

The effects of variable nutrient additions on a pond mesocosm community

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Abstract The effects of nutrient additions on aquatic systems have been frequently studied. Typically, these studies report an increase in algal biomass and a decrease in species diversity in response to nutrient increases. However, it is not clear why comparable aquatic communities respond differently to nutrient additions of similar magnitudes. We tested the effects of the rate and amount of nutrient load on community structure in 760 l mesocosms; treatments manipulated the total amount of nutrients that entered an aquatic system (small versus large load) and the temporal pattern in which these nutrients entered the system (annually, monthly, or weekly). We found that the effects of the loading rate of nutrients were at least as important as the total amount of the nutrients for several response variables. Although these effects were manifested in

several ways, the response to the different rates was most prominent within groups of the primary producers, which showed large shifts in composition and abundance.

Keywords Load · Loading rate · Variability · Ponds · Mesocosms · Primary productivity

Introduction

Limiting nutrients, such as nitrogen and phosphorus, strongly influence the productivity of an ecosystem, which can then affect trophic level complexity and stability, community attributes (e.g., species richness and abundance distribution), and ecosystem functioning (reviewed in Vitousek et al., 1997; Carpenter et al., 1998). The assembly and function of natural communities, as well as the reclamation of damaged systems, can be better understood with knowledge of how nutrient availability can affect community properties (NRC 1992; Vitousek et al., 1997; Carpenter et al., 1998).

Aquatic ecosystems almost invariably exhibit strong and highly variable responses to both natural and experimental manipulation in nutrient loading (Smith 1998; Dodson et al., 2000). For example, Leibold et al. (1997) analyzed published experiments that manipulated nutrient levels and found that once

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standardized to account for treatment differences among studies, the primary producers and the herbivores did not respond consistently; sometimes, producers had a much stronger response, while herbivores responded more other times. Furthermore, Schindler et al. (1978) found that the total nutrient load explained about half the range of productivity in a number of lakes, but the variance of productivity in similar systems remained large once nutrient effects were statistically removed.

In addition to a lack of consistency between study results, empirical studies sometimes do not support predictions of theoretical models. A metaanalysis (Brett & Goldman, 1997) showed that when systems varying in the number of trophic levels were subjected to increased productivity, the models of Oksanen et al. (1981; Oksanen & Oksanen, 2000) did not successfully predict the response of each level. Furthermore, models that attribute phytoplankton abundance and composition solely to variation in nutrient availability (e.g., Tilman, 1977) were incompatible with patterns observed in natural systems (Leibold, 1997).

In light of inconsistent findings on effects of nutrients on aquatic ecosystems, it may be necessary to recognize that the influence of nutrients is more complex than initially thought. Aquatic systems, in particular, are thought to be especially sensitive to environmental variability (Steele, 1985). For example, the phytoplankton diversity of lakes may decline with decreased frequency of wind disturbance (Sommer, 1993), and plankton communities can be influenced by different light regimes (Floder et al., 2002; Floder & Burns, 2005). Nutrients neither rarely enter an aquatic system at a constant rate during the year, nor do they show the same annual pattern over time (e.g., Soranno et al., 1996; Ostfeld & Keesing, 2000). Theoretical models (e.g., Harris, 1980), laboratory studies (e.g., Sommer, 1985; Grover, 1997; Merriman & Kirk, 2000), and a few field studies (e.g., Hann & Goldsborough, 1997; McDougal et al., 1997; Beisner, 2001) have explored effects of nutrient variability, but these studies have focused on simple ecosystems with few species and trophic levels. It remains to be seen what the relative effects of total nutrient load versus the temporal pattern of this loading (nutrient loading rate) will be to community structure and ecosystem functioning in a more realistic and complex ecosystem.

We conducted a mesocosm experiment designed to mimic natural wetland communities by examining how aquatic communities responded to varied total nutrient load, the nutrient loading rate, and their interaction. In a survey of natural wetlands in Northwestern Pennsylvania, we found that concentrations and variability of nitrogen and phosphorus (the primary limiting nutrients in these ecosystems) differed among wetlands; nutrient inputs ranged from relatively constant throughout the year to highly variable over time. Because theory, models, and results from previous studies have indicated responses at several levels of taxonomic resolution, we evaluated this experiment at three levels to identify any general ecological relationships: the effects of nutrient variability among trophic levels, functional groups within trophic levels, and species within trophic levels.

