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THE TEMPORAL SCALE OF VARIANCE IN LIMNETIC PRIMARY PRODUCTION

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The productivity of temperate lakes spans a thousandfold range. Nutrient loading explains nearly half ($r^2 = 0.48$) of this variability, yet when nutrient effects are removed statistically, the range of productivities about the regression line is still a hundredfold (Schindler 1978). Regional climate and methodology account for some of this variability, but even when lakes lie in similar watersheds, experience the same weather, and are sampled by standardized methods, their productivity varies about tenfold (Schindler et al. 1978). Many physical and biological processes, with time scales ranging from minutes to years, could contribute to variability in productivity (Harris 1980). This spectrum of variability has not been analyzed by limnologists. Generally, we sample regularly (weekly, biweekly) and calculate annual production, thereby limiting our analyses to one or two time scales. The unexplained variability that we observe may be caused by a host of dynamic processes occurring at time scales that have been neglected (Harris 1980).

Better understanding of the variability of productivity is necessary for the advancement of both basic research on lake ecosystems and lake management. Because whole-ecosystem experiments on lakes (e.g., Hasler 1964; Schindler 1974) are generally not replicated, they have low statistical power and must achieve massive treatment effects to succeed (Hurlbert 1984). However, responses that are not statistically detectable by present methods may be very significant ecologically. Knowledge of typical variability, the time scales on which it occurs, and the mechanisms that generate it will enhance the sensitivity of ecosystem experiments. Such basic information about variability is also needed to detect effects of pollutants, watershed changes, or management schemes on lake productivity (Likens 1983).

We have suggested a hypothesis, cascading trophic interactions, for the unexplained variability in lake productivity (Carpenter et al. 1985). A predator-induced cascade of effects is clearly demonstrated at the community level through food-web interactions (Paine 1980). We extend these effects to the ecosystem level by proposing that fluctuations in piscivory propagate through the food web, causing

changes in planktivory, herbivory, and primary production. The resulting dynamics of primary production result from variable recruitment of fishes (Pitcher and Hart 1982) and their consequent effects on food webs. Variability in recruitment success seems an inherent property of many fish populations, as might be expected given the huge fecundities of most fish species (Stearns 1977). The processes that regulate year-class strength are many and complex, differing among years and species. Regardless of the cause, the effects of a large or small year class are transient since the diets of the fishes change during ontogeny (Werner and Gilliam 1984). Consequently, the food web varies at all trophic levels (Carpenter et al. 1985). We propose that a large component of the observed variance in primary production is evoked through feedback from the top carnivore.

This paper estimates the potential variability in primary production that results from variability in fish populations and compares it with the observed variability in productivity known from many lakes. We used a simulation model to estimate the variability in primary production caused by food-web effects. Model results were then compared with the known variability of both fish populations and primary production.

As advocated by Allen et al. (1984), we explicitly discuss the time scales on which variance is expressed. In the familiar formula for the sample variance,

$$s^2 = \sum_{i=1}^n (x_i - \bar{x})^2 / (n - 1),$$

the x_i are measurements of production for a specified time period (hourly, daily, annually, etc.) and \bar{x} is the mean of a series of these x_i . Two time scales are evident in the formula: that of an individual measurement (x_i), and that of the series of measurements. Here the time scale of a variance refers to the time scale of an individual measurement.

The time scales of variance in productivity caused by piscivore effects are dictated by the life histories of the fishes. Results of previous studies of food-web effects on phytoplankton prompted us to focus our efforts on two time scales: (1) among days within the period of stable summer stratification, and (2) among summers within a series of several years. Algal dynamics depend heavily on physical factors during periods of mixing (Reynolds 1984; Ashton 1985), thereby muting food-web effects. However, systems that have experienced massive changes in fish-community composition exhibit marked changes in chlorophyll concentration and productivity during summer periods of thermal stratification (Henriksen et al. 1980; Shapiro and Wright 1984; Mills et al. 1987; Scavia et al. 1986; Carpenter et al., MS). These changes are evident on at least two time scales. First, the day-to-day progression of chlorophyll concentration and productivity during summer stratification depends on fish-community structure (Mills et al. 1987; Scavia et al. 1986; Carpenter et al., MS). Second, changes in summer mean production and chlorophyll concentration were documented in all of these studies. Paleolimnological analyses suggest that food-web changes can systematically alter the interannual variability of plankton for periods of a decade or more (Kitchell and Carpenter 1987, unpubl. data).

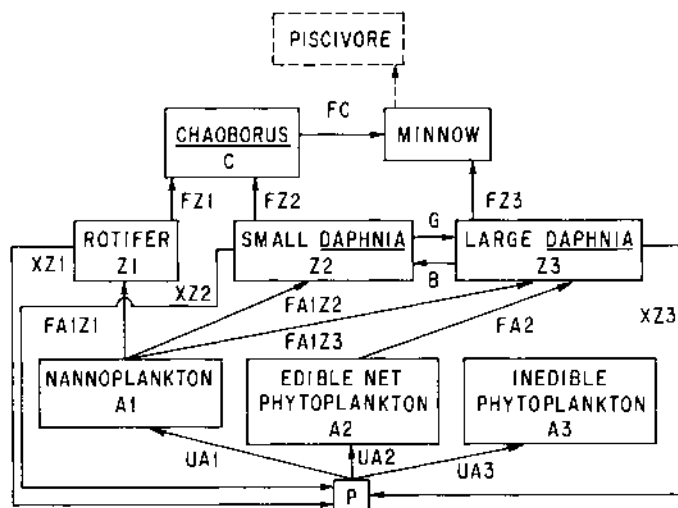


FIG. 1.—Compartments and interactions considered in the model. Symbols are given for dynamic variables and their interactions. *Dashed lines*, the regulation of the minnow population by piscivory.

