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Impact of Bythotrephes Invasion on Zooplankton Communities in Acid-Damaged and Recovered Lakes on the Boreal Shield

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Impact of *Bythotrephes* invasion on zooplankton communities in acid-damaged and recovered lakes on the Boreal Shield

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Abstract

Invasive species introductions into freshwater ecosystems have had a multitude of effects on aquatic communities. Few studies, however, have directly compared the impact of an invader on communities with contrasting structure. Historically high levels and subsequent reductions of acid deposition have produced landscapes of lakes of varying acidity and zooplankton community structure. We conducted a 30 day enclosure experiment in Killarney Provincial Park, Ontario, Canada to test the effects of *Bythotrephes longimanus,* an invasive invertebrate predator, on two contrasting zooplankton communities at different stages of recovery from acidification; recovered and acid-damaged. *Bythotrephes* significantly decreased zooplankton biomass and abundance in both communities, but had a greater negative effect on the abundance of zooplankton in the recovered community. *Bythotrephes* reduced species diversity of the recovered zooplankton community but not of the acid-damaged community. Species richness of both community types was unaffected by *Bythotrephes* predation. The effect of *Bythotrephes* on small cladocerans, a preferred prey type, differed between the community types and appeared related to density-dependent predation by *Bythotrephes*. Both community- and species-level results suggest that recovered and acid-damaged zooplankton assemblages may be negatively affected by an invasion of *Bythotrephes*, but that the specific response is dependent on the original community structure.

Key words: crustacean zooplankton, boreal lakes, Canadian Shield, recovery from acidification, invasive species

Introduction

The invasion of non-indigenous species into freshwater ecosystems has altered food webs worldwide, severely affecting ecosystem processes, destroying habitats, and driving native species to local extinction (Spencer et al. 1991; Ricciardi and Rasmussen 1998). In the next century, biodiversity scenarios predict that invasive species will be the single most important driver of change in aquatic ecosystems (Sala et al. 2000). Case studies of species introductions into the Laurentian Great Lakes make it clear that invasive species present an imminent threat to freshwater resources (Vanderploeg et al. 2002). *Bythotrephes longimanus* (Cercopagidae), until recently called *B. cederstroemi* (Berg et al. 2002), is a large predatory zooplankter that invaded the Great Lakes in the mid-1980s from Eurasia (Lehman 1987). It subsequently spread into inland lakes in Canada and the United States in the 1990s (Yan et al. 1992), expanding its range into at least 55 Ontario lakes (F. MacDonald, Ontario Federation of Anglers and Hunters, 4601 Guthrie Drive, Peterborough, Ontario K9J 8L5, personal communication) and several lakes in northern Minnesota (Forman and Whiteside 2000) and Upper Michigan (Jarnagin et al. 2000).

In North America, invasions of *Bythotrephes* have resulted in various responses of zooplankton communities. A survey of 30 Canadian Shield lakes with and without the invader found significantly lower biomass and species richness of zooplankton in single, mid-summer samples taken from lakes containing *Bythotrephes* (Boudreau and Yan 2003). In Harp Lake, a small inland lake in Ontario, the invasion of *Bythotrephes* caused a decrease in crustacean zooplankton species richness and a size shift from small- to large-bodied zooplankton, owing to the decline and disappearance of small species (Yan et al. 2001). However, other studies have suggested that these responses may not be universal. Zooplankton samples from Lake Michigan and laboratory feeding experiments have indicated that *Bythotrephes* may have negative effects on large-bodied zooplankton, including several species of *Daphnia* (Lehman and Cáceres 1993; Schulz and Yurista 1999). Taken together, these studies suggest that the effect of *Bythotrephes* on zooplankton communities may be dependent on the structure of the initial community that is invaded.

Human activities have led to innumerable changes in aquatic environments (Schindler 1998*a*), and thus, created a mosaic of different aquatic communities across the landscape. One example of this is the large-scale acidification of lakes and their watersheds, and subsequent loss of biodiversity, in the area around Sudbury, Ontario (Beamish and Harvey 1972). Reductions in SO_2 emissions from Sudbury smelters have led to improvements in lake pH and biological recovery of some aquatic communities (Gunn and Keller 1990; Holt and Yan 2003), though recovery of zooplankton in many lakes is slow and not uniform across the landscape (Keller et al. 2002). Although recovery endpoints are difficult to establish because historic, pre-disturbance data are rarely available, the recovery status of a community is often compared with that of more pristine natural communities in similar biogeographical settings (see Yan et al. 1996b for description of reference lake approach). Many of the lakes recovering from acidification are extremely clear due to thin soils, exposed bedrock, and small catchment areas, resulting in low dissolved organic carbon (DOC) inputs (Gunn et al. 2001). These clear lakes are especially vulnerable to invasion by *Bythotrephes* (MacIsaac et al. 2000). Although *Bythotrephes* tends to occupy circumneutral lakes, it is tolerant of a wide range of pH (Grigorovich et al. 1998) and is currently spreading into lakes that were historically acidified (A. Strecker, personal observation). It is uncertain what impact *Bythotrephes* will have on lakes in different stages of recovery and therefore, with different zooplankton community structure.

We tested the effects of *Bythotrephes* on two ecologically disparate zooplankton communities at different stages of recovery from historic acidification (recovered vs acid-damaged) using a field enclosure experiment. Specifically, our objectives were to: 1) examine community- and species-level responses of zooplankton to an invasion of *Bythotrephes*; and 2) determine if the responses were dependent on the recovery status of the community. We hypothesized that *Bythotrephes* would: 1) cause declines in all community metrics and prey selectively on small cladocerans (Lehman and Cáceres 1993; Yan et al. 2001; Boudreau and Yan 2003); and 2) have a greater negative effect on the zooplankton in the acid-damaged community type because it has a lower species richness than the recovered community and therefore, fewer species to compensate for those preyed upon by *Bythotrephes* (McNaughton 1977; Naeem and Li 1997).

Methods

Study site and experimental design

Experiments were conducted in Kakakise Lake (46º03' N, 81º03' W; Fig. 1), located in Killarney Provincial Park, situated 40-60 km southwest of metal smelters in Sudbury, Ontario. Due to the large amounts of sulphur deposition received from Canada and the USA, this was one of the first regions to be affected by atmospheric pollution (Beamish and Harvey 1972). While many lakes are approaching their historical pre-acidification pH, some of the highly acidified lakes located on orthoquartzite ridges have shown little improvement in pH (Keller et al. 2003). Kakakise Lake is a relatively small (113 ha), mesotrophic boreal lake (Table 1) that was historically acidified to pH 5.6 (Sprules 1975), but has now chemically recovered to levels consistent with diatom-inferred pre-industrial pH (Keller et al. 2003).

A two-factor enclosure experiment was conducted in Kakakise Lake during July and August 2002 to test for the effect of *Bythotrephes* on zooplankton communities at different stages of recovery from acidification. The effects of acidification on zooplankton communities in lakes have been well-documented. In general, acidified lakes have low species richness and are dominated by a few acid-tolerant species, while neutral or buffered lakes have more diverse assemblages (Sprules 1975). Our experimental treatments were designed to reflect these differences in community structure. The experiment consisted of two treatments, each with two levels: *Bythotrephes* (*Bythotrephes*, no *Bythotrephes*) and zooplankton community (recovered, acid-damaged). The four treatment combinations were each replicated three times, for a total of 12 enclosures. However, one replicate of the recovered, no *Bythotrephes* treatment was discarded after a northern pike (*Esox lucieus)* invaded the enclosure. In each zooplankton community treatment (recovered vs. acid-damaged), the enclosures with no *Bythotrephes* present are the controls for that community.

Due to the sensitive nature of conducting experiments with invasive species, Kakakise Lake was chosen as the location for the experiment because previous data indicated that the lake had been invaded by *Bythotrephes* prior to 1997 (B. Keller, Cooperative Freshwater Ecology Unit, Laurentian University, Sudbury, Ontario, P3E 2C6, unpublished data). In July 2002, *Bythotrephes* was present in the lake in low densities; < 0.1 ind·m^{-3} (A. Strecker, unpublished data).

Bell Lake (46º08' N, 81º26' W; Fig. 1) and Ruth Roy Lake (46º05' N, 81º14' W; Fig. 1) were chosen as the recovered and acid-damaged zooplankton source lakes, respectively. These lakes have contrasting zooplankton assemblages as a result of their different acidification histories and lake geologies. The Bell Lake zooplankton community was typical of recovered zooplankton assemblages that are species-rich and contain both acid-tolerant and acid-sensitive species (Holt and Yan 2003). Ruth Roy is typical of other acid-damaged communities with low species richness and dominance by a few acid-tolerant species; 77% of the zooplankton biomass was contributed by two acid-tolerant species (*Leptodiaptomus minutus* and *Diaphanosoma birgei)*. A correspondence analysis (CA) of 21 reference lakes from the Dorset, Ontario region, compared with the two study lakes confirmed their recovery status (A. Strecker, unpublished data).

