in herbivores. Predation pressure from *Chaoborus*, as judged from biomass, was typically higher during the stratification season than during the mixing season. Significant changes in predation pressure on the herbivores might therefore have given rise to the higher standing stock of herbivores in the mixing season. If the causal connection existed, it was not entirely uncomplicated, as shown by the failure of total herbivore biomass to be reversed in its seasonal maximum in 1980, when *Chaoborus* was, atypically, slightly more abundant during the mixing season than during stratification (Fig. 2).

The biomass ratios in Fig. 3 show that the herbivore taxa differed in their seasonal patterns of abundance. *Keratella* and the Cladocera seemed to have a strong dependence on the mixing season, while the other common herbivores were more evenly distributed over time. The seasonal summaries are evidence for a certain amount of temporal segregation of the taxa, suggesting that the two sets of taxa, which we designate as opportunistic and core species, respectively, were favored by distinct, annually recurring sets of conditions that were at least partially associated with the seasonal cycle of the lake.

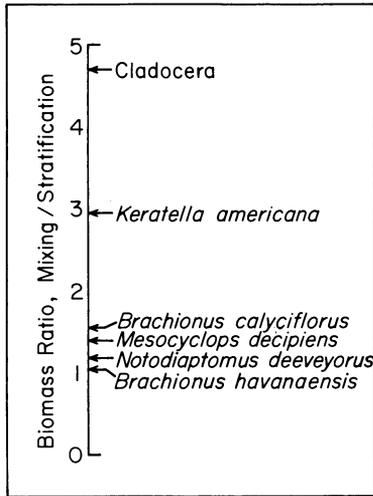


FIG. 3. Ratio of the 5-yr mean standing stock for the mixing season to the 5-yr mean standing stock for the stratification season in Lake Valencia.

Development and production

For the copepod *Mesocyclops decipiens*, our laboratory studies of egg development produced results in good agreement with general predictions for egg development at this temperature (Burgis 1970, Bottrell et al. 1976). The N1 stage, which does not feed (Comita and Tommerdahl 1960, Cooley 1973), was found by direct observation to have a development time of ≈ 9 h. All naupliar stages were enumerated separately for one of the cohorts, and this resulted in an estimate of 8.4 d for the combined development of all naupliar stages. A development time of 7 d was obtained independently with experimental enclosures. Frequently, cohorts that were at first distinct became indistinct prior to completion of development, possibly due to temporal variations in food availability. Consequently, the development times were averaged from various segments of the developmental sequence obtained from the individual cohorts (Table 1). The combined results of cohort analysis and enclosure studies indicate that the time required for an egg to develop to the adult stage under field conditions was 21 d.

Cohorts of *Notodiptomus deeveyorus* were much more distinct than those of *Mesocyclops*. Cohort analysis produced an estimate of 8 d for naupliar development time. This was confirmed almost exactly by laboratory studies in which mean development from egg to N6 was 7.8 d ($s = 1.0$, $N = 9$ clutches). As with *Mesocyclops*, complete development from egg to adult female required 21 d (Table 1).

Development times were not measured for *Mesocyclops meridianus* because of the rarity of the species; we assumed that this species developed at a pace similar to that of the other copepods.

Extensive data on the three major rotifer populations showed egg development times of 18–20 h for all taxa

(J. F. Saunders 1980 and *personal observation*). Eggs were deposited in the evening hours and eclosed during the following afternoon (Saunders 1980). Typically a female rotifer in Lake Valencia produced only one subitaneous egg per day, although two eggs per female were occasionally observed for *Brachionus calyciflorus*.

Initial production estimates of herbivores (Table 2) were based on the assumption that development times were constant at the measured growth rates shown in Table 1. This is the standard method for calculating production. We will show, however, that this method is seriously biased, at least for Lake Valencia, because it fails to account for sporadic suppression of growth by inadequate food. Production estimates can be revised on the basis of known loss and recruitment by a method we will describe after the rate data have been presented. The revised production estimates, which take into account periods of slowed growth, are shown along with the standard estimates in Table 2 and will be used henceforth in the text. It was not possible to revise production estimates for *M. meridianus*, *Polyarthra*, or *Hexarthra* because population densities were too low for loss-rate analysis.

Several lines of evidence suggested a general suppression of growth rates in Lake Valencia. The develop-

TABLE 1. Measured development times and growth rates (mass), and actual growth rates for major herbivores in Lake Valencia. Actual growth rate reflects adjustment of measured growth rate for growth suppression.

Species/stage	Copepod development time (d)	Measured growth rate (d ⁻¹)	Actual growth rate (d ⁻¹)
<i>Notodiptomus</i>			
Adult female		0.058*	0.058*
C5 female	2.8	0.179	0.089
C5 male	2.8	0.141	0.069
C4	2.1	0.256	0.095
C3	2.0	0.259	0.135
C2	2.0	0.275	0.096
C1	2.0	0.303	0.079
Nauplii	8.3	0.121	0.030
Eggs	1.3		
<i>Mesocyclops</i>			
Adult female		0.063*	0.063*
C5 female	2.1	0.179	0.130
C4 female	3.2	0.185	0.131
C3	2.1	0.173	0.103
C2	2.1	0.190	0.081
C1	2.1	0.205	0.128
Nauplii	8.4	0.214	0.107
Eggs	1.3		
<i>Moina</i>		0.236	0.072
<i>Diaphanosoma</i>		0.117	0.053
<i>Ceriodaphnia</i>		0.176	0.079
<i>Keratella</i>		0.143	0.069
<i>Brachionus calyciflorus</i>		0.272	0.170
<i>B. havanaensis</i>		0.212	0.069

* Egg production rate.

