

# Temporal variance in lake communities: blue-green algae and the trophic cascade

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## Abstract

Two examples, blue-green algal blooms and the fish-driven trophic cascade, illustrate important consequences of time scale dependency in lakes. Blue-green algae and fish populations are notably variable components of lake communities. The timing of colonization of the water column by blue-green algae, relative to population oscillations of grazers and other algal groups, determines the magnitude of subsequent blooms. Variability in colonization acts jointly with dynamic variability in herbivory to produce large fluctuations in blue-green algal concentration at time scales of weeks to years. Fishes exhibit high interannual variance in recruitment. Episodes of high recruitment cascade through lake food webs, inducing fluctuations in lower trophic levels at time scales of years to decades. Fishes, through their effects on herbivores, contribute to variability in blue-green algal blooms. Blue-green algae and fishes are foci of lake management, so analyses of their variable and scale-dependent interactions are important for applied limnology. Theories and models that address nonequilibrium dynamics, analyses of effects of time scale on correlations and experiments, and improved paleolimnological capabilities will yield valuable progress on temporal scale issues in limnology and ecology.

## Introduction

Much variability in community and ecosystem dynamics involves irruptions and fluctuations of interacting populations. Population outbreaks, with attendant cascades through food webs (Paine 1980), are among the most spectacular community phenomena. Examples are known from most biomes and taxocenes and include epidemic disease, red tides, various weeds, many insect taxa (*e.g.*, migratory locusts, spruce budworm), forest birds, fishes, small mammals and their predators, and ungulates (Watt 1969; Odum 1971; Krebs 1985; Colinvaux 1986).

Many extreme population fluctuations derive from the dynamics of extant assemblages. Other irruptions occur when invading species encounter unexploited resources and few negative interactions (Elton 1958; Mooney and Drake 1986). In most cases, analyses are complicated by long lags between cause and response and by responses which appear much larger than the causes (Elton 1958; Watt 1969; Krebs 1985; Mooney and Drake 1986). Most examples are anecdotal (Kareiva 1987), experimental field studies are rare, and models are case specific (Ehrlich 1986; Orians 1986), often with stochasticity lending predictions the 'status

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## TIME SCALES OF MAJOR PROCESSES AFFECTING LAKE ECOSYSTEMS

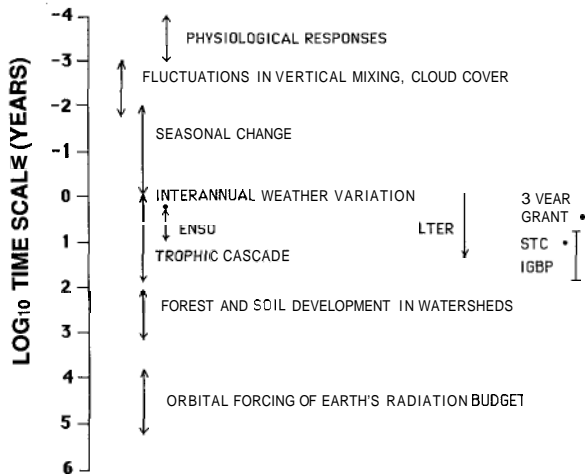


Fig. 1. Time scales of major processes affecting lake ecosystems. ENSO = El Niño – Southern Oscillation. Time scales of selected research programs are shown at the right of the diagram. LTER = Long-Term Ecological Research; STC = Science and Technology Centers; IGBP = International Geosphere-Biosphere Program. Sources: Harris 1980; Strub *et al.* 1985; Likens 1983; NRC 1986; Carpenter and Kitchell 1988.

of a weather report' (Roughgarden 1986).