Material and methods

Experimental design

Our mesocosm experiment, which was conducted from 1 June to 15 October 1999 at the University of Pittsburgh's Pymatuning Laboratory of Ecology (Pennsylvania), examined effects of total nutrient load (μg of nutrient/l) and loading rate on experimental aquatic ecosystems. Twenty-four replicate mesocosms (760-l stock tanks) were filled with 5 cm of top soil and nutrient-poor well water. The mesocosms were tested for initial nutrient levels and ratios ($\sim 110 \mu\text{g/l}$ N:20 $\mu\text{g/l}$ P), and each mesocosm received enough nutrients to raise the N:P ratio to 30:1, so that the ecosystems were not co-limited. Each mesocosm was inoculated with phytoplankton, periphyton, macrophytes, zooplankton, benthic invertebrates, and associated microbes collected from 10 ponds. Zooplankton were collected using a 64- μm plankton net and distributed into each mesocosm. Periphyton scraped from substrate found in 10 ponds was added to each mesocosm. Floating filamentous algae (primarily *Cladophora* spp. and *Oedogonium* spp.), submerged macroalgae (*Chara* sp.), and common vascular macrophytes (*Potamogeton crispus*, *Ceratophyllum demersum*, *Elodea canadensis*) were collected, cleaned, and added in small amounts (~ 35 g dry weight) to each mesocosm; macrophytes

were rooted by hand, which resulted in no noticeable plant mortality. Common detritivorous, herbivorous, and predaceous macroinvertebrates (pulmonate snails (Planorbellidae and Physidae), and several groups of insects, including hemipterans (Belostomidae, Corixidae, Naucoridae, and Notonectidae), coleopterans (Dytiscidae), and odonates (Libellulidae, Aeshnidae, Coenagrionidae and Lestidae)), were collected from various ponds and added to each mesocosm in identical numbers (the specific number for each group varied depending on their relative size and how many we could catch).

Most species (>90% by biomass) that were inoculated into these mesocosms have generation times on the order of days to months. In addition, although they did not go through more than one generation over the course of the experiment, the macrophytes and several of the animals have highly variable growth rates that respond rapidly to variation in resource availability. Thus, we feel that the time span of the experiment (a single season) allowed us to capture much of the variation in community and ecosystem responses that resulted from the experimental manipulation. The mesocosms were left uncovered, permitting immigration and emigration of many species, including many of those macroinvertebrates that we inoculated into the experiments, as well as anuran larvae (Hylidae). Similar methods have been shown to create communities that resemble natural ponds within a relatively short time span (Leibold & Wilbur, 1992, J. M. Chase, unpublished data).

The experiment was a 2×3 factorial design that manipulated the total nutrient load for a single growing season (2 levels) and the nutrient loading rate (3 levels). Each treatment was replicated four times. We used nitrogen (NaNO_3) and phosphorus

(NaH_2PO_4) for the experimental nutrient addition; these nutrients have been found to be the most limiting resources in aquatic systems (Lampert et al., 1997; Wetzel, 2001). Two weeks after the community was inoculated, we added nutrients at three rates: (a) a single large addition; (b) 4 monthly additions; and (c) 16 weekly additions. The total amount of nutrients was kept equal across each of these treatments; so only the temporal pattern of the nutrient addition differed between systems. We repeated these three different rate treatments at two levels of total nutrient load: 75 $\mu\text{g/l}$ P:2,250 $\mu\text{g/l}$ N (hereafter “small”) and 200 $\mu\text{g/l}$ P:6,000 $\mu\text{g/l}$ N (hereafter “large”) (Table 1). These nutrient regimes were chosen such that the weekly pulses (4.69 or 12.5 $\mu\text{g/l}$ P every 7 days for small or large total loads, respectively) spanned a range that is characteristic of a precipitation event in a eutrophic system of the Pymatuning area (Butzler, 2002). The large nutrient pulses (a single pulse of 75 or 200 $\mu\text{g/l}$ P for small or large loads, respectively) are representative of an extreme precipitation event in a eutrophic system of the Pymatuning area. The N:P ratio was maintained in all treatments at 30:1 to ensure that P would be the limiting nutrient, as is typical for most freshwater ecosystems (Wetzel, 2001).

