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Measurement and Mechanisms

Author(s): Janet M. Fischer, Thomas M. Frost and Anthony R. Ives

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COMPENSATORY DYNAMICS IN ZOOPLANKTON COMMUNITY RESPONSES TO ACIDIFICATION: MEASUREMENT AND MECHANISMS

JANET M. FISCHER,^{1,3} THOMAS M. FROST,¹ AND ANTHONY R. IVES²

¹*Center for Limnology, University of Wisconsin, 680 North Park Street, Madison, Wisconsin 53706 USA*

²*Department of Zoology, University of Wisconsin, 430 Lincoln Drive, Madison, Wisconsin 53706 USA*

Abstract. Previous studies indicate substantial variation in ecological responses to perturbation. In some cases, ecosystems are resilient to perturbation due to compensatory dynamics in which losses of sensitive species are offset by population increases of species that perform similar ecological functions. Here, we report a detailed evaluation of compensatory dynamics in zooplankton community responses to the experimental acidification of Little Rock Lake, Wisconsin, USA. We used a variance ratio to quantify compensatory dynamics in functional groups of zooplankton containing species that use similar resources and are vulnerable to the same predators. We also used first-order autoregressive models to explore mechanisms driving the dynamics of each functional group. Our results indicate that responses of functional groups to acidification can be highly variable. Herbivorous copepods and medium-sized herbivorous cladocerans exhibited significant compensatory dynamics in response to acidification, whereas other functional groups exhibited independent or synchronous dynamics. First-order autoregressive models indicated that groups exhibiting compensatory dynamics contained both acid-tolerant and acid-sensitive species that competed. In contrast, groups that contained only acid-sensitive or acid-tolerant species exhibited more independent or synchronous dynamics. Overall, our study highlights the combined roles of sensitivity to environmental perturbation and species interactions in determining the extent of compensatory dynamics in zooplankton functional group responses to acidification.

Key words: acidification; community ecology; compensatory dynamics; functional compensation; functional redundancy; zooplankton.

INTRODUCTION

Predicting the effects of environmental change on ecosystems is a major challenge in ecology. Recent studies demonstrate that the effects of environmental change on ecosystems can sometimes be tempered by compensatory dynamics, wherein losses of sensitive species are offset by population increases of species that perform similar ecological functions (e.g., Weinstein and Birk 1989, Schindler 1990, Howarth 1991, Frost et al. 1995, Tilman 1996, Havens and Carlson 1998). However, there are also examples where compensatory dynamics have not occurred, and ecological processes (e.g., total community biomass or productivity) have changed dramatically following a perturbation (Howarth 1991, Pratt and Cairns 1996, Cottingham and Carpenter 1998).

In order to anticipate ecological responses to perturbation, it is important to understand the ecological processes underlying compensatory changes among functionally similar species. Theory predicts that the extent of compensatory dynamics will depend both on the species-specific effects of the perturbation and the

strength of competitive interactions among species (Ives 1995). When only a subset of species is adversely affected by the environmental change and species compete strongly, compensatory dynamics are likely as tolerant species increase in response to environmentally driven declines in their competitors. If competition among species is weak, however, decreases in sensitive species may have little impact on the population dynamics of tolerant species. Compensatory dynamics will also be unlikely if all species are adversely affected by the change in the environment. For this reason, theory predicts that more diverse communities may be more resilient to perturbation because they are more likely to contain tolerant species (Ives et al. 1999b).

In this study, we quantify compensatory dynamics in zooplankton community dynamics during a whole-lake acidification experiment, and explore mechanisms leading to compensatory dynamics by fitting autoregressive models to time-series data. Freshwater zooplankton provide an interesting system in which to examine compensatory dynamics in community responses to perturbation. The relatively short generation times of zooplankton (weeks to months) permit rapid responses to environmental change (Moore and Folt 1993). In addition, the trophic interactions of many species have been well studied (e.g., Morgan 1980, Williamson 1983, Lazzaro 1987, Moore 1988). This

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³ Present address: Department of Biology, Franklin and Marshall College, Lancaster, Pennsylvania 17604 USA.
E-mail: j_fischer@acad.fandm.edu

information can be used to group species into functional groups containing species that have similar ecological characteristics. Finally, numerous laboratory studies have documented the responses of zooplankton species to a variety of environmental variables including pH (e.g., Locke 1991).

Here, we present a detailed evaluation of the role of compensatory dynamics in zooplankton community responses to the experimental acidification of one basin of Little Rock Lake, Wisconsin. Frost et al. (1992, 1995) reported that compensatory dynamics within taxonomic groups of zooplankton (e.g., total copepods) are a prevalent feature of zooplankton community responses to acidification in this system. We expand on this earlier analysis by examining compensatory dynamics within more finely resolved functional groups of zooplankton (e.g., small herbivorous cladocerans). We used a variance ratio to characterize covariation among species as independent, compensatory, or synchronous. This approach has been used previously to describe community dynamics in long-term data from the reference basin in a whole-lake experiment (Frost et al. 1995), to quantify community responses in perturbation experiments (Klug et al. 2000), and to test for species associations across space or time (Schluter 1984, McCulloch 1985). Additionally, we explored the mechanisms driving population dynamics of zooplankton, using first-order autoregressive time-series models (Ives 1995, Ives et al. 1999a). These models describe direct and indirect effects pathways through which zooplankton respond to acidification. Together, our analyses provide insights into the underlying processes that determine the extent of compensatory dynamics in functional group responses to perturbation.

METHODS

Study site

Little Rock Lake, an 18-ha lake located in the Northern Highlands Lake District of Wisconsin, USA (Vilas County, 45°59'55" N, 89°42'15" W), is the site of an ongoing investigation of the effects of acidification on lake ecosystems. In 1984, the two basins of Little Rock Lake were separated with an inert plastic curtain. Beginning in 1985, the pH of the lake's northern basin was reduced from an initial pH of 6.1 with sulfuric acid, in a series of three steps lasting 2 yr each. Target values of pH 5.6, 5.1, and 4.7 were attained during the acidification. A detailed description of Little Rock Lake's basic limnology, and summaries of lake responses to acidification are provided by Frost and Montz (1988), and Brezonik et al. (1993). Experimental acidification was completed in 1990, and the treatment basin is currently in a recovery phase in which chemical and biological conditions are returning to preacidification levels.

Throughout the experiment, abundance of zooplankton (crustaceans and rotifers) was monitored in the

treatment and reference basins of Little Rock Lake. During open-water periods, zooplankton were collected approximately every 2 wk using a 33-L Schindler-Pattalas trap (53- μ m Nitex mesh) at permanent sampling stations located at the deepest point in each basin (Frost and Montz 1988). All samples were collected between 1000 and 1600 on the same day in both basins. Samples were collected using this 0.5 m long trap from fixed depths (0, 4, and 8 m in the treatment basin and 0, 4, and 6 m in the reference basin) and were preserved with 4% sucrose-buffered formalin. With the exception of the surface sample, the middle of the trap was positioned at the target depth. Hypsometrically weighted average abundances were calculated for each basin. Zooplankton abundance was converted to biomass using length-mass relationships determined directly for Little Rock Lake species or from the literature (Ruttner-Kolisko 1977, Pace and Orcutt 1981, Culver et al. 1985, Yan and Mackie 1987).

Abundance of the invertebrate predator, *Chaoborus* spp., was also monitored in treatment and reference basins of Little Rock Lake throughout the experiment (Sierzen and Frost 1993, Fischer and Frost 1997). In Little Rock Lake, *Chaoborus* species consist almost entirely of *Chaoborus punctipennis* (>95%), with rare occurrences of *Chaoborus albatus*. *Chaoborus* were collected approximately every 2–4 wk using vertical tows from 0.5 m above the lake bottom to the surface of the lake with a plankton net (0.5 m diameter, 1.5 m long, 253- μ m mesh). All samples were collected roughly 1 h after sunset and preserved with Lugol's iodine solution. Because timing of *Chaoborus* sampling was less frequent than zooplankton sampling, we used monthly averages to estimate *Chaoborus* abundance for dates on which crustacean and rotifer were sampled. For some years, *Chaoborus* was not sampled in October. *Chaoborus* abundance on these dates was estimated by applying an average proportional decrease from September, calculated for years where *Chaoborus* were sampled in both months.