Variability demands consideration of temporal scales. This paper develops two examples of temporal scaling in lakes. Both present substantial challenges to basic research and significant problems to lake managers. Blue-green algal blooms occur on subannual scales and exhibit the multiple causal factors, time lags, explosive growth, and catastrophic declines characteristic of irruptions in many communities. Trophic cascades emanating from variability in fish populations occur on multiyear time scales and illustrate the community and ecosystem consequences of fluctuations in strongly interacting populations (Carpenter and Kitchell 1987; 1988). I emphasize temporal scales because spatial scales are thoroughly covered by other contributors to this volume and have received extensive attention from aquatic ecologists (Steele 1978). Indeed, the earliest quantitative arguments about spatial heterogeneity vs. homogeneity arose in plankton ecology (McIntosh 1985). Benthic ecologists are especially concerned with the landscape pattern is-

sues emphasized by terrestrial ecologists (Fisher 1983; Lodge *et al.* 1988).

Lakes are excellent systems for studies of temporal variance and scaling (Carpenter 1988a). They are bounded and offer a natural spatial scale for analyses of processes spanning a broad range of time scales (Fig. 1). Irruptions and extirpations are prominent in lake community dynamics (Murdoch and Bence 1987). 'Big effects from small causes' (Ricker 1963) are perhaps best known for fish populations (Walters 1986). Other freshwater examples of outbreaks include crayfish (Lodge and Lorman 1987), macrophytes (Carpenter 1980), and blue-green algae (Paerl 1988a). Excellent long-term records exist for some lakes (Brock 1985; Kratz *et al.* 1987; Schindler 1988; Strub *et al.* 1985). Moreover, lakes record their own temporal dynamics in the fossil archive stored in their sediments (Binford *et al.* 1983). Thus lakes provide a landscape-wide array of sensors and recorders of long-term environmental change (O'Sullivan 1983).

The variability discussed in this paper derives from system dynamics and/or stochastic components of lake systems. Measurement and sampling errors will not be discussed. In the terminology of Walters (1986), this paper concerns process variance, not observation variance.

### Blue-green algal blooms

Blooms of blue-green algae are common summer phenomena in productive lakes. Their noxious, malodorous, and toxic properties have drawn considerable interest as water quality problems (Cooke *et al.* 1986). Blooms form and disappear quickly (Reynolds and Walsby 1975) and 'exhibit rather profound sensitivity to rapid but minor shifts in environmental conditions' (Paerl 1988b, p. 271). Even in lakes where blue-green blooms are common, the timing, magnitude, and dominant species of the next bloom often cannot be predicted by experienced investigators (Brock 1985). Numerous control measures have been devised, but their success is variable from lake to lake and from time to time (Carlson and Schoenberg 1983; Shapiro 1984; Cooke *et al.* 1986; Benndorf 1987).

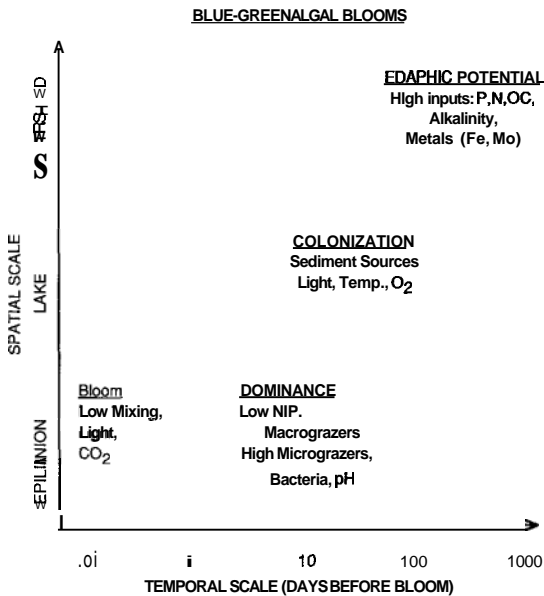


Fig. 2. Causal hierarchy that governs blue-green algal blooms. Major regulatory factors that determine edaphic potential, colonization of the water from the sediments, dominance of the phytoplankton, and bloom formation are organized according to spatial and temporal scales.

