THE ROLE OF NUTRIENT VARIABILITY IN AQUATIC ECOSYSTEMS

by

Julia M. Butzler

B.S., University of Pittsburgh, 1996

Submitted to the Graduate Faculty of

Arts and Sciences in partial fulfillment

of the requirements for the degree of

Masters of Science

University of Pittsburgh

2002

UNIVERSITY OF PITTSBURGH

FACULTY OF ARTS AND SCIENCES

This dissertation was presented

by

Julia M. Butzler

It was defended on

November 28, 2001

and approved by

Thesis Advisor: Dr. Jonathan M. Chase, Assistant Professor, Department of Biological Sciences

Dr. Ricky Relyea, Assistant Professor, Department of Biological Sciences

Dr. Susan Kalisz, Professor, Department of Biological Sciences

THE ROLE OF NUTRIENT VARIABILITY IN AQUATIC ECOSYSTEMS

Julia M. Butzler, M.S.

University of Pittsburgh, 2002

The effects of nutrient input into aquatic systems has been studied frequently; typically, these studies report an increase in algal biomass and a decrease in species diversity in response to an increase of nutrients. However, it is not clear why similar aquatic communities will respond differently to nutrient additions of similar magnitudes, resulting in alternative communities. Because variance in natural ecosystems is pervasive, perhaps it is this variability that helps determine the final community. I proposed that the total amount of nutrient input and the variability of nutrient input would affect the abundances and composition of species. A natural survey was conducted to measure the variable levels of nutrients in several aquatic systems. Experimental ponds were used to test the effects of variable rates and timing of nutrient inputs upon an aquatic community; experimental treatments manipulated the total amount of nutrient input (high v. low), the rate of nutrient input (annually, monthly or weekly), the timing of the nutrient input (early v. mid- season), and the trophic status at which these treatments were imposed (mesotrophic v. eutrophic). The effects of the variability of nutrient input was at least as important as the total amount of the nutrient input. There were large impacts upon species diversity, abundances and composition. Although these effects were manifested in many trophic groups, the response to the variability was most strikingly found within the primary producers, which showed large shifts in abundance and composition.

ACKNOWLEDGMENTS

Endless thanks to Dr. Jonathan Chase for guidance, independence, and friendship.

Thanks to Dr. Susan Kalisz and Dr. Ricky Relyea for support and direction.

Many thanks to Emily Bond (partner in crime), Dr. Tiffany Knight (for ponds in March and thousands of *Trillium grandiflorum*), and Janette Steets; the Second Floor Girls Club was my link to sanity (or insanity?).

Special thanks to Mom and Daddy, for (not so) silently suffering through my idiosyncratic ways; Mo, Steve, Rachel, Kathy, Todd and Nick, and Tom, Kelly, Jacob, Emma and the little one, for being family; Pepper, Herky, Coco, Charlie, Jack and Harry, for company; Todd and Mike, the clean-up crew.

And last, David, my thanks and so much more.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1: The effects of nutrient input variance upon aquatic communities

Introduction

Changes in nutrient regimes can have drastic effects. Limiting nutrients, such as nitrogen and phosphorus, play a large role in determining the productivity of a ecosystem, which in turn can affect the number of trophic levels in a food web and it's stability (Oksanen et al. 1981, Abrams 1993, Kaunzinger and Morin 1998), the abundance and composition of the species making up the community (Tilman 1982, Abrams 1995, Dodson et al. 2000), and ecosystem functioning (Tilman et al. 1997, Hooper and Vitousek 1998). Because changes in the availability of nutrients can affect community properties, it is important to understand the role of nutrients within ecosystems to describe how natural communities assemble, interact and function, as well as to apply this knowledge to address the cause, effect and the reclamation of damaged ecosystems (NRC 1992, Vitousek et al. 1997, Carpenter et al. 1998).

The effects that nutrient addition will have on an aquatic ecosystem remain unclear, despite many experimental manipulations. There is a lack of consistency in the experimental studies performed that explore how nutrient dynamics will affect aquatic communities (e.g. Gabor et al. 1994, Murkin et al. 1994). Leibold et al. (1997) analyzed data from a number of published studies that manipulated total nutrient input and found that, once standardized to account for treatment differences between studies, the disparity between studies was large. And while Schindler (1978) found that total nutrient input explained about half of the range of productivity in lakes, after statistically removing nutrient effects and limiting the analysis to include similar systems, the range of productivity remained large (Schindler et al. 1978). This emphasizes the unpredictability of results from studies that manipulate or monitor resources, and suggests that factors in addition to total nutrient addition may be important.

In addition to a lack of consistency between study results, empirical studies oftentimes do not support the predictions of theoretical models. A recent meta-analysis (Brett and Goldman 1997) showed that when systems varying in the number of trophic levels were subjected to increased productivity, the models of Oksanen and colleagues (Oksanen et al. 1981, Oksanen and Oksanen 2000) did not successfully predict the response of each trophic level. Furthermore, models that attribute phytoplankton abundance and composition solely to nutrient processes have been found to be incompatible with patterns in natural systems (Leibold 1997).

One feature of ecosystems that has remained relatively unexplored is the inherent variability lost by averaging values or by only presenting a single sample. Nutrients rarely enter an aquatic system at a constant rate during the year (Brenner et al. 1996), nor do they show the same pattern on a year-to-year basis (e.g. Brenner et al. 1999, Ostfeld and Keesing 2000). The land surrounding aquatic systems often varies in usage (e.g. agricultural, industrial, forested), history (e.g. glaciated, nonglaciated), and topography (e.g. flat, mountainous). The shape and function of land can directly affect the amount, rate and timing of nutrients entering an aquatic system (Brenner et al. 1996, Soranno et al. 1996). Thus, variability in the total input, through the rate and the timing of nutrient input, are commonplace in aquatic ecosystems. It has been well documented that varying magnitudes of nutrient loading can affect aquatic ecosystems (Rader and Richardson 1992, Koelmans et al. 2001). Variability of the rate and timing could also have large effects upon the structure and the function of the ecosystem, as indicated by theoretical models (Harris 1980, Ruel and Ayres 1999) and laboratory studies done on simple systems (Sommer 1985, Grover 1997, Merriman and Kirk 2000). These laboratory studies and the few field studies that have explored the effects of nutrient variability to date have focused on competition within a trophic level (e.g. Hann and Goldsborough 1997, McDougal et al. 1997, see

also Grover 1997, Lampert and Sommer 1997). But what is unknown is the response to nutrient variability *between* trophic levels. Because aquatic communities are complex systems that are often comprised of multiple trophic levels, and populations can be regulated by inter-trophic level interactions (e.g. bottom-up and top-down effects) as well as intra-trophic level interactions (e.g. competition), it is important to understand the responses at both levels.

In this study, I asked whether total nutrient input, variance of nutrient input, and their interaction were important in aquatic communities. I first documented the degree to which natural systems varied in nutrient levels by conducting a natural survey of aquatic systems. Next, I conducted a mesocosm experiment designed to explicitly look at the consequences of nutrient input variability. Specifically, I looked at the effects of three nutrient addition regimes (one large addition, four monthly additions and sixteen weekly additions), crossed with two total nutrient loads (low and high), on a multi-trophic level aquatic community. I examined the effects of nutrient variability *within* a trophic level, as well as *among* multiple trophic levels. The response to the manipulations was measured through effects at the community level (composition and abundance of species).

Methods

Natural survey. A natural survey was conducted to examine the degree of variability of nutrient availability in aquatic systems in the Pymatuning Watershed of Northwestern Pennsylvania, USA. Seven aquatic systems located within a five mile radius were sampled bi-weekly from mid-March to September of 2000. These aquatic systems were located in areas that varied in land use and topography, ranging from highly degraded farm land to protected state game lands. Because these systems varied in many ways (size, depth, canopy cover, temperature, etc), the nutrient variability should reflect the natural range found in aquatic

habitats in this landscape. Water samples were taken from the middle of the water column and analyzed in the lab for total nitrogen (TN) and total phosphorus (TP) (using standard methods; Clesceri 1998).

Experimental design. A mesocosm experiment manipulated the total nutrient input and variance of nutrient input in experimental aquatic ecosystems. The experiment was conducted from 1 June 1999 to 15 October 1999 at the Pymatuning Laboratory of Ecology, Pennsylvania. I chose to use mesocosms because replicated experimental ecosystems could easily be created. Performing a mesocosm experiment also allowed me to evaluate the effects of nutrient input with all influences of history removed.

