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PLANKTON COMMUNITY STRUCTURE AND LIMNETIC
PRIMARY PRODUCTION

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In the view of systems ecologists, the ecosystem is an entity which persists regardless of fluctuations in its component populations (Odum 1969, 1977; O'Neill 1976a; O'Neill and Reichle 1979). Some ecosystem biologists have extended this concept and rejected the notion that the ecosystem can be studied as the sum of its parts (Innis 1976). Others see "no a priori reason to believe that ecosystem phenomena are to be found by examining populations" (O'Neill 1976b, p. 18). O'Neill and Reichle (1979) propose nutrient-limited primary production as an example of an ecosystem phenomenon that is independent of the dynamics of the underlying populations. Support for this example is provided by O'Neill and Giddings' (1979) analysis of a model of phytoplankton populations competing for a limiting nutrient, which showed that perturbations that substantially affected algal community structure had only weak effects on primary production.

There is substantial variability in lake productivity that cannot be explained by nutrient loading (Harris 1980). The correlation of phosphorus loading and primary production of lakes is low, though significant ($r^2 = 0.476$; Schindler 1978). Phosphorus loading is more successful as a predictor of chlorophyll concentrations; published r^2 values range from 0.792 (Schindler 1978) to 0.951 (Dillon and Rigler 1974). Oglesby (1977, p. 2,267) concludes that "BAP (biologically available phosphorus) loading is obviously a more accurate predictor of standing crop than of annual productivity and this seems unlikely to change with the addition of more data." Graphs of chlorophyll concentration versus primary production show considerable scatter (Brylinsky and Mann 1973; Oglesby 1977). We infer that primary production depends on how chlorophyll is allocated among phytoplankters of differing metabolic activities and on the recycling rates of nutrients within the plankton community. Such processes depend on size-structured interactions within limnetic food webs.

The size distribution of herbivorous zooplankton is determined by predation to a great extent (Brooks and Dodson 1965; Hall et al. 1976). The zooplankton size distribution influences per capita grazing and nutrient excretion rates (Peters and Rigler 1973; Peters 1975; Hall et al. 1976; Bartell and Kitchell 1978). Regeneration by herbivores is a major nutrient source for limnetic phytoplankton (Kitchell et al.

1979; Lehman 1980*a*, 1980*b*; Axler et al. 1981). Zooplankton influence the phytoplankton size distribution by grazing some size classes more heavily than others (Porter 1977; Steele and Frost 1977; Gliwicz 1977, 1980; DeMott 1982). Smaller phytoplankters have higher maximum growth rates (Fenchel 1974; Banse 1976; Malone 1980), are nearer their maximum growth rate at low nutrient concentrations (Malone 1980), and sink more slowly (Smayda 1970; Walsby and Reynolds 1980) than large phytoplankters.

Collectively, these observations suggest that modulation of planktonic size spectra by trophic interactions could produce coupled shifts in plankton community composition and primary productivity. Here we analyze a dynamic model of phytoplankton size structure that incorporates grazing and nutrient cycling, to explore the potential effects of these processes on primary production. Significant implications for ecosystem theory and predictive models of lake productivity are noted.

PHYTOPLANKTON SIZE DISTRIBUTION MODEL

The model evaluates changes in the limiting nutrient concentration and phytoplankton size distribution over time scales short enough that the zooplankton biomass can be considered static. The dynamics of the abundance of algae of radius R [$A(R)$, in $\mu\text{g C L}^{-1}$ size class $^{-1}$] and nutrient concentration N (μM) are given by

$$\frac{dA(R)}{dt} = [g(R, N) - h(R, Z, W) - D]A(R) \quad (1)$$

$$\frac{dN}{dt} = D(N_0 - N) + \frac{E}{Y} \sum_R h(R, Z, W)A(R) - \frac{1}{Y} \sum_R g(R, N)A(R). \quad (2)$$

The functions describing growth (g) and herbivory (h) are described below. D is the dilution rate and N_0 is the influent nutrient concentration. Y is the amount of cell carbon maintained per unit nutrient. E is the proportion of ingested nutrients that is recycled by excretion.