TABLE 2. Annual means for the dry mass production of herbivores in Lake Valencia ($\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$) computed with constant development time (standard estimates), and with development times varying in relation to food (revised estimates; see text for further explanation). Standard errors (SE) of the means are shown for random error in the revised production estimates.

Species	Standard production estimates							Revised production estimates	
	1977	1978	1979	1980	1981	Mean	Mean %	1977	1978
<i>Notodiaptomus</i>	1.48	1.47	4.41	7.56	4.04	3.79	38.1	1.21	1.37
<i>Mesocyclops decipiens</i>	1.92	1.39	0.92	1.69	2.11	1.61	16.1	1.93	1.40
<i>M. meridianus</i>	0.24	0.21	0.05	0.15	0.02	0.13	1.3
<i>Moina</i>	0.04	0.00	0.11	0.69	0.93	0.35	3.6	0.01	0.00
<i>Diaphanosoma</i>	0.11	0.00	0.00	0.00	0.06	0.03	0.3	0.05	0.00
<i>Ceriodaphnia</i>	0.05	0.00	0.07	1.79	2.63	0.91	9.1	0.02	0.00
<i>Keratella</i>	0.16	0.20	0.25	0.17	0.17	0.19	1.9	0.06	0.11
<i>Brachionus calyciflorus</i>	3.76	2.26	1.92	3.02	1.69	2.53	25.4	1.96	1.05
<i>B. havanaensis</i>	0.26	0.31	0.43	0.34	0.57	0.38	3.8	0.05	0.07
<i>Polyarthra</i>	0.01	0.01	0.05	0.00	0.01	0.02	0.2
<i>Hexarthra</i>	0.00	0.01	0.00	0.00	0.00	0.00	0.0
Total	8.03	5.85	8.21	15.41	12.22	9.94	100.0	5.28	4.00

ment rate observed for *Notodiaptomus* in Lake Valencia was almost identical to that observed by Landry (1983) for seven marine copepods reared at 15°C. It is surprising that the Valencia copepods did not develop faster than this. However, food supply is known to have a strong influence on development time (e.g., Coker 1934a, b, Klein-Breteler et al. 1982, Piyasiri 1985). The measured growth rates of all herbivores in Lake Valencia were low compared to maximum growth rates reported in the literature. For example, Huntley and Boyd (1984) obtained a relationship between maximum growth rate and temperature for marine zooplankton (mainly copepods) that predicts a rate of 0.85 d⁻¹ at 25°. Similarly, Stemberger and Gilbert (1985) predict a value for r_{max} , which exhibits a very close empirical relationship to optimum individual growth rate (Peters 1983), for *B. calyciflorus* of 0.63 d⁻¹. The growth rates for the populations in Lake Valencia (Table 1) did not approach these optimal values.

For a given species, the ratio of production to biomass (P/B) is thought to be relatively constant and the P/B ratio is inversely related to adult mass for organisms spanning a broad range of sizes and habitats (Banse and Mosher 1980). All species in Lake Valencia, however, had annual P/B ratios well below those predicted by Banse and Mosher (1980: 362, Eq. 10) on the basis of adult mass, and there was no correspondence between P/B and adult mass. This deviation suggests a general resource-based suppression of production in Lake Valencia.

Loss rates

The loss-rate estimates obtained as described in that section of Methods represent the changes in abundance not explained by recruitment or maturation (Table 3). Loss rates were partly accounted for by predation. In addition, if the development times from which we predicted recruitment and maturation were sometimes lengthened by poor nutrition, suppression of growth

would contribute to calculated loss rates (small negative loss rates for postembryonic stages are explained by growth rates that exceed those used in the production calculations). Loss rates for the two copepod species were distributed differently over the developmental stages. *Notodiaptomus* nauplii experienced very high losses, and losses of the copepodid stages and of the adults were typically less than those of the corresponding stages of *Mesocyclops*. The very different patterns of loss for the two species of copepods were a major cause of the different ratios of abundance for the developmental stages.

Seasonal differences in loss rates, although large in absolute terms, were typically not great when expressed as percentages (Table 3). Loss per capita for *Notodiaptomus* was higher during the circulation period for five of the eight stages, whereas the reverse was true for six of the eight stages of *Mesocyclops*. Higher relative loss rates of *Notodiaptomus* nauplii during stratification resulted in poor recruitment to all postembryonic stages in that season. Loss per capita for the most common cladoceran, *Ceriodaphnia*, was higher during stratification than during circulation (Table 3). The three rotifer species experienced higher loss per capita during circulation.

Predation

In accounting for the losses of herbivores in Lake Valencia, we first consider predation, which was estimated on the basis of predator abundances and predator feeding rates. In the limnetic zone of Lake Valencia, there were three predators. The rotifer *Asplanchna* preys on small rotifers such as *Keratella* or *Anuraeopsis*, but was too rare to account for significant loss of any herbivore category. In addition, the atherinid fish *Xenomelaniris* feeds upon herbivores to some degree. Unger's (1985) study of the *Xenomelaniris* population, however, showed that *Xenomelaniris* never became sufficiently abundant to suppress the herbivore com-

TABLE 2. Continued.

