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Author(s): Anthony R. Ives, Stephen R. Carpenter and Brian Dennis
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COMMUNITY INTERACTION WEBS AND ZOOPLANKTON RESPONSES TO PLANKTIVORY MANIPULATIONS

ANTHONY R. IVES,[1,3,4] STEPHEN R. CARPENTER,[1,3] AND BRIAN DENNIS[2,3]

[1]*Department of Zoology, University of Wisconsin, Madison, Madison, Wisconsin 53706 USA*
[2]*Department of Fish and Wildlife Resources, and Division of Statistics, University of Idaho, Moscow, Idaho 83844 USA*
[3]*National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, Santa Barbara, CA 93101 USA*

Abstract. The response of a species to an environmental perturbation depends on both the direct effect of the perturbation on the population growth rate of the species and the indirect effects operating through interactions among species in a community. To estimate the importance of indirect effects, we analyzed the population dynamics of nine zooplankton species or species groups in a lake subjected to experimental manipulations of the fish community. The manipulations included additions and removals of planktivorous and piscivorous fish over a period of seven years, thereby producing changes in planktivory rates on the zooplankton community. Applying autoregressive models to time-series data, collected during weekly samples, we estimated the direct interaction strengths between species, thereby constructing a quantitative interaction web for the zooplankton community. We then used this interaction web to explore the roles of direct and indirect interactions between species in determining the long-term changes in zooplankton biomasses that were observed over the course of the experimental manipulations. The analysis identified *Daphnia pulex* as a keystone species. This large herbivore had strong direct interactions with other zooplankton species and was strongly affected by changes in planktivory. Consequently, changes in the biomasses of other zooplankton species during the planktivory manipulations were influenced strongly by indirect interactions acting through changes in *D. pulex* biomass. In addition, we used the analysis to ask whether information about the response of species to planktivory manipulations could be used to anticipate species' responses to other types of perturbation. If the direct effects of a novel perturbation on each species in a community were known, then the interaction web would help to anticipate how a novel perturbation will affect each species via direct and indirect effects through the community.

Key words: autoregressive models; community ecology; Daphnia pulex; *food webs; species interactions; time-series analysis; trophic cascade; zooplankton.*

INTRODUCTION

Food webs are among the most compelling conceptual constructs in ecology. Food webs (and their more general relatives, interaction webs) show which species in a community interact with each other (Paine 1966, 1980, Pimm 1982). Since interactions among species are a fundamental component of how communities and ecosystems function, interaction webs are central to a large number of ecological questions: (1) Are large communities more or less resilient to environmental stress than small communities (May 1974, Pimm 1984, Cohen and Newman 1985, Lawler and Morin 1993)? (2) What is the maximum number of trophic levels likely to occur in any community (Pimm and Lawton 1977, Cohen et al. 1986)? (3) Do changes in species abundance or composition at one trophic level create cascading effects to other trophic levels (Hairston et al. 1960, Carpenter et al. 1985, Power 1992)? (4) For a community subjected to an exogenous perturbation, do decreases in the densities of some species lead to compensatory increases in the densities of functionally similar species, thereby preserving the ecosystem level processes performed by the community (Lawton and Brown 1993, Frost et al. 1995, Tilman 1996)?

To answer these questions, it is often not enough to know which species interact with each other. It is also necessary to know the strengths of interactions (Paine 1980). To illustrate this, consider the case of two herbivores that share common food resources and a predator that attacks both herbivores. Suppose further that the predator increases in density due to some exogenous factor, such as long-term climate or habitat changes. The question is how the densities of the two herbivores respond to this change in predator density. The outcome of this hypothetical situation might be a trophic cascade (Carpenter et al. 1985): an increase in density at the predator trophic level leads to decreases in densities of both herbivores in the trophic level below. Alternatively, the outcome might be dictated by compensatory dynamics (Frost et al. 1995): the in-

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[4] E-mail: arives@facstaff.wisc.edu

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crease in predator density may decrease the density of one of the herbivores, while the other herbivore shows a compensatory increase in density. Whether both herbivores decrease in density, or one increases while the other decreases, depends on the strengths of interactions among all three species (Holt 1977, Abrams 1987). The point of this example is that, even for a simple three-species community, it is necessary to know the strengths of species interactions to predict how densities will respond to an external perturbation.

The objective of this article is to quantify the strengths of interactions among zooplankton species in order to understand how biomasses of different species changed in response to an experimental perturbation of planktivorous fish abundance (Carpenter and Kitchell 1993). Over a seven-year period, Tuesday Lake was subjected to whole-lake manipulations in which piscivorous and planktivorous fish were added and removed. The manipulations of the fish community led to dramatic changes in the zooplankton community. With increases in the abundance of planktivorous fish, some zooplankton species decreased in biomass, while others increased. Some of the observed changes appear to be direct responses to the manipulations: species that are preferred prey of planktivorous fish decreased in biomass with increases in the abundance of their predators. Other observed changes appear to be indirect: species of nonpreferred prey increased with increasing planktivore abundance. Our goal is to use the data from the lake manipulations to quantify interactions between species and thereby interpret the observed responses of species to the manipulations.

To quantify the strengths of interaction between species, we analyze the data to take advantage of the short-term changes in population biomasses between weekly samples, using multispecies autoregression analysis (Ives 1995, Elkington et al. 1996, Solow and Sherman 1997). This approach regresses the biomass of each species in a sample against the biomasses of all species and planktivory rates measured in the preceding sample. Because direct effects lead to relatively rapid responses of population growth rates, analyzing weekly changes in biomasses makes it possible to quantify both the strengths of interaction between species and the direct effects of planktivory on changes in species' biomasses. Thus, the result of the autoregression analysis is a quantitative interaction web of the zooplankton community along with interaction links between zooplankton and planktivorous fish.

In order to understand the response of the zooplankton community to experimental planktivory manipulations conducted over several years, it is necessary to consider the indirect effects of planktivory on each species acting through changes in other species' biomasses. For example, consider those zooplankton species that increased in biomass when planktivory increased. This increase could be due to competitive release caused by the reduction in the biomass of competitors that are susceptible to planktivory. Alternatively, it could be due to the reduction in abundance of predatory zooplankton when they are eaten by planktivorous fish. Distinguishing between these alternatives requires knowing both the strength of competitive and predatory interactions on the species that increased in biomass, and how much the biomasses of potential competitors and predators decreased in response to fish predation. To study the outcome of direct and indirect effects, we derive a formula that uses the interaction coefficients obtained from the autoregression analysis to predict the average annual biomass of each zooplankton species as a function of average annual planktivory. This makes it possible to determine whether the interaction coefficients obtained from short-term changes in zooplankton biomasses are consistent with the long-term changes in biomasses measured across the seven years of the experiment.

This formula also provides a tool to investigate which pathways through the community interaction web are the most important in understanding the long-term responses of the zooplankton community to the experimental manipulations. To measure the importance of the interaction pathway through a particular species, we set the coefficient for the effects of planktivory on that species to zero. We then predict the changes in biomasses of all species in the community caused by changing average annual planktivory, and we compare these predictions to the observed changes. The greater the difference between predicted and observed changes, the more important is the effect of planktivory on the particular species in question. Thus, performing this analysis for each species susceptible to planktivory identifies which pathways through the interaction web are the most important in explaining how the entire zooplankton community changed in response to planktivory manipulations.

Finally, the autoregression analysis separates endogenous interactions between species within the community from the exogenous forces that affect the species. We treat planktivory as an exogenous factor because it was manipulated during the experiment. Even in unmanipulated systems, from the perspective of zooplankton community dynamics, it makes sense to consider planktivory as an exogenous factor. This is because fish population dynamics occur on a much slower time scale than zooplankton dynamics and are sensitive to many environmental factors (such as human fishing pressure and winter anoxic events) that do not directly affect zooplankton. By separating the exogenous from the endogenous interactions, we can ask how important are the endogenous interactions in determining the sensitivities of species to planktivory manipulations. If the responses of species are dominated by indirect effects determined by interactions with other species, rather than the direct effects of planktivory on each species, then endogenous interactions will play a large role in

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determining the sensitivities of species to the planktivory manipulations (Ives 1995).

This question is central to the more general problem of understanding how the same community might respond to different types of exogenous perturbation. Any given community is susceptible to numerous types of exogenous perturbation, and it is unrealistic to expect that we can study all possible perturbations as independent phenomena. Our analysis makes it possible to use data from one perturbation to quantify the interaction strengths among species. Armed with a quantitative interaction web, anticipating the community response to a different perturbation requires knowing only the direct effects of the perturbation on species in the community.

Methods

Experiment

The data we analyze were collected as part of the "trophic cascade" project conducted on three lakes in the Upper Peninsula of Michigan, USA (Carpenter and Kitchell 1993). Two of the lakes, Tuesday and Peter Lakes, were manipulated, while the third lake, Paul Lake, was an unmanipulated control. Details of the experimental manipulations, study organisms, and sampling methods are given in Carpenter and Kitchell (1993), and we only present an overview here. The experiment was designed to test the hypothesis that increases in planktivory will result in lower abundances of zooplankton, which, in turn, will lead to increased phytoplankton abundances and increased primary productivity. Manipulations of planktivory were achieved by both the removal and addition of planktivorous fish, and by the addition and removal of piscivorous fish that preyed on planktivorous fish. In general, the hypothesis was supported, with increasing planktivory leading to increased phytoplankton abundance. However, the decrease in zooplankton abundance with increasing planktivory pressure was not uniform across all zooplankton species, and several species of zooplankton increased in abundance with increasing planktivory.

For the analyses reported here, we used only the data from Tuesday Lake. The zooplankton communities in the three lakes were not identical, making the joint analysis of all three lakes complicated. We selected Tuesday Lake over the other two lakes, because it experienced the most dramatic changes in zooplankton abundances in response to changes in planktivory. Premanipulation sampling of Tuesday Lake started in the spring of 1984. In early summer 1985, ~90% of the planktivorous minnows were removed using minnow traps. Simultaneously, a roughly equal mass of piscivorous bass was collected by electrofishing and angling from Peter Lake and added to Tuesday Lake. The reduction in planktivory was reversed after the summer of 1986 when all bass were removed and a small number of planktivorous minnows were added. This led to a large minnow recruitment event in 1987, with planktivore abundance reaching levels found in 1984 before the initial manipulations. Tuesday Lake then remained unmanipulated until mid-summer of 1990 when some juvenile bass were added. This did not result in a significant drop in planktivore abundance in 1990. Sampling intensity of Tuesday Lake was reduced after 1990, so we use only the 1984–1990 data set.

