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Whole-lake experiments: Is grazer functional response stable?

S. R. Carpenter, X. He, J. F. Kitchell and P. A. Soranno

Introduction

Whole-lake experiments are usually used to test specific ecological hypotheses (SCHINDLER 1990, CARPENTER & KITCHELL 1993). Data from large-scale manipulations can also be used to fit and compare ecosystem models (WALTERS 1986). Time series data from manipulated ecosystems often include wide fluctuations that facilitate model fitting (WALTERS 1986, CARPENTER & KITCHELL 1993).

Many difficulties that arise in the estimation of parameters for ecosystem models are related to the fact that the state variables are necessarily rather complex aggregations (O'NEILL & RUST 1979). For example, edible phytoplankton may be modeled as a homogeneous state variable, even though it consists of many species that may respond differently to grazing. One troublesome consequence of aggregation is that parameter values can change through time, due to changes in the underlying composition of the aggregate. WALTERS (1986) refers to this situation as "parameters that aren't". Ecosystem experiments may provide valuable information on the range of possible values and the rate of change when parameters are dynamic (WALTERS 1987).

In models of zooplankton-algae interactions, the functional response influences the clear water phase and bloom formation (CARPENTER 1992). However, predictions of algal fluctuations will be much more difficult if the parameters of the functional response are dynamic. In this paper, we use data from 3 experimental lakes over 7 years to assess temporal variation in the functional response for grazing.

Methods

We studied 3 mesotrophic lakes near Land o' Lakes, Wisconsin, USA (CARPENTER & KITCHELL 1993). As a consequence of massive fish manipulations, zooplankton of Tuesday Lake were dominated by small copepods and cladocerans in 1984 and 1989–1990, by large *Daphnia* in 1986–1987, and by transitional zooplankton assemblages in 1985 and 1988. A series of brief fish manipulations in Peter Lake caused substantial fluctuations in the zooplankton community in 1985 and 1988–1990. Paul Lake was an undisturbed reference system throughout this study.

Lakes were sampled weekly during summer stratification (approximately mid-May to mid-September) each year. Zooplankton were collected in vertical net hauls, preserved, enumerated, and measured. Phytoplankton samples were composited from profiles of Van Dorn casts, preserved, enumerated, and measured. For this study, edible phytoplankton biomass was defined as the biovolume of all cells and colonies having volume less than that of a 30 μm sphere. Method details appear in CARPENTER & KITCHELL (1993).

Time series of edible algal biomass were fit to the model:

$$A(t+1) = \mu(t) + g(t)A(t) + r'(t)A(t)^2 + c(t)A(t)Z(t)$$

where A is biomass of edible algae, Z is biomass of zooplankton, and t is time. The parameters estimated by the fitting procedure are mean biomass (μ), algal growth rate (g), density dependence of algal growth (r', equal to r/K of the logistic equation), and the grazing rate parameter (c). Negative values of r' indicate negative density dependence. Negative values of c indicate grazing loss.

In this paper, we are concerned with changes in c. Models were fit by time series dynamic modeling (WEST & HARRISON 1989). Initial parameter estimates and standard errors needed for this method were obtained by ordinary least squares regression.

Results

Predictions of edible algal biomass one week in the future were reasonably close to observed values (Fig. 1 A, C, E). This model performed better than several alternatives that we examined. We concluded that the model fit acceptably well.

Grazing rate coefficients fluctuated in all 3 lakes (Fig. 1 B, D, F). If zooplankton biomass is 1 g · m^{-2}, a grazing rate coefficient of −1 causes a turnover of the edible algal biomass once per week. This value is a convenient reference point, because herbivore biomasses in these lakes average about 1 g · m^{-2} (CARPENTER & KITCHELL 1993). Positive grazing rate coefficients indicate stimulation of algal growth by zooplankton, possibly through nutrient regeneration. Coefficients were generally negative, with a few exceptions. Exceptions oc-

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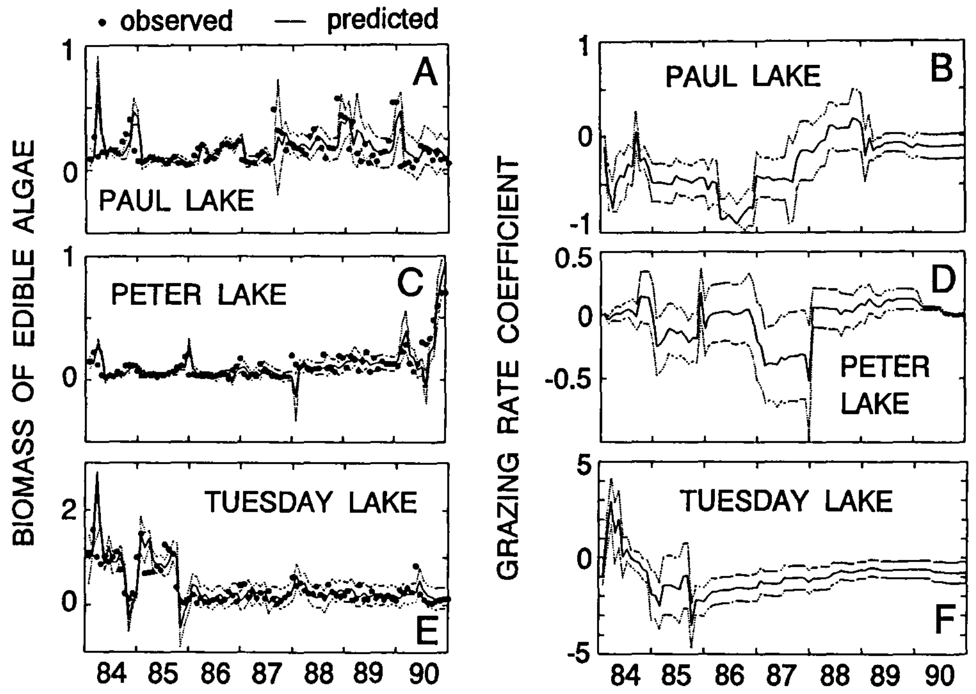

