

Asymmetrical food web responses in trophic-level richness, biomass, and function following lake acidification

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Abstract We tested for disproportional changes in annual and seasonal species richness and biomass among five trophic levels (phytoplankton, herbivorous, omnivorous, and carnivorous zooplankton, and fish) as well as altered trophic structure and ecosystem function following the 5-year experimental acidification of Little Rock Lake (Wisconsin, USA) from pH 6.1 to 4.7. Abiotic and biotic controls of trophic level response during acidification were also identified. Asymmetric reductions of species richness among trophic levels, separated by life stage and feeding type, were evident and changes in trophic structure were most pronounced by the end of the acidification period. Relative declines in richness of fish and zooplankton were greater than phytoplankton, which were generally unaffected, leading to a reduction of upper trophic level diversity. Each of the lower four trophic levels responded to a distinct combination of abiotic and biotic variables during acidification. pH was identified as a direct driver of change for only carnivorous zooplankton, while all

other trophic levels were affected more by indirect interactions caused by acidification. Fluctuations in ecosystem function (zooplankton biomass and primary production) were also evident, with losses at all trophic levels only detected during the last year of acidification. The acidified basin displayed a tendency for greater variation in biomass for upper trophic levels relative to reference conditions implying greater unpredictability in ecosystem function. Together, these results suggest that trophic asymmetry may be an important and recurring feature of ecosystem response to anthropogenic stress.

Keywords Aquatic food web · Ecosystem function · Fish · Phytoplankton · Zooplankton

Introduction

Trophic sensitivity to ecosystem stress is predicted to be greater for upper trophic levels, thereby disrupting fundamental food web interactions and processes (Odum 1985; Menge and Sutherland 1987). As such, predation by consumers can be significantly reduced while primary production and decomposition rates, mediated by lower trophic levels, should not be altered as much (e.g., Schindler et al. 1985; Stenson et al. 1993). Theoretical modeling of changes in habitat quality has shown more rapid loss of species belonging to upper trophic levels in freshwater, marine, and

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terrestrial environments (Dobson et al. 2006). However, emerging empirical evidence from impacted aquatic and terrestrial systems exist to support increased species and biomass losses at higher trophic levels (Dodson et al. 2000; Jackson et al. 2001; Vinebrooke et al. 2003; Voigt et al. 2003). These disproportionate losses at higher trophic levels can generate asymmetrical responses in food web structure and have important implications for the flow of energy in aquatic systems.

The prevalence of trophic asymmetry as a response to stress, and precisely whether or how ecosystem function might be altered as a result, is not well-established. Dispersal limitation, reduced functional redundancy, or increased physiological sensitivity to environmental stress for species in higher trophic levels are potential mechanisms that may directly result in trophic asymmetry (e.g., Menge and Sutherland 1987; Ives et al. 1999). However, given the complexity of many aquatic food webs, the potential for a myriad of indirect effects also exists (e.g., Yodzis 1980; Martinez 1991). Further examination of this trophic response in similar, stressed systems is needed to test its generality and investigate the causal mechanisms underlying this pattern.

Factors regulating community structure in stressed ecosystems vary according to trophic position (Menge and Sutherland 1987) and acidification is known to alter the relative importance of these factors (e.g., Locke 1992). As a result, different trophic levels may respond to different combinations of abiotic and biotic factors during acidification. Many previous studies have highlighted the importance of concomitant changes in abiotic factors and biotic interactions to alter community responses during acidification. For example, the reduced availability of dissolved inorganic carbon (DIC) has been linked to the proliferation of filamentous green algae in the littoral zones of acidified lakes (Turner et al. 1987). Similarly, increased water clarity, owing to acidification-induced declines in dissolved organic carbon (DOC), is responsible for increases observed in deepwater phytoplankton production (Dillon et al. 1984). On the whole, however, most changes have been discussed with little regard for their trophic dependence, although the experimental work of Frost et al. (1999) in Little Rock Lake (LRL) begins to document the diversity of responses from an organismal perspective. We build on that work by revisiting the LRL experiment to test for the hypothesized asymmetry in trophic level response to disturbance.

Given the seasonality of aquatic communities, the intra-annual dynamics characteristic of different trophic levels also needs to be examined for a complete picture of the trophic dependence of species loss. Species generally abundant in the spring might be more sensitive to a given stress than those found during fall. Such patterns of seasonal sensitivity have been documented for zooplankton in response to ultraviolet radiation (Xenopoulos et al. 2000) and methylmercury contamination (Cleckner et al. 2003). Seasonal dynamics in the taxonomic composition of zooplankton can be a regular feature of lakes (e.g., Frost and Montz 1988), but has not yet been exploited for its potential to improve our understanding of the hypothesized heterogeneity in trophic level response.

Finally, the nature of the response of trophic levels to ecosystem disturbance may be linked to altered variability of that trophic level associated with the disturbance (Cottingham et al. 2000; Vogt et al. 2006). If sustained, increases in variability for a given trophic level will reduce our ability to predict its dynamics. Subsequent transmission of this variability throughout the food web may result in altered dynamics for the entire ecosystem (Carpenter 1988). We test for increased variability of species richness and biomass at different trophic levels due to acidification which continues to be a globally important stress on aquatic ecosystems particularly in many developing countries where sulphur dioxide and nitrogen oxide emissions are now on the rise (e.g., Seip et al. 1999).

In this article, we use data from LRL to test the hypothesis that acidification results in asymmetric changes in richness, biomass, and ecosystem function (i.e., primary productivity) among trophic levels and to identify potential mechanisms associated with this response. Trophic levels were distinguished based on functional traits (i.e., zooplankton were divided by life stage and feeding type). In addition to changes in water quality, many ecological changes occurred in LRL following experimental acidification (summarized in Brezonik et al. 1993 and Frost et al. 1999). Species richness and food web structure were affected in a complex manner due to differing tolerances to decreased pH (e.g., Frost and Montz 1988; Eaton et al. 1992; Fischer et al. 2001a), altered species interactions (Fischer et al. 2001b), increased food availability (Webster et al. 1992), reduced grazing pressure (Fischer et al. 2001b), and compensatory dynamics (Frost et al. 1995, 1998). We do not

focus on these species-specific responses, instead, we test the trophic dependence of these changes with the specific objectives of (1) documenting species loss by trophic level following lake acidification at both annual and seasonal time-scales as well as the interactions with abiotic and biotic factors resulting from acidification, (2) examining the relationships between species loss and ecosystem function at a whole-lake scale, and (3) testing the hypothesis of increased trophic level variability in response to acidification. Thus, this study goes beyond the somewhat more descriptive work that precedes it by testing for an emergent property of response to aquatic ecosystem stress—one that may have wider applicability to other perturbations as well as other ecosystems.