Data

Planktivorous fish populations were assessed every 2 wk from May–September using minnow traps. Planktivory rates were estimated with bioenergetics calculations that use planktivore densities, the average growth rates of fish, temperature, and gut content analysis (He et al. 1993). Since planktivorous fish may also feed in the benthos, including gut content analysis makes the estimate of planktivory reflect consumption rates of zooplankton only.

We focused on five species of cladocerans and four groups of other zooplankton: omnivorous copepods, carnivorous copepods, rotifers, and predatory phantom midges in the genus *Chaoborus*. (For the remainder of the article, we will refer to the lumped groups of species simply as "species.") Table 1 lists the zooplankton species and gives brief descriptions. The most efficient herbivores are the large-bodied *Daphnia pulex* (Dp) and *Holopedium gibberum* (Hg); with the smaller cladocerans, *D. rosea* (Dr), *Bosmina longirostris* (Bl), and *Diaphanosoma birgei* (Db) being less efficient (DeMott and Kerfoot 1982, Vanni 1986). The large size of Dp makes it particularly vulnerable to fish predation, and it may also be vulnerable to invertebrate predation during juvenile stages (MacKay et al. 1990). Adult Hg have a gelatinous mantle that is thought to protect against predation, although juveniles and recently molted adults are highly vulnerable (Tessier 1986). The small cladocerans appear to be less susceptible to fish predation than Dp and typically occur in lakes with high densities of planktivorous fish, although they are highly vulnerable to invertebrate predation (Lane 1978, Elser et al. 1987).

We divided copepods into an omnivorous and a carnivorous group. The omnivorous group consists of five genera of small- to large-bodied species and the juvenile stages (nauplii and copepodids) of all copepods (including the carnivorous copepods). The omnivorous copepods (Ocop) range from primarily herbivores (e.g., *Diaptomus oregonensis* and the juvenile copepod stages) to the omnivorous *Orthocyclops modestus,* which can prey on rotifers, juvenile copepods, and small cladocerans. Owing to their size and strictly carnivorous diet, we used a separate category for adult *Mesocyclops edax* (Ccop), which prey on rotifers, copepods, and small cladocerans (Gilbert and Williamson 1978, Williamson 1980). The rotifers (Rot) are all small herbivores except *Asplanchna* spp., which preys on

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TABLE 1. Summary of species/groups of zooplankton.

Species or group	Abbreviation	Description	Approximate generation time	M_i†
Daphnia pulex	Dp	Large-bodied cladoceran; susceptible to fish predation; juveniles susceptible to invertebrate predation.	2 wk	−0.59
Daphnia rosea	Dr	Medium-sized cladocerans; susceptible to fish and invertebrate predation.	2 wk	−0.059
Holopedium gibberum	Hg	Large-bodied cladoceran; gelatinous mantle thought to reduce predation by invertebrate predators and possibly small fish.	2 wk	−0.33
Bosmina longirostris	Bl	Small-bodied cladoceran; not preferred by fish predators; vulnerable to invertebrate and copepod predation.	2 wk	0.79
Diaphanosoma birgei	Db	Small-bodied cladoceran; not preferred by fish predators; vulnerable to invertebrate and copepod predation.	2 wk	0.59
Omnivorous copepods	Ocop	Five genera of small- to large-bodied herbivores and omnivores; larger species may prey on small cladocerans and rotifers; includes nauplii and copepodid stages of all species; large individuals susceptible to fish predation, and small individuals susceptible to invertebrate predation.	4 wk	0.26
Carnivorous copepods	Ccop	Consists solely of adult *Mesocyclops edax*; feeds on small cladocerans, rotifers, nauplii, and copepodids.	4 wk	0.24
Rotifers	Rot	18 species of small herbivores; susceptible to invertebrate predation.	<1 wk	0.11
Chaoborus	Chao	Three species of phantom midges, *Chaoborus trivittatus, C. flavicans,* and *C. punctipennis*; predators on small to medium zooplankton at different instars.	1–2 generations/yr	−0.21

† Slopes of yearly average log biomass against yearly average log planktivory.

other rotifers. Because *Asplanchna* spp. only appeared in significant numbers in the final year of the study, we did not give it a separate category. Finally, we grouped the three species of *Chaoborus* together (Chao). Despite our grouping, there were changes in the composition of Chao, with the smallest species (*C. punctipennis*) dominating the two larger species (*C. flavicans* and *C. trivittatus*) when planktivory was high (Soranno et al. 1993*b*).

In addition to zooplankton biomasses and planktivory, we included primary productivity in the analysis of zooplankton responses to the planktivory manipulations. Primary productivity is an overall measure of turnover in the phytoplankton community that is sensitive to fluctuations in nutrient abundance. We included primary productivity to account for possible changes in the biomass of the total zooplankton community, due to fluctuations in food supply. Primary productivity was measured weekly at three depths representing 100%, 50%, and 25% surface irradiance (Carpenter et al. 1993), and, for the analyses, we averaged across depths.

Zooplankton other than Chao were sampled each week during May–September. Abundances of each species were converted to biomass using the average size of a subsample of individuals in each collection. Chao biomass and primary productivity were sampled every other week (Soranno et al. 1993*a*, Soranno et al. 1993*b*). To match the zooplankton sampling dates, Chao biomass, primary productivity, and planktivory data were log-linearly interpolated.

For the analyses, zooplankton biomasses and planktivory were log-transformed. Data for most zooplankton species included zeros when densities dropped below the detection limit of the sampling program. Before the log transformation, zero values were replaced by 0.5× the lowest nonzero biomass of that species observed in the data set.

Analysis

The analysis uses short-term fluctuations in species' biomasses to estimate the direct effects of planktivory on population growth rates and the interaction strengths between zooplankton species (Ives 1995). For each species other than *Chaoborus,* we fitted the first-order autoregressive model

$$x_i(t+1) = x_i(t) + c_i + \left[\sum_{j=1}^{9} b_{i,j}x_j(t)\right] + \left[\sum_{k=1}^{4} a_{i,k}u_k(t)\right] \quad (1)$$

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where $x_i(t)$ is the log biomass of species i in sample t, $u_k(t)$ is value of exogenous variable k [$u_{\text{plk}}(t)$ = log planktivory, $u_{\text{pp}}(t)$ = primary productivity, $u_{\text{day}}(t)$ = day-of-year, and $u_{\text{day}^2}(t)$ = day-of-year squared], and c_i, $b_{i,j}$, and $a_{i,k}$ are regression coefficients. We have included day-of-year and day-of-year squared to account for possible seasonal effects on changes in biomass.

We fit the set of nine equations given by Eq. 1 simultaneously, using two different estimation procedures. The first, conditional least-squares estimation (CLS), is most appropriate when all unexplained variability is due to process error; while the second, total least-squares estimation (TLS), is most appropriate when all unexplained variability is due to measurement error. Of course, the unexplained variability in our data set is due to both types of error. However, fitting the model assuming the extremes of all process and all measurement error spans the range of possibilities for the relative contributions of process and measurement error.

For CLS, we estimated parameters by minimizing the sum of squared differences between observed and predicted values from Eq. 1 (Klimko and Nelson 1978, Dennis et al. 1995). This method is algebraically the same as standard least-squares regression. We included only consecutive samples within the same year, so changes in biomasses from the last sample of one year to the first sample of the next were excluded.

When measurement error is large, CLS is inappropriate, because the biomasses of species in sample t, needed to predict the biomass of species i in sample $t + 1$, are not known precisely, due to the measurement error. Therefore, we used TLS (Ludwig and Walters 1989, Hilborn and Walters 1992). To describe the procedure for TLS, let the function $G(\boldsymbol{\theta})$ give the sum of squared differences between predicted and observed species biomasses for a particular set of coefficients contained in the vector $\boldsymbol{\theta} = [c_1, \ldots, c_9, b_{1,1}, \ldots, b_{9,9}, a_{1,1}, \ldots, a_{9,4}]$. The objective is to find that set of coefficients $\boldsymbol{\theta}$ that minimizes the function $G(\boldsymbol{\theta})$. For a particular set of coefficients, the function $G(\boldsymbol{\theta})$ was calculated as follows:

1) At the start of each year, we estimated the biomass of all species as the average biomass from the first three samples.

2) From these starting biomasses, we generated time series of species biomasses by iterating Eq. 1 for the number of samples in the year. For each iteration, we used the observed values of the exogenous variables $u_k(t)$. However, the only biomass data used to generate the time series were those data used to estimate initial biomasses for each year.

3) We then calculated the sum of squared differences between observed and predicted biomasses, for all species and all samples, to give the function $G(\boldsymbol{\theta})$.

To find the set of coefficients $\boldsymbol{\theta}$ that minimizes $G(\boldsymbol{\theta})$, we started with the coefficient values calculated using CLS, and then we used a Nelder–Mead simplex method to minimize $G(\boldsymbol{\theta})$ (MathWorks 1996).

The difference between CLS and TLS can be explained as follows. When predicting species biomasses at time $t + 1$, CLS uses the observed biomasses at time t, since these are assumed to be known without measurement error. In contrast, when predicting species biomasses at time $t + 1$, TLS uses the *predicted* biomasses at time t, since the observed biomasses are assumed to contain measurement error. In turn, the predicted biomasses at time t are obtained from the predicted biomasses at time $t - 1$. Thus, in TLS the estimated coefficient values are those that give the best fitting time-series trajectory as calculated simultaneously from the set of nine equations given by Eq. 1.

Although the number of data points in the data set is large (107 consecutive samples × 9 species = 973), the number of coefficients to be estimated is also large (117 total). To avoid the problem of overparameterization, we imposed an a priori structure to the model. Philosophically, this is similar to path analysis, in which interactions between particular species are either included or excluded in the analysis (e.g., Wootton 1994*a*). Rather than including or excluding particular interactions, however, we constrained the signs of the coefficients to be biologically plausible. Specifically, we assumed that planktivory and Chao could only have negative effects on changes in zooplankton biomass. Furthermore, we assumed that herbivorous and omnivorous zooplankton could only have negative effects on changes in each other's biomasses. For the carnivorous copepod, we assumed that it could only have negative effects on changes in the biomasses of other zooplankton (excluding the omnivorous copepods), while the other zooplankton could have only positive effects on changes in carnivorous copepod biomass. We let omnivorous and carnivorous copepods have either negative or positive effects on each other, because the omnivorous copepod category includes the juvenile stages of the carnivorous copepod. Thus, although carnivorous copepods may prey on omnivorous copepods, they also produce omnivorous juvenile stages. Finally, we assumed that Dp was competitively superior to Bl and Db, and, therefore, that these two small cladocerans have no effect on changes in the biomass of Dp. This assumption has empirical support from other studies (DeMott and Kerfoot 1982, Vanni 1986). We assumed this because there were strong negative correlations both between Dp and Bl biomasses and between Dp and Db biomasses. Since Dp is known to be the superior competitor, these negative correlations will be driven by the negative effect of Dp on Bl and Db, rather than the other way around.