Fig. 1. Time series dynamic modeling results for Paul Lake (A, B), Peter Lake (C, D) and Tuesday Lake (E, F). Panels A, C, and E show observed biomasses of edible algae (mg wet mass l^{-1}) and one-week-ahead predictions of the model, ± one standard error. Panels B, D, and F show dynamics of the grazing rate parameter c (proportion of algal biomass consumed $\cdot$ g^{-1} zooplankton dry biomass $\cdot$ m^{-2} $\cdot$ $week^{-1}$), ± one standard error.

curred during blooms of inedible algae. Slightly positive coefficients in Peter Lake 1988–1990 correspond with periods of blooms by colonial green algae. Positive coefficients in Tuesday Lake in 1984 correspond with high biomasses of large dinoflagellates.

Grazing rate coefficients fluctuated the least in Peter Lake. Over the entire data set, the coefficient was not significantly different from zero (mean = -0.0022, s.e. = 0.0092, n = 91).

In Paul Lake, grazing rate coefficients were somewhat lower in 1984–1987 than in 1988–1990. Over the entire data set, the coefficient was -0.095 (s.e. = 0.072, n = 91).

Shifts in the grazing rate coefficient were greatest in Tuesday Lake. Over the entire data set, the coefficient was -0.93 (s.e. = 0.29, n = 91). Over 1984–1985, the coefficient was relatively high (mean = -0.91) but variable (s.e. = 0.82, n = 22). Over 1986–1990, the coefficient was -0.46 (s.e. = 0.21, n = 69).

Discussion

Our model uses a linear (type I) functional response. Laboratory data for zooplankton grazing often fit an asymptotic (type II) functional response (Porter et al. 1982). If an asymptotic functional response is appropriate for our data, then values of the grazing rate coefficient c(t) should be positively related to edible algal biomass A(t), and scatterplots of c(t) versus A(t) should appear asymptotic. In all 3 lakes, c(t) and A(t) are weakly correlated (r values: Paul 0.229; Peter 0.261; Tuesday 0.312). Scatterplots appear asymptotic in Peter Lake, but not in Paul or Tuesday lakes. Evidence for a type II functional response is weak in these lakes. Algal biomass may be too low to saturate grazing rates, so a linear relationship is a good approximation for the functional response.

Herbivore size is often a reliable indicator of grazing effects in lakes (Pace 1984, Carpenter & Kitchell 1993). Correlations of cladoceran length with c(t) are evident in Tuesday Lake (r = 0.504), modest in Peter Lake (r = 0.304), and weak in Paul Lake (r = −0.081). However, cladoceran length is poorly correlated with residuals of all three models (r values: Paul 0.025; Peter −0.105; Tuesday 0.073). Therefore, adding herbivore size to the dynamic-parameter models is not likely to improve predictions. However, the correlation of c(t) with cladoceran size in Peter and Tuesday lakes suggests that predictions of a static-parameter model could be improved by including an index of herbivore size in the functional response.

We obtained satisfactory estimates of the grazing rate coefficient only in Tuesday Lake. In the other lakes, confidence bands were relatively wide and coefficients were not significantly different from zero. In Tuesday Lake, strong, sustained fish manipulations produced large limnological responses, allowing parameters to be estimated with relatively low uncertainty. The brief perturbations in Peter Lake and the natural fluctuations of Paul Lake did not yield sustained ecosystem changes conducive to good parameter estimates. Ecosystem analysis is best served by time series data from strong, sustained manipulations at the ecosystem scale (Walters 1986, Carpenter & Kitchell 1993).

In view of the dramatic changes that occurred in the herbivore community, the fluctuations in the grazing rate coefficient in Tuesday Lake are relatively modest. From the standpoint of ecosystem modeling, this result is encouraging. It suggests that the assumption of static parameters for grazing rates will not lead to large errors. If static parameters are used, errors may be further reduced by incorporating effects of herbivore size in the functional response.

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