Methods

Study lake and acidification history

LRL, a small (18-ha) low-conductivity, clear water, mesotrophic seepage lake in northern Wisconsin (45°59'55" N, 89°42'15" W), was the site of a whole-lake acidification experiment from 1984 to 1991. The two basins of LRL were separated with a plastic curtain and monitored during 1984 prior to the start of the experimental phase in the northern basin (treatment) in 1985. During sulfuric acid addition the pH was lowered from 6.1 to 4.7 in a stepwise fashion with intermediate target values of 5.6 and 5.1 being maintained for 2 years each. A detailed description of LRL responses to acidification are provided by Frost and Montz (1988), Eaton et al. (1992), and Brezonik et al. (1993). Briefly, concurrent with the experimental reduction in pH, the treatment basin experienced an increase in major cations (Ca in particular) as well as several minor and trace elements (Al, Mn, Fe, and Zn) relative to the reference basin (Frost et al. 1999). In addition, microbial activity rose substantially in the treatment basin as sulfate from the acid additions was processed by sulfate-reducing bacteria—a process that likely also enhanced methyl mercury formation and its increased bioaccumulation throughout the treatment food web (Frost et al. 1999). Water clarity also increased in the treatment basin which allowed greater penetration of both photosynthetically active as well as harmful UV-A and UV-B radiation (Frost et al. 1999).

Sampling and taxonomic analyses

The methods for sampling, preparation, and analysis of physical and chemical variables, as well as phytoplankton, zooplankton, and fish populations were undertaken using standard limnological techniques and are detailed elsewhere (Frost and Montz 1988; Swenson et al. 1989; Eaton et al. 1992; Brezonik et al. 1993). However, because our focus is on biological response variables, we briefly outline sampling for the phytoplankton, zooplankton, and fish communities here. Integrated whole-water column phytoplankton samples were collected from a central sampling station using 10 mm diameter plastic tubing and a 5 ml subsample was identified and enumerated at 400× with an inverted microscope (Merz 2003). Zooplankton were also collected at a central station in each basin with a 30-l Schindler-Patalas trap equipped with a 53-μm mesh that sampled 0, 4, and 6 m in the reference basin and 0, 4, and 8 m in the treatment basin (Frost and Montz 1988). Fish abundances were determined using a combination of techniques including fyke nets, angling, electrofishing, and minnow traps (Swenson et al. 1989). We note that sampling for all variables was generally conducted throughout the ice-free season at fortnightly intervals and approximately once per month throughout the winter, with the exception of fish population estimates which were primarily conducted during intensive spring and fall sampling periods. All organisms were identified to species, with the exception of a limited number of phytoplankton taxa which were grouped as genera. Copepod zooplankton and fish were also identified to their life cycle stage according to size and appearance. Whole-basin zooplankton biomass was estimated using published (e.g., Culver et al. 1985) and derived length-weight regressions applied to hypsometrically-weighted density estimates and mean lengths measured for each species (or life cycle stage) from a subset of the sampled individuals.

Trophic-level assignments

The analysis presented here focused on five trophic levels: primary producers, primary consumers (herbivorous zooplankton), secondary consumers (omnivorous zooplankton), tertiary consumers (carnivorous zooplankton) and quaternary consumers (all fish). This

latter trophic level was summarized at annual intervals while all others are represented at both annual and seasonal time scales (three seasons: spring, summer and fall/winter combined). We also aggregated the zooplankton into a single trophic group as is commonly done in many lake studies (e.g., Micheli et al. 1999).

All phytoplankton counted from LRL treatment and reference basin were grouped and assigned to trophic level 1 (primary producers). Zooplankton, including rotifers which are often excluded when characterizing zooplankton communities, were combined and divided into three trophic levels (levels 2–4) based on their life stage and feeding type following Thorp and Covich (2001), Hutchinson (1967), and Fischer et al. (2001b): (a) trophic-level 2 was comprised of primary consumers and included all herbivorous zooplankton; (b) trophic level 3, secondary consumers, combining all omnivorous zooplankton; and (c) trophic level 4, tertiary consumers, combining all carnivorous zooplankton. Copepods, originally identified by species and copepodid stages, were counted as separate “species” if the bulk of their diet changed between life cycle stages. For example, *Mesocyclops edax* copepodids 1 and 2 were counted as herbivorous, copepodids 3, 4 and 5 as omnivorous, and copepodid 6 as carnivorous. This separation was necessary for two reasons. First, more useful information on zooplankton population dynamics can be obtained if the stages in the life history of species are analyzed separately than if only the total population is measured (Wetzel 2001). Second, this separation allowed us to examine specific responses of the different trophic levels that may in themselves be differentially sensitive (e.g., *Mesocyclops* copepodid 1 may be more sensitive to acidification than *Mesocyclops* copepodid 6, etc). Most studies of zooplankton trophic structure ignore the ontogenetic shifts in diet observed in many taxa (Thorp and Covich 2001). Here, we explicitly consider these functional traits (cf. Barnett et al. 2007) when assessing trophic level response to stress. All five fish species [yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*), largemouth bass (*Micropterus salmoides*), black crappie (*Pomoxis nigromaculatus*) and mudminnows (*Umbra limi*)] in LRL were placed into trophic level 5, quaternary consumers and all fish species were used in the richness analyses and thus represent a mix of planktivorous and piscivorous species. Biomass data, however, were only available for young-of-the-year (YOY) yellow perch (Eaton et al. 1992; Brezonik et al. 1993) and are thus confined to a

single trophic level (planktivorous fish) (Appendix 1: Trophic level assignments).

The 6-year duration of the LRL acidification experiment was not long enough to detect declines in the abundance of adult fishes. However, in another whole-lake acidification experiment (Lake 223, Experimental Lakes Area, Ontario, Canada; Schindler et al. 1985), a decline of adult fishes was detected following complete recruitment failure of all seven species originally present in the lake after 20 years. Therefore, in our analysis, recruitment failure (absence of YOY for a given fish species) was treated as species extirpation.

Data analysis

We used photosynthetic rates measured as ^{14}C -uptake (Fee 1990) as a direct measurement of primary productivity. These latter data were available for the open water season (June–August) from 1985 to 1989 and were only used in the annual analysis (average of six measurements per year). For the seasonal analysis, we used mean phytoplankton biomass, measured as chlorophyll *a* concentration, as a potential correlate of phytoplankton production (Morin et al. 1999). Similarly, we analyzed zooplankton and fish biomass, but note that they tend to be correlated with secondary and fish production (Plante and Downing 1989; Shuter and Ing 1997; Randall et al. 1995). Differences in secondary production rates have also been inferred from differences in biomass in LRL previously (Frost et al. 1995).