In this study, we focused our analyses on the dynamics of crustacean zooplankton species, and limited our time scale to the period May–October, which corresponds roughly to the ice-free season. We considered only the dynamics of dominant crustacean zooplankton species (those crustacean species that were >10% of total zooplankton biomass in either the reference or treatment basin at any time in the experiment). Due to the difficulties of accurately identifying copepod nauplii to species, nauplii were not included in our analyses.

Compensatory dynamics

We grouped Little Rock Lake zooplankton species into functional groups using a classification scheme developed by consensus by the Community Dynamics Working Group at the National Center for Ecological

TABLE 1. Functional groups represented by the Little Rock Lake zooplankton.

Functional group	Diet	Species
Herbivorous copepods	H	<i>Leptodiaptomus minutus</i> <i>Tropocyclops extensus</i> †
Predatory copepods	P	<i>Diacyclops thomasi</i> <i>Mesocyclops edax</i>
Small cladocerans	H	<i>Bosmina longirostris</i> <i>Diaphanosoma birgei</i>
Medium cladocerans	H	<i>Daphnia catawba</i> <i>Daphnia dubia</i> <i>Daphnia parvula</i>
Large cladocerans	H	<i>Holopedium gibberum</i>

Notes: Only dominant species constituting >10% of zooplankton biomass in the reference or treatment basin in any sample were included. Diet codes indicate herbivorous (H) and predatory (P) zooplankton.

† Studies by Adrian and Frost (1992, 1993) indicate that *Tropocyclops extensus* is primarily herbivorous in Little Rock Lake.

Analysis and Synthesis.⁵ This scheme groups zooplankton species according to trophic position, by incorporating information on resource consumption and vulnerability to predators (Table 1). These functional groups represent “trophic species” that use similar resources and are vulnerable to the same predators.

We quantified the extent of compensatory dynamics among species within functional groups using a variance ratio (Schluter 1984, McCulloch 1985, Frost et al. 1995, Klug et al. 2000). For each aggregated group of species (G), variance is a function of the variance of individual species (S_i) and the covariance among species (Box et al. 1978):

$$G = \sum_{i=1}^n S_i$$

$$\text{var}(G) = \left[\sum_{i=1}^n \text{var}(S_i) \right] + \left[2 \sum_{i=1}^n \sum_{j=1}^{i-1} \text{cov}(S_i, S_j) \right].$$

It is important to note that this relationship does not hold if data have been transformed (e.g., as a logarithm) prior to aggregation. We used variance ratio (VR) calculated on untransformed biomass data as an index of compensatory dynamics:

$$\text{VR} = \frac{\text{var}(G)}{\sum_{i=1}^n \text{var}(S_i)}.$$

This approach provides a measure of the magnitude of covariation among species in a functional group, relative to the variation of the constituent species. Variance ratios <1 result when the sum of covariances among species is negative, and indicate compensatory dynamics among species. In contrast, variance ratios >1 occur when the sum of covariances among species is positive, and indicate synchronous dynamics among

species. Finally, variance ratios equal to one occur when the sum of the covariances is zero, and indicate that species vary independently.

We calculated variance ratios for four periods: 1984, 1984–1986, 1984–1988, and 1984–1990. These expanding time periods corresponded to preacidification and three acidification stages in Little Rock Lake. We hypothesized that variance ratios would change as the time period was extended to include progressively lower pH conditions (and thus, more dramatic changes in population dynamics). In order to capture species replacements that occurred among years, we chose to calculate variance ratios using expanding, overlapping time periods, rather than nonoverlapping time periods. For example, in the situation where species A dominates in 1984–1986, and species B dominates in 1986–1990, a variance ratio including data from 1984–1990 is necessary to capture negative covariation between species A and B .

We used variance ratios as a summary of the degree of compensatory dynamics or synchrony in population responses for the finely resolved functional groups of zooplankton listed in Table 1, as well as for more coarsely resolved functional groups (total zooplankton and herbivorous zooplankton). We expected compensatory dynamics to be more prevalent in the finely resolved groups where species interact strongly. We expected compensatory dynamics to be weaker in coarsely resolved functional groups like “total zooplankton” and “all herbivorous zooplankton,” because positive and negative covariances can cancel each other out in groups containing many species.

To help interpret variance ratio results for the treatment basin, we conducted parallel analyses using reference-basin data. Variance ratios for reference-basin data provide a description of the degree of compensation or synchrony in population dynamics in the absence of experimental acidification. Using reference-basin variance ratios as a baseline, it is possible to ask whether functional group dynamics in the treatment basin represent a change in degree of compensation or synchrony compared to dynamics under unperturbed conditions. For example, if variance ratios are <1 in both the reference and treatment basins, compensatory dynamics in the treatment basin may not represent a change in the degree of compensation. However, if variance ratios are >1 in the reference basin but <1 in the treatment basin, then a dramatic change has occurred in the pattern of dynamics among species.

We used a randomization procedure to assess whether the extent of compensation or synchrony among species in a functional group was greater than what would be expected if species varied independently. The goal of randomization was to generate distributions of variance ratios using data sets for each functional group of interest where population dynamics of constituent species were independent. Variance ratios for randomized data sets have been shown to be approximately

⁵ <http://www.nceas.ucsb.edu>

normal with a mean of one, indicating neither synchrony nor compensation (N. J. Gotelli, *personal communication*). Our approach was to randomize (i.e., scramble) the time-series data for each individual species in the functional group of interest. Then, we calculated a variance ratio for the new data set, which contained scrambled data for each species. For each functional group, we calculated variance ratios for 1000 scrambled data sets. Finally, actual variance ratios were compared to the distribution of variance ratios from the scrambled data sets for the same basin. We considered actual variance ratios greater or less than 95% of variance ratios from scrambled data sets to be indicative of significant synchronous or compensatory dynamics, respectively.

Autoregressive models

Quantification of strong compensatory or synchronous dynamics does not necessarily point to any particular ecological mechanism. For example, Schluter (1984) provides a list of mechanisms that can lead to negative and positive associations among species. To explore the mechanisms driving zooplankton responses to acidification in Little Rock Lake, we developed a set of descriptive autoregressive models (Ives 1995) for each functional group. These models predicted the temporal dynamics for the members of each functional group. A separate model was fit for each species. In each model, biomass of this focal species in the next time step (time $t + 1$) was predicted using current data (time t) for biomass of the focal species, combined biomass of species in other functional groups, and pH. The multivariate linear autoregressive model had the form

$$n_i(t + 1) = n_i(t) + b_{i0} + \sum b_{ij}n_j(t) + \sum a_{ij}u_j(t) + e(t)$$

where $n_i(t + 1)$ is the $\ln(x + 1)$ -transformed biomass of species i at time $t + 1$, $n_i(t)$ is $\ln(x + 1)$ -transformed biomass of species i at time t , u_j is either $\ln(x + 1)$ -transformed pH or the $\ln(x + 1)$ -transformed combined biomass of species in another functional group, and $e(t)$ is variability that is not explained by the linear terms of the model. Coefficients (a_{ij} and b_{ij}) indicate the strength of each effect considered in the model. Environmental variability is contained within $e(t)$, as is variability associated with possible nonlinear interactions among variables in the model. Because autoregressive models require evenly spaced data, we have coded the model to ignore data that span the winter period. That is, we do not attempt to predict spring biomass using data from the previous fall. Although the model cannot account for nonlinear population dynamics, it nonetheless is a first-order approximation that can be used to estimate the main effects of pH and species interactions on changes in biomass of focal species. By explicitly separating the direct pH effects on species from the indirect effects acting through

changes in other species, the autoregressive models revealed why some functional groups exhibited compensatory dynamics while other groups did not.

