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Many studies have examined the effects of high level nutrient additions (up to 10x ambient loading rate) to lake ecosystems. This study examined microplankton response to low-level nitrogen and phosphorus additions (nominally 2X ambient loading rate) in lakes with and without fish at the Arctic LTER site. Annual variation in microplankton abundance in experimental and reference lakes was high. Lakes with fish had fewer large microplankton taxa. Overall, the response of microplankton to fertilization was unremarkable except for *Vorticella* whose average total biomass at 1 meter in the experimental lake containing fish increased significantly over the experimental period (regression coefficient = 1.264; F = 18.27; p = 0.007; d.f. = 5). Microplankton biomass trended downward in reference lakes while remaining relatively stable in experimental lakes, thus a subtle positive response may have occurred. Assessing changes in intermediate trophic levels in response to low-level fertilization is difficult because of high inter-annual variation in temperature and rainfall and a high coefficient of variation in direct count data (range 2 – 244%). Long term experiments and observations (10 years or greater) may be required to definitively assess such subtle impacts.

EFFECT OF LOW LEVEL FERTILIZATION ON MICROPLANKTON IN ARCTIC LTER LAKES

By

Alison Lisa Boyko

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the Faculty of the Graduate School at
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Approved by

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APPROVAL PAGE

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CHAPTER I

INTRODUCTION

The availability of nutrients within an aquatic system can be a major limiting factor for productivity within that system. Much research has focused on this because of changing inputs due to cultural eutrophication resulting from changing population patterns. This is the addition of nutrients to aquatic systems which includes the dumping of treated or untreated effluent, and runoff from farms, industrial sites, and residential areas. Additionally, there is the current concern of global climate change including increased temperature and changes in precipitation patterns. This change is predicted to include a disproportionate increase in temperature (IPCC 2001) and rainfall in the arctic regions and in the higher latitudes may lead to permafrost thaw releasing a large amount of nutrients and a large and previously inaccessible carbon pool (Mack *et al.* 2004; Rouse *et al*. 1997).

The addition of high levels of nutrients to a system can lead to reduced biodiversity and high levels of organic production (eutrophication). Many studies have been conducted to examine the effects of high level nutrient addition on aquatic systems and the general response, including increases in production and biomass, is well known (Carpenter 1988; O'Brien *et al.* 2005). Carpenter (2001) found that in Wisconsin lakes, nutrient additions lead to variable responses of fish and zooplankton populations while primary producers appeared to be inhibited by the trophic cascade. Another study

conducted by Vanni and Layne (1996) also found evidence for the occurrence of nutrient mediated effects of top predators on primary producers.

Several models are used to explain the effects of nutrient addition to aquatic systems. These include bottom-up models, cascading trophic level (top-down) interaction models, and food webs. Each of these models varies in complexity, emphasis and its ability to explain response in a natural system.

The simplest of the models is the bottom-up interaction model. It is a model dependent on a well defined food chain with discrete trophic levels. In this model an increase in the lowest trophic level leads to resource movement upward through the food chain and causes an increase the biomass in all trophic levels. Because communities are made up of multiple types of organisms and therefore have complex interactions this model is oversimplified and may not account for dietary variability or predation. Therefore it is of limited applicability to natural systems.

The cascading trophic level interaction model (top-down) commonly defined as 'the reciprocal effects of predators on prey which alter the abundance, biomass, or productivity of a population, community, or trophic level' (Carpenter *et al.* 2001; Carpenter *et al.* 1985; Pace *et al.* 1999; Polis *et al.* 2000) also requires a simplified food chain. However, unlike the bottom-up model it emphasizes the effects of predation. This allows for a slightly more complex approach which makes it more realistic for modeling a natural system. However, this model is inadequate for use in many systems as it still does not reflect the full complexity within that system. For example, it cannot easily account for species which feed on multiple trophic levels and selective predation. Some

believe that communities are in fact too complex to show general patterns and due to this no natural grouping of organisms into distinct trophic levels is really possible (Polis and Strong 1996).

Natural systems are complex, thus food webs based on trophic level functional feeding groups maybe a more realistic choice for modeling the interactions and predicting changes in a natural system. By separating trophic levels into functional groups based on feeding and vulnerability to consumption, effects that were obscured when the system was viewed as a food chain should be visible (Persson *et al.* 2001). Although these trophic level groupings are more complex then the other commonly used models (Figure 1) their use of convenient functional feeding groups can also be somewhat challenging because many species don't fall into a discrete feeding group and there may be limited available data on some species. Also, changes in community structure such as the 'appearance' of a new species or the 'disappearance' of a sensitive species are not easily accounted for. It is also difficult to account for the altered importance of particular taxa which may result from selective predation (Abrams and Walters 1996; Hall *et al*. 2006; Leibold and Wilbur 1992; Persson *et al.* 2001).

The bottom-up effects of resource availability and the top-down effects of predation and trophic cascade have been important foci of aquatic research in the last 30 years (Carpenter 1988, 2003; Carpenter *et al.* 2001; Carpenter and Kitchell 1993; Carpenter *et al.* 1985; Hambright 1994; Herendeen 2004; Kitchell *et al.* 1994; Persson *et al.* 1992). Some studies have supported the bottom-up model by showing that over time increased nutrient inputs into aquatic system tends to increase the productivity in that

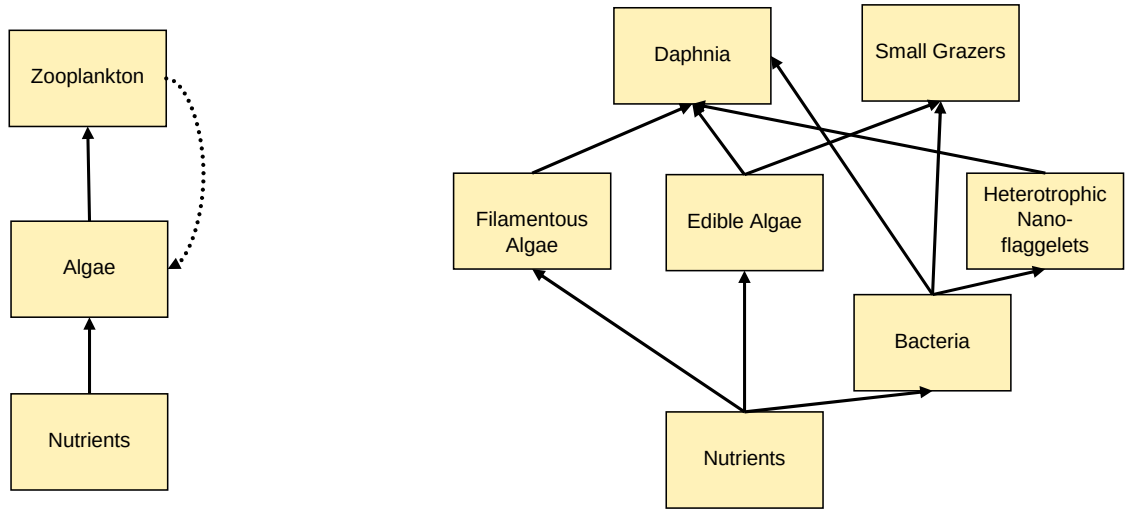

Figure 1. Comparison of cascading trophic level interaction food chain (left) and functional feeding group specific food web in a simplified experimental system. Adapted from Persson *et al.* 2001.

system (Carpenter 1988). The cascading trophic interaction model has been supported in studies were alterations of the higher trophic levels resulted in top-down pressures acting upon the lower trophic levels and causing subsequent increases or decreases in biomass (Lewis 1979; McQueen and Post 1986). However, there are also studies whose results do not support this model (Brett and Goldman 1997; Bronmark and Weisner 1996; Pace and Funke 1991).

Food web experimental manipulations can be highly complex and with each additional trophic level the response is likely to grow more difficult to predict (Abrams and Roth 1994; Fussmann and Heber 2002; Rozenzweig 1971). One reason for this within aquatic systems is that the intrinsic dynamics of higher trophic level populations usually involve large amplitude changes with long time lags (Persson *et al.* 2004). Also,

high predator diversity causes predictions pertaining to the effects of trophic cascade to be much more tenuous, as higher predator diversity weakens the trophic cascade and dampens the effects of predation on lower trophic levels (Finke and Denno 2004). Trophic level uncoupling is another factor that makes it difficult to predicting trophic level responses. McQueen *et al.* (1989) found that although most adjacent trophic levels had a direct effect on one another, an uncoupling occurred at the zooplankton-phytoplankton link, specifically at the level of protozoans (Pace and Funke 1991). This means that the predator effects on zooplankton may not be good predictors of phytoplankton response.