MODEL: RATIONALE AND GENERAL STRUCTURE

The variability of fish populations and physical and chemical factors in lakes both have proximal causes in the vagaries of climate. However, meteorological effects and food-web effects on productivity are not linked because they operate on different time scales. In general, meteorological events directly affect phytoplankton within days (Reynolds 1984). Variability in production induced by climate is evident in seasonal patterns of production (Ashton 1985) and in the tendency of productivity to become more variable as latitude increases (Melack 1979). However, ecosystem effects of a strong year class of fishes are felt for years after its spawning and could cause substantial variability at time scales of one to many years (Carpenter et al. 1985).

Our goal was to estimate the potential variability in production attributable to fish populations but independent of short-term meteorological fluctuations. Therefore, we used a deterministic model that assumed constant temperature, irradiance, and nutrient supply, such that the emerging temporal variability was caused entirely by system dynamics and could not be attributed to methodology, weather, or nutrient loading. Each run of the model simulated 100 days in the epilimnion during summer stratification. Each run was identical except for the parameters determining fish predation. The rate and selectivity of planktivory by fishes was varied to simulate different levels of fish biomass and species composition. Thus, the model addressed variability at two time scales: (1) among days within 100-day periods of stratification, and (2) among 100-day periods of stratification.

Our choice of compartments for the model reflected our experience with lakes of the upper Midwest (fig. 1). However, the functional groups represented in the

model (vertebrate planktivore, invertebrate planktivore, large and small herbivores, and large and small algae) are major food-web components in most temperate lakes. We included compartments representing planktivorous fishes (minnows), an invertebrate planktivore (*Chaoborus*), three size classes of herbivore (rotifers, juvenile *Daphnia*, and adult *Daphnia*), three size classes of phytoplankton, and the limiting nutrient, phosphorus (fig. 1). Phytoplankton classes represented groups of algae that respond differently in grazing experiments (Bergquist 1985; Bergquist et al. 1985; Bergquist and Carpenter 1986): nanoplankton (1–10 μm), edible net plankton (10–60 μm), and inedible plankton (greater than 60 μm).

Fish effects were introduced through changes in predation rates of minnows on *Chaoborus* and adult *Daphnia*. Raising or lowering these predation rates simulated increases or decreases in the minnow populations as a result of piscivory. Adjustments in the relative magnitudes of the two predation rates represented changes in the proportions of *Chaoborus* and *Daphnia* in the minnows' diets. Thus, we were able to simulate the effects of planktivory by a full range of fish-community types, from assemblages that prey heavily on zooplankton to assemblages dominated by piscivores that consume few zooplankton (Tonn and Magnuson 1982).

METHODS AND MODEL DETAILS

This section presents the equations used in the model. Parameter values used in the simulations reported here are shown in the Appendix.

The dynamics of *Chaoborus* were modeled after those of *C. flavicans*. In this species, reproduction occurs in June and most of the stratified summer period is spent as a third- or fourth-instar larva (von Ende 1982). The population of larvae, C (animals per liter), declines because of mortality and predation:

$$dC/dt = -(MC + FC). \quad (1)$$

The instantaneous rate of nonpredatory mortality, MC , was set to zero in the simulations reported here. Thus, attrition of the invertebrate planktivore was due entirely to predation by minnows, FC .

The two *Daphnia* compartments ($Z2$ = small *Daphnia*, $Z3$ = large *Daphnia*, both in animals per liter) were linked by growth and reproduction:

$$dZ2/dt = B - G - FZ2 - MZ2, \quad (2)$$

$$dZ3/dt = G - FZ3 - MZ3. \quad (3)$$

Growth (G) and reproduction (B) functions were fit to the data of Porter et al. (1983) for *Daphnia magna*. Reproduction rates depended on the concentration of edible algae, A_E (equal to $A1 + A2$):

$$B = r_{\max} \{1 - [\log(A_E/A_o)/\log(A_o/A_{\min})]^2\} Z3. \quad (4)$$

A_o , the optimum algal concentration, was 2 mg carbon (C) per liter and A_{\min} , the minimum algal concentration for reproduction, was 0.02 mg C per liter (Porter et al. 1983). Maximum reproduction rate, r_{\max} , was scaled to ingestion rate (see below) using a ratio of growth to ingestion of 0.21 (Peters 1983). The rate of

growth of juvenile *Daphnia* to adults was a function of ingestion by the juvenile *Daphnia*:

$$G = 0.21 (FA1Z2/W) Z2, \quad (5)$$

where 0.21 is the ratio of growth to ingestion (Peters 1983), I is the daily ingestion rate per juvenile *Daphnia* (see below), and W is the mass gain necessary to grow from the $Z2$ category to the $Z3$ category (set at 50 $\mu\text{g C}$ per animal for these simulations).

Losses from both *Daphnia* size classes occurred through predation ($FZ2$, $FZ3$) and nonpredatory mortality ($MZ2$, $MZ3$). Above the minimum food concentration (0.02 mg C per liter; Porter et al. 1983), nonpredatory mortality was set to zero in simulations reported here. Below the minimum food concentration, the starvation rate was estimated from the data of Threlkeld (1976). Predation on small *Daphnia* by *Chaoborus* followed the function of Ivlev (1961):

$$FZ2 = a[1 - \exp(-bZ2)]C. \quad (6)$$

The coefficients of the Ivlev function, a and b , were estimated by nonlinear regression using the data of Fedorenko (1975).