Available data relating cell size to growth and herbivory express cell size in different units, either carbon content per cell or equivalent spherical radius. We convert radius (R) in μm to carbon content (x) in pg C/cell as

$$x = c4\pi R^3/3 \quad (3)$$

where $c = 0.1 \text{ pg C}/\mu\text{m}^3$ (Vollenweider 1974).

The growth function $g(R, N)$ is a hyperbolic function of nutrient concentration that depends on cell size in two ways: maximum growth rate $V(x)$ decreases with cell carbon content as a power function (Banse 1976) and the half saturation constant $K_m(R)$ increases linearly with cell radius (Malone 1980):

$$g(R, N) = V(x)N/[K_m(R) + N]. \quad (4)$$

The value of $V(x)$ is determined by a maximum possible rate V_{\max} multiplied by a size-dependent ratio that varies from 0 to 1:

$$V(x) = V_{\max}(x/x_{\min})^{-\alpha}. \quad (5)$$

The carbon content of the smallest cell size class is x_{\min} . α is the exponent of the power function that couples growth rate to size. The value of K_m is given by

$$K_m(R) = K_{\max}(R/R_{\max}) \quad (6)$$

where K_{\max} is the half-saturation constant of the largest algae, which have radius R_{\max} .

The herbivory rate $h(R, Z, W)$ depends on both phytoplankter radius and the biomass (Z , mg dry mass/L) and mean individual mass (W , mg dry mass/animal) of zooplankton:

$$h(R, Z, W) = a \left(\frac{Z}{W} \right) W^\beta S(R). \quad (7)$$

Grazing rate per animal, a power function of body mass with exponent β , is multiplied by the number of animals/L (Z/W), a grazing coefficient a , and a selectivity function $S(R)$. A wide variety of selectivity curves has been described for zooplankton (cf. Gliwicz 1980; Richman et al. 1980, e.g.). Our analyses are based on the shape that Gliwicz (1980) finds most characteristic of cladoceran assemblages:

$$\begin{aligned} S(R) &= 1 - (R/R_{\text{lim}})^2 \quad \text{for } R < R_{\text{lim}} \\ S(R) &= 0 \quad \text{for } R \geq R_{\text{lim}}. \end{aligned} \quad (8)$$

$S(R)$ thus ranges from 0 (for algae that exceed R_{lim} , the radius of the largest particle ingested) to 1 (for the smallest and most heavily grazed algae). R_{lim} increases with zooplankter length following Burns' (1968) regression based on seven species of *Bosmina* and *Daphnia*. Length and mass of zooplankters were interconverted using a regression for *Daphnia* (Rosen 1981).

Model estimates of chlorophyll concentrations and primary productivity are the focus of this paper. Chlorophyll concentration in $\mu\text{g/L}$ is given by

$$Chl = 10^3 \sum_R Q(R)A(R) \quad (9)$$

where the function $Q(R)$ gives the chlorophyll:carbon ratio for cells of radius R . $Q(R)$ was estimated by fitting a straight line to Malone's (1980) fig. 12.2:

$$Q(R) = \frac{1}{c} \{ \text{antilog} [-1.43(\log 2R) + 2.43] \}. \quad (10)$$

Primary production over any time interval t_1 to t_2 is

$$\int_{t_1}^{t_2} \left[\sum_R g(R, N) A(R) \right] dt. \quad (11)$$

Results presented here center on a reference run of the model. Consequences of selected assumptions were explored by altering the appropriate functions or parameters and comparing results with the reference run.

