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COMPENSATORY DYNAMICS IN PLANKTONIC COMMUNITY RESPONSES TO pH PERTURBATIONS

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Abstract. Compensatory population dynamics, in which species that decline in response to an environmental perturbation are replaced by similar species, may be crucial in maintaining processes performed by functional groups of species. Compensatory dynamics may be produced by negative interactions among species, such that the decrease in abundance of a species releases the suppression of another species and allows it to increase. We conducted a mesocosm experiment in Trout Lake, Wisconsin, USA, to test the hypothesis that compensatory shifts in species abundances play a role in overall planktonic community response to pH perturbation. In 2000-L mesocosms over a period of six weeks, we contrasted a control treatment with two acidified treatments (press, sustained pH = 4.7; and pulse, alternating pH = 4.7 and ambient pH). In the acidified treatments, we saw changes in abundance of the major zooplankton and phytoplankton species, but we observed few cases of compensatory dynamics. Nonetheless, when present, compensatory dynamics could be strong. Analyses using autoregressive models revealed negative interactions among species that could potentially lead to compensatory dynamics. However, this potential for compensatory dynamics was not realized in cases where all species were sensitive to the pH perturbations. Therefore, compensatory dynamics that buffer community responses to perturbations may be limited in communities in which many species are sensitive to the perturbation.

Key words: acidification; community dynamics; compensatory dynamics; LTER; perturbation; phytoplankton; Trout Lake, Wisconsin; zooplankton.

INTRODUCTION

Ecological communities are frequently exposed to environmental perturbations, and predicting community responses to perturbation has become crucial in applied environmental fields such as conservation biology, ecosystem management, and ecological restoration. Understanding community responses is difficult, in part because population abundances fluctuate widely even under stable environmental conditions and can change rapidly when the system is later exposed to perturbations.

If populations change in a compensatory manner (i.e., decreases in the abundances of some species are coupled to increases in the abundances of other functionally similar species), community function and/or functional group biomass will be partially or wholly maintained during environmental perturbations (MacArthur 1955, McNaughton 1977, Schindler 1987, Howarth 1991, Walker 1992, Lawton and Brown 1993, Carpenter et al. 1994, Frost et al. 1995, Tilman 1996, Peterson et al. 1998). The maintenance of ecological processes despite shifts in the populations that contribute to the process is called functional compensation. Compensatory dynamics among populations occur when some species increase and others decrease so that negative covariances among functionally similar species outweigh positive covariances (Frost et al. 1995, Tilman 1996). Functional compensation is an extreme case of compensatory dynamics, one where species' increases and decreases are perfectly balanced. In other cases, changes in community function and/or functional group biomass occur despite negative covariance among species and/or functional groups (i.e., compensatory dynamics), hence the distinction between functional compensation and compensatory dynamics.

Compensatory dynamics may arise when there are negative interactions among species. For example, consider a hypothetical community with two competitors, species A and species B. Following a decrease in pH, species A declines in abundance because its population growth rate is negatively affected by acidity. Compensatory dynamics arise if species B is acid-tolerant and increases in response to the decline of species A. In this hypothetical example, the abundances of species A and B negatively covary because the two competing species have contrasting direct responses to the perturbation.

On the other hand, negative interactions among species do not guarantee compensatory dynamics. Con-

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sider another case, where the competitors (species C and species D) have similar direct responses to a pH perturbation. Following a decrease in pH, species C and species D decline because the growth rates of both species are negatively affected by acidity. Although there is potential for compensatory dynamics, the abundances of species C and D positively covary because of their similar direct responses to acidification. To determine whether compensatory dynamics can arise between competing species, it is necessary to quantify both the direct effects of an environmental perturbation on the population growth rate of each species and the strength of interactions between the species (Ives 1995).

To explore the role of compensatory dynamics in community responses to perturbation, we performed a mesocosm experiment to assess how planktonic communities changed in response to pH perturbations. We examined the effects of long-term and short-term perturbations by employing both press and pulse manipulations (Bender et al. 1984). In the press manipulation, the pH was dropped and sustained at a low level for the duration of the experiment. In the pulse manipulation, the pH was dropped for a short time and then brought back up to the pre-manipulation level. Two pulses were administered over the duration of the experiment.

We used conventional statistics to assess changes in individual taxa and functional groups. We identified compensatory dynamics by quantifying patterns of covariance within and among groups of functionally similar taxa using a variance ratio technique (Frost et al. 1995). In the cases where compensatory dynamics were most evident, we examined the mechanisms underlying the pattern using first-order autoregressive models to quantify the direct effects of pH on taxa and the interactions among taxa. We used these models to hypothesize the interactions that led to compensatory dynamics and to understand why compensatory dynamics were not more prevalent.

Methods and Materials

Study site

Trout Lake (46°00′ N, 89°40′ W) is one of seven lakes in the North Temperate Lakes Long-Term Ecological Research site located in Vilas County, Wisconsin, USA (for further site information see the Center for Limnology, University of Wisconsin–Madison web site).[5] Trout Lake is an oligotrophic drainage lake with an area of 1608 ha, mean depth of 14.6 m, and maximum depth of 35.7 m. Acid neutralizing capacity (ANC) is 829 μeq/L, and mean summer pH is 8.1.

Experimental design

The experiment was conducted 19 June–29 July 1995. Three replicate control mesocosms remained at the ambient pH of 8.1. Two acidified treatments, press and pulse, with three replicates each were employed after one pretreatment sample. In the press treatment, we lowered pH to 4.7 ± 0.2. In the pulse treatment, we lowered pH to 4.7 ± 0.2 for the first week of the experiment. In the second week, we raised pH to 8.1 ± 0.2 for two weeks. We again lowered pH to 4.7 ± 0.2 in the fourth week, then raised it to 8.1 ± 0.2 in the fifth week. We manipulated pH using 1.0 mol/L sulfuric acid and 1.0 mol/L sodium hydroxide. All mesocosms (including controls) were thoroughly mixed after each manipulation, and pH was measured three times a week. The experiment was terminated after six weeks.

Mesocosm design

We used nine polyethylene bags (Laird Plastics, Madison, Wisconsin), 0.8 m in diameter and 4.0 m deep (~2000 L), as mesocosms. The bags were open at the top to allow exchange with the atmosphere and closed at the bottom to prevent mixing with lake water. We attached the bags to a floating wooden frame, which was oriented in a north/south direction. We stocked phytoplankton, protozoans, and bacteria into each bag by pumping water from 2 m depth through a 80-μm mesh screen to exclude zooplankton. We stocked zooplankton at ambient lake density by taking net tows with an 80-μm net. Tows were taken at dusk to include zooplankton that migrate vertically throughout the day.