Revised production estimates					
1979	1980	1981	Mean	Mean %	SE
3.50	8.05	3.96	3.62	52.0	0.17
0.92	1.58	1.65	1.49	21.5	0.05
...
0.06	0.20	0.16	0.10	1.2	0.01
0.00	0.00	0.02	0.01	0.2	0.003
0.06	0.63	0.95	0.33	4.7	0.02
0.07	0.03	0.07	0.07	1.0	0.002
0.94	1.25	1.04	1.25	17.9	0.05
0.11	0.07	0.21	0.10	1.5	0.005
...
...
5.65	11.82	8.04	6.96	100.0	

munity as a whole, although it might have affected the abundance of *Ceriodaphnia* or *Notodiaptomus* during stratification. The third predator in the limnetic zone, *Chaoborus*, was the only one that reached sufficiently high abundance to have accounted for large losses within the herbivore community. We thus begin our analysis with a consideration of mortality caused by *Chaoborus* for the herbivores as a group, and then consider more specifically the mortality of individual taxa caused by *Chaoborus* and by *Xenomelaniris* given the feeding preferences of these two predators.

Cressa (1985: Fig. 22) provided instar-specific estimates of the growth efficiency (K_1) of each *Chaoborus* instar from Lake Valencia; K_1 values for instars I-IV were 0.21, 0.46, 0.46, and 0.41. Growth efficiencies appeared not to have been greatly influenced by prey type; assimilation efficiencies of instar IV ranged from 0.57 to 0.65 for three prey types (Cressa 1985). From the growth efficiencies, growth rates, and abundances of the four instars, we calculated for each date the potential of the *Chaoborus* population to consume prey biomass. The potential consumption rate should be realized as long as the appropriate food items are relatively abundant. As will become evident, however, the *Chaoborus* population often became so large that the food required to sustain the growth rate of *Chaoborus* exceeded the production of the prey. When this occurred, the growth rate of *Chaoborus* would have been retarded by lack of food. Switching to alternative food items was not possible because *Chaoborus* fed on all available prey species.

Table 4 gives annual and seasonal estimates of the potential consumption rate of the *Chaoborus* population and provides comparisons of the consumption rates with herbivore production. Herbivore community production is the biomass that can be harvested by *Chaoborus* without reducing prey standing stock. Comparison of consumption with production rates shows that the growth rate of the *Chaoborus* population was constrained by the availability of food under most conditions. The constraint was not without interrup-

TABLE 3. Absolute (organisms · L⁻¹ · d⁻¹) and relative (%/d) loss rates of herbivores in Lake Valencia.

Species/stage	Annual							Seasonal			
	1977	1978	1979	1980	1981	Mean	Relative (%/day)	Mean		Relative (%/day)	
								Circ.*	Strat.*	Circ.	Strat.
<i>Notodiaptomus</i>											
Female	0.09	0.06	0.29	0.77	0.22	0.29	10.6	0.41	0.25	13.3	10.1
Male	0.09	0.06	0.30	0.77	0.19	0.28	11.0	0.42	0.24	14.4	10.2
C5	0.03	0.00	0.18	-0.09	0.08	0.04	2.5	0.20	-0.03	8.3	-1.9
C4	0.04	-0.01	0.02	-0.12	-0.09	-0.03	-2.5	0.05	-0.06	2.3	-6.1
C3	-0.09	-0.02	-0.05	-0.08	0.10	-0.03	-2.4	-0.22	0.02	-9.1	3.0
C2	0.06	0.05	0.16	-0.17	0.08	0.04	3.2	-0.09	0.09	-4.6	10.0
C1	0.49	0.29	0.60	0.06	0.11	0.31	25.6	0.48	0.28	28.2	27.6
Nauplii	2.64	4.67	4.79	5.80	10.76	5.73	74.3	5.73	5.39	52.7	79.2
<i>Mesocyclops</i>											
Female	0.96	0.66	0.45	0.75	0.61	0.69	31.8	0.71	0.67	28.8	33.5
Male	0.95	0.65	0.48	0.77	0.64	0.70	15.9	0.71	0.68	14.2	16.6
C5	-0.51	0.14	-0.09	-0.09	0.48	-0.01	-0.5	0.13	-0.12	4.1	-4.2
C4	0.26	-0.15	0.38	0.91	0.63	0.41	9.8	0.38	0.39	7.1	10.3
C3	0.19	0.22	0.32	0.15	0.50	0.28	7.9	-0.10	0.36	-2.2	11.2
C2	2.09	1.36	0.39	1.52	1.77	1.43	34.4	1.17	1.34	28.5	33.3
C1	2.16	0.14	-0.06	-0.41	2.56	0.88	12.6	1.54	0.45	23.4	6.8
Nauplii	0.25	3.95	1.88	3.54	4.81	2.89	8.1	2.65	2.26	6.7	7.8
<i>Moina</i>											
Female	0.07	0.00	0.20	1.33	1.25	0.57	30.8	0.41	0.44	28.9	27.4
<i>Diaphanosoma</i>											
Female	0.15	0.00	0.00	0.00	0.06	0.04	12.3	0.09	0.04	9.6	15.1
<i>Ceriodaphnia</i>											
Female	0.12	0.00	0.15	4.05	5.50	1.96	21.2	1.96	1.30	21.2	28.4
<i>Keratella</i>											
Female	19.43	21.89	28.86	16.96	28.49	23.12	23.1	49.95	12.61	24.6	19.4
<i>Brachionus calyciflorus</i>											
Female	14.59	8.67	7.26	11.46	7.46	9.89	36.4	12.14	8.57	37.8	34.7
<i>B. havanaensis</i>											
Female	4.15	4.17	7.55	4.80	10.45	6.22	28.9	5.60	6.37	37.3	28.1

* Circ. = circulation season; Strat. = stratification season.