Clear plastic cylindrical enclosures (1 m diameter, total volume 6830 L; Filmtech Plastics, 125 East Dr., Brampton, Ontario L6T 1B5) were suspended between the cross-bars of three 4.9 m long floating wooden frames. The top of the enclosures were 0.3 m above the water level to prevent the immigration of new species and extended down to a depth (approx. 8.7 m) that was just below the thermocline. The enclosures were covered with mesh (approx. 5 mm) to prevent aerial zooplankton colonization by macroinvertebrate and bird vectors, and were closed at the bottom. Frames were oriented in a north-south direction so that all enclosures received comparable light.

Water from Kakakise Lake was pumped from the central region of the euphotic zone into the enclosures and filtered through a 50 µm mesh to remove all zooplankton. Zooplankton were collected first from Bell Lake and the following day from Ruth Roy Lake with an 80 µm mesh net and added to the enclosures in Kakakise Lake at ambient lake densities, filtering lake water at a volume equal to the volume of enclosure. Samples collected with a 0.5 m diameter, 250 µm mesh net in June and July 2002 verified the absence of *Bythotrephes* from the zooplankton source lakes. Because the concentration of *Bythotrephes* was low in Kakakise Lake, *Bythotrephes* for the experiment were collected from another invaded lake, Ahmic Lake (45°37'

N, 79°42' W). Ahmic Lake is circumneutral (pH = 6.58), and has calcium and DOC concentrations that are similar to values in Kakakise Lake (Boudreau 2002). *Bythotrephes* were collected using a 0.5 m diameter, 400 µm mesh net. During transport to Kakakise Lake, samples were kept cool and held at low densities in opaque 20 L carboys surrounded by icepacks. On the same day, live *Bythotrephes* were added to each enclosure at a density (10 $\text{ind}\cdot\text{m}^{-3}$) comparable to mid-summer population maxima that have been reported in an early invasion year in Harp Lake, Ontario (Yan et al. 2001).

Sampling protocol and analyses

Enclosures were sampled once a week for a period of four weeks. Zooplankton abundance and composition, temperature, oxygen concentration, and total chlorophyll *a* concentrations were estimated every week. Conductivity and pH were measured on Weeks 0, 2 and 4, and total phosphorus and edible chlorophyll *a* (< 30 µm) were measured on Weeks 0 and 4. Zooplankton samples were obtained by taking two 8 m hauls with a 0.15 m diameter plankton net (80 µm mesh size). The combined hauls represented approx. 3.4% of the volume of the enclosure. Zooplankton were preserved in 4% sugared and buffered formalin.

Temperature and dissolved oxygen data were measured at 1 m intervals using a YSI Model 95 dissolved oxygen and temperature meter (YSI Incorporated, Yellow Springs, Ohio). Water samples for chemistry and chlorophyll *a* were obtained using an 8 m composite tube sampler with a diameter of 16 mm. A 1.0 L subsample was filtered through Pall™ Ultipor glass fiber filters (1.2 µm pore size) which were then frozen and kept in darkness for chlorophyll *a* analysis. Edible chlorophyll *a* was sampled in the same manner, except that it was filtered through 30 µm mesh prior to its concentration onto a glass fiber filter. Chlorophyll *a* samples were extracted in methanol for 24 hours before fluorometric analysis (Welschmeyer 1994) using the TD 700 Fluorometer (Turner Designs, Sunnyvale, California). Total phosphorus was analyzed following Ontario Ministry of the Environment protocols (Ontario Ministry of the Environment 1983). Conductivity was measured with a YSI Model 32 conductance meter (YSI Incorporated, Yellow Springs, Ohio) and pH with a PHM 80 portable pH meter (Radiometer A/S, Copenhagen, Denmark).

During our routine zooplankton sampling, we infrequently encountered *Bythotrephes* in the samples because we were sampling with a small diameter net. When we collected them, they were enumerated and returned to the enclosure live. We did not want to risk damaging the *Bythotrephes* in our experimental treatments and therefore did not attempt to quantitatively sample them throughout the experiment. Instead, *Bythotrephes* was sampled with a 250 µm mesh net (0.5 m diameter) on the last day of the experiment. Samples were preserved in 4% sugared and buffered formalin until enumeration.

Zooplankton samples were enumerated using a protocol designed to target mature individuals, as well as rare species (Girard and Reid 1990). Samples were subsampled using a Folsom plankton splitter, and a total of at least 250 individuals were enumerated, such that no more than 50 individuals were counted for the dominant taxa, no more than 50 copepodids per order were counted, and no more than 30 nauplii per order were counted. Zooplankton were identified and counted on a Leica MZ 12.5 dissecting microscope and individuals were measured using the semi-automated zooplankton counting system ZEBRA2 (Allen et al. 1994).

Taxonomic keys that were used included Hebert (1995) for *Daphnia*, Smith and Fernando (1978) for copepods, Dodson and Frey (1991) for cladocerans, Taylor et al. (2002) for Bosminidae, and Smith (2001) for general zooplankton identification. The taxa *Bosmina*

(Bosmina) and *Alona* were only identified to subgenera and genera, respectively, due to taxonomic difficulties in distinguishing species.

Statistical analyses

This experiment was designed to test the impacts of *Bythotrephes* on an acid-damaged and recovering lake zooplankton community. By design, there were initial differences between the two community types, i.e. the acid-damaged community had lower species richness and diversity than the recovered community. However, initial differences between communities can confound the interpretation of univariate statistics. In instances of significantly different starting communities, the Time × *Bythotrephes* interaction and Time × Recovery × *Bythotrephes* interaction statistic were used to assess the effects of *Bythotrephes*.

A multivariate analysis of variance (MANOVA) was used to test the effects of *Bythotrephes* and community recovery on zooplankton functional group abundance from Weeks 1-4, excluding Day 0, the first sampling date. We defined functional groups by taxonomic groupings (calanoid and cyclopoid copepods), and further subdivided by size differences (small vs large cladocerans) and habitat preferences of cladocerans (littoral vs pelagic) (Smith 2001). Assumptions of normality were tested using the Kolmogorov-Smirnov goodness-of-fit test and the Shapiro-Wilks *W*-statistic, homoscedasticity using Levene's test, and equal covariance using Box's M-test. Functional group abundances were log(x+1)-transformed to improve unequal variance and non-normal treatments; however, some groups still violated these assumptions. MANOVA is considered to be robust to violations of these assumptions, especially when using the more robust Pillai trace method (Zar 1999).

Zooplankton responses to experimental treatments, including community biomass, abundance, species richness, Shannon-Wiener species diversity (Zar 1999), functional group abundance, and individual species abundances were tested with a two-factor repeated measures analysis of variance (RM-ANOVA) for Weeks 1-4. Total chlorophyll *a*, edible chlorophyll *a,* and water chemistry responses were tested with a two-factor RM-ANOVA on all dates, as the first chlorophyll *a* samples were taken three days after treatments were established. Two-factor ANOVAs were also used to test for differences among community metrics at the beginning of the experiment. All metrics were tested for normality and homoscedasticity, and sphericity was tested using the less conservative Huynh-Feldt adjusted *p*-value, as in this type of experiment, it is of greater importance to reduce the probability of a Type II error (Zar 1999). Total zooplankton biomass and edible chlorophyll *a* were log(x+1)-transformed to equalize variance. Some non-normal treatments remained, however, since the analysis of variance test is robust to departures from normality and equal variance (Zar 1999), the parametric version of the test was used.

Results

Environmental conditions

There was no difference in water chemistry samples for pH (*Bythotrephes* $F_{1,7} = 1.034$, $p = 0.343$; Recovery $F_{1,7} = 4.090$, $p = 0.083$), total phosphorus (*Bythotrephes* $F_{1,7} = 1.594$, $p = 0.247$; Recovery $F_{1,7} = 3.237$, $p = 0.115$), and conductivity (*Bythotrephes* $F_{1,7} = 0.359$, $p = 0.568$; Recovery $F_{1,7} = 0.730$; $p = 0.421$) (Table 2). Total phosphorus tended to be variable within treatments, likely due to the low numbers of replicates. As well, there was one particularly high total phosphorus value, which suggests that the sample may have been contaminated by an organism which would increase phosphorus levels (B. Clark, Ontario Ministry of the Environment, P.O. Box 39, Dorset, Ontario P0A 1E0, personal communication). There was no difference between the ambient lake and enclosure values for temperature and O_2, indicating that they efficiently tracked the thermal and oxygenic regimes of the lake. There was also no effect of treatment on temperature (*Bythotrephes* $F_{1,7} = 1.594$, $p = 0.939$; Recovery $F_{1,7} = 0.627$, $p = 0.454$) or O_2 (*Bythotrephes* $F_{1,7} = 3.485$, $p = 0.104$; Recovery $F_{1,7} = 2.322$, $p = 0.171$) of the enclosures (Table 2).