Rotifer dynamics ($Z1$, animals per liter) followed

$$dZ1/dt = B - FZ1 - MZ1. \quad (7)$$

Reproduction of rotifers, B , followed equation (4), with A_0 and A_{\min} calculated by curve fits to the data of King (1967) for *Euchlanis dilatata*, $A_E = A1$, and r_{\max} estimated from the maximum ingestion rate (see below) and a ratio of growth to ingestion of 0.21 (Peters 1983). Predation by *Chaoborus* on rotifers ($FZ1$) followed equation (6), with $Z1$ replacing $Z2$ in the exponent. *Chaoborus* were not selective in the model; they consumed rotifers and young *Daphnia* in direct proportion to their densities. Nonpredatory mortality of rotifers ($MZ1$) was set to zero when the food supply exceeded A_{\min} . At food levels below A_{\min} , the starvation rate was estimated from the data of Threlkeld (1976).

Dynamics of the algae and phosphorus were taken directly from our model of zooplankton-phytoplankton interactions (Carpenter and Kitchell 1984), as were the conversion factors for algal cell volume, carbon content, and chlorophyll content. Equations for the algal and nutrient compartments are

$$dA1/dt = g(A1) - DA1 - (FA1Z1 + FA1Z2 + FA1Z3), \quad (8)$$

$$dA2/dt = g(A2) - DA2 - FA2, \quad (9)$$

$$dA3/dt = g(A3) - DA3, \quad (10)$$

$$d[P]/dt = D([P]_0 - [P]) + (XZ1 + XZ2 + XZ3) - [g(A1) + g(A2) + g(A3)]/Y. \quad (11)$$

Algal concentrations ($A1$, $A2$, and $A3$) were in $\mu\text{g C}$ per liter, and phosphorus concentrations $[P]$ were micromolar. Growth rates $g(X)$ for algal group X followed hyperbolic functions of phosphorus concentration:

$$g(X) = V_{\max}[P]/(K_m + [P]). \quad (12)$$

Maximum growth rates (V_{\max}), half-saturation constants (K_m), nongrazing loss rates (D), and cell carbon per unit of phosphorus (Y) were taken from Carpenter and Kitchell (1984). Grazing functions ($FA1Z1$, $FA1Z2$, $FA1Z3$, and $FA2$) followed the Ivlev (1961) equation, where $L(X, H)$ is loss from algal compartment X from grazing by zooplankton compartment H :

$$L(X) = a[1 - \exp(-bX)]H. \quad (13)$$

The data of Porter et al. (1982) provided estimates of b . The maximum ingestion rates, a , were calculated from the cladoceran regression of Peters and Downing (1984) for each alga-grazer combination at the optimum food concentration of 2 mg C per liter (Porter et al. 1983) and median values of all other variables. Excretion of phosphorus ($XZ1$, $XZ2$, and $XZ3$) was equal to 50% of the phosphorus ingested by each zooplankton compartment (Peters 1975).

Primary production (PPR) equaled the combined growth rates of all three algal groups:

$$PPR = g(A1) + g(A2) + g(A3). \quad (14)$$

This definition of PPR approximates measurements of ^{14}C fixation during incubations lasting less than a day (Reynolds et al. 1985). Our PPR data, and most of the literature PPR values that we present, used this method.

The model was implemented in FORTRAN using the Adams-Bashforth integration method (Hildebrand 1976), a time step of 0.04 days, and double-precision arithmetic. Coefficients of variation and correlations as a function of time scale were calculated by the random-pairing method (Goodall 1974) using the program of Carpenter and Chaney (1983).

Literature data were used to calculate some variances of primary production and to estimate all parameters of the model. When possible, data or curve fits were obtained directly from tables or the text. Otherwise, data were obtained from published graphs by analyzing photographic enlargements with an electronic digitizer. Phosphorus-loading effects were removed from temperate-lake and Experimental Lakes Area data by fitting a power function using nonlinear regression. Coefficients of variation were calculated as the ratio of the standard deviation of the residuals to the grand mean. Other data were not analyzed by regression, and coefficients of variation were calculated by standard procedures.

RESULTS

Time courses generated by the model exhibited patterns of zooplankton biomass, chlorophyll, and primary production similar to those observed in lakes during summer stratification. For example, *Daphnia* oscillations, algal blooms, transitions among algal groups, and clear-water phases occurred at various levels of planktivory by minnows. When phosphorus levels and predation intensities on *Chaoborus* and *Daphnia* were adjusted to those found in Peter Lake, Michigan (Carpenter et al. 1986), model predictions were similar to our observations (fig. 2). We conclude that the range of dynamic behavior expressed by the model is a reasonable representation of the dynamics occurring in the mixed layers of lakes during summer stratification.

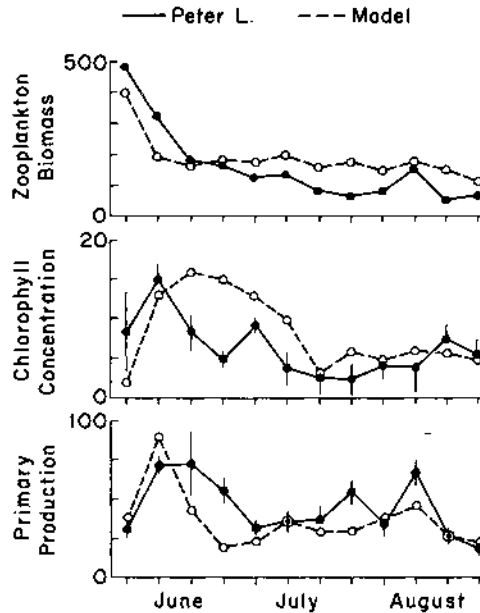


FIG. 2.—Predictions of the model and observations in Peter Lake, June 5–August 21, 1984. *Top*, zooplankton biomass, mg dry mass m^{-3} ; *middle*, chlorophyll *a* concentration in the epilimnion, mg m^{-3} ; *bottom*, primary production in the mixed layer, mg C m^{-3} day $^{-1}$. Vertical bars denote 95% confidence intervals based on three mixed-layer samples.