In the language of hierarchy theory, bloom-forming blue-green algae succeed by breaking constraints (Allen and Starr 1982; O'Neill *et al.* 1986). Several distinctive characteristics enable blue-green colonies to dominate the phytoplankton through mechanisms not available to their competitors. These include (1) low  $\text{CO}_2$  compensation points, which permit rapid carbon fixation at low concentrations; (2) capacity of some taxa to fix nitrogen; (3) gas vacuoles, which permit rapid vertical movements via floating and sinking; and (4) resistance to grazing afforded by large size and low palatability (Paerl 1988a; b).

Extensive observational and physiological studies show that sequences of multiple causal factors govern blue-green algal blooms (Paerl 1988a; b). The unpredictability of the populations and the variable effectiveness of management suggest that causal factors interact with varying intensities through time.

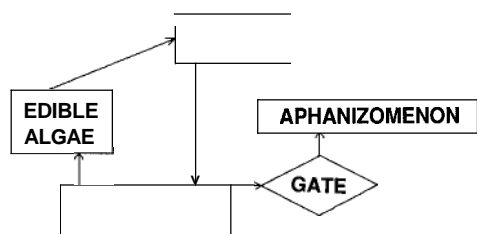
Major factors in blue-green algal blooms form four clusters on axes of spatial and temporal scale (Fig. 2). Three spatial scales are involved: the

watershed, lake, and epilimnion. Temporal scales are less discrete and range from many years to hours before the bloom. The clusters of Fig. 2 are hierarchical (Allen and Starr 1982; O'Neill *et al.* 1986). Events at coarse scales set the range of possibilities at finer scales. Complex, tightly coupled interactions occur among processes operating at similar scales.

The edaphic potential for blue-green blooms is established over years or decades and includes high inputs of alkalinity, the macronutrients N and P, organic carbon, and the micronutrients Fe and Mo (Howarth *et al.* 1988; Paerl 1988b; Schindler 1988). Nutrient recycling from sediments creates favorable conditions for blue-green algae in some lakes (Cooke *et al.* 1986). Colonization of the water column from benthic resting cells or colonies antedates bloom formation by 1 to 16 weeks (Trimbee and Prepas 1988). Light, temperature, and oxygen conditions at colonization differ among blue-green species (Lynch 1980; Reynolds *et al.* 1981; Trimbee and Harris 1984; Trimbee and Prepas 1988). Dominance of the phytoplankton by blue-green algae is promoted by low N/P ratio, high pH (hence low  $\text{CO}_2$  concentration), low populations of large herbivores (*e.g.*, *Daphnia pulex*), and a vigorous microbial food web that includes bacteria, protozoa, and rotifers (Smith 1983; Shapiro 1984; Paerl 1988b; Schindler 1988). Blooms occur during calm periods as the buoyant colonies rise, concentrating the entire blue-green algal biomass of the lake at the surface (Reynolds and Walsby 1975). Increased buoyancy is stimulated by low light intensity and  $\text{CO}_2$  concentration in deep waters prior to the bloom (Paerl 1988a).

The public perceives blue-green algae at the finest scales, *i.e.*, during blooms. Comprehensive explanations for blooms and effective management actions require additional information from coarser scales (Fig. 2). Many of the correctives used for blue-green algal problems operate at the coarser scales of Fig. 2 (Cooke *et al.* 1986).

The variable effectiveness of management techniques in controlling blue-green algal blooms may be explained by temporal variation of the causal factors. Attention to timing of critical factors may improve the success rate of management. For



**Fig. 3.** Compartments and interactions of the model used to study *Aphanizomenon* blooms in Lake Mendota. The herbivore, *Daphnia*, feeds on both highly edible algae (eukaryotic nanoplankton) and the less edible *Aphanizomenon* and excretes phosphorus, the limiting nutrient. *Aphanizomenon* is ingested and assimilated at lower rates than the edible algae. The 'gate' controls entry of *Aphanizomenon* into the water column from the sediments.