Sampling procedure and laboratory analyses

We collected phytoplankton from each bag twice a week by lowering a length of 6 mm diameter Tygon tubing to 3.5 m. An integrated water sample was contained in the tube by raising the tube from the bottom. We preserved phytoplankton with gluteraldehyde (1% final concentration) and enumerated the samples using the Utermohl method (Utermohl 1958). Preserved 25-mL subsamples were gravity settled for at least 22 h and counted on an inverted microscope at 400×. At least 25 fields or 200 cells were counted per sample. We calculated biovolume using geometrical formulas according to the shape of each alga (Wetzel and Likens 1991). Most phytoplankton were identified to genus. Genera names followed by sp. indicate that only one species was found in that genus.

Zooplankton were collected from each bag once a week at 0.5, 1.5, 2.5, and 3.5 m below the surface using a 12-L Schindler-Patalas trap (constructed by G. Lee, University of Wisconsin Center for Limnology) with an 80-μm mesh net. All four samples were combined and preserved with sucrose-buffered formalin (5% final concentration). We counted and measured zooplankton length at 50× on a dissecting microscope. Cladocerans and adult copepods were identified to species. Copepod copepodites were combined into two categories: calanoid or cyclopoid. We calculated biomass using length–weight regressions after McCauley (1984), with

[5] URL: ⟨www.limnology.wisc.edu⟩

TABLE 1. Results from repeated-measures ANOVA for time, treatment, and time × treatment effects.

Response variable	Time	TRT	Contrasts	Times × TRT	Contrasts
Total phytoplankton	0.0007*	NS		0.0001*	C PU PR
Chlorophyte phytoplankton	0.0001*	0.0603		0.0001*	C PU PR
Chlorococcalean A	0.0008*	0.0322		0.0037†	
Chlorococcalean B	0.0008*	NS		0.0619	
Chlorococcalean C	0.0001*	NS		0.0001*	C PU PR
Chlorococcalean D	NS	NS		NS	
Crucigenia sp.	0.0001*	NS		0.0004*	C PU PR
Mougeotia sp.	0.0001*	0.0033†		0.0028†	
Oocystis A	NS	NS		NS	
Oocystis B	0.0470	NS		0.0149	
Sphaerocystis sp.	0.0039†	NS		NS	
Spondylosium sp.	NS	NS		NS	
Chrysophyte phytoplankton	NS	NS		NS	
Dinobryon sp.	0.0040†	NS		0.0195	
Flagellate A	0.0010*	NS		NS	
Flagellate B	NS	NS		NS	
Ochromonas sp.	0.0001*	0.0002*	C PU PR	0.0031†	
Cyanobacteria	0.0154*	0.0323		NS	
Aphanocapsa sp.	NS	0.0315		NS	
Chroococcus A	0.0248	0.0010*	C PU PR	0.0847	
Chroococcus B	NS	NS		NS	
Chroococcalean unicell	0.0391	NS		NS	
Filament	0.0001*	NS		NS	
Nostoc sp.	0.0001*	0.0001*	C PU PR	0.0061	
Diatom phytoplankton	0.0001*	0.0923		0.0006*	C PU PR
Asterionella sp.	0.0001*	NS		0.0155	
Fragilaria A	0.0001*	0.0225		0.0004*	C PU PR
Fragilaria B	NS	NS		NS	
Melosira sp.	NS	NS		NS	
Rhizosolenia sp.	0.0001*	NS		NS	
Stephanodiscus sp.	0.0003*	NS		0.0007*	C PU PR
Tabellaria sp.	0.0891	NS		NS	
Total zooplankton	0.0001*	0.0001*	C PU PR	0.0001*	C PU PR
Large herbivorous zooplankton	0.0001*	0.0001*	C PU PR	0.0001*	C PU PR
Calanoid copepodites	0.0002*	0.0030*	C PU PR	0.0005*	C PU PR
Cyclopoid copepodites	0.0022†	0.0405		NS	
Daphnia galeata mendotae	0.0001*	0.0002*	C PU PR	0.0001*	C PU PR
Daphnia retrocurva	0.0010†	0.0595		0.0034*	C PU PR
Holopedium gibberum	0.0001*	0.0142†		0.0001*	C PU PR
Leptodiaptomus minutus	NS	0.0109†		0.0680	
Scapholeberis mucronata	0.0410	0.0536		NS	
Sida crystallina	0.0029†	NS		NS	
Tropocyclops extensus	0.0001*	0.0064†		0.0039*	C PU PR
Small herbivorous zooplankton	0.0001*	NS		0.0014*	C PU PR
Bosmina longirostris	0.0011†	NS		0.0380	
Chydorus sphaericus	0.0001*	NS		NS	
Carnivorous zooplankton					
Diacyclops thomasi	0.0001*	0.0030*	C PU PR	0.0536	

Notes: All P values < 0.10 are reported (NS signifies $P > 0.10$). Symbols indicate significance after sequential Bonferroni correction for number of species tested († $P < 0.10$; * $P < 0.05$). Underlining indicates treatments that were not significantly different after Bonferroni correction ($P > 0.05$). C = control; PU = pulse treatment; PR = press treatment.

the exception of *Holopedium gibberum*, whose biomass without the gelatinous sheath was estimated using the equation in Peters and Downing (1984).

Construction of functional groups

We divided the phytoplankton and zooplankton communities into functional groups to assess how similar groups of species responded to pH perturbations. Construction of functional groups is subjective and may be based on a number of characteristics depending on how function is defined. For example, all phytoplankton could be aggregated into the same functional group if photosynthesis is the function of interest. We defined our functional groups based on a priori knowledge of the organisms rather than on their observed response to the perturbation. Therefore, although our selection of functional groupings was subjective, it was unbiased by our experimental results.

Phytoplankton were divided into four functional groups (chlorophytes, chrysophytes, cyanobacteria, or diatoms) based on taxonomy (Table 1). Cryptophytes and dinoflagellates were rare throughout the experiment. The four functional groups share common resources: all require a carbon source, nutrients, and some need additional vitamins and/or minerals. In most cases, these requirements are similar within the major

taxonomic groups of phytoplankton but differ among groups. For example, diatoms generally have a lower phosphorus requirement than chlorophytes (Sommer 1989). In addition, the relative ability to take up nutrients from the water column differs among groups (Sandgren 1988).