For the functional groups used as predictor variables, we considered not only the other crustacean functional groups, but also two rotifer functional groups (herbivorous rotifers and predatory rotifers) and *Chaoborus*. Previous studies document dramatic increases in herbivorous rotifers and *Chaoborus* during the last stage of the acidification, and virtual extinction of predatory rotifers (Fischer and Frost 1997, Frost et al. 1999). We did not include effects of planktivorous fish in our models, because their abundance did not differ between basins or change with acidification (Eaton et al. 1992).

To select the best fitting autoregressive model, we used the Akaike Information Criterion (AIC), a measure of model fit (measured by log-likelihood) that includes a penalty for the number of parameters:

$$\text{AIC} = -2 \times L + 2 \times p$$

where L is the log-likelihood and p is the number of parameters in the model (Akaike 1973, 1974). We used a search algorithm that fit 10 000 randomly constructed models for each focal species, to find the best-fitting model. When evaluating models, we considered only those coefficients that were biologically plausible (i.e., negative interactions among competitors, positive effects of prey on predators, and negative effects of predators on prey). In addition, we considered only detrimental effects of acidification because direct, positive effects of acidity have never been demonstrated for zooplankton, although they have been tested for experimentally (Locke 1991, Fischer 1997). For each model, we standardized the variability in $\ln(x + 1)$ -transformed data for dependent and independent variables by dividing by the standard deviation calculated across samples. Differences in means are incorporated into the constant term in the model and, thus, do not influence the estimated coefficients for interactions between species. With this standardization, model coefficients represent an aggregate effect that combines per capita effects and variation. Thus, coefficients are comparable in terms of the overall impact of predictors on the dependent variable (Neter et al. 1989).

RESULTS

Compensatory dynamics

Acidification caused changes in the degree of compensation or synchrony among species for some groups of zooplankton (Figs. 1, 2). For coarsely resolved groups (total zooplankton and all herbivores), variance ratios indicated that patterns of covariance among species were not significantly synchronous or compensatory (Fig. 1). That is, variance ratios were never significantly different from one, for either of the coarsely resolved groups. Total crustacean zooplankton biomass was dominated by herbivores (Fig. 3).

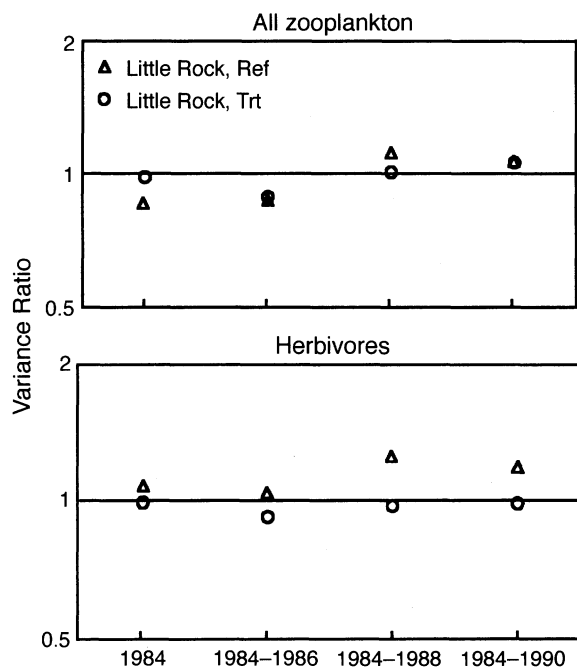


FIG. 1. Variance ratios for coarsely resolved functional groups of crustacean zooplankton in the reference (Ref) and treatment (Trt) basins of Little Rock Lake. Variance ratios were calculated for four expanding time periods that correspond to preacidification and three acidification stages. Variance ratios for these groups were not greater or less than 95% of variance ratios generated using randomization procedures during any time period.

The finely resolved functional groups showed both compensation and synchrony. For both herbivorous copepods and medium cladocerans, variance ratios indicated significant compensatory dynamics among species in the acidified basin (Fig. 2). In both cases, the degree of compensation measured represented a departure from independent or synchronous dynamics observed in the reference basin during the same time periods (e.g., dynamics of medium cladocerans were synchronous in the reference basin in 1984–1990).

In the herbivorous copepod functional group, compensatory dynamics were driven by a decrease in *Leptodiptomus minutus*, followed by an increase in *Tropocyclops extensus* (Fig. 4). *Leptodiptomus minutus* declined to levels below detection limits during the last phase of the acidification, whereas *Tropocyclops extensus* increased with acidification and was abundant even under the most severe acid conditions. Compensatory dynamics in the medium herbivorous cladoceran functional group reflected a shift from dominance by *Daphnia dubia* in 1984 and 1985, to *Daphnia catawba* in 1987–1990. The year 1986 served as a transition year, when both *Daphnia dubia* and *Daphnia catawba* were present (Fig. 5). A third species, *Daphnia parvula*, was present throughout the experiment as a small proportion of medium herbivorous cladoceran biomass.

Other finely resolved functional groups exhibited increases in the degree of synchrony with acidification (Fig. 2). For predatory copepods, species exhibited significant compensatory dynamics in the reference basin but independent dynamics in the treatment basin. Therefore, patterns of covariance among species in this

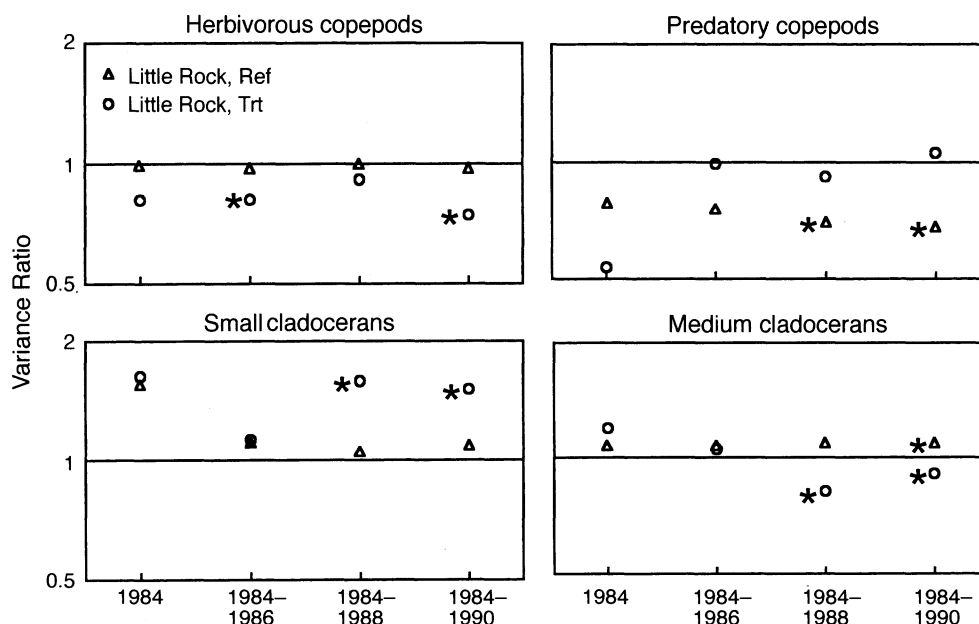


FIG. 2. Variance ratios for finely resolved functional groups of crustacean zooplankton in the reference (Ref) and treatment (Trt) basins of Little Rock Lake. Layout and symbols are the same as in Fig. 1. Asterisks indicate variance ratios that were greater or less than 95% of variance ratios generated using randomization procedures.