Average concentrations of total chlorophyll *a* in the *Bythotrephes* treatment enclosures increased by 17% over concentrations in no *Bythotrephes* enclosures from Week 0 to 4 ($F_{1,7} = 6.982$, $p = 0.033$; Fig. 2). Edible chlorophyll *a* also increased in response to *Bythotrephes* (Time × *Bythotrephes*: $F_{1,7} = 4.031$, $p = 0.085$), such that concentrations were 32% higher in *Bythotrephes* treatments by the end of the experiment, although this increase was primarily observed in the recovered community. Although total chlorophyll *a* was slightly higher in the acid-damaged enclosures on our first sampling date ($F_{1,7} = 5.977$, $p = 0.044$), it declined throughout the remainder of the experiment, and was 25% lower ($F_{1,7} = 12.913$, $p = 0.009$) than the recovered enclosures from Week 1 to 4. Edible chlorophyll *a*, which had similar concentrations on our first sampling date, was also lower in the acid-damaged community on Week 3 ($F_{1,7} = 9.036$, $p = 0.020$, effect size = 15%).

Zooplankton community responses to *Bythotrephes*

Total zooplankton biomass and abundance were both significantly decreased by the addition of *Bythotrephes* (Table 3, Fig. 3). Our experimental design resulted in differences in initial biomass (*Bythotrephes* $F_{1,7} = 7.846$, $p = 0.026$; Recovery $F_{1,7} = 17.439$, $p = 0.004$), richness (Recovery $F_{1,7} = 54.716$, $p < 0.001$; Recovery × *Bythotrephes* $F_{1,7} = 9.569$, $p = 0.017$), and Shannon-Wiener diversity (Recovery $F_{1,7} = 76.011$, $p < 0.001$). Therefore, the Time × *Bythotrephes* interaction statistic was used. The effect of *Bythotrephes* on community biomass became more pronounced over time, such that biomass in the *Bythotrephes* treatment declined by

> 50% in both acid-damaged and recovered enclosures at the conclusion of the experiment. Species richness was not affected by the *Bythotrephes* treatment, but diversity increased through time in *Bythotrephes* treatments (Time × *Bythotrephes* interaction, Table 3, Fig. 3). Individual ANOVAs on functional groups revealed significant negative effects of *Bythotrephes* on biomass of calanoid copepods (*Bythotrephes* $F_{1,7} = 6.259$, $p = 0.041$) and small cladocerans (*Bythotrephes* $F_{1,7} = 16.779$, $p = 0.005$).

Zooplankton species responses to *Bythotrephes*

RM-ANOVA revealed significant effects of *Bythotrephes* on individual species (Table 4, Fig. 4). *Bythotrephes* significantly increased average *Holopedium glacialis* concentration by 89 ind·m^{-3} and average cyclopoid copepodid concentration by 21 ind·m^{-3}, from Week 1 to 4. Average abundances of *L. minutus* declined by 53 ind·m^{-3} in *Bythotrephes* treatments throughout the experiment. *Bythotrephes* had a negative effect over time (Time × *Bythotrephes* interaction) on *Eubosmina longispina, Bosmina (Bosmina)* spp., and calanoid copepodids, where average concentrations were reduced by > 300, 173, and 115 ind·m^{-3}, respectively in *Bythotrephes* treatments compared to no *Bythotrephes* treatments from Week 1 to 4.

Recovered vs acid-damaged zooplankton responses to *Bythotrephes*

MANOVA showed a significant interaction between recovery and *Bythotrephes* (Pillai = 0.948, $F = 11.028$, $p = 0.038$; Fig. 5), suggesting that *Bythotrephes* had a different effect on some functional groups, depending on whether or not they were in a recovered community. For example, average cyclopoid copepod abundance increased by 9 ind·m^{-3} in the *Bythotrephes* treatment in the acid-damaged community, but declined by 12 ind·m^{-3} in the recovered community on Weeks 1 to 4 (Fig. 4). The addition of *Bythotrephes* had a greater negative impact on the recovered community than the acid-damaged community. Throughout the experiment, *Bythotrephes* caused a 32% decline in the average total zooplankton abundance of the recovered community, but only an 8% decline in acid-damaged average total zooplankton abundance (Time × Recovery × *Bythotrephes* interaction; Fig. 3). There was also an interaction between recovery and *Bythotrephes* on species diversity, such that *Bythotrephes* had a negative effect on diversity in the recovered treatment, but increased diversity in the acid-damaged community.

There was a significant interaction between *Bythotrephes* and recovery on abundances of *E. longispina* and cyclopoid copepodids (Fig. 4). Averaged over Week 1 to 4, these taxa declined in abundance by 90 ind·m^{-3} (*E. longispina*) and 31 ind·m^{-3} (cyclopoid copepodids) in the presence of *Bythotrephes* in the recovered treatment, but increased their abundances in the acid-damaged community by 79 ind·m^{-3} and 32 ind·m^{-3}, respectively. *Mesocyclops edax* concentration also declined by 14 ind·m^{-3} in the recovered treatment, but increased by 8 ind·m^{-3} in the acid-damaged treatment, although it was not statistically significant.

Bythotrephes

We were able to detect *Bythotrephes* at low abundances (< 2 individuals per enclosure) throughout the experiment in four of the six invaded enclosures, using the 15 cm diameter net during routine zooplankton sampling. At the conclusion of the experiment, we suspect that *Bythotrephes* abundances had declined because we were only able to retrieve live individuals from two enclosures. Both dead specimens and broken tail spines were recovered in all enclosures.

Discussion

The results of our study indicate that *Bythotrephes* can have negative effects on several measures of community structure, but that the initial community composition is an important determinant of the extent of the effect of *Bythotrephes*. In the context of this experiment, the degree to which the zooplankton community in a lake had recovered from acidification influenced the outcome of the invasion. This interactive effect of an invader with different stages of recovery from acidification gives important evidence that the invasion of *Bythotrephes* into different systems will have complex and unpredictable effects. In our study we found that *Bythotrephes* negatively affected total community biomass and abundance, and caused compositional shifts due to the loss of small cladoceran taxa. Surprisingly, *Bythotrephes* had a stronger impact on the recovered zooplankton assemblage in terms of both total zooplankton abundance and diversity, contrary to our expectation that the more diverse community would be more resistant to stress.

Our experimental invasion of *Bythotrephes* into two distinct zooplankton communities in different stages of recovery had a significant negative effect on the total abundance and total biomass of zooplankton communities (Fig. 3). These results are consistent with previous studies of invasions, where total zooplankton community abundance declined in mesocosms with *Bythotrephes* (Wahlström and Westman 1999), and in Harp Lake, Ontario, where total zooplankton abundance in pre-invasion years was greater than in post-invasion years (Yan et al. 2001). In addition, total mid-summer zooplankton biomass was 41% lower in lakes which had been invaded by *Bythotrephes* in a one-time survey of 30 Shield lakes with and without the invader (Boudreau and Yan 2003). The response of zooplankton in our enclosures was unlikely caused by factors other than *Bythotrephes*. We detected no statistical differences in conductivity, temperature, dissolved oxygen, or nutrients among our experimental treatments. There were significant increases in total chlorophyll *a* in invaded enclosures, which is a response consistent with declines in zooplankton abundance or biomass (i.e., decreased grazing rates). On Week 0 there tended to be higher levels of phosphorus in the invaded treatment, which may have also contributed to the higher abundance of chlorophyll *a*. Thus, declines in abundance and biomass seem to be a consistent response of zooplankton communities to a *Bythotrephes* invasion, regardless of the initial state or recovery status of the community.

A major factor in the decrease in total community abundance in our experiment was the negative effect *Bythotrephes* had on *E. longispina* and *Bosmina (Bosmina)* spp. in the recovered community. Our results concur with previous studies that have suggested that *Bythotrephes* has a preference for bosminids (Wahlström and Westman 1999; Yan et al. 2001). However, in the acid-damaged community, *Bythotrephes* had no effect on *Bosmina* (*Bosmina*) spp. and a positive effect on *E. longispina*. This difference in response to *Bythotrephes* probably occurred because *Bosmina (Bosmina) spp*. and *E. longispina* were able to escape heavy predation because of their relatively low abundance. We found that the effect of *Bythotrephes* on individual species tended to be dependent on the initial density of the prey species, which may have enabled some species to escape predation and increase in abundance due to release from competition, e.g., *E. longispina*. In a regression of the relative effect size of *Bythotrephes* against log(x+1)-transformed abundances in the absence of the invader, zooplankton abundance explained a highly significant amount of variation in the effect size of *Bythotrephes* on prey species ($r^2 = 0.706$, $p < 0.001$). This suggests that, although *Bythotrephes* exhibits a strong preference for cladocerans, it tends to prey on the most abundant species present.