example, effects of artificial mixing are time scale specific. Over the long term, mixing to aerate the hypolimnion immobilizes phosphorus in sediments, reducing recycling and the edaphic potential for blue-green algal blooms (Cooke *et al.* 1986). During the colonization phase, mixing promotes invasion of some blue-green algae and suppresses invasion of others (Lynch 1980; Reynolds *et al.* 1981; Trimbee and Prepas 1988). During the dominance phase, effects of mixing depend on chemical conditions at the time. Mixing has stimulated blue-green algae by increasing the vertical flux of nutrients from the hypolimnion to the epilimnion (Stauffer and Lee 1973). Conversely, mixing has suppressed blue-green algae by increasing the CO<sub>2</sub> concentration (Shapiro 1984) and decreasing the flux of phosphorus from sediments (Cooke *et al.* 1986). After blue-green algae have become dominant, mixing prevents bloom formation because maximum flotation rates of blue-green algae are much slower than typical wind-driven vertical currents (Reynolds and Walsby 1975). In sum, the effect of mixing on bloom-forming blue-green algae depends critically upon when the mixing occurs.

Subtle biotic interactions with massive consequences occur during colonization, dominance, and bloom phases. A model of colonization and dominance of Lake Mendota, Wisconsin, by *Aphanizomenon flos-aquae* during May and June illustrates one complex interaction (Fig. 3). For this paper, I analyzed a simple set of equations based on

a much more complex simulation model by Vanni *et al.* (in prep.). My model included density-dependent algal growth and a type II functional response. McCauley *et al.* (1988) showed that models with these features explained the dynamics of *Daphnia* and their prey in most lakes.

Dynamic equations for the relatively edible phytoplankton *E*, the relatively inedible *Aphanizomenon* *A*, and the herbivore *H* were

$$\begin{aligned} dE/dt &= r_1 E [1 - (E + A)/K] - c_1 Z [1 - \exp(-s_1 E/c_1)] \\ dA/dt &= G + r_2 A [1 - (E + A)/K] - c_2 Z [1 - \exp(-s_2 E/c_2)] \\ dZ/dt &= B_1 c_1 Z [1 - \exp(-s_1 E/c_1)] + B_2 c_2 Z [1 - \exp(-s_2 E/c_2)] - DZ \end{aligned}$$

where *r* is growth rate, *K* is the upper bound for algal biomass, *c* is maximum ingestion rate, *s* is slope of the functional response for grazing at low algal concentration, *B* is assimilation efficiency, and *D* is zooplankton death rate. Values of these parameters were estimated from data on Lake Mendota (Brock 1985; M. Vanni, pers. comm.) and from simulations using the more complex model of Vanni *et al.* (in prep.). *G* is colonization rate of *Aphanizomenon* and corresponds to the 'gate' in Fig. 3. When the gate for colonization is open, *G* is a positive value equal to the maximum *Aphanizomenon* growth rates observed in Lake Mendota (M. Vanni, pers. comm.). When the gate is closed, *G* is zero. In various simulations, the gate was opened at different times and for different periods of time.

In the absence of *Aphanizomenon*, the *Daphnia*-edible algae system oscillates (Fig. 4), a phenomenon known from other predator-prey models of enriched systems (Rosenzweig 1972) and from many *Daphnia*-alga systems (Murdoch and McCauley 1985; McCauley *et al.* 1988; Mills and Forney 1988). *Aphanizomenon* can successfully enter the system only during times when edible algae are declining due to overgrazing and *Daphnia* densities subsequently decline due to food limitation (invasible region in Fig. 4). These conditions occur at the end of the spring clear water period in Lake Mendota and other lakes, a time when *Aphanizomenon* commonly becomes dominant (Brock 1985; Lynch 1980; Trimbee and Prepas 1988). When *Aphanizomenon* colonizes during this period, the system