An additional problem arose for Chao. Chao population dynamics occur on a much slower time scale than for the other zooplankton species, since Chao have only one generation per year in Tuesday Lake. Moreover, Chao adults fly and are therefore not confined to

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a lake. Thus, the only component of Chao demography necessarily tied to the lake community is mortality. As a consequence, changes in Chao abundance between samples were not great enough to identify the effects of other zooplankton species on Chao, and the predicted biomass of Chao in sample $t + 1$ was dominated by the Chao biomass at time t. Therefore, in Eq. 1, we set coefficients for the effects of other zooplankton species on Chao equal to zero, and the coefficient for the effect of Chao on itself, we set equal to one. This assumes that Chao biomass is determined by the level of planktivory and the time-dependent influx of Chao into the lake [included in Eq. 1 as $u_{\text{day}}(t)$ and $u_{\text{day}^2}(t)$; Primary productivity, $u_{\text{pp}}(t)$, was included in the statistical model but was never significant.]

To select the best model structure, we used Akaike's Information Criterion (AIC) while estimating coefficients using CLS. AIC incorporates a "penalty factor" for the number of parameters in a model, thereby selecting a model that includes only those parameters that provide a minimum amount of additional information about the system (Box et al. 1994, Dennis et al. 1998). The number of possible model structures is large; since there are 117 coefficients, there are 2^{117} possible model structures, depending on which coefficients are included. To select the best model (i.e., the model with the lowest AIC), we used the following procedure. We randomly constructed 100 model structures by including or excluding coefficients with probability 0.5, and, from these, we selected the best fitting model. We repeated this 100 times, to give 100 models that were the best out of 100 randomly constructed models (10 000 total model structures). If a coefficient occurred in <15 of the 100 "best-of-100" models, we set the coefficient to zero. Then, we repeated the procedure to produce another 100 "best-of-100" models and set coefficients to zero if they occurred in <15 models. Repeating this procedure led to a single model with the lowest AIC. We checked that this model in fact had the lowest AIC both by repeating the procedure described above using different random numbers, and by exhaustively searching all models that differed from the best model by the inclusion or exclusion of individual coefficients. We selected the best model structure using only CLS, because TLS was computationally too intensive to investigate many different model structures. For TLS, we included all coefficients, but constrained the signs of interactions as we have described. The magnitudes of the estimated coefficients reveal the importance of different interactions.

The autoregression models were fit without any nonlinear higher order interaction terms among species. To try to identify higher order interactions, we regressed residuals for each species from the best fitting model obtained by CLS in a pair-wise fashion against each higher order quadratic term of the form $(x_i(t) - \bar{x}_i) \times (x_j(t) - \bar{x}_j)$ for all i and j, where $\bar{x}$ is the mean log biomass; this produced 594 pair-wise regressions (residuals for each of nine species × 66 higher order interaction terms). For each regression, we calculated the F ratio, and we selected the strongest higher order interaction terms as those with the largest F ratios (Larsen and Marx 1981). F ratios can be used comparatively to rank the higher order interactions, because they are monotonic functions of the likelihood ratio statistic (Dennis and Taper 1994). However, the F ratios in this context do not have F distributions, and so tables of F distribution percentiles cannot be used with time-series data for hypothesis testing or estimating confidence intervals (Dennis and Taper 1994).

To measure the long-term changes in biomasses in response to planktivory, we calculated the average species' biomasses for each of the seven years of study and regressed these against the average annual planktivory rate. The slope of this regression for species i is denoted M_i, and values of M_i for all species are given in Table 1. Negative and positive values of M_i correspond to decreases and increases, respectively, in average annual species' biomasses with increases in average annual planktivory rates. We will compare these values of long-term changes in species' biomasses with those predicted by the autoregression model, using an analysis described in the *Results* section.

Results

Fitted autoregressive model

Table 2 gives the coefficients for the autoregressive model fitted using CLS and TLS. For CLS (Table 2A), only those coefficients included in the best fitting model are shown, and R^2 values give the amount of explained variance in the change in biomass from one sample to the next (i.e., $x_i(t + 1) - x_i(t)$). For TLS (Table 2B), all coefficients with magnitude >0.02 (or >0.0001 for day-of-year and day-of-year squared) are shown, and R^2 values give the amount of explained variance in the biomass (i.e., $x_i(t)$).

In general, the coefficients given by CLS and TLS are similar. The main differences are the coefficients for the effects of Ocop on Dr ($b_{\text{Dr,Ocop}}$), Dr on itself ($b_{\text{Dr,Dr}}$), and Dp on Bl ($b_{\text{Bl,Dp}}$). The R^2 values reported for CLS are generally lower than those reported for TLS. This reflects differences in how these R^2 values were calculated; for CLS, R^2 was based on the variance in $x_i(t + 1) - x_i(t)$, whereas for TLS, R^2 was based on the variance in $x_i(t)$.

Fig. 1 gives zooplankton biomasses and planktivory rates for the period 1984–1990, with zooplankton biomasses predicted by the autoregressive model using CLS (dashed lines) and TLS (solid lines). The lines were fit to the data by estimating the first point of each year as the average of the biomasses in the first three samples of the year, and then generating predicted time series using Eq. 1. The lines obtained by CLS and TLS are similar, although they differ for a few species in a few years, for example, for Dp in 1987, for Dr in 1988,

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and for Bl in 1988. Also, although the fitted lines capture much of the variability in species' biomasses, the models do not capture some dynamical features of the data, for example, the very high biomasses of Dr in 1988 and of Hg in 1985. It is unclear what caused these particularly high biomasses, but it is likely that exogenous factors other than those included in the model (planktivory, primary productivity, and day-of-year) were involved.

Fig. 2 summarizes the autoregressive model in the form of an interaction web. Species that decreased in biomass with increasing planktivory are shown in black, species that increased are white, and the species that remained unchanged, Dr, is shown with hatching (Table 1). Lines connecting species denote the interactions given by the coefficients obtained from CLS (Table 2A), with negative coefficients shown with arrows and positive coefficients shown with dots. The best fitting model included coefficients for intraspecific effects, b_{ii}, for all species, although these are not shown in the figure.

Higher order interactions

We searched for higher order interactions by regressing residuals from the best fitting model obtained using CLS against all quadratic terms of the form $(x_i(t) - \bar{x}_i) \times (x_j(t) - \bar{x}_j)$ for all i and j. Of the 594 resulting regressions, the three with the highest F ratios were for Ccop residuals regressed against the interaction term Ccop × Bl, Ccop residuals against Ccop × Db, and Dr residuals against Dr × Dp; the corresponding F ratios were 15.08, 10.97, and 10.05, respectively. Fig. 3 shows the strongest of these: Ccop residuals regressed against Ccop × Bl. The negative correlation between Ccop residuals and Ccop × Bl implies that the increase in biomass of Ccop was relatively high when either Ccop had high biomass and Bl had low biomass, or when Ccop had low biomass and Bl had high biomass. We can think of no biological reason for this to be the case. Furthermore, although this is the strongest higher order interaction, it does not explain much variance in the residuals from the best fitting linear model.

This analysis highlights the difficulty of detecting higher order interactions in complex communities using time series techniques. Although higher order interactions may exist, the large number of possible higher order interactions makes detecting real higher order interactions statistically problematic. Furthermore, large amounts of unexplained variability in natural systems will obscure the effects of higher order interactions.

Long-term changes in average annual biomass

The coefficients from the autoregressive model measure the direct effects of species interactions on short-term changes in biomass, assuming that changes in biomasses between weekly samples are too rapid to be the result of indirect interactions acting through changes in the biomasses of other species. In contrast, long-term changes in species' biomasses depend on both direct interactions and indirect interactions operating through long-term changes in biomasses of other species in the community (Bender et al. 1984, Yodzis 1989, Ives 1995). To investigate the importance of these indirect effects, in Appendix A we derive a mathematical formula that uses the coefficients estimated from the autoregressive model to predict the long-term changes in species biomass. This formula can be expressed in terms of vectors $\mathbf{B}_j = [b_{1j}, b_{2j}, \ldots, b_{9j}]$ and $\mathbf{A}_{\text{plk}} = [a_{1,\text{plk}}, a_{2,\text{plk}}, \ldots, a_{9,\text{plk}}]$; $\mathbf{B}_j$ contains the coefficients for the effects of species j on all other species in the community, and $\mathbf{A}_{\text{plk}}$ contains the coefficients for the effect of planktivory on all species. The predicted long-term change in biomass of species i, L_i, is then given by

$$L_i = -\frac{\det(\mathbf{B}_1, \ldots, \mathbf{B}_{i-1}, \mathbf{A}_{\text{plk}}, \mathbf{B}_{i+1}, \ldots, \mathbf{B}_9)}{\det(\mathbf{B}_1, \ldots, \mathbf{B}_9)}. \quad (2)$$

By comparing values of L_i to the observed changes in average annual species biomasses with changes in average annual planktivory (given by M_i in Table 1), we can determine whether the direct interactions obtained from the autoregressive model are consistent with long-term changes in the zooplankton community. When assessing the predicted changes in zooplankton biomasses, we excluded Chao, since the autoregressive model did not include coefficients for the effects of other zooplankton species on changes in Chao biomass.

Fig. 4 graphs the predicted changes in average annual zooplankton biomasses with changes in average annual planktivory, L_i, against the actual changes, M_i. This relationship is based on CLS (Fig. 4A) and TLS (Fig. 4B). For CLS, the match between L_i and M_i is very close. The match is poorer for TLS. The two low values of L_i for TLS correspond to Dr and Ccop. Considering the similarity in coefficients obtained from CLS and TLS (Table 2), the differences in values of L_i for Dr and Ccop are surprisingly large. Trying to determine exactly which coefficients are responsible for the differences in the predicted values of L_i is difficult, because the values of L_i depend on all coefficients, not just those involving the particular species i. Because the coefficient values obtained from CLS give better predictions of the long-term changes in zooplankton biomasses, we will use these values in further analyses.

In this analysis, L_i and M_i were both derived from the same data. Therefore, the match between L_i and M_i should not be interpreted as a test of the fit of the autoregressive model to the data. Instead, the formula for L_i should be viewed as a tool to investigate the interaction web derived from the autoregressive model and how indirect interactions acting through this web explain the community responses to planktivory manipulations.

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TABLE 2. Regression coefficients c_i, $b_{i,j}$, and $a_{i,k}$ obtained from (A) conditional least-squares estimation, and (B) total least-squares estimation.