We set the year 1985 as the baseline to begin estimating loss in species richness and ecosystem function because the acidification treatment began in the spring of this year. Richness counts included rare species. Loss was calculated as natural log percent change from the 1985 baseline values (as $100 \cdot \log_e (y/x)$)—Tornqvist et al. 1985, where $y = 1986, 1987, 1988, 1989, 1990$ and $x = 1985$) either annually or for the three different seasons beginning with spring 1985, followed by summer 1985, and fall/winter 1985–1986. Log percent change is the only symmetric, additive, and normed indicator of relative change (Tornqvist et al. 1985). It alleviates, to the greatest extent possible, the problem of unequal richness across trophic levels (e.g., carnivorous zooplankton = 5 species vs. phytoplankton = 159 species) which could have a confounding effect. We analyzed species loss and changes in biomass and primary productivity between the two basins during

the three seasons as follows: (1) spring open water (April–June); (2) open water (July–September); (3) fall overturn and winter (October–March).

We used Spearman rank correlations to detect relationships in the reference and treatment basins between species richness and biomass or primary production of all trophic levels at both annual and seasonal scales ($n = 5$). Richness is expected to be, in general, positively correlated with biomass and function (sensu Tilman 1996). We also tested whether the interannual variability of richness or function was altered as a result of acidification for the period 1985–1991 using Levene's test for homogeneity of variance (e.g., Levene 1960; Schultz 1985). In this procedure, we \log_{10} -transformed each time series to control variance from scaling as a function of mean (Underwood 1997); then compared reference and treatment basins with a Levene's test via a one-way analysis of variance (cf. Cottingham et al. 2000; Rusak et al. 2001). We used a conservative formulation of Levene's test that calculates absolute deviations from a median fit to both basins individually (Cottingham et al. 2000).

Community change within each trophic level, with the exception of planktivorous fish, was estimated as Euclidean distance (Legendre and Legendre 1998) between every other sampling event (effectively changing biweekly sampling to monthly to reduce any potential autocorrelation effects). Euclidean distance characterizes community resemblance, based on the simultaneous changes in a matrix of species abundances overtime, where larger distances indicate greater change in community structure between samplings. Relationships between change for each trophic level, again except fish, and several abiotic and biotic variables were analyzed using multiple regression based on the model of best fit as determined by Akaike's Information Criterion (AIC). AIC generates the most parsimonious regression model by discounting fit by the number of parameters in the final solution. Water temperature ($^{\circ}\text{C}$), oxygen saturation (%), conductivity ($\mu\text{S cm}^{-1}$), dissolved organic carbon (mg l^{-1}), NO_3 (mg l^{-1}), NH_4 (mg l^{-1}), PO_4 (mg l^{-1}), total phosphorus (unfiltered water sample; mg l^{-1}), total nitrogen (unfiltered water sample; mg l^{-1}), and dissolved reactive Si (filtered water sample; mg l^{-1}) from approximately monthly sampling intervals were included as abiotic variables. Total herbivorous, omnivorous, and carnivorous zooplankton biomass and chlorophyll *a* plus

phaeopigments ($\mu\text{g l}^{-1}$) were included as biotic variables for adjacent trophic levels. Specifically, each data point represents the date, once monthly, when biotic and abiotic variables were sampled on the same day, throughout the experiment. Due to some missing data, samples sizes varied slightly between basins (treatment/reference) for phytoplankton (48:42), herbivorous zooplankton (65:69), omnivorous zooplankton (65:69), and carnivorous zooplankton (65:69). Abiotic and biotic variables were transformed, if necessary, to ensure normality. Data on *Chaoborus*, a carnivorous zooplankton species, were not included in this analysis as they were sampled at a different frequency and their dynamics covaried with changes in pH (see Fischer and Frost 1997). The influence of *Chaoborus* on the zooplankton community has been noted elsewhere (e.g., Neill 1981; Yan et al. 1991; Fischer and Frost 1997).

Results

Altered species richness

After acidification, there was a greater reduction in species richness in the treatment basin and with increasing trophic level (compared to 1985 baseline) regardless of the season (Fig. 1). In contrast, species richness in the reference basin decreased in the summer, slightly decreased in the spring, and varied or remained unchanged for all trophic levels (Fig. 1). Likely due to natural fluctuations, the year from which we measured log percent change (1985) had slightly lower richness and biomass values than typically found in LRL. Therefore, the observed increases in the reference basin are not related to the experiment. This is supported by long-term richness and abundance data from adjacent Sparkling Lake which also had depressed values in this year (online dataset: North Temperate Lakes Long Term Ecological Research site <http://lter.limnology.wisc.edu/>).

The loss of species in the acidified basin was most apparent during the last year of the experiment (Fig. 2a). On an annual basis, no species were lost over this same time period in the reference basin (Fig. 2b). Fish recruitment ceased or was significantly reduced for all five species. We found a significant increase in trophic level variability in the treatment basin for annual carnivorous zooplankton richness alone (Table 1a).