The response of phytoplankton, zooplankton, and fish (Bertolo *et al.* 2000; Carpenter 1988, 2003; Carpenter *et al.* 2001; Carpenter and Kitchell 1993; Carpenter *et al.* 1985; Jeppesen *et al.* 2003; Olsson *et al.* 1992; Pace and Orcutt 1981; Persson *et al.* 2004) have historically been the focus of nutrient addition studies. Due to this, the important role that microplankton may play in the aquatic ecosystem has largely been ignored in such studies. Microplankton act as grazers and also may play a critical role as food for larval fish and crustacean zooplankton (Guma'a 1987; Williamson 1983). They are important in nutrient cycling and organic matter decomposition (Arndt 1993; Markarewicz and Likens 1979; Rieman and Christoffersen 1993) and are consumers of microplankton secondary production because large rotifers and protozoans often feed on smaller ones (Rublee 1998b; Rublee and Bettez 1995).

Over the last 30 years research at the Toolik Lake Arctic Long Term Ecological Research center (LTER) has given scientists insight into the inner workings of both

aquatic and terrestrial arctic systems. Since 1985 the arctic LTER and surrounding area has been the location of many lake manipulations including whole-lake fertilization studies, limnocorral studies, and organism surveys (Hershey 1992; O'Brien 1992; O'Brien *et al.* 2005). Earlier studies investigating the effects of both long and short term fertilization on arctic lakes found a dramatic response to large nutrient additions (≈ 4-10 times ambient loading) by microplankton (Bettez *et al.* 2002; O'Brien *et al.* 2005; Rublee 1998a; Rublee and Bettez 1995).

A fertilization study of lake N2 at the arctic LTER was conducted from 1985 to 1990 when half of the lake was fertilized at approximately 10 times the ambient loading rate. Rublee and Bettez (1995) found that both microplankton biomass and abundance was lower in the oligotrophic half of the lake compared to the experimentally fertilized half of the lake. This is consistent with bottom-up regulation of microplankton abundance (Rublee 1992). Another study using limnocorrals to examine the effects of high and low inorganic nitrogen and phosphorus addition and high and low free-swimming fish additions was performed in an isolated bay of Toolik Lake (O'Brien *et al.* 1992; O'Brien *et al.* 2005). Although this study did not examine microplankton directly it found that as a result of the nutrient additions there was a rapid and dramatic increase in phytoplankton activity and microbial production. By the third year zooplankton density had also increased. Hobbie and colleagues (Hobbie *et al.* 1999; Rublee 1992) also performed a smaller microcosm study in which addition of litter leachate resulted in rapid dramatic increases in primary producer biomass followed by rapid increases in the microplankton biomass.

Rublee and colleagues examined the effects of fertilization on the microplankton community structure in fertilized arctic lakes (Bettez *et al.* 2002; Rublee 1992; Rublee and Bettez 1995). Lake N1 was fertilized at 5-10 times the ambient nutrient loading rate from 1989-1992. Fertilization resulted in a statistically significant increase in both protozoan numbers and biomass. This included a change in the dominant species from oligotrichs to the bacterivorous peritrich *Epistylis rotans* in later years. Rotifer biomass and abundance did not change significantly during this study but there was a sudden appearance of *Conochilus natans*, a rotifer species not seen prior to fertilization in these lakes.

These studies, like most studies examining the effects of nutrient additions to aquatic systems utilized high levels of nutrient addition (5 – 10 times ambient loading) while few studies have examined the effects of low level nutrient additions. A low-level addition study was started in lakes near the Toolik Lake LTER site in 2001. Using a food chain model one would expect to find that a low-level nutrient addition would result in a response of increasing biomass of organisms at different trophic levels that equilibrates at a new baseline approximately double the pre-fertilization biomass found in each trophic level (Figure 2). This would be a much more muted response then that found in the previous high level fertilization studies also conducted at the Toolik Lake Arctic LTER (Bettez *et al.* 2002; Rublee 1992, 1998b; Rublee and Bettez 1995, 2001). However, these food web interactions may not be quite so simple due to a number of factors including the complex and dynamic nature of natural systems. This is compounded by the diversity of microplankton species in these lakes. For example, there are at least 127 species of

rotifers identified from arctic sites (Chengalath and Koste 1989) and because of their varying dietary preferences (Rublee 1998a) it is difficult to propose an adequate food chain structure.

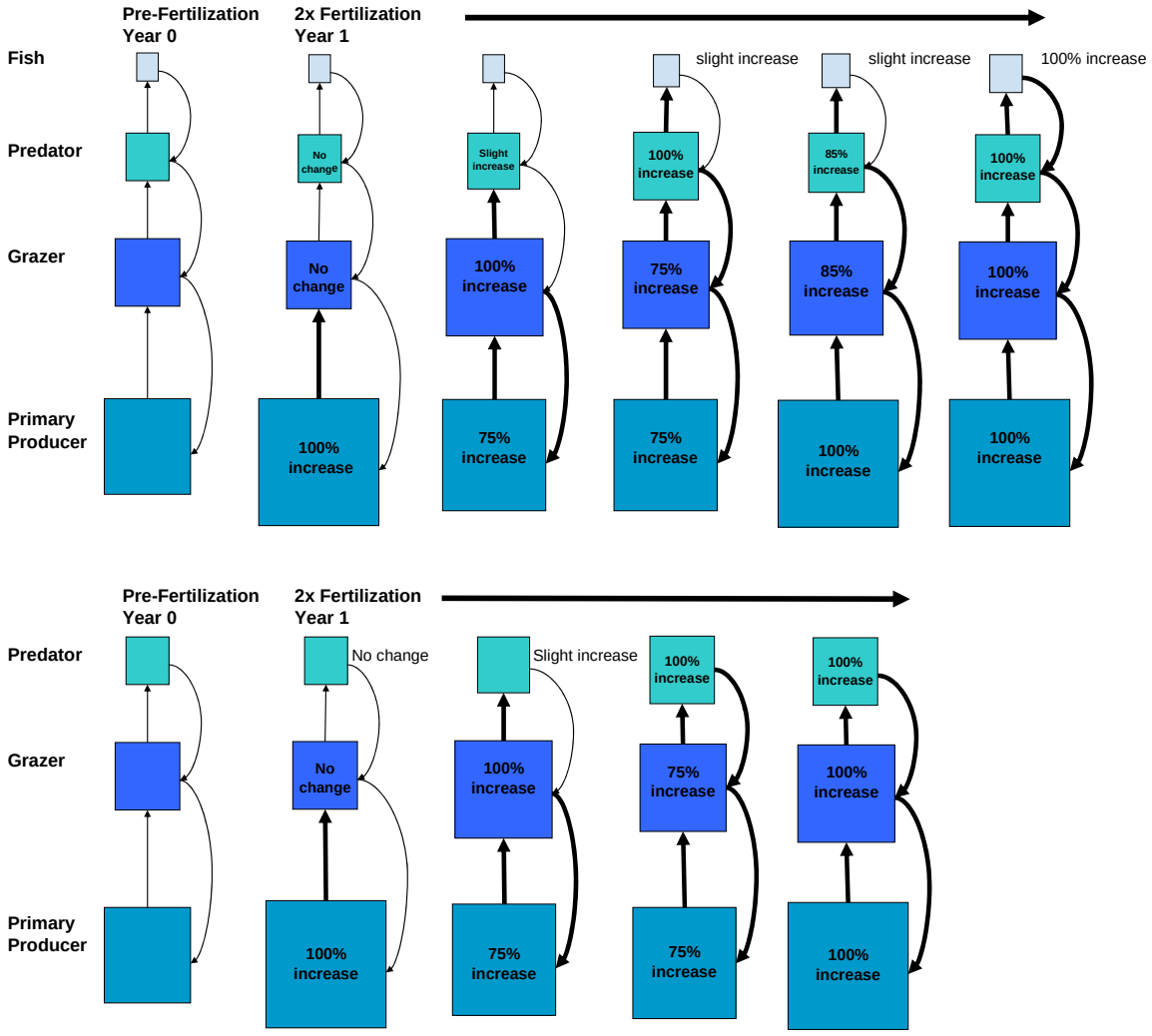

Figure 2. Hypothetical bottom-up and top-down responses to low level fertilization of arctic aquatic ecosystems. Thicker arrows indicate increased energy flow or predatory impact compared to year 0. Similarly, size of boxes indicates biomass. Top: lakes containing fish; Bottom: lakes without fish

Generalized food web models have been published for these arctic lakes (Rublee 1998a; Rublee and Bettez 1995). However, microplankton play such a large variety of roles within the aquatic ecosystems that it is difficult to determine exactly how the food web functions at the microbial level and thus, how the system will respond to perturbations. Finally, as noted in previous studies, perturbations may alter foods webs and community structure, by the appearance or disappearance of species or changes in the dominant species (Bettez *et al.* 2002; Persson *et al.* 2001; Sladecek 1983; Stemberger and Gilbert 1985; Sudzuki 1989). Thus, it is likely that a more complex response will occur then the example of Figure 2 would predict.