Twenty-four replicate mesocosms (760-L stock tanks) were filled with two inches of topsoil and nutrient-poor well water. Each mesocosm was inoculated with algae, zooplankton, macrophytes, invertebrates, and associated micro organisms (e.g. bacteria), collected from several local aquatic systems that spanned the range of variable nutrient levels found in natural systems. These ecosystems were initiated at low abundances of diverse composition of organisms. Phytoplankton and zooplankton were collected from ten ponds using a 64 μm plankton net; approximately 400 mL of combined phytoplankton was added to each mesocosm five days prior to zooplankton to allow for the establishment of a suitable and sustainable habitat for the zooplankton. Approximately 200 mL of combined concentrated zooplankton was added to each mesocosm. Periphyton was scraped from substrate found in ten ponds; approximately 50 mL of combined periphyton was added to each mesocosm. Floating filamentous algae (primarily *Cladophora* spp. and *Oedogonium* spp.) and common macrophytes (*Chara* sp., *Potomageton crispus*, *Cerataphyllum* sp., *Elodea* sp.) were collected and cleaned, and small amounts (approximately five grams) of each were added to every mesocosm. Common detritivorous,

herbivorous, and predaceous macro invertebrates (*Helisoma trivolovis*=12, *Physella gyrina*=15, *Gyrallus* sp.=5, Corixidae=7, *Notonecta* sp.=5, Naucoridae=3, *Belostoma* sp.=4, and several species of larval beetles (Hydrophilidae=3 and Dytiscidae=4), larval dragonflies (Libellulidae=3 and Aeshnidae=3) and larval damselflies (Coenagrionidae=3 and Lestidae=3), were collected from various ponds and added to mesocosms. The community in each replicated mesocosm assembled for two weeks. Most of the species (>90% by biomass) that were inoculated have short generation times (2 weeks to a month) that allowed population growth, or response time (days) that allowed an increase in biomass, in response to the experimental treatments within a season. The mesocosms were left uncovered, permitting immigration and emigration of many species, including Corixidae, *Notonecta* sp., *Belastoma* sp., *Chaoborus* sp., beetles, dragonflies and damselflies. Similar methods have been shown to create communities that resemble natural ponds (Leibold and Wilbur 1993, J. M. Chase, unpublished data).

The experiment was a 2 x 3 completely random factorial design manipulating the total nutrient input (2 levels) and the nutrient input rate (variance) (3 levels). Each treatment was replicated 4 times. Nutrients for the experimental treatments were nitrogen (added in the form of $NaNO_3$) and phosphorus (added in the form of NaH_2PO_4), which have been found to be the most limiting nutrients in aquatic systems (Lampert and Sommer 1997, Wetzel 2001). The experimental treatments were as follows: a single large nutrient addition, 4 smaller monthly additions, or 16 weekly additions (while maintaining the same total amount of nutrients); these rates of nutrient addition simulated a gradient of variability, ranging from nutrient levels that vary greatly through the season (single addition) to smaller, more consistent nutrient levels (weekly additions). The three rate treatments were conducted at two levels of total nutrient input: 75 μg/L P: 2250 μg/L N (low) and 200 μg/L P: 6000 μg/L N (high). The mesocosms

were tested for initial nutrient levels and ratios (approximately 110 μg/L N: 20 μg/L P); each mesocosm then received a nutrient addition to bring the N: P ratio up to 30:1, in order to ensure the ecosystems were not co-limited. 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. I sampled the biotic variables in each mesocosm at the conclusion of the experiment. Phytoplankton biomass was analyzed using chlorophyll-*a* analysis (cold ethanol extraction method; using standard methods, Clesceri 1998). Periphyton was collected from artificial substrate that had been placed in the mesocosms at the start of the experiment, and was analyzed using chlorophyll-*a* analysis (Clesceri 1998). Filamentous algae and macrophytes were quantified by visually estimating the percent cover in each mesocosm. Volume-weight regressions created from dried and weighed samples taken from similar mesocosms (see Appendix C) were then applied to obtain an estimate of biomass of primary producers. Zooplankton sub samples were collected from four corners and the center of each mesocosm using a water column tube sampler, concentrated through a 64 μm mesh net and preserved in Lugol's for later enumeration and identification to species (genus when necessary), using taxonomical keys (Balcer et al. 1984, Pennak 1989); biomass was obtained through species-specific length-weight regressions (McCauley 1984, Lawrence et al. 1987). Macro invertebrates were censused visually; sub samples of the macro invertebrates were measured for length. Biomass was obtained using length-weight regressions or species-specific weights (see Appendix C).

Sub sampled biomasses for all organisms were scaled to obtain the biotic response measured in biomass of entire mesocosm. All visual assessments were validated or standardized

by applying census techniques to mesocosms that were established in the same fashion of the experiment. The values obtained were then compared (and subsequently standardized when necessary) to a manual quantification of the organisms in the mesocosm (J. M. Butzler, unpublished data).

Data analysis. I examined the effects of variable total and rate of nutrient input and their interaction on several dependent community variables: composition, abundance and relative abundance of species. The responses were explored within trophic levels and between trophic levels. All statistical analyses presented are from the final sampling date, when the total amount of nutrients added to each mesocosm was the same. The results of the mesocosm experiment were analyzed using analysis of variance ([M]ANOVA). The data was ln-transformed to correct for any non-normality or heteroscedasticity of the error terms.

I conducted three sets of analyses to examine the effects of variable nutrient input. A multivariate analysis of variance (MANOVA) was conducted on primary producers, herbivores and predators to test for overall treatment differences. Then, I separated each trophic level (producer, herbivore, predator) into functional subgroups. These subgroups were as follows: filamentous algae (including periphyton), phytoplankton and macrophytes; pelagic herbivores and benthic herbivores; pelagic predators and benthic predators. Due to constraints of time, the species of algae were not identified; as a result, for the sake of this analysis, filamentous algae was considered a "species" as well as a functional group, and phytoplankton was considered a "species" as well as a functional group. MANOVAs were used to determine whether there were any significant treatment differences within trophic levels. If the MANOVA results were significant, ANOVAs were then performed on each subgroup. Finally, I separated all groups by species. MANOVAs were used to determine whether there were any significant treatment

differences on the species within each trophic level. If the MANOVAs were significant, ANOVAs were then performed. Because there were three input rates, Tukey's *hsd* was used to test for significant pair wise differences.

Results

Natural survey. The natural survey illustrates the temporally variable nutrient levels among these sampled aquatic systems. The variability of available nutrients is manifested in three ways (Figure 1). First, within a single pond, the nutrient levels varied through time. For example, Geneva Pond showed low phosphorus levels in the beginning of the season and higher nutrient levels towards the end of the season. Second, this variation through time differed between ponds. This can be seen by comparing the phosphorus levels of Geneva Pond (where the nutrient levels varied greatly throughout the season) and Wheeler Pond (where the nutrient levels were very consistent throughout the season). Finally, the totaled amount of nutrients available for a season varied between ponds, as can be seen between Wheeler Pond and Geneva Pond.

Mesocosm experiment. The analyses of the trophic levels are reported in Table 1. Overall, there was no significant multivariate effect of the variability of total nutrient input, input rate or the interaction. There were significant effects within trophic levels when species were lumped by functional group (Figure 2, Table 2). The multivariate analysis for the variability of total nutrient input and input rate was significant, but the interaction between rate and total was not. Univariate results showed that both macrophytes and filamentous algae responded significantly to the rate treatment and the total input treatment (Figure 2A, B). The biomass of filamentous algae increased with an increase in total nutrient input, whereas the biomass of macrophytes decreased. In response to the nutrient input rate, filamentous algae was more

abundant with the weekly additions than with the single addition (Tukey's hsd; $P<0.01$), whereas macrophyte biomass was higher with a single addition and lower with the weekly additions (Tukey's hsd; $P=0.03$). Phytoplankton showed a marginally significant increase in biomass with an increase in total nutrient load (Figure 2A, B). The pelagic functional group within the herbivores responded significantly to both rate and total nutrient input (Figure 2C, D). Pelagic herbivores decreased with increased nutrient load and decreased with an increase in nutrient input rate (Tukeys hsd; $P=0.05$). Predator functional groups were unaffected by the nutrient treatments (Figure 2E, F).

When the community was analyzed by individual species (Table 3), multivariate analysis showed that predator and herbivore species were unaffected by variable total and rate of nutrient input, and the interaction. Only the primary producer species showed significant results in response to variable input rate and total nutrient load. Univariate analyses of the primary producer species established that these results are primarily due to grouping filamentous algae as both a functional group and a species, and these results will not be discussed further.