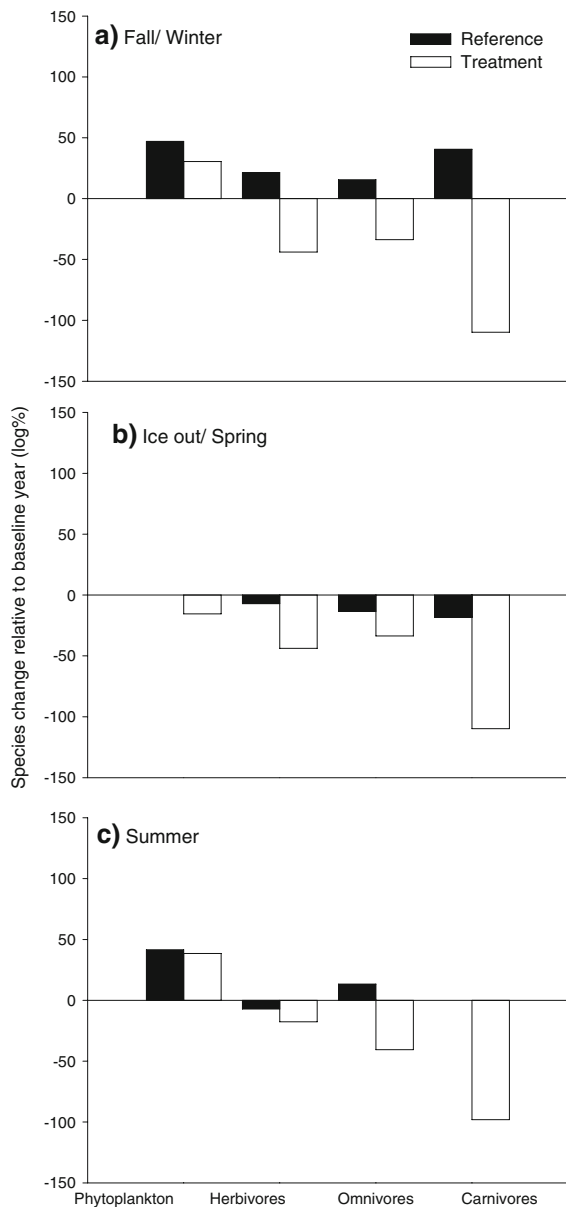


Fig. 1 Log percent species loss or gain after 6 years of acidification in the treatment and reference basins based on maximum annual richness. Species loss/gain is calculated from the baseline year of 1985

Changes were not significant for other trophic levels and both increases and decreases in variability were detected.

Altered primary production and zooplankton biomass

There were very few significant relationships between annual averages of trophic level biomass

and species richness in both basins of LRL (Table 2). However, significant positive relationships were evident for phytoplankton (in both basins), as well as for total zooplankton, and fish in the treatment basin only (Table 2). Examined visually, we found that both richness and biomass declined simultaneously in the upper trophic levels in the acidified basin but not in the reference basin.

Variability in biomass data among years following acidification appeared greater in the treatment basin than the reference basin (Fig. 2c, d). However, examined statistically, biomass variability in reference and treatment basins was largely homogeneous (Table 1b), with the exception of the carnivorous zooplankton which had significantly increased variability in the treatment basin in the summer only. Although not significant, variability did show a consistent average increase in the treatment basin for all other trophic levels and seasons (Table 1b), with the exception of a small decline in spring carnivorous zooplankton.

During acidification, biomass and photosynthetic rates increased in the treatment basin relative to the reference basin and remained high in 1989 (no data were available for 1990; Fig. 2c, d). To quantify a community-wide response for the zooplankton, we combined all zooplankton species into one assemblage and compared this to the annual averages for phytoplankton and fish. Consistent with our predictions, there was greater loss of fish and zooplankton species compared to phytoplankton in the treatment basin but no loss detected in the reference basin (Fig. 3). Biomass losses at all trophic levels were most evident in the last year of acidification, particularly for YOY yellow perch which declined to near zero when biomass in the reference basin was increasing nearly four-fold over pre-acidification estimates (Fig. 3). By the summer of 1989, the carnivorous zooplankton community was reduced to a single species, *Tropocyclops prasinus* (copepodid 6).

Influence of abiotic and biotic factors on trophic level responses

During the acidification of LRL, the degree of change within trophic levels was influenced by distinct groups of abiotic and biotic factors (Table 3a). Multiple regressions showed that the phytoplankton community became more similar (lower values of community change) with declining % oxygen saturation and nitrate,

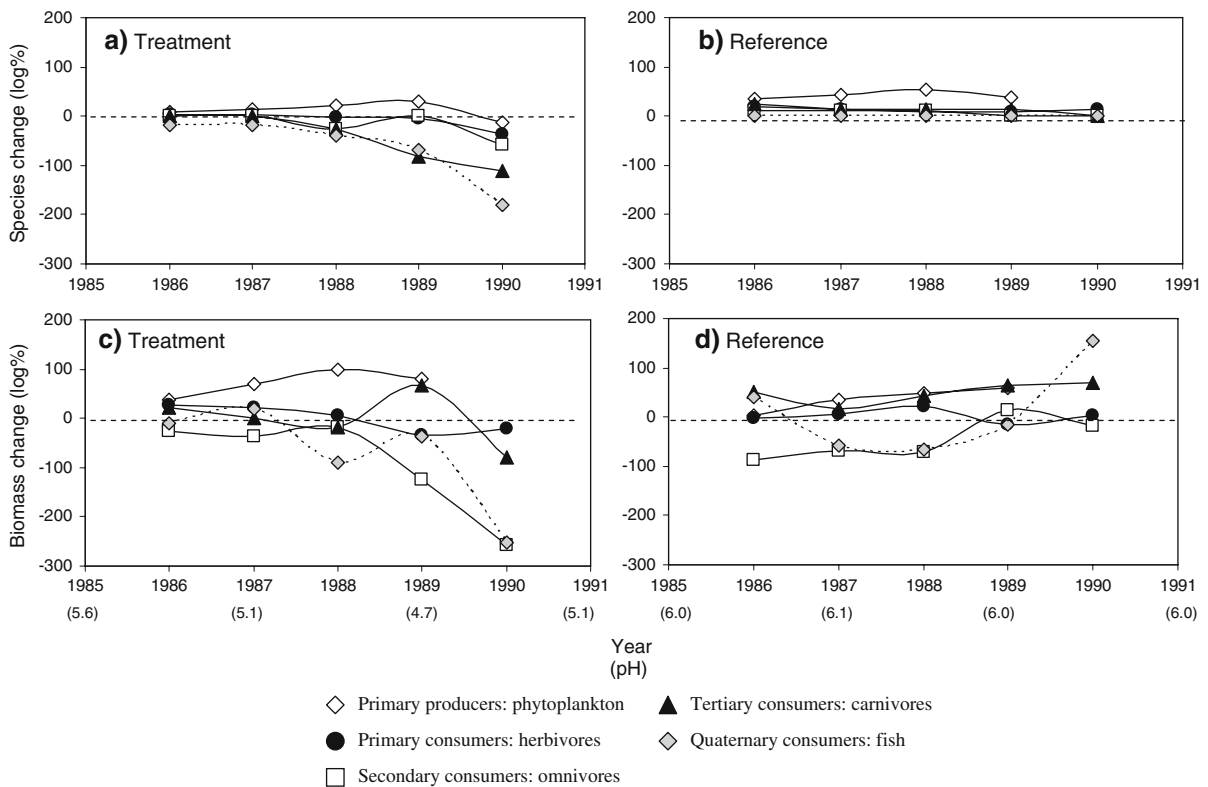


Fig. 2 Time-series change of the log percentage of species loss or gain in the (a) treatment and (b) reference basins based on maximum annual richness and the log percentage of biomass and primary productivity (phytoplankton) lost or