Sampling methods

We sampled each mesocosm destructively at the conclusion of the experiment (Oct. 15). Phytoplankton were sampled with an integrated tube sampler, and periphyton were collected from a 100 cm^2 section of artificial substrates (plastic flagging) suspended from the side of the mesocosm for this purpose. Both groups of algae were analyzed for chlorophyll-*a* concentration using a Turner[®] fluorimeter following

Table 1 Values for N and P used to analyze the effect of total nutrient load and nutrient loading rate on a model pond community

Total nutrient load ^a		Nutrient loading rate ^b		
		Single pulse/season (annual)	Four pulses/season (monthly)	Sixteen pulses/season (weekly)
SMALL	75 $\mu\text{g/l}$ P	75 $\mu\text{g/l}$ P	18.75 $\mu\text{g/l}$ P	4.69 $\mu\text{g/l}$ P
	2,250 $\mu\text{g/l}$ N	2,250 $\mu\text{g/l}$ N	562.5 $\mu\text{g/l}$ N	140.63 $\mu\text{g/l}$ N
LARGE	200 $\mu\text{g/l}$ P	200 $\mu\text{g/l}$ P	50 $\mu\text{g/l}$ P	12.5 $\mu\text{g/l}$ P
	6,000 $\mu\text{g/l}$ N	6,000 $\mu\text{g/l}$ N	1,500 $\mu\text{g/l}$ N	375 $\mu\text{g/l}$ N

Notes: ^a Total is the nutrient concentration or the mass of nutrients added to a mesocosm per season. ^b Loading rate is the mass of nutrients added to the experimental unit with each pulse

methods described in Clesceri (1998). The biomass of the remaining primary producers in each tank was determined by drying and weighing the filamentous algae and macrophytes.

Zooplankton samples were collected from the water column using a 1-l integrated tube sampler. Five samples taken from within each mesocosm were poured through a 64- μ m mesh net to concentrate the 5 l of sampled water into \sim 50 ml and were preserved in Acid Lugol's solution for later analysis. We subsampled 5–25 ml of this sample and counted at least 200 individuals per sample before scanning the entire sample for rare species. Individuals were identified to species (where possible) using taxonomic keys of Balcer et al. (1984) and Pennak (1989). We measured 20 individuals (or the total number observed if less than 20) of each species per sample and estimated biomass using species-specific, length–weight regressions (McCauley, 1984, Lawrence et al., 1987).

We surveyed macroinvertebrate and anuran larval densities in mesocosms from a quarter subsection of the mesocosm. We then scanned the entire mesocosm search for anurans and larger species of rarer invertebrate species. This method correlated well with other methods such as sweeping a net through each mesocosm, and the various methods were standardized by destructively sampling a subset of the mesocosms, and identifying, measuring, and enumerating individuals. We converted these censuses to biomass using length–weight regressions or species-specific weights.

Data analysis

The biomass data was natural log-transformed to correct for non-normality or heteroscedasticity of the error terms. We employed three sets of analyses to examine the effects of variable nutrient addition on biomass. A factorial multivariate analysis (MANOVA) was conducted on the primary producers, herbivores, and predators to test for overall treatment differences on trophic levels. Then, we separated each trophic level (producer, herbivore, and predator) into the following functional subgroups: producers—filamentous algae (including periphyton), phytoplankton and vascular macrophytes; herbivores—pelagic herbivores (those that swim and forage in the water column, e.g., zooplankton) and benthic herbivores (those that

primarily remain on the substrate and forage there, e.g., snails and tadpoles); predators—pelagic predators (e.g., Notonectidae and Pleidae) and benthic predators (e.g., dragonfly larvae). MANOVAs were used to detect significant treatment differences within trophic levels. If the MANOVA results were significant, ANOVAs were then used within each subgroup to determine univariate responses. We further analyzed the responses of each individual species, where species information could be ascertained, to the treatments; again, if the MANOVA results were significant, ANOVAs were then performed at the species level. Because there were three loading rates, we used Tukey's *HSD* to test for significant pairwise differences.