Discussion

Although total load or average input has been the focus of most ecological research to date (e.g. Peterjohn and Correll 1984, Carpenter et al. 1991, Cooke and Prepas 1998), my results suggest that the variance of nutrient input can also play an important role in determining community patterns. In fact, my results are surprising in that we found the effect of variance was often greater than the effect of total nutrient load.

Variation of nutrient input is pervasive in nature and has been measured in aquatic systems (Brenner et al. 1991, Soranno et al. 1996). The natural survey illustrated that, indeed, aquatic ecosystems in the Pymatuning area vary in available nutrient levels at a given moment.

In addition to variability of nutrients between ponds, this survey also illustrates the flux of available nutrients throughout the season.

In my mesocosm experiment, the manipulations of variable nutrient rate and total input failed to produce a response 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 none were manifested at any of the trophic levels. In fact, this lack of trophic interaction contests the predictions of many theoretical models (e.g. Oksanen et al. 1981, DeAngelis 1992, Grover and Holt 1998), and the results of previous studies (e.g. Pace et al. 1999, Ostfeld and Keesing 2000). But many of the classic models and theory that predict an effect of increased productivity on trophic levels (e.g. Oksanen et al. 1981, DeAngelis 1992), consider the entire trophic level as being homogeneous, ignoring importance of species composition. Models that do allow heterogeneity within trophic levels (e.g. Abrams 1993, Chase 1999) have been suggested to better explain 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, it is easy to imagine that a lake study focusing on the pelagic food web could misinterpret trophic interactions by ignoring the energy that "escaped" into the benthos (certainly part of the lake food web)!

When the trophic levels were broken down into functional groups, however, I found strong results at the primary producer level. First, there was a main effect of total nutrients; as the total nutrient load increased, filamentous algae biomass increased and macrophyte biomass decreased. Second, there was an effect of variable rate; filamentous algae biomass was significantly higher with weekly nutrient additions than with a single addition whereas macrophyte biomass was significantly higher with a single nutrient addition than with weekly

additions. That is, with more frequent, but less intense nutrient input, species composition shifted from macrophytes to filamentous algae. Filamentous algae and macrophytes increased and decreased (respectively) in biomass in response to the total nutrient load. There are several examples of similar systems persisting in these two different states (e. g. Hann and Goldsborough 1997, McDougal et al. 1997; see also Lampert and Sommer 1997). Phytoplankton biomass, like filamentous algae, showed a tendency to increase with an increase in total nutrient load. This increase in phytoplankton biomass is likely due simply to the increase in nutrients for reproduction and population growth.

While my study did not allow me to examine the mechanisms behind these results, these outcomes could have been the result of the faster uptake rate by filamentous algae, or by light limitation of macrophytes caused by the increased volume of filamentous algal mats. Indeed, previous studies have shown large responses of primary production, particularly algae and macrophytes, to an input of resources; but these two functional groups have very different utilization methods (reviewed in Wetzel 2001, Kalff 2002). Algae can uptake nutrients in the water column at a much faster rate than macrophytes, allowing for maximum food utilization. Algae can also form reserves of particular nutrients. However, if the supply of nutrients is large enough that the algal cells are overwhelmed, the excess nutrients will precipitate out of the water column to accumulate at the bottom. Because macrophytes are rooted, they obtain the majority of their resource requirements from the sedimented nutrients. Thus, a large single pulse of nutrients might favor macrophyte growth because these nutrients are likely to only remain in the water column for a short period, quickly falling to the sediment; any reserves that the algal cells may have would soon be depleted, limiting growth. Alternatively, periodic replenishment of the nutrients in the water column might favor algal growth because of consistent nutrient

availability.

In conjunction with different utilization strategies, two other factors may facilitate the alternative producer communities in the presence of different resource regimes. First, the consistently high nutrient levels in the water column that result from weekly nutrient additions could alleviate the competitive exclusion of filamentous algae by the edible (by zooplankton) algae, which are supposed to be the superior competitor (Sommer 1989, Graham and Wilcox 2000). Filamentous algae biomass significantly increased with weekly nutrient additions, indicating that the availability of nutrients was likely high enough to support both filamentous algae and phytoplankton. Secondly, because filamentous algae mats float on the surface of the water and have been measured to reduce light by 60 to 90% (J. M. Butzler, unpublished data, also see Hann and Goldsborough 1997), the established filamentous algae mats are likely to occlude light from reaching the sediments, potentially resulting in competitive exclusion of macrophytes.

Pelagic herbivores (primarily zooplankton) actually decreased in biomass with increasing total nutrient load. One reason for this decrease in herbivore biomass could be due to a shift in phytoplankton composition. It has been shown that phytoplankton vary in edible attractiveness to zooplankton, differing in size, digestibility, and nutritional value (Reynolds 1997, Brett et al. 2000). Additionally, environmental factors such as nutrient availability and disturbance can influence variables of the phytoplankton community, such as plankton strategy, size, and composition (Reynolds 1984). Thus, although the total biomass of phytoplankton did not decrease, a shift in species composition could have resulted in phytoplankton that were unpalatable, inedible or nutritionally deficient.

The lack of response at the predator trophic level could be a result of the large difference

in response time between the primary producers (days), consumers (weeks) and predators (a season or more). A second possibility and limitation of my experiment, is that the mesocosms were left uncovered and open to colonization; random colonization could potentially have damped out any effect experienced by a mesocosm. However, species that have a high colonizing ability characteristically trade off a high competitive or predation ability (Tilman 1994); these species are likely to have small impacts upon the community. Also, dispersal in and out of systems is a reality in nature. Although colonizing species add more variation to the system, controlling dispersal would make the experimental mesocosms more artificial and the results less likely to reflect how natural systems would respond.

In conclusion, I suggest that to determine the effects of important variables such as nutrient input, rainfall, and temperature, it is important to explore the not only the mean value, but also the magnitude, the variance, and the timing of the occurrence. It has been previously suggested that nutrient variability could affect the outcome of resource competition (Grover 1997, Merriman and Kirk 2000). My study provides evidence that, in addition to competition and predator-prey interactions, nutrient variability can affect community structuring. Also, this study emphasizes the importance of examining a community not only within a trophic level, but also among trophic levels, in order to gain a better understanding of the factors that influence natural ecosystems. I suggest that ecologists will gain a deeper understanding of the structuring and functioning of communities and ecosystems by considering the variability that occurs naturally. Understanding community responses to nutrient input is important to value, protect and restore aquatic ecosystems.

Chapter 2: The effects of timing of nutrient input on aquatic communities

Introduction

Changes in nutrient input have been shown to greatly influence community dynamics. Increases in limiting nutrients, such as nitrogen and phosphorus, available to the biota can influence both community and ecosystem attributes such as species abundance and composition (Siegel 1998, Srivastava and Lawton 1998, Dodson et al. 2000), and diversity, stability, and ecosystem functioning (Pimm and Kitching 1987, Vanni and de Ruiter 1996, Tilman et al. 1997, Hooper and Vitousek 1998, Kaunzinger and Morin 1998, Koelmans 2001).

While it has been well documented that varying magnitudes of nutrient input can affect aquatic ecosystems (Rader and Richardson 1992, Koelmans et al. 2001), there has been considerably less focus on the effects of other variables related to nutrient addition, such as the temporal pattern (e.g. rate, timing) in which nutrients enter an aquatic system. The land surrounding aquatic systems often varies in usage (e.g. agricultural, industrial, forested), history (e.g. glaciated, nonglaciated), and topography (e.g. flat, mountainous). The shape and function of land can directly affect the amount, rate and timing of nutrients entering an aquatic system (Brenner et al. 1996, Soranno et al. 1996, Allan et al. 1997). In addition, seasonality is an important factor that influences the temporal pattern of nutrient input. Despite the acknowledged variability of nutrient input, little is known about the affects on a community.

The rate at which the nutrients enter a system should affect the nutrients available to the biota. Variability of the rate could have large effects upon the structure and the function of the ecosystem, as has been indicated in theoretical models (Harris 1980, Ruel and Ayres 1999) and laboratory studies (Sommer 1985, Grover 1988, Grover 1997, Merriman and Kirk 2000). Recently, I experimentally manipulated both the total and rate of nutrient addition and found

large effects on community structure in response to both treatments (this thesis, first chapter; Butzler and Chase, submitted).

It is possible that other variables, in addition to rate, are as important as magnitude in determining nutrient availability. In particular, the timing of nutrients entering a system in a seasonal environment can cause temporal variation in the resources available to organisms. Because several groups of organisms show seasonal succession (Reynolds 1980, 1984, Sommer et al. 1986) and seasonal phenology (Miao and Bazzaz 1990, Neto 2000), temporal variation in available resources could have drastic effects on community structure. In models that incorporate resource depletion or limitation, temporally varying nutrient additions can alter the seasonal development of species composition and abundance (Sommer et al. 1986). It has also been shown that individual species showing seasonal phenology will respond differently to the timing of nutrient pulses (Miao and Bazzaz 1990, Miao et al. 1991).