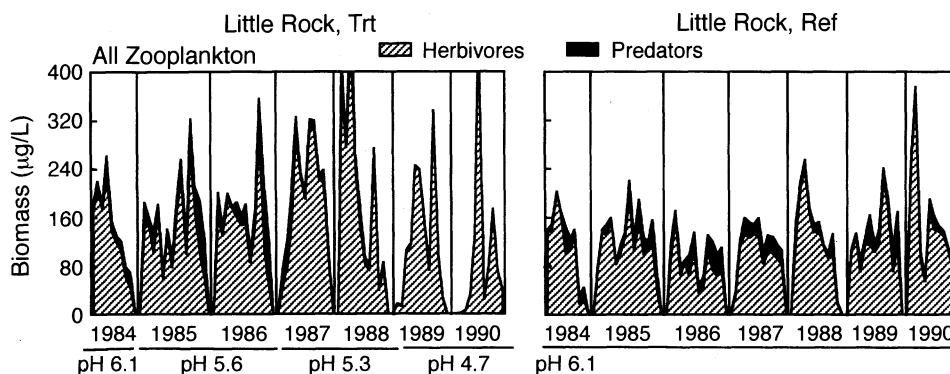


FIG. 3. Biomass plots for crustacean zooplankton in the reference (Ref) and treatment (Trt) basins of Little Rock Lake during 1984–1990. The total filled area in these stacked area plots indicates the summed biomass of herbivores and predators.

group were relatively more synchronous in the treatment basin than in the reference basin. This pattern reflects dramatic decreases in all predatory copepod species (Fig. 4). Both *Diacyclops thomasi* and *Mesocyclops edax* were below detection limits by the end of the experiment. The decrease in *Diacyclops thomasi* biomass occurred during the second step of the acidification, whereas *Mesocyclops edax* decreased during the final acidification.

For small cladocerans, variance ratios indicated significant synchronous dynamics among species in the acidified basin, whereas dynamics were independent in the reference basin during the same time periods (Fig. 2). In this functional group, *Bosmina longirostris* and *Diaphanosoma birgei* were present throughout all phases of the acidification, although *Diaphanosoma birgei* appeared to decrease somewhat during the last phase of the acidification (Fig. 5).

Variance ratios could not be calculated for large herbivorous cladocerans because this group contained a single species. *Holopedium gibberum* decreased in the acidified basin in 1988, and was below detection limits by 1990 (Fig. 5). Biomass of *Holopedium gibberum* remained high in the reference basin throughout the experiment.

Autoregressive models

The fit of the first-order autoregressive models varied among functional groups. On average, the models explained ~50% of the temporal variation in population biomass. R^2 values for the relationship between predicted and observed biomass ranged from 0.23 to 0.72 (Tables 2, 3).

The autoregressive models for the two functional groups showing compensatory dynamics (herbivorous copepods and medium cladocerans) shared two features. First, the models suggested that both groups contained acid-sensitive and acid-tolerant species. In the herbivorous copepod model, a detrimental pH effect (indicated by the positive pH coefficient) was detected for *Leptodiantomus minutus*, but not for *Tropocyclops extensus* (Fig. 6, Table 2). For medium cladocerans, a

detrimental pH effect was detected for *Daphnia dubia*, but not *Daphnia catawba* (Fig. 7, Table 3). Second, the models suggested that competitive interactions occurred within each functional group that exhibited compensatory dynamics. For medium cladocerans, the model indicated negative interactions between *Daphnia dubia* and *Daphnia catawba*. Interestingly, the coefficient describing the effect of *Daphnia dubia* on *Daphnia catawba* was greater than the coefficient for the effect of *Daphnia catawba* on *Daphnia dubia*. For herbivorous copepods, the model suggested that the more tolerant *Tropocyclops extensus* had a negative effect on the acid-sensitive *Leptodiantomus minutus* (Fig. 6, Table 2). In addition, the covariates, *Chaoborus* and large cladocerans, negatively affected *Leptodiantomus minutus*, and herbivorous rotifers and large cladocerans negatively affected the dynamics of some medium cladoceran species.

In groups where synchronous dynamics occurred, models described more uniform patterns of acid sensitivity within functional groups. In the case of the predatory copepods, model results suggested that both *Diacyclops* and *Mesocyclops* were acid sensitive (Fig. 6, Table 2). In addition, model results indicated that the covariates, predatory rotifers and small cladocerans, affected the dynamics of *Mesocyclops edax*. In contrast to the results for predatory copepods, the models for small cladocerans suggested that both *Bosmina longirostris* and *Diaphanosoma birgei* were acid tolerant. Models indicated that the synchrony in the dynamics of these small cladocerans during the 1984–1990 time period may have been driven by interactions with medium cladocerans (Fig. 7, Table 3). Finally, model results indicated that the dynamics of *Diaphanosoma birgei* were affected by herbivorous rotifers.

The model for *Holopedium gibberum* indicated that this species is acid sensitive. In addition, the model detected negative effects of the predator *Chaoborus*.

DISCUSSION

In this study, we found that the responses of crustacean zooplankton to acidification were highly vari-

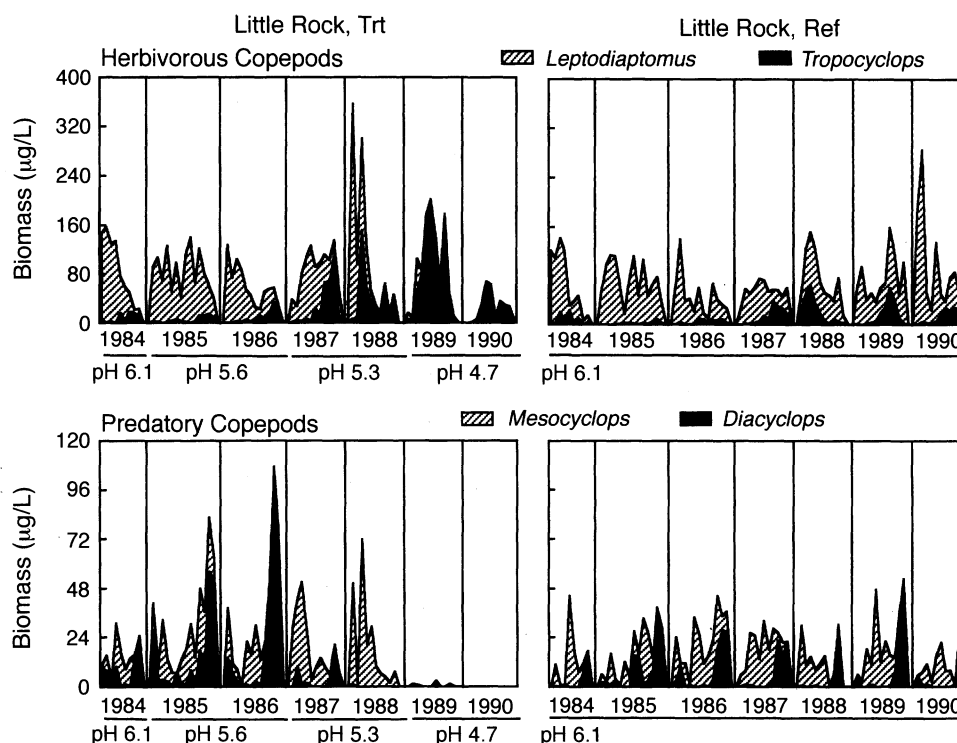


FIG. 4. Biomass plots for herbivorous and predatory copepods in the reference (Ref) and treatment (Trt) basins of Little Rock Lake during 1984–1990. Layout is the same as in Fig. 3.

able among functional groups. Predatory copepods and large herbivorous cladocerans decreased to virtual extinction with acidification, whereas herbivorous copepods, small cladocerans, and medium cladocerans changed little with acidification. Some functional groups that were relatively stable during acidification exhibited compensatory dynamics, in which abundance of some species increased to compensate for population decreases by other species. In effect, these functional groups were preserved by a constituent acid-tolerant species.

We used a variance ratio to explore patterns of synchrony or compensation among species within a functional group. Parallel calculations of variance ratios for the reference basin provided a baseline for comparison to the treatment basin. For example, the degree of compensatory dynamics among medium herbivorous cladocerans in the treatment basin was a dramatic shift from the independent or synchronous dynamics observed in the reference basin during the same time periods. Similarly, independent dynamics for predatory copepods during 1984–1988 and 1984–1990 time periods represented an increase in degree of synchrony relative to the significant compensatory dynamics observed in the reference basin. Thus, calculations of variance ratios for reference systems can be critical to interpretation of dynamics in perturbed systems.

Our results are consistent with other studies indicating that compensatory dynamics among species

within a functional group can reduce more aggregate responses to perturbation (Frost et al. 1995, Tilman 1996, Havens and Carlson 1998, Micheli et al. 1999, Klug et al. 2000). To predict ecosystem responses to environmental change, however, ecologists must understand the mechanisms controlling functional group responses to perturbations like acidification. The results of descriptive autoregressive models can provide insights into the causes of compensation vs. synchrony in functional group dynamics.