This study will examine the response of the microplankton community in the low level fertilization study in arctic lakes begun in 2001. Based on the results of previous studies the following hypotheses are proposed:

Hypotheses

$H1_{O.}$ There will be no change in microplankton biomass or community structure as a result of low level fertilization.

$H1_{A1.}$ There will be a change in microplankton biomass as a result of low level fertilization.

$H1_{A2.}$ There will be a change in microplankton community structure as a result of low level fertilization.

$H2_{O}$. There will be no change in microplankton species composition as a result of low level fertilization.

$H2_A$. There will be a change in microplankton species composition as a result of low level fertilization.

$H3_O$. Lakes with fish will respond identically as lakes without fish to low level nutrient addition.

$H3_A$. Lakes with fish will respond differently from lakes without fish to low level nutrient addition.

In addition to the hypotheses, the appropriateness of the reference lakes was evaluated by comparing the species composition of the lakes during the first few years of the study.

CHAPTER II

MATERIALS AND METHODS

Site Description

The Toolik Lake Arctic Long term Ecological Research Station is located in the northern foothills of the Brooks Mountain Range in Alaska (Figure 3) and has been extensively described (Bettez *et al.* 2002; O'Brien 1992; O'Brien *et al.* 1997; O'Brien *et al.* 2005; Rublee 1998a, 1992, 1998b; Rublee and Bettez 1995, 2001). Briefly, this site includes a variety of oligotrophic, glacial lakes and ponds with varying microplankton, zooplankton and fish populations. These systems have been studied for over three decades and some have undergone experimental manipulations (O'Brien *et al.* 1997). The region has an extreme climate with a mean annual temperature of -9°C and is classified as arctic tundra having permafrost. The annual precipitation is about 31 cm with approximately half of that falling from late May through September. In late September or October ice up to 2 m thick forms on the water and remains until thawing in June. The water temperature in the epilimnion may rise to 12-15° C by late summer. This combination of low rainfall and a cold climate makes nutrients a major limiting factor in the Arctic water bodies. Because of this, these waters are highly oligotrophic (Miller *et al.* 1986), making them an ideal study site for nutrient manipulations.

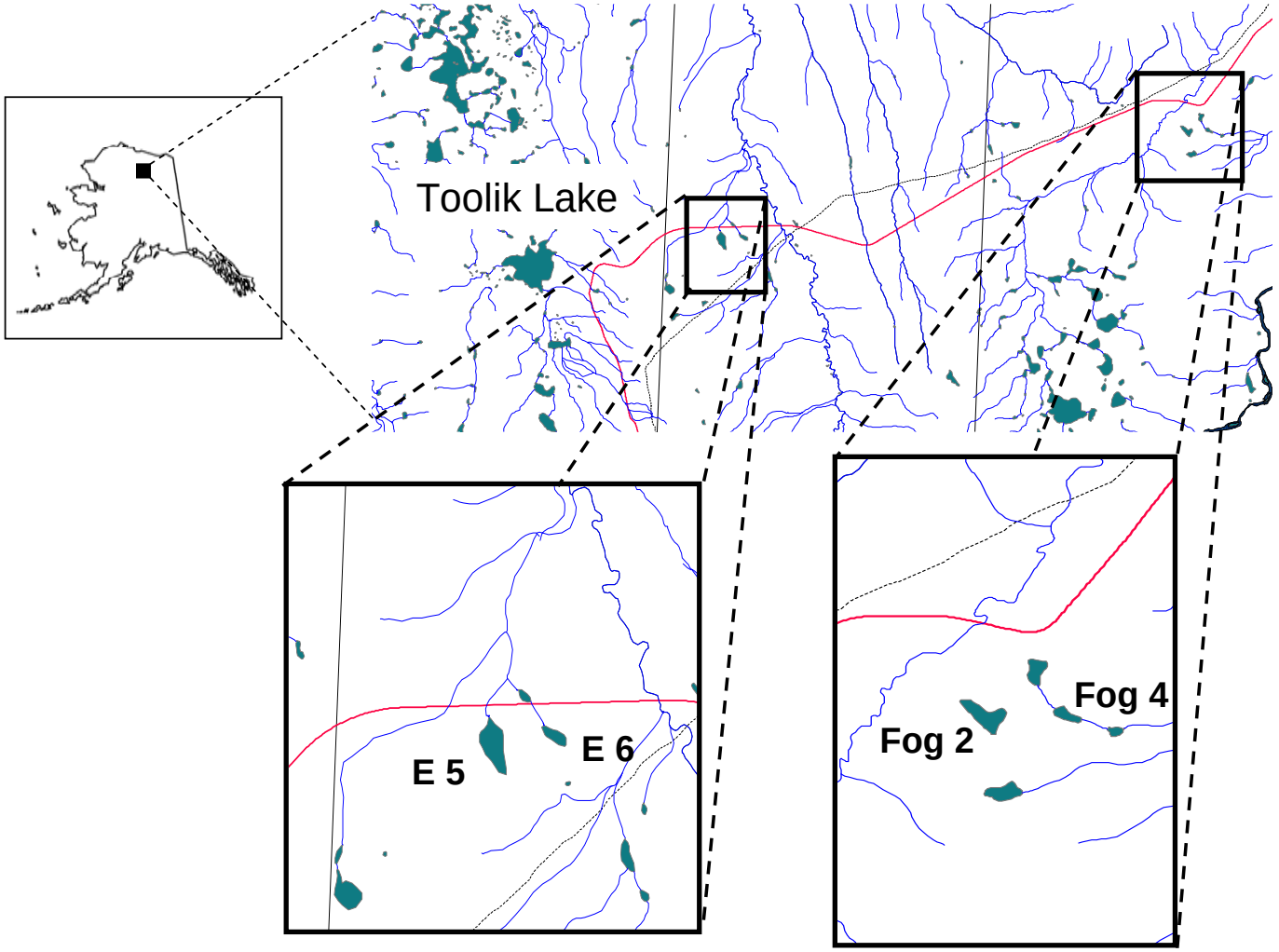

Figure 3. Toolik Lake arctic LTER study sites in the northern foothills of the Brooks Mountain Range in Alaska. (68° 38' N, 149° 43' W).

A fertilization study currently conducted at the arctic LTER site increased nutrients by approximately 2x ambient loading rates in two lakes with the addition of 3 mmol inorganic phosphorus m^{-2} (as H_3PO_4) and 48 mmol inorganic nitrogen m^{-2} ($(NH_4)_2NO_3$). This nutrient addition is similar to what might be found in a realistic scenario of ecosystem alteration as a result of increased human presence in the arctic and should give insight into what actually may occur as a result of low level nutrient addition to an aquatic system. Possible causes of such nutrient additions to arctic lakes include runoff from increased rainfall and increased drainage as a result of permafrost thawing due to climactic shifts (Rouse *et al*. 1997) and possibly human disturbances such as airborne dust from the unpaved access roads.

Methods

This study took advantage of existing samples from these sites to enumerate and identify protozoans and rotifers from experimentally fertilized lakes E5, E6 and reference lakes Fog 2 and Fog 4 over a period of 6 years (1999-2005). Lakes E5 (which contains fish) and E6 (a fishless lake) have been fertilized weekly during the summer at 2x ambient loading starting in 2001. Lake Fog 2 (which contains fish) is a reference for lake E5 and is similar in size and depth and has identical fish species composition (Table 1). Lake Fog 4 (a fishless lake) is a reference for lake E6 (also a fishless lake) both of which are similar in size, depth, and species composition (Table1).