TABLE 4. Potential consumption by *Chaoborus* in relation to herbivore production.

	1977	1978	1979	1980	1981	Mean
Circulation season						
Potential consumption rate ($\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$)	2.25	23.77	17.93	11.61	3.22	11.76
Prey production ($\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$)	7.05	3.55	8.59	15.74	9.44	8.87
Relative consumption (%)	32	669	209	74	34	204
Consumption exceeds production (% of dates)	33	81	70	33	33	50
Stratification season						
Potential consumption rate ($\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$)	16.84	28.13	24.34	9.36	15.16	18.77
Prey production ($\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$)	5.13	3.79	3.80	9.56	7.60	5.98
Relative consumption (%)	328	742	640	98	200	402
Consumption exceeds production (% of dates)	82	100	89	50	41	72
Annual composite						
Potential consumption rate ($\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$)	12.94	28.81	21.95	8.02	13.56	17.06
Prey production ($\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$)	5.28	4.00	5.65	11.82	8.04	6.96
Relative consumption (%)	245	720	389	68	169	245
Consumption exceeds production (% of dates)	72	96	82	42	37	66

tion, however. Potential consumption exceeded prey availability on 66% of the dates during the 5-yr period and exceeded prey availability more often during stratification than it did during circulation.

The data in Table 4 suggest that *Chaoborus* controlled the herbivore community. If so, there should be an inverse relationship between herbivore production and the potential consumption of herbivores by *Chaoborus*. A very strong inverse relationship existed between potential consumption and herbivore production during the stratification season ($r^2 = 0.86$; Fig. 4). For the circulation season, there was no significant linear relationship because abiotic factors had a strong effect on abundance in some years. At the beginning of overturn in some years, the zooplankton, including *Chaoborus*, experienced catastrophic mortality, the extent of which depended on the suddenness with which the hypolimnion was incorporated into the mixed layer (Infante et al. 1979). Mortality in the *Chaoborus* population was by no means complete, but was significant. Potential consumption of herbivores by *Chaoborus* fell to a minimum 4–6 wk after overturn and did not reach normal levels for another month. The time to recovery represented approximately two generations for *Chaoborus*. The herbivores, which had shorter generation times, typically rebounded from the effect of overturn more quickly than *Chaoborus*. Herbivore production began increasing almost immediately, but decreased again ≈ 8 –10 wk after overturn, which corresponded to the recovery of the *Chaoborus* population. Abrupt overturn thus temporarily broke the coupling between *Chaoborus* and the herbivores, and provided some release from predation for ≈ 2 mo.

Although *Xenomelaniris* feeds readily on prey < 1 mm in length (Unger and Lewis 1983), it was a much less important predator on herbivores than was *Chaoborus*. The effect of *Xenomelaniris* was quantified by a method similar to that used for *Chaoborus*, with data from Unger (1985). Accurate fish population data were available only for the year 1980, but, based on more

limited data, Unger (1985) concluded that seasonal biomass variations for 1977–1979 were similar to those in 1980. Unger (1985) has shown that *Xenomelaniris* abundance passes through a regular seasonal cycle caused by the recruitment and maturation of a single major cohort over the course of each year. Fish population density is very low during January and February when only adult (yearling) fish are present. Density of the adult fish declines steadily until the end of September, at which time they have virtually disappeared. The impact of the larger fish on the herbivore populations is negligible because of the low density of the fish and their strong preference for *Chaoborus* instead of herbivores. Although young-of-the-year fish begin to appear early in the year, their main effect is restricted to the stratification season (after April); their low densities and small size preclude major effects prior to that time.

The average food requirement of the *Xenomelaniris* population during the stratification season was ≈ 1

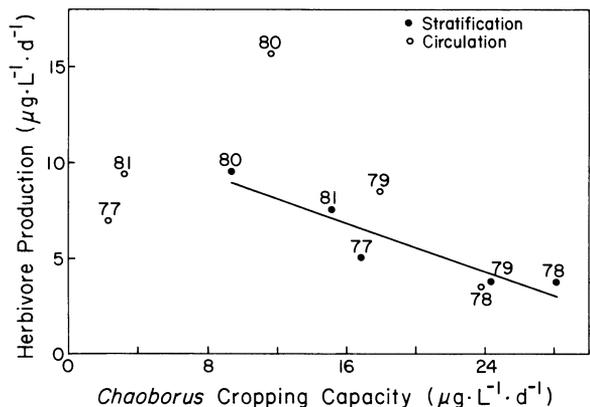


FIG. 4. Relationship between seasonal herbivore production and the capacity of *Chaoborus* to crop herbivore biomass. Circulation and stratification seasons for each year are shown as separate points. A least squares linear regression has been fitted to the stratification-season data.

TABLE 5. Herbivore mortality attributable to *Chaoborus* predation. The value is given only where density exceeded the detection limit on at least five dates.