gained following acidification in the (c) treatment and (d) reference basins based on annual averages. Target values for pH for the treatment basin and average annual actual pH values for the reference basin are located below the year on the x-axis

increased ammonium, dissolved reactive silica, DOC, and warmer water temperatures. These factors accounted for 45% of the variation in phytoplankton community change ($P = 0.0003$). Change in the herbivorous zooplankton community was best explained by changes in % oxygen saturation, conductivity, DOC, and nitrate during acidification ($R^2 = 0.18$, $P = 0.02$). Chlorophyll *a*, total nitrogen, ammonium, and % oxygen saturation were associated with observed changes in the omnivorous zooplankton community, accounting for 16% of the total variation ($P = 0.03$). Significant predictors of carnivorous zooplankton change were pH, chlorophyll *a*, % oxygen saturation, and total omnivorous zooplankton biomass ($R^2 = 0.51$, $P < 0.0001$). Residual error reported for carnivorous zooplankton in the treatment basin was almost half of that seen in the reference basin, highlighting the better fit of abiotic variables to the treatment model (Table 3).

Different predictors of community change were identified in the reference basin for almost all

trophic levels (Table 3b) although the relative amount of explained variance was generally much lower in the control. In particular, PO_4 concentrations were the only significant predictor of phytoplankton community change ($R^2 = 0.08$, $P = 0.04$) whereas ammonium explained 15% of the change in herbivorous zooplankton ($P = 0.005$). Community change in omnivorous zooplankton was attributed to changes in the available biomass of herbivorous zooplankton ($R^2 = 0.06$, $P < 0.04$). Water temperature, chlorophyll *a*, PO_4 , and total nitrogen were identified as significant predictors of carnivorous zooplankton community change ($R^2 = 0.20$, $P = 0.02$). Based on these regression analyses, chlorophyll *a* was the only predictor of community change in carnivorous zooplankton that was comparable between the reference and treatment basin. The residual variances reported for the reference basin are indicative of background variability in a system not under stress.

Table 1 Levene's test of homogeneity of variance between the reference and treatment basin of LRL for log₁₀-transformed (a) richness and (b) biomass

	Annual			Spring			Summer			Fall/winter		
	<i>F</i>	<i>P</i> (% change)	MS _{residual}	<i>F</i>	<i>P</i> (% change)	MS _{residual}	<i>F</i>	<i>P</i> (% change)	MS _{residual}	<i>F</i>	<i>P</i> (% change)	MS _{residual}
(a) Richness												
Phytoplankton	0.14	0.72 (-10.3)	44.61	1.87	0.21 (-62.3)	58.15	0.26	0.63 (-17.5)	47.25	1.16	0.31 (-20.8)	34.88
Herbivores	0.23	0.64 (19.4)	8.90	3.92	0.08 (63.6)	1.25	0.46	0.52 (21.7)	5.45	0.11	0.75 (-7.6)	3.13
Omnivores	0.26	0.62 (25.0)	1.69	1.60	0.24 (-50.0)	0.25	0.00	1.00 (0.0)	0.55	0.43	0.52 (16.6)	0.77
Carnivores	7.64	0.02 (68.8)	1.11	0.62	0.46 (16.7)	0.65	2.97	0.12 (41.2)	1.65	1.29	0.28 (28.6)	1.03
Fish ^a	10.00	0.01 (100)	-	-	-	-	-	-	-	-	-	-
(b) Biomass												
Phytoplankton	0.49	0.49 (16.9)	0.01	2.35	0.15 (29.9)	0.00	0.99	0.34 (29.0)	0.01	0.00	0.99 (0.3)	0.04
Herbivores	1.53	0.24 (27.9)	0.00	2.64	0.13 (42.2)	0.02	0.09	0.77 (7.5)	0.01	0.34	0.57 (12.6)	0.00
Omnivores	1.43	0.26 (36.3)	0.06	3.89	0.07 (40.6)	0.07	1.45	0.25 (44.4)	0.04	1.03	0.33 (27.1)	0.07
Carnivores	0.48	0.50 (16.1)	0.01	0.03	0.86 (-4.5)	0.03	5.80	0.03 (52.1)	0.02	0.76	0.40 (23.0)	0.04
Fish ^a	0.02	0.66 (7.3)	-	-	-	-	-	-	-	-	-	-

Positive % change values quantify the magnitude of the increase in treatment basin variability over reference, while negative values document decreases. Highlighted in bold are significant results ($n = 7$, $df_{\text{model}} = 1$)

^a seasonal data not available for fish

Table 2 Spearman rank correlation coefficient of the relationship between species richness and primary production (phytoplankton) or consumer biomass (other trophic levels) for the treatment and reference basins of LRL

Group	Treatment basin	Reference basin
Phytoplankton	0.91**	0.82*
Herbivores	0.44	-0.04
Omnivores	0.36	0.08
Carnivores	-0.11	0.33
Fish	0.85*	0
Total zooplankton	0.86*	0.14

Correlation coefficients are calculated for annual averages of years 1985–1990 ($n = 5$; one for each year for each season; * $P < 0.05$, ** $P < 0.01$)

Discussion

Overall, our results provide support for asymmetric trophic responses for richness, biomass, and production to an ecosystem-level stress. Trophic levels had

differential sensitivities to acidification, which were reflected in the increased loss of species richness with increasing trophic level. Biomass and function (primary productivity) varied in its response to acidification, with substantial reductions reported for higher trophic levels (e.g., zooplankton and fish) by the final year of the experiment, whereas phytoplankton remained largely insensitive to acidification. The prevalence of water quality parameters (habitat) altered by acidification (e.g., pH, DOC, conductivity) in predicting trophic level responses in the treatment basin was contrasted with more typical predictors of zooplankton communities (nutrients and chlorophyll concentrations) in the reference basin. In particular, regression results for treatment basin carnivorous zooplankton suggested the importance of pH and reduced prey availability as contributing to observed asymmetric patterns. Differential trophic sensitivities to acidification were also identified on a seasonal time-scale with omnivorous and carnivorous zooplankton

