

Invasive Predator, *Bythotrephes*, has Varied Effects on Ecosystem Function in Freshwater Lakes

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ABSTRACT

Bythotrephes longimanus is an invertebrate predator that has invaded the North American Great Lakes and a number of inland lakes, where it preys on crustacean zooplankton. We examined the effect of *Bythotrephes* on two measures of ecosystem function during a four-month observational study of freshwater lakes on the boreal shield. *Bythotrephes*-invaded lakes had significantly lower epilimnetic zooplankton abundance and production compared to reference lakes. On average, *Bythotrephes* consumed 34% of zooplankton production when it was present in lakes. There was some evidence of changes in the timing of zooplankton production, as well as shifts to cooler, less productive habitats, which may lessen the overall effect of the invader

on the transfer of energy to higher trophic levels. We experimentally demonstrated a weak trophic cascade where invader predation reduced zooplankton biomass, and subsequently increased phytoplankton growth. However, the response was small in magnitude and not biologically relevant at the whole lake-scale. The most conspicuous effect of *Bythotrephes* that we measured was a diversion of energy away from native predators at higher trophic levels.

Key words: invasive species; ecosystem function; crustacean zooplankton; *Bythotrephes*; freshwater lakes; secondary production; zooplankton grazing.

INTRODUCTION

The introduction of non-indigenous species is expected to be one of the greatest threats to species across all ecosystems (Wilcove and others 1998; Sala and others 2000) and the single most important driver of biodiversity loss in freshwater lakes (Sala and others 2000). Although there is evidence that invasive species can alter ecosystem function (Brooks and others 2004; Zhu and others 2006), we currently lack understanding of how newly intro-

duced species may affect ecosystem processes (Millennium Ecosystem Assessment 2005). Thus, the invasion of a non-native species presents a unique opportunity to understand how complex ecosystems operate.

Bythotrephes longimanus (Crustacea, Branchiopoda, Onychopoda) is a parthenogenetic invertebrate predator that has invaded all of the North American Great Lakes (Jin and Sprules 1990), and more than 100 inland lakes in North America, including waterbodies in Ontario (N. Yan, unpublished data), Minnesota (Branstrator and others 2006), and Michigan (Jarnagin and others 2000). Although studies have indicated that *Bythotrephes* prefers large, deep, low productivity lakes in both its native Eurasia and in invaded regions (MacIsaac

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and others 2000), it has been found in smaller shallow waterbodies and higher productivity lakes as well (Jarnagin and others 2000). *Bythotrephes* has the potential to invade many boreal shield and northern temperate lakes, especially those visited by human vectors.

Bythotrephes can have substantial effects on the community structure of its primary prey, crustacean zooplankton, and although there is some degree of among-lake variability in the response to invasion, the general trend has been reductions in species richness (Yan and others 2002; Strecker and others 2006), total community biomass (Boudreau and Yan 2003; Strecker and Arnott 2005), and total community abundance of zooplankton (Yan and others 2001; Strecker and Arnott 2005; Strecker and others 2006). These trends follow from dramatic declines in cladoceran zooplankton richness and abundance (Yan and others 2001; Boudreau and Yan 2003; Strecker and others 2006).

Zooplankton are a central component in freshwater food webs, transferring energy to young-of-year (YOY) and planktivorous fish via production of biomass, grazing on phytoplankton biomass, and recycling dissolved nutrients to phytoplankton. Foraging success of juvenile fish can be greatly influenced by variability in zooplankton populations in freshwater ecosystems (Chick and van den Avyle 1999; Beauchamp and others 2004). In one study, it was observed that *Bythotrephes* consumed large portions of zooplankton production in Harp Lake, Ontario during summer (Dumitru and others 2001), potentially decreasing the amount of production available to other components of the aquatic food web. Additionally, when *Bythotrephes* was present, total consumption of the invertebrate predator guild increased by greater than 300% (S. Foster, personal communication), potentially reducing the efficiency of energy transfer to higher trophic levels (Sprules 1980).

The impact of zooplankton on phytoplankton is influenced by zooplankton biomass and community composition—and is therefore potentially affected by *Bythotrephes* predation. Zooplankton grazing and nutrient recycling can have a greater effect on phytoplankton biomass in lakes than nutrient recycling of fish (Sarnelle and Knapp 2005), and grazing by large cladoceran zooplankton can exert strong top-down control on phytoplankton (Elser and Goldman 1991). Thus, zooplankton community structure in lakes can be a primary determinant of the flow of energy and nutrients to all trophic levels; however, few studies have examined the effects of invaders on nutrient and energy flow at multiple levels of organization

in freshwater systems (Simon and Townsend 2003).

The overall purpose of this study was to determine the effects of the invasive predator, *Bythotrephes*, on ecosystem function in boreal lakes. Ecosystem function is commonly measured as changes in rates of productivity, decomposition, nutrient cycling, and resistance and resilience to perturbations (Loreau and others 2001). In our study, we measured ecosystem function as changes in rates of secondary productivity and the combined effects of zooplankton grazing and nutrient cycling on phytoplankton. The two main objectives of our study were to examine: (1) the effect of *Bythotrephes* on crustacean zooplankton production within each lake stratum and throughout the ice-free season; and (2) if zooplankton impact on phytoplankton is influenced by *Bythotrephes*-induced changes in community composition and biomass.

Based on reductions in zooplankton abundance observed in previous studies (Yan and others 2001; Strecker and others 2006), we hypothesized that *Bythotrephes* would negatively affect zooplankton production. *Bythotrephes* tends to be absent in lakes until middle-to-late June (Yan and others 2001), creating a window of opportunity before this time period for zooplankton to increase their reproduction. Therefore, we expect to see a less pronounced effect of *Bythotrephes* on coarse measures of overall seasonal and whole-water column production, but differences in fine-scale temporal (biweekly) and spatial (variation between strata) patterns of zooplankton production. Secondly, the effects of zooplankton grazing and nutrient recycling on phytoplankton are significantly influenced by both community biomass and composition (Elser and Goldman 1991; Cyr 1998; Elser and others 2000), thus, we would expect zooplankton communities in invaded lakes to have a lessened impact on phytoplankton as a result of *Bythotrephes*-induced reductions in total zooplankton biomass and selective predation on cladocerans.