The autoregressive models suggest that compensatory dynamics occur when a functional group contains at least one species that can attain a positive population growth rate under acidic conditions, and this acid-tolerant species increases in response to population declines by acid-sensitive species. For example, the autoregressive model for medium cladocerans suggested that *Daphnia catawba* was acid tolerant and experienced competitive release following a decrease in acid-sensitive species in the same functional group. This result is supported by laboratory tests showing that the increase in *Daphnia catawba* biomass in the treatment basin cannot be explained as a direct positive response to acidity (T. M. Frost, unpublished data), as well as by lake surveys showing that *Daphnia catawba* is the most acid-tolerant daphnid in Canada (Keller and Pitblado 1984). Similar mechanisms (differential responses to acid, coupled with competitive release) have been proposed to explain compensatory dynamics between

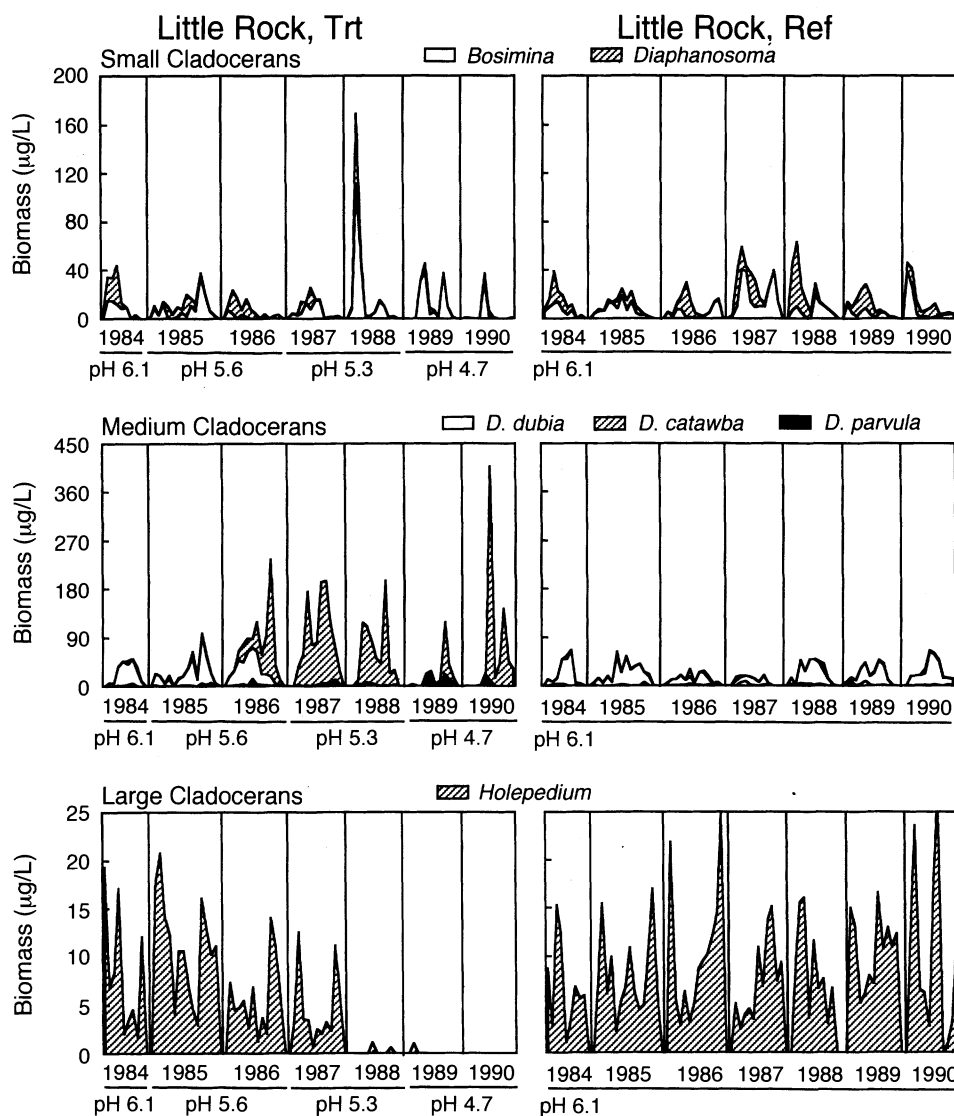


FIG. 5. Biomass plots for small, medium, and large cladocerans in the reference (Ref) and treatment (Trt) basins of Little Rock Lake during 1984–1990. Layout is the same as in Fig. 3.

TABLE 2. Coefficients for the autoregressive models describing dynamics of herbivorous and predatory copepods.

Species	pH	<i>Tropo</i>	<i>Dia</i>	Large clad	<i>Chaob</i>	R^2
Herbivorous copepods						
<i>Tropocyclops</i>		−0.40		−0.20		0.53
<i>Leptodiaptomus</i>	0.17	−0.10	−0.34		−0.06	0.72
Species	pH	<i>Dia</i>	<i>Meso</i>	Small clad	Predatory rotifers	R^2
Predatory copepods						
<i>Diacyclops</i>	0.14	−0.33				0.41
<i>Mesocyclops</i>	0.27		−0.68	0.23	−0.27	0.38

Notes: Coefficients represent effects of pH and species interactions (columns) on focal species (rows). Note that a positive coefficient for pH indicates a negative effect of acidity. R^2 values are for the relationship between predicted and observed biomass for each species ($n = 143$).

TABLE 3. Coefficients for the autoregressive models describing dynamics of small, medium, and large cladocerans.

Species	pH	<i>Bos</i>	<i>Diaph</i>	Medium clad	Herbivorous rotifers	<i>R</i> ²	
Small cladocerans							
<i>Bosmina</i>		−0.51		−0.26		0.31	
<i>Diaphanosoma</i>			−0.34	−0.30	−0.14	0.54	
Medium cladocerans							
Species	pH	<i>D. cat</i>	<i>D. dub</i>	<i>D. par</i>	Large clad	Herbivorous rotifers	<i>R</i> ²
<i>D. catawba</i>		−0.35	−0.09		−0.18		0.59
<i>D. dubia</i>	0.24	−0.10	−0.46			−0.14	0.69
<i>D. parvula</i>				−0.57	−0.19		0.23
Large cladocerans							
Species	pH	<i>Holo</i>	<i>Chaob</i>	<i>R</i> ²			
<i>Holopedium</i>	0.41	−0.62	−0.10	0.61			

Notes: Coefficients represent effects of pH and species interactions (columns) on focal species (rows). Note that a positive coefficient for pH indicates a negative effect of acidity. R^2 values are for the relationship between predicted and observed biomass for each species ($n = 143$).

diatoms and chrysophytes in an acidification experiment conducted in mesocosms (Klug et al. 2000).