We divided the zooplankton into three functional groups based on feeding mode and body size after Sprules and Holtby (1979). Zooplankton were classified as either large herbivores, small herbivores, or carnivores (Table 1). We used a cutoff of 0.50 mm to separate small and large herbivores. We considered *Tropocyclops extensus* an herbivore because previous feeding experiments with *T. extensus* (formerly *T. prasinus mexicanus*) from lakes in the area indicate that *T. extensus* is largely herbivorous; daily mass-specific uptake rates for algae were 2 to 34 times higher than those for invertebrate prey under in situ food concentrations (Adrian and Frost 1992).

Analyses

We used repeated-measures analysis of variance (ANOVAR) to assess time effects, treatment effects, and time × treatment interactions on the biomass/biovolume of individual species and functional groups (Gurevitch and Chester 1986). One of the control bags was excluded from our analyses because we believe this bag was invaded by fish. We applied a square-root transformation to normalize the data and homogenize variances. The symmetry of the covariance matrix did not meet the assumptions of ANOVAR. However, the Huynh-Feldt (H-F) conditions were satisfied, and therefore we used H-F corrected *P* values (Potvin et al. 1990). We applied separate sequential Bonferroni corrections (Rice 1989) for the number of species and number of functional groups tested. For example, when we were interested in how many of the 12 zooplankton taxa responded to the manipulations, we used a sequential Bonferroni correction of 12 on the zooplankton taxa. If a significant treatment or time × treatment interaction (after correction, using $\alpha < 0.05$) was found, pairwise contrasts were used to assess which of the treatments were different. A sequential Bonferroni correction was applied to the three contrasts. All repeated-measures analyses were performed using SAS (SAS Institute 1990).

Compensatory dynamics

Compensatory dynamics exist when there is greater negative than positive covariance among species within a functional group and consequently reduced variance in the group taken as a whole. We used the variance ratio given in Frost et al. (1995) to assess the degree of compensatory dynamics within and among functional groups. The variance ratio is based on the relationship between the variance of the functional group and the variance of the component taxa (Box et al. 1978):

$$\mathrm{Var}\left(\sum_{i=1}^{n} S_i\right) = \left[\sum_{i=1}^{n}\left(\mathrm{Var}\ S_i\right)\right] + \left[2\sum_{i=1}^{n}\sum_{j=1}^{i-1}\mathrm{Cov}(S_iS_j)\right] \quad (1)$$

where S_i is the biomass of species i, Var is the variance, and Cov is the covariance. The variance ratio relates the variance of a functional group to the variance of the component taxa and is given as

$$\mathrm{Var}\left(\sum_{i=1}^{n} S_i\right) \Bigg/ \left[\sum_{i=1}^{n}(\mathrm{Var}\ S_i)\right]. \quad (2)$$

When species vary independently, their covariance is zero, and the variance ratio is one. When compensatory dynamics exist, the sum of the pairwise covariances between species is negative, and the variance ratio is less than one. When the sum of pairwise covariances between species is positive, the variance ratio is greater than one indicating synchronous dynamics. For each trophic level, we quantified patterns of covariance both within and among functional groups. To identify patterns within functional groups, we calculated the variance ratio using Eq. 2 with S_i denoting the species within the functional group. To quantify patterns among functional groups, we calculated the variance ratio using Eq. 2 with S_i denoting functional groups. Because we were interested in compensatory dynamics resulting from response to pH perturbations, we calculated the variance ratio for each bag and then averaged the replicates from the same treatment. Average values less than one in any treatment indicate compensatory dynamics because the sum of the variances of the component taxa is less than the variance of the functional group taken as a whole. Lower average variance ratios in the acidified treatments compared to the control treatment indicate a greater degree of negative covariance among taxa in the acidified treatments. This pattern demonstrates enhanced compensatory dynamics in response to the pH manipulations.

Autoregressive models

We used first-order autoregressive models to identify the potential mechanisms generating compensatory dynamics. Specifically, we were interested in which interactions were important in generating the pattern of negative covariance among species or functional groups of species (Ives 1995). The objective of our analyses was to select the best-fitting autoregressive model, and we did not attempt to distinguish potentially competing models statistically. The methods required for statistical inference in multispecies autoregressive models have yet to be developed in detail, and for our purposes, selecting the best-fitting model is a good first step in explaining the responses we observed in our experiment.

We used the results from the variance ratio calculations to choose which taxa to include in the models. To describe the mechanisms driving compensatory dynamics, we chose the cases with the lowest variance

TABLE 2. Focal taxa and covariates in autoregressive models.

Model	Focal taxa	Covariates
Phytoplankton	diatoms, chlorophytes	pH†, temperature, small herbivores†, large herbivores†, chrysophytes†, cyanobacteria, treatment × pH†
Zooplankton	*Daphnia galeata mendotae, Holopedium gibberum, Sida crystallina*	pH†, temperature, small phytoplankton, large phytoplankton†, small herbivores†, other large herbivores, treatment × pH†

† Covariates that are included in the best-fitting subset models.

ratios. Average variance ratios were lowest among phytoplankton functional groups in the pulse and press treatments and among large herbivores in the pulse treatment. In both cases, the variance ratio in at least one acidified treatment was substantially lower than the variance ratio in the control treatment (i.e., two case studies of enhanced compensatory dynamics in response to acidification). Thus, we created a phytoplankton model to predict the biovolume of the dominant phytoplankton functional groups, the chlorophytes and diatoms. Likewise, we created a zooplankton model to predict the biomass of the dominant large herbivores, *Daphnia galeata mendotae*, *Holopedium gibberum*, and *Sida crystallina.* We used only the dominant taxa as dependent variables because our short time series limited the number of variables we could fit. This limitation means that when working with short time series, autoregressive models are best suited for analyzing communities that contain a few species, a few clearly dominant species, or communities that are readily amenable to combining species into functional groups. We fit separate phytoplankton and zooplankton models to ensure that the focal taxa in each model were operating on similar time scales.