Species (i)	c_i	$b_{i,j}$ Dp	Dr	Hg	Bl	Db	Ocop	Ccop	Rot	Chao	Plk
A) Conditional least-squares estimation											
Dp	1.17	−0.59					−0.40				−0.26
Dr	0.18		−0.19				−0.13		−0.14		
Hg	−1.17	−0.19		−0.28	−0.22						−0.09
Bl	−0.23	−0.05			−0.07					−0.11	
Db	−0.47	−0.16		−0.18		−0.27					
Ocop	0.30	−0.06					−0.14				
Ccop	−0.07		0.12					−0.10	0.15		
Rot	−0.33			−0.13				−0.05	−0.37		
Chao	−1.91									1‡	−0.21
B) Total least-squares estimation											
Dp	1.49	−0.45	−0.03				−0.57				−0.16
Dr	0.23	−0.03	0.0				−0.02		−0.11		
Hg	−0.79	−0.20		−0.25	−0.19						−0.11
Bl	−0.34	−0.16			−0.13	−0.02				−0.21	
Db	−0.11	−0.24	−0.03	−0.12		−0.27					
Ocop	0.34	−0.09					−0.14				
Ccop	−0.06		0.07					−0.07	0.12		
Rot	−0.29			−0.16					−0.39	−0.02	
Chao	−2.17									1‡	−0.21

Note: In (B), only values with magnitude ≥0.02 shown, except for Day and Day^2, where only values ≥0.00001 are shown.
† In (A), R^2 is calculated for changes in log biomasses between consecutive samples. In (B), R^2 is calculated for total variation in log biomasses.
‡ Regression coefficient set to 1.

Pathways of the effects of planktivory

The equation for L_i (Eq. 2) gives a tool that can be used to explore the pathways by which changes in planktivory change the biomasses of zooplankton in the community. From the autoregressive model, planktivory has its main effects through Dp, Hg, and Chao (Table 2, Fig. 2). It is natural to ask which of these three pathways is the most important in explaining the long-term changes in zooplankton biomasses in response to changes in planktivory.

To address this, we sequentially set the coefficients for the effects of planktivory on Dp, Hg, and Chao to zero, and recalculated the predicted long-term change in biomass, L_i, for all species. Comparing the resulting values of L_i to the observed values M_i shows that removing the effect of planktivory on Dp causes the greatest decrease in the correlation between L_i and M_i (Fig. 5). Therefore, the effect of planktivory on Dp is the most important in explaining the changes in average annual zooplankton biomasses observed over the course of the experiment. Nonetheless, even after the removal of the effect of planktivory on Dp, the correlation between L_i and M_i is 0.71, implying that the effects of planktivory on Hg and Chao also play an important role.

Endogenous vs. exogenous interactions

The autoregressive model (Eq. 1) separates the endogenous interactions between species within the community that are given by coefficients $b_{i,j}$, from the exogenous interactions between species and planktivory that are given by coefficients $a_{i,\mathrm{plk}}$. The long-term responses of zooplankton biomasses to changes in planktivory, L_i, depend on both the endogenous and exogenous interactions. Nonetheless, Eq. 2 breaks L_i down into a denominator, which is independent of the effects of planktivory on species in the community ($\mathbf{A}_{\mathrm{plk}}$), and a numerator, which is independent of the effects of species i on species in the community ($\mathbf{B}_i$). This makes it possible to ask, for a given species i, whether its sensitivity to long-term planktivory manipulations can be predicted from only endogenous interactions between species (denominator of Eq. 2); whether its sensitivity can be predicted without knowing its effects $\mathbf{B}_i$ on other species (numerator of Eq. 2); or whether both of these components are needed to predict a species' sensitivity to planktivory manipulation.

Fig. 6 shows the magnitudes of L_i, the denominator of Eq. 2, and the numerator of Eq. 2 graphed against the magnitude of the observed long-term change in the biomass of species i, M_i. Variation in the magnitude of the denominator of Eq. 2 explains little of the variation in $|M_i|$ (Fig. 6B). Therefore, endogenous interactions alone are not sufficient to predict the sensitivity of species to planktivory perturbations. The numerator of Eq. 2 explains more of the variation in $|M_i|$ (Fig. 6C), although not as much as the product of the numerator and denominator, that is, L_i (Fig. 6A). We therefore conclude that to predict the sensitivity of species i to planktivory perturbations, it is necessary to know how planktivory effects all species, how species i effects all species, and how all of the other species interact in the community.

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TABLE 2. Extended.

Pp	$a_{i,k}$ Day	$a_{i,k}$ Day^2	R^2†
			0.30
			0.11
	0.0038	−0.00031	0.27
			0.05
	−0.0029	−0.00038	0.19
			0.08
			0.14
−0.19			0.21
	0.0067	−0.000082	0.25
	−0.00031		0.73
	−0.00072		0.64
	0.0033	−0.00041	0.49
	−0.0010		0.72
	−0.0048	−0.00031	0.78
	−0.00089		0.79
	−0.00045		0.75
−0.25	−0.00061		0.33
	0.0070	0.00016	0.23

Arguing from this result for planktivory perturbations, it is likely that predicting how species will respond to any other type of perturbation will require knowing how that perturbation affects the population growth rates of all species in the community. Knowing only the interaction strengths between species is not enough. However, once the interaction web for a community is quantified using data from one perturbation, it can be used to predict species' responses to another perturbation, when combined with information on how the perturbation affects each species. This argument assumes that the quantitative interaction web, as calculated from data collected during one type of perturbation, would correctly describe interactions experienced during a different type of perturbation. In the *Discussion,* we consider whether this assumption is likely to be valid.

In Appendix B, we break down Eq. 2 still further and show that the sensitivity of a species to a perturbation decreases with the following: (1) the strength of interactions of that species on other species in the community (measured by the magnitude of $\mathbf{B}_i$), (2) the ecological distinctiveness of the species in the community (measured by the dissimilarity between $\mathbf{B}_i$ and the $\mathbf{B}_j$'s for all other species in the community), and (3) the similarity between the effects of planktivory and the effects of species other than species i (measured by the similarity between $\mathbf{A}_{\mathrm{plk}}$ and all $\mathbf{B}_j$'s except for $\mathbf{B}_i$). This analysis reveals several interesting patterns. For example, the magnitudes of responses of both Dp and Db to long-term planktivory manipulations were that same ($|M_{\mathrm{Dp}}| = |M_{\mathrm{Db}}| = 0.59$). Dp had strong effects on other species, while Db had weak effects. This should buffer Dp against long-term perturbations relative to Db. Nonetheless, Dp was ecologically similar to Hg and Ocop (Table 2, Fig. 2), and this greater ecological similarity counteracted the buffering effect of having strong interactions with other species. The net result is that Dp was as sensitive as Db to the planktivory perturbations. Appendix B summarizes the results of this analysis for all species in the community, showing that no single factor was responsible for differences among species' in their sensitivity to planktivory manipulations.

DISCUSSION

Our goal has been to understand the observed changes in the zooplankton community of Tuesday Lake caused when planktivory rates were experimentally manipulated. Using weekly changes in species biomasses over the seven-year period of the experiment, we constructed a quantitative interaction web for the zooplankton community, using autoregression to estimate the direct interaction strengths between species (Table 2, Fig. 2). We then used the interaction web to investigate how direct and indirect interactions combine to explain the long-term changes in species biomasses with changes in average annual planktivory rates.

Biological plausibility of the interaction web

When interpreting the interaction web produced by the autoregressive model, two caveats are needed. First, the autoregressive model relies on correlated changes in species' biomasses to infer interactions between species. The best fitting model gives the best post hoc description of changes in species' biomasses, but, as with any model based on correlation, it does not constitute a test of species interactions. Second, for interactions between species to be detected, the interactions must be involved in the observed changes in species' biomasses. For example, even though a species may have a negative effect on another, this effect will not be found using autoregression unless the biomass of the first species changes. Therefore, the ability of autoregression to identify species interactions depends on the response of the entire community to a perturbation.

Despite these caveats, the autoregressive model gives a biologically plausible depiction of the main interactions within the zooplankton community (Fig. 2). Planktivory has greatest impact on the large-bodied zooplankton species, *D. pulex* (Dp), *Chaoborus* (Chao), and *H. gibberum* (Hg), as expected from size-selective predation (Brooks and Dodson 1965, Hall et al. 1976). Dp interacts strongly with the other herbivores, and this pattern is consistent with the view that Dp is the most critical zooplankton species for successful biomanipulation (Shapiro 1990, Carpenter and Kitchell 1993). Its broad diet and rapid numerical response make it a formidable grazer and competitor (Lynch 1979, Vanni 1986). The negative effect of Chao on *B. longirostris* (Bl) is consistent with predation known from Tuesday and other lakes (Elser et al. 1987). The

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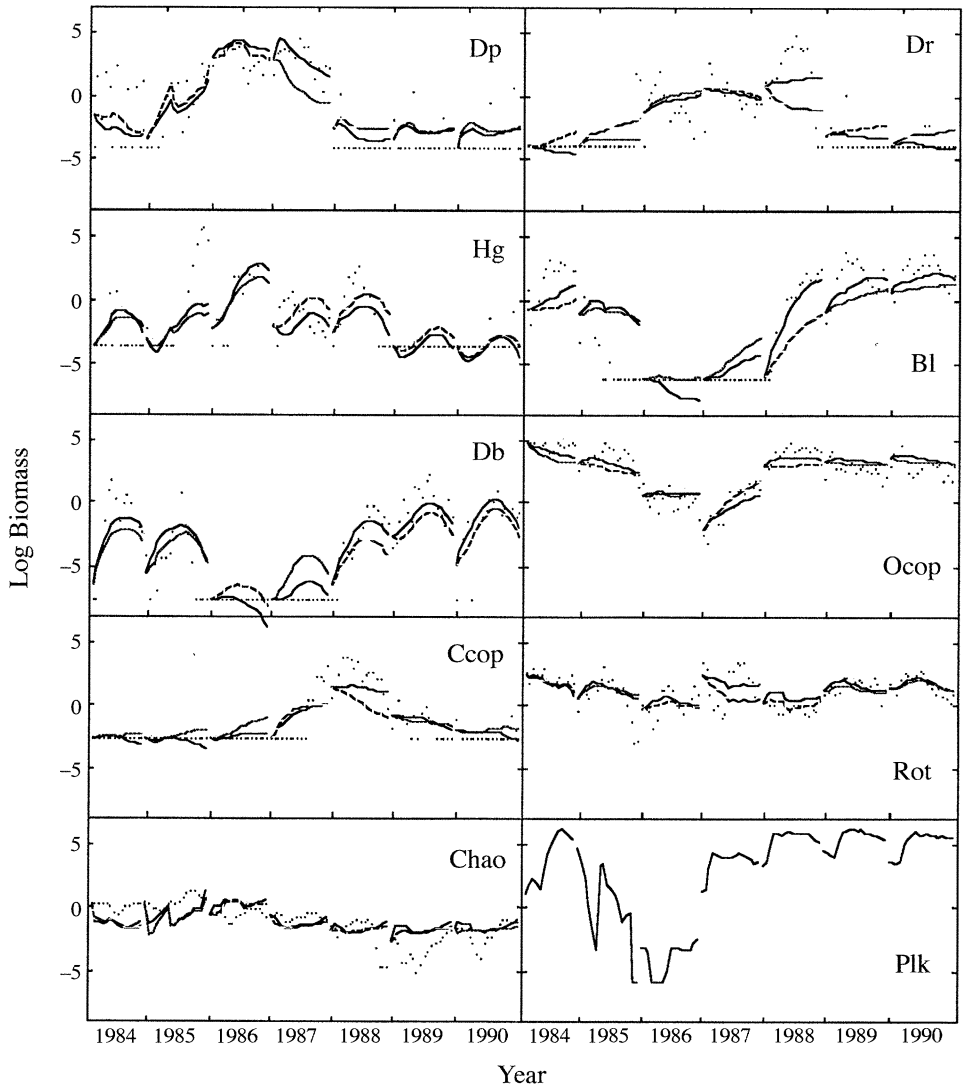