The autoregressive models also highlighted mechanisms that cause synchrony in functional group responses to environmental change. In general, synchrony occurred when all species within a functional group had similar acid tolerance. For example, the predatory

copepods *Diacyclops thomasi* and *Mesocyclops edax* were both acid sensitive, and the dynamics of these species were more synchronous in the acidified basin than in the reference basin. A similar pattern was observed for small cladocerans. In this case, however, model results suggested that synchrony in the dynamics of the two acid-tolerant small cladoceran species in the

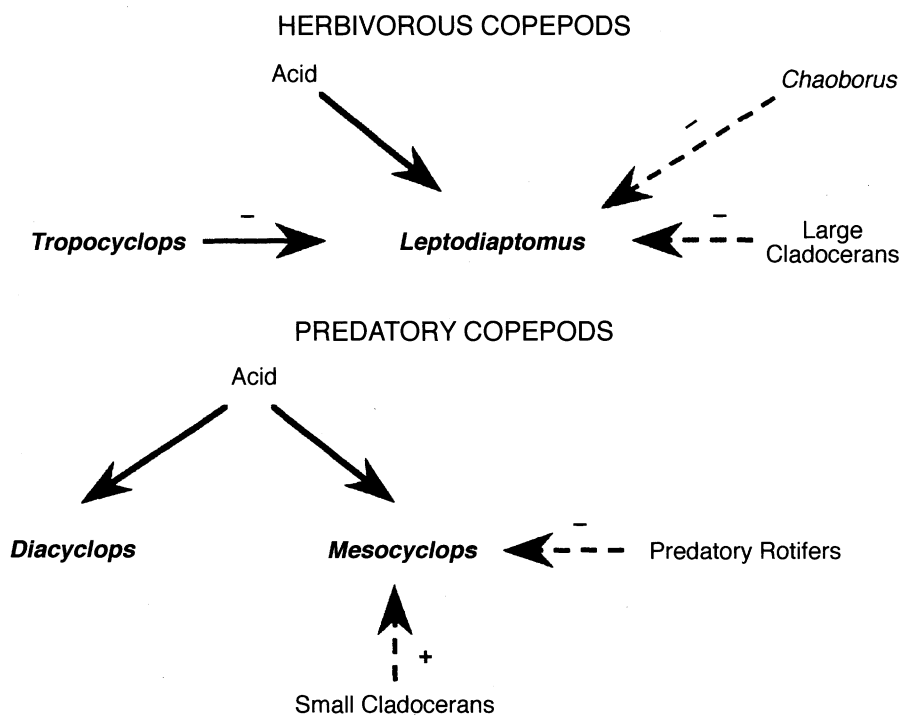


FIG. 6. Interaction webs describing factors affecting population dynamics of copepods in Little Rock Lake. Coefficients for the descriptive autoregressive models are presented in Table 2.

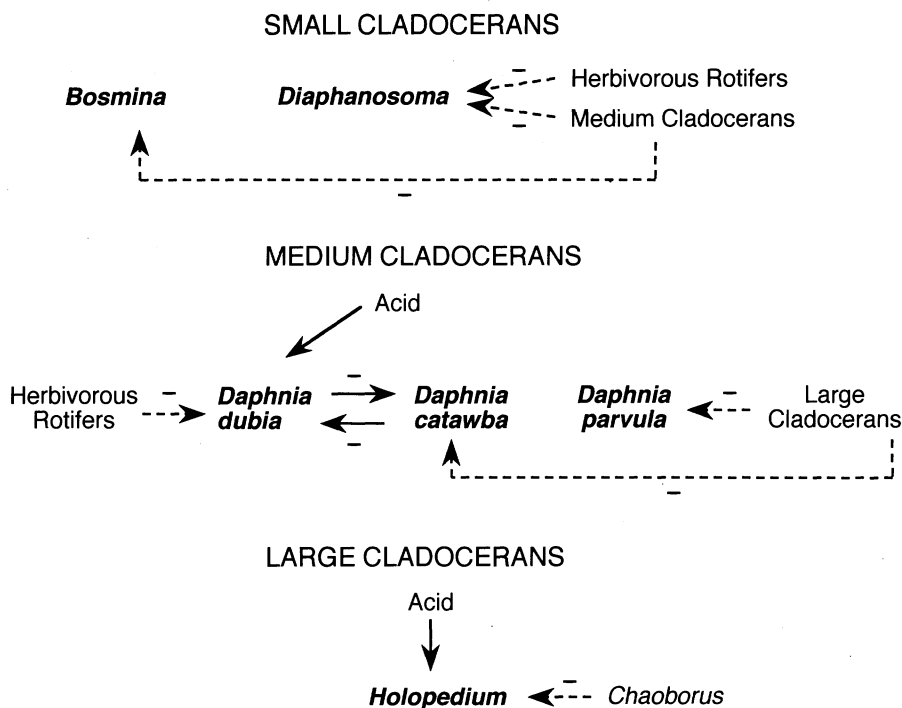


FIG. 7. Interaction webs describing factors affecting population dynamics of cladocerans in Little Rock Lake. Coefficients for the descriptive autoregressive models are presented in Table 3.

acidified basin was caused by a similar response to medium cladocerans.

As is the case for all models based on correlation, autoregressive models provide post hoc descriptions of relationships among variables. Model results do not constitute a test of interactions; however, they give a way to systematize and quantify the patterns of correlation among species, and they produce testable hypotheses. Although detailed experimental tests of each potential mechanism are beyond the scope of this study, our model results were consistent with other studies of zooplankton acid sensitivity and species interactions. For example, other studies have documented similar patterns of acid sensitivity for many of the crustacean zooplankton species found in Little Rock Lake (Table 4). One notable exception is *Leptodiptomus minutus*, which responded sensitively to acidification in bioassays conducted in Little Rock Lake (Fischer 1997), but has been reported to increase with acidification in synoptic lake surveys (Sprules 1975). Previous studies have also reported competitive interactions between herbivorous copepods, small cladocerans, medium cladocerans, and large cladocerans, with competitive asymmetries in which the larger species are typically competitively dominant (Brooks and Dodson 1965, DeMott and Kerfoot 1982, Smith and Cooper 1982, Vanni 1986). Rotifers and medium cladocerans interact via interference and exploitative competition, and rotifers can have a detrimental effect on some small *Daphnia* species (Gilbert 1988, MacIsaac and Gilbert 1989, 1991). Williamson (1980, 1986) reports that the

predatory copepod *Mesocyclops edax* can consume small cladocerans. The predatory invertebrate *Chaoborus* increased dramatically with acidification in Little Rock Lake (Fischer and Frost 1997), and experiments conducted in Little Rock Lake show that predation by *Chaoborus* can cause dramatic decreases in abundance of *Leptodiptomus minutus* and *Holopedium gibberum* (T. Frost, unpublished data). These experimental results indicating relatively high *Chaoborus* predation rates on *Holopedium* (~3 *Holopedium* per *Chaoborus* per day) are at odds with conventional wisdom that *Holopedium* is invulnerable to *Chaoborus* predation, due to its large gelatinous sheath. However, other studies (e.g., Allan 1973, Moore 1988) have found that *Chaoborus* can consume *Holopedium*, although they are not preferred relative to other crustaceans like *Bosmina*, *Daphnia*, and copepods. Overall, we conclude that there is general agreement between our autoregressive models and previous mechanistic studies of zooplankton ecology.

Analyses of crustacean zooplankton functional group responses to acidification can be sensitive to the scheme used to categorize species into functional groups. Previous studies by Frost et al. (1992, 1995) have reported extensive compensatory dynamics in Little Rock Lake zooplankton responses to acidification. In their analyses, zooplankton were grouped taxonomically (e.g., cladocerans, copepods, and rotifers). In addition, Havens and Carlson (1998) report compensatory changes among zooplankton taxa that maintained total herbivorous zooplankton biomass in 50 Adirondack Mountain

TABLE 4. Comparison of autoregressive model results to previous studies of zooplankton acid tolerance.

Species	Model results	Results of mechanistic studies	
		Fischer (1997) [†]	Other studies
<i>Bosmina longirostris</i>	T	T	T (Ivanova 1969) [‡] T (Havens 1990) [‡] T (Havens et al. 1993)
<i>Daphnia catawba</i>	T	S/T	S (Havas and Likens 1985 ²)
<i>Daphnia dubia</i>	S	S	not tested
<i>Daphnia parvula</i>	T	T	not tested
<i>Diacyclops thomasi</i>	S	S/T [§]	not tested
<i>Diaphanosoma birgei</i>	T	T	S (Havens et al. 1993)
<i>Holopedium gibberum</i>	S	S/T	S (Bruns and Wiersma 1988 ²) S (Havas and Likens 1985 ²)
<i>Leptodiantomus minutus</i>	S	S	not tested
<i>Mesocyclops edax</i>	S	S/T	S (Price and Swift 1985 ²) S (Havens et al. 1993)
<i>Tropocyclops extensus</i>	T	S/T	not tested

Notes: S and T indicate acid-sensitive and acid-tolerant taxa, respectively.