We fit autoregressive models of population growth rate between successive samples. For each model, we focused on quantifying the effects of interactions among focal taxa (presumably competition), as well as the effects of covariates such as pH, nonfocal taxa, and temperature (Table 2). Data from all bags were combined in the analysis. The model was of the form

$$x_i(t + 1) = a_i + \sum_{j=1}^{n} b_{ij}x_j(t) + \sum_{k=1}^{m} c_{ik}u_k(t) + \varepsilon_i(t) \quad (3)$$

where $x_i(t)$ is the biomass of species i in the sample at time t, $u_k(t)$ is the value of a covariate in the model (such as pH, temperature, or the biomass of a nonfocal species), a_i is a constant, b_{ij} is the effect of species j on the change in biomass of species i, c_{ik} is the effect of $u_k(t)$ on the change in species i, and $\varepsilon_i(t)$ is unexplained variability. Due to the structure of the model, the covariates can only affect the focal taxa. For the phytoplankton autoregressive model, an equation of the form of Eq. 3 was fit for each of the two dominant phytoplankton functional groups, while for the zooplankton model, an equation was fit to the biomass of each of the three dominant large herbivores. Data were $\log(x + c)$ transformed before analysis where c is a constant. We chose the value of c to normalize the error term $\varepsilon_i(t)$.

We fit the autoregressive models using least-squares techniques. The best-fitting subset model was chosen as that with the lowest Akaike Information Criterion (AIC) (Box et al. 1994). AIC is a measure of model fit that includes a penalty for the number of parameters. We used a search algorithm to identify the parameters in the best-fitting subset model. Covariates in the phytoplankton model included pH, temperature, small herbivores, large herbivores, other phytoplankton functional groups, and a treatment × pH interaction (Table 2). We included a treatment × pH interaction to account for the possibility of different effects of pH in the different treatments. It is possible that the responses of species in the pulse treatment were dominated by the initial pulse (i.e., very little recovery occurs after the first pulse). To allow for this possibility, we used a dummy variable coded to identify periods during which pH was experimentally brought to ambient after being experimentally reduced in the pulse treatment (ambient = 1, acidic = 0). Covariates in the zooplankton model included pH, temperature, small phytoplankton, large phytoplankton, small herbivores, other large herbivores, and a treatment × pH interaction (Table 2). We used cutoff values of 30 μm to separate small and large phytoplankton (Lehman 1988) and 0.5 mm to separate small and large zooplankton.

The approach outlined above yields a best-fitting subset model that identifies all the direct effects on the focal taxa. However, we were also interested in the indirect effects of acidification. To identify the potential indirect effects, we performed similar autoregression analyses on each of the covariates in the best-fitting models (phytoplankton and zooplankton) to determine if they were directly affected by acidity. For example, we found that large herbivores (a covariate in the phytoplankton model) had a negative effect on diatoms (a focal taxon), and therefore we performed an autoregression analysis on large herbivores and found that they were negatively affected by acidity. This suggests that acidity has an indirect positive effect on diatoms via large herbivores. For clarity, we present only the results for the covariates for which autoregression suggests direct effects of acidity (i.e., only the covariates that are involved in indirect effects of acidity on the focal taxa).

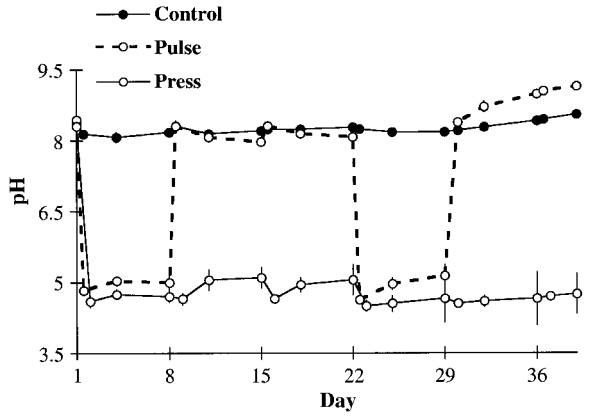

FIG. 1. Mean (± 1 SE) of pH throughout the course of the experiment.

RESULTS

Manipulations of pH

The pH levels attained in our mesocosms closely followed our experimental design (Fig. 1). Control bag pH was similar to pH in the lake and remained relatively constant throughout the six-week period. The pH in one of the press treatment bags drifted slightly upwards and had to be corrected each week. This may have been due to a small hole. However, because its biological dynamics were similar to the other press bags, we included it in the analyses.

Phytoplankton responses

Total phytoplankton biovolume diverged among treatments. At the end of the experiment, total phytoplankton biovolume was much higher in the pulse treatment relative to the press and control treatments (Fig. 2, Table 1). In general, diatoms and chlorophytes had much higher biovolume than cyanobacteria and chrysophytes. Diatoms, primarily *Asterionella* sp., *Fragilaria* sp. A, and *Tabellaria* sp., dominated the phytoplankton community at the beginning of the experiment but decreased in abundance in all three treatments. Diatoms showed an initial increase and then gradual decrease in the control treatment and a drastic reduction following acidification in the pulse and press treatments (Fig. 3). Chlorophytes comprised a small percentage of the total biovolume at the beginning of the experiment. The taxa present were primarily small unicellular chlorococcalean algae or small colonies such as *Crucigenia* sp. Large colonies and filaments, primarily *Sphaerocystis* sp. and *Mougeotia* sp., increased near the end of the experiment in all three treatments, although for *Mougeotia* sp., the magnitude of the increase was much greater in the pulse treatment (Fig. 3). The biovolume of chrysophytes and cyanobacteria was not significantly different among treatments (Table 1). Chrysophytes were dominated by small flagellates, and cyanobacteria were dominated by *Aphanocapsa* sp.

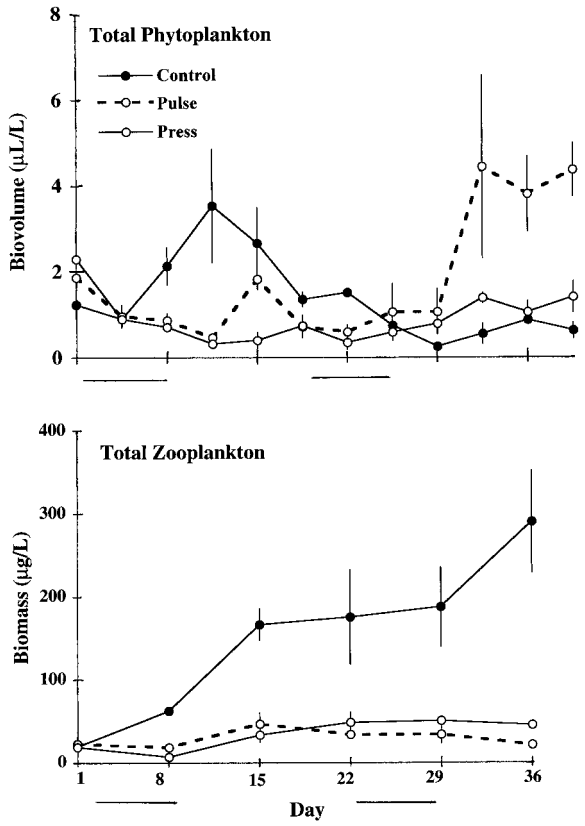

FIG. 2. Mean (± 1 SE) total phytoplankton biovolume and total zooplankton biomass in control and two acidified treatments over time. Note difference in scale on *y*-axis. Bars under the *x*-axis represent the portions of the pulse treatment where the pH was low.