MATERIALS AND METHODS

Study Site and Sampling

Eight lakes in the Parry Sound and Muskoka districts of south-central Ontario were chosen for our study (Table 1). The study lakes are located in mixed-forest catchments, have low productivity (oligo-mesotrophic), and are circumneutral. Lakes are relatively deep, ranging from 23 to 59 m, and have surface areas ranging from 72 to 2058 ha

Table 1. Morphometric, Physical, Chemical, and Biotic Characteristics of Study Lakes

Lake	Lat. Long.	Z _{max} (m)	Area (ha)	Ca (mg l ⁻¹)	DOC (mg l ⁻¹)	Cond. (µmhos cm ⁻¹)	pH	TP (µg l ⁻¹)	Mean total chl <i>a</i> (µg l ⁻¹)
Reference									
Buck ^a	45°25'N 79°23'W	23.0	656.0	2.6	10.7	25.6	6.3	13.3	2.8
Doe ^a	45°32'N 79°25'W	23.0	1187.0	3.6	7.0	46.0	7.1	12.0	3.4
Pickereel ^a	45°41'N 79°18'W	38.0	513.0	2.8	6.7	32.4	6.8	8.1	4.4
Sand	45°37'N 79°10'W	59.0	568.2	3.5	6.0	37.2	6.8	7.1	2.0
Mean		35.8	731.1	3.1	7.6	35.3	6.8	10.1	3.1
Invaded									
Harp ^a	45°23'N 79°07'W	37.5	71.7	3.0	6.7	38.0	7.0	7.2	1.7
Vernon ^a	45°20'N 79°17'W	37.2	1505.1	3.0	7.1	36.8	6.8	7.9	2.8
Bernard	45°45'N 79°23'W	47.9	2057.7	4.1	3.4	65.2	7.1	9.6	2.8
Peninsula	45°20'N 79°06'W	34.1	864.8	4.4	6.1	70.6	7.1	9.0	2.6
Mean		39.2	1124.8	3.6	5.8	52.7	7.0	8.4	2.5
F-ratio		0.14	0.75	1.04	1.74	3.10	1.96	1.16	1.51
P-value		0.72	0.42	0.35	0.23	0.13	0.21	0.32	0.27

^aLakes included in grazing experiment.

A one-way ANOVA was performed on parameters ($n = 4$, treatment $df = 1$, error $df = 6$). Lakes sorted by increasing *Bythotrephes* abundance. Lat. = latitude; long. = longitude; Z_{max} = maximum depth; Ca = calcium; DOC = dissolved organic carbon; Cond = conductivity; TP = total phosphorus; chl *a* = chlorophyll *a*.

(Table 1). Lakes were chosen based on prior knowledge of the invasion of *Bythotrephes* (invaded lakes had *Bythotrephes* for at least 5 years), proximity, and similarity of chemical, physical, and morphometric characteristics. As well, all of the lakes contained the glacial relict *Mysis relicta*, which is indicative of a similar post-glacial history, and planktivorous fish communities, including yellow perch (*Perca flavescens*) and a combination of cisco (*Coregonus artedii*), rainbow smelt (*Osmerus mordax*), and lake whitefish (*Coregonus clupeaformis*) (Appendix 1).

Lakes were visited every two weeks from May to September 2003 ($n = 9$), and samples were generally taken within a five-day time period. At a deep station in the lake, temperature, dissolved oxygen, and Secchi depth were measured, and samples were taken for zooplankton, *Bythotrephes*, and chlorophyll *a* (chl *a*). Four additional sample stations for *Bythotrephes* collection were chosen along a transect, starting at the deep station and moving toward shore, marking each station with a GPS to locate it on the next sampling date (see Strecker and others 2006 for sampling details). Logistical constraints prevented sampling at night so all

samples were taken during the day. Chl *a* samples were taken from the epilimnion using a 2.5-cm diameter integrated tube sampler. The integrated tube sampler was also used to collect water from the epilimnion on the week of 14 July 2003 for analysis of water chemistry variables.

Zooplankton were sampled with a 110-µm mesh conical closing net that was 0.5 m in diameter. Samples were taken in the epilimnion, metalimnion, and hypolimnion (from 5 m off the lake bottom to the top of the hypolimnion) after thermal strata were determined from a temperature profile taken at 1-m intervals. The top of the metalimnion was defined as a change of more than 1°C per meter, and the top of the hypolimnion by a change of less than 0.2°C per meter. On the first sampling date, stratification had not yet been achieved in Bernard Lake, so the depth of the entire water column was roughly divided into 3 and samples were taken from those depths. Average temperatures from each strata in Bernard Lake on the first date were consistent with other lakes, thus, we do not believe that this method affected our results. The hypolimnion of Doe Lake could not be sampled on seven dates because it was too shallow;

therefore, this lake was excluded from hypolimnetic abundance and production estimations. Samples for *Bythotrephes* were taken over the entire water column, starting from 5 m off the lake bottom, using a 400- μm mesh conical net that was 0.5 m in diameter. *Bythotrephes* and zooplankton samples were anesthetized and preserved in 5.5% sugared and buffered formalin.

Zooplankton samples were enumerated and measured on a Leica MZ12.5 dissecting microscope using the semi-automated counting system ZEBRA2 (Allen and others 1994). Subsamples of a known volume were taken and a minimum of 350 individuals were identified to genus, with the exception of *Daphnia mendotae*, *Eubosmina* (*Neobosmina*) *tubicen*, *Eubosmina* (*Eubosmina*) *coregoni*, *Eubosmina* (*Eubosmina*) *longispina*, and other species which are the only representative of their genus in the area. Diaptomid calanoid copepods belonging to the genera *Leptodiaptomus* and *Skistodiaptomus* were grouped simply as *Diaptomus* spp. To obtain a representative enumeration of all zooplankton genera present, only 40–50 individuals of the dominant taxa, 40–50 copepodids per order, and 20–30 nauplii per order were counted. Both loose and attached eggs were counted in the subsamples, stopping either when the minimum number of individuals was reached or more than 700 loose eggs were counted. Loose eggs were designated as cladoceran or copepod and apportioned to the number of adults present. *Bythotrephes* samples containing less than 32 individuals were counted in their entirety, whereas samples with greater numbers were split with a Folsom plankton splitter and mixed to ensure that clumping did not occur. All instars were enumerated and abundances were averaged across the five sampling stations.

Zooplankton Production

Although *Bythotrephes* (Pangle and Peacor 2006) and other visual predators (Lampert 1989) can induce diel vertical migration of zooplankton, we chose to sample during the day to specifically examine the vertical distribution of productivity available to visually foraging predators, such as cisco, which are daytime feeders (Milne and others 2005). Comparisons of day and night vertically stratified samples of zooplankton taken in 2007 in most of our study lakes suggest that some zooplankton migrated downwards in invaded lakes during the day, whereas diel migrations in non-invaded lakes tended to be small in magnitude (S. Arnott, unpublished data). There was variability in the extent of migration in invaded lakes: on

average 15% of total zooplankton (range: –13 to 31%; negative value represents migration in the opposite direction) moved from the metalimnion to the epilimnion at night, but migration of zooplankton away from the hypolimnion to warmer temperatures at night was small (mean: 9%, range: –9 to 28%). We acknowledge that as a result of these migrations, our calculations may underestimate metalimnetic production in invaded lakes by including organisms that have spent nights at warmer temperatures.