Species assemblages vary along productivity gradients (Reynolds 1980, 1984, Sommer et al. 1986). Therefore, systems of different *trophic status* (a classification of aquatic systems based on production) could respond in different ways to variable timing of nutrient pulses. Algal blooms are more pronounced in meso- and eutrophic systems than in oligotrophic systems (Seip and Reynolds 1995), and macrophytes tend to be in higher abundances in systems of lower trophic status (Spence 1982, Harper 1986). Also, the trophic status of a system could influence the strength of a trophic cascade (McQueen et al. 1986, Elser et al. 1990, Strauss et al. 1994). Thus, the timing of nutrient input could affect high and low productive systems differently. The trophic status tends to be more consistent and stable, reflective of the long-term local conditions; nutrient pulses, on the other hand, are short-term changes to the system (Miao et al. 1991). Thus, these two factors could potentially affect the community in different ways.

In this study, I asked whether the timing of nutrient input (pulses), trophic status and their interaction were important in seasonal aquatic communities. I first documented the degree to which natural systems varied in nutrient availability by conducting a natural survey of aquatic systems. Next, I conducted a mesocosm experiment designed to explicitly look at the consequences of the timing of nutrient input and trophic status. Specifically, I looked at the effects of two nutrient pulses (early spring or mid-summer), and two trophic states (mesotrophic and eutrophic) on a complex aquatic community. I examined effects within and among each trophic level. The response to the manipulations was measured through effects at the community level as composition and abundance of species.

Methods

Experimental design. In order to examine the effects of trophic status and seasonal timing of nutrient pulses on experimental aquatic ecosystems, I conducted a replicated mesocosm experiment from 1 April 2000 to 15 September 2000 at the Pymatuning Laboratory of Ecology, Pennsylvania. Twenty-four replicate mesocosms (760-L stock tanks) were filled with two inches of topsoil and nutrient-poor well water. Each mesocosm was inoculated with algae, zooplankton, macrophytes, invertebrates, and associated microbes, collected from a wide variety of natural systems. Phytoplankton and zooplankton were collected from ten ponds using a 64 μm plankton net, concentrated and added to each mesocosm. Periphyton was scraped from substrate found in ten ponds, concentrated and added to each mesocosm. Floating filamentous algae (primarily *Cladophora* spp. and *Oedogonium* spp.) and common macrophytes (*Chara* sp., *Potomageton crispus*, *Cerataphyllum* sp., *Elodea* sp.) were collected and cleaned, and small amounts of each were added to every mesocosm. Common detritivorous, herbivorous, and

predaceous macro invertebrates (*Helisoma trivolovis*, *Physella gyrina*, *Gyrallus* sp., Corixidae, *Notonecta* sp., Naucoridae, *Belostoma* sp., and several species of larval beetles (Hydrophilidae and Dytiscidae), dragonflies (Libellulidae and Aeshnidae) and damselflies (Coenagrionidae and Lestidae), were collected from various ponds and added to mesocosms. The community in each mesocosm assembled for two weeks. Most of the species (>90% by biomass) that were inoculated have short generation times (2 weeks to a month) that allowed population growth, or response time (days) that allowed an increase in biomass, in response to the experimental treatments within a season. The mesocosms were left uncovered, permitting immigration and emigration of many species, including Corixidae, *Notonecta* sp., *Belastoma* sp., *Chaoborus* sp., beetles, dragonflies and damselflies. Similar methods have been shown to create communities that resemble natural ponds (Leibold and Wilbur 1992; J. M. Chase, unpublished data).

The experiment was a 2 x 2 factorial design manipulating the timing of the nutrient pulse (2 times) and the trophic status (2 levels). Each treatment was replicated five times. Nutrients for the experimental treatments were nitrogen (added in the form of $NaNO_3$) and phosphorus (added in the form of NaH_2PO_4), which have been found to be the most limiting nutrients in aquatic systems (Lampert and Sommer 1997, Wetzel 2001). The experimental treatments were as follows: a pulse of nutrients in early spring (1 April 2000), or a pulse of nutrients mid summer (1 June 2000) (each pulse equaling the same total amount of nutrients). The two timing treatments were conducted at two trophic levels: 5 μg/L P: 150 μg/L N added per week (mesotrophic) or 8 μg/L P: 240 μg/L N added per week (eutrophic); the total nutrient load for mesotrophic was 220 μg/L P: 6600 μg/L N, eutrophic was 352 μg/L P: 10560 μg/L N. These trophic states were within the range of natural levels in local systems (J. M. Butzler, unpublished

data). 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 (Moss 1998, Wetzel 2001).

Sampling methods. I sampled each mesocosm at the conclusion of the experiment. Phytoplankton was collected from the water column and periphyton was collected from artificial substrates (plastic flagging), and analyzed for chlorophyll-*a* concentration (Clesceri 1998). Filamentous algae and macrophytes were estimated for percent cover in each mesocosm. To estimate biomass of the primary producers, volume-weight regressions were created from dried and weighed samples (see Appendix C). Zooplankton sub samples were collected from the water column using an integrated tube sampler, concentrated through a 64 μm mesh net and preserved for later enumeration and identification to species (genus when necessary), using taxonomical keys (Balcer et al. 1984, Pennak 1989); biomass was obtained through species-specific length-weight regressions (McCauley 1984, Lawrence et al. 1987). Macro invertebrates were censused visually. Biomass was obtained using length-weight regressions or species-specific weights (see Appendix C). All visual assessments were standardized by validating census techniques in mesocosms that were established in the same fashion of the experiment.

Data analysis. All data analyses were from the final sampling date when the total amount of nutrients added to each mesocosm was the same. The data was ln-transformed to correct for any non-normality or heteroscedasticity of the error terms. I conducted three sets of analyses to examine the effects of variable nutrient input. A multivariate analysis of variance (MANOVA) was conducted on primary producers, herbivores and predators to test for treatment differences. Then, I separated each trophic level (producer, herbivore, predator) into functional subgroups. These subgroups were as follows: filamentous algae (including periphyton), phytoplankton and macrophytes; pelagic herbivores and benthic herbivores; pelagic predators

and benthic predators. MANOVAs were used to determine whether there were any significant treatment differences within trophic levels. If the MANOVA results were significant, ANOVAs were then performed on each subgroup. I further analyzed the response by individual species, but multivariate analysis showed no effect of the treatments (Table 5), and these results will not be discussed further.

Results

Natural survey. The natural survey illustrates temporally variable nutrient availability among these sampled aquatic systems (Figure 1). First, within a single pond, the nutrient availability varied through time. For example, Geneva Pond showed low nutrient values in the beginning of the season and larger nutrient values towards the end of the season. Second, this variation through time varied between ponds. This can be seen by comparing the nitrogen levels of Geneva Pond (where there were large levels of nutrients in the end of the season) and Wheeler Pond (where there were large levels of nutrients in the beginning of the season). Finally, the total amount of nutrients levels over the season varied between ponds, as can be seen between RRditch Pond and Geneva Pond.

Mesocosm experiment. The response of the trophic groups (primary producers, herbivores and predators) to the timing of the nutrient pulse (MANOVA; $F_{3,14}$=0.66, P=0.59), trophic status (MANOVA; $F_{3,14}$=3.12, P=0.07) or their interaction (MANOVA $F_{3,14}$=0.48, P=0.70) was not significant. Multivariate analysis showed that the functional groups did not respond to the trophic status or the interaction between timing and trophic status, but did significantly respond to the timing of the nutrient input (Table 4, Figure 3). Univariate analysis showed that both macrophytes and phytoplankton responded significantly to the timing treatment (Figure 3A, B). The biomass of macrophytes was higher with an earlier pulse of nutrients,

whereas phytoplankton biomass was higher with a later pulse of nutrients. Filamentous algae did not respond to variable timing of nutrient input. The herbivore functional groups were unaffected by the nutrient treatments (Figure 3C, D). Benthic predator biomass was significantly higher with an early pulse of nutrients than with the mid summer pulse (Figure 3E, F).