Species/stage	Instantaneous loss rate (d ⁻¹)					Mean		
	1977	1978	1979	1980	1981	Annual	Circ.*	Strat.*
<i>Notodiaptomus</i>								
Female	0.06	0.17	0.09	0.06	0.07	0.09	0.09	0.09
Male	0.08	0.14	0.12	0.12	0.08	0.11	0.10	0.12
C5	0.02	0.12	0.04	0.01	0.01	0.04	0.06	0.04
C4	0.02	0.07	0.07	0.02	0.00	0.04	0.04	0.10
C3	0.00	0.06	0.06	0.01	0.01	0.03	0.03	0.07
C2	0.03	0.10	0.04	0.02	0.01	0.04	0.04	0.05
C1	0.04	0.21	0.09	0.03	0.01	0.08	0.03	0.12
Nauplii	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Mesocyclops decipiens</i>								
Female	0.26	0.72	0.33	0.18	0.12	0.32	0.19	0.31
Male	0.09	0.18	0.12	0.06	0.04	0.10	0.09	0.12
C5	0.03	0.29	0.14	0.07	0.08	0.12	0.13	0.14
C4	0.10	0.16	0.17	0.12	0.10	0.13	0.18	0.19
C3	0.11	0.14	0.07	0.03	0.02	0.07	0.03	0.09
C2	0.18	0.19	0.11	0.03	0.06	0.11	0.06	0.13
C1	0.08	0.13	0.05	0.01	0.06	0.07	0.01	0.04
Nauplii	0.04	0.12	0.06	0.04	0.03	0.06	0.09	0.05
<i>Moina</i>	0.03	...	0.24	0.10	0.09	0.12	...	0.27
<i>Diaphanosoma</i>	0.06	0.06
<i>Ceriodaphnia</i>	0.05	...	0.24	0.08	0.06	0.11	...	0.25
<i>Keratella</i>	0.18	0.18	0.20	0.16	0.07	0.16	0.16	0.19
<i>Brachionus calyciflorus</i>	0.19	0.32	0.21	0.12	0.10	0.19	0.18	0.24
<i>B. havanaensis</i>	0.06	0.14	0.05	0.03	0.06	0.07	0.03	0.06

* Circ. = circulation season; Strat. = stratification season.

$\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$, dry mass. For purposes of calculating the maximum possible effect of *Xenomelaniris*, we assumed that the diet consisted exclusively of herbivores. Given this assumption, which does not take into account the fact that *Xenomelaniris* consumes *Chaoborus* as well, *Xenomelaniris* would use only 14% of herbivore production to meet its growth requirements. Thus while *Xenomelaniris* may have exerted some effect on herbivore species composition, it did not suppress the herbivore community, nor did its potential consumption approach that of the *Chaoborus* population.

From the electivities, the daily food requirements and abundances of the *Chaoborus* instars, and the mean abundances of the herbivores, we computed for each species and developmental stage of herbivore the instantaneous mortality due to *Chaoborus* (Table 5). These computations incorporated an upper bound so that consumption by *Chaoborus* did not exceed the total food supply on any given date. For all herbivores, mortality of eggs was assumed to be dependent only on mortality of adult females.

The electivities of each instar of *Chaoborus* were computed on the basis of data from > 1000 crops. All instars of *Chaoborus* fed on the smallest prey items, but electivities for small prey declined as *Chaoborus* body size increased. Electivities of the larger instars of *Chaoborus*, which consumed all common herbivore species, were not related consistently to the size of the prey.

Predation pressure was distributed quite unevenly over the herbivore taxa (Table 5). Two rotifer species and the late life history stages of the copepods received the most intense predation pressure. Seasonal data show that predation pressure on preferred prey was often more intense during stratification. Copepod nauplii and the younger copepodid stages were not well exploited by *Chaoborus*. Despite their relatively high abundance at certain times of the year, the naupliar stages of *Notodiaptomus* were not found in any of the *Chaoborus* crops. The nauplii of *Mesocyclops* were found on a few occasions, but the electivities were quite low ($r_i/p_i = 0.55$ for *Chaoborus* instar IV, where r_i is the proportion of item i in the diet, and p_i is the proportion of item i in the lake). The resistance of the younger copepod stages to predation provides a mechanism by which the population can be maintained in the face of extreme predation pressure by *Chaoborus* on the older stages.

The coexistence of predator and prey in Lake Valencia represents a balance of reproductive strategy and vulnerability to predation. Only species that can offset predation losses by reproductive output will coexist continually with *Chaoborus* (cf. Neill 1981). The two copepod species and the two *Brachionus* species had this ability; these four species persisted throughout the year and thus formed the core of the herbivore community. *Brachionus* reproduced with sufficient speed to offset predation. The copepods were able to persist in the face of predation only because the pre-adult

TABLE 6. Nonpredation losses as a percent of total losses. The value is given only where density exceeds the detection limits on at least five dates.