FIG. 1. Log biomass of zooplankton species and planktivory rates over seven years of experimental manipulation in Tuesday Lake. The lines in the graphs for each species give the population dynamics predicted by iterating the autoregressive model, using the coefficients obtained from conditional least-squares estimation (·····) and total least-squares estimation (– – –), given in Table 2. The data are given as sequential points, and the years are separated by breaks in the fitted lines. The acronyms for the different species are given in Table 1. Planktivory (Plk) is log-transformed and rescaled so that it fits on the same scale as the log biomasses of the zooplankton.

strong predator–prey interaction between carnivorous copepods (Ccop) and rotifers (Rot) makes sense (Soranno et al. 1993*b*), although Ccop were abundant in only one year of the study.

Some other interactions are plausible but not well studied. For example, the negative effects of omnivorous copepods (Ocop) on Dp and *D. rosea* (Dr), and of Dp on Ocop, could represent competition with, or predation on, juveniles. Although we do not understand the mechanism of these interactions, they appear to have substantial effect and could be investigated experimentally. The negative effect of Rot on Dr is puzzling, but does appear as important in our autoregressions.

We expected seasonal patterns to be weak, because our sampling program was designed to focus on summer stratification and avoid strongly seasonal patterns. The species that show seasonal effects (Chao, Hg, and *D. birgei* [Db]) are those that typically show a cycle within the summer season in these lakes (Carpenter et al. 1987, Elser et al. 1987, Soranno et al. 1993*b*). During the course of the summer, Chao undergoes the major events of its life cycle: pupating, emerging, ovipositing, and growth through four larval instars. Thus, a strong seasonal effect is expected.

In other cases, we were surprised by interactions that were not revealed by autoregression. While numerous negative effects of competition or predation are evident, positive effects of prey on predators are rare. This

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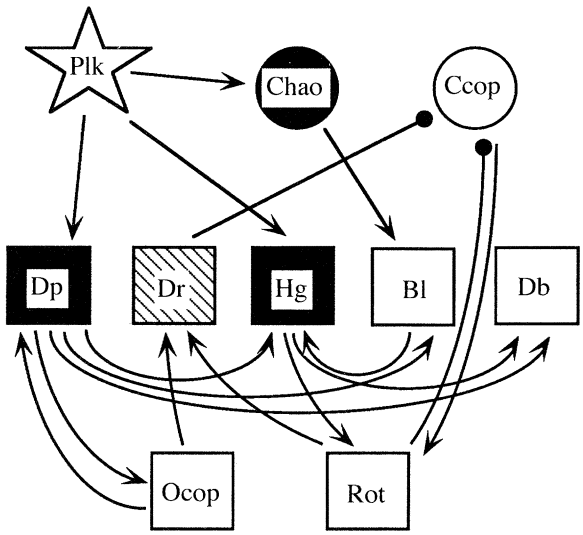

FIG. 2. Interaction web derived from the best fitting autoregressive model with coefficients obtained from conditional least-squares estimation (Table 2A). The abbreviations of species names are explained in Table 1. The shading corresponds to decreasing (black), increasing (white), or unchanging (hatching) biomass of the species with increasing planktivory. Boxes are used for mainly herbivorous species, while circles denote predatory species. Arrows denote negative coefficients on the species to which the arrow is directed, and solid dots denote positive coefficients. Although not shown, the best fitting model includes negative coefficients for intraspecific effects for all species.

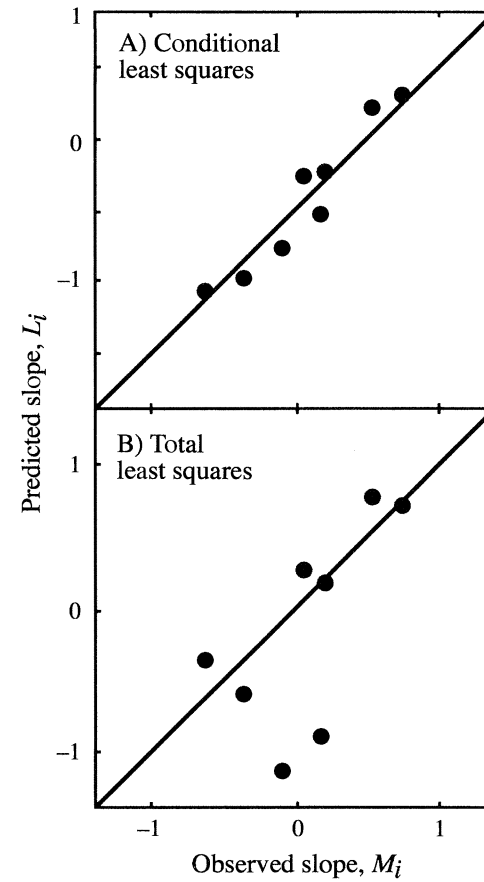

FIG. 4. The predicted change in average annual biomass with average annual planktivory for each species, L_i, vs. the observed change, M_i. (A) L_i was predicted using coefficients obtained from conditional least-squares estimation. (B) L_i was predicted using coefficients obtained from total least-squares estimation. Each point corresponds to a zooplankton species, although *Chaoborus* is excluded (see *Results: Long-term changes*).

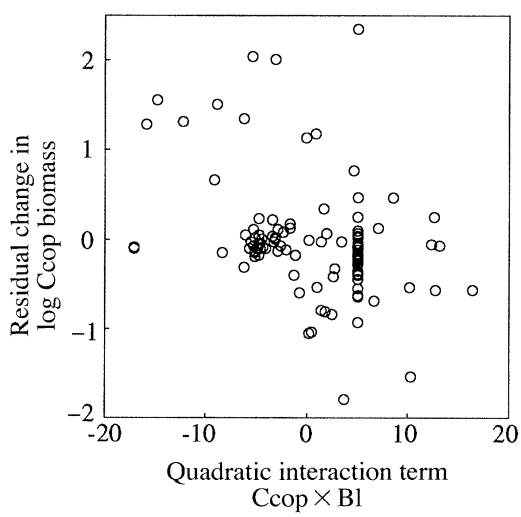

FIG. 3. Graph of the strongest quadratic higher order interaction. The residual change in log biomass of carnivorous copepods (Ccop) from the best fitting autoregressive model is regressed against the interaction term between carnivorous copepod and *B. longirostris* log biomasses, $[x_{\mathrm{Ccop}}(t) - \bar{x}_{\mathrm{Ccop}}] \times [x_{\mathrm{Bl}}(t - \bar{x}_{\mathrm{Bl}}]$.

may indicate that predators can be sustained by a number of prey species and consequently are not sensitive to shifts in the availability of any one prey item. Based on diet analyses (Elser et al. 1987), we expected Chao to have a negative impact on Rot. Because of interference competition (Gilbert 1988), we also expected Dp and Dr to have negative impacts on Rot. There are at least two biological explanations for the absence of these negative effects. (1) Rotifers have relatively fast growth rates (Downing and Rigler 1984), and rapid growth may obscure effects in measurements made at 1-wk intervals. (2) Rotifers are the most speciose of the lumped groups in the analysis (Soranno et al. 1993*b*), and shifts in species composition could prevent changes in total rotifer biomass (Frost et al. 1995). We expected primary production to have a generally positive effect on zooplankton biomass, as has occurred in whole-lake nutrient enrichments (Carpenter et al. 1996). However, effects of primary production were

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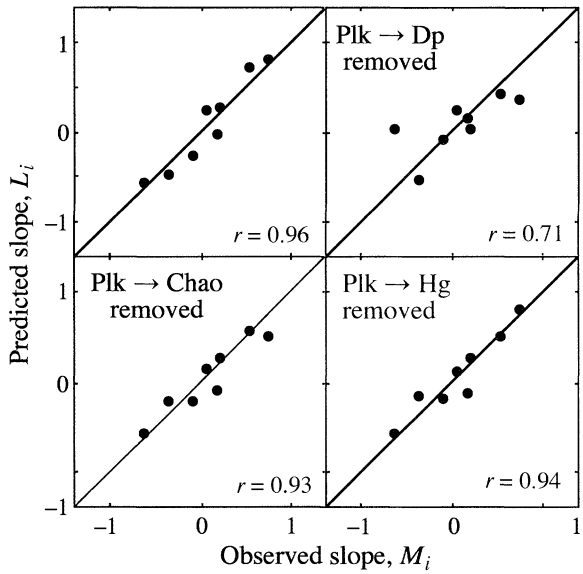

FIG. 5. The predicted change in average annual biomass with average annual planktivory for each species, L_i, vs. the observed change, M_i, when different interactions between planktivory and zooplankton are removed. The coefficients used to calculate L_i were obtained from conditional least-squares estimation. The top left-hand panel corresponds to Fig. 4A. The panel labels "Plk → j removed" denote that the coefficient for the effect of planktivory on species j is set to zero. The abbreviations of species names are explained in Table 1.

weak. Primary production varied far more in nutrient enrichment experiments than in the Tuesday Lake planktivory manipulation, and the range of primary production was probably insufficient to detect its effects on zooplankton. Because autoregression analyses can fail to detect effects for a number of reasons, the interaction web of Fig. 2 should be viewed as a minimal map of the most strongly apparent interactions.