[†] In the Fischer (1997) study, zooplankton from Little Rock Lake reference basin were incubated in situ for 1 wk at four pH levels (ambient, 5.3, 4.7, and 4.0). Acid sensitivity was concluded when population density was significantly lower in an acidified treatment than in the control. Indirect effects mediated by food web structure were not observed during this short-term experiment (Fischer 1997). T indicates that a species was tolerant in all pH treatments, S indicates that a species was sensitive to acidification at pH 4.7, and S/T indicates that a species was tolerant to acidification at pH 4.7 but sensitive to acidification at pH 4.0.

[‡] Cited in Locke (1991), a literature review of laboratory bioassays for zooplankton taxa. Original citations are given in parentheses.

[§] Results for *Diacyclops thomasi* from Little Rock Lake treatment basin. This species was absent from the reference basin at the time of the experiment.

^{||} Fischer (1997) reports rapid evolution of acid tolerance by *Tropocyclops extensus* in Little Rock Lake treatment basin.

Lakes spanning an acidity gradient. Clearly, the functional group scheme should be tailored to the function of interest. Our grouping scheme was more finely resolved in order to represent "trophic species," which use similar resources and are vulnerable to the same predators. However, more coarsely resolved schemes may be appropriate for some ecological functions and for broad comparisons among systems.

Formation of zooplankton functional groups can be complicated by factors such as ontogenetic diet shifts. Many zooplankton species have complex stage-structured life cycles involving changes in body size and/or diet. In this analysis, we lumped juvenile and adult stages of the same species. While this scheme accurately reflects similarity of juvenile and adult diets for most cladocerans and herbivorous copepods, it does not recognize diet shifts in predatory copepods, which are generally more herbivorous as juveniles (reviewed in Williamson 1991). We found, however, that exclusion of juveniles (i.e., copepodites) from the analysis did not change our results qualitatively (Fischer 1997). Omnivory can also complicate the assignment of zooplankton species to functional groups based on diet. For example, adults of cyclopoid copepods like *Tropocyclops extensus*, *Diacyclops thomasi*, and *Mesocyclops edax* are typically considered to be omnivores capable of consuming both algae and small animal prey (e.g., rotifers). We relied on the studies of Adrian and Frost (1992, 1993) for each of these species

in Little Rock Lake and nearby Trout Lake to classify species as primarily herbivorous or predatory.

Overall, we found the combination of the variance ratio and autoregressive models to be useful for investigating compensatory dynamics in community response to perturbation. The variance ratio is a powerful summary statistic that, by quantifying the degree of compensation or synchrony in complex time series data, offers substantial advantages over simply eyeballing the data. That is, the variance ratio is a more objective means of classifying the dynamics of a functional group as compensatory, independent, or synchronous. The autoregressive models provided additional insights by serving as hypotheses for mechanisms driving population dynamics of species that make up a functional group.

The nature of zooplankton functional group responses to acidification can potentially affect ecosystem processes. For example, medium herbivorous cladocerans like *Daphnia* spp. can control phytoplankton biomass and primary production in some lakes (Shapiro 1980, Pace 1984, Leibold 1989, Carpenter et al. 1996). In addition, daphnids are often a preferred prey resource by planktivorous fish and can control fish growth rates (e.g., Mittelbach and Osenberg 1993) and, potentially, nutrient excretion. The lack of change in medium cladoceran biomass in the acidified basin suggests that these functions may have been maintained during acid-

ification. In contrast, the virtual extinction of predatory copepods represented the loss of a trophic level in the Little Rock Lake food web. This dramatic change in the food web may have had consequences for energy and nutrient transfer. For example, the extinction of predatory copepods may have led to increases in prey items like small cladocerans and rotifers, which may be an important food source for larval fish.

Overall, our study highlights the combined roles of sensitivity to environmental perturbation and species interactions in determining the extent of compensatory dynamics in zooplankton functional group responses to acidification. Previous studies (Walker 1992, 1995, Tilman 1996) have argued that species diversity increases the potential for compensatory dynamics by increasing the likelihood that a tolerant species is present. While this may be true, our study demonstrates that compensatory dynamics can occur in functional groups containing as few as three species. Our findings suggest that predictions of functional group responses to environmental change will be limited in the absence of prior knowledge of species interactions and species-specific responses to the environmental variable of interest.

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LITERATURE CITED

- Adrian, R., and T. M. Frost. 1992. Comparative feeding ecology of *Tropocyclops prasinus mexicanus* (Copepoda, Cyclopoida). *Journal of Plankton Research* **14**:1369–1382.
- Adrian, R., and T. M. Frost. 1993. Omnivory in cyclopoid copepods: comparisons of algae and invertebrates as food for three differently sized species. *Journal of Plankton Research* **15**:643–658.
- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petra and F. Csáki, editors. *Proceedings of the Second International Symposium on Information Theory*. Second edition. Akadémiai Kiadó, Budapest, Hungary.
- Akaike, H. 1974. A new look at the statistical model identification. *Institute of Electrical and Electronic Engineers Transactions on Automatic Control* **AC-19**:716–723.
- Allan, J. D. 1973. Competition and the relative abundance of two cladocerans. *Ecology* **54**:484–498.
- Box, G. E. P., W. G. Hunter, and J. S. Hunter. 1978. *Statistics for experimenters*. Wiley, New York, New York, USA.
- Brezonik, P. L., J. G. Eaton, T. M. Frost, P. J. Garrison, T. K. Kratz, C. E. Mach, J. H. McCormick, J. A. Perry, W. A. Rose, C. J. Sampson, B. C. L. Shelley, W. A. Swenson, and K. E. Webster. 1993. Experimental acidification of Little Rock Lake, Wisconsin: chemical and biological changes over the pH range 6.1 to 4.7. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:1101–1121.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of the plankton. *Science* **150**:28–35.
- Bruns, D. A., and G. B. Wiersma. 1988. Laboratory acidification of a crustacean zooplankton assemblage from a Rocky Mountain subalpine lake (USA). *Environmental Toxicology and Chemistry* **7**:807–814.
- Carpenter, S. R., J. F. Kitchell, K. L. Cottingham, D. E. Schindler, D. L. Christensen, D. M. Post, and N. Voichick. 1996. Chlorophyll variability, nutrient input, and grazing: evidence from whole-lake experiments. *Ecology* **77**:725–735.
- Cottingham, K. L., and S. R. Carpenter. 1998. Population, community, and ecosystem variates as indicators: phytoplankton response to whole-lake enrichment. *Ecological Applications* **8**:508–530.
- Culver, D. A., M. M. Boucherle, D. J. Bean, and J. W. Fletcher. 1985. Biomass of freshwater crustacean zooplankton from length–weight regressions. *Canadian Journal of Fisheries and Aquatic Sciences* **42**:1380–1390.
- DeMott, W. R., and W. C. Kerfoot. 1982. Competition among cladocerans: nature of the interaction between *Bosmina* and *Daphnia*. *Ecology* **63**:1949–1966.
- Eaton, J. G., W. A. Swenson, J. H. McCormick, T. D. Simonson, and K. M. Jensen. 1992. A field and laboratory investigation of acid effects on largemouth bass, rock bass, black crappie, and yellow perch. *Transactions of the American Fisheries Society* **121**:644–658.
- Fischer, J. M. 1997. Zooplankton community responses to acidification: the role of rapid evolution and compensatory dynamics. Dissertation. University of Wisconsin, Madison, Wisconsin, USA.
- Fischer, J. M., and T. M. Frost. 1997. Indirect effects of lake acidification on *Chaoborus* population dynamics: the role of food limitation and predation. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:637–646.
- 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, New York, USA.
- Frost, T. M., S. R. Carpenter, and T. M. Kratz. 1992. Choosing ecological indicators: effects of taxonomic aggregation on sensitivity to stress and natural variability. Pages 215–227 in D. H. McKenzie, D. E. Hyatt, and V. J. McDonald, editors. *Ecological indicators*. Elsevier Applied Science, London, UK.
- Frost, T. M., and P. M. Montz. 1988. Early zooplankton response to experimental acidification of Little Rock Lake, Wisconsin, USA. *Internationale Vereinigung für theoretische und angewandte Limnologie* **23**:2279–2285.
- Frost, T. M., P. K. Montz, M. J. Gonzalez, B. L. Sanderson, and S. E. Arnott. 1999. Rotifer responses to increased acidity: long-term patterns during the experimental manipulation of Little Rock Lake. Pages 141–152 in E. Wurdak, R. Wallace, and H. Segers, editors. *Rotifera VIII: a comparative approach*. *Hydrobiologia* **387/388**:141–152.
- 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.
- Havas, M., and G. E. Likens. 1985. Toxicity of aluminum and hydrogen ions to *Daphnia catwaba*, *Holopedium gibberum*, *Chaoborus punctipennis*, and *Chironomus anthracinus* from Mirror Lake, New Hampshire. *Canadian Journal of Zoology* **63**:1114–1119.