Results

We found that community response to nutrient addition varied with taxonomic resolution. At both a low and high taxonomic resolution, there was no response to nutrient variability. When the community was grouped by trophic level, we found no significant response of total nutrient load (MANOVA; $F_{3,16} = 0.76$, $P = 0.53$), loading rate (MANOVA; $F_{6,32} = 1.37$, $P = 0.26$), the interaction (MANOVA; $F_{6,32} = 1.09$, $P = 0.39$). Moreover, individual species within the functional group did not respond to variability in nutrient addition (Table 2). The significant values of the primary producers obtained here are spurious because they are driven solely by the species “filamentous algae,” which was not broken down into true species because of logistical constraints. Filamentous algae was therefore resolved to be a functional group, and discussed as such.

In contrast, when the community was examined by functional groups, we found responses to the nutrient addition. Multivariate analyses for total nutrient load and loading rate were significant but the interaction between rate and total was not (Fig. 1, Table 3). Univariate results showed that the biomass of filamentous algae increased with an increase in total nutrient load, whereas the biomass of macrophytes decreased (Fig. 1A, B). Filamentous algae biomass was higher with the weekly additions than with the single addition (Tukey's *HSD*; $P < 0.05$), whereas macrophyte biomass was higher with a single addition and lower with the weekly additions (Tukey's *HSD*; $P < 0.05$). The phytoplankton response to the

Table 2 MANOVA results when community was broken down by species

Factor	df	F	P
Multivariate response			
<i>Primary producers</i>			
Rate	10, 28	2.16	0.05
Total	5, 14	6.35	<0.01
Rate × total	10, 28	0.21	0.99
<i>Herbivores</i>			
Rate	26, 12	0.83	0.67
Total	13, 6	1.08	0.49
Rate × total	26, 12	0.68	0.81
<i>Predators</i>			
Rate	16, 22	1.22	0.33
Total	8, 11	0.86	0.58
Rate × total	16, 22	0.53	0.90

Bold numbers denote significant responses

nutrient addition showed a marginally significant increase in biomass with an increase in total nutrient load (Fig. 1A, B). Biomass of pelagic herbivores decreased with increased nutrient load and decreased with a more frequent nutrient addition (Tukey’s *HSD*; $P = 0.05$) (Fig. 1C, D). Differences registered for benthic herbivores were not statistically significant. Predator functional groups were unaffected by the nutrient treatments (Fig. 1E, F).

Discussion

Environmental variability has long been recognized as an important factor influencing community structure. For example, Hutchinson’s (1961) “Paradox of the plankton” suggested that variability of environmental conditions within the water column can allow

Fig. 1 The response of the functional groups within each trophic level to the nutrient treatments. Functional groups were as follows: filamentous algae, phytoplankton, and macrophytes; pelagic herbivores and benthic herbivores; pelagic predators and benthic predators. Response was measured as standing crop biomass (g) Figs. 1A and B represent primary producer responses to three different loading rates (single, monthly, or weekly) for SMALL total nutrient load and LARGE total nutrient load, respectively. Figures 1C and D represent herbivore responses to loading rates (single, monthly, or weekly) for SMALL and LARGE total nutrient load, respectively. Figures 1E and F represent predator responses to nutrient loading rates (single, monthly, or weekly) for SMALL and LARGE total nutrient load, respectively