Samples were collected according to Arctic LTER lakes field season protocol by the summer research staff at the Toolik Lake Arctic LTER. Generally, water samples

were collected weekly or biweekly at the surface and at depths of 1, 3, 5, 8, and 12 meters. Samples were taken using a VanDorn bottle then emptied into a bucket. Of this sample 2 liters were concentrated by reverse-flow concentration through a 20-µm Nitex mesh net (Dodson and Thomas 1964). A final volume of 60 ml was preserved with 1% cold glutaraldehyde in 60 ml polypropylene bottles and stored at room temperature until the sample was counted.

Table 1. Characteristics of Arctic LTER lakes sampled in this study. (after Kling *et al.* 1992, and http://ecosystems.mbl.edu/ARC/). List of taxa includes protozoans and rotifers identified in this study

		Lake E5	Fog 2	Lake E6	Fog 4
Area		9.1 ha	6.1 ha	3 ha	2.3 ha
Maximum Depth	**Feeding Type**	10 m	10.5 m	3 m	3.6 m
Ciliated Protozoans					
Oligotrichs	Herbivore*	x	x	x	x
Peritrichs	Herbivore	x	x	x	x
Rotifers					
Keratella cochlearis	Herbivore	x	x	x	x
Keratella quadrata	Herbivore	x	x	x	x
Kellicottia longispina	Herbivore	x	x	x	x
Polyarthra sp.	Herbivore	x	x	x	0
Chromogaster ecaudis	Predator	x	x	x	x
Synchaeta sp.	Herbivore	x	x	0	x
Conochilus unicornis	Predator	x	x	x	x
Conochilus natans	Herbivore	x	x	0	x
Filinia longiseta	Herbivore	x	x	0	0
Gastropus stylifer	Specialist Herbivore**	x	x	x	x
Colletheca mutabilis	Herbivore	x	x	x	x
Crustacean Zooplankton					
Diaptomus pribilofensis	Herbivore	x	x	x	x
Daphnia middendorffiana	Herbivore	0	x	x	x
Daphnia longiremis	Herbivore	0	x	0	x
Bosmina longirostris	Herbivore	x	x	x	x
Cyclops scutifer	Predator	x	x	x	x
Heterocope septentrionalis	Predator	x	x	x	x
Holopedium gibberum	Herbivore	x	x	x	x
Fish Species					
Cottus cognatus	Predator	x	x	0	0
Thymallus arcticus	Predator	x	x	0	0
Salvelinus alpinus	Top Predator	x	x	0	0
Lota lota	Top Predator	x	x	0	0

* feeds on phytoplankton but may also consume bacteria
** feeds on dinoflagellates

Samples were prepared following the method of Baldock (1986). 5 - 10 ml of each sample was stained with 0.25% Rose Bengal solution. The solution was then drawn onto an 8.0 μm pore cellulose acetate filter, and the filter was mounted in 47% sucrose solution. The entire filter surface was then examined at 100x magnification using a light microscope (Zeiss) for microplankton enumeration. Magnification of 400X was used to aid in species identification when necessary. Individual rotifers were identified to species when possible and protozoans were identified to genera using available taxonomic keys (Lee *et al.* 2000; Needham and Needham 1930; Pennak 1989; Ruttner-Kolisko 1974) and information about species composition of those lakes (Chengalath and Koste 1989; De Smet 1994; Rublee 19925;1998; Rublee and Bettez 2001). Nauplii were enumerated but not taxonomically distinguished.

All biomass values (as μg carbon 1^{-1}) were estimated as in Rublee (1982) who based his calculations on measurements of preserved biovolumes and literature values. Briefly, he placed protozoans into size categories and estimated mean biovolume by appropriate geometric formulas for volumes of a cone or sphere. Protozoan biovolume was then converted to protozoan biomass using a conversion factor of 0.14 pg C μm-3 (Putt and Stoecker 1989). For rotifers, Rublee (1992) estimated mean biomass values for individuals of each species from direct measurements of dimensions and appropriate conversion factors to biomass via methods described by Makarewicz and Likens (1979) Pauli (1989) and Ruttner-Kolisko (1977).

Two approaches were used to assess microplankton trends over time in this study. First, samples from all depths were counted from two dates (mid-June and early August)

from each lake in each year. Counts were integrated over depth to estimate mean values. Second, all samples from 1 meter depth were counted for all sampling dates from all lakes in each year. This group of samples allowed a comparison among lake of microplankton in the eplimnetic mixed layer. Linear regression analysis was performed on both sets of data using microplankton biomass as the dependent variable and time (year) as the independent variable to assess trends. Due to the non-normal distribution of direct counts, raw data was log-transformed (log (x +1)) prior to statistical analysis.

Community Measures

Community structure was assessed using three measures. First, Shannon Weaver species diversity index which takes into account both richness and evenness (Smith and Smith 1998) was determined using the annual average abundance of taxa at 1 m. Two measures were used to compare communities: 1) Sorensen's coefficient of community similarity, and 2) Sorensen's percent similarity which takes into account the relative abundance of species in each community (Smith and Smith 1998). Comparisons included: 1) pre-fertilization experimental lakes compared to their reference lake; 2) post-fertilization experimental lakes compared to their reference lake; 3) pre-fertilization experimental lakes compared to their post-fertilization values; 4) lakes with fish lakes compared lakes without fish.

CHAPTER III

RESULTS

Overview

Microplankton observed in lakes E5, E6, Fog 2 and Fog 4 included rotifers, ciliated protozoans and crustacean zooplankton (Table 1). Eleven species of rotifers were identified and *Concohilus unicornis* was the most common. Most ciliates were small oligotrichs (largest ≈50 μm) of the genera *Halteria, Strombidium,* and *Strobilidium*, but the peritrichs *Vorticella* and *Epistylis* were also seen. Most taxa were seen in all lakes.

The range of microplankton biomass observed in all lakes over time was 4.6-31.8 μg $C1^{-1}$ with a mean of 13 μg $C1^{-1}$. Abundance in all lakes over time ranged from 49-1456 individuals l^{-1} with a mean of 501 individuals l^{-1}. The coefficient of variation of count data was high (from 2 to greater than 244%) for yearly average values of counts of major taxa reflecting the high variability often found in direct count data.

Seasonal patterns varied within and among lakes with peaks in biomass occurring at inconsistent times during the year (Figure 4). Abundance of microplankton generally increased with increasing depth of sample (Figure 5). Rotifer abundance at the start of the summer was generally low, and was highest in the experimental lakes (1273 individuals l^{-1} in lake E5, July, 2003). In general, crustacean nauplii biomass equaled or exceeded rotifer biomass and tended to increase over the course of the summer. Early in