The individual species and community responses to *Bythotrephes* were dependent on the recovery status of the zooplankton community. In our experiment, the presence of *Bythotrephes* had a greater negative effect on the abundance of the recovered zooplankton community. Three taxa (*E. longispina, M. edax*, and cyclopoid copepodids) were more negatively affected by

Bythotrephes in the recovered treatment, in agreement with other experimental and survey data in systems which were not damaged by acidification (Wahlström and Westman 1999; Boudreau and Yan 2003). Communities structured by past acidification and at different stages of recovery have species present in abundances that reflect their tolerance for the abiotic conditions of the lake. In lakes invaded by *Bythotrephes*, the species most tolerant to the local abiotic environment, and therefore the species with the highest concentrations, will be the most susceptible to density-dependent predation. This effect will be exacerbated in recovered communities where acid-sensitive cladocerans have returned to high concentrations. Dumitru et al. (2001) calculated that *Bythotrephes* can remove > 100% of total zooplankton production per day in Harp Lake, a Precambrian Shield lake. On average, cladocerans contribute > 40% of the total zooplankton biomass in these lakes (Arnott et al. 2001). Therefore, density-dependent predation, combined with feeding preferences for small cladocerans, makes this zooplankton group particularly vulnerable to *Bythotrephes* predation. In acid-damaged lakes, small cladocerans are likely to experience a reduced impact of *Bythotrephes* because of their low proportional abundance. The reduced effect of *Bythotrephes* on *E. longispina* in the acid-damaged community in our experiment supports this hypothesis.

Alternatively, the acid-damaged zooplankton community may have been suffering from stress associated with being moved to higher pH. This stress may have prevented the community from experiencing a rapid increase in the absence of predators, as shown in the recovered community. However, if the acid-damaged zooplankton were stressed by the change in pH, they likely would have decreased in abundance within the first few weeks of the experiment. There was no significant difference in the abundance of acid-damaged zooplankton in the no

Bythotrephes treatment between Weeks 0 and 1 (*t*-test, $p = 0.646$), thus, pH stress is an unlikely explanation for differences in acid-damaged and recovered community responses to invasion.

Density dependent predation likely explains the observed effect of *Bythotrephes* on species diversity. In the acid-damaged community, > 90% of species abundance was attributable to two acid-tolerant species, *L. minutus* and *D. birgei*. By preying on the most abundant species, *Bythotrephes* allowed other species to be released from competition for resources, resulting in increased levels of diversity in the acid-damaged community.

We were surprised by the lack of a significant effect of *Bythotrephes* on species richness. Yan et al. (2002) detected a 17% decline in species richness in Harp Lake over a period of seven years following the invasion of *Bythotrephes*. As well, Boudreau and Yan (2003) found a 30% decrease in species richness in 13 boreal Shield lakes invaded by *Bythotrephes*. Our inability to detect an effect of *Bythotrephes* on crustacean zooplankton richness was probably because of the short-term scale of our experiment. The long-term monitoring program of Harp Lake generated a database with 12 and seven years of pre- and post-invasion samples, respectively (Yan et al. 2001; Yan et al. 2002). Boudreau and Yan (2003) sampled lakes which may have been invaded for up to 10 years and thus had several years for *Bythotrephes* to impact the zooplankton community. Our experiment lasted four weeks, and while this duration was long enough to detect changes in species concentrations, it may not have been long enough for the extirpation of species to take place.

In summary, recovered and acid-damaged zooplankton communities responded differently to *Bythotrephes* in terms of individual species concentrations and for more aggregate community structure metrics, including total zooplankton concentration and diversity. We were surprised to find that the impact of *Bythotrephes* was greater in the recovered than the acid-damaged zooplankton community. This suggests that when an invasive species enters a system that is being influenced by other anthropogenic stressors, the results may be complex and difficult to predict. In our experiment, the initial composition of the community, especially the abundance of favoured prey, small cladocerans, seemed to influence the magnitude of the effect that *Bythotrephes* had on the community. Similarly, other studies have found that the interaction of multiple stressors had varying and surprising results on aquatic communities. In their study, Folt et al. (1999) found that the combination of 30 °C temperature with either low food or a toxin was more harmful to daphniids than the effects of either one of the stressors alone. In other cases, the combination of the toxin and low temperature (20 °C) was less stressful than the effect of the single worst stressor by itself (Folt et al. 1999). In Swan Lake, near Sudbury, Ontario, chemical and biotic recovery from long-term acid deposition was interrupted by an additional stressor: a two year drought which caused the lake to re-acidify (Yan et al. 1996a). This interaction between climate and acidification had unpredictable effects, including a temporary increase in crustacean zooplankton species richness resulting, partially, from the appearance of acid-sensitive species (Arnott et al. 2001). A review of marine and estuarine non-indigenous species invasions found that a high percentage of invasions occurred with other stressors, but that these effects were seldom quantified (Ruiz et al. 1999). To date, ours is the first study that we have knowledge of that quantitatively examines how an invasive species can interact with biological recovery from acidification.

Our study provides evidence that the concerted effect of invasion and acidification will have substantial negative impacts on crustacean zooplankton in lakes. This is especially important for crustacean zooplankton, which are generally slow to recover from acidification (Locke et al. 1994) and are the primary prey items for *Bythotrephes*. In Yan et al.'s (2003) conceptual framework of biological recovery, suitable water quality, followed by availability of colonists, and overcoming demographic and stochastic hurdles are the main steps to recovery. The last step in this framework is influenced by community-level factors, such as predation, which will modify the population growth of the target organism, and thus affect biological recovery (Yan et al. 2003). The invasion of *Bythotrephes* in lakes may effectively implement a roadblock to recovery by preying on species in the process of recovery. A > 64% decline in the abundance of *L. minutus* in our acid-damaged treatment that was exposed to *Bythotrephes* predation, suggests that *Bythotrephes* will likely have a substantial impact on acid-damaged lakes where *L. minutus* dominates the community. This is of particular importance because a recent study revealed that *L. minutus* is currently the dominant crustacean zooplankton species in 35% of the lakes in Killarney Park (Arnott, unpublished manuscript). Sprules (1975) identified six main species that occur in Killarney lakes across a broad pH range: *Diaptomus minutus, Bosmina longirostris, Holopedium gibberum, Mesocyclops edax, Cyclops bicuspidatus thomasi*, and *Diaphanosoma leuchtenbergianum* (see Table 5 for taxonomic revisions). Of these acid-tolerant species, *Bythotrephes* negatively affected abundances of three in both recovered and acid-damaged communities in our study, and negatively affected two others in the recovered community only (Table 5). As well, the abundances of two acid-sensitive species, *Daphnia retrocurva* and *Epischura lacustris*, which were rare in the Sprules (1975) survey, were negatively impacted by *Bythotrephes* in the recovered community in our study (Table 5). This suggests that invasion of *Bythotrephes* into regions affected by acidification, can impact not only species that are widely distributed across the landscape, but also rarer species that may exist in small isolated populations. The reduction or loss of these isolated, potential sources of colonists may reduce dispersal rates to other lakes, thereby having important negative consequences for regional recovery of the biota.

A long-term study of recovering lakes has shown that failed colonization events can occur frequently, even when conditions are suitable for the establishment of species (Keller et al. 2002). In one of the study lakes, species were able to arrive via internal and/or external modes of colonization, but failed to establish lasting populations, in part due to biological resistance from the invertebrate predator, *Chaoborus* (Keller et al. 2002), which can prey on many smaller species of zooplankton, including some species of *Daphnia* (Vanni 1988). It is likely that *Bythotrephes*, which has high predation rates (Lehman and Cáceres 1993; Dumitru et al. 2001), would have a similar effect on colonizing species of zooplankton, preventing their establishment in recovering lakes. Our study suggests that *Bythotrephes* will disrupt the structure of communities that are acid-damaged and those at more advanced stages of recovery, changing the probable biological endpoint of recovery, such that it will no longer possible for the community to return to its former composition.

Although the direct effects of *Bythotrephes* on zooplankton have been observed in other systems, previous studies have not shown an indirect effect of *Bythotrephes* on chlorophyll *a* (Lehman and Cáceres 1993; Wahlström and Westman 1999). In our experiment, the *Bythotrephes* treatments had significantly higher concentrations of chlorophyll *a*. This indirect effect of *Bythotrephes* on phytoplankton in the enclosures suggests that by altering the composition of the zooplankton community, the invader can cause a trophic cascade of effects in the food web. The invasion of another exotic species of the Cercopagid family, *Cercopagis pengoi*, has resulted in numerous changes to the food web of Lake Ontario. High abundances of *C. pengoi* resulted in declines of the herbivores *Daphnia retrocurva* (reduced from 4650 ind·m^{-3}

to 120 ind·m^{-3}) and *Bosmina longirostris* (reduced from 32 000 ind·m^{-3} to 125 ind·m^{-3}) in 1999, which led to an increase in phytoplankton biomass (Laxson et al. 2003). Our experimental results indicate that more moderate declines in zooplankton abundance (32% and 8% reduction in recovered and acid-damaged communities, respectively) can still precipitate changes in the lower trophic levels.