Species/stage	1977	1978	1979	1980	1981	Mean		
						Annual	Circ.*	Strat.*
<i>Notodiaptomus</i>								
Female	50	22	28	70	78	50	59	37
Male	32	0	17	58	74	36	50	28
C5	79	24	59	91	98	70	75	60
C4	85	0	86	90	...	65	69	73
C3	83	98	98	93	...	93
C2	90	85	84	97	98	91	82	91
C1	98	86	94	95	98	94	97	94
Nauplii	100	100	100	100	100	100	100	100
<i>Mesocyclops decipiens</i>								
Female	25	15	14	48	75	36	30	32
Male	54	69	41	73	84	64	69	49
C5	...	0	0	65	92	39	28	25
C4	0	0	32	71	24	25	33	25
C3	14	51	56	86	96	61	52	60
C2	68	59	68	92	82	74	83	69
C1	81	72	0	7	92	50	77	77
Nauplii	0	50	33	87	79	50	58	40
<i>Moina</i>								
<i>Diaphanosoma</i>	95	...	37	66	79	69	68	56
<i>Ceriodaphnia</i>	67	67	47	75
<i>Keratella</i>	79	...	13	66	75	59	65	59
<i>Brachionus calyciflorus</i>	37	18	23	35	67	36	45	27
<i>B. havanaensis</i>	48	31	36	64	70	50	59	44
	85	54	83	88	77	77	84	73

* Circ. = circulation season; Strat. = stratification season.

stages had low vulnerability to predation; the adults experienced high predation losses. Thus high losses during the adult stage were subsidized by recruitment from less vulnerable stages. The other species (cladocerans and *Keratella*), which were not able to coexist continually with *Chaoborus*, were opportunistic in the sense that they became abundant only when there was a decline in the *Chaoborus* population. Because the circulation period is the most predictable time of decline for *Chaoborus*, opportunistic species tended to be more abundant during circulation than stratification (Fig. 3). Opportunistic species appeared when predation pressure was low (i.e., most circulation periods).

Losses in excess of predation

Not all losses could be explained by predation. Some herbivores were not consumed by *Chaoborus*, and *Chaoborus* population density was sometimes too low to affect even those herbivores that were its preferred food. For each herbivore stage or species, predation loss was subtracted on each date from total loss to give non-predation loss (Table 6). Nonpredation losses were high in 1980 and 1981 when the *Chaoborus* population was small, and were relatively low in 1978 and 1979 when *Chaoborus* was more abundant. Nonpredation losses were typically higher during the circulation season, although the pattern was not entirely consistent. Nonpredation loss as a percent of total loss indicates the relative importance of predation in the different herbivore groups. As shown by the percent nonpre-

dition loss (Table 6), two of the three common rotifer species experienced high loss to *Chaoborus*, particularly during 1978 and 1979, when the *Chaoborus* population was large. *Brachionus havanaensis*, on the other hand, experienced lower loss to *Chaoborus*. Cladocerans were typically absent when *Chaoborus* was abundant; the percentages given in Table 6 thus may underestimate the potential effect of *Chaoborus* on these species. Nevertheless, predation had a strong effect on cladocerans: about one-third of the cladoceran losses for 1980 could be explained by predation at a time when *Chaoborus* population density was relatively low.

Data for the copepods present a more complex picture in that loss mechanisms changed during development. For *Notodiaptomus*, predation explained a substantial portion of total losses only in the adults. For *Mesocyclops*, predation also played an important role in the large subadult stages. Mechanisms other than predation must therefore be invoked to account for losses in the smaller developmental stages. For both species, the stages that were most affected by predation comprised $\approx 70\%$ of population biomass, including the reproductive stage.

Mechanisms other than predation strongly affected most taxa (Table 6), which would seem to contradict the conclusion that *Chaoborus* was often food-limited (Table 4). The contradiction is only apparent, however, since predation fell most heavily on the most important species. Weighting the predation loss rate of each taxon by its numerical representation in the herbivore com-

munity results in a weighted average for community predation mortality of 0.123 d^{-1} (49% of total loss).

Resource limitation

Several factors could account for nonpredation loss. Parasitism and disease are occasionally invoked to explain suppression of populations (Hoenicke 1984, Burns 1985). We observed a few parasitized rotifers, but the frequency of parasitism was so low in Lake Valencia that there is no reason to suspect a measurable effect on population dynamics.

Another possible cause of nonpredation loss would be diversion of energy into predation defenses, such that growth rates are reduced even though survival may be enhanced. We believe, however, that such an explanation was not important in Lake Valencia for several reasons. Only two of the major herbivore species, *Brachionus calyciflorus* and *Ceriodaphnia cornuta*, are known to produce morphotypes bearing defensive structures. The small-eyed morph of *Ceriodaphnia*, which has a reproductive potential inferior to that of the large-eyed morph (Zaret 1972a, b), was not common in Lake Valencia, nor would it be expected in the absence of intense visual predation. In *B. calyciflorus*, spine development was variable, but not clearly related to predation intensity.

The only realistic explanation for most nonpredation loss is inadequate food supply. In Lake Valencia total algal biomass was quite high (Fig. 1; Lewis 1986). Nevertheless, if algal biomass is not ingestible or is of low food value, herbivore growth rates will be suppressed. For example, Coker (1934b) documented a prolongation by a factor of 5–6 in the development of poorly nourished cyclopoid copepods. We conclude from the Lake Valencia data that the resource base, although abundant, was unavailable to or suboptimal nutritionally for certain species and stages. In most cases, nutritionally inadequate food did not cause death, but the resultant growth suppression appeared as nonpredation losses. Even though some other kinds of losses may have made small contributions, we will henceforth refer to the nonpredation losses (Table 6) as growth suppression.

Notodiaptomus nauplii were exceptional in their high degree of growth suppression. In fact, mere suppression cannot explain the observed ratio of naupliar density to egg density (Table 7). Given continuous recruitment and no mortality, ratios of numerical abundance for different stages should equal ratios of their development times. The great disparity between these ratios for nauplii and eggs of *Notodiaptomus* (Table 7) shows that nauplii were actually lost in substantial numbers, even though predation could not explain the loss. Nonpredation loss in this case thus probably included starvation.