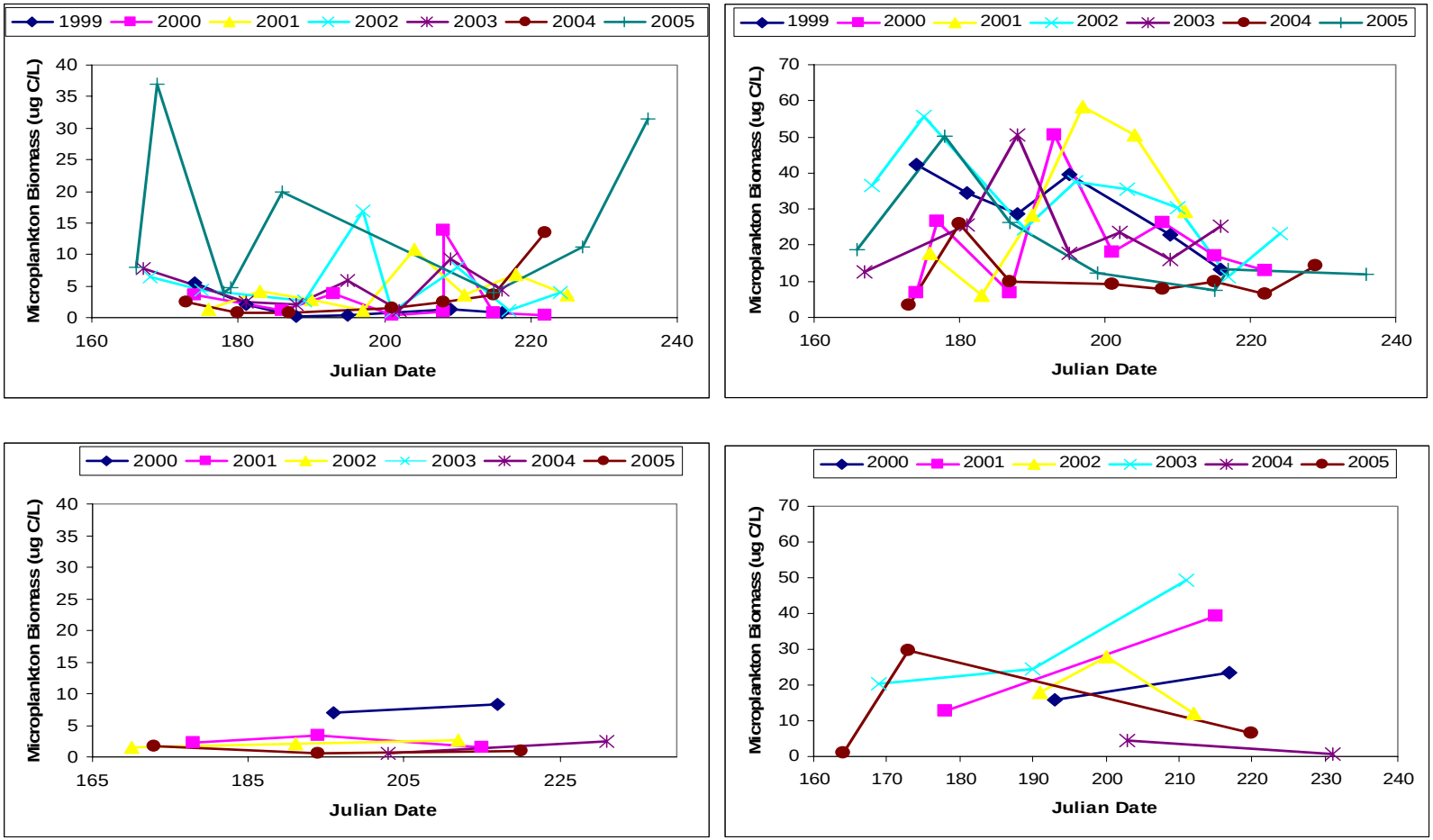

Figure 4. Seasonal variability in microplankton biomass. Top left: lake E5; Bottom left: lake Fog 2; Top right: lake E6; Bottom right: lake Fog 4

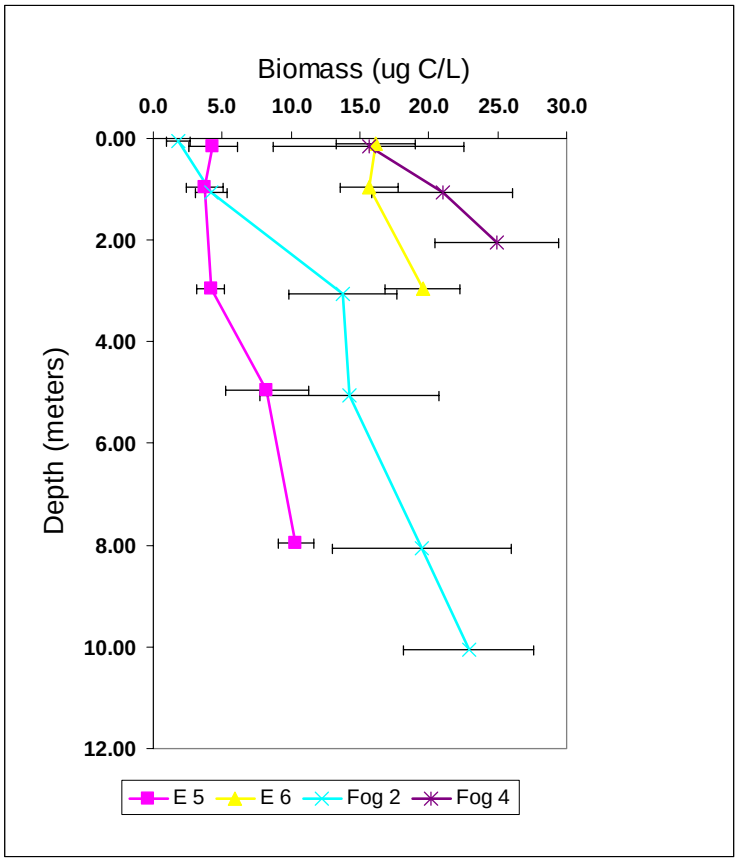

Figure 5. Microplankton distribution by depth. All years are averaged together for each lake. The standard error of each mean is represented by error bars.

the summer protozoans were more numerous than rotifers (range 0 – 4110 protozoans l^{-1} versus 0-576 rotifers l^{-1}) at 1 meter depth.

Overall, the reference lakes, Fog 2 and Fog 4, had lower average microplankton biomass over the 6 years at 1 meter (Fog 2 with 51µg C l^{-1}; Fog 4 with 239 µg C l^{-1}) than the experimental lake each was paired with (E5, 217µg C l^{-1}; E6, 400µg C l^{-1}). Lake E5 had over 4 times more biomass then its reference Fog 2 and lake E6 had about 2 times more biomass then its reference Fog 4. Protozoan abundance at 1 meter was highest in

experimental lake E5 and reference lake Fog 4. Total protozoan biomass was greatest in experimental lake E6 and reference lake Fog 4. Experimental lakes had higher total rotifer biomass then did the reference lakes. Experimental lake E6 and reference lake Fog 4 had the highest abundance and the highest total biomass of crustacean nauplii (Figure 6).

Raw data has been made available on the Toolik Lake LTER website.

Community Comparisons

Microplankton diversity determined as the Shannon Weaver species diversity index (Smith and Smith 1998) showed little change over time within lakes, except for a downward trend in experimental Lake E5 (Figure 7). Comparisons of microplankton community among lakes using Sorensen's coefficient of community and percent similarity indices found that community indices were generally high (>90%) and community similarity was also usually above 50% (Table 2). Exceptions to this were a lower community similarity between pre and post fertilization communities in Lake E5, and lower percent similarity values between lakes with and without fish and in comparisons with post fertilization communities in Lake E-5.