Zooplankton responses

Zooplankton biomass was low in the acidified treatments relative to the control treatment (Fig. 2, Table 1). Large-bodied herbivores, such as *Daphnia galeata mendotae* and *Holopedium gibberum*, were dominant in the control treatment, whereas small-bodied herbivores, such as *Bosmina longirostris* and *Chydorus sphaericus*, were dominant in the acidified treatments (Fig. 4). Although *Diacyclops thomasi*, the dominant carnivore, was abundant at the beginning of the experiment (biomass ~30% of total), its average biomass over the course of the experiment was <9% in every bag. Total zooplankton and large herbivore biomass was lower in the acidified treatments than in the control treatment throughout the experiment (Fig. 4). During the first three weeks of the experiment, small herbivore biomass was lower in acidified treatments relative to the control treatment. However, small herbivore biomass was greater in the acidified treatments than in the control treatment for the second half of the experiment (Fig. 4).

Compensatory dynamics

Most of the variance ratio values calculated within and among functional groups were close to or greater

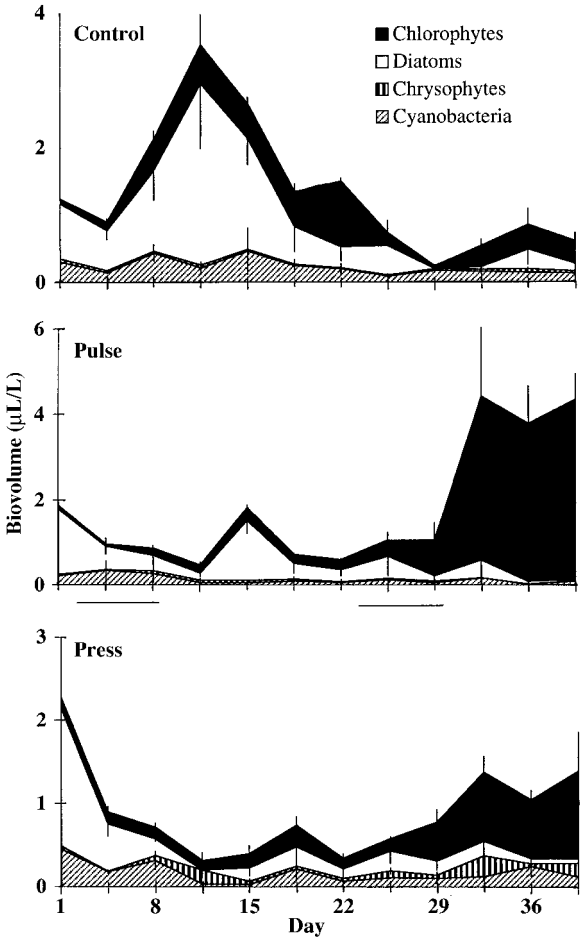

FIG. 3. Mean (± 1 SE) chlorophyte, diatom, chrysophyte, and cyanobacteria biovolume in the control, pulse, and press treatments over time. Note difference in scale on *y*-axis. Bars under the *x*-axis represent the portions of the pulse treatment where the pH was low.

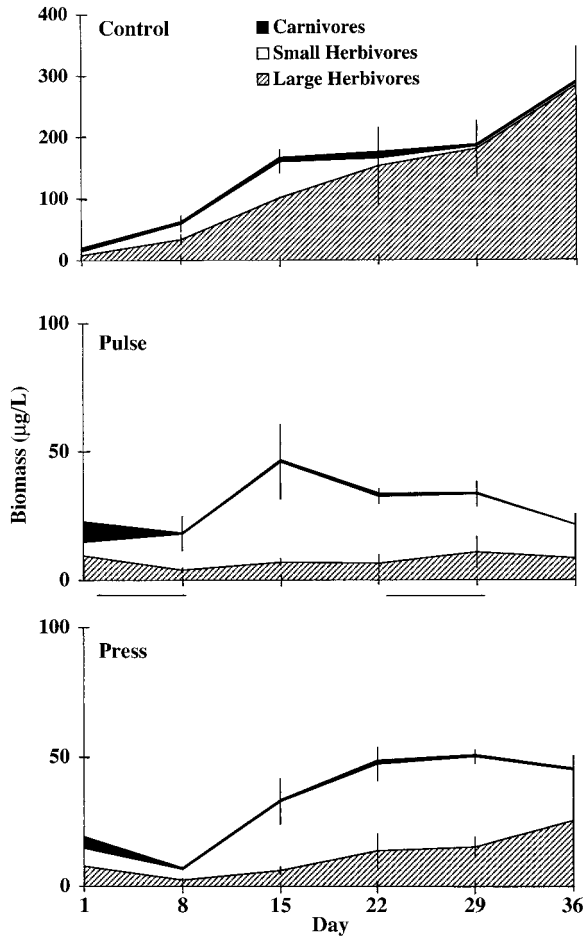

FIG. 4. Mean (± 1 SE) carnivore, small herbivore, and large herbivore biomass in the control, pulse, and press treatments over time. Note difference in scale on *y*-axis. Bars under the *x*-axis represent the portions of the pulse treatment where the pH was low.

than one, indicating independent or synchronous dynamics (Table 3). Only 9 of 24 variance ratio averages were less than one, and five of these cases were in the control treatment (Table 3). The lowest variance ratios were observed among phytoplankton functional groups in both acidified treatments and within the large herbivore functional group in the pulse treatment (Table 3). These were also cases where the values of the variance ratio in one or more acidified treatments were lower than the values in the control treatment.