Discussion

The results from this experiment suggest that the timing of nutrient pulses play an important role in determining community composition and relative abundance in aquatic systems. Although for simplicity, many ecological studies focus on the total or average nutrient input, the findings from this study support the indications of theoretical models (Harris 1980, Ruel and Ayres 1999) and laboratory studies of simple systems (Sommer 1985, Grover 1988, 1997, Merriman and Kirk 2000) that suggest significant effects from variability of nutrient input. The natural survey illustrates that, indeed, in addition to different overall levels of nutrients, the ponds in this survey also have a large range in variance in the temporal pattern of the nutrient availability. The variation in timing of nutrient pulse is not a unique property of this watershed, and has been indicated in other systems (Brenner et al. 1991, Soranno et al. 1996).

The effects of variable timing of the nutrient pulses were seen most strongly at the primary producer level. Phytoplankton biomass was significantly higher with the early pulse than with the mid-summer pulse of nutrients, whereas macrophyte biomass was significantly higher with the mid-summer pulse than with the early pulse of nutrients. These outcomes could have resulted from both faster uptake by phytoplankton, or light limitation of macrophytes caused by the increase of algal mats. Empirical studies have shown large responses of primary production, particularly algae and macrophytes, to an input of resources; but these two functional groups have very different utilization methods (reviewed in Wetzel 2001, Kalff 2002). Algae

can uptake nutrients in the water column at a much faster rate than macrophytes, allowing for maximum food utilization. Because macrophtyes are rooted, they obtain the majority of their resource requirements from the sedimented nutrients. Also, macrophytes die down each winter, requiring re-growth in the spring. If the nutrients enter the system early in the season, the phytoplankton could potentially exploit this short pulse while macrophyte biomass is low. If the phytoplankton became established, background nutrients might sustain the high abundance of phytoplankton. A large abundance of phytoplankton in the water column has been shown to reduce light penetration (Reynolds 1987), thus likely to suppress any further macrophyte growth.

The results were seen strongly at the primary producer level. When analyzed as species, both herbivores and predators did not respond to the nutrient treatments. Of the higher trophic levels, benthic predators were the only functional group to show a significant response to the timing of nutrient input. This raises the question of why were these results constrained mainly to the primary producers. Because of domination by alternative primary producers, one might have expected to see the effects more strongly manifested in higher trophic levels. A large difference in generation times could be a possible explanation. Whereas algae and macrophytes can respond in a matter of days (or hours), the response of the herbivores and predators may be one of weeks or even months. Also, despite a shift in the dominant primary producer, perhaps this shift was not indicative of a decrease or increase of the edible primary producer, which would be largely responsible for any response at the higher trophic levels.

There was no difference between trophic states. It has been suggested that the interactions between zooplankton and phytoplankton could be affected by the trophic status of the system; McQueen et al. (1986) proposed that the effects of trophic status would be most strongly manifested in oligotrophic systems, whereas Elser et al. (1990) suggested that the

effects would be seen most strongly in mesotrophic systems, and weakly at very high or low productivity. This study showed no significant relationship between trophic status and various measures of community structure. The difference between the mesotrophic treatment and the eutrophic treatment may not have been enough to elicit a significant response. Because this study did not span the range of oligotrophic to hypereutrophic trophic states, this question remains unresolved and warrants further consideration. Interestingly, the total biomass of all the primary producers did not increase in response to an increase in nutrient input, while the timing of nutrient input produced significant responses at both trophic states. This suggests that at a certain magnitude, the total amount ceases to be an important factor and other variables of nutrient addition, such as timing, play a defining role in an aquatic community.

Although anthropogenic eutrophication of aquatic systems has received much attention in the recent years, the focus has been on the magnitude of the nutrient input, and the variables such as seasonality, land use and riparian zones, affecting this measure of nutrient input. But these same variables can affect the rate and the timing of the nutrients entering the system. The data presented here and in the first chapter illustrate the importance of understanding the role of variance of nutrient input in aquatic systems. In addition to the consequences that variable nutrient input may have on the ecology of an aquatic community, this variability may also have significant implications for the economic value of wetlands as a control of excessive nutrient pollution (Bystrom et al. 2000). If wetlands are to be used to reduce point and nonpoint pollution (e.g. Greenway and Woolley 1999, Cardoch et al. 2000), it is important to understand how variable nutrient regimes will influence their effectiveness. Also, because many aquatic systems are surrounded by land that includes practices that affect these systems, concurrent

management of a watershed and the surrounding lands is necessary to protect aquatic ecosystems.

APPENDICES

Appendix A: Tables

Table 1. MANOVA results from the mesocosm experiment when analysed by trophic level.

	Factor	df	F	P
		Multivariate response		
OVERALL RESPONSE	rate	6, 32	1.37	0.26
	total	3, 16	0.76	0.53
	rate x total	6, 32	1.09	0.39

Table 2. [M]ANOVA results of mesocosm experiment when the community was broken down by function. See text for functional groupings.

	Factor	df	F	P
		Multivariate response		
PRIMARY PRODUCERS	rate	6, 32	4.23	**<0.05**
	total	3, 16	15.12	**<0.01**
	rate x 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	11.21	**<0.01**
macrophytes	rate	2	4.38	**0.03**
	total	1	18.92	**<0.01**
		Multivariate responses		
HERBIVORES	rate	4, 34	3.47	**0.02**
	total	2, 17	13.68	**<0.01**
	rate x 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
		Multivariate responses		
PREDATORS	rate	4, 34	0.21	0.93
	total	2, 17	2.98	0.08
	rate x total	4, 34	0.96	0.44

Table 3. MANOVA results when community was broken down by species.

	Factor	df	F	P
		Multivariate response		
PRIMARY PRODUCERS	rate	10, 28	2.16	**0.05**
	total	5, 14	6.35	**<0.01**
	rate x total	10, 28	0.21	0.99
HERBIVORES	rate	26, 12	0.83	0.67
	total	13, 6	1.08	0.49
	rate x total	26, 12	0.68	0.81
PREDATORS	rate	16, 22	1.22	0.33
	total	8, 11	0.86	0.58
	rate x total	16, 22	0.53	0.90

Table 4. [M]ANOVA results of mesocosm experiment when the community was broken down by function. See text for functional groupings.

	Factor	df	F	P
		Multivariate response		
PRIMARY PRODUCERS	Trophic status	3, 14	1.47	0.26
	Timing	3, 14	3.15	**0.05**
	Trophic status x timing	3, 14	2.95	0.07
		Univariate responses (timing)		
phytoplankton		1	6.81	**0.02**
filamentous algae		1	1.55	0.23
macrophytes		1	4.63	**0.05**
		Multivariate responses		
HERBIVORES	Trophic status	2, 15	2.38	0.13
	Timing	2, 15	1.12	0.35
	Trophic status x timing	2, 15	0.07	0.94
		Multivariate responses		
PREDATORS	Trophic status	2, 15	0.76	0.49
	Timing	2, 15	7.68	**<0.01**
	Trophic status x timing	2, 15	2.45	0.12
		Univariate responses (timing)		
Pelagic predators		1	6.98	0.30
Benthic predators		1	1.16	**0.02**

Table 5. MANOVA results when community was broken down by species.

	Factor	df	F	P
		Mulitvariate responses		
PRIMARY PRODUCERS	Trophic status	6, 11	1.02	0.46
	Timing	6, 11	2.70	0.07
	Trophic status x timing	6, 11	1.59	0.24
HERBIVORES	Trophic status	15, 2	0.92	0.64
	Timing	15, 2	2.69	0.30
	Trophic status x timing	15, 2	0.86	0.66
PREDATORS	Trophic status	6, 11	1.64	0.23
	Timing	6, 11	0.51	0.79
	Trophic status x timing	6, 11	0.81	0.58