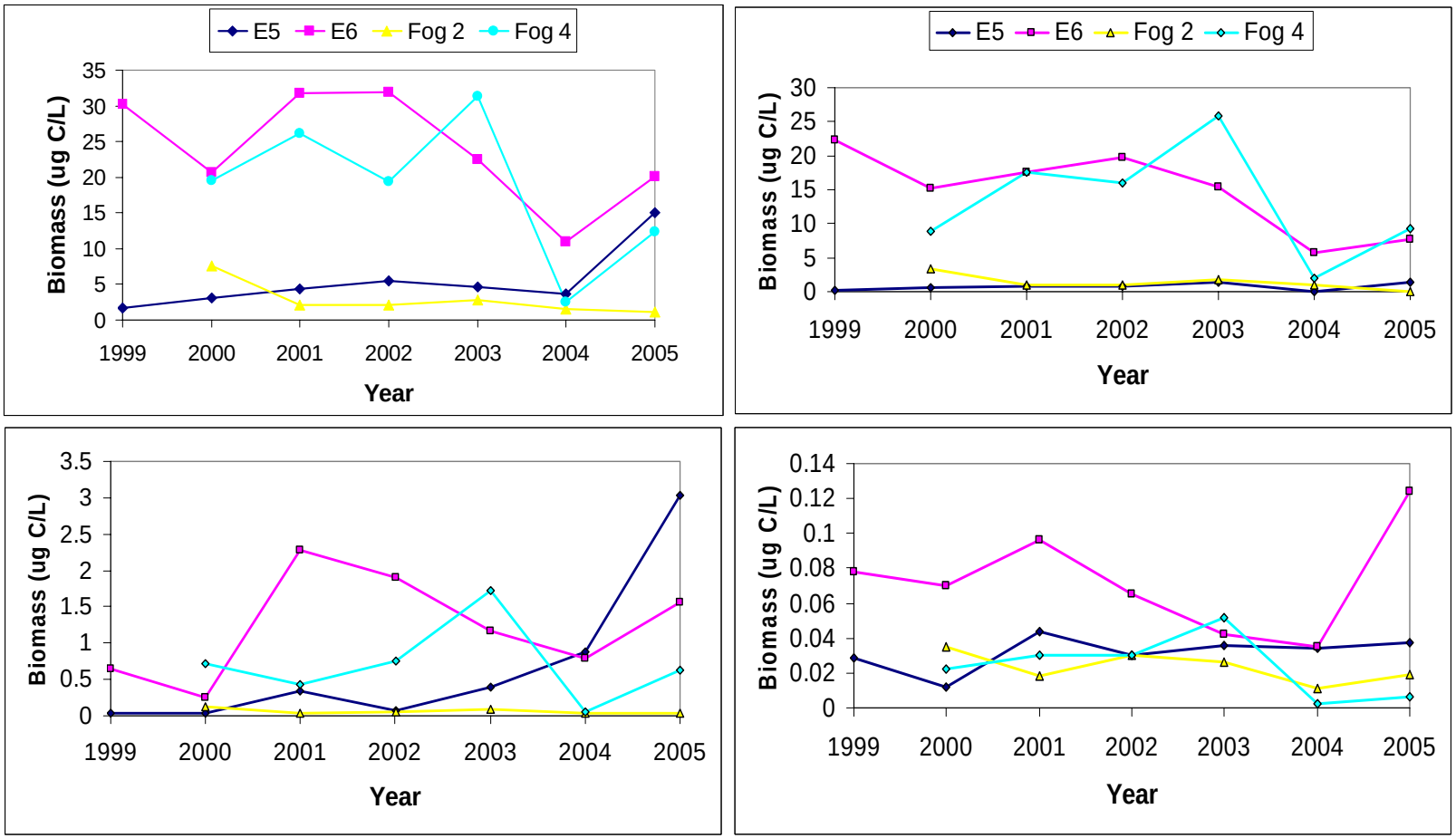

Figure 6. Average total biomass at 1 meter. Top left: total microplankton; Top right: crustacean nauplii; Bottom left: protozoans; Bottom right: rotifers

Table 2. Lake comparisons according to Sorensen's Coefficient of Community Similarity and Percent Similarity.

Comparison Lakes		Sorensen's Coefficient of Community Similarity	Sorensen's Percent Similarity
E5 (pre-fert)	Fog 2	0.92	55.6
E6 (pre-fert)	Fog 4	0.94	51.5
E5 (post-fert)	Fog 2	0.98	22.9
E6 (post-fert)	Fog 4	0.92	50.5
E5 (pre-fert)	E5 (post-fert)	0.80	31.6
E6 (pre-fert)	E6 (post-fert)	0.94	71.7
E5 (fish)	E6 (fishless)	0.90	88.1
Fog 2 (fish)	Fog 4 (fishless)	0.95	34.8

Analysis

Linear regression analysis of total microplankton biomass at 1 meter versus year found that the slope was not statistically different from zero in either experimental lake although there appeared to be a slight increase with the start of fertilization in Lake E5 (Table 3). Except for *Vorticella* in lake E5 there were no significant changes in biomass over time. Regression analysis of change in protozoan biomass at 1 meter in lake E5 (post-fertilization) over time was statistically significant. There were no significant changes in abundance or total biomass of rotifers or crustacean nauplii as a result of fertilization in the experimental lakes (Figure 6).

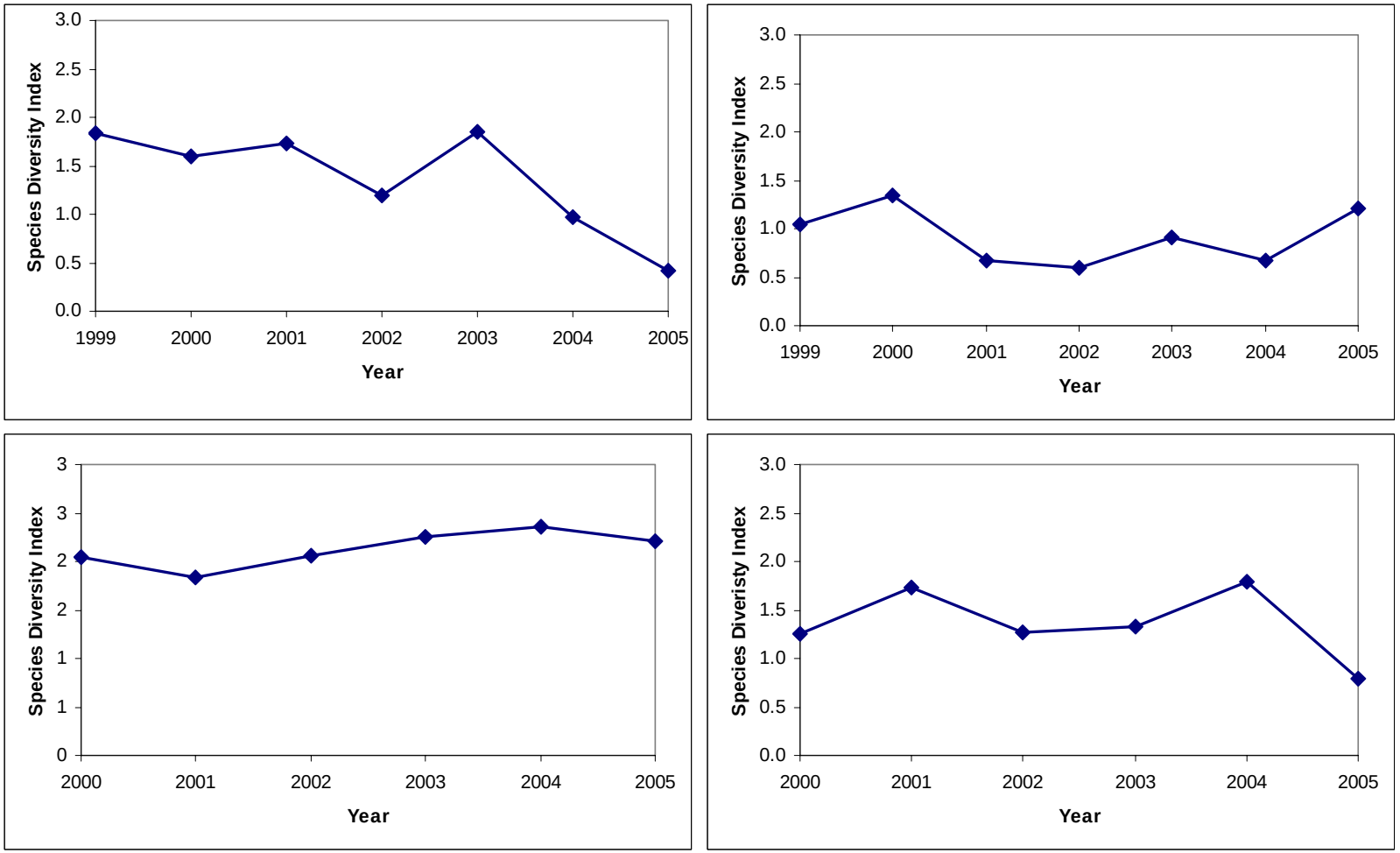

Figure 7. Shannon Weaver Species diversity index, Top left: lake E5; Top right: lake E6: Bottom left: lake Fog 2; Bottom right: lake Fog 4.

Table 3. Regression analysis of total microplankton biomass at 1 meter over the study period

Lake	Coefficent	F	P value	d.f.
E5	0.356	5.521	0.066	5
E6	-0.163	2.612	0.167	5
Fog 2	-0.583	5.020	0.089	4
Fog 4	-0.092	1.340	0.311	4

Regression analysis was also run for each microplankton taxa. In lake E5 regression analysis of *Vorticella* biomass at 1 meter over time had a slope that was significantly different from zero (regression coefficient = 1.264; F = 18.27; p=0.007; d.f. =5) (Figure 6) as was protozoan biomass over time (regression coefficient = 0.495; F = 7.381; p= 0.041; d.f. =5). However, analysis of protozoan biomass over time, with *Vorticella* excluded, found no statistically significant pattern (regression coefficient = 0.451; F = 1.780; p= 0.239; d.f. =5) (Figure 6). No significant correlations existed for any other taxa.

Linear regression analysis of total microplankton biomass as a depth integrated sample found only one significant result: a negative trend in lake Fog 2 (regression coefficient = -0.5706; F = 37.316; p= 0.003; d.f.= 4) (Figure 8).