Parameter values for the reference run were based on the assumption that phosphorus was the limiting nutrient. Influent phosphorus concentration (N_0) was $0.1 \mu\text{M}$. The dilution rate (D) was $0.1 d^{-1}$. The molar carbon:phosphorus ratio was 106 (Parsons et al. 1977). The maximum half-saturation constant of the largest cells (K_{\max}) was $0.25 \mu\text{M}$. The maximum growth rate (V_{\max}) was $3 d^{-1}$. The exponent of the power function relating maximum growth rate and cell size (α) was $\frac{1}{4}$ (Banse 1976). The exponent of the power function relating grazing rate and zooplankton mass (β) was $\frac{2}{3}$ (Hall et al. 1976). The grazing coefficient (a) was 10^3 . Excretion efficiency was 0.5 (Peters 1975). Ten algal size classes ranging in mean radius from $5 \mu\text{m}$ (R_{\min}) to $95 \mu\text{m}$ (R_{\max}) were used. Initially, each size class contained $10 \mu\text{g C}$. The equations were solved recursively with a time step of $0.05 d$ using a double-precision computer program.

RESULTS

In the absence of grazers ($Z = 0$) equations (1) and (2) reduce to the Monod model of many species competing for a limiting nutrient in a continuous culture. Only the species with the lowest half-saturation constant and highest maximum growth rate, in this case the smallest species, would remain at equilibrium (Tilman 1977). However, when zooplankton are present the smallest phytoplankton is not necessarily the dominant competitor.

Preliminary simulations showed that phytoplankton biomass and nutrient levels did not reach equilibrium in 15 days. In nature, it is likely that zooplankton individual mass, total biomass, or some environmental factor would change before equilibrium is reached. Therefore, we examined dynamic results under non-equilibrium conditions over short time periods. In preliminary simulations, consistent trends of productivity with zooplankton biomass were reached in 2 to 4 days and maintained for the remainder of the 15-day simulations. All results shown here are based on day 6 of the simulations.

Reference run calculations were made over a logarithmic scale of zooplankton sizes from 10^{-5} to 1 mg/animal . The smallest sizes correspond to small rotifers and nauplii; sizes of ca. 10^{-4} to $10^{-3} \text{ mg/animal}$ are represented by *Bosmina*; sizes of ca. 10^{-3} to $10^{-2} \text{ mg/animal}$ are represented by *Daphnia rosea* and *Mesocyclops*; and the largest sizes correspond to large copepods and *Daphnia* spp. (Edmondson and Winberg 1971; Rosen 1981; A. M. Bergquist, unpubl. data). Response surfaces were calculated for a logarithmic range of zooplankton biomass from 10^{-5} to 1 mg/L , which spans the range typical of temperate lakes.

The radius of the fastest-growing algal size class depended on both grazer size and zooplankton biomass (fig. 1A). Large phytoplankton predominated when large grazers were present at high biomass levels. The smallest phytoplankters predominated when grazers were small or when biomass of zooplankton was low. Chlorophyll concentrations showed the opposite trends (fig. 1B). High chlorophyll concentrations occurred where grazers were small or zooplankton biomass