Appendix B: Figures

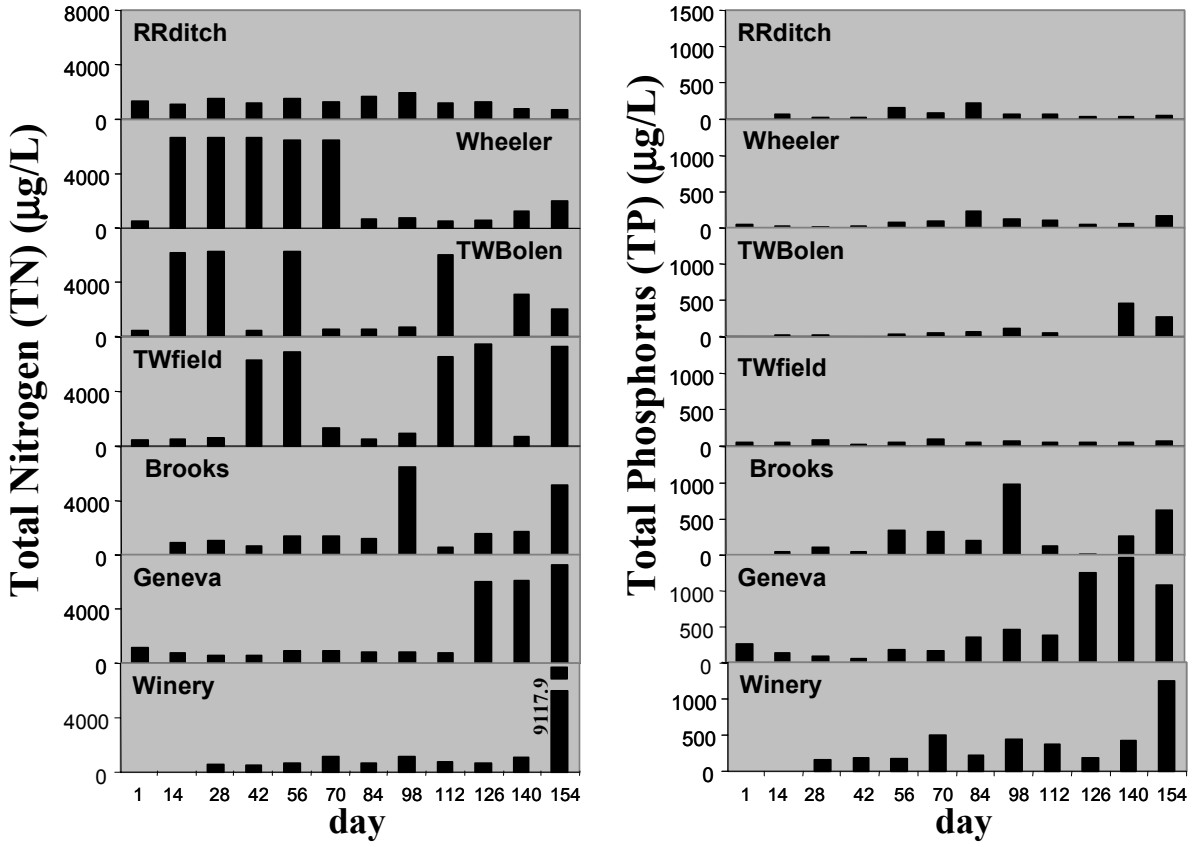

Figure 1. The natural variation of nutrient levels in seven aquatic systems in the Pymatuning watershed. Reported are bi-weekly samples of surface waters tested for levels of TN and TP. Note the variation within, as well as between, the aquatic systems.

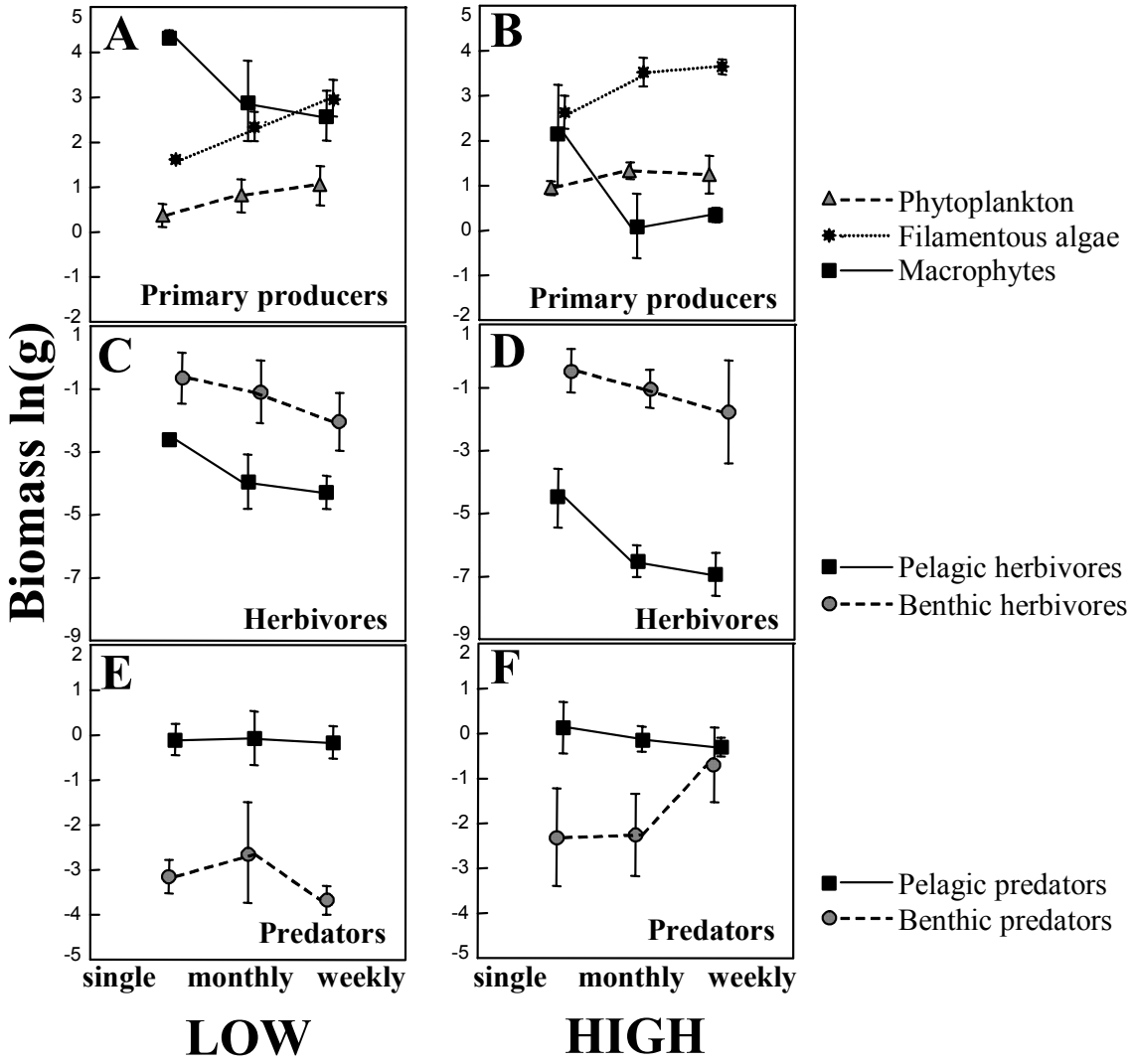

Figure 2. The response of the functional groups within each trophic level to the nutrient treatments. Functional groups were as follows: filamentous algae, phytoplankton and macrophytes; pelagic herbivores and benthic herbivores; pelagic predators and benthic predators. Response was measured as standing crop biomass (g). A. and B. represent primary producer responses to variable nutrient input (single, monthly or weekly) for

LOW total nutrient load and HIGH total nutrient load. C. and D. represent herbivore responses to variable nutrient input (single, monthly or weekly) for LOW and HIGH total nutrient load. E. and F. represent predator responses to variable nutrient input (single, monthly or weekly) for LOW and HIGH total nutrient load. The community responded to variable nutrient input most significantly within the primary producers.