We recovered few *Bythotrephes* at the end of the experiment. Several factors may be responsible. First, *Bythotrephes* populations may not have been successfully established in the enclosures. This explanation seems unlikely, as third instar individuals, carrying eggs in the late stage of development, were detected near the end of the experiment. This suggests that there were adequate resources to support healthy, reproducing individuals and that new individuals were entering the populations. Second, the conical net used for routine sampling was small (0.15 m diameter). Small nets can be avoided more easily than large nets (Fleminger and Clutter 1965), especially by large-bodied zooplankton, such as *Bythotrephes,* that have a compound eye and can swim more quickly than some smaller zooplankton (see Muirhead and Sprules (2003) for a comparison of swimming velocities). The use of the larger net at the conclusion of the experiment should have reduced this problem. While some *Bythotrephes* may have been able to avoid the net, it may be that populations were reduced at this point in the experiment, compared to the starting concentrations. Another possibility is that there was greater mortality of *Bythotrephes* individuals collected in routine sampling for other zooplankton. This seems unlikely as no more than two individuals were ever captured from an enclosure, compared to a total of 68 that were initially stocked. In other experimental enclosures, there was a reduction in *Bythotrephes* concentration throughout the experiment when concentrations were high (37.5 and 62.5 *Bythotrephes* ind·m^{-3}) (Wahlström and Westman 1999), likely due to cannibalism between conspecifics at high densities. Although our starting concentration was much lower (10 ind·m^{-3}) and cannibalism was probably not a factor controlling populations, we suspect that *Bythotrephes* populations in our experiment may have also declined throughout the experiment. However, the fact that we captured reproducing individuals and that we detected significant differences in many parameters of zooplankton community structure in our experiment, leads us to conclude that our *Bythotrephes* treatment was maintained, although perhaps at lower concentrations toward the end of the experiment. If *Bythotrephes* densities did indeed decline through our experiment, as in Wahlström and Westman (1999), our results are probably conservative estimates of the magnitude of effects of *Bythotrephes* on recovered and acid-damaged zooplankton communities.

A criticism of enclosure studies is that they lack the complexity of an entire ecosystem (Schindler 1998*b*). Our study was a unique attempt to experimentally unravel the direct consequences of an invasion on different zooplankton communities, while removing confounding factors, such as competition with other invertebrates and predation from fish. However, the absence of planktivorous fish to prey on *Bythotrephes* in our experiment may create an unrealistic scenario for the invasion of this species into small inland lakes. *Bythotrephes*' role in restructuring the zooplankton community of Harp Lake has occurred under intensive fish predation, where lake herring (*Coregonus artedtii*) selectively feed on the invader, even though its relative abundance and biomass is lower than other preferred prey items (Coulas et al. 1998). Decreases in the abundances of four species of native cladocerans were observed in Lake Michigan after the invasion of *Bythotrephes*, where all but *Daphnia galeata mendotae* were decimated, despite the presence of planktivorous fish (Lehman and Cáceres 1993). Past studies have suggested that invertebrate predators can only structure zooplankton communities when planktivorous fish are absent or in low abundance (Black II and Hairston Jr. 1988). However, *Bythotrephes* has demonstrated the ability to structure zooplankton communities, regardless of whether or not it is in the presence of fish, suggesting that it can be an important component of lake food webs, and thus, that our manipulation was realistic. An additional criticism of enclosure studies is the brevity of the experimental manipulation and the applicability of the results in the long term. Studies of this nature can be looked upon as models that examine specific questions, which can then be tested in increasingly complex ways, exploring a range of possibilities that can occur in natural systems (Drake et al. 1996). At this level of organization, the direct effects of invertebrate predation on zooplankton communities occur quickly, due to the short generation times of these organisms, but can be important in the long-term structuring of the community. For example, a feeding experiment with *Chaoborus* conducted in < 6 d found results that were consistent with field studies of the size-selective predation of *Chaoborus* on *Daphnia* (MacKay and Elser 1998). In addition, the indirect consequences of predation, such as release from competition, can also cause changes to occur rapidly in the zooplankton community, as some taxa can increase their abundance quickly due to parthenogenic reproduction. Our experiment provides a stepping stone for future predictions about the effects of *Bythotrephes* in boreal lakes. Due to the rapid spread of *Bythotrephes* in inland lakes, many natural whole-lake experiments will be created, allowing for further tests of the specific hypotheses generated by our experiment.

The invasion of exotic species is a problem of growing concern, as both terrestrial and aquatic ecosystems are susceptible to introductions from a variety of sources, e.g., ballast water, aquaculture, intentional introductions (see Ricciardi and Rasmussen 1998). In this study, the effects of an invasive species on two very different communities were experimentally tested.

Bythotrephes negatively affected community and species parameters in both recovered and acid-damaged zooplankton communities. This will have serious implications for the continued success of biological recovery in the wake of decreased sulphur dioxide emissions and improved water chemistry.

At the community-level, both acid-tolerant species, such as *L. minutus*, which occupies a large fraction of lakes and dominates zooplankton assemblages in acidification events, as well as acid-sensitive species, such as *E. longispina*, which are recolonizing lakes in the improved environment, were negatively affected. At the ecosystem-level, declines of 32% and 28% in the biomass of recovered and acid-damaged zooplankton, respectively, will likely have severe effects on several trophic levels throughout the food web. Planktivorous fish rely on zooplankton as a food source, and will likely suffer from both decreases in prey availability and increased competition from *Bythotrephes*, resulting in greater energetic costs to obtain food. A previous study has also shown that other invertebrate predators may be outcompeted for food and directly preyed upon by this voracious invader (Branstrator 1995). Phytoplankton populations may proliferate in the absence of herbivorous zooplankton, as these experimental results suggest that release from predation pressure by *Bythotrephes* can increase phytoplankton biomass. Overall, the results from our experiment suggests that *Bythotrephes* will not only affect zooplankton communities directly through changes to its structure, but will indirectly alter other trophic levels in boreal lakes, leading to unexpected food web changes in different lake types.

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Table 1. Summary of water chemistry variables of Kakakise Lake, Bell Lake, and Ruth Roy Lake, Killarney Park, Ontario from data collected from a surface water sample (3-4 July 2001; J. Heneberry, Cooperative Freshwater Ecology Unit, Laurentian University, Sudbury, Ontario P3E 2C6, unpublished data).

Limnological variable	Kakakise	Bell	Ruth Roy
Lake surface area (ha)	112.6	347.4	54.5
Maximum depth (m)	30.5	26.8	18.0
Mean depth (m)	13.5	8.1	4.3
pH	6.91	6.35	4.82
Conductivity ($\mu S \cdot cm^{-1}$)	28.8	26.5	21.9
Ca ($mg \cdot L^{-1}$)	2.25	2.0	1.0
SO_4 ($mg \cdot L^{-1}$)	6.5	7.0	7.0
Al ($\mu g \cdot L^{-1}$)	27.8	53.8	335
Cu ($\mu g \cdot L^{-1}$)	1.02	2.14	1.78
Ni ($\mu g \cdot L^{-1}$)	2.45	7.63	12.5
Total phosphorus ($\mu g \cdot L^{-1}$)	6.0	6.0	4.0
Total Kjeldahl nitrogen ($mg \cdot L^{-1}$)	0.20	0.24	0.16
Dissolved organic carbon ($mg \cdot L^{-1}$)	3.0	5.3	1.9

Table 2. Average pH, conductivity (μS·cm^{-1}), total phosphorus (μg·L^{-1}), surface temperature (°C), and dissolved oxygen (mg·L^{-1}) measured on each enclosure on selected dates during the experiment. The standard deviations of the measurements are in parentheses.

		Recovered		Acid-damaged	
Variable	Week	*Bythotrephes*	No *Bythotrephes*	*Bythotrephes*	No *Bythotrephes*
pH	0	6.8 (0.03)	6.8 (0.01)	6.8 (0.09)	6.8 (0.05)
	2	6.7 (0.03)	6.7 (0.01)	6.7 (0.07)	6.7 (0.02)
	4	6.7 (0.01)	6.6 (0.02)	6.6 (0.05)	6.6 (0.02)
Conductivity (μS·cm^{-1})	0	26.1 (0.10)	26.1 (0.00)	26.2 (0.17)	31.6 (10.3)
	2	26.2 (0.40)	26.0 (0.00)	26.4 (0.44)	25.9 (0.31)
	4	26.2 (0.25)	26.0 (0.28)	26.4 (0.30)	26.1 (0.25)
Total phosphorus (μg·L^{-1})	0	12.9 (6.37)	7.5 (1.27)	9.7 (1.62)	4.4 (0.99)
	4	3.2 (0.85)	2.5 (2.83)	2.7 (0.40)	3.3 (1.12)
Temperature (°C)	0	19.8 (0.21)	19.6 (0.13)	19.8 (0.17)	19.7 (0.16)
	2	20.5 (0.04)	20.7 (0.04)	20.3 (0.27)	20.3 (0.01)
	4	21.2 (0.08)	21.1 (0.01)	21.25 (0.09)	21.2 (0.09)
Dissolved oxygen (mg·L^{-1})	0	10.4 (0.08)	10.1 (0.03)	10.2 (0.13)	10.3 (0.11)
	2	10.1 (0.15)	9.9 (0.31)	10.1 (0.18)	10.1 (0.12)
	4	10.2 (0.07)	10.0 (0.07)	9.9 (0.07)	10.0 (0.19)