TABLE 1

ANALYSIS OF VARIANCE FOR SIMULATIONS IN A FACTORIAL DESIGN WITH SIX LEVELS OF PREDATION BY MINNOWS ON *Daphnia* BY SIX LEVELS OF PREDATION BY MINNOWS ON *Chaoborus*

Source of Variance	df	Variance
Among summers		
Fish predation on large <i>Daphnia</i>	5	3288
Fish predation on <i>Chaoborus</i>	5	830
Interaction	25	374
Within summers	468	92

NOTE.—The dependent variable was daily primary production, which was recorded 14 times at 7-day intervals in each of the 36 simulations.

Effects of minnow predation on primary production were assessed in a factorial design with six levels of predation on *Chaoborus* and six levels of predation on *Daphnia*. For each independent variable, the minimum predation rate was zero and the maximum predation rate resulted in extinction of the prey population within 20 days. The simulations were sampled every 7 days to mimic the typical weekly sampling regimen of limnologists. An analysis of variance was used to summarize the results (table 1). Fish predation on both *Chaoborus* and *Daphnia*

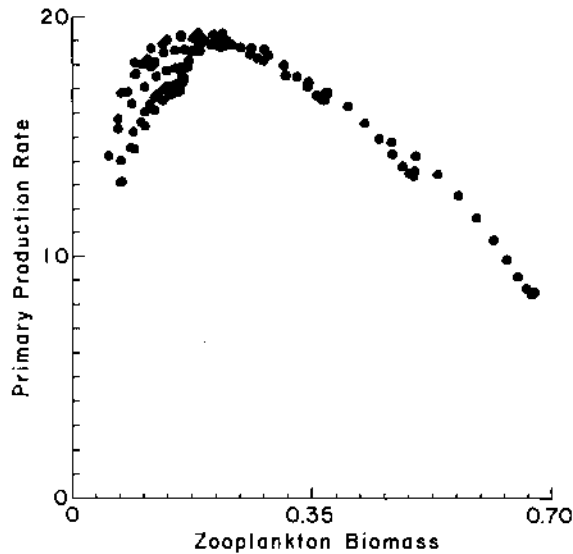


FIG. 3.—Mean daily primary production ($\text{mg C m}^{-3} \text{ day}^{-1}$) versus mean zooplankton biomass ($\text{mg dry mass per liter}$) from 100-day simulations over a range of predation intensities on large *Daphnia* and *Chaoborus*.

affected primary production. Predation on *Daphnia* had the strongest effect on primary production. Whole-lake experiments in which planktivore populations were manipulated have produced similarly strong effects on large, crustacean grazers and phytoplankton (Henrikson et al. 1980; Shapiro and Wright 1984; Carpenter et al., MS).

At the seasonal scale, primary production was related unimodally to zooplankton biomass, with maximum production occurring at intermediate zooplankton biomass (fig. 3). Carpenter and Kitchell (1984) predicted a similar unimodal relationship at shorter time scales of a few days. Bergquist and Carpenter (1986) found such a unimodal relationship empirically for grazed algae in 4-day, in situ, mesocosm experiments.

The correlation between zooplankton biomass and primary production depended on the time scale (fig. 4). For example, when daily mean production and daily mean zooplankton biomass were calculated for 10-day periods, their correlation coefficient was $+0.90$. In contrast, when daily mean production and daily mean zooplankton biomass were calculated for 3-day periods, their correlation coefficient was -0.67 . Significant negative correlations occurred at time scales of 3–4 days, whereas significant positive correlations occurred at sampling intervals of 10 to 20 days. At longer time scales (more than 50 days), the unimodal relationship (fig. 3) appeared. These results help to reconcile short-term grazing experiments, in which enhanced grazing frequently decreases chlorophyll and primary production, with correlations on an annual scale, which show positive relationships of zooplankton and phytoplankton biomass (McCauley and Kalff 1981).

It is fortuitous that the weekly sampling interval typically practiced by lim-

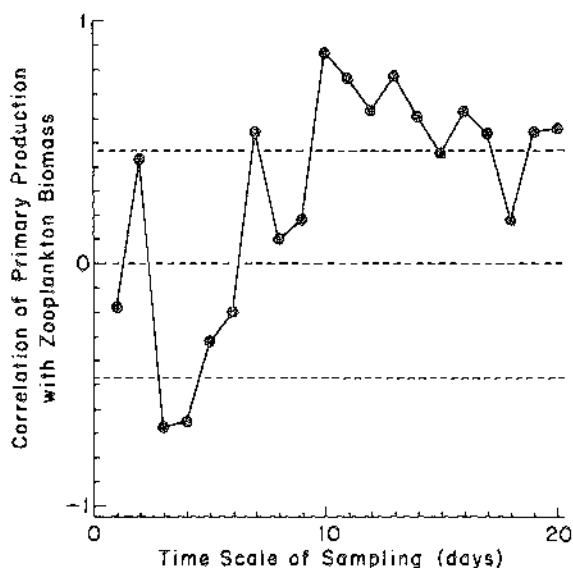


FIG. 4.—Pearson product-moment correlation coefficient of primary production with zooplankton biomass versus time scale (days) for a time series calculated by the model. Dashed lines: upper and lower denote statistically significant correlations ($P < 0.05$); middle line denotes zero correlation.

nologists yielded a significant positive correlation (fig. 4). Even though primary production and zooplankton biomass are directly linked in the model, they are uncorrelated at certain time scales (fig. 4). Increasing the sample size is the usual means of resolving a poor correlation among variables that are known to be strongly related in principle. However, more-intensive sampling without attention to time scale is likely to increase the confusion, rather than resolve the correlation. Substantial amounts of data collected at a fixed sampling scale may never appear in published reports because the strong correlations expected by the investigators did not occur. The time-scale effects evident in the results of our model emphasize the importance of sampling design in empirical analyses of dynamic systems.