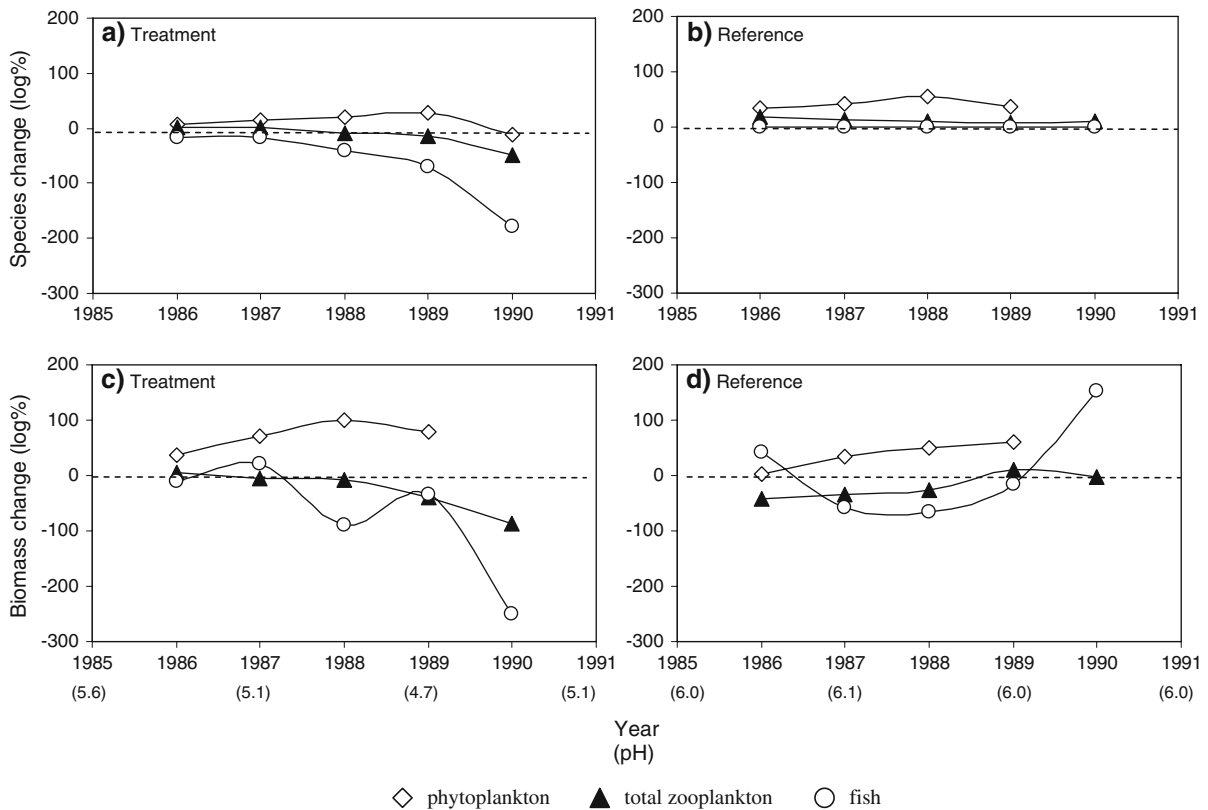


Fig. 3 Time-series change for three major trophic levels of the percentage of species loss or gain in the (a) treatment and (b) reference basins and of the percentage of biomass lost or gained following acidification in the (c) treatment and (d)

reference basins. Target values for pH for the treatment basin and average annual actual pH values for the reference basin are located below the year on the x-axis

Table 3 Multiple regression models indicating the relationship between abiotic and biotic variables and degree of assemblage change for each trophic level in the (a) treatment and (b) reference basin

Trophic level (<i>n</i> =)	Model	<i>R</i> ²	df	MS _{residual}	<i>F</i>	<i>P</i>
(a) Treatment basin						
Phytoplankton (48)	$\Delta PP = -0.24NH_4 + 0.51\%O_2 - 26.45Si - 1.95WTEMP - 4.74DOC + 68.05NO_3 + 2.36$	0.45	6	0.07	5.61	<0.001
Herbivorous zooplankton (65)	$\Delta HZ = -0.16O_2SAT - 1.71COND + 1.39DOC + 1.74NO_3 + 0.54$	0.18	4	0.05	3.21	0.02
Omnivorous zooplankton (65)	$\Delta OZ = 0.001TN + 0.31CHLP - 0.22NH_4 + 0.06O_2SAT - 0.16$	0.16	4	0.13	2.88	0.03
Carnivorous zooplankton (65)	$\Delta CZ = 0.37PH - 0.33CHLP - 0.04O_2SAT + 0.29TOZBIO - 1.59$	0.51	5	0.06	15.62	<0.001
(b) Reference basin						
Phytoplankton (42)	$\Delta PP = 0.429PO_4 + 0.414$	0.08	1	0.05	4.39	0.04
Herbivorous zooplankton (69)	$\Delta HZ = 0.15NH_4 + 0.223$	0.15	4	0.02	4.06	0.005
Omnivorous zooplankton (69)	$\Delta OZ = -0.278THZBIO + 0.215$	0.06	3	0.14	3.29	0.04
Carnivorous zooplankton (69)	$\Delta CZ = -0.454WTEMP - 0.421CLP - 0.519PO_4 - 0.001TN + 1.914$	0.20	5	0.11	4.30	0.02

CHLP, chlorophyll *a* plus phaeopigments; NO₃, nitrate; NH₄, ammonium; TN, total nitrogen; TP, total phosphorus; PO₄, phosphate; Si, dissolved reactive Si; WTEMP, water temperature; % O₂, percent oxygen saturation; COND, conductivity; TOZBIO, total omnivorous zooplankton biomass; TCZBIO, total carnivorous zooplankton biomass; THZBIO, total herbivorous zooplankton biomass

Models of best fit were determined using AIC

appearing to be somewhat more sensitive to low pH during spring and summer months. Variability in biomass, although only significantly increased for carnivorous zooplankton, was almost always greater in the treatment basin. Not only are losses from upper trophic levels more strongly affected by acidification, these changes have the potential to be less predictable than lower trophic levels.

We did not find evidence of top-down or bottom-up effects as predicted by trophic cascade theory. Even though many interactions and indirect effects were documented over the course of the whole-lake experiment (Frost et al. 1998, 1999), the multiple regressions suggest that pH was the driving factor of loss in upper trophic levels (predators and carnivorous zooplankton). The weak relationships between abiotic and biotic predictors shown for herbivorous and omnivorous zooplankton during acidification provide further support for this phenomenon. While a trophic cascade was not evident in the upper trophic levels, the loss of species with important functional or life history traits (Barnett et al. 2007) may have occurred in the lower ones. For example, the increase in phytoplankton biomass after acidification may have been due to the loss of *Daphnia*

species, an efficient grazer in the treatment basin. Similarly, this same increase in phytoplankton biomass did not appear to affect upper trophic levels, suggesting that bottom-up processes were not particularly important either, or at least were quickly dampened in the food web. Clearly, additional work will be required to model the gains and losses of specific functional groups to further understand the biological and mechanistic basis of asymmetric change in trophic structure.