Quantifying the importance of indirect interactions

We used the quantitative interaction web to integrate the direct and indirect effects of planktivory manipulations and, thereby, explain the long-term responses of species to changing planktivory. The coefficients of the autoregressive model obtained from conditional least-squares (CLS) estimation gave predictions for the effect of planktivory on average annual species' biomasses that are consistent with the observed average annual biomasses. In contrast, the coefficients obtained from total least-squares (TLS) estimation gave poor predictions, especially for *D. rosea* and the carnivorous copepods. This occurs despite the similarity between coefficients obtained using both estimation procedures (Table 2), and despite the similarity in trajectories of the models fitted to the data (Fig. 1). This result emphasizes how predicting long-term changes in species abundances may be sensitive to the magnitudes of the estimated strengths of interaction between species.

From the analysis of the interaction web with coefficients obtained from conditional least-squares estimation, planktivory appears to have its main effect on the zooplankton community through its effect on *D. pulex*; setting the coefficient for the effect of planktivory on *D. pulex* to zero leads to poor predictions of the long-term changes in zooplankton biomasses (Fig. 5). This identifies *D. pulex* as a keystone species with respect to changes in the community brought about by changes in planktivory. Despite the importance of *D. pulex,* the effects of planktivory on *H. gibberum* and

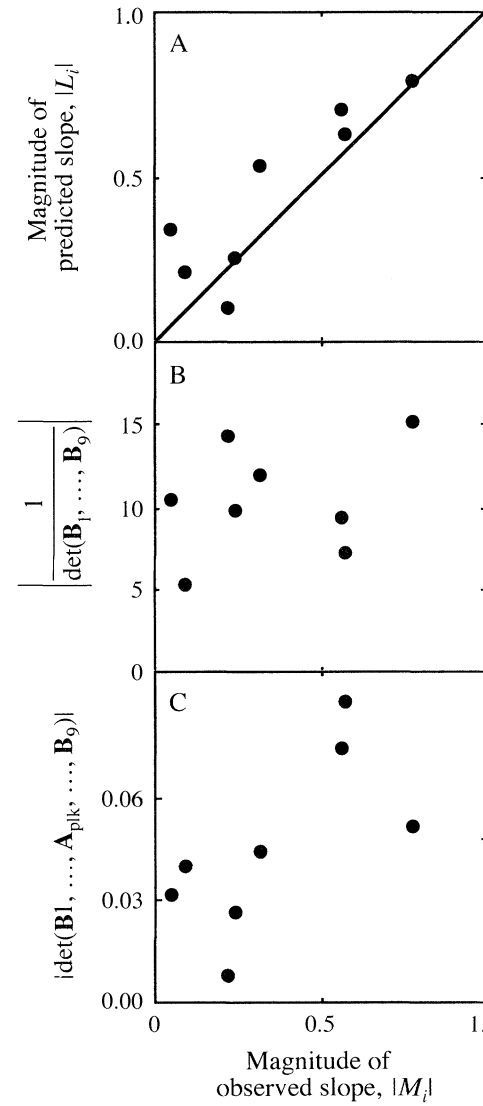

FIG. 6. Magnitude of the predicted change in average annual biomass of each species (excluding *Chaoborus*), with changes in average annual planktivory, vs. the magnitude of the observed changes $|M_i|$. (A) Prediction based on $|L_i|$, given by Eq. 2. (B) Prediction based only on the magnitude of the denominator of Eq. 2, $|1/\det(\mathbf{B}_1, \ldots, \mathbf{B}_9)|$. (C) Prediction based only on the magnitude of the numerator of Eq. 2, $|\det(\mathbf{B}_1, \ldots, \mathbf{B}_{i-1}, \mathbf{A}_{plk}, \mathbf{B}_{i+1}, \ldots, \mathbf{B}_9)|$.

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Chaoborus are also important, and together, in the absence of the effects on *D. pulex,* they can explain much of the observed long-term responses in the zooplankton community (Fig. 5).

The interaction web can also be used to quantify how the patterns of interaction between zooplankton within the community either buffer or accentuate the effects of planktivory. Theory predicts that, all else being equal, species that have distinct ecological roles and exert large effects on other species in the community will be relatively buffered against long-term exogenous perturbations (Appendix 2; Ives 1995). In principle, this makes it possible to predict which species are the least sensitive to environmental perturbations, based solely on how they interact with other species. However, our analysis shows this does not work for planktivory manipulations (Fig. 6). Instead, knowing how planktivory effects all zooplankton species is essential for making predictions about which species will change to the greatest extent when the community experiences planktivory manipulations. Thus, although theory makes predictions about which species will be most sensitive assuming all else is equal, for the community and manipulation we analyzed, all else is not equal.

Assumptions underlying the quantitative interaction web

A central assumption of the autoregressive model is that, over the weekly intervals between samples, changes in zooplankton biomasses are driven by direct interactions between species. By inferring direct interactions using weekly data, we are assuming that indirect interactions between two species, acting via changes in the biomass of a third species, do not occur rapidly enough to be observed on a weekly time scale. For example, consider three competing species, x, y, and z, with y having a direct effect on x, and z having a direct effect on y, but not on x. Suppose that the biomass of species z was high in week t, and this led to a decrease in biomass of species y. If species x responded rapidly to this decrease in y, then the increase in z would appear to create an increase in the biomass of species x. Although this example highlights the potential danger of inferring direct interactions from weekly samples, two things reduce this danger. First, the biomass of species y, in week t, itself appears in the regression for the change in the biomass of species x. Therefore, the indirect positive effect of species z on x will only appear if the change in biomass of species y, after the sample in week t, explains a substantial amount of variance in the change in biomass of species x *beyond* that already explained by the biomass of species y in week t. Second, in Tuesday Lake, the generation times of all zooplankton except rotifers are at least twice as long as the weekly sampling interval, thereby limiting the magnitude of possible indirect interactions.

The autoregressive model also assumes that changes in species' biomasses between successive samples are explained by the biomasses of all species at the initial sample, with no effect of biomasses measured in preceding weeks. The potential for time-delayed effects exists if there are changes in the age structure of populations. For example, if predators selectively killed juvenile stages of a species, then the effect of predation on the species' reproduction rate would be delayed by the time required for juveniles to reach reproductive age. The potential for time-delayed effects is reduced at longer intervals between sampling, since longer sampling intervals will incorporate time-delayed effects. Thus, the sampling interval of roughly half a generation time of many of the zooplankton species we analyzed decreases the likelihood of time-delayed effects. Notice that there is a conflict between sampling at short intervals to reduce the confounding effects of indirect interactions, and sampling at long intervals to reduce the potential for time-delayed effects. The weekly sampling interval of the data we analyzed should be a reasonably good compromise of this conflict.

Finally, the autoregressive model assumes that interactions between the log-transformed biomasses of species are linear. To search for potential nonlinear interactions, we regressed residuals from the best fitting log-linear model against all quadratic terms of the form $(x_i(t) - \bar{x}_i) \times (x_j(t) - \bar{x}_j)$. Even the strongest nonlinear interaction (Fig. 3) did not explain much of the residual variation in changes in biomasses. A problem of detecting nonlinear higher order interactions is the large number of possible nonlinear interactions, even when there are relatively few species in a community; for our data set, there are 594 possible quadratic interaction terms. Nonlinear interactions might occur in real communities, but only very strong nonlinearities are likely to be detected in time-series data sets, especially if the natural variability in the community is large. Although a log-linear model may not be biologically accurate, it may nonetheless be sufficient to characterize the major patterns of interactions between species and make predictions about long-term responses to environmental perturbations (Ives 1995, Ives and Jansen 1998).

Predicting the response of the community to other perturbations

The magnitude of changes in average annual biomasses of species, with respect to changes in average annual planktivory, depends on both endogenous interactions within the community and the direct effects of exogenous manipulations of planktivory on each of the individual species. In principle, it is possible to anticipate the magnitude of these changes from knowledge of only the endogenous interactions. Nonetheless, for the case of planktivory perturbations, we showed that it is necessary to know both endogenous and exogenous patterns of interactions. Thus, to predict how a novel perturbation will affect the zooplankton community, it will be necessary to know how this pertur-

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bation directly affects all species in the community. This is not to say, however, that information obtained from analyzing the community responses to the planktivory manipulation is useless. The quantitative interaction web can be combined with information on the direct effects of a novel perturbation to predict how the community will respond to the perturbation. The direct effects of factors such as pH, temperature, food abundance, and chemical pollutants are often measured in laboratory and enclosure experiments (Graney et al. 1994). Our approach may make it possible to use the results of small-scale, single-species experiments to predict the response of an entire community to perturbations, thereby making a bridge between small-scale experiments and community responses to novel perturbations.

Although it is possible to use the interaction web estimated from the planktivory manipulations to predict how the Tuesday Lake community will respond to a novel perturbation, this relies on the assumption that the interactions revealed by the planktivory manipulations will be the same as those that drive the response of the community to the novel perturbation. Because the ability of autoregression to detect interactions between species depends on the amount of variation explained by the interactions, which interactions are detected may depend on the perturbation that drives the pattern of variation in species' biomasses. Unfortunately, Tuesday Lake was subjected to only a single kind of perturbation, thereby making it impossible to assess whether our analysis could predict community responses to a different perturbation. A thorough assessment of the possibility of using information from one perturbation to predict the responses to another requires a different data set.

Linear autoregression provides a relatively simple tool for quantifying how direct and indirect interactions affect the response of species to environmental perturbations. Of course, many complexities of the interactions among species are ignored. For example, we measured interaction strengths as linear regression coefficients, even though interactions between species are almost certainly nonlinear (Vandermeer 1969, Case and Bender 1981, Gilpin et al. 1986, Billick and Case 1994, Wootton 1994*b*). Although nonlinear modeling approaches are possible, these often require estimates of large numbers of parameters and make numerous assumptions about the particular forms of nonlinearities (Walters 1986, DeAngelis 1988). A different approach to quantifying interactions between species in a community is to manipulate the biomasses of individual species independently and measure the resulting changes in biomasses of other species (Bender et al. 1984). Although this approach has been applied to laboratory (Case and Bender 1981, Gilpin et al. 1986, Worthen and Moore 1991) and field communities (Moran et al. 1988, Wootton 1993, 1994*a*, Menge 1995), it is not possible at the scale of whole lakes. Furthermore, although it is possible to manipulate abundances of species in smaller-scale mesocosm experiments, interactions among species within mesocosms are often poor predictors of interactions at the scale of whole lakes (Carpenter 1996, Pace et al. 1998). Therefore, given the constraints inherent when studying whole-lake communities, we believe that our method is more direct, simpler, and, therefore, more robust than other methods we could have used to assess the role of species interactions in the response of the Tuesday Lake zooplankton community to planktivory.