Table 3. Two-factor repeated measures analysis of variance on zooplankton community metrics in enclosures comparing the effect of an invasion *Bythotrephes (Bytho)* on recovered and acid-damaged (Recov) communities across the length of the experiment (Time). Values reported are F-ratios. † $p < 0.1$, * $p < 0.05$, ** $p < 0.01$

	Recov	*Bytho*	Recov × *Bytho*	Time	Time × Recov	Time × *Bytho*	Time × Recov × *Bytho*
Log biomass	30.494**	7.984*	0.010	18.423**	7.527**	5.099 **	1.764
Abundance	59.103**	7.690*	5.406†	6.400**	4.115*	2.907 †	4.181*
Species richness	73.279**	0.003	0.686	0.949	1.314	1.999	0.125
Species diversity	17.528**	1.003	4.197†	4.867*	4.685*	2.849 †	0.649

Table 4. Two-factor repeated measures analysis of variance on abundance of zooplankton species in enclosures comparing the effect of an invasion of *Bythotrephes (Bytho)* on recovered and acid-damaged (Recov) communities across the length of the experiment (Time). Values reported are F-ratios. † $p < 0.1$, * $p < 0.05$, ** $p < 0.01$

	Recov	*Bytho*	Recov × *Bytho*	Time	Time × Recov	Time × *Bytho*	Time × Recov × *Bytho*
Eubosmina longispina	54.735**	0.186	16.527**	10.371**	1.478	4.173*	2.243
Bosmina (Bosmina) spp.	3.654†	0.867	0.815	2.431†	2.466	7.906**	2.704†
Holopedium glacialis	360.801**	5.638*	0.781	59.378**	23.653**	3.356*	1.754
Diaphanosoma birgei	1.176	2.366	1.269	2.819†	14.457**	0.969	1.262
Sida crystallina	0.142	1.760	0.868	1.818	0.813	0.183	2.738†
Leptodiaptomus minutus	0.025	6.330*	0.686	18.124**	0.303	3.295*	2.779†
Diacyclops bicuspidatus thomasi	12.936**	<0.001	1.031	1.243	1.325	0.885	1.309
Mesocyclops	183.811**	1.496	4.941†	13.699**	6.623**	0.655	0.510

edax							
Tropocyclops extensus	41.634**	0.253	0.001	1.248	2.525†	1.002	0.656
Calanoid copepodid	6.191*	2.940	0.111	10.542**	4.122*	4.143*	0.520
Cyclopoid copepodid	78.189**	5.862*	8.002*	3.018	0.225	0.031	0.332
Calanoid nauplii	27.086**	3.805†	1.6971	25.648**	2.227	1.334	0.406
Cyclopoid nauplii	32.675**	1.010	1.678	2.285	0.402	2.164	1.104

Table 5. A summary of the effects of *Bythotrephes* on species in acid-damaged and recovered enclosures, listed from the least pH tolerance to the greatest. Species included occur on at least four dates in the experiment. The tolerance ranges reported are limited to the geographic region of our study, as species responses may vary in different locales.

	pH tolerance*	Acid-damaged (% change in abundance)	Recovered (% change in abundance)
Epischura lacustris	5.9-7.0	---	-51.4
Eubosmina longispina	5.4-7.0	878.7	-82.3
Daphnia retrocurva	5.2-6.4	---	-90.5
Tropocyclops extensus [a]	5.2-7.0	---	21.6
Sida crystallina	≥ 5.0	31.9	-61.2
Diacyclops bicuspidatus thomasi [b]	4.2-7.0	214.3	-26.4
Diaphanosoma birgei [c]	4.2-7.0	-40.6	-31.6
Holopedium glacialis [d]	4.2-7.0	344.4	30.0
Mesocyclops edax	4.2-7.0	276.2	-13.0
Polyphemus pediculus	4.1-5.6	-7.7	---
Bosmina (Bosmina) spp.[e]	4.0-7.0	-60.9	-70.0
Leptodiaptomus minutus [f]	4.0-7.0	-39.1	-38.2

* Source for *Eubosmina longispina*: Keller and Yan (1998), *Sida crystallina*: Walseng et al. (2003), all others from Sprules (1975)

[a] Formerly *Tropocyclops prasinus mexicanus*

[b] Formerly *Cyclops bicuspidatus thomasi*

[c] Formerly *Diaphanosoma leuchtenbergianum*

[d] Formerly *Holopedium gibberum*

[e] Formerly *Bosmina longirostris*

[f] Formerly *Diaptomus minutus*

Figure 1. Study site in Killarney Wilderness Park, Ontario, Canada.

Figure 2. Chlorophyll *a* concentration ($\mu g \cdot L^{-1}$) in response to experimental treatments: (a) total and (b) edible (< 30 µm). Symbols indicate the four treatment combinations: acid-damaged and no *Bythotrephes* (○), acid-damaged and *Bythotrephes* (●), recovery and no *Bythotrephes* (□), recovery and *Bythotrephes* (■). Vertical bars represent standard error (n = 3 for all treatments except recovery and no *Bythotrephes* where n = 2).

Figure 3. Community responses of zooplankton to *Bythotrephes* and recovery treatments: (a) log (x+1) biomass ($mg \cdot m^{-3}$), (b) abundance ($ind \cdot m^{-3}$), (c) species richness, (d) species diversity. Symbols indicate the four treatment combinations: acid-damaged and no *Bythotrephes* (○), acid-damaged and *Bythotrephes* (●), recovery and no *Bythotrephes* (□), recovery and *Bythotrephes* (■). Vertical bars represent standard error (n = 3 for all treatments except recovery and no *Bythotrephes* where n = 2).

Figure 4. Log (x+1) abundance ($ind \cdot m^{-3}$) of zooplankton species and juveniles in response to experimental treatments. Symbols indicate the four treatment combinations: acid-damaged and no *Bythotrephes* (○), acid-damaged and *Bythotrephes* (●), recovery and no *Bythotrephes* (□), recovery and *Bythotrephes* (■). Vertical bars represent standard error (n = 3 for all treatments except recovery and no *Bythotrephes* where n = 2).

Figure 5. Log (x+1) abundance ($ind \cdot m^{-3}$) of zooplankton functional groups in response to experimental treatments: (a) calanoid copepods, (b) cyclopoid copepods, (c) large cladocerans, (d) littoral cladocerans, and (e) small cladocerans. Symbols indicate the four treatment combinations: acid-damaged and no *Bythotrephes* (○), acid-damaged and *Bythotrephes* (●), recovery and no *Bythotrephes* (□), recovery and *Bythotrephes* (■).

Vertical bars represent standard error (n = 3 for all treatments except recovery and no *Bythotrephes* where n = 2).