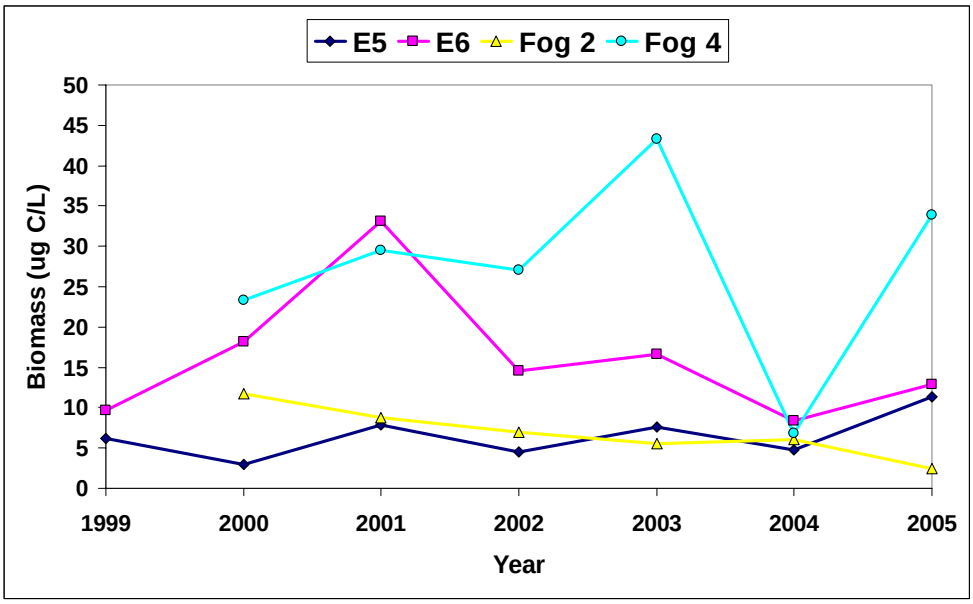

Figure 8. Total microplankton biomass as a depth integrated sample. Regression analysis found a statistical significant negative trend in reference lake Fog 2 which contains fish (regression coefficient = -0.5706; F = 37.316; p= 0.003; d.f.= 4)

CHAPTER IV

DISCUSSION

The purpose of this study was to address specific hypotheses concerning the effects of low levels of nutrient addition on microplankton in arctic aquatic systems and to compare these results to the findings from high level nutrient addition studies. First, it should be noted that there was response to nutrient addition in these lakes documented by LTER researchers who studied other taxa. There was an increase in biomass of the primary producers as indicated by chlorophyll *a* values (Figure 9, and G. Kling, University Michigan, personal communication). There was no clear pattern or statistically significant change in zooplankton biomass or abundance in the experimental or reference lakes, although there was a slight increase in the predatory zooplankter *Heterocope* over time (C. Luecke, Utah State University, personal communication). Also, in experimental lake E5 there was no increase in fish biomass over time (C. Luecke, Utah State University, personal communication).

Overall, the microplankton communities observed in this study were similar to those found in other arctic LTER lakes. Rotifer species found in this study have been reported on species lists of arctic lakes (Chengalath and Koste 1989; Rublee 1992) and protozoan taxa were also similar to those reported in arctic LTER lake studies (Rublee 1992; 1998; Rublee and Bettez 2001). Average yearly microplankton biomass and

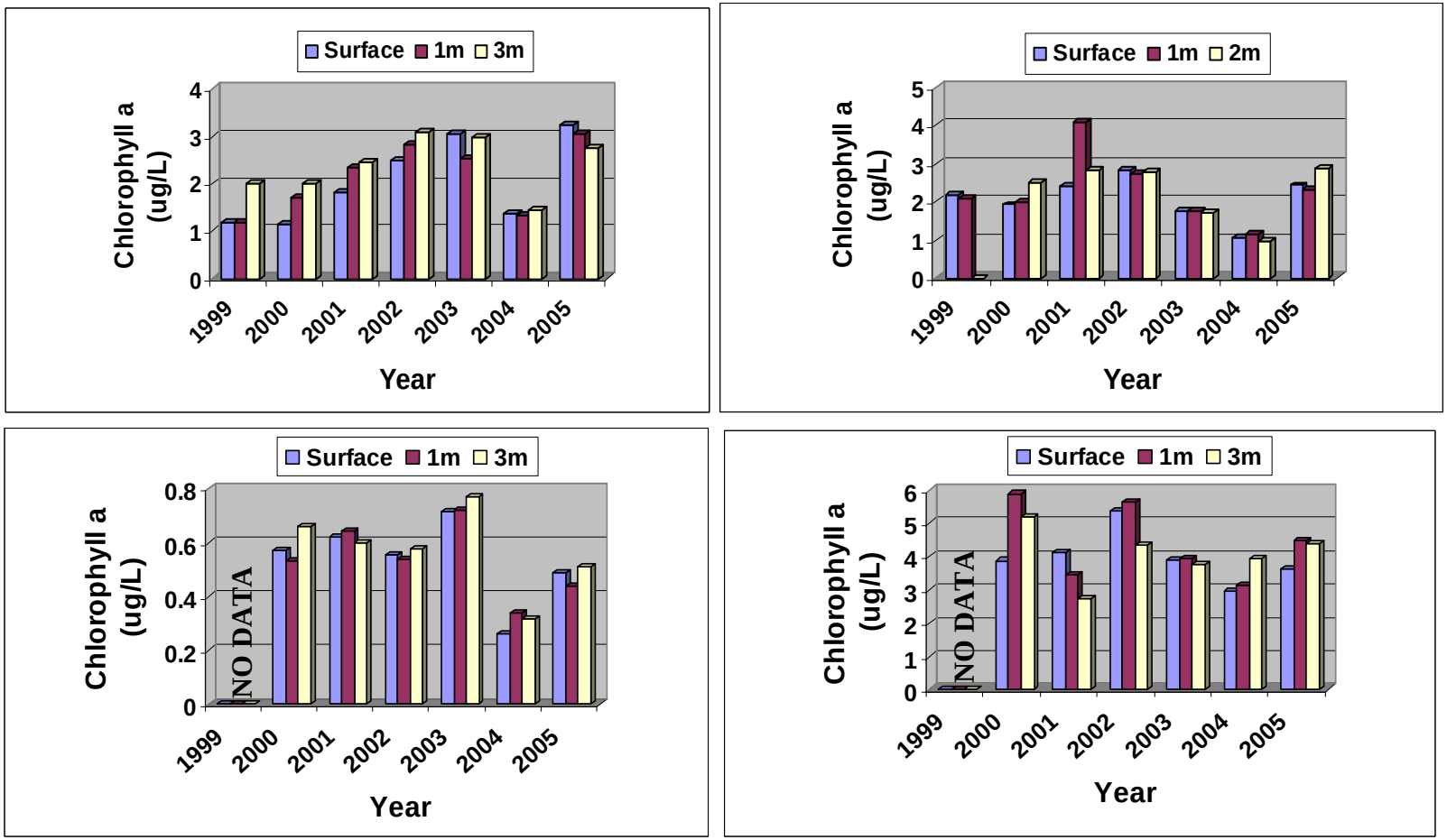

Figure 9. Chlorophyll *a* concentration in study lakes over time. Top left: lake E5, Bottom left: lake Fog 2, Top right: lake E6, Bottom right**:** lake Fog 4. Data from Toolik Lake LTER (http://www.lternet.edu/sites/arc/)

abundance at 1 meter in all lakes were within the range of numbers found by Rublee (1992) for other arctic LTER lakes. Finally, seasonal patterns (Figure 4), though variable, and depth distribution patterns (Figure 5) are also consistent with previous reports (Rublee 1992; 1998; Rublee and Bettez 2001).

Reference lakes were considered to be a reasonable comparison (Table 1) for the experimental lakes although they were not perfect. Pre-fertilization experimental lake E5 had a very similar species composition (coefficient 0.92) to reference lake Fog 2. However, these lakes had only moderate similarity when it came to the abundance of the species (55.6% similar) present (Table 2). Pre-fertilization lake E6 also had very similar species composition (coefficient 0.94) to reference lake Fog 4. But, there was also moderate similarity when it came to the abundance of the species (51.5% similar) present (Table 2).

I hypothesized that there would be a change in microplankton biomass or community structure as a result of low-level fertilization (H1). Overall, there was no significant change in microplankton biomass in the experimental lakes based on the result of regression analysis. However, the biomass of one taxon of microplankton, *Vorticella,* in lake E5 did exhibit a significant increase in abundance over the course of the study. In experimental lake E5 (which contains fish) total protozoan biomass increased significantly over time (Figure 7). Closer examination of the protozoan community found that a large portion of the community (80%) was comprised of *Vorticella.* When *Vorticella* was omitted from regression analysis there was no statistically significant change in protozoan biomass over time (Figure 7). Because there was a change in

community structure and no change in biomass, $H1_O$ was rejected as was alternative hypothesis $H1_{A1}$. Alternative hypothesis $H1_{A2}$, that there would be a change in community structure as a result of low level fertilization, was accepted.