While the direct and indirect effects of low pH are important to the disproportionate losses of species observed at upper trophic levels, our results suggest that the interactions among trophic levels and the transmission of this trophic asymmetry may also be dampened by the relative stability observed in the phytoplankton and herbivore communities. An analysis of LRL zooplankton response to acidification by Fischer et al. (2001b) revealed significant compensatory responses among herbivorous cladocerans and herbivorous copepods (calanoids were not stratified by copepodid stage as we have done in this study). Our results agree well with compensation documented for lower trophic levels elsewhere (e.g., Ives et al. 1999; Fischer et al. 2001b). The fact that compensation is not

present, or not possible given reduced diversity, in upper trophic levels may lead to the observed asymmetric responses. As our regression analysis generates the best predictors of trophic level change per se, the low amount of variation explained by abiotic and biotic variables for changes in herbivorous and omnivorous zooplankton assemblages may only be due to compensatory dynamics if species replacements within a trophic level are responding to different factors.

The asymmetric responses observed in richness and biomass following the acidification of LRL may also be attributed to differences in the diversity and dispersal potentials on a trophic level basis. Previous studies have concluded that speciose communities are more likely to contain a stress-tolerant species that can potentially compensate for losses from stress-sensitive species (Walker 1992; Tilman 1996; Ives et al. 1999). Wider dispersal potentials typical of lower trophic levels are also thought to increase the probability of a tolerant species being present to compensate for losses of sensitive species (Vinebrooke et al. 2003). In contrast, acid-tolerant fish would be limited by physical barriers imposed by distance or lack of connectivity.

The lack of decline in biomass and primary productivity, except for higher trophic levels at the end of the acidification period, agrees with earlier results from experimentally- (Schindler et al. 1991) and culturally-acidified lakes (Nicholls et al. 1992; Havens and Carlson 1998) which have shown that acidification has little effect on algal and herbivorous zooplankton biomass. This result was further substantiated in Little Rock Lake by results for zooplankton grazing rate (another key functional attribute) which remained relatively constant throughout the acidification period (Sierszen and Frost 1990). In LRL, compensatory dynamics were commonly observed in major zooplankton groups in response to acidification (Frost et al. 1995). However, we show that variability in biomass also increased as acidification proceeded, suggesting that ecosystem function may become less predictable with greater stress. Cottingham et al. (2000) demonstrated this positive relationship between variability and unpredictability and noted a similar pattern for a different stressor (eutrophication) in aquatic ecosystems. This response of increasing variability may also have a trophic asymmetry, as it generally was more prevalent in the upper trophic levels.

We detected some differential sensitivity to acidification among seasons for the various trophic levels, however patterns were not strong. This may be because LRL was not directly acidified in the winter, although the pH remained low even under the ice (Brezonik et al. 1993). Metabolism rates would also remain low in the winter, potentially reducing exposure to low pH. In tropical and sub-tropical lakes the effects of acidification may be realized much more quickly than in temperate systems.

Our results provide further support for the idea that a decline in habitat quality, in this case acidification, leads to a gradual and asymmetrical loss of species diversity and trophic complexity and function (e.g., Schindler et al. 1985; Vinebrooke et al. 2003). How such trophic asymmetry applies to larger lakes is unknown and may be confounded by greater species diversity and longer food chains (Post et al. 2000) which could reduce susceptibility to the trophic collapse that we document here. The emerging consensus on the asymmetric change in stressed lake ecosystems needs to be investigated with further experiments to distinguish among the roles that food web structure, diversity, and other factors play in determining this response.

Some acidified lakes in North America have now recovered or are recovering from low pH (Keller et al. 1992; Driscoll et al. 2001) based on changes in water chemistry, although others continue to acidify (Jefferies et al. 2003) and drought-induced setbacks can and do occur (Arnott et al. 2001). However, the top-down dismantling of food web structure may negatively affect biological recovery. When acidification-induced effects are focused on upper trophic levels rather than distributed equally, the resilience of the entire food web may be compromised. Delayed biological recovery has now been documented in a number of whole-lake manipulation studies (e.g., Yan et al. 1996, 2004; Frost et al. 1999). Although additional studies are needed to test for the occurrence of asymmetrical food web responses to other aquatic stressors and in other ecosystems, the prospects for understanding this phenomenon as a common ecological response to disturbance appear promising.

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Appendix 1

Trophic level assignments (M = male, F = female)