Autoregressive models

The best-fitting phytoplankton model is summarized in Fig. 5 in the form of an interaction web (Ives et al. 1999). Arrows represent coefficients in the model (see *Methods*). Phytoplankton model results suggest that diatoms and chrysophytes had negative effects on the growth rate of chlorophytes. The model also suggests a direct negative effect of acidity on both focal groups of species. The effect of acidity in the pulse treatment is obtained by combining the pH and treatment × pH coefficients. The treatment × pH interaction was negative for diatoms and positive for chlorophytes sug-

TABLE 3. Variance ratio within and among phytoplankton and zooplankton functional groups. Data are means (with 1 SE in parentheses).

Group	Control	Pulse	Press
Total phytoplankton	1.36 (0.01)	0.75 (0.10)	0.85 (0.14)
Total zooplankton	0.87 (0.07)	0.89 (0.13)	1.29 (0.21)
Phytoplankton functional groups			
Chlorophytes	0.91 (0.13)	1.42 (0.32)	1.12 (0.16)
Chrysophytes	0.94 (0.13)	1.08 (0.14)	1.27 (0.25)
Cyanobacteria	0.92 (0.09)	1.26 (0.20)	1.27 (0.19)
Diatoms	1.38 (0.44)	1.30 (0.02)	1.96 (0.47)
Zooplankton functional groups			
Large herbivores	0.90 (0.02)	0.66 (0.14)	1.24 (0.20)
Small herbivores	1.08 (0.18)	1.09 (0.30)	1.17 (0.07)

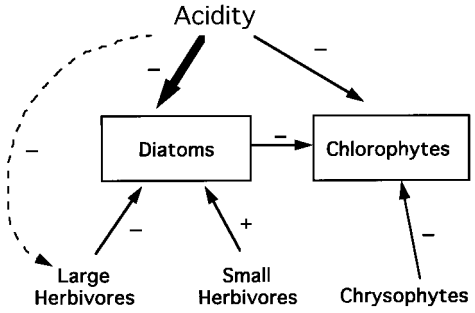

FIG. 5. Interactions in the best-fitting phytoplankton model. Each solid arrow represents a term in the model. The size of the acidity arrows is representative of the magnitude of the effect. Pluses and minuses indicate positive or negative effects. Note that a negative effect of acidity equals a positive effect of pH since acidity increases as pH declines. Dashed arrows represent direct effects of acidity on covariates.

gesting that diatoms recovered only weakly with the increase in pH following an experimental pulse, while chlorophytes responded strongly to the increase in pH. In addition, large herbivores had a negative effect and small herbivores had a positive effect on the growth rate of diatoms (Fig. 5, Table 4a). Small herbivores are not likely to eat diatoms but could exert a positive effect by recycling nutrients (Sterner 1989). Our analysis of the covariates in the model suggests a direct negative effect of acidity on large herbivores, which translates into an indirect positive effect of acidity on diatoms (Fig. 5, Table 4b). We calculated model fit by comparing predicted change in biovolume from time t to time $t + 1$ to observed changes in biovolume from time t to time $t + 1$. The R-square values for diatoms and chlorophytes were 0.46 and 0.21, respectively (Table 4a).

We used the model results to hypothesize the mechanisms causing the patterns of phytoplankton functional group abundance. Model results suggest that diatoms decreased in the control treatment due to increases in large herbivores (presumably a grazing effect), while the decrease in diatoms in the acidified treatments was due to the negative effect of acidity. Thus, the indirect positive effect of acidity on diatoms was offset by the direct negative effect. The model suggests that chlorophyte increases in all treatments were due to the decline of diatoms. The magnitude of chlorophyte increase was different in the two acidified treatments. Chlorophyte increases in the pulse treatment were quite dramatic once pH was raised after the second pulse (Fig. 3). In contrast, we suggest that a direct effect of low pH on chlorophytes in the press treatment prevented the bloom seen in the pulse treatment.

The best-fitting zooplankton model is summarized in Fig. 6. The model indicates that *D. galeata mendotae* had a negative effect on the growth rate of *H. gibberum.* There was a negative effect of acidity on all three species. The treatment × pH interaction was negative for *D. galeata mendotae* and *H. gibberum,* and positive for *S. crystallina.* The model indicates a negative effect of large phytoplankton on *S. crystallina* (Table 5a). Toward the end of the experiment, *Mougeotia* sp. was the dominant large phytoplankton species and this filamentous chlorophyte may interfere with the filtering mechanism of *S. crystallina.* Other filamentous algae have been shown to clog filtering appendages in some zooplankton species (Hayward and Gallup 1976). The mechanism underlying the positive effect of small herbivores on *H. gibberum* is unclear but could reflect common responses to *D. galeata mendotae.* Autoregression analysis of the model covariates suggests a direct negative effect of acidity on large phytoplankton, which translates to an indirect positive effect of acidity on *S. crystallina* (Fig. 6, Table 5b). We compared predicted change in biomass to observed change in biomass as in the phytoplankton model. The R-square values for *D. galeata mendotae, H. gibberum,* and *S. crystallina* were 0.46, 0.65, and 0.32, respectively (Table 5a).

As in the phytoplankton model, we used the best-

TABLE 4. (a) Model coefficients and diagnostics for the phytoplankton model fitted to the two dominant functional groups and (b) model coefficients and diagnostics for the covariate in the phytoplankton model that was directly affected by acidity.

Functional Group	Coefficients							R^2	Variance-covariance matrix of error terms		Autocorrelation of error terms
	Diatoms	Chlorophytes	pH	Treatment × pH	Large herbivores	Small herbivores	Chrysophytes		Diatoms	Chlorophytes	
a) Phytoplankton model											
Diatoms	0.3561		0.1673	−0.0656	−0.1263	0.1722		0.4579	0.1397	0.0036	−0.0861
Chlorophytes	−0.1246	0.7738	0.0050	0.0313			−0.7849	0.2101	0.0036	0.1332	−0.0682
b) Covariate in phytoplankton model											
Large herbivores			0.3591	−0.1832				0.4446			−0.1958

Note: For part (b), the model is the best-fitting subset model which originally contained small herbivores, chrysophytes, diatoms, chlorophytes, cyanobacteria, temperature, pH and treatment × pH as predictor variables.