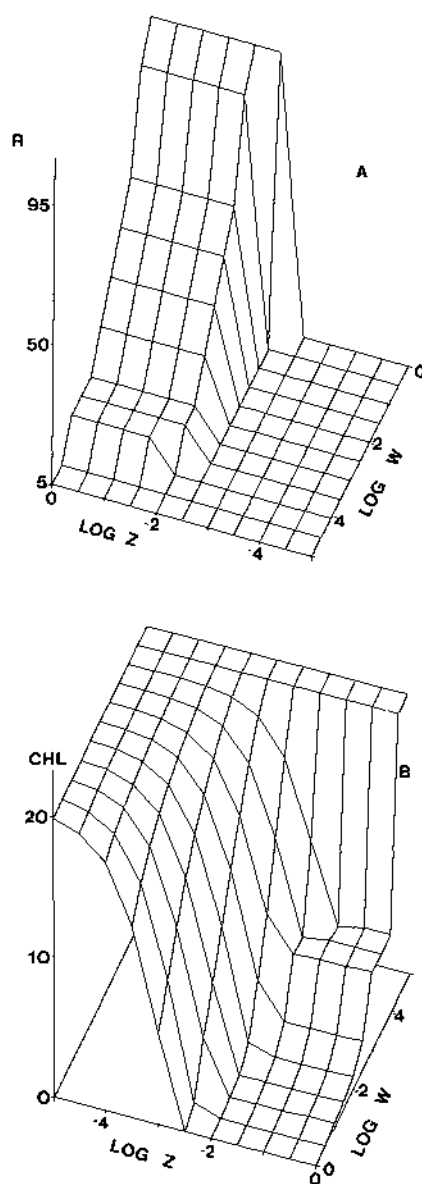


FIG. 1.—Response surfaces of the phytoplankton to zooplankton biomass (concentration) (Z , mg/L) and mean individual zooplankton mass (W , mg) on day 6 of the reference run. Z and W are plotted as base 10 logarithms. Note that Z and W scales in panel A are the reverse of those in panels B and C . A , Radius of the fastest-growing algal size class, R (μm). B , Chlorophyll a concentration ($\mu\text{g/L}$).

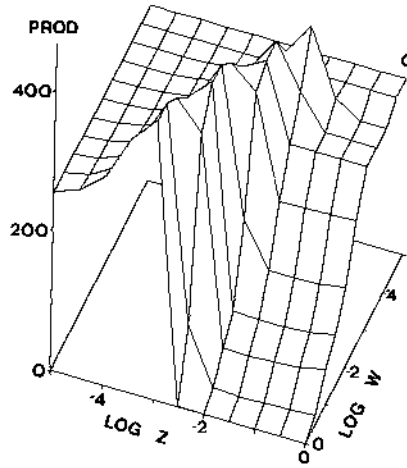


FIG. 1. (Continued)—C, Primary productivity ($\mu\text{g C} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$).

was low. Very low chlorophyll concentrations occurred when large grazers were present at high biomass. Productivity was maximal at intermediate zooplankton biomass (fig. 1C). The zooplankton biomass that optimized productivity depended on herbivore size.

The optimization of productivity at intermediate levels of zooplankton biomass was not sensitive to changes in our assumptions. Effects of selected parameters and functions were determined by modifying them and then calculating productivity response surfaces (e.g., fig. 2). Because the resulting response surfaces were similar in shape, we conserved space by plotting optimum zooplankton biomass versus mean mass of individual zooplankters (fig. 3). These graphs trace the ridges of productivity response surfaces such as figures 1C and 2.

Selectivity curves of herbivorous zooplankters take on a wide variety of shapes (cf., e.g., Gliwicz 1977 and Richman et al. 1980). We compared four alternative selectivity curves to the results of the reference run. In the first alternative, zooplankton showed no preference:

$$S(R) = 1. \quad (12)$$

In the second alternative, selectivity was maximum for cells of intermediate size:

$$S(R) = 2R/R_{\max} \quad \text{for } R \leq R_{\max}/2 \quad (13)$$

$$S(R) = 2(R_{\max} - R)/R_{\max} \quad \text{for } R \geq R_{\max}/2.$$

In the third alternative, selectivity declined linearly with cell radius:

$$S(R) = 1 - (R/R_{\max}). \quad (14)$$

Selectivity increased linearly with cell radius in the fourth alternative:

$$S(R) = R/R_{\max}. \quad (15)$$

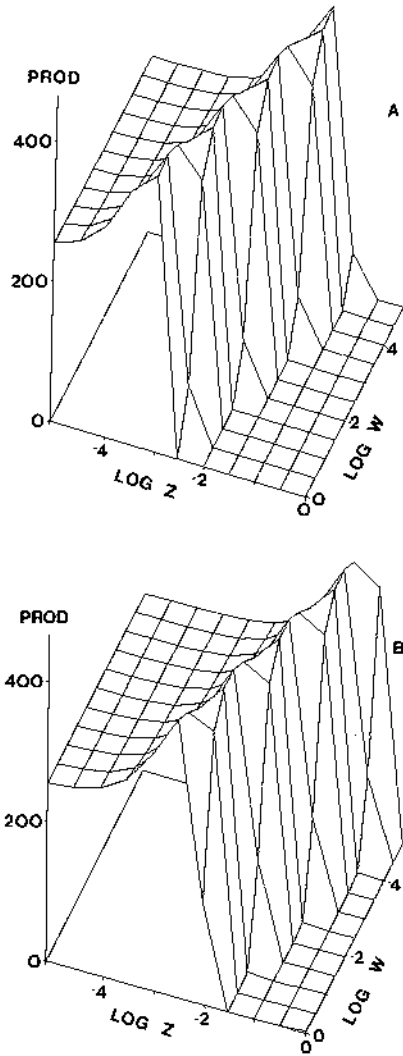


FIG. 2.—Response surfaces of primary productivity ($\mu\text{g C}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$) to zooplankton biomass (Z , mg/L) and mean zooplankton mass (W , mg) on day 6 of simulations with alternative selectivity functions. Axis scales and perspective points are identical to fig. 1C. *A*, no selectivity (eq. [12]). *B*, unimodal selectivity function (maximum selectivity for intermediate cell sizes; eq. [13]).

Productivity response surfaces were similar despite changes in selectivity functions (figs. 1C, 2). Only minor differences in the optimal zooplankton levels resulted from changing the selectivity function (figs. 3A–E). In all cases, optimal productivity occurred at intermediate zooplankton biomass.

Phosphorus excretion efficiencies of zooplankton range between ca. 20% and 80% (Peters 1975). Regardless of excretion efficiency, productivity is optimized at

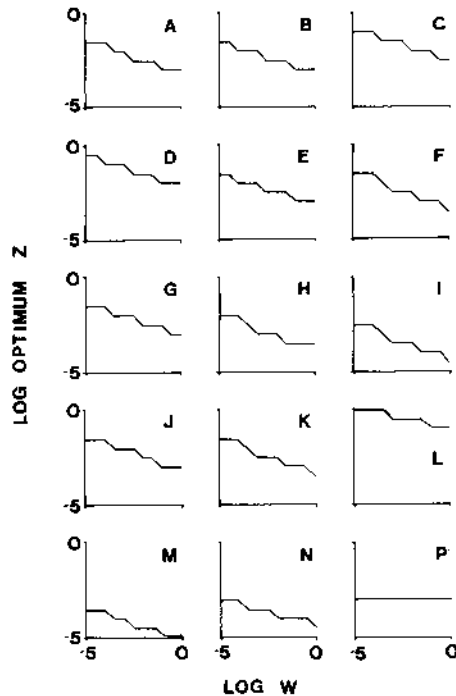


FIG. 3.—Optimum zooplankton biomass (Z , mg/L.) versus mean zooplankton mass (W , mg) for 15 versions of the model. Both axes are scaled as base 10 logarithms. *A*, reference run (cf. fig. 1C); *B*, no grazing selectivity (eq. [12], cf. fig. 2A); *C*, unimodal grazing selectivity (eq. [13], cf. fig. 2B); *D*, grazing selectivity declines with cell size (eq. [14]); *E*, grazing selectivity increases with cell size (eq. [15]); *F*, excretion efficiency = 0.2; *G*, Excretion efficiency = 0.8; *H*, influent phosphorus concentration = 0.01 μM ; *I*, influent phosphorus concentration = 1 μM ; *J*, dilution rate = 0.05 d^{-1} ; *K*, dilution rate = 0.5 d^{-1} ; *L*, grazing coefficient = 10; *M*, grazing coefficient = 10^5 ; *N*, $\alpha = 0.1$; *P*, $\beta = 1$.

intermediate zooplankton biomass (fig. 3A, F, G). Productivity increased by a factor of ca. 1.5 when excretion efficiency was raised from 0.2 to 0.8.