Trophic level 1—primary producers

<i>Chlorophyta</i>	<i>Chrysophyta</i>	<i>Cyanophyta</i>
<i>Actinastrum hantzschii</i>	<i>Achnanthes minutissima</i>	<i>Anabaena flos-aquae</i>
<i>Ankistrodesmus falcatus</i>	<i>Actinella punctata</i>	<i>Anabaena plactonica</i>
<i>Ankistrodesmus</i> spp.	<i>Amphora ovalis</i>	<i>Anabaena spiroides</i>
<i>Ankyra judayi</i>	<i>Asterionella formosa</i>	<i>Apanizomenon flos-aquae</i>
<i>Arthrodesmus</i> spp.	<i>Asterionella ralfsii</i>	<i>Apanizomenon gracile</i>
<i>Bambusina</i> spp.	<i>Bicosoeca cylindrica</i>	<i>Aphanocapsa</i> spp.
<i>Botryococcus braunii</i>	<i>Bitrichia</i> spp.	<i>Aphanothece clathrata</i>
<i>Chlamydomonas</i> spp.	<i>Chromulina</i> spp.	<i>Arthrospira</i> spp.
<i>Closterium</i> spp.	<i>Chrysochromulina</i> spp.	cf. <i>Synechococcus</i> spp.
<i>Coelastrum cambrium</i>	<i>Chrysococcus</i> spp.	<i>Chroococcus limneticus</i> var <i>distans</i>
<i>Cosmerarium</i> spp.	<i>Chrysolykos planktonicus</i>	<i>Chroococcus minimus</i>
<i>Crucigenia rectangularis</i>	<i>Chrysosphaerella longispina</i>	<i>Chroococcus minutus</i>
<i>Crucigenia tetrapedia</i>	<i>Cyclotella</i> spp.	<i>Chroococcus turgidus</i>
<i>Dictyosphaerium ehernbergianum</i>	<i>Cymbella ventricosa</i>	<i>Cloethece rupestris</i>
<i>Dictyosphaerium pulchellum</i>	<i>Diceras chodati</i>	<i>Coelosphaerium</i> spp.
<i>Elakatothrix</i> spp.	<i>Dinobryon bavaricum</i>	<i>Gloeocapsa punctata</i>
<i>Euastrum</i> spp.	<i>Dinobryon divergens</i>	<i>Gloeocapsa</i> spp.
<i>Euastrum</i> spp. Small	<i>Dinobryon sertularia</i>	<i>Gomposphaeria naegeliana</i>
<i>Gloeococcus</i> spp.	<i>Dinobryon sociale</i>	<i>Merismopedia glauca</i>
<i>Gloeocystis</i> spp.	<i>Dinobryon</i> spp.	<i>Merismopedia minutissima</i>
<i>Mougeotia</i> spp.	<i>Eunotia fallax</i>	<i>Merismopedia tenuissima</i>
<i>Nephrocytium obesum</i>	<i>Fragilaria crotonensis</i>	<i>Microcystis incerta</i>
<i>Nephrocytium</i> spp.	<i>Gomphonema</i> spp.	<i>Oscillatoria</i> spp.
<i>Oedogonium</i> spp.	<i>Kephyrion</i> spp.	<i>Rhabdoderma lineare</i>
<i>Oocystis lacustris</i>	<i>Mallomonas</i> spp.	Unidentified small bluegreens
<i>Oocystis</i> spp.	<i>Melosira ambigua</i>	
<i>Pediastrum tetras</i>	<i>Melosira granulata</i> var <i>angustissima</i>	<i>Phyrrhophyta</i>
<i>Quadrigula lacustris</i>	<i>Navicula</i> spp.	<i>Glenodinium</i> spp.
<i>Quadrigula</i> spp.	<i>Nitzschia gracilis</i>	<i>Gymnodinium</i> sp. 2
<i>Scenedesmus quadricauda</i>	<i>Nitzschia</i> spp.	<i>Gymnodinium</i> spp.
<i>Scenedesmus</i> spp.	<i>Ochromonas</i> spp.	<i>Peridinium cintum</i>
<i>Scourfeldia cordiformis</i>	<i>Ophiocytium</i> sp.	<i>Peridinium inconspicuuum</i>
<i>Sphaerocystis Schroeteri</i>	<i>Pinnularia</i> spp.	<i>Peridinium</i> spp.
<i>Spondylium</i> spp.	<i>Pseudokephyrion</i> spp.	<i>Peridinium willei</i>
<i>Staurastrum</i> spp.	<i>Stephanodiscus niagarae</i>	<i>Unknown phyrrhophyta</i>
<i>Temnogametum</i> spp.	<i>Stichogloea doederleinii</i>	
<i>Tetraedron</i> spp.	<i>Stichogloea doederleinii</i> round	
<i>Ulothrix</i> spp.	<i>Stichogloea</i> spp.	

Appendix continued

Unidentified small greens	<i>Synedra</i> sp.	
Unknown green filament 1	<i>Synura</i> spp.	
<i>Xanthidium</i> spp.	<i>Tabellaria fenestrata</i>	
<i>Zygnema</i> spp.	<i>Tabellaria flocculosa</i>	
<i>Zygonium</i> spp.	Unidentified flagellate sp. A	
	Unidentified small chrysophytes	
<i>Cryptophyta</i>		
cf. <i>Chroomonas</i>	<i>Euglenophyta</i>	
<i>Cryptomonad</i> 1	<i>Euglena acus</i>	
<i>Cryptomonas</i> sp. 3	<i>Euglena</i> spp.	
<i>Cryptomonas</i> sp. 3b	<i>Phacus longicauda</i>	
<i>Cryptomonas</i> sp. 4	<i>Phacus</i> spp.	
<i>Cryptomonas</i> sp. 5	<i>Trachelomonas</i> spp.	
<i>Cryptomonas</i> sp. 6	<i>Trachelomonas volocina</i>	
<i>Chroomonas</i> spp.		
<i>Cryptomonas erosa</i>		
<i>Cryptomonas marsonii</i>		
<i>Cryptomonas ovata</i>		
<i>Cryptomonas</i> spp. (small)		
<i>Rhodomonas minutus</i>		
Trophic level 2—primary consumers, including all herbivorous zooplankton		
<i>Copepod nauplii</i>	<i>Polyarthra dolichoptera</i>	
<i>Cyclopoid copepod</i> 1-2	<i>Polyarthra remata</i>	
<i>Bosminid</i> sp.	<i>Polyarthra vulgaris</i>	<i>Daphnia dubia</i> M & F
<i>Chydorus</i> sp.	<i>Trichocerca</i> sp.	
<i>Diaphanosoma birgei</i>	<i>Trichocerca birostris</i>	
<i>Holopedium gibberum</i>	<i>Trichocerca cylindrica</i>	<i>Daphnia parvula</i> M & F
<i>Ascomorpha</i> sp.	<i>Trichocerca multirinis</i>	
<i>Ascomorpha ecaudis</i>		
<i>Ascomorpha ovalis</i>		<i>Daphnia catawba</i> M & F
<i>Conochiloides</i> sp.	<i>Diacyclops thomasi</i> 1-2	
<i>Conochilus</i> sp.		
<i>Gastropus hyptopus</i>		
<i>Gastropus stylifer</i>	<i>Mesocyclops edax</i> 1-2	
<i>Kellicottia bostoniensis</i>		
<i>Kellicottia longispina</i>		
<i>Keratella cochlearis</i>	<i>Orthocyclops modestus</i> 1-2	
<i>Keratella crassa</i>	<i>Tropocyclops prasinus</i> 1-2	
<i>Keratella hiemalis</i>		
<i>Keratella taurocephala</i>		
<i>Lecane</i> sp.		
<i>Monostyla</i> sp.	<i>Leptodiptomus minutus</i> 1-3	

Appendix continued

Trophic level 3—secondary consumers, combining all omnivorous zooplankton

Collotheca mutabilis

Synchaeta sp.

Diacyclops thomasi 3-5

Mesocyclops edax 3-5

Orthocyclops modestus 3-5

Tropocyclops prasinus 3-5

Leptodiatomus minutus 4-5

Leptodiatomus minutus 6 M & F

Trophic level 4—tertiary consumers, combining all carnivorous zooplankton

Diacyclops thomasi 6 M & F

Mesocyclops edax 6 M & F

Orthocyclops modestus 6 M & F

Tropocyclops prasinus 6 M & F

Asplanchna sp.

Trophic level 5—fish

Perca flavescens

Ambloplites rupestris

Micropterus salmoides

Pomoxis nigromaculatus

Umbra limi

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