The variance of actual primary-productivity data similarly depends on the time scale. We used polynomial regression to remove irradiance effects from summer volumetric productivity of three lakes with contrasting plankton assemblages. Details of the ^{14}C -fixation determinations and productivity calculations appeared elsewhere (Carpenter et al. 1986).

Substantial variance was not explained by fluctuations in irradiance, and this residual variance depended on the time interval over which production was averaged (fig. 5). The variance at a scale of zero, which corresponds to the variance among replicate carbon-fixation profiles on the same day, is much less than the variance at other time scales. Therefore, the variance in figure 5 is not a consequence of methodology, but results from system dynamics independent of variability in irradiance. In Paul and Peter lakes, the coefficient of variation rose to a peak at a scale of 7 days, and did not increase substantially at longer scales.

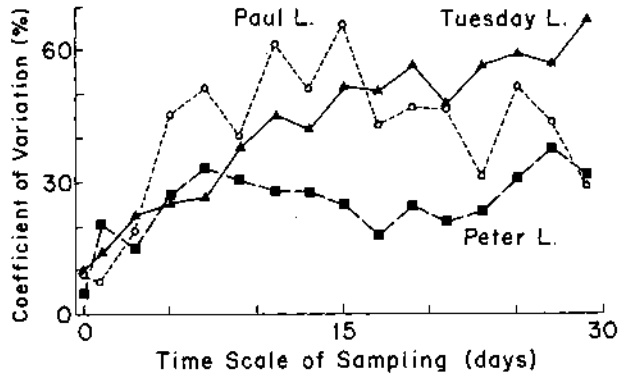


FIG. 5.—Coefficient of variation versus sampling scale (days) for variability in primary production not explained by irradiance in Paul (circles), Peter (squares), and Tuesday (triangles) lakes, June–August 1984.

Thus, the full range of variation in summer production of these lakes occurred in the average 7-day period. In Tuesday Lake, the coefficient of variation rose throughout the range of scales that we studied, and at least 30 days of data were needed to characterize the full range of variation in summer production. This longer variance component in Tuesday Lake is related to the ontogeny of the minnows dominating its food web. Paul and Peter lakes lack minnows and are dominated by piscivorous bass (Carpenter et al., MS).

The coefficients of variation of primary production from several sources are collected in table 2. These data show comparable variability at several different spatial and temporal scales. For temperate, phosphorus-limited lakes ($[N]/[P] > 5$), the coefficient of variation of annual primary production was nearly 100% when phosphorus-loading effects were removed. This variability includes effects of regional geology and climate, as well as methodological differences among laboratories. The Experimental Lakes Area lakes, which lie within a single geologic formation, experience the same climate, and have been sampled by standardized methods, have a much lower coefficient of variation of 43%. Within-lake variability of annual primary production has coefficients of variation of 16% to 30% for oligotrophic Castle Lake, mesotrophic Lawrence Lake, and eutrophic Lake Wingra. Variability among samples within a year is somewhat greater. Coefficients of variation through the annual cycle at scales of 1 wk to 3 mo were 15% to 86% for tropical lakes and 29% to 155% for temperate lakes. The temperate lakes were significantly more variable than the tropical lakes (Melack 1979). During summer stratification, we found coefficients of variation of 35% to 48% for daily primary production in Paul, Peter, and Tuesday lakes.

The variability in primary production in mesocosms and models that simulate food-web effects is similar to the variability known from lakes (table 2). Coefficients of variation of primary production among grazer treatments in mesocosms incubated in situ ranged from 18% to 108%. Our earlier model (Carpenter and Kitchell 1984, fig. 1C), which essentially simulated mesocosm experiments, gave a coefficient of variation among grazer treatments of 47%. The present model

TABLE 2
COEFFICIENTS OF VARIATION FOR PRIMARY PRODUCTION AT SEVERAL SCALES

Spatial Scale	Temporal Scale	Coefficient of Variation (%)	Source
Temperate lakes	annual	91	Schindler 1978
Experimental Lakes Area lakes	annual	43	Fee 1979
Within lake	annual	16-30	Goldman & de Amezaga 1984; Wetzel 1983; Prentki et al. 1977
Within lake	1 wk-3 mo, annual cycle	15-86	Melack 1969, tropical
Within lake	daily, summer only	29-155	Melack 1969, temperate
Among food-web treatments	4-14 days	35-48	Carpenter et al. 1986
	6 days	18-108	Bergquist 1985, mesocosms
	100 days	47	Carpenter and Kitchell 1984, model
	daily	23	this paper
		44-142	this paper

exhibits coefficients of variation of 44% to 142% on a daily scale and of 23% on a 100-day scale among levels of planktivory by minnows.

DISCUSSION

The model results depend, of course, on the compartments that were included as well as the specific functions and parameters that were selected to represent the interactions. Structural changes in the model would alter both the magnitude and the time scale of the variability in production. For example, inclusion of bacterioplankton that competed with phytoplankton for excreted nutrients would weaken and delay the positive feedback between zooplankton and algae. Variance of productivity would increase at certain scales, because recycling would be less effective in compensating for grazing losses. At other scales, variance of productivity would decrease because phosphorus flux to the algae was delayed and smoothed by transfer through the bacterioplankton compartment. This example is one of many conceivable modifications that would alter the variance structure of the model results. However, two important points are quite general. (1) The variance of primary production and its covariance with other dynamic variables are a function of sampling scale. (2) Variance in biomass of the top carnivore evokes substantial variance in primary production at certain time scales.