The conclusion that *Notodiaptomus* nauplii starved is supported by Infante's (1981) dietary analysis. Her data showed no feeding during N1 and N2, and only

TABLE 7. Ratios of densities and development times for sequences of stages of the two copepods.

Stages	<i>Mesocyclops</i>		<i>Notodiaptomus</i>	
	Density	Develop-ment time	Density	Develop-ment time
C5/C4	0.69	0.66	1.24	1.33
C4/C3	1.17	1.52	1.07	1.05
C3/C2	0.85	1.00	1.05	1.00
C2/C1	0.59	1.00	0.97	1.00
C1/nauplius	0.20	0.25	0.16	0.24
Nauplius/egg	3.90	6.72	0.97	6.64

limited feeding during N3. Because most workers agree that only N1 is a nonfeeding stage, we conclude that the two subsequent stages were often simply unable to ingest suitable food. It is unlikely that survival to N4 is possible without food intake. In laboratory studies of *Mesocyclops* from Lake Valencia, we observed that development stopped in N2 if suitable food was unavailable. The inability of the early naupliar stages to obtain adequate food would thus result in a bottleneck for the population.

The growth rates that we measured for the herbivores (Table 1) may not have been sustained throughout the year. Growth suppression of the natural populations would cause the actual growth rates to be less than those measured directly in the laboratory. The same could also be true of our cohort analyses, even though they were based on field data, because distinct cohorts appeared to be associated with times of strong population growth. In either case, the measured growth rates were higher than the actual growth rates of the natural populations by an amount equal to growth suppression. The difference between the measured growth rate and nonpredation losses, which we interpreted as growth suppression, gives the actual growth rate (Table 1). The revised production estimates in Table 2 are the product of actual growth rate and population biomass.

The mechanism of growth suppression is not obvious. Although the standing crop of phytoplankton was very large, the herbivores may only have utilized a small subset determined by the size, shape, taxonomy, or other characteristic of the algae. This possibility was investigated in great detail with correlation analysis, but we were unable to find more significant relationships between the abundance trends of the herbivores and the phytoplankton than would be expected by chance. No clear evidence identified a specific food item as a regulator of herbivore abundance, although the possibility cannot be eliminated that such existed. Alternatively, herbivore growth rates may have been suppressed by a general nutritional inadequacy common to the food items used by the herbivores, a prospect made more plausible by the considerable dietary similarity among the major herbivores in Lake Valencia (Infante 1978, 1981). Low nitrogen content would be one such mechanism, and has been proposed for

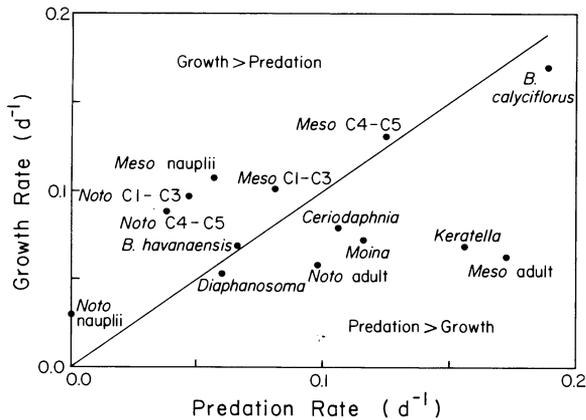


FIG. 5. Relationship between mortality due to predation and herbivore growth rate.

the limitation of terrestrial herbivores (White 1978) and marine plankton (Checkley 1980, Durbin et al. 1983). Checkley (1980) found that energy conversion efficiencies of a marine copepod were inversely related to the C:N ratio of its food. High C:N ratios, and thus low conversion efficiencies for zooplankton, are characteristic of N-limited phytoplankton, and would thus be expected in Lake Valencia (cf. Lewis 1983b).

Herbivore community organization and structure

All herbivore species in Lake Valencia were affected simultaneously by growth suppression and by predation. The balance of these two factors determined the relative abundance of species and the seasonal timing of population growth for individual species. A line defined by the equivalence of growth and predation rates divides the species of the herbivore community into two groups (Fig. 5). *Keratella* and the cladocerans, which we have classified as opportunistic species on the basis of temporal abundance patterns, fell well below the line, and thus on average had growth rates less than predation rates. The opportunistic species populations tended to expand when *Chaoborus* was scarce; this was possible by virtue of their high growth rates, which allowed them to exploit more quickly any favorable shift in conditions. However, maximum growth rates will not be realized when food quality is suboptimal, and this appeared to occur often. Occasional, brief release from growth suppression did occur. For example, during a 2-wk interval in 1979, the *Keratella* population expanded from nearly undetectable levels to almost 1700 individuals/L ($r = 0.25 \text{ d}^{-1}$). Although the *Keratella* population density soon returned to very low levels, this brief episode was responsible for >25% of the annual production of *Keratella*. The extent of nutritional growth suppression generally appeared to be sufficient, however, to shift the actual growth rate below that required to balance removal by predation. The opportunistic species became very rare for extended periods of time, especially during the stratification sea-

son, and extremely low abundance must have provided an escape from predation.