Biweekly zooplankton production was calculated using two methods. For the calanoid copepod species that do not carry their eggs in an egg sac (for example, *Senecella calanoides*), the cohort method was used (Downing 1984). For all other zooplankton, the egg-ratio method was used (Borgmann and others 1984), following Paloheimo (1974). Temperature and species-specific values for egg development time were determined from the literature (see Kuns and Sprules 2000), and the mean temperature of each stratum was used. Mean dry weights for zooplankton were calculated using length–weight regressions (McCauley 1984; Culver and others 1985; Yan and Mackie 1987; Yan and Pawson 1997; W.G. Sprules unpublished data). Areal biweekly production was calculated by multiplying volumetric production by the depth of the stratum. All of our production estimates were calculated at the genus level and then summed across all taxa to obtain total crustacean zooplankton production. *Bythotrephes* production was calculated separately from the crustacean zooplankton community, as we wanted to examine the effects of

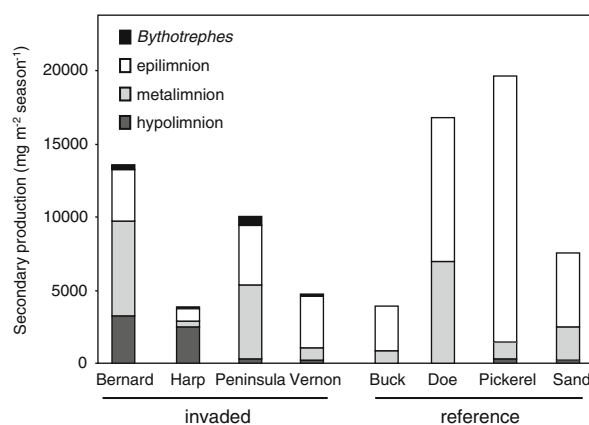


Figure 1. Total secondary production ($\text{mg m}^{-2} \text{season}^{-1}$) of *Bythotrephes* (■) and zooplankton in the epilimnion (□), metalimnion (▨), and hypolimnion (■) of invaded and reference lakes. For the purposes of our study, we define the season as the middle of May to the middle of September.

Bythotrephes as a predator on zooplankton productivity, exclusive of its contribution to total zooplankton productivity (for comparison, *Bythotrephes* production is displayed in Figure 1). Biweekly *Bythotrephes* consumption ($\text{mg m}^{-2} \text{ fortnight}^{-1}$) was estimated by dividing *Bythotrephes* biweekly production ($\text{mg m}^{-2} \text{ fortnight}^{-1}$; calculated by the egg-ratio method from whole-water column samples) by growth efficiency, which was estimated at 27% for a population of mixed instars (Dumitru and others 2001). Consumption by *Bythotrephes* was contrasted with zooplankton production from the epilimnion and metalimnion, as a concurrent study in a subset of the lakes in our study suggests that this is where the invader is generally found (Young and Yan 2008).

Impact of Zooplankton on Phytoplankton

To assess the effects of *Bythotrephes* on trophic interactions between zooplankton and phytoplankton, an in situ experiment was conducted three times in a subset of the study lakes: two invaded and three reference lakes. Using a technique modified from Elser and Goldman (1991), Cyr (1998), and Sommer and others (2001), we measured zooplankton impact on the phytoplankton community, including direct grazing effects, but also indirect effects, such as nutrient recycling, as no nutrients were added to the carboys. Four translucent 20-l carboys were deployed for 72 h in each lake, once during June, July, and August, approximately 4 weeks apart. Carboys were filled with water and incubated at a depth corresponding to 50% light penetration, thereby minimizing between lake differences in light exposure. Water was filtered through 80- μm mesh to remove zooplankton and added to each carboy. Zooplankton were added to each of the carboys at several densities (0, 1, 2, and 3 \times ambient) by taking discrete hauls with a closing net through each of the strata (epi-, meta-, and hypolimnion), thus compensating for any diel vertical migration that may have been occurring, but also likely overestimating grazing due to the presence of hypolimnetic taxa that would not be feeding in the epilimnion during the day. The carboys were then sealed, weighted, and incubated for 72 h. All predaceous macroinvertebrates, such as *Bythotrephes*, were excluded from the carboys. By removing *Bythotrephes* from the carboys, we are thus explicitly testing how zooplankton communities shaped by invasion will influence algal community biomass in short-term experiments in invaded and reference lakes. Although initial differences in the composition of phytoplankton communities could

influence zooplankton grazing, the invaded and reference lakes in this study have similar proportions of edible phytoplankton cells (B. Beisner, unpublished data), suggesting that conditions were relatively comparable in invaded and reference lakes. Chl *a* samples from each carboy were taken at the beginning and end of the experiment, concentrating water samples onto 1.2- μm glass fiber filters, and measured using fluorometry. Following Cyr (1998), the realized algal growth rates per day for the carboys that contain zooplankton (r) were calculated from

$$r = \ln(C_1/C_0)/T \quad (1)$$

where C_0 and C_1 are the chl *a* concentrations ($\mu\text{g l}^{-1}$) at the beginning and end of the experiment, respectively, and T is the length of time the experiment ran (days). Zooplankton impact was calculated as the slope (b) of the equation

$$r = b(ZB) + a \quad (2)$$

where ZB is the zooplankton biomass at 0, 1, 2, or 3 \times ambient biomass and a is the growth rate in the absence of zooplankton. Zooplankton biomass was determined from the average of the two survey sampling dates that surrounded the experiment. The coefficients of the equation were estimated by linear regression. Percent change in algae (per day) was calculated as $-(1 - e^b) \times 100$. Although this experiment and others upon which it was modeled (Elser and Goldman 1991; Cyr 1998) are brief, our experiment was designed to provide insight into possible trophic interactions that may result from changes in lake food webs and should be looked upon as a simplified test of the interaction between zooplankton and phytoplankton without confounding factors from higher trophic levels.

Statistical Analyses

One-way ANOVAs were used to examine differences in physical, chemical, and morphological characteristics of study lakes. Repeated measures ANOVAs were used to test if there were differences between invaded and reference lakes for chl *a*, secondary production, zooplankton abundance, and egg ratio (eggs individual $^{-1}$). Because of non-normality and heteroskedasticity in some of the above measures, all values were log ($x + 1$)-transformed. The Huynh–Feldt adjusted P -value was used in situations where the assumption of sphericity was not met for repeated measures analyses. Although we would expect to observe seasonal changes in zooplankton communities, independent of invasion status, it was not our intention to

describe these changes; therefore, we will not discuss time effect results unless there is an interaction with invasion. A two-factor ANOVA was used to test for differences in zooplankton grazing impact over all three experimental time periods in invaded and reference lakes, with time as a block factor. Statistical analyses were performed using Statistica 6.0 (StatSoft 2001).