These results show that variation in primary production caused solely by food-web effects is similar in magnitude to the known variability that cannot be explained by nutrient supply. On a daily scale, the coefficients of variation of production are similar for lakes and for the model. In the model, variance results from food-web interactions only; the variance of the lake data results from additional meteorological factors as well as food-web dynamics. On an annual

scale, the coefficients of variation of production are similar for the model and for data sets of many years from temperate lakes. The variance of the lake data results from fluctuations in the water-renewal time (Schindler et al. 1978; Goldman and de Amezaga 1984) as well as food-web dynamics. Interlake variability in annual production, which reflects morphometric factors (Fee 1979) and hydrologic factors (Schindler et al. 1978) as well as food-web differences, is greater than the variability shown by the model. Collectively, these data show that fish population dynamics, translated through the food web, could be a major factor in the variability of primary production. Experimental manipulations of lake fish assemblages confirm this inference (Henrikson et al. 1980; Shapiro and Wright 1984; Carpenter et al., MS). The known variability in fish populations indicates that food-web effects on productivity may be very common in lakes.

Fish populations are highly variable. With few exceptions, empirical, experimental, and theoretical assessments of fish population dynamics reveal highly stochastic recruitment (Connell and Sousa 1984; Pitcher and Hart 1984). An analysis of recruitment found coefficients of variation of 25% to 143%, and ratios of high to low year classes ranging from 2.5 to 2700, for 18 intensively monitored marine fish stocks (Hennemuth et al. 1980). The distribution of year-class sizes was lognormal. Large year classes were more common than reproductive failures, and neither was predictable. No general pattern of density dependence or density independence could be discerned. In most cases, there was no correlation among sequential year classes. Variability of similar magnitude occurs in freshwater fish populations (LeCren 1962). For example, ratios of high to low year classes in percids are 10 to 400 (Koonce et al. 1977), and those for largemouth bass range up to 2000 (Summerfelt 1975).

Stock-recruitment models are a cornerstone of fisheries biology, yet are considered an example of models that consistently fail (Hall and DeAngelis 1985). Fish recruitment is "density-vague" (Strong 1984); that is, recruitment is only weakly explained by stock size. Density dependence is most evident at low stock densities, where recruitment and stock size are positively related, and at high stock densities, where recruitment declines as the stock increases. Over a broad intermediate range of stock densities, recruitment is highly variable and may be uncorrelated with stock size (cf. Pitcher and Hart 1984, fig. 6.6, with Strong 1984, fig. 1).

Although the mechanisms of variability in fish recruitment remain problematic, two conclusions can be drawn with regard to the cascade hypothesis: (1) the magnitude of variation in recruitment is equal to or greater than the unexplained variance of primary production, and (2) the effects of a large cohort will be expressed in food-web interactions throughout the lifetime of the fishes. Variability at lower trophic levels is enhanced through trophic ontogeny as members of a year class grow and feed on progressively larger prey and/or become large enough to avoid predation (Werner and Gilliam 1984). Predation by a large year class may alter food-web structure for many years as the adult fishes continue to prey on smaller fish ("predatory inertia"; Stewart et al. 1981) and episodically produce large numbers of recruits, which in turn undergo trophic ontogeny ("storage effect"; Warner and Chesson 1985).

Two examples illustrate cascading food-web effects at different time scales.

Long-term studies at Oneida Lake, New York, revealed that year-class strength of yellow perch (*Perca flavescens*) varied by about 400-fold. In 6 of the 18 years of observation, strong year classes caused collapse of *Daphnia* populations in mid-summer, resulting in reduced grazing, increased algal concentrations, and lower water transparencies (Mills et al. 1987). Thus, the trophic ontogeny of a single year class of one species was expressed as intra-annual variance of aggregate limnological variables. Among-year variability is demonstrated by recent changes in Lake Michigan (Kitchell and Carpenter 1987; Kitchell and Crowder 1986). Predation by stocked salmon and trout increased mortality and reduced the biomass of planktivorous alewife, which, since 1983, has resulted in dramatic late-summer increases in large *Daphnia*, greater grazing, lower algal densities, and increased water transparencies (Scavia et al. 1986). Over a decade of observations, the magnitude of interannual difference induced through food-web effects in 1983–1985 was about the same as that induced by severe meteorological conditions in 1977 (Scavia et al. 1986).

A paradox emerges from our analysis. The fish populations of most lakes are managed and exploited. The goal of management is to achieve stock densities that permit near-maximal, predictable, sustainable yields (Pitcher and Hart 1982). These are the intermediate stock densities at which variability in recruitment is maximal. Thus, the result of carefully considered and closely regulated harvest strategies is the maximization of variation in recruitment, its expression through food-web interactions, and the unexplained variance in ecosystem behavior. When fish-population models are applied to such stochastic systems, they will likely be judged as failures (Hall and DeAngelis 1985). This has been a common experience for fisheries managers, and has led them to seek alternatives. Among these has been a plea to limnologists and ecologists for help in assembling empirical models that will yield better predictions of fishery yields (Rigler 1982). Of course, the researchers will be studying lakes in which plankton communities are highly variable because of food-web effects deriving from the management of the fishery. It should be no surprise, then, that fishery yield correlates only weakly with primary production (Brylinsky and Mann 1973).

The unpredictability of ecosystems remains a major challenge for researchers and managers. Much of this variance originates in the weather, but feedbacks within ecosystems alter the time scales at which variability is expressed, thereby increasing the apparent stochasticity of ecosystems. Thus, attempts to analyze ecosystems by direct regression methods leave much variance unexplained and yield conflicting results when relationships are unimodal or a function of sampling scale. More-explicit attention to the scales at which variance occurs would be profitable, because the predominant mechanisms may be predictable and manageable at certain time scales.