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Literature Cited

Abrams, P. 1987. Indirect interactions between species that share a predator: varieties of indirect effects. Pages 38–54 *in* W. C. Kerfoot and A. Sih, editors. Predation. University Press of New England, Hanover, New Hampshire, USA.

Apostol, T. M. 1969. Calculus. Volume 2. Blaisdell Publishing Company, Waltham, Massachusetts, USA.

Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology **65**:1–13.

Billick, I., and T. J. Case. 1994. Higher order interactions in ecological communities: what are they and how can they be detected? Ecology **75**:1529–1543.

Box, G. E. P., G. M. Jenkins, and G. C. Reinsel. 1994. Time series analysis: forecasting and control. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and the composition of plankton. Science **150**:28–35.

Carpenter, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology **77**:677–680.

Carpenter, S. R., and J. F. Kitchell. 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Carpenter, S. R., J. F. Kitchell, K. L. Cottingham, D. E. Schindler, D. L. Christensen, P. D. M., and N. Voichick. 1996. Chlorophyll variability, nutrient input and grazing: evidence from whole-lake experiments. Ecology **77**:725–735.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. Bioscience **35**:634–639.

Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He, and C. N. von Ende. 1987. Regulation of lake primary production by food web structure. Ecology **68**:1863–1878.

Carpenter, S. R., J. Morrice, P. A. Soranno, J. J. Elser, N. A. MacKay, and A. St. Amand. 1993. Primary production and its interactions with nutrients and light transmission. Pages 189–209 *in* S. R. Carpenter and J. F. Kitchell, editors. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Case, T. J., and E. A. Bender. 1981. Testing for higher order interactions. American Naturalist **118**:920–929.

Cohen, J. E., F. Briand, and C. M. Newman. 1986. A sto-

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chastic theory of community food webs. III. Predicted and observed lengths of food chains. Proceedings of the Royal Society of London **B228**:317–353.

Cohen, J. E., and C. M. Newman. 1985. When will a large complex system be stable? Journal of Theoretical Biology **113**:153–156.

DeAngelis, D. L. 1988. Strategies and difficulties of applying models to aquatic populations and food webs. Ecological Modelling **43**:57–73.

DeMott, W. R., and W. C. Kerfoot. 1982. Competition among cladocerans: nature of the interaction between *Bosmina* and *Daphnia.* Ecology **63**:1949–1966.

Dennis, B., R. A. Desharnas, and J. M. Cushing. 1995. Nonlinear demographic dynamics: mathematical models, statistical methods, and biological experiments. Ecological Monographs **65**:261–281.

Dennis, B., W. P. Kemp, and M. L. Taper. 1998. Joint density dependence. Ecology **79**:426–441.

Dennis, B., and B. Taper. 1994. Density dependence in time series observations of natural populations: estimation and testing. Ecological Monographs **64**:205–224.

Downing, J. A., and F. H. Rigler. 1984. A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters. Blackwell, London.

Elkington, J. S., W. M. Healy, J. P. Buonaccorsi, G. H. Boettner, A. M. Hazzard, H. R. Smith, and A. M. Liebhold. 1996. Interactions among gypsy moths, white-footed mice, and acorns. Ecology **77**:2332–2342.

Elser, M. M., C. N. von Ende, P. A. Soranno, and S. R. Carpenter. 1987. *Chaoborus* populations: response to food web manipulation and potential effects on zooplankton communities. Canadian Journal of Zoology **65**:2846–2852.

Frost, T. M., S. R. Carpenter, A. R. Ives, and T. K. Kratz. 1995. Species compensation and complementarity in ecosystem function. Pages 224–239 *in* C. G. Jones and J. H. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York.

Gilbert, J. J. 1988. Suppression of rotifer populations by *Daphnia*: a review of the evidence, the mechanisms, and the effects on zooplankton community structure. Limnology and Oceanography **33**:1286–1303.

Gilbert, J. J., and C. E. Williamson. 1978. Predator–prey behavior and its effect on rotifer survival in associations of *Mesocyclops edax, Asplanchna giroldi, Polyarthra vulgaris,* and *Keratella cochlearis.* Oecologia **37**:13–22.

Gilpin, M. E., M. P. Carpenter, and M. Pomerantz. 1986. The assembly of a laboratory community: multispecies competition in *Drosophila.* Pages 23–40 *in* J. M. Diamond and T. J. Case, editors. Community ecology. Harper and Row, New York, New York, USA.

Graney, R. L., J. H. Kennedy, and J. H. Rodgers. 1994. Aquatic mesocosm studies in ecological risk management. Lewis Publishers, Boca Raton, Florida, USA.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **94**:421–425.

Hall, D. J., S. T. Threlkeld, C. W. Burns, and P. H. Crowley. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. Annual Review of Ecology and Systematics **7**:177–208.

He, X., J. F. Kitchell, J. R. Hodgson, R. Wright, P. A. Soranno, D. M. Lodge, P. A. Cochran, D. Benkowski, and N. Bouwes. 1993. Roles of fish predation: piscivory and planktivory. Pages 85–102 *in* S. R. Carpenter and J. F. Kitchell, editors. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment. Chapman and Hall, New York, New York, USA.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology **12**:197–229.

Ives, A. R. 1995. Predicting the response of populations to environmental change. Ecology **76**:926–941.

Ives, A. R., and V. A. A. Jansen. 1998. Complex dynamics in stochastic tritrophic models. Ecology **79**:1039–1052.

Klimko, L. A., and P. I. Nelson. 1978. On conditional least squares estimation for stochastic processes. Annals of Statistics **6**:629–642.

Lane, P. A. 1978. Role of invertebrate predation in structuring zooplankton communities. Verhandlungen-Internationale Vereinigung fur theoretische und angewandte Limnologie **20**:480–485.

Larsen, R. J., and M. L. Marx. 1981. An introduction to mathematical statistics and its applications. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Lawler, S. P., and P. J. Morin. 1993. Food web architecture and population dynamics in laboratory microcosms of protists. American Naturalist **141**:675–686.

Lawton, J. H., and V. K. Brown. 1993. Redundancy in ecosystems. Pages 255–270 *in* E. D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer-Verlag, Berlin, Germany.

Leibold, M. A. 1995. The niche concept revisited: mechanistic models and community context. Ecology **76**:1371–1382.

Ludwig, D., and C. J. Walters. 1989. A robust method for parameter estimation from catch and effort data. Canadian Journal of Fisheries and Aquatic Sciences **46**:137–144.

Lynch, M. 1979. Predation, competition and zooplankton community structure: an experimental study. Limnology and Oceanography **24**:253–272.

MacKay, N. A., S. R. Carpenter, P. A. Soranno, and M. J. Vanni. 1990. The impact of two *Chaoborus* species on a zooplankton community. Canadian Journal of Zoology **68**: 981–985.

MathWorks. 1996. MATLAB. The MathWorks, Natick, Massachusetts, USA.

May, R. M. 1974. Stability and Complexity in Model Ecosystems. Second edition. Princeton University Press, Princeton, New Jersey, USA.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: pattern and importance. Ecological Monographs **65**:21–74.

Moran, P. J., S. P. Lawler, and E. A. Johnson. 1988. Competition between aquatic insects and vertebrates: experimental measures of interaction strengths and higher order interactions. Ecology **69**:1401–1409.

Pace, M. L., J. J. Cole, and S. R. Carpenter. 1998. Trophic cascades and compensation: differential responses of microzooplankton in whole-lake experiments. Ecology **79**: 138–152.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65–75.

———. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology **49**: 667–685.

Pimm, S. L. 1982. Food Webs. Chapman and Hall, London, UK.

———. 1984. The complexity and stability of ecosystems. Nature **307**:321–326.

Pimm, S. L., and F. H. Lawton. 1977. Number of trophic levels in ecological communities. Nature **268**:329–331.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology **73**:733–746.

Shapiro, J. 1990. Biomanipulation: the next phase—making it stable. Hydrobiologia **200/201**:13–27.

Solow, A. R., and K. Sherman. 1997. Testing for stability in a predator–prey system. Ecology **78**:2624–2627.

Soranno, P. A., S. R. Carpenter, and X. He. 1993*a*. Zoo-

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plankton biomass and body size. Pages 172–188 *in* S. R. Carpenter and J. F. Kitchell, editors. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Soranno, P. A., S. R. Carpenter, and S. M. Moegenburg. 1993*b*. Dynamics of the phantom midge: implications for zooplankton. Pages 103–115 *in* S. R. Carpenter and J. F. Kitchell, editors. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Tessier, A. J. 1986. Comparative population regulation of two planktonic cladocera (*Holopedium gibberum* and *Daphnia catawba*). Ecology **67**:285–302.

Tilman, D. 1996. Biodiversity: population vs. ecosystem stability. Ecology **77**:350–363.

Vandermeer, J. H. 1969. The competitive structure of communities: an experimental approach with protozoans. Ecology **50**:362–371.

Vanni, M. J. 1986. Competition in zooplankton communities: suppression of small species by *Daphnia pulex*. Limnology and Oceanography **31**:1039–1056.

Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan, New York, New York, USA.

Williamson, C. E. 1980. The predator behavior of *Mesocyclops edax*: Predator preferences, prey defenses, and starvation-induced changes. Limnology and Oceanography **25**: 903–909.

Wootton, J. T. 1993. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. American Naturalist **141**:71–89.

———. 1994*a*. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology **75**:151–165.

———. 1994*b*. Putting the pieces together: testing the independence of interactions among organisms. Ecology **75**: 1544–1551.

Worthen, W. B., and J. L. Moore. 1991. Higher order interactions and indirect effects: a resolution using laboratory *Drosophila* communities. American Naturalist **138**:1092–1104.

Yodzis, P. 1989. Introduction to theoretical ecology. Harper and Row, New York, New York, USA.