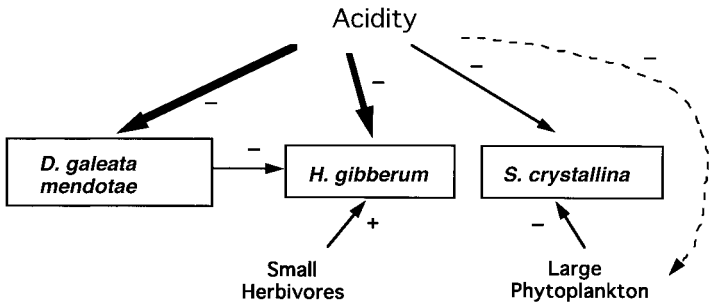

FIG. 6. Interactions in the best-fitting zooplankton model. Each arrow represents a term in the model. The size of the acidity arrows is representative of the magnitude of the effect. Pluses and minuses indicate positive or negative effects. Note that a negative effect of acidity equals a positive effect of pH since acidity increases as pH declines. Dashed arrows represent direct effects of acidity on covariates.

fitting zooplankton model to identify the potentially important mechanisms generating compensatory dynamics among the three dominant large herbivores. *D. galeata mendotae* and *H. gibberum* were the dominant species in the control treatment. *D. galeata mendotae* increased steadily whereas *H. gibberum* declined due to negative interaction with *D. galeata mendotae* (Fig. 7). Model results suggest that both of these species were negatively affected by the pH perturbations and the data show dramatic declines in both acidified treatments relative to the control treatment. For *H. gibberum*, the decline was slightly less in the press treatment than in the pulse treatment. *S. crystallina* became the dominant large herbivore in the pulse treatment because of the declines in the other two species. However, *S. crystallina* did not interact with either *D. galeata mendotae* or *H. gibberum* (Fig. 6) and thus its increase cannot be explained by decline of *D. galeata mendotae* and *H. gibberum*. Model results suggest both a small direct negative effect and an indirect positive effect of acidity on *S. crystallina*. These effects were not strong enough to statistically affect *S. crystallina*'s dynamics (i.e., the biomass of *S. crystallina* is not significantly different among treatments, Table 1). However, the indirect positive effect outweighing the direct negative effect explains *S. crystallina*'s increasing trend during the second period of low pH in the pulse treatment.

We used several diagnostic tools to test the assumptions of the autoregressive models. Normal probability plots and plots of the residuals vs. observed values suggested no deviation from normality. The errors for the predicted values (with the exception of *H. gibberum* and large phytoplankton) were negatively autocorrelated. This is to be expected if there is measurement error.

A caveat is needed when interpreting the interaction webs produced by the autoregressive models. Autoregressive models rely on correlated changes in biomasses. The best-fitting models give the best post hoc descriptions of changes in species' biomasses, but as with all models based on correlation, they do not constitute tests of species interactions.

DISCUSSION

As in previous studies of planktonic responses to acidification (Schindler et al. 1985, Findlay and Kasian 1990, Brezonik et al. 1993), we detected changes in phytoplankton and zooplankton communities in response to pH perturbations (Table 1, Fig. 2). The changes in these communities allowed us to explore whether populations changed in a compensatory manner. For many functional groups, we observed little or no compensatory dynamics (Table 3). However, we did observe enhanced compensatory dynamics in response to pH perturbations among phytoplankton functional groups and within the large herbivore functional group. The autoregressive models suggest that the strongest compensatory dynamics (i.e., lowest variance ratios) occurred when two taxa interacted and at least one of the taxa was directly affected by the perturbation. Compensatory dynamics among taxa can lead to maintenance of functional group biomass despite changes in species composition (Carpenter et al. 1994, Frost et al. 1995). In this study, compensatory dynamics among phytoplankton groups led to increased biovolume in the acidified treatments relative to the control. In contrast, compensatory dynamics within large herbivores resulted in only partial compensation of large herbivore biomass (i.e., large herbivore biomass is much lower in the acidified treatments than the control treatment despite the presence of compensatory dynamics, Fig. 4).

The proposed negative interaction between chlorophytes and diatoms led to compensatory dynamics in response to perturbation because the stronger competitors (diatoms) were more affected by the perturbation than the weaker competitors (chlorophytes). In the pulse treatment, diatoms declined when acidity was high, and chlorophytes increased after the second pulse, when acidity was low. We hypothesize that the chlorophyte increase was due to competitive release. In the press treatment, chlorophytes increased somewhat following the decrease in diatoms, although the slight direct pH effect prevented the bloom formation seen in the pulse treatment. Similar mechanisms (i.e., differential responses to acid coupled with competitive release) are proposed to explain compensatory dynamics between *Daphnia catawba* and *Daphnia dubia* during a whole-lake acidification (Fischer 1997).

The compensatory dynamics within the large herbivore functional group were a result of negative co-

TABLE 5. (a) Model coefficients and diagnostics for the zooplankton model fitted to the three dominant large herbivores and (b) model coefficients and diagnostics for the covariate in the zooplankton model that was directly affected by acidity.

Species	Coefficients							
	Daphnia galeata	*Holopedium gibberum*	*Sida crystallina*	pH	Treatment × pH	Small herbivores	Large phytoplankton	Temperature
a) Zooplankton model								
Daphnia galeata	0.7609			0.2914	−0.1802			
Holopedium gibberum	−0.4080	0.6444		0.3069	−0.2048	0.3254		
Sida crystallina			0.6886	0.0560	0.0281		−0.3575	
b) Covariate in zooplankton model								
Large phytoplankton				0.1313	0.0366	0.3253		0.2555

Note: For part (b), the model is the best-fitting subset model which originally contained *D. galeata*, *H. gibberum*, and *S. crystallina*, other large herbivores, small herbivores, temperature, pH, and treatment × pH as predictor variables.