SUMMARY

Substantial variability in the productivity of the world's lakes cannot be explained by methodology, weather, hydrology, or nutrient supply. A deterministic model shows that variable piscivory, cascading through the food web and causing fluctuations in planktivory, herbivory, and primary production, can bring about variability in primary production comparable in magnitude and time scale to the

variability that cannot be explained by physical or chemical factors. The variance of productivity and the correlation between primary production and zooplankton biomass are functions of the time scale over which model results were averaged. The scatter of data around regressions of annual production versus nutrient loading represents internal system dynamics at a host of time scales, some of which may be regulated by fish populations. An important consequence of these dynamics is that variances and covariances of limnological variables are strongly related to sampling scale. Nutrient loading, hydrology, and spring mixing establish the potential summer productivity of lakes. The realized productivity depends in part on the configuration and dynamics of the food web, which are largely determined by the top carnivore in the system.

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APPENDIX

PARAMETERS USED IN THE SIMULATIONS

Parameter	Equation	Value and Units
a	2,6,7	21 prey predator ⁻¹ day ⁻¹
	8,13	3.04 $\mu\text{g C animal}^{-1}$ day ⁻¹ for large <i>Daphnia</i> 0.34 $\mu\text{g C animal}^{-1}$ day ⁻¹ for small <i>Daphnia</i> and rotifers
A_{min}	9,13	210 $\mu\text{g C animal}^{-1}$ day ⁻¹
	2,4	0.02 mg C/liter
A_{o}	2,4	2 mg C/liter
b	2,6,7	0.033 liter/prey
	8,13	4.3×10^{-3} liter/ $\mu\text{g C}$
D	9,13	3.4×10^{-5} liter/ $\mu\text{g C}$
	8,11	0.02 day ⁻¹
FC	1	variable between 0 and 0.3 day ⁻¹
$FZ3$	3	variable between 0 and 0.3 day ⁻¹
K_{m}	8,11,12,14	0.26 μM
	9,11,12,14	1.3 μM
	10,11,12,14	3.1 μM
MC	1	0 day ⁻¹
$MZ1, MZ2, MZ3$	2	0 day ⁻¹ when $A_{\text{E}} > A_{\text{min}}$
		0.1 day ⁻¹ when $A_{\text{E}} < A_{\text{min}}$
P_{o}	11	0.025 μM
V_{max}	8,11,12,14	3 day ⁻¹
	9,11,12,14	2 day ⁻¹
	10,11,12,14	1.6 day ⁻¹
W	2,3,5	50 $\mu\text{g C/animal}$
Y	8-12,14	1.272 $\mu\text{g C}/\mu\text{mole P}$

NOTE.—Equations and the sources of the data are given in the text.

LITERATURE CITED

- Allen, T. F. H., R. V. O'Neill, and T. W. Hoekstra. 1984. Interlevel relations in ecological research and management: some working principles from hierarchy theory. U.S. For. Serv. Tech. Rep. RM-110.
- Ashton, P. J. 1985. Seasonality in Southern Hemisphere freshwater phytoplankton assemblages. *Hydrobiologia* 125:179-190.
- Bergquist, A. M. 1985. Effects of herbivory on phytoplankton community composition, size structure, and primary production. Ph.D. diss. University of Notre Dame, Notre Dame, Ind.
- Bergquist, A. M., and S. R. Carpenter. 1986. Limnetic herbivory: effects on phytoplankton populations and primary production. *Ecology* 67:1351-1360.
- Bergquist, A. M., S. R. Carpenter, and J. C. Latino. 1985. Shifts in phytoplankton size structure and community composition during grazing by contrasting zooplankton assemblages. *Limnol. Oceanogr.* 30:1037-1045.
- Brylinsky, M., and K. H. Mann. 1973. An analysis of factors governing productivity in lakes and reservoirs. *Limnol. Oceanogr.* 18:1-14.
- Carpenter, S. R., and J. E. Chaney. 1983. Scale of spatial pattern: four methods compared. *Vegetatio* 53:153-160.
- Carpenter, S. R., and J. F. Kitchell. 1984. Plankton community structure and limnetic primary production. *Am. Nat.* 124:159-172.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634-639.
- Carpenter, S. R., M. M. Elser, and J. J. Elser. 1986. Chlorophyll production, degradation, and sedimentation: implications for paleolimnology. *Limnol. Oceanogr.* 31:112-124.
- Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. *Am. Nat.* 121:789-824.
- Fedorenko, A. Y. 1975. Feeding characteristics and predation impact of *Chaoborus* (Diptera, Chaoboridae) larvae in a small lake. *Limnol. Oceanogr.* 20:250-258.
- Fee, E. J. 1979. A relation between lake morphometry and primary productivity and its use in interpreting whole-lake experiments. *Limnol. Oceanogr.* 24:401-416.
- Goldman, C. R., and E. de Amezaga. 1984. Primary productivity and precipitation at Castle Lake and Lake Tahoe during 24 years. *Int. Ver. Theor. Angew. Limnol. Verh.* 22:591-599.
- Goodall, D. W. 1974. A new method for the analysis of spatial pattern by random pairing of quadrats. *Vegetatio* 29:135-146.
- Hall, C. A. S., and D. L. DeAngelis. 1985. Models in ecology: paradigms found or paradigms lost? *Bull. Ecol. Soc. Am.* 67:339-346.
- Harris, G. P. 1980. Temporal and spatial scales in phytoplankton ecology: mechanisms, methods, models, and management. *Can. J. Fish. Aquat. Sci.* 37:877-900.
- Hasler, A. D. 1964. Experimental limnology. *BioScience* 14:36-38.
- Hennemuth, R. C., J. E. Palmer, and B. E. Brown. 1980. A statistical description of recruitment in eighteen selected fish stocks. *J. Northwest Atl. Fish. Sci.* 1:101-111.
- Henrikson, L., H. G. Nyman, H. G. Oscarson, and J. A. E. Stenson. 1980. Trophic changes, without changes in the external nutrient loading. *Hydrobiologia* 68:257-263.
- Hildebrand, F. B. 1976. *Advanced calculus for applications*. Prentice-Hall, Englewood Cliffs, N.J.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54:187-211.
- Ivlev, V. A. 1961. *Experimental ecology of the feeding of fishes*. Yale University Press, New Haven, Conn.
- King, C. E. 1967. Food, age, and the dynamics of a laboratory population of rotifers. *Ecology* 48:111-128.
- Kitchell, J. F., and S. R. Carpenter. 1987. Piscivores, planktivores, fossils, and phorbins. Pages 132-146 in W. C. Kerfoot and A. Sih, eds. *Predation: direct and indirect effects on aquatic communities*. University Press of New England, Hanover, N.H.
- Kitchell, J. F., and L. B. Crowder. 1986. Predator-prey systems in Lake Michigan: model predictions and recent dynamics. *Environ. Biol. Fishes* 16:205-211.