RESULTS

Zooplankton Production

Reference and invaded lakes were similar in surface area, maximum depth, and primary productivity (chl *a* and total phosphorus) (Table 1), as well as thermal structure (epilimnetic temperature: $F_{1,6} = 0.01$, $P = 0.98$). There was also no significant difference in concentrations of calcium and dis-

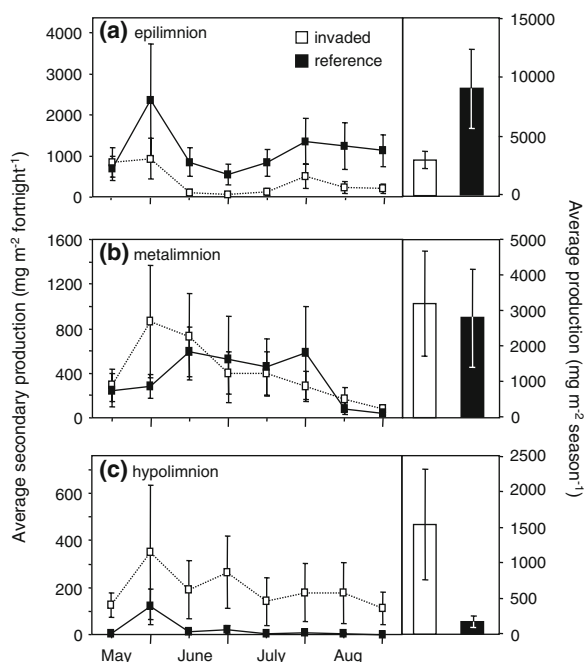


Figure 2. On the left axis, average secondary production of zooplankton of invaded (□) and reference (■) lakes ($\text{mg m}^{-2} \text{ fortnight}^{-1}$) and on the right axis, average seasonal production ($\text{mg m}^{-2} \text{ season}^{-1}$) of invaded (□) and reference (■) lakes in the (a) epilimnion, (b) metalimnion, and (c) hypolimnion ($n = 4$, except reference lake hypolimnion where $n = 3$). Production is calculated from two adjacent sampling dates, so the value shown represents that of the following two-week interval, that is, the value from the middle of May represents the sampling period from then until early June. Sampling occurred approximately fortnightly (mean: 13.5 days) and we define the season as the middle of May to the middle of September. Error bars are ± 1 standard error.

solved organic carbon, pH, and conductivity between lake categories (Table 1).

Zooplankton production was significantly lower in the epilimnion of *Bythotrephes*-invaded lakes throughout the summer, declining on average by more than $6000 \text{ mg m}^{-2} \text{ season}^{-1}$, or about 67% (Figure 2, Table 2). There was no difference in metalimnetic or hypolimnetic production between invaded and reference lakes (Figure 2, Table 2), although the hypolimnions of two of the four invaded lakes, Bernard and Harp, were 18 \times and 13 \times more productive than the average hypolimnetic productivity of reference lakes (Figure 1). When all of the strata were combined, there was no statistical difference in whole-water column zooplankton production between invaded and reference lakes (Figures 1, 2 and Table 2).

In the epilimnion, production of calanoid copepods, cyclopoid copepods, and small cladocerans was significantly reduced in *Bythotrephes*-invaded lakes (Figure 3 and Table 3). Epilimnetic production by large cladocerans tended to be reduced in *Bythotrephes*-invaded lakes, although not significantly. There was a significant Time \times Invasion interaction for small cladocerans, where production in invaded lakes was high early in the season, but declined precipitously from an average of $442 \text{ mg m}^{-2} \text{ fortnight}^{-1}$ in May and early June to less than $2 \text{ mg m}^{-2} \text{ fortnight}^{-1}$ over the remainder of the sampling dates (Figure 3 and Table 3). In the metalimnion, production by cyclopoids, calanoids, and small cladocerans was similar in reference and invaded lakes, whereas large cladoceran production was 90% lower in invaded lakes compared to reference lakes, averaging $13 \text{ mg m}^{-2} \text{ fortnight}^{-1}$ over the season (Figure 3 and Table 3). In the hypolimnion, cyclopoid copepods had higher production in invaded lakes early in the season, followed by a decrease beginning in mid-June, and calanoid copepod production was significantly greater in invaded lakes (Figure 3 and Table 3). There was no difference in large and small cladoceran hypolimnetic production between lake groups (Figure 3 and Table 3).

The abundance of crustacean zooplankton in the epilimnion was significantly affected in invaded lakes, with declines of more than 33,000 individuals m^{-3} over the summer, on average (Figure 4 and Table 2). There was also a significant Time \times Invasion interaction, such that abundances were similar in invaded and reference lakes in May and early June, but showed significant declines in the invaded lakes after this time. There was no difference between invaded and reference lake zooplankton abundance in the metalimnion,

Table 2. Repeated Measures ANOVAs on Stratified and Whole-Water Column Zooplankton Secondary Production, Total Zooplankton Abundance, and Eggs Individual⁻¹

Measure	Stratum	Invasion		Time		Time × Invasion		Mean effect size (%)
		$F_{1,6}$	P	$F_{7,42}^a$	P	$F_{7,42}^a$	P	
Secondary production	Epilimnion	9.68	0.02**	2.13	0.11	1.31	0.29	-67
	Metolimnion	0.03	0.87	5.19	<0.01**	0.58	0.75	+15
	Hypolimnion [†]	3.46	0.12	1.77	0.13	0.43	0.88	+766
	All strata	1.24	0.31	1.85	0.14	0.64	0.65	-35
Total abundance	Epilimnion	16.91	<0.01**	17.48	<0.01**	6.55	<0.01*	-59
	Metolimnion	0.80	0.40	8.08	<0.01**	0.80	0.56	+55
	Hypolimnion [†]	1.78	0.24	4.02	<0.01**	0.50	0.85	+137
	All strata	0.42	0.54	12.03	<0.01**	0.80	0.61	-17
Eggs individual ⁻¹	Epilimnion	1.90	0.22	1.56	0.19	1.06	0.41	-17
	Metolimnion	0.01	0.91	2.86	0.08*	0.19	0.88	+10
	Hypolimnion [†]	6.04	0.06*	4.70	0.02**	1.63	0.23	+213
	All strata	1.74	0.24	3.58	<0.01**	1.52	0.20	-20

* $P < 0.10$; ** $P < 0.05$.

[†]Invasion error $df = 5$, Time × Invasion error $df = 35$; total abundance Time × Invasion error $df = 40$.

^aTotal abundance: $F_{8,48}$.

The mean effect size of production is calculated by summing all the sampling dates and then averaging between lakes in each category. The mean effect size of abundance and eggs individual⁻¹ is calculated by averaging all of the lakes in each category on all dates.

hypolimnion, and when all strata are combined, nor were there any interactions between invasion status and time (Figure 4 and Table 2).

Bythotrephes-invaded lakes had a marginally significant increase in numbers of eggs produced per individual zooplankton in the hypolimnion, which was most noticeable early in the summer (Figure 5 and Table 2). This peak was likely driven by extremely high egg production by hypolimnetic cyclopoid copepods, producing on average more than 9000 eggs m^{-3} between the first and second sampling dates (A. Strecker, unpublished data), far greater numbers than other zooplankton of a similar size, and had greater numbers of eggs per individual in invaded lakes compared to reference lakes (Figure 5 and Table 4). When all strata were combined, there was a marginally significant increase in eggs produced per individual zooplankton in invaded lakes compared to reference lakes on the first sampling date ($F_{1,6} = 3.82$, $P = 0.10$). This early season peak in number of eggs per individual in invaded lakes came mostly from small cladoceran and cyclopoid functional groups (Figure 5). There was no significant effect of invasion on total or functional group eggs per individual in the epilimnion, metalimnion, or when all strata were combined, nor were there any significant Time × Invasion interactions (Figure 5 and Table 2).