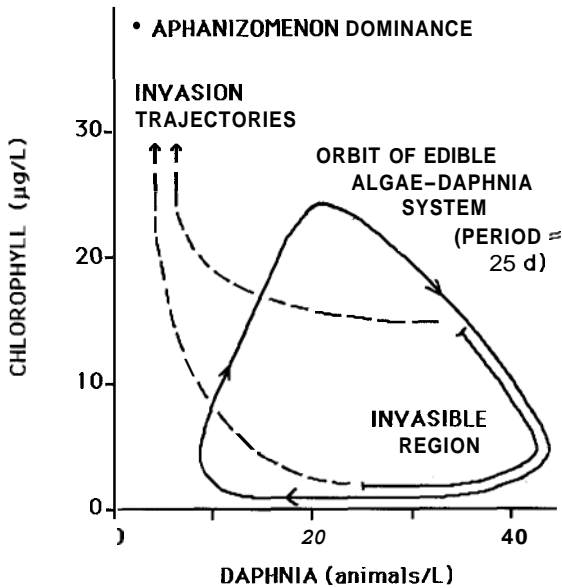


Fig. 4. Major dynamic features of chlorophyll concentration and herbivore (*Daphnia*) density from the model used to study *Aphanizomenon* blooms in Lake Mendota. See text for further explanation.

moves toward a state of abundant algae and few herbivores (dashed trajectories in Fig. 4). Some trajectories fall back toward the main oscillation, depending on the exact time of colonization.

If colonization occurs outside the invulnerable region, *Aphanizomenon* is suppressed by increasing or high *Daphnia* densities driven by increasing or high concentrations of edible phytoplankton. This is a transient case of apparent competition (Holt 1977) as elaborated by Abrams (1987). Rising densities of edible algae suppress their competitor, *Aphanizomenon*, by promoting growth of their common herbivore.

In sum, blue-green algal dynamics are determined by multi-scaled physical, chemical, and biotic processes. The physical and chemical processes are usually modeled as forcing functions, extrinsic to the system. On the other hand, biotic processes such as grazing are tightly coupled to dynamics of other system components. The scale of variance in herbivory is set by higher trophic levels through the trophic cascade.

## Trophic cascades

The trophic structure of lakes is largely determined by predation (Kerfoot and Sih 1987; Carpenter 1988a). Within broad constraints established by physiochemical factors, piscivory structures planktivore assemblages (Tonn and Magnuson 1982), planktivorous fishes govern zooplankton size structure and species composition (Brooks and Dodson 1965), and herbivory influences phytoplankton community structure (Carpenter and Kitchell 1984; Bergquist and Carpenter 1986; Elser and Carpenter 1988).

Fish recruitment exhibits interannual coefficients of variation of 25% to 143%, with ratios of high to low year classes as large as 2,700 (Carpenter and Kitchell 1987). Fishes are among the best examples of density-vague population dynamics (Strong 1986). Dominant predators are often generalists, and their interactions tend to be strong ones (*sensu* Paine 1980) that rapidly extirpate prey species (Murdoch and Bence 1987). Trophic cascades result from fluctuations in carnivory propagated through chains of strong interactions (Paine 1980). In lakes, variations in fish community structure cascade through the food web, ultimately affecting phytoplankton community structure, biomass, and productivity (Carpenter *et al.* 1987; Carpenter and Kitchell 1988).

For lakes in which management or disturbance are not overriding factors, the time scale of the trophic cascade is set by the lifespan of the dominant predator. The scaling effect of predator lifespan is illustrated by a food-chain model fit to data from three intensively studied experimental lakes in northern Wisconsin. The model can include either deterministic or stochastic terms for the effects of weather on phytoplankton, planktivore recruitment, and piscivore recruitment. Model equations and coefficients were presented by Carpenter (1988b; 1989).