- Koonce, J. F., T. B. Bagenal, R. F. Carline, K. E. F. Hokanson, and M. Naglec. 1977. Factors influencing year-class strength of percids: a summary and model of temperature effects. *J. Fish. Res. Board Can.* 34:1900-1909.
- LeCren, E. D. 1962. The efficiency of reproduction and recruitment in freshwater fish. *Symp. Br. Ecol. Soc.* 2:283-296.
- Likens, G. E. 1983. A priority for ecological research. *Bull. Ecol. Soc. Am.* 64:234-243.
- McCauley, E., and J. Kalff. 1981. Empirical relationships between phytoplankton and zooplankton biomass in lakes. *Can. J. Fish. Aquat. Sci.* 38:458-463.
- Melack, J. M. 1979. Temporal variability of phytoplankton in tropical lakes. *Oecologia (Berl.)* 44:1-7.
- Mills, E., J. Forney, and K. Wagner. 1987. Fish predation and its cascading effect on the Oneida Lake food chain. Pages 118-131 in W. C. Kerfoot and A. Sih, eds. *Predation: direct and indirect effects on aquatic communities*. University Press of New England, Hanover, N.H.
- Paine, R. T. 1980. Food webs, linkage interaction strength, and community infrastructure. *J. Anim. Ecol.* 49:667-685.
- Peters, R. H. 1975. Phosphorus regeneration by natural populations of limnetic zooplankton. *Int. Ver. Theor. Angew. Limnol. Verb.* 19:273-279.
- . 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Peters, R. H., and J. A. Downing. 1984. Empirical analysis of zooplankton filtering and feeding rates. *Limnol. Oceanogr.* 29:763-784.
- Pitcher, T. J., and P. J. B. Hart. 1984. *Fisheries ecology*. Croom Helm, Beckenham, Kent, United Kingdom.
- Porter, K. G., J. Gerritsen, and J. D. Orcutt, Jr. 1982. The effect of food concentration on swimming patterns, feeding behavior, ingestion, assimilation, and respiration by *Daphnia*. *Limnol. Oceanogr.* 27:935-949.
- . 1983. Functional response and fitness in a generalist filter feeder: *Daphnia magna* (Cladocera: Crustacea). *Ecology* 64:735-742.
- Prentki, R. T., D. S. Rogers, V. J. Watson, P. R. Weiler, and O. L. Loucks. 1977. Summary tables of Lake Wingra basin data. Rep. 85, Institute of Environmental Studies, University of Wisconsin, Madison.
- Reynolds, C. S. 1984. *The ecology of freshwater phytoplankton*. Cambridge University Press, Cambridge.
- Reynolds, C. S., G. P. Harris, and D. N. Gouldney. 1985. Comparison of carbon-specific growth rates and rates of cellular increase of phytoplankton in large limnetic enclosures. *J. Plankton Res.* 7:791-820.
- Rigler, F. H. 1982. The relation between fisheries management and limnology. *Trans. Am. Fish. Soc.* 111:121-132.
- Scavia, D., G. L. Fahnenstiel, M. S. Evans, D. J. Jude, and J. T. Lehman. 1986. Influence of salmonine predation and weather on long-term water quality trends in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 43:435-443.
- Schindler, D. W. 1974. Eutrophication and recovery in experimental lakes: implications for lake management. *Science (Wash., D.C.)* 184:897-898.
- . 1978. Factors regulating phytoplankton production and standing crop in the world's lakes. *Limnol. Oceanogr.* 23:478-486.
- Schindler, D. W., E. J. Fee, and T. Rusczyński. 1978. Phosphorus input and its consequences for phytoplankton standing crop and production in the Experimental Lakes Area and in similar lakes. *J. Fish. Res. Board Can.* 35:190-196.
- Shapiro, J., and D. Wright. 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. *Freshwater Biol.* 14:371-383.
- Stearns, S. C. 1977. The evolution of life history traits. *Annu. Rev. Ecol. Syst.* 8:145-171.
- Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Trans. Am. Fish. Soc.* 110:751-763.
- Strong, D. R. 1984. Density-vague ecology and liberal population regulation in insects. Pages 313-327 in P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, eds. *The new ecology: a novel approach to interactive systems*. Wiley, New York.

- Summerfelt, R. C. 1975. Relationship between weather and year-class strength of largemouth bass. Pages 166-174 in R. Clepper, ed. Black bass biology and management. Sport Fishing Institute, Washington, D.C.
- Threikeld, S. T. 1976. Starvation and the size structure of zooplankton communities. *Freshwater Biol.* 6:489-496.
- Tonn, W. M., and J. J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* 63:1149-1166.
- von Ende, C. N. 1982. Phenology of four *Chaoborus* species. *Environ. Entomol.* 11:9-16.
- Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *Am. Nat.* 125:769-787.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.* 15:393-425.
- Wetzel, R. G. 1983. *Limnology*. Saunders, Philadelphia.