Bythotrephes consumed substantial portions of the total seasonal zooplankton production in three of the four invaded lakes (Figure 6), on average

consuming more than 1000 $mg\ m^{-2}\ season^{-1}$ or about 17% of secondary production from the middle of May to the middle of September. However, *Bythotrephes* did not tend to appear until mid-June in our samples, thus zooplankton production consumed after *Bythotrephes* starts reproducing is, on average, about 34% (Figure 6). *Bythotrephes* consumed greater than 100% of zooplankton production on two sampling dates in Bernard Lake and Harp Lake, but its consumption never exceeded zooplankton production in Peninsula and Vernon lakes. In general, *Bythotrephes* production was low, only comprising less than 6% of total zooplankton production, on average (Figure 1).

Impact of Zooplankton on Phytoplankton

In each grazing experiment, algae decreased in reference lakes and increased in invaded lakes (Figure 7a). There was a significant effect of invasion on zooplankton impact on the algal community (invasion: $F_{1,8} = 23.13$, $P < 0.01$, time: $F_{2,8} = 0.85$, $P = 0.46$), such that % change in algae increased in the invaded lakes. However, this increase is likely not biologically meaningful in the long term, as changes in chl *a* in the experimental carboys were typically less than 1 $\mu g\ l^{-1}$. Indeed, there was no significant difference in epilimnetic chl *a* concentrations between lakes with and without *Bythotrephes* throughout the entire season in the entire subset of lakes sampled (Figure 7b and Table 1).

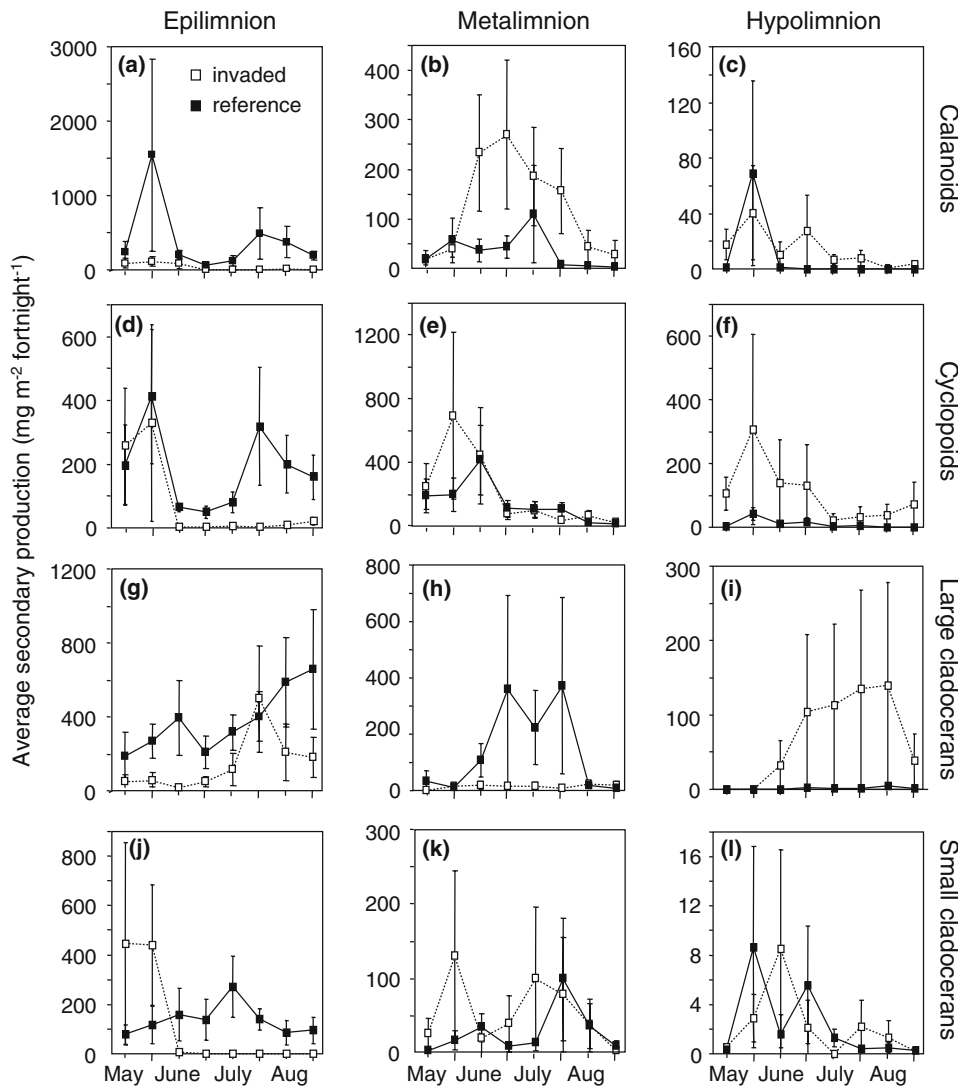


Figure 3. Average biweekly secondary production ($\text{mg m}^{-2} \text{ fortnight}^{-1}$) in calanoids (a–c), cyclopoids (d–f), large cladocerans (g–i), and small cladocerans (j–l) in the epi-, meta-, and hypolimnion of invaded (\square) and reference (\blacksquare) lakes ($n = 4$, except reference lake hypolimnion where $n = 3$). Sampling occurred approximately fortnightly (mean: 13.5 days). Error bars are ± 1 standard error.

DISCUSSION

We found that the invasive invertebrate predator, *Bythotrephes*, altered some measures of ecosystem function in freshwater lakes, such as epilimnetic secondary production, but that other measures were generally unchanged. There was some evidence for seasonal shifts in the production of different functional groups and individual egg production in invaded lakes in May and early June, but this was not great enough to balance production lost to *Bythotrephes* consumption later in the season. The effects of *Bythotrephes* on whole lake productivity may be moderated by behavioral shifts in zooplankton abundance to the cool dark waters of the hypolimnion and/or increased abundance of hypolimnetic species, and consequently, increased production in the hypolimnion of some lakes. *Bythotrephes* cannot compensate for the declines in biomass production observed in invaded lakes, as it

generated less than 6% of total zooplankton production. Our study provides compelling evidence that *Bythotrephes* can alter the flow of energy in parts of freshwater lakes, but may leave other measures of ecosystem function relatively unaffected. Changes in energy flow will likely have implications for growth and reproduction of other trophic levels in the food web, including macroinvertebrates, planktivorous fish, and young-of-year piscivorous fish, because these organisms all rely on zooplankton as a major food source.