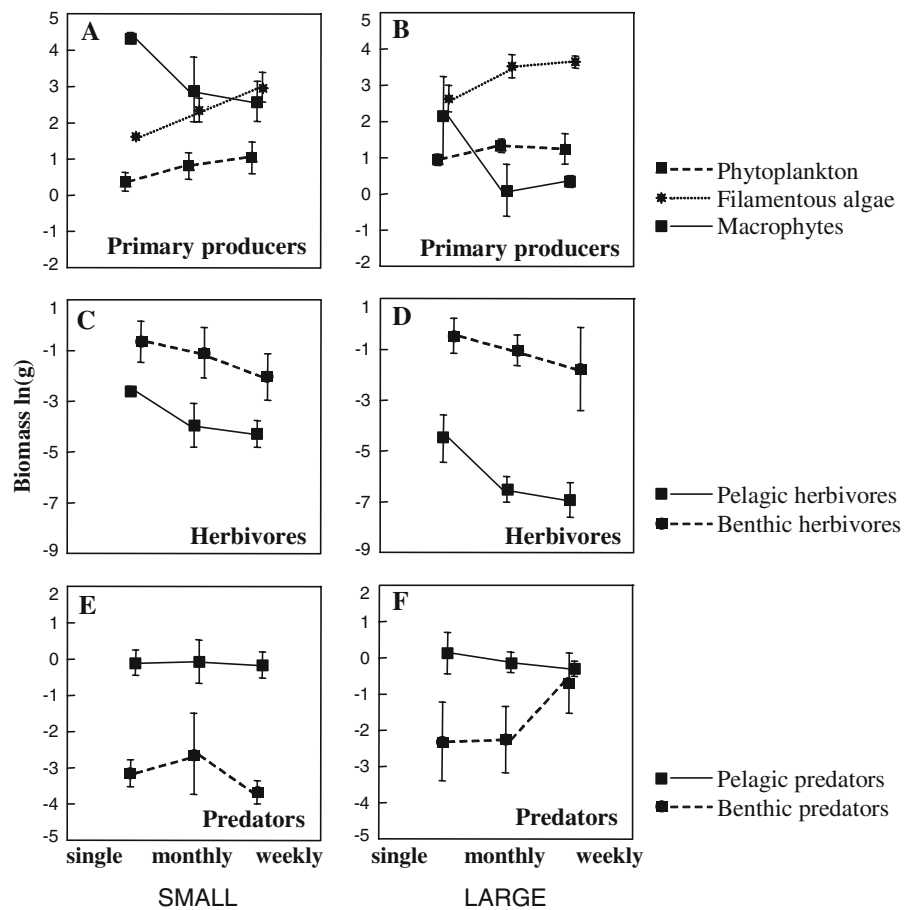


Table 3 [M]ANOVA results of mesocosm experiment when the community was broken down by function. See text for functional groupings

	Factor	df	<i>F</i>	<i>P</i>
<i>Primary producers</i>				
Multivariate response				
	Rate	6, 32	4.23	<0.01
	Total	3, 16	15.12	<0.01
	Rate × total	6, 32	0.27	0.95
Univariate responses (rate and total)				
Phytoplankton	Rate	2	1.77	0.20
	Total	1	3.88	0.06
Filamentous algae	Rate	2	6.11	<0.01
	Total	1	11.20	<0.01
Macrophytes	Rate	2	4.38	0.03
	Total	1	18.92	<0.01
<i>Herbivores</i>				
Multivariate responses				
	Rate	4, 34	3.47	0.02
	Total	2, 17	13.68	<0.01
	Rate × total	4, 34	0.12	0.97
Univariate responses (rate and total)				
Pelagic herbivores	Rate	2	17.91	<0.01
	Total	1	3.57	0.05
Benthic herbivores	Rate	2	1.55	0.23
	Total	1	0.07	0.79
<i>Predators</i>				
Multivariate responses				
	Rate	4, 34	0.21	0.93
	Total	2, 17	2.98	0.08
	Rate × total	4, 34	0.96	0.44

Bold numbers denote significant responses

coexistence of many algal species. Subsequent theoretical and empirical work showed how variability in environmental conditions influences interactions and coexistence among resource competitors (reviewed in Chesson & Huntly, 1997; Chesson, 2000). However, these studies have rarely considered multi-trophic level interactions. Most studies that consider the responses of food web structure to different environmental conditions have only considered the average conditions of the environment (e.g., Oksanen et al., 1981; Leibold et al., 1997). In contrast, our experimental results suggest that nutrient loading rate can play an important role in determining patterns in a complex community consisting of multiple species, functional groups, and trophic levels. In fact, our results are surprising in that we found that the effect of rate of nutrient addition was sometimes greater than that of the total

amount of nutrients on patterns of biomass and community composition.