The core species, with the exception of copepod adults, had average growth rates that equalled or exceeded predation rates. The favorable balance of growth and predation allowed these species to persist throughout the year. Adults of the two copepods, which had actual growth rates lower than predation rates, persisted because of recruitment from younger, faster growing stages that were much less vulnerable to predation. *B. calyciflorus* contended with very intense predation pressure. It was apparently able to do this because it had a considerable capacity to respond to brief releases from growth suppression, as indicated by episodes similar to the one described above for *Keratella*. *B. calyciflorus* was probably very sensitive to changes in food quality.

The convergence of control pathways on herbivores has been predicted by other studies (Lewis 1979, McQueen et al. 1986). In eutrophic lakes, McQueen et al. (1986) predict that maximum attainable herbivore biomass is set by algal biomass ("bottom-up" control) and that a departure from the maximum would be attributable to planktivores ("top-down" control). Although trophic relationships in Lake Valencia generally conformed to those predicted by McQueen et al., there were differences. Despite high primary production ($\approx 84 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$; W. M. Lewis, Jr., *personal observation*), top-down effects remained very prominent. We attribute this to a suppression of herbivore growth rates by qualitative inadequacy of the algal food base.

In some ways, the trophic relationships in Lake Valencia may be better described by the model of Carpenter et al. (1985). The relative abundance of the trophic levels in Lake Valencia (high algal biomass, low herbivore biomass, and high planktivore biomass) was consistent with "cascading trophic interaction" at low piscivore biomass. Once again, however, the model does not describe fully the situation in Lake Valencia. Given the dominance of an invertebrate planktivore in open water, the model predicts a shift in species composition toward larger herbivores and higher biomass. There is no evidence that this occurs in Lake Valencia, apparently because *Chaoborus* is able to ingest even the largest herbivores in the community.

CONCLUSION

Overview of control mechanisms

Food and predation simultaneously controlled planktonic herbivore populations in Lake Valencia. The food supply, while abundant, appears to have been qualitatively poor to the extent that herbivore growth rates were greatly suppressed. Predation by *Chaoborus*, which exerted especially tight control during the stratification season, accounted for removal of virtually all herbivore production. Temporary release of the herbivores from control by *Chaoborus* occurred when

mixing of the lake led to a decline in the *Chaoborus* population.

With the onset of stable stratification, nutrient supplies in the epilimnion and oxygen in the hypolimnion were depleted rapidly. Herbivore populations were thus restricted to the mixed layer. The herbivores grew slowly on food that was probably of poor quality and were subject to intense predation pressure from *Chaoborus*. Thus during stratification, which prevailed for much of the year, strong control was exerted on the herbivores by the two adjacent trophic levels (Fig. 6).

Disruptions in stratification altered the strength of the control pathways. Strong winds during the stratification season can thicken the mixed layer and increase nutrient supplies. Such an event may produce an improvement in food quality, which would allow herbivores to grow faster. Because the effects of mixed-layer thickening persisted on a time scale of days, response to the brief improvement in food quality was restricted to the fast-reproducing species. Moreover, thickening of the mixed layer did not provide any release from predation (Fig. 6); brief increases in herbivore growth were quickly consumed by the food-limited *Chaoborus* population.

Annual overturn, which marks the beginning of the circulation season, may have improved food quality, but often resulted in substantial mortality of zooplankton. Thus, while overturn reduced the effect of both biotic control mechanisms on the herbivores (Fig. 6), the reduction in herbivore populations may have precluded a major response by the herbivores.

Control mechanisms affecting herbivores in Lake Valencia operated hierarchically in three levels. Abiotic conditions constituted the most basic level of control on herbivore production. Temperature, which was relatively constant over time and space in Lake Valencia, fixed optimum growth rates for the herbivores, and thus set an upper boundary for the production of the community at a given standing stock. In addition, overturn could interrupt and override controls at other levels by imposing catastrophic mortality on the zooplankton populations.

A second level in the hierarchy was food quality. In Lake Valencia, poor food quality apparently depressed herbivore growth rates and thereby reduced the tolerance of herbivores to predation pressure. Because food quality depends ultimately on abiotic factors, it will vary over time in response to changes in the thickness of the mixed layer, which affects nutrient availability (Lewis 1986). As a direct consequence of temporal changes in food quality there were variations over time in herbivore growth rates and hence the yield available to predators.

Predation constituted the third and final level of control on herbivore populations. Predation control was hierarchical in the sense that predation was imposed on populations already suppressed by food quality and thus regulated in sustainable yield. Moreover, despite

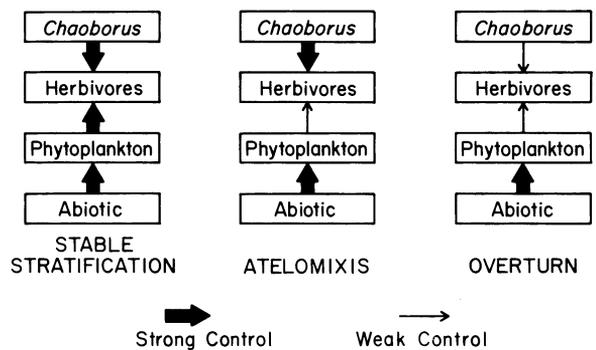


FIG. 6. Relationship between control pathways and mixing patterns in Lake Valencia. "Atelomixis" is a thickening of the mixed layer of a tropical lake that does not lead to complete mixing (see Description of Lake Valencia).

the strong control that predators exerted on herbivores in Lake Valencia, it could be overridden by abiotic factors that resulted in catastrophic mortality.

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