Zooplankton Production

There was a significant decrease in epilimnetic zooplankton production in lakes invaded by *Bythotrephes*. This was likely the result of significant reductions in zooplankton abundance in the epilimnion, as there was no difference in other factors that influence productivity, such as egg production,

Table 3. Repeated Measures ANOVAs on Zooplankton Secondary Production for Each Functional Group

Stratum	Functional group	Invasion		Time		Time × Invasion		Mean effect size (%)
		$F_{1,6}$	P	$F_{7,42}$	P	$F_{7,42}$	P	
Epilimnion	Calanoids	10.50	0.02**	3.95	<0.01**	0.77	0.62	-90
	Cyclopoids	54.02	<0.01**	4.10	<0.01**	1.64	0.17	-57
	Large cladocerans	2.48	0.17	1.62	0.21	0.14	0.95	-61
	Small cladocerans	24.97	<0.01*	3.45	0.02**	5.45	<0.01**	-17
Metalimnion	Calanoids	2.71	0.15	3.79	0.02**	0.53	0.71	+250
	Cyclopoids	0.05	0.83	4.61	0.01**	0.56	0.65	+45
	Large cladocerans	2.07	0.20	4.01	<0.01**	2.12	0.07*	-90
	Small cladocerans	0.04	0.85	1.64	0.19	1.47	0.24	+96
Hypolimnion [†]	Calanoids	9.70	0.03**	1.15	0.36	0.43	0.81	+61
	Cyclopoids	0.35	0.58	5.48	<0.01**	1.97	0.09*	+964
	Large cladocerans	0.57	0.48	2.08	0.17	0.52	0.61	+6188
	Small cladocerans	0.03	0.88	1.77	0.18	0.79	0.53	-4

* $P < 0.10$; ** $P < 0.05$.

[†]Invasion error $df = 5$, Time × Invasion error $df = 35$.

The mean effect size of production is calculated by summing all the sampling dates and then averaging between lakes in each category.

chl *a*, and temperature, in invaded lakes compared to non-invaded lakes. Although previous studies have observed declines in overall zooplankton abundance (Yan and others 2001; Strecker and others 2006), this is the first study to detect negative effects of *Bythotrephes* on epilimnetic zooplankton production in multiple lakes and reduced production in several functional groups (calanoids, cyclopoids, and small cladocerans) within the epilimnion. The substantial declines in epilimnetic production are likely the result of a combination of direct predation on zooplankton by *Bythotrephes*, as well as behavioral shifts away from the epilimnion to cooler darker habitat. Although we cannot determine the relative importance of predation vs. migration, what remains is that the epilimnion of lakes has dramatically changed following the invasion of *Bythotrephes*, and that there is significantly less productivity available to foraging species. Although few studies exist that compare secondary productivity across different predatory regimes, our results are similar in magnitude to those observed in a fish biomanipulation experiment, where the introduction of piscivores into a piscivore-free lake resulted in reductions in planktivorous fish, increased biomass of the native invertebrate predator *Chaoborus*, and significant declines in zooplankton productivity (Ramcharan and others 2001). This suggests that the introduction of non-native species can act in an analogous fashion to the complete restructuring of a lake food web by the introduction of a top predator.

We observed an increase in productivity in the hypolimnion in some invaded lakes, which likely

results from predator-induced habitat shifts. As discussed above, diel vertical migrations of zooplankton can confound estimations of secondary productivity. However, it is unlikely that these migrations influenced our estimates of epilimnetic or hypolimnetic production because we have no evidence that zooplankton migrated downwards from the epilimnion at night, and zooplankton migration upwards from the hypolimnion at night was minor (S. Arnott, unpublished). However, we may have underestimated metalimnetic production in invaded lakes, as diel migrations from the warmer epilimnion at night to the cooler metalimnion during the day may be a response of some zooplankton taxa to *Bythotrephes*. Dumitru and others (2001) examined the effect of *Bythotrephes* on whole-water column zooplankton production in a single lake, and therefore did not consider the spatial distribution of production. Pangle and Peacor (2006) and Pangle and others (2007) demonstrated that *Bythotrephes* can induce cladoceran taxa to migrate into the hypolimnion to avoid predation, with significant costs as a result of exposure to cooler temperatures: our results extend their findings to the entire zooplankton community over a greater part of the ice-free season. The non-lethal costs of these migrations may be substantial. Using Harp Lake as an example, we estimate that epilimnetic production would be about 44% greater if approximately 50% of zooplankton (based on differences in hypolimnetic abundance between Harp and reference lakes) in the hypolimnion of Harp Lake are epilimnetic species that have behaviorally shifted habitats to avoid *Bythotrephes*.

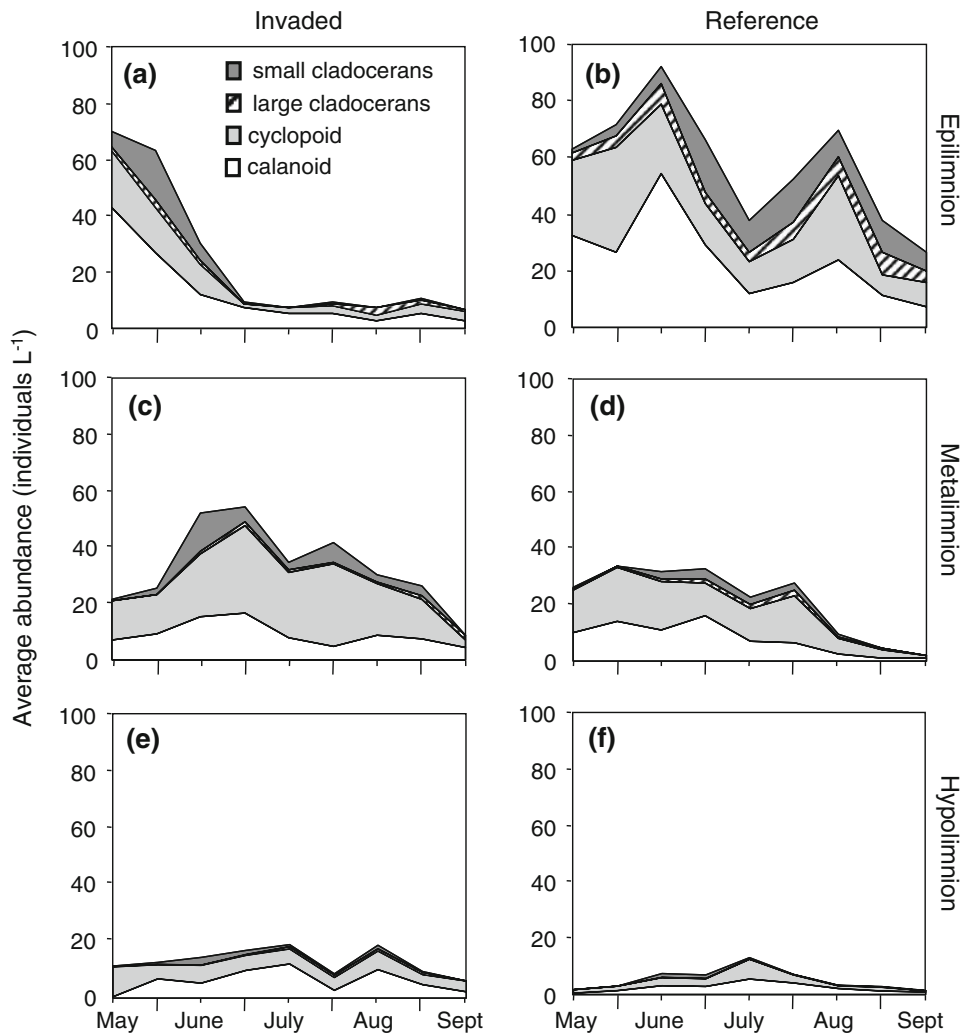


Figure 4. Average abundance of small cladocerans, large cladocerans, cyclopoids, and calanoids (individuals L⁻¹) in the epilimnion (a, b), metalimnion (c, d), and hypolimnion (e, f) of invaded and reference lakes.