The strongest responses to the nutrient addition were seen when the community was evaluated by its constituent functional groups (Fig. 1), and within these, at the primary producer level. First, algae (filamentous and phytoplankton) increased and macrophytes decreased in biomass in response to the total nutrient load. Second, with more frequent but less intense nutrient additions, species composition shifted from macrophytes to filamentous algae. While our study did not allow us to examine the mechanisms behind these results, we suspect that these outcomes could have been the result of the faster uptake rate of suspended nutrients by algae, or by light limitation of macrophytes caused by the increased volume of filamentous algal mats. These two functional groups have very different nutrient utilization strategies

(reviewed in Wetzel, 2001). Algae can absorb nutrients in the water column at a much faster rate than macrophytes and can more efficiently store particular nutrients for later use. Because vascular macrophytes used in our study are rooted, they obtain the majority of their nutrient requirements from the sediment. Thus, a single pulse of nutrients might have favored macrophyte growth because the nutrients would have remained in the water column for only a short period, quickly falling to the sediment. Alternatively, periodic replenishment of nutrients in the water column might have favored algal growth because of more consistent nutrient availability through time. The consistently high nutrient levels in the water column that resulted from weekly nutrient additions could also have reduced the intensity of competition between filamentous algae and phytoplankton, which have been shown to be superior competitors (Sommer, 1989; Graham & Wilcox, 2000). Because filamentous algae mats float on the surface of the water and have been measured to reduce light by 60–90% (Butzler, 2002), the established filamentous algae mats probably occluded light from reaching the sediments, potentially resulting in competitive exclusion of macrophytes.

Pelagic herbivores (primarily zooplankton) decreased in biomass with increasing total nutrients. Nutrient availability and disturbance can influence phytoplankton community characteristics, such as plankton strategy, size, and composition (Reynolds, 1984), which can influence zooplankton herbivory (Reynolds, 1997; Brett et al., 2000). Although phytoplankton biomass did not decrease, a shift in species composition could have resulted in unpalatable, inedible, or nutritionally deficient phytoplankton, causing the observed decrease in herbivore biomass.

Several examples are present in similar aquatic systems persisting in two different states, one in clear water and another in high turbidity. These states are usually characterized by an abundance of macrophytes and algal species, respectively (e.g., Blindow et al., 1993; Korner, 2001). While primary producers are tightly coupled with resources (Wetzel, 2001), the occurrence of a particular state cannot be predicted by nutrient load alone, as both states can be achieved within a certain range of nutrient levels (Scheffer, 1989), suggesting that additional factors may determine and maintain the state of a system. Our study suggests that not only is nutrient loading important, but the temporal pattern of these additions may also

influence the abundance and composition of the primary producers. Our study also suggests that there may be additional effects of nutrient variability at the higher trophic levels, as illustrated by the response of the pelagic herbivores. Few studies have examined the role of higher trophic levels in driving the system (but see Janse et al., 1998) and their response to the alternative states (but see Meerhoff et al., 2003).

We found no effect of either nutrient loading rate or total load when the community was analyzed by trophic levels. When considering the many interactions in a food web that can be affected by an increase of nutrients (e.g., predator–prey dynamics, coexistence of species), it is surprising that no effects were manifested at any of the trophic levels. In fact, the lack of support for any trophic interaction contests the predictions of many theoretical models (e.g., Oksanen et al., 1981) and the results of previous studies (e.g., Leibold et al., 1997). However, many of the classic models and theories that predict an effect of increased productivity on trophic levels (e.g., Oksanen et al., 1981; DeAngelis, 1992), considered the entire trophic level as being homogenous, thereby ignoring importance differences among species. Theoretical models that allow for heterogeneity within trophic levels (e.g., Abrams, 1993; Chase, 1999) have been suggested to better explain some of the variation in patterns observed in nature (Leibold et al., 1997; Chase et al., 2000). Also, many studies ignore large components of the community (Micheli, 1999). For example, many studies focus only on the pelagic community, ignoring the potential role of the benthos in nutrient acquisition.

In conclusion, we suggest that to determine the effects of important abiotic factors, such as nutrient addition, rainfall, and temperature, it is important to explore not only the mean value, but also rate, magnitude, and timing of the occurrence. It has been previously suggested that nutrient variability could affect the outcome of resource competition (Grover, 1997; Merriman & Kirk, 2000). Our study provides evidence that nutrient variability can also affect community composition in more complex food webs.

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