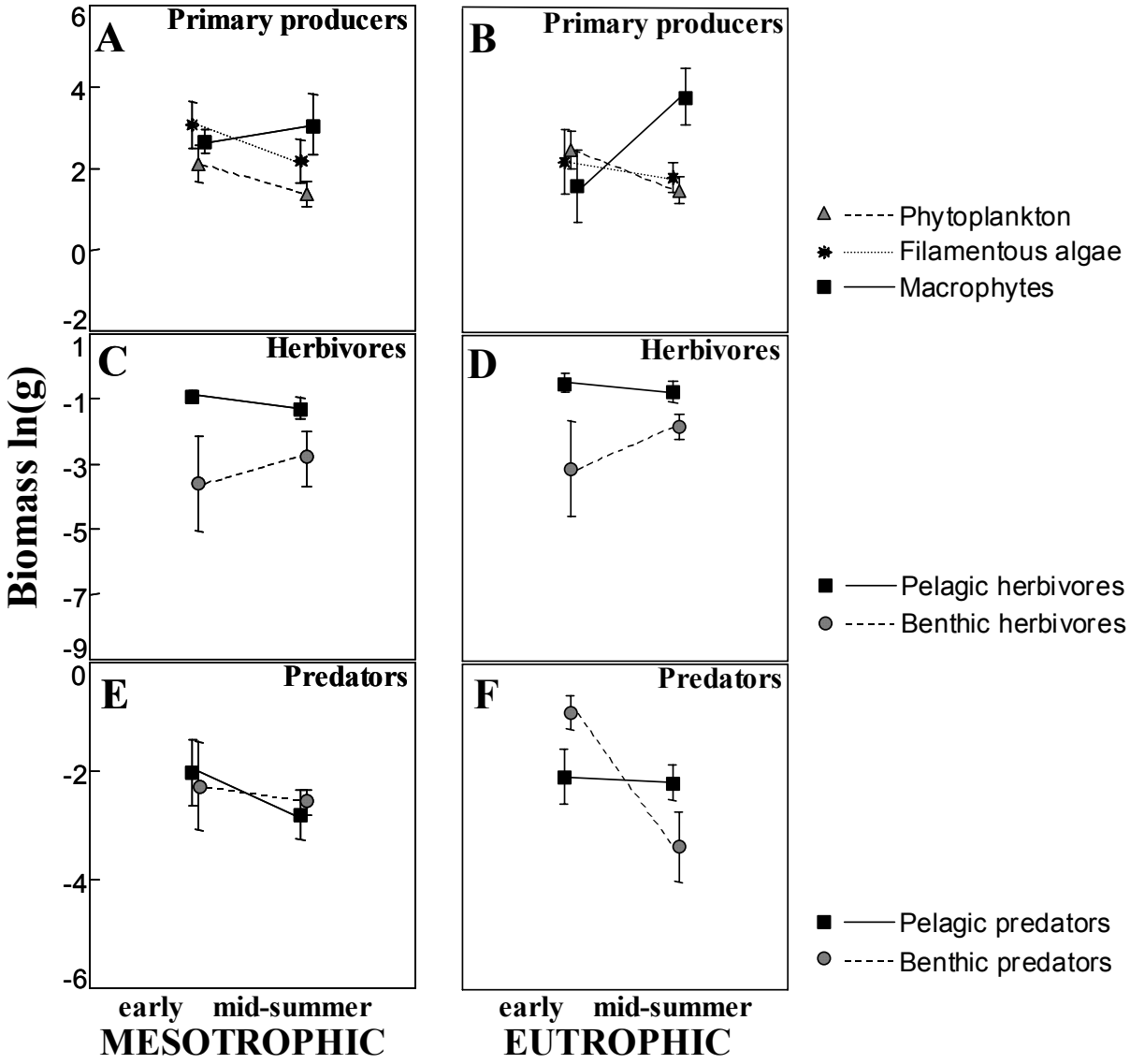

Figure 3. Results from the mesocosm experiment manipulating nutrient input timing and background nutrient level. The response of the functional groups within each trophic level to the nutrient treatments. Functional groups were as follows: filamentous algae, phytoplankton and macrophytes; pelagic herbivores and benthic herbivores; pelagic predators and benthic predators. Response was measured as standing crop biomass (g). A.

and B. represent primary producer responses to variable timing (early spring or mid-summer) for EUTROPHIC systems and MESOTROPHIC systems. C. and D. represent herbivore responses to variable timing (early spring or mid-summer) for EUTROPHIC systems and MESOTROPHIC systems. E. and F. represent predator responses to variable nutrient timing (early spring or mid-summer) for EUTROPHIC systems and MESOTROPHIC systems.

Appendix C: Biomass relationships

Table 6. Length –weight relationships for primary producers and two species of snails collected from mesocosm experiment.

species	slope (a)	intercept (b)	r^2
Filamentous algae	0.0002	2.265	0.63
Chara sp.	0.004	1.437	0.96
Potomageton crispus	0.004	0.005	0.44
Cerataphyllum sp.	0.005	0.001	0.82
Elodea sp.	0.004	0.041	0.41
Helisoma trivolovis	2.57	0.0000468	.094
Physella gyrina	2.34	0.000040	0.85

Notes: The slope (a), the intercept (b), and the r^2 value are presented for the general relationship:

$y=b+a(L)$

where y is the biomass estimate (g). The length (L) was measured in millimeters (mm). Because the relationships for both snails were not linear, the slope (a) and the intercept (b) are presented for the modified relationship (length-weight relationships for snails were provided by C. Boes, unpublished data):

$\ln(y)=\ln(b)+a(\ln L)$

where ln(y) is the logarithm of the biomass estimate.

Table 7. Estimated biomass for biota collected from the mesocosm experiment. All values reported are estimates of adults or individuals in final instar.

Species	Average biomass
Corixidae	0.025g/individual
Notonecta spp.	0.032g/individual
Belostoma sp.	0.071g/individual
Hydrophilidae	0.028g/individual
dragonflies	0.030g/individual
damselflies	0.006g/individual

BIBLIOGRAPHY

Bibliography

Abrams, P. A. 1993. Effect of increased productivity on the abundance of trophic levels. American Naturalist **14**:351-371.

Abrams, P. A. 1995. Monotonic or unimodal diversity productivity gradients: what does competition theory predict? Ecology **76**:2019-2027.

Allan, J. D., D. L. Erickson and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biology **37**:149-161.

Balcer, M. D., N. L. Korda and S. I. Dodson. 1984. Zooplankton of the Great Lakes. University of Wisconsin Press, Madison, Wisconsin, USA.

Brenner, F. J., J. J. Mondok and R. J. McDonald. 1991. Impact of riparian areas and land use on four non-point source pollution parameters in Pennsylvania. Journal of the Pennsylvania Academy of Science **65**:65-70.

Brenner, F. J., R. P. Steiner and J. J. Mondok. 1996. Groundwater-surface water interaction in an agricultural watershed. Journal of the Pennsylvania Academy of Science **70**:3-8.

Brenner, M., T. J. Whitmore, M. A. Lasi, J. E. Cable and P. H. Cable. 1999. A multi-proxy trophic state reconstruction for shallow Orange Lake, Florida, USA: possible influence of macrophytes on limnetic nutrient concentrations. Journal of Paleolimnology **21**:215-233.

Brett, M. T. and C. R. Goldman. 1997. Consumer versus resource control in freshwater pelagic food webs. Science **275**:384-386.

Brett, M. T., D. C. Muller-Navarra and S. K. Park. 2000. Emperical analysis of the effect of phosphorus limitation on algal food quality for freshwater zooplankton. Limnology and Oceanography **45**:1564-1575.

Bystrom, O., H. Andersson and I. M. Gren. 2000. Economic criteria for using wetlands as nitrogen sinks under uncertainty. Ecological Economics **35**:35-45.

Cardoch, L., J. W. Day, J. M. Rybczyk and G. P. Kemp. 2000. An economic analysis of using wetlands for treatment of shrimp processing wastewater - a case study in Dulac, LA. Ecological Economics **33**:93-101.

Carpenter, S. R., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley and V. H. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecological Applications **8**:559–568.

Carpenter, S. R., T. M. Frost, J. F. Kitchell, T. K. Kratz, D. W. Schindler, J. Shearer, W. G. Sprules, M. J. Vanni and A. P. Zimmerman. 1991. Patterns of primary production and herbivory in 25 North American lake ecosystems. Pages 67-96 in J. Cole, G. Lovett and S. Findlay, editors. Comparative Analysis of Ecosystems: Patterns, Mechanisms, and Theories. Springer-Verlag, New York, New York, USA.

Chase, J. M. 1999. Food web effects of prey size refugia: variable interactions and alternative stable equilibria. American Naturalist **154**:559-570.

Chase, J. M., M. A. Leibold, A. L. Downing and J. B. Shurin. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. Ecology **81**:2485-2497.

Clesceri, L. S., A. E. Greenberg and A. D. Eaton. 1998. Standard Methods for the Examination of Water and Waste Water. 20th edition. American Public Health Association, Washington, DC, USA.

Cooke, S. E. and E. E. Prepas. 1998. Stream phosphorus and nitrogen export from agricultural and forested watersheds on the Boreal Plain. Canadian Journal of Fisheries and Aquatic Sciences **55**:2292-2299.

DeAngelis, D. 1992. Dynamics of Nutrient Cycling and Food Webs. Chapman and Hall, London.

Dodson, S. I., S. E. Arnott and K. L. Cottingham. 2000. The relationship in lake communities between primary productivity and species richness. Ecology **81**:2662-2679.

Elser, J. J., H. J. Carney and C. R. Goldman. 1990. The zooplankton-phytoplankton interface in lakes of contrasting trophic status: an experimental comparison. Hydrobiologia **200**:69-82.

Gabor, T. S., H. R. Murkin, M. P. Stainton, J. A. Boughen and R. D. Titman. 1994. Nutrient additions to wetlands in the Interlake region of Manitoba, Canada: effects of a single pulse addition in spring. Hydrobiologia **279/280**:497-510.

Graham, L. E. and L. W. Wilcox. 2000. Algae. Prentice Hall, New Jersey, USA.