The deterministic model stabilizes with no interannual variance in primary production (Fig. 5). With stochastic weather effects on phytoplankton, interannual variance in primary production develops but at no particular time scale. With the addition of stochastic planktivore recruitment, a

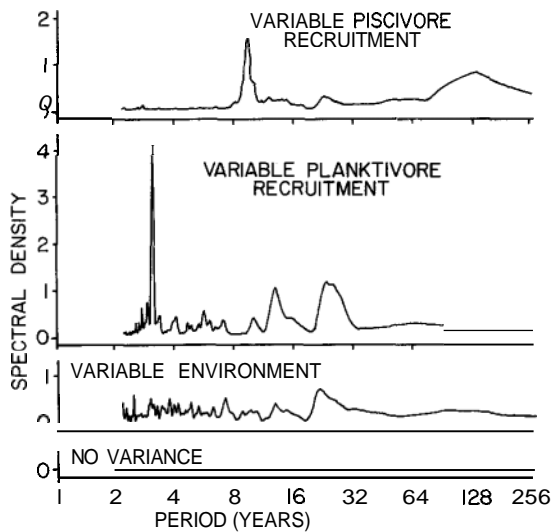


Fig. 5. Variance (spectral density) of primary production vs. time period (years) for lake food chain model. Peaks indicate the time scales of the most important variance components. No variance = run of deterministic model with no stochastic parameters; variable environment = run with stochastic weather effects on phytoplankton; variable planktivore recruitment = run with stochastic weather effects on phytoplankton and recruitment of planktivorous fish; variable piscivore recruitment = run with stochastic weather effects on phytoplankton and recruitment of both planktivorous and piscivorous fishes.

dominant variance component in primary production appears with a period of about 3 years, the lifespan of the planktivore in the model. With the further addition of stochastic piscivore recruitment, the dominant variance component in primary production shifts to a period of about 10 years, the lifespan of the piscivore in the model. Over a diverse range of life history scenarios, the dominant variance component of primary production tracks the lifespan of the piscivore (Carpenter 1988b).

The hypothesis that algal variance scales with the lifespan of the top carnivore is testable by paleolimnology. Deposition rates of algal fossils provide proxy data for productivity. Annually resolved long-term stratigraphies can be examined for periodicities consistent with cascading effects (Carpenter and Leavitt, in prep.).

Predator-induced and weather-induced perturbations travel down and up the food chain at different phases and frequencies. Complicated interference patterns and variable correlations result.

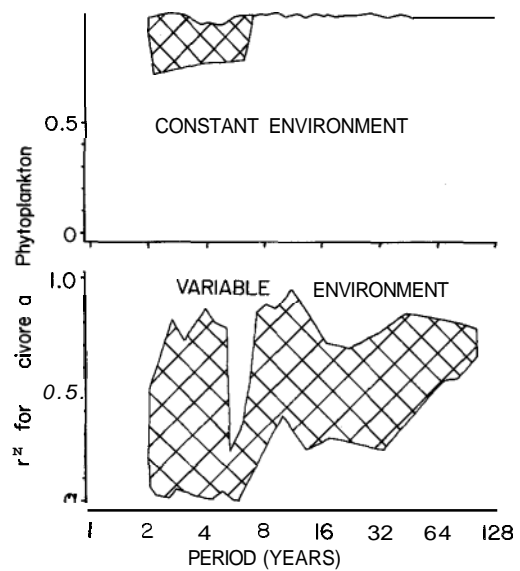


Fig. 6. Squared correlation coefficient of piscivore biomass and primary production as a function of time period (years) for lake food chain model. Correlation coefficients were calculated by cospectral analysis (Chatfield 1980). The hatched areas enclose the range of correlation coefficients observed at each time period for 100 runs of the stochastic model. Constant environment = runs with constant weather effects on phytoplankton, but stochastic fish recruitment; variable environment = runs with stochastic weather effects on phytoplankton and fish recruitment.

When the model is run with no stochastic terms, piscivore density and primary production are perfectly correlated. Stochastic piscivore recruitment causes lower and variable  $r^2$  values at scales shorter than the piscivore lifespan (Fig. 6). When the weather effect on phytoplankton is also stochastic,  $r^2$  becomes much lower and more variable at all scales and is often nonsignificant even with large samples.