- Havens, K. E. 1990. Aluminum binding to ion exchange sites in acid-sensitive versus acid-tolerant cladocerans. *Environmental Pollution* **64**:133–141.
- Havens, K. E., and R. E. Carlson. 1998. Functional complementarity in plankton communities along a gradient of acid stress. *Environmental Pollution* **101**:427–436.
- Havens, K. E., N. D. Yan, and W. Keller. 1993. Lake acidification: effects on crustacean zooplankton populations. *Environmental Science and Technology* **27**:1621–1624.
- Howarth, R. W. 1991. Comparative responses of aquatic ecosystems to toxic chemical stress. Pages 169–195 in J. Cole, G. Lovett, and S. Findlay, editors. *Comparative analyses of ecosystems*. Springer-Verlag, New York, New York, USA.
- Ivanova, M. B. 1969. The influence of active water reaction on the filtration rate of cladocera. *Polskie Archiwum Hydrobiologii* **16**:115–124.
- Ives, A. R. 1995. Predicting the response of populations to environmental change. *Ecology* **76**:926–941.
- Ives, A. R., S. R. Carpenter, and B. Dennis. 1999a. Community interaction webs and zooplankton responses to planktivory manipulations. *Ecology* **80**:1405–1421.
- Ives, A. R., K. Gross, and J. L. Klug. 1999b. Stability and variability in competitive communities. *Science* **286**:542–544.
- Keller, W., and J. R. Pitblado. 1984. Crustacean plankton in northeastern Ontario lakes subjected to acid deposition. *Water, Air, and Soil Pollution* **23**:271–291.
- Klug, J. L., J. M. Fischer, A. R. Ives, and B. Dennis. 2000. Compensatory dynamics in planktonic community responses to pH perturbations. *Ecology* **81**:387–389.
- Lazzaro, X. 1987. A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. *Hydrobiologia* **146**:97–168.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* **134**:922–949.
- Locke, A. 1991. Zooplankton responses to acidification: a review of laboratory bioassays. *Water, Air, and Soil Pollution* **60**:135–148.
- MacIsaac, H. J., and J. J. Gilbert. 1989. Competition between rotifers and cladocerans of different body sizes. *Oecologia* **81**:295–301.
- MacIsaac, H. J., and J. J. Gilbert. 1991. Competition between *Keratella cochlearis* and *Daphnia ambigua*: effects of temporal patterns of food supply. *Freshwater Biology* **25**:189–198.
- McCulloch, C. E. 1985. Variance tests for species association. *Ecology* **66**:1676–1681.
- Micheli, F., K. L. Cottingham, J. Bascompte, O. N. Bjornstad, G. L. Eckert, J. M. Fischer, T. H. Keitt, B. E. Kendall, J. L. Klug, and J. A. Rusak. 1999. The dual nature of community variability. *Oikos* **85**:161–169.
- Mittelbach, G. G., and C. W. Osenberg. 1993. Stage-structured interactions in bluegill: consequences of adult resource variation. *Ecology* **74**:2381–2394.
- Moore, M. V. 1988. Differential use of food resources by the instars of *Chaoborus punctipennis*. *Freshwater Biology* **19**:249–268.
- Moore, M., and C. Folt. 1993. Zooplankton body size and community structure: effects of thermal and toxicant stress. *Trends in Ecology and Evolution* **8**:178–183.
- Morgan, N. C. 1980. Secondary production. Pages 247–523 in E. D. L. Cren, editor. *The functioning of freshwater ecosystems*. Cambridge University Press, Cambridge, UK.
- Neter, J., W. Wasserman, and M. H. Kutner. 1989. *Applied Linear Regression Models*. Irwin, Homewood, Illinois, USA.
- Pace, M. L. 1984. Zooplankton community structure, but not biomass, influences the phosphorus-chlorophyll a relationship. *Canadian Journal of Fisheries and Aquatic Sciences* **41**:1089–1096.
- Pace, M. L., and J. D. Orcutt, Jr. 1981. The relative importance of protozoa, rotifers, and crustaceans in a freshwater zooplankton community. *Limnology and Oceanography* **26**:822–830.
- Pratt, J. R., and J. Cairns, Jr. 1996. Ecotoxicology and the redundancy problem: understanding effects on community structure and function. Pages 134–174 in M. C. Newman and C. H. Jagoe, editors. *Ecotoxicology: a hierarchical approach*. CRC Lewis, New York, New York, USA.
- Price, E. E., and M. C. Swift. 1985. Inter- and intra-specific variability in the response of zooplankton to acid stress. *Canadian Journal of Fisheries and Aquatic Sciences* **42**:1749–1754.
- Ruttner-Kolisko, A. 1977. Suggestions for biomass calculation of planktonic rotifers. *Archiv für Hydrobiologie Ergebnisse der Limnologie* **8**:71–76.
- Schindler, D. W. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos* **57**:25–41.
- Schluter, D. 1984. A variance test for detecting species associations, with some example applications. *Ecology* **63**:998–1005.
- Shapiro, J. 1980. The importance of trophic-level interactions to the abundance and species composition of algae in lakes. Pages 105–115 in J. Barica and L. Mur, editors. *Hyper-eutrophic ecosystems*. Dr. W. Junk bv, Publishers, The Hague, The Netherlands.
- Sierszen, M. E., and T. M. Frost. 1993. Response of predatory zooplankton populations to the experimental acidification of Little Rock Lake, Wisconsin. *Journal of Plankton Research* **15**:553–562.
- Smith, D. W., and S. D. Cooper. 1982. Competition among cladocera. *Ecology* **63**:1004–1015.
- Sprules, W. G. 1975. Midsummer crustacean zooplankton communities in acid-stressed lakes. *Journal of the Fisheries Research Board of Canada* **32**:389–395.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* **77**:350–363.
- Vanni, M. J. 1986. Competition in zooplankton communities: suppression of small species by *Daphnia pulex*. *Limnology and Oceanography* **31**:1039–1056.
- Walker, B. 1995. Conserving biological diversity through ecosystem resilience. *Conservation Biology* **9**:747–752.
- Walker, B. H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* **6**:18–23.
- Weinstein, D. A., and E. M. Birk. 1989. The effects of chemicals on the structure of terrestrial ecosystems: mechanisms and patterns of change. Pages 181–209 in S. A. Levin, M. A. Harwell, J. R. Kelly, and K. D. Kimball, editors. *Ecotoxicology: problems and approaches*. Springer-Verlag, New York, New York, USA.
- Williamson, C. E. 1980. The predatory behavior of *Mesocyclops edax*: predator preferences, prey defenses, and starvation-induced changes. *Limnology and Oceanography* **25**:903–909.
- Williamson, C. E. 1983. Invertebrate predation on planktonic rotifers. *Hydrobiologia* **104**:385–396.
- Williamson, C. E. 1986. The swimming and feeding behavior of *Mesocyclops*. *Hydrobiologia* **134**:11–19.
- Williamson, C. E. 1991. Copepoda. Pages 787–822 in J. H. Thorp and A. P. Covich, editors. *Ecology and classification of North American freshwater invertebrates*. Academic Press, San Diego, California, USA.
- Yan, N. D., and G. L. Mackie. 1987. Improved estimation of the dry weight of *Holopedium gibberum* (Crustacea, Cladocera) using clutch size, a body fat index, and lake water total phosphorus concentration. *Canadian Journal of Fisheries and Aquatic Sciences* **44**:382–389.