Greenway, M. and A. Woolley. 1999. Constructed wetlands in Queensland: Performance efficiency and nutrient bioaccumulation. Ecological Engineering **12**:39-55.

Grover, J. P. 1988. Dynamics of competition in a variable environment: phytoplankton growing according to Monod's model. American Naturalist **136**:771-789.

Grover, J. P. 1997. Resource competition. Chapman and Hall, New York, New York, USA.

Grover J. P. and R. D. Holt. 1998. Disentangling resource and apparent competition: realistic models for plant-herbivore communities. Journal of Theoretical Biology **191**:353-376.

Hann, B. J. and L. G. Goldsborough. 1997 Responses of a prairie wetland to press and pulse additions of inorganic nitrogen and phosphorus: invertebrate community structure and interactions. Archiv für Hydrobiologie **140**:169-194.

Harper, D. 1992. Eutrophication of Freshwaters: Principles, Problems and Restoration. Chapman and Hall, New York, New York, USA.

Harris, G. P. 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models, and management. Canadian Journal of Fisheries and Aquatic Sciences **37**:877-900.

Hooper, D. U. and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. Ecological Monographs **68**:121-149.

Kalff, J. 2002. Limnology: Inland Water Ecosystems. Prentice Hall, New Jersey, USA.

Kaunzinger, C. M. K. and P. J. Morin. 1998. Productivity controls food-chain properties in microbial communities. Nature **395**:495-497.

Koelmans, A. A., A. Van der Heijde, L. M. Knijff and R. H. Aalderink. 2001. Integrated modeling of eutrophication and organic contamination: fate and effects in aquatic ecosystems. A review. Water Research **35**:3517-3536.

Lampert, W. and U. Sommer. 1997. Limnoecology: the Ecology of Lakes and Streams. Oxford University Press, New York, New York, USA.

Lawrence, S. G., D. F. Malley, W. J. Findlay, M. A. MacIver and I. L. Delbaere. 1987. Method for estimating dry weight of freshwater planktonic crustaceans from measures of length and shape. Canadian Journal of Fisheries and Aquatic Sciences **44**:264-274.

Leibold, M. A. 1997. Do nutrient-competition models predict nutrient availabilities in limnetic ecosystems? Oecologia **110**:132-142.

Leibold, M. A. and H. M. Wilbur. 1992. Interactions between food-web structure and nutrients on pond organisms. Nature **360**:341-343.

Leibold, M. A., J. M. Chase, J. B. Shurin and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. Annual Review of Ecology and Systematics **28**:467-494.

Maberly, S. C. and D. H. N. Spence. 1983. Photosynthetic inorganic carbon use by freshwater plants. Journal of Ecology **71**:705-724.

McCauley, E. 1984. The estimation of the abundance and biomass of zooplankton in samples. Pages 228-265 in J. A. Downing and F. H. Rigler, eds. A Manual on Methods for the

Assessment of Secondary Productivity in Fresh Waters. Blackwell Scientific, Oxford, UK.

McDougal, R. L., L. G. Goldsborough and B. J. Hann. 1997. Responses of a prairie wetland to press and pulse additions of nitrogen and phosphorus: production by planktonic and benthic algae. Archiv für Hydrobiologie **140**:145-167.

McQueen, D. J., J. R. Post, and E. L. Mills. 1986. Trophic relationships in pelagic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences **43**:1571-1581.

Merriman, J. L. and K. L. Kirk. 2000. Temporal patterns of resource limitation in natural populations of rotifers. Ecology **81**:141-149.

Miao, S. L., and F. A. Bazzaz. 1990. Responses to nutrient pulses of two colonizing species requiring differing disturbance frequencies. Ecology **71**:2166-2178.

Miao, S. L., F. A. Bazzaz and R. B. Primack. 1991. Effects of maternal nutrient pulse on reproduction of two colonizing plantago species. Ecology **72**:586-596.

Micheli, F. 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. Science **285**:1396-1398.

Moss, B. 1998. Ecology of Freshwaters: Man and Medium, Past to Future. Blackwell Science, Inc., Malden, Massachusetts, USA.

Murkin, H. R., J. B. Pollard, M. P. Stainton, J. A. Boughen and R. D. Titman. 1994. Nutrient additions to wetlands in the interlake region of Manitoba, Canada: effects of periodic additions throughout the growing season. Hydrobiologia **280**:483-495.

National Research Council. 1992. Restoration of Aquatic Ecosystems. National Academy Press, Washington, DC, USA.

Neto, A. I. 2000. Observations on the biology and ecology of selected macroalgae from the littoral of Sao Miguel (Azores). Botanica Marina **43**:483-498.

Oksanen, L. and T. Oksanen. 2000. The logic and realism of the hypothesis of exploitation ecosystems. American Naturalist **155**:703-723.

Oksanen, L., S. D. Fretwell, J. A. Arrunda and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist **118**:240-261.

Ostfeld, R. S. and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution **15**:232-237.

Pace, M. L., J. J. Cole, S. R. Carpenter and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution **14**:483-488.

Pennak, R. W. 1989. Fresh-water Invertebrates of the United States, 3rd Edition: Protozoa to Mollusca. Wiley and Sons, New York, New York, USA.

Peterjohn, W. T. and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology **65**:1466-1475.

Pimm, S. L. and R. L. Kitching 1987. The determinants of food chain lengths. Oikos **50**:302-307.

Rader, R. B. and C. J. Richardson. 1992. The effects of nutrient enrichment on algae and macroinvertebrates in the everglades- a review. Wetlands **12**:121-135.

Reynolds, C. S. 1980. Phytoplankton assemblages and their periodicity in stratifying lake ecosystems. Holartic Ecology **3**:141-159.

Reynolds, C. S. 1984. Phytoplankton periodicity: the interaction of form function and environmental variability. Freshwater Biology **14**:111-142.

Reynolds, C. S. 1997. Vegetation Process in the Pelagic: a Model for Ecosystem Theory. Ecology Institute, Oldendorf/Luhe, Germany.

Ruel, J. J. and M. P. Ayres. 1999. Jensen's inequality predicts effects of environmental variation. Trends in Ecology and Evolution **14**:361-366.

Schindler, D. W. 1978. Factors regulating phytoplankton production and standing crop in the world's lakes. Limnology and Oceanography **23**:478-486.

Schindler, D. W., E. J. Fee and T. Ruszczynski. 1978. Phosphorus input and its consequences for phytoplankton standing crop and production in the Experimental Lakes Area and in similar lakes. Journal of Fish Research Board Canada **35**:190-196.

Siegel, D. A. 1998. Resource competition in a discrete environment: why are plankton distributions paradoxical? Limnology and Oceanography **43**:1133-1146.

Seip, K. L. and C. S. Reynolds. 1995. Phytoplankton functional attributes along trophic gradient and season. Limnology and Oceanography **40**:589-597.

Sommer, U. 1985. Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. Limnology and Oceanography **30**:335-346.

Sommer, U. 1989. Nutrient status and nutrient competition of phytoplankton in a shallow, hypertrophic lake. Limnology and Oceanography **34**:1162-1173.

Sommer, U., Z. Maciej Gliwicz, W. Lampert and A. Duncan. 1986. The PEG*-model of seasonal succession of planktonic events in freshwaters. Archiv für Hydrobiologie **106**:433-471.

Soranno, P. A., S. L. Hubler and S. R. Carpenter. 1996. Phosphorus loads to surface waters: a simple model to account for spatial pattern of land use. Ecological Applications **6**:865-878.

Srivastava, D. S. and J. H. Lawton. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. American Naturalist **152**:510-529.

Strauss, E. A., W. K. Dodds and C. C. Edler. 1994. The impact of nutrient pulses on trophic interactions in a farm pond. Journal of Freshwater Ecology **9**:217-228.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, New Jersey, USA.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology **75**:2-16.

Tilman, D. C. L. Lehman and K. T. Thomson. 1997. Plant diversity and ecosystem productivity: theoretical considerations. Proceedings of the National Academy of Sciences **94**:1857-1861.

Vanni, M. J. and P. C. de Ruiter. 1996. Detritus and nutrients in food webs. Pages 25-29 in G. A. Polis and K. O. Winemiller, editors. Food webs: Integration of Patterns and Dynamics. Chapman and Hall, New York, New York, USA.

Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger and D. G. Tilman. 1997. Human alteration of the global nitroden cycle: sources and consequences. Ecological Applications **7**:737–750.

Wetzel, R. G. 2001. Limnology: Lake and River Ecosystems. 3rd ed. Academic Publishing, San Diego, USA.