Influent phosphorus concentrations were varied over a hundredfold range (0.01 μM to 1 μM). Optimal productivity always occurred at intermediate zooplankton biomass (figs. 3H, I). The logarithm of productivity increased linearly with the logarithm of phosphorus supply.

Changes in dilution rate had only slight effects on productivity, and scarcely altered optimum zooplankton biomasses (figs. 3J, K).

The grazing coefficient (a) is probably the most variable parameter in the model. Values calculated from short-term grazing studies range from less than unity to more than 10^6 (S. R. Carpenter, personal observation). At very low grazing coefficients ($a = 10$) productivity was optimized at relatively high zooplankton biomass (fig. 3L). When the grazing coefficient was very high ($a = 10^5$) productivity was optimized at relatively low zooplankton biomass (fig. 3M).

Banse (1982) suggests that the exponent of the power function relating algal

metabolism and cell mass (α) may be nearer 0.1 than 0.25. When α was decreased to 0.1, optimal productivity occurred at lower, but intermediate zooplankton biomass (figs. 3A, N).

Some published evidence shows that zooplankter feeding rates are linearly proportional to zooplankter mass (Hall et al. 1976). When $\beta = 1$, the optimum zooplankton biomass is 10^{-3} mg/L regardless of zooplankter mass (fig. 3P).

DISCUSSION

The model predicts trends in algal size structure and biomass (represented by chlorophyll concentrations) that are supported by field studies. Large zooplankters and high zooplankton biomass are commonly associated with assemblages of large phytoplankters (Brooks 1969; Porter 1977; Gliwicz 1977), consistent with figure 1A. Chlorophyll *a* concentrations and phytoplankton biomass decline with increased zooplankter size (Lynch and Shapiro 1981; Shapiro and Wright 1984), consistent with figure 1B.

The general shape of the productivity response surface (fig. 1C) is a unimodal relationship between primary production and total grazing pressure, represented by zooplankton biomass. Herbivore size also influences productivity, reflecting the importance of nutrient recycling. This unimodal response is remarkably robust (figs. 2, 3). It is consistent with theoretical considerations of behavior of the system components (Glasser 1979; Huston 1979; Kitchell 1980): under moderate grazing, reduced competition enhances growth rates of surviving algae, and their small mean size increases specific nutrient uptake and recycling rates (Bartell and Kitchell 1978). Such effects are evident in herbivore regulation of primary production in terrestrial systems (Matson and Addy 1975; McNaughton 1979) as well as in aquatic systems (Hurlbert et al. 1972; Porter 1977; Wiegert et al. 1981, fig. 9.5).

In stream ecosystems, invertebrate consumers affect the rate of nutrient cycling in many ways analogous to those we develop here for zooplankton-algae interactions (Webster and Patten 1979). Newbold et al. (1982) present a modeling analysis of nutrient spiraling in streams which is similar to our model in that they conclude that optima commonly occur when invertebrate consumers alter particle size distributions and enhance nutrient recycling through excretory remineralization.

Several examples exist of consumer regulation of primary production in aquatic systems. Cooper (1973) reported highest production rates of filamentous algae in aquaria at intermediate densities of a herbivorous fish. Seale's (1980) field study recorded highest specific production rates of phytoplankton grazed by an intermediate biomass of suspension-feeding tadpoles. Low tadpole biomass levels had little effect on algal and nutrient dynamics while high tadpole biomass resulted in intense grazing which depressed both algal biomass and specific production rates. Similar enhancement effects occurred when a microbial community was selectively grazed by amphipods (Smith et al. 1982). Microcosm studies of stabilized primary production and detrital output rates by odd versus even length food chains (Elliott et al. 1983) resulted in (1) highest phytoplankton biomass in microcosms without zooplankton; (2) lowest phytoplankton biomass in microcosms with zooplankton; and (3) highest gross primary and secondary productivities in

microcosms with fish that preyed on the zooplankton. Detrital output was highest in the latter microcosms. The principles represented in these studies are currently the basis for a biomanipulation approach to water quality management (Shapiro 1980; Shapiro and Wright 1983) and fisheries management problems (Kitchell et al. 1982).