Post-fertilization experimental lake E5 was more similar to reference lake Fog 2 then it was before nutrients were added to the system. Sorensen's community similarity coefficient dropped from 0.98 to 0.92. However, when abundance of species was taken into account the lakes were less similar after fertilization (22.9% similar) then before (55.6% similar) fertilization (Table 2). This is likely due to the increased abundance of the protist *Vorticella.* The lake E5 pre-fertilization community compared to its post-fertilization community showed reduced community similarity (coefficient 0.80) and based on species abundance was very different (31.6% similar) after the addition of nutrients (Table 2).

Pre-fertilization lake E6 was similar to its reference lake (similarity coefficient = 0.92). This changed little with the addition of nutrients (similarity coefficient = 0.94). Sorensens's percent community similarity found moderate similarity both pre-fertilization (51.5% similarity) and post fertilization (50.5% similarity) between the two lakes (Table 2). When pre-fertilization lake E6 was compared to itself post-fertilization the communities were found to be very similar (similarity coefficient = 0.94). When species abundance was taken into account the two were still generally similar (71.7% similarity) (Table 2).

The significant increase in *Vorticella* biomass only occurred in the experimental lake containing fish (E5) and is consistent with results of high level nutrient addition

studies in arctic lakes N1 and N2 (Bettez *et a*l. 2002; Rublee 1992; Rublee and Bettez 1995) and may indicate a top-down effect of fish predation on crustacean zooplankton predators or an increase in available food. *Vorticella* is a bacterivore and in a limnocorral study by Hobbie *et al.* (1999) the abundance of both bacteria and heterotrophic nanoflagellates increased with increased nutrient input, both which went unmeasured in this study.

The Shannon Weaver species diversity index (Smith and Smith 1998), which takes into account both species richness and evenness, was used to assess community trends (Figure 6). Both reference lakes and experimental lake E6 experienced no change in diversity over time. In experimental lake E5 there was a statistically significant loss of diversity over time (coefficient = -0.19; F= 7.34; p = 0.042; d.f. = 5) which was attributable to the increase in *Vorticella* abundance.

The null hypothesis $H2_{O,}$ that there would be no change in species composition as a result of low level fertilization, was accepted. The low level addition of nutrients to experimental lakes did not bring about changes in microplankton species composition. This is different from the results of other high level nutrient addition LTER lake studies (Bettez *et al.* 2002; Rublee 1992, 1998; Rublee and Bettez 1995) where 'new' microplankton species appeared following nutrient addition to the system.

Null hypothesis 3, which stated that lakes with fish and lakes without fish will respond identically to low level fertilization, was rejected and the alternative hypothesis, that lakes with fish will respond differently then lakes without fish, was accepted. The microplankton community of experimental lake E5, which contains fish, was less like its

reference lake after the addition of nutrients (Table 2). Experimental lake E6, which doesn't contain fish, was still very similar to its reference lake after the nutrient addition (Table 2).

The picture painted by these results is a complicated one due to variability in the data which partly results from the use of microscopic count data (with high coefficient of variation) and also to inter-annual variability in temperature and rainfall. Assessing the response of intermediate trophic levels to low level fertilization is difficult because the signal may be small relative to biologically important forcing variables such as temperature and rainfall. During the period of this study inter-annual variation (temperature) was high (personal communication C. Luecke, Utah State University; data provided by Toolik Lake Arctic LTER station) and could have masked small changes that occurred as a result of nutrient additions. For example, in lake E5 the summer season average (June-August) for water temperature at 1 meter ranged from 9.8 °C in 2003 to 14.5 °C in 2004 while the temperature in lake E6 ranged from 11.8 °C in 2002 to 15.3 °C in 2004.

Although low level nutrient addition did not elicit a large scale microplankton response such as seen in previous studies, a subtle response may have occurred. Three factors indicate this: 1) experimental lakes maintained microplankton biomass and abundance while both declined within the reference lakes; 2) previous studies by Hobbie and colleagues (1999) show rapid "pulsed" microplankton response (1-3 days) that may have been missed by the sampling frequency of this study (7-10 days); 3) there is some evidence of an increase in zooplankton within the experimental lakes. Increased

zooplankton could decrease microplankton abundance and mask any increases that had occurred.

Hobbie and colleagues (1999) observed that, as a result of dissolved organic nutrient addition to mesocosms in an arctic lake, there was an increase in chlorophyll *a* levels and bacteria abundance. This was quickly followed (days) by increased abundance of protozoans then by an increase in rotifers and next by a subsequent increase in zooplankton. Had sampling of the lakes in the current study occurred more often (such as every other day) it is possible that a similar pattern would have been observed in the experimental lakes. However, the goal of this study was to document long term changes, so higher frequency of sampling was not desirable.

There is evidence of an increase in crustacean zooplankton abundance and biomass in experimental lakes at 1 meter (personal communication C. Luecke, Utah State University). Predatory *Heterocope* zooplankton responded slightly to the low level nutrient addition however no changes were seen in other zooplankton species. This might be expected as changes in zooplankton and higher trophic levels such as fish are subject to longer time lags and in other studies zooplankton took up to a year to respond to high-level nutrient additions (Hobbie 1999; Rublee and Bettez 1995). Also, if zooplankton abundance or biomass increased in the lakes containing fish, it's likely that predation would quickly reduce it. This would occur within a short period, likely days, and due to the sampling interval of this study these short term responses may have been missed.

There was no increase in fish biomass in experimental lake E6 compared to its reference lake Fog 4 (personal communication, C. Luecke; Utah State University), this differs from the results of other arctic lake studies (Lienesch *et al.* 2005). However, because fish are long lived and slow to grow, especially in the cold climates, this would be better studied over a much longer time period. Because of the difference in life histories between the high trophic levels and lower trophic levels, responses may have a time delay before they become established or appear significant.

The response of lake E5 and lack of response in lake E6 communities, to low level nutrient addition, was considerably less that that found in high level nutrient additions in other arctic lake studies. Rublee and Bettez (1995) and Hobbie *et al.* (1999) found an increase in protozoa abundance and biomass in experimentally fertilized lake N1 as well as in mesocosms experiments. However, both studies also found little response by rotifers and only a slight increase in crustacean zooplankton abundance which is similar to the results of this study. Rotifer biomass and abundance were not significantly different among years in the current study which is consistent with other studies of arctic lakes (Rublee and Bettez 1995). Rotifer biomass and total microplankton biomass varied over time in lake E5 and Fog 2 (Figure 6).

There are many possible reasons for little change in microplankton abundance and biomass in response to low level nutrient addition. Other studies which found responses used high levels of nutrient additions (4-10 times the annual ambient loading rate) in arctic lakes (Bettez *et al*. 2002; Hershey 1992; Rublee 1992; Rublee 1998a; Rublee and Bettez 1995) while the nutrient addition levels used in this study, approximately 2 times

the annual ambient loading, rate may have been too low to initiate a response. Also, estimates of loading rates were extrapolated from Toolik Lake, not each individual experimental lake, and because of this could have been lower than the estimated 2 times ambient loading. More information on sediment types of each lake may be beneficial, as other studies (Rublee and Bettez 2001) suggested that the structure of lake sediments may affect the amount of added nutrients that are available for uptake within that system.

Studying the effects of low level nutrient addition to aquatic systems poses many difficulties. Some of these difficulties are easily resolved while the logistics of resolving others may prove to be too costly. Increasing sample size and sampling frequency would provide a more complete picture of changes in the system and increase the accuracy of statistical analysis. Sampling more often (every other day) would allow for more accurate analysis of trophic level interactions by accounting for rapid responses from organisms with high metabolic rates and short generation times that make up the lower trophic levels.

Although not as drastic as those found in previous arctic lake studies, changes did occur within this system the significance of which is still unclear. Thus, continuation of this study is important for insight into the long term effects of enrichment on aquatic systems. This is valuable because these nutrient addition rates are approximate to those expected from anthropogenic sources. Once humans impact an area the impacts are not likely to lessen. This makes understanding the effects of long term nutrient addition both important and valuable.

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