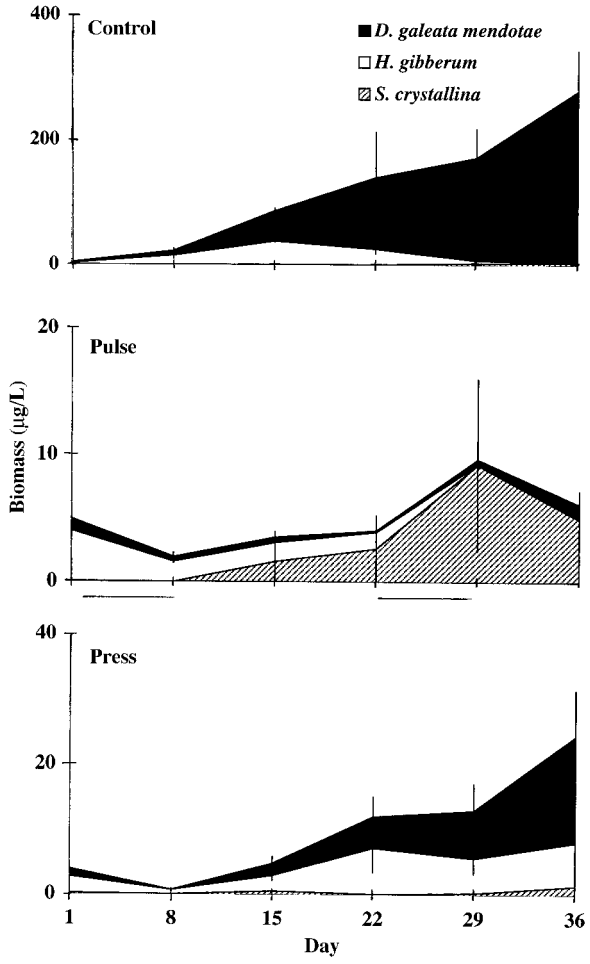

FIG. 7. Mean (± 1 SE) *Daphnia galeata mendotae*, *Holopedium gibberum*, and *Sida crystallina* biomass in the control, pulse, and press treatments over time. Note difference in scale on *y*-axis. Bars under the *x*-axis represent the portions of the pulse treatment where the pH was low.

variance between *Sida crystallina* and the other large herbivores. This is a surprising result because we expect that compensatory dynamics occur among strongly interacting taxa. The autoregressive model suggests that *S. crystallina* does not interact with either of the other dominant large herbivores, and we hypothesize that its slight but nonsignificant increase in the pulse treatment during the second pulse of low pH is due to an indirect positive effect of acidity operating via the large phytoplankton. This increase is highest in the replicate which had the lowest biovolume of large phytoplankton (J. L. Klug, *unpublished data*). This result shows that compensatory dynamics, measured by negative covariances among species, do not require negative interactions among species. The hypothesized competitive interaction between *D. galeata mendotae* and *H. gibberum* suggests a potential for strong compensatory dynamics between these two species following perturbation. However, the potential compensatory dynamics between *D. galeata mendotae* and *H. gibberum* were not realized because both species had strong negative responses to the reductions in pH. The model suggests that the negative effect of acidity was greater than the competitive release experienced by *H. gibberum* following the decline of *D. galeata mendotae*.

There is an important distinction to make between the two examples of compensatory dynamics described above. The phytoplankton example is a case of compensatory dynamics among functional groups whereas the zooplankton example is a case of compensatory dynamics within a functional group. Compensatory dynamics among functional groups may lead to maintenance of total community function (e.g., primary production); nonetheless, more specific functions may be lost. Functional groups perform different roles in a community, and the replacement of one functional group by another will likely change processes such as nutrient cycling and food web interactions. For example, replacement of diatoms with chlorophytes will alter cycling of silica because diatoms require silica and chlorophytes do not. In contrast, compensatory dy-

TABLE 5. Extended.

R^2	Variance-covariance matrix of error terms: *D. galeata*	*H. gibberum*	*S. crystallina*	Autocorrelation of error terms
0.4638	0.2823	0.0296	−0.0212	−0.4924
0.6492	0.0296	0.1390	−0.0223	0.1337
0.3245	−0.0212	−0.0223	0.1051	−0.0222
0.7111				0.2341

namics within functional groups should lessen the chance that particular functions will be interrupted. Although taxa within a functional group are not equal, by definition they are similar and can partially or wholly perform the same role in the community.

The phytoplankton community showed different patterns in the pulse and press treatments whereas zooplankton dynamics in the two acidified treatments were similar (Table 1). This contrast may be due in part to differences in generation time between phytoplankton and zooplankton. The periods of high pH in the pulse treatment may not have been long enough to allow acid-sensitive zooplankton species to recover. In addition, colonization from other lakes or resting stages may be important in community recovery following perturbation. The spatial and temporal extent of our experiment did not allow these processes to occur.

The phytoplankton community in our experiment appears less sensitive to decreased pH than the zooplankton community. Zooplankton biomass decreased greatly in both acidified treatments, whereas at the end of the experiment, phytoplankton biovolume was higher in the acidified treatments than in the control treatment (Fig. 2). A whole-lake acidification of Little Rock Lake in Wisconsin showed a similar pattern of declining crustacean zooplankton biomass and constant phytoplankton biomass (Brezonik et al. 1993). In our study, the proportion of species that responded immediately to a pH decrease was much lower in the phytoplankton than the zooplankton (J. L. Klug, *unpublished analysis*), suggesting that more zooplankton taxa were directly affected by the acidification. In addition, phytoplankton species richness was much higher than zooplankton species richness (27 and 10, respectively). Other studies have suggested that species-rich communities are more resistant to perturbation (McNaughton 1977, Tilman 1996). All else being equal, species-rich communities are more likely to have at least one species tolerant to a given perturbation. Further, phytoplankton have faster growth rates and shorter generation times than zooplankton, and this could enable them to respond more quickly to the pH perturbations imposed during our experiment.

Both species interactions and taxa-specific sensitivity play a large role in determining how communities change in response to perturbations. Previous studies have shown that compensatory dynamics occur in response to a perturbation when there are strong competitive interactions among species (Tilman 1996). The proposed competitive interaction between chlorophytes and diatoms did lead to strong compensatory dynamics in response to perturbation because the stronger competitors (diatoms) were more affected by the perturbation than the weaker competitors (chlorophytes). However, negative interactions among species do not guarantee compensatory dynamics. Autoregression analysis identifies strong negative interactions between *Daphnia galeata mendotae* and *Holopedium gibberum*, yet the potential for compensatory dynamics between these two species was not realized because both were sensitive to reduced pH. Compensatory dynamics among large herbivores in the pulse treatment were driven by a species, *Sida crystallina*, that had been rare at the start of the experiment and increased in all treatments. Our study suggests that the potential for compensatory dynamics is controlled both by the tolerance of the species pool to a particular perturbation and the strength of the interactions between the members of the community. The fraction of the total species pool sensitive to a perturbation depends on both the community and perturbation in question. Therefore, the potential for compensatory dynamics to buffer community response to perturbation is likely to vary widely.

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