APPENDIX A

Long-term Changes in Species Biomasses

Here we derive Eq. 2, giving the long-term change in a species' biomass with long-term changes in planktivory. Eq. 1 can be written in matrix form as

$$\mathbf{X}(t+1) = \mathbf{X}(t) + \mathbf{C} + \mathbf{B}\mathbf{X}(t) + \mathbf{A}\mathbf{U}(t) \qquad \text{(A.1)}$$

where

$$\mathbf{X}(t) = [x_1(t), \ldots, x_9(t)]'$$

$$\mathbf{U}(t) = [u_1(t), \ldots, u_4(t)]'$$

$$\mathbf{C} = [c_1, \ldots, c_9]'$$

$$\mathbf{B} = \begin{bmatrix} b_{1,1} & \cdots & b_{1,9} \\ \vdots & \ddots & \vdots \\ b_{9,1} & \cdots & b_{9,9} \end{bmatrix}$$

$$\mathbf{A} = \begin{bmatrix} a_{1,1} & \cdots & a_{1,4} \\ \vdots & \ddots & \vdots \\ a_{9,1} & \cdots & a_{9,4} \end{bmatrix}$$

and the prime symbol (′) denotes transpose. Let $\mathbf{E}_{m,n}(\mathbf{X})$ denote the vector of average values of $\mathbf{X}(t)$ for samples m–n within the same year; $\mathbf{E}_{m,n}(\mathbf{X}) = [1/(n - m + 1)] \sum_{t=m}^{n} \mathbf{X}(t)$. If there are T samples in a year, then taking the average of the first $T - 1$ samples on both sides of Eq. A.1 gives

$$\mathbf{E}_{2,T}(\mathbf{X}) = \mathbf{E}_{1,T-1}(\mathbf{X}) + \mathbf{C} + \mathbf{B}\mathbf{E}_{1,T-1}(\mathbf{X}) + \mathbf{A}\mathbf{E}_{1,T-1}(\mathbf{U}). \qquad \text{(A.2)}$$

If the number of samples per year is large, and the biomasses in the last sample are similar to the average annual biomasses, then $\mathbf{E}_{1,T-1}(\mathbf{X}) \approx \mathbf{E}_{1,T}(\mathbf{X})$, since $\mathbf{E}_{1,T-1}(\mathbf{X}) = \mathbf{E}_{1,T}(\mathbf{X}) + [1/(T-1)][\mathbf{E}_{1,T}(\mathbf{X} - \mathbf{X}(T)]$. Similarly, $\mathbf{E}_{1,T-1}(\mathbf{U}) \approx \mathbf{E}_{1,T}(\mathbf{U})$, and $\mathbf{E}_{2,T}(\mathbf{X}) \approx \mathbf{E}_{1,T}(\mathbf{X})$. Using these approximations,

$$\mathbf{E}_{1,T}(\mathbf{X}) \approx \mathbf{E}_{1,T}(\mathbf{X}) + \mathbf{C} + \mathbf{B}\mathbf{E}_{1,T}(\mathbf{X}) + \mathbf{A}\mathbf{E}_{1,T}(\mathbf{U}). \qquad \text{(A.3)}$$

This gives a set of 9 equations with 9 unknowns, which can be solved to give

$$\mathbf{E}_{1,T}(\mathbf{X}) \approx -\mathbf{B}^{-1}[\mathbf{C} + \mathbf{A}\mathbf{E}_{1,T}(\mathbf{U})]. \qquad \text{(A.4)}$$

The predicted change in average annual biomass of species i with changes in average annual planktivory, L_i, is the slope of $\mathbf{E}_{1,T}(x_i)$ against $\mathbf{E}_{1,T}(u_{\text{plk}})$ which is given by the ith element of the vector $-\mathbf{B}^{-1}\mathbf{A}_{\text{plk}}$. Applying Cramer's Rule leads directly to Eq. 2 (Apostol 1969, Ives 1995).

APPENDIX B

Factors Affecting the Sensitivity of Species to Perturbations

From Eq. 2, the predicted change in the average annual biomass of species i with changes in average annual planktivory, L_i, can be expressed as follows (Ives 1995):

$$L_i = -\frac{\|\mathbf{A}_{\text{plk}}\| \cos \alpha_i}{\|\mathbf{B}_i\| \cos \beta_i} \qquad \text{(B.1)}$$

where $\| \, \|$ denotes the magnitude of a vector (e.g., $\|\mathbf{B}_i\| = (b_{1,i}^2 + b_{2,i}^2 + \ldots + b_{9,i}^2)^{1/2}$). This equation has a graphical interpretation that is illustrated in Fig. B1 for the case of a three-species community. $\|\mathbf{A}_{\text{plk}}\|$ and $\|\mathbf{B}_i\|$ are the lengths of $\mathbf{A}_{\text{plk}}$ and $\mathbf{B}_i$, while α_i and β_i are the angles between $\mathbf{A}_{\text{plk}}$ and $\mathbf{B}_i$, respectively, and the vector which is perpendicular to the vectors $\mathbf{B}_j$ for the species other than species i. The angle β_i can be interpreted as giving the "ecological role" or "Eltonian niche" of species i, since it measures how distinctly species i affects all species in the community (Leibold 1995). When β_i is close to 90°, $\mathbf{B}_i$ lies close to the plane defined by the vectors $\mathbf{B}_j$ for species $j \neq$ i. This implies that the ecological effect of species i is similar to the combined ecological effects of other species in the community, in the sense that $\mathbf{B}_i$ is nearly equal to a linear combination of $\mathbf{B}_j$ ($j \neq i$). When β_i is small, $\mathbf{B}_i$ lies far from the plane defined by the vectors $\mathbf{B}_j$, for species $j \neq i$. In this case, there is no combination of changes in the biomasses of other species that would have the same effect on all species in the community as changing the biomass of species i. This implies that species i is ecologically distinct from all other species. In a similar fashion, α_i measures how planktivory affects species in the community, relative to the effects of all species other than species i. If α_i is close to 90°, then changing planktivory has a similar

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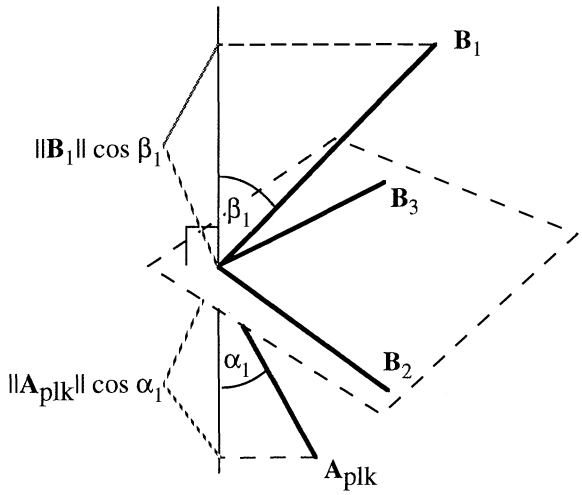

FIG. B1. Graphical interpretation of Eq. B.1 for a three-species community. The vectors $\mathbf{B}_i$ are defined by the points $[b_{1,i}, b_{2,i}, b_{3,i}]$, and $\mathbf{A}_{plk}$ is defined by $[a_1, a_2, a_3]$. The quantities $\|\mathbf{B}_1\| \cos \beta_1$ and $\|\mathbf{A}_{plk}\| \cos \alpha_1$ are, respectively, the projections of $\mathbf{B}_1$ and $\mathbf{A}_{plk}$ onto the line perpendicular to the surface spanned by $\mathbf{B}_2$ and $\mathbf{B}_3$.

effect as changing a combination of biomasses of species j ($j \neq i$). Conversely, if α_i is small, then the pattern of planktivory effects on species in the community is distinct from those of all species other than species i.

From Eq. B.1, three factors decrease the magnitude of the species-specific response to long-term changes in planktivory: (1) strong effects exerted by species i on other species in the community ($\|\mathbf{B}_i\|$ large), (2) a distinctive ecological role for species i (β_i small and $\cos \beta_i$ large), and (3) a pattern of planktivory that is similar to the vectors $\mathbf{B}_j$ for species other than species i (α_i large and $\cos \alpha_i$ small). The fourth term to consider in Eq. B.1, $\|\mathbf{A}_{plk}\|$, is the same for all species and, therefore, does not contribute to the relative sensitivities of different species. Values of $\|\mathbf{B}_i\|$, $\cos \beta_i$, and $\cos \alpha_i$ are given for each species in Table B1. Dp has the greatest value of $\|\mathbf{B}_i\|$, implying that the magnitude of effects of Dp on all species in the system is greatest. This buffers Dp against long-term changes. The next two species in order of $\|\mathbf{B}_i\|$ are Ocop and Rot. For Ocop, the high value of $\|\mathbf{B}_i\|$ is largely due to its negative effect on Dp; for Rot, the high value of $\|\mathbf{B}_i\|$ is due to its negative effect on itself.

Ecological distinctiveness, measured by $\cos \beta_i$, is greatest for Ccop, which is not surprising since this is the only carnivorous species. The next species in terms of ecological distinctiveness is Rot, largely owing to its large negative effect on itself and its positive effect on Ccop. The three groups containing large herbivores, Dp, Hg, and Ocop, all have low ecological distinctiveness, since they are all similar to each other. This similarity may lead to compensatory changes in biomasses, with increases in the biomass of any one of them causing compensatory decreases in the biomasses of the others. Therefore, the low ecological distinctiveness of these three species will tend to make each more prone to change (either increase or decrease) when the community experiences an exogenous perturbation.

Finally, the magnitude of $\cos \alpha_i$ is greatest for Dp. This implies that the effect of Dp on other species in the community is the most similar to that of planktivory (Fig. B1). The large value of $\cos \alpha_i$ increases the long-term change in Dp biomass with changes in planktivory (Eq. B.1). The species with the lowest value of $\cos \alpha_i$ is Ccop, thereby giving it the lowest value of L_i.

These three components, $\|\mathbf{B}_i\|$, $\cos \beta_i$, and $\cos \alpha_i$, combine in different ways to explain the long-term changes in species' biomasses to changes in planktivory. Considering the three species with the largest values of M_i, Dp, Bl and Db, the explanation for Dp's sensitivity to long-term changes in planktivory is different from Bl and Db. Dp has a strong effect on other species (i.e., a large $\|\mathbf{B}_i\|$), thereby buffering it against long-term changes. Nonetheless, this buffering effect is overwhelmed by Dp's similarity to other species (small $\cos \beta_i$) and its similarity to the effects of planktivory (large $\cos \alpha_i$). In contrast, both Bl and Db are relatively weak interactors with other species, and they have relatively large values of $\cos \alpha_i$ that drive large changes in average annual biomasses.

TABLE B1. Values of terms in Eq. B.1 for zooplankton in Tuesday Lake.

Species	M_i	L_i	$\|\mathbf{B}_i\|$	$\cos \beta_i$	$\cos \alpha_i$
Dp	−0.59	−0.61	0.64	−0.23	0.090
Dr	−0.059	−0.32	0.22	−0.45	0.032
Hg	−0.33	−0.52	0.35	−0.24	0.044
Bl	0.79	0.78	0.23	−0.29	−0.052
Db	0.59	0.68	0.27	−0.40	−0.076
Ocop	0.26	0.24	0.45	−0.24	−0.025
Ccop	0.24	−0.089	0.11	−0.67	0.0063
Rot	0.11	0.20	0.42	−0.49	−0.040

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