There was considerable among-lake variability in response to the invasion of *Bythotrephes*. Although the hypolimnion of some invaded lakes made substantial (>25%) contributions to total seasonal productivity, the hypolimnion contributed very little to overall productivity in other invaded lakes (<4%). This variability in invaded lakes may be partly due to differing planktivore communities. Planktivores may influence the vertical distribution of *Bythotrephes*, which may, in turn, influence the distribution of zooplankton. A concurrent study in two of our invaded lakes revealed that *Bythotrephes* distribution is indeed related to the presence of the cold-water planktivore, cisco (Young and Yan 2008), suggesting that other components of the food web may mediate the effects of *Bythotrephes* on crustacean zooplankton.

In addition to spatial shifts in productivity, we observed seasonal shifts in invaded lakes during periods when *Bythotrephes* was not present, that is, in the spring before population growth rates in-

crease. In three of the four invaded lakes, there was a large pulse in small cladoceran epilimnetic production early in the season, likely from above average egg production per individual small cladoceran in two of the invaded lakes, in combination with greater abundances in May and early June. This suggests that small cladocerans may alter their life history, at least in some lakes, by shifting reproduction to earlier in the season to avoid the invader. This is in agreement with another field study, where temporal shifts in copepod egg production were observed as a result of the presence of a fish predator (Hairston and Walton 1986).

Increased production of other intermediate trophic levels may offset reduced epilimnetic crustacean production. For instance, rotifers were more abundant in lakes invaded by *Bythotrephes*, especially the colonial *Conochilus* (Hovius and others 2006), which has high intrinsic rates of increase (Allan 1976) and is probably an inedible prey item for *Bythotrephes*. However, rotifers likely do not

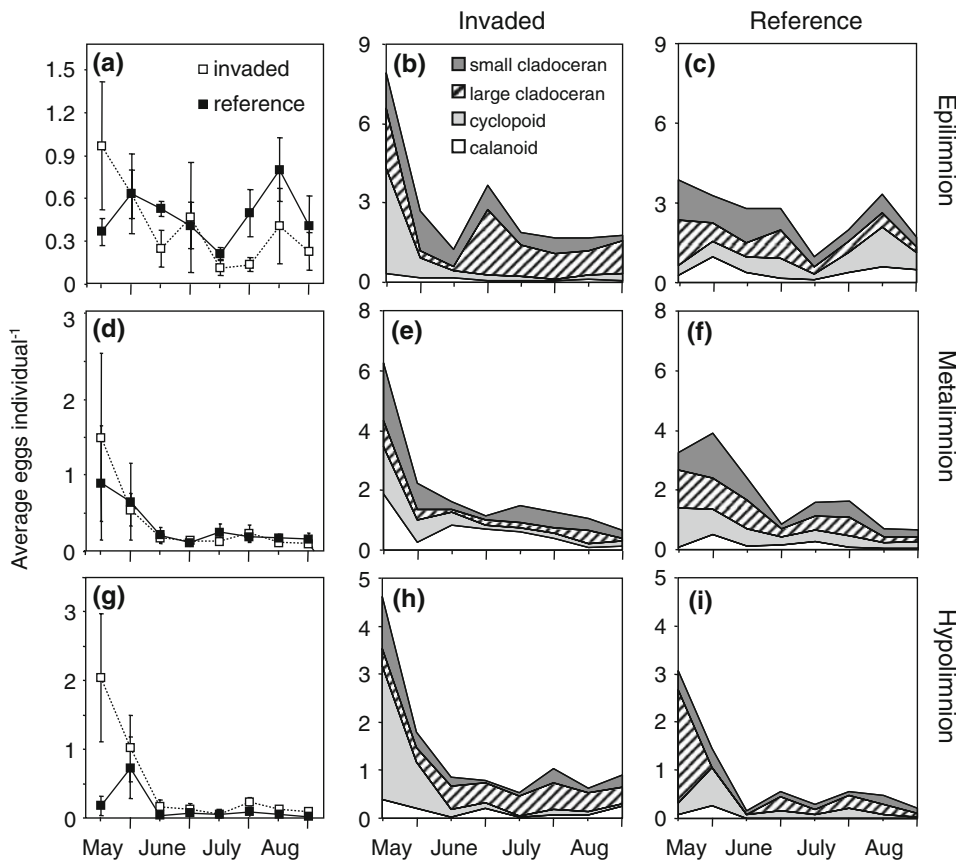


Figure 5. Average number of eggs individual⁻¹ of entire zooplankton community in each strata in invaded (□) and reference (■) lakes (left column: a, d, g) and for each functional group in the epilimnion (b, c), metalimnion (e, f), and hypolimnion (h, i) of invaded and reference lakes ($n = 4$, except reference lake hypolimnion where $n = 3$). Error bars are ± 1 standard error. Note that the ratio of eggs to individuals for separate functional groups does not sum to equal the average of the entire community as a result of different densities of zooplankton in each group.

Table 4. Repeated Measures ANOVAs on Zooplankton Egg Production per Individual for Each Functional Group

Stratum	Functional group	Invasion		Time		Time \times Invasion		Mean effect size (%)
		$F_{1,6}$	P	$F_{7,42}$	P	$F_{7,42}$	P	
Epilimnion	Calanoids	3.15	0.13	1.16	0.35	1.01	0.40	-72
	Cyclopoids	0.01	0.92	0.95	0.40	1.37	0.29	7
	Large cladocerans	0.65	0.45	2.42	0.09*	0.67	0.59	75
	Small cladocerans	0.02	0.89	2.58	0.05**	0.41	0.82	-4
Metalimnion	Calanoids	3.02	0.13	0.61	0.54	0.71	0.49	295
	Cyclopoids	0.09	0.77	2.59	0.12	0.08	0.92	-17
	Large cladocerans	1.90	0.22	1.26	0.32	0.40	0.77	-54
	Small cladocerans	0.07	0.80	3.01	0.05**	1.55	0.23	11
Hypolimnion [†]	Calanoids	2.54	0.17	0.95	0.44	0.51	0.69	253
	Cyclopoids	4.04	0.10*	4.92	0.03**	3.44	0.07*	157
	Large cladocerans	0.01	0.99	1.20	0.34	1.26	0.33	-2
	Small cladocerans	1.20	0.32	3.12	0.08*	1.06	0.39	67

* $P < 0.10$; ** $P < 0.05$.