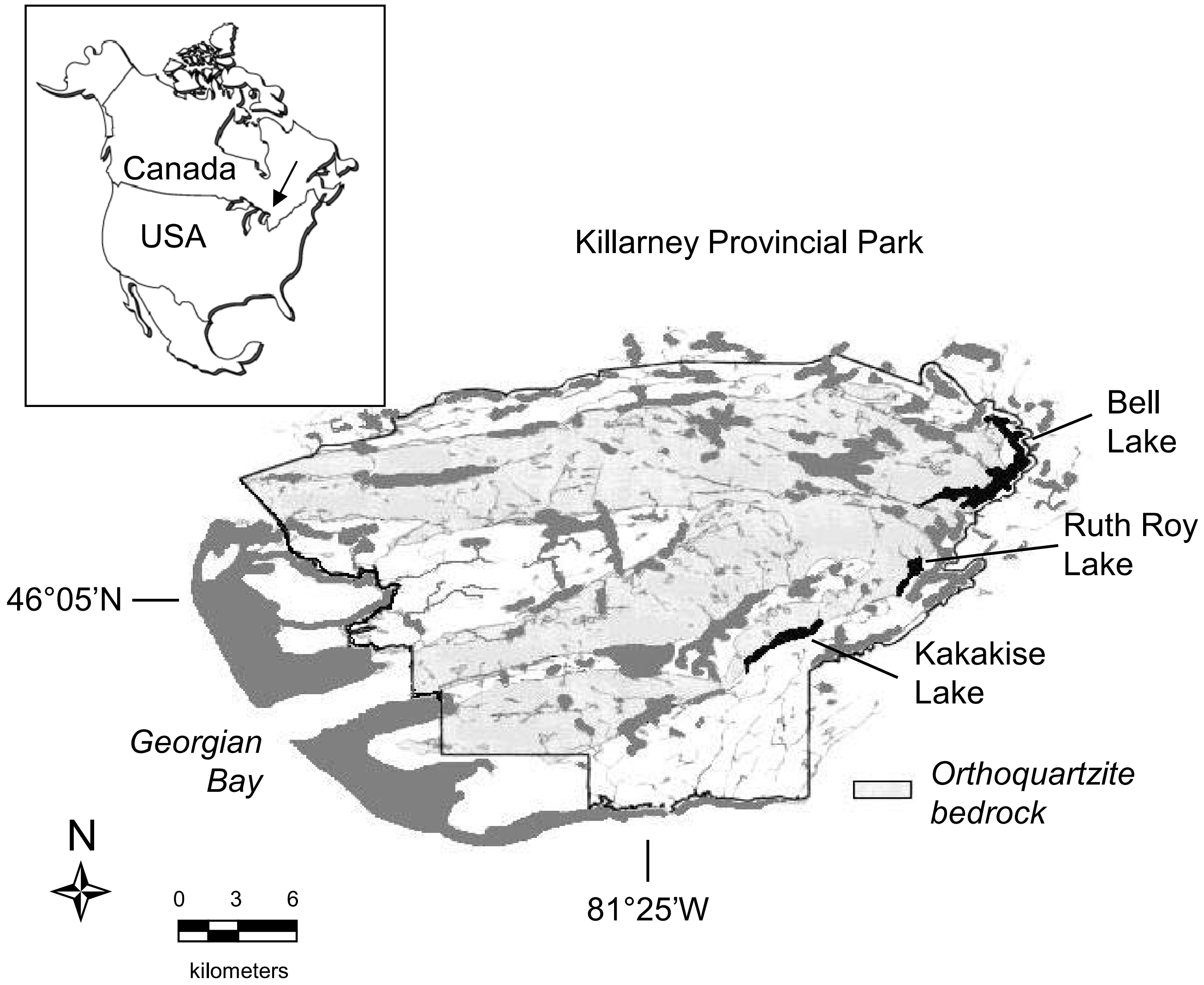

Canada
USA
Killarney Provincial Park
Bell Lake
Ruth Roy Lake
Kakakise Lake
46°05'N
Georgian Bay
Orthoquartzite bedrock
N
0 3 6
kilometers
81°25'W

Figure 1

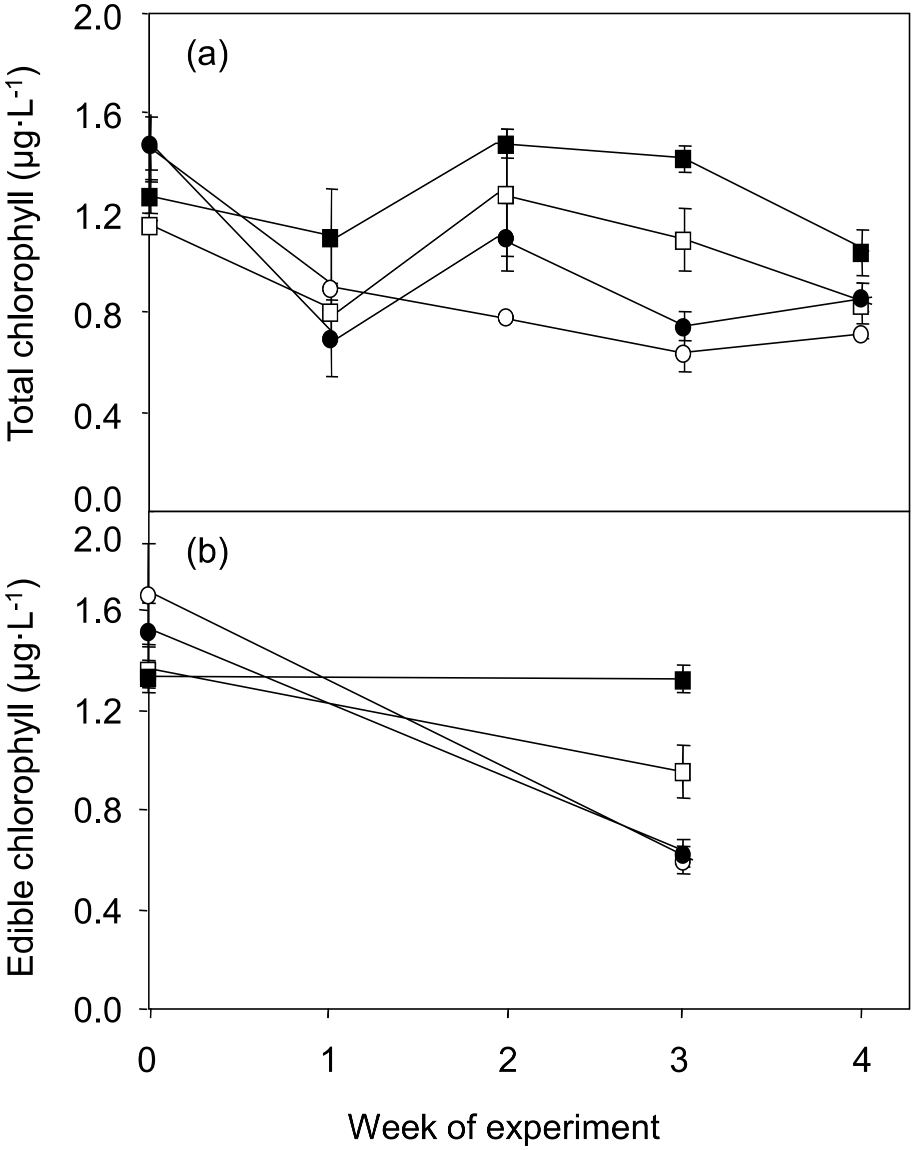
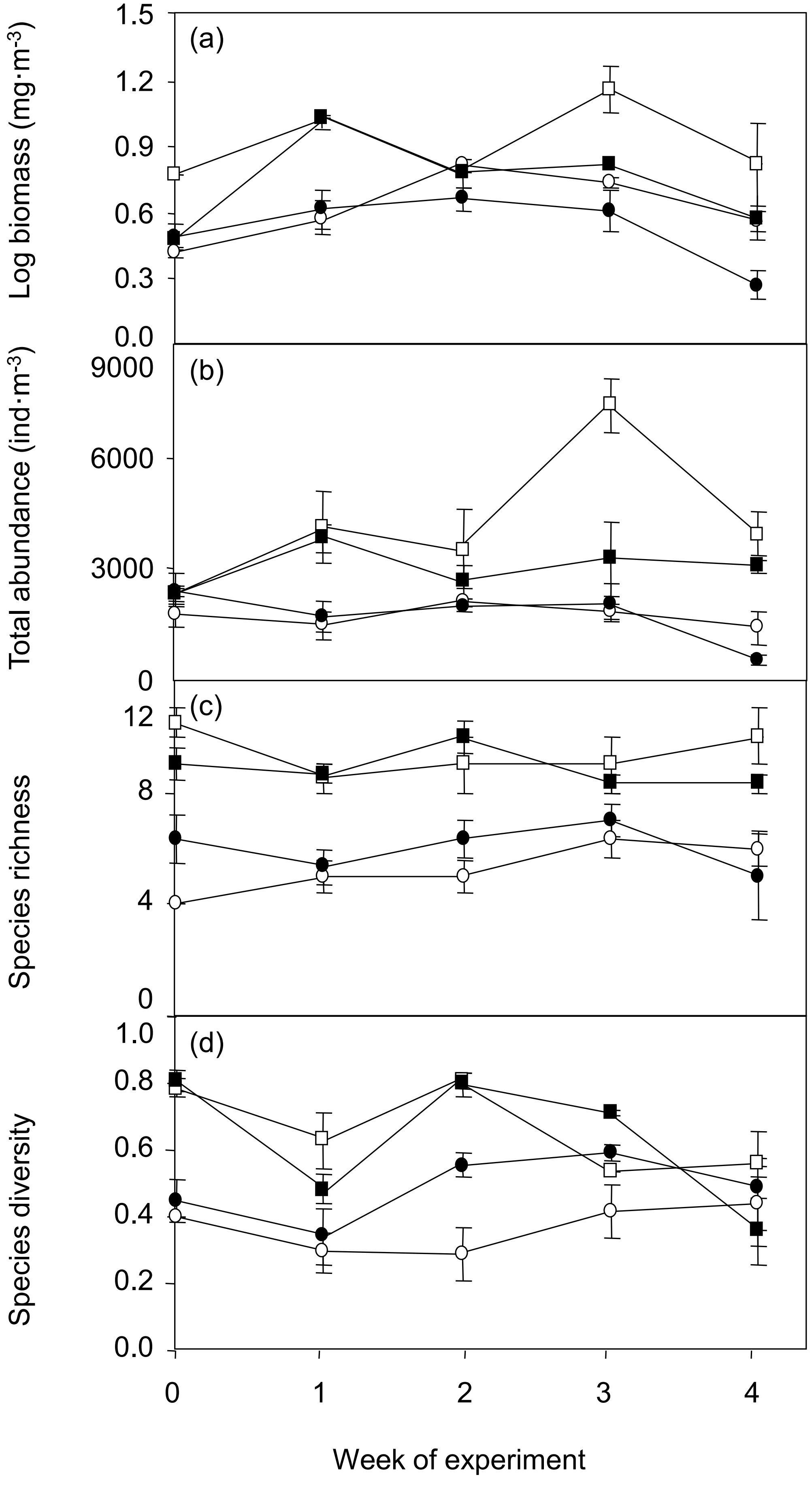
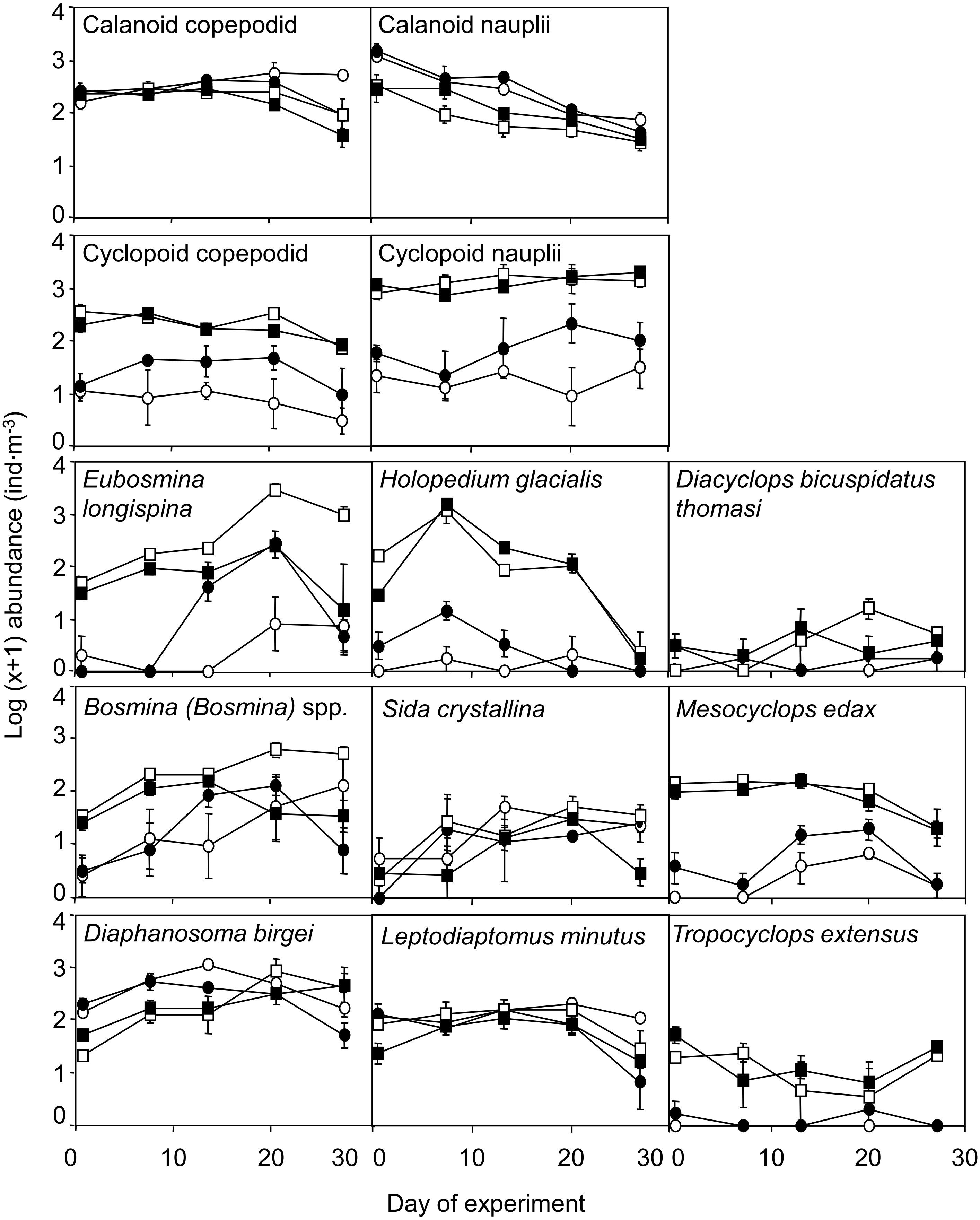