Model results indicate that biologically reasonable shifts in zooplankton biomass and/or size structure can alter primary productivity by a factor as large as several hundred (fig. 1C). For example, Kitchell and Kitchell (1980) used fossil zooplankton to document a size structure shift in Peter Lake at the University of Notre Dame Environmental Research Center. *Daphnia pulex* (mean mass ca. 0.022 mg) were substantially replaced by *Bosmina* spp. (mean mass ca. 0.006 mg) following zooplanktivore manipulations. This size shift is predicted to increase primary productivity by tenfold or more, depending on zooplankton biomass (fig. 1C). Changes in chlorophyll concentrations of comparable magnitude have occurred in biomanipulated lakes (Shapiro and Wright 1984). Lakes with the same phosphorus loading, corrected for hydraulic retention time, vary in productivity by factors as large as one hundred (Schindler 1978, fig. 3). Herbivory is sufficiently potent to account for productivity variations of 10- to 100-fold. Herbivore community structure may hold the key to much of the unexplained variance in productivity-phosphorus loading data.

Productivity was maximal at intermediate chlorophyll concentrations in the model results (fig. 4). This result indicates that linear correlations of productivity and chlorophyll should be poor, which is the case (Brylinski and Mann 1973; Oglesby 1977).

Many simple models of population dynamics, such as the logistic, postulate a unimodal relationship between growth rate and abundance (May 1981). The relationship between production and chlorophyll (fig. 4) is superficially similar to these assumptions, but results from a complex set of multispecies interactions, including competition for a limiting nutrient, grazing, and nutrient recycling by herbivores.

Our analysis illustrates a mechanistic relationship between plankton community structure and lake ecosystem primary productivity. Dependence of ecosystem processes on community or population processes in no way detracts from the appropriateness of the ecosystem as an object of scientific study. The distillation from detailed mechanistic models of simple relationships among aggregate variables (such as primary productivity, chlorophyll, and zooplankton biomass) complements and strengthens comparative studies of aggregate properties of ecosystems. If the apparently conflicting paradigms of population and ecosystem biology (McIntosh 1980) are to be evaluated and perhaps ultimately reconciled, then links between ecosystem, community, and population phenomena are especially worthy of study.

SUMMARY

A mechanistic, size-structured model was used to analyze effects of grazers on lacustrine primary productivity. Dependence of grazing and nutrient excretion

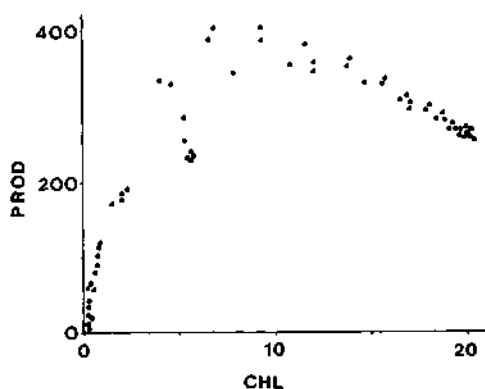


FIG. 4.—Primary productivity ($\mu\text{g C}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$) vs. chlorophyll *a* concentration ($\mu\text{g/L}$) for the reference run (cf. figs. 1B, 1C).

rates on herbivore size, and dependence of algal metabolic rates on cell size, interacted to produce strong responses in primary productivity. Productivity was maximum at intermediate concentrations of chlorophyll and zooplankton biomass. This unimodal response is consistent with data from aquatic systems, terrestrial systems (where the underlying mechanisms are different), and theoretical expectations. Substantial variability in lake productivity (2 to 3 orders of magnitude) exists that cannot be explained by nutrient supply. Food web interactions can regulate herbivorous zooplankton size and abundance, independent of nutrient supply. The resultant variability in herbivory influences nutrient recycling and the size distribution of the phytoplankton, and can alter lake primary productivity by as much as two orders of magnitude.

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