Since correlations based on field data are often used to derive predictions (Peters 1986), scale dependency is cause for caution (Carpenter and Kitchell 1987; Carpenter 1988b; Carpenter and Kitchell 1988). Empirical studies should consider the effects of scale on correlations. Experiments are a powerful alternative (or supplement) to correlations (Carpenter and Kitchell 1988). Paine (1980; 1988) points out the general importance of experimentation in food web studies. Box (1966) concludes: "To find out what happens to a system when

you interfere with it, you have to interfere with it (not just passively observe it)'.

The scale dependencies of lake primary production suggest a three-level hierarchy of control (Carpenter and Kitchell 1987; 1988). The broad regional differences among lakes and the development of lake ecosystems over centuries are set by edaphic, climatic, and morphometric factors that determine nutrient loading and hydraulic residence time. The trophic cascade acts at lakewide spatial scales and intermediate temporal scales of years to decades. At subannual scales, a host of short-term physical and chemical effects produces further variance in primary production (Harris 1980).

The time scales of the trophic cascade (years to decades) are also those of lake management. Much of the temporal variability of lakes arises from fisheries management practices that seek intermediate fish stock levels at which recruitment variance and its cascading effects are maximized (Carpenter and Kitchell 1987). In theory, alternative fisheries management practices can reduce temporal variance and reduce nuisance chlorophyll levels in lakes (Carpenter and Kitchell 1987; 1988). Fishes and blue-green algae are coupled through their interactions with herbivorous zooplankton. The scale dependencies of these interactions must be analyzed to assess the potential effects of fish management on blue-green algal blooms.

### Research needs and opportunities

The theoretical, analytical, and methodological challenges of time scales are potentially unifying ones because they pervade all of ecology. Apparently contrasting equilibrium and nonequilibrium views can be reconciled by recognizing that equilibrium is scale dependent (DeAngelis and Waterhouse 1987). However, major sources of variability and apparently nonequilibrium dynamics are evident at many scales (Fig. 1). Among these scales are those at which society asks ecologists for predictions and management advice (Kitchell *et al.* 1988). If basic ecology is to serve management interests (Slobodkin 1988), then ecologists must address the issues of temporal variance and scaling.

Effective approaches to variable systems will be quite different from some current emphases in ecology. Temporal heterogeneity deflects attention from equilibria and average system states. Averages and regression lines can be simply artifices, rarely describing variable systems. Unpredictability forces attention to frequency distributions and variance spectra. The trajectories, variances, and covariances resulting from sequences of perturbations are the key data for analyzing and managing stochastic systems (Walters 1986).

In closing, I suggest three areas where progress on temporal scale problems is possible and would be widely beneficial to ecology.

1. Theories and models that address nonequilibrium dynamics, population irruptions, and extirpations are needed. Existing models that incorporate temporal variability of communities and ecosystems are usually very limited in scope (Roughgarden 1986; Carpenter 1988b). Several potentially useful approaches are emerging for modeling temporal variance (Steele 1985; Walters 1986; Shaffer and Kot 1985).

2. Relationships between correlative and manipulative studies and among experiments at different scales need to be examined. In temporally variable systems, correlations are dependent on time scale (Fig. 6). Several scale considerations, including time, influence the outcome of manipulative experiments (Frost *et al.* 1988; Carpenter and Kitchell 1988). Are there general rules for scaling experiments or for comparing results of differently scaled experiments? Are there general scales of correspondence between correlative and manipulative approaches?

3. Important opportunities exist to improve paleoecological methods for investigating long time scales beyond the grasp of current research. Paleolimnological records have only rarely been calibrated against coeval data. Long-term data sets make such calibrations possible. Technological advances could create prospects for fine-interval sectioning of cores. New separation methods may dramatically increase rates of sample processing. Paleoeological information is the grist for both the models and the understanding needed to anticipate ecosystem responses in a changing global context.

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