(a)
Total chlorophyll (µg·L⁻¹)
0.0
0.4
0.8
1.2
1.6
2.0
(b)
Edible chlorophyll (µg·L⁻¹)
0.0
0.4
0.8
1.2
1.6
2.0
0
1
2
3
4
Week of experiment

Figure 2



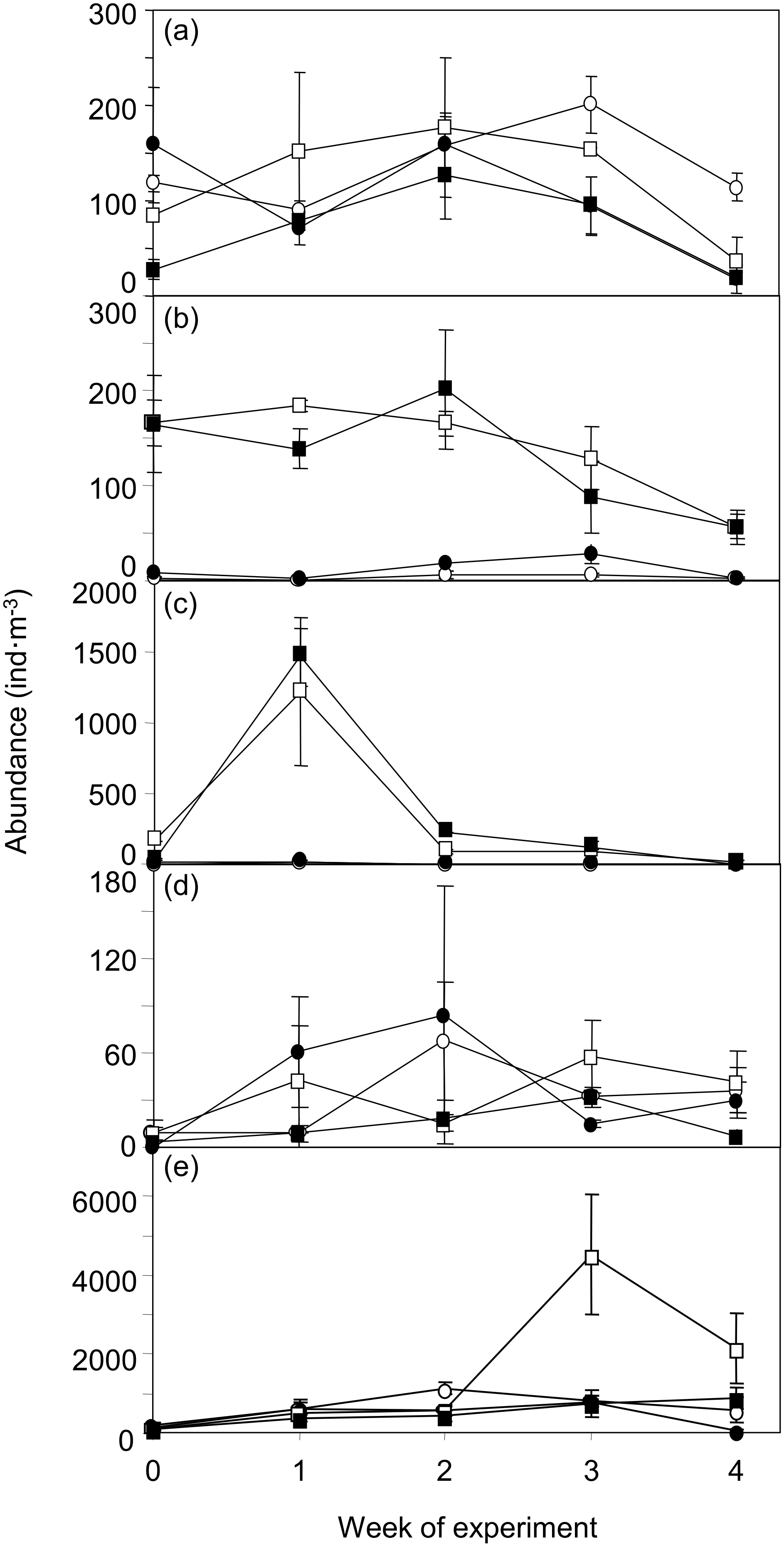
(a)
Log biomass (mg·m-3)
1.5
1.2
0.9
0.6
0.3
0.0
(b)
Total abundance (ind·m-3)
9000
6000
3000
0
(c)
Species richness
12
8
4
0
(d)
Species diversity
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
Week of experiment

Figure 3



Calanoid copepodid
Calanoid nauplii
Cyclopoid copepodid
Cyclopoid nauplii
Eubosmina longispina
Holopedium glacialis
Diacyclops bicuspidatus thomasi
Bosmina (Bosmina) spp.
Sida crystallina
Mesocyclops edax
Diaphanosoma birgei
Leptodiaptomus minutus
Tropocyclops extensus
Log (x+1) abundance (ind·m-3)
0
1
2
3
4
0
10
20
30
Day of experiment

Figure 4



(a)
(b)
(c)
(d)
(e)
300
200
100
0
300
200
100
0
2000
1500
1000
500
0
180
120
60
0
6000
4000
2000
0
Abundance (ind·m⁻³)
0
1
2
3
4
Week of experiment

Figure 5