[†]Invasion error $df = 5$, Time \times Invasion error $df = 35$.

The mean effect size is calculated by averaging all of the lakes in each category on all dates.

substitute for crustacean zooplankton as prey for fish (Threlkeld 1988). In addition, Sherwood and others (2002) showed that the lack of large-bodied prey groups could reduce the efficiency of energy

transfer to fish in metal-polluted lakes with simplified food webs, implying that the loss of typical prey in invaded lakes may prevent higher trophic levels from reaching their normal body size.

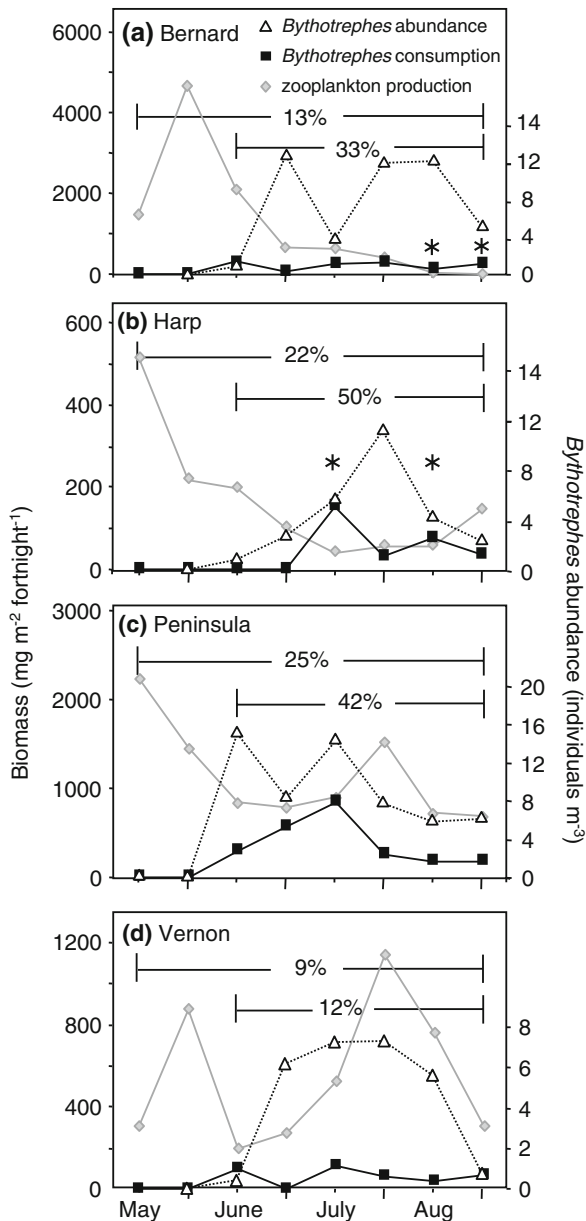


Figure 6. Epi- and metalimnetic zooplankton production (\blacklozenge ; $\text{mg m}^{-2} \text{ fortnight}^{-1}$) and *Bythotrephes* consumption (\blacksquare ; $\text{mg m}^{-2} \text{ fortnight}^{-1}$) in invaded lakes, contrasted with *Bythotrephes* abundance (\triangle ; individuals m^{-3}) on the right axis. In each panel, the top bracketed value is the percent of total seasonal zooplankton production consumed by *Bythotrephes*, and the bottom bracketed value is the percent of seasonal production consumed by *Bythotrephes* starting in the middle of June. Asterisk (*) indicates the dates on which *Bythotrephes* consumption exceeded zooplankton production. Sampling occurred approximately fortnightly (mean: 13.5 days).

The spatial, temporal, and taxonomic redistribution of secondary production in *Bythotrephes*-invaded lakes will likely have important implications for aquatic food webs. Shifts in zooplankton

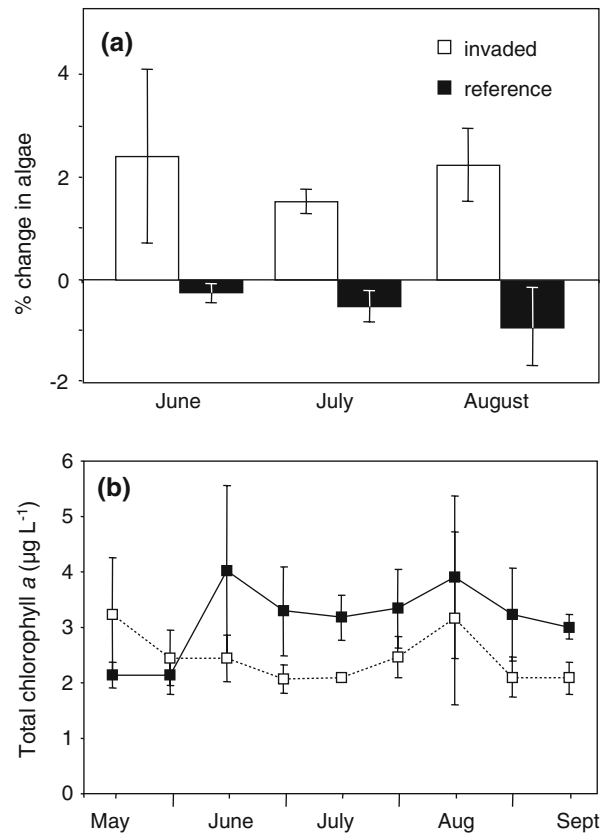


Figure 7. (a) Percent change in algae during zooplankton impact experiment in invaded (\square ; $n = 2$) and reference lakes (\blacksquare ; $n = 3$). Positive values indicate that phytoplankton increased during the experiment, whereas negative numbers indicate a decrease in algae. (b) Total chl a ($\mu\text{g L}^{-1}$) of all invaded (\square) and reference (\blacksquare) lakes ($n = 4$). Error bars are ± 1 standard error.

reproduction from the epilimnion to the hypolimnion may negatively affect epilimnetic-feeding fish species that rely on zooplankton, such as larval cisco, which inhabit surface waters (Oyadomari and Auer 2004), and are highly reliant on crustaceans as their prey (Davis and Todd 1998). In addition, cold-water planktivores (that is, adult cisco) would be unlikely to benefit from this shift because they have reduced foraging success in poorly lit waters (Milne and others 2005) and tend to prefer temperatures around 12°C (Rudstam and Magnuson 1985), which falls into the metalimnion in most of our lakes.

Impact of Zooplankton on Phytoplankton

Despite experimental results that were suggestive of reduced control of the algal community by the zooplankton community, we did not observe the expected changes in phytoplankton biomass (as measured by chl a) at the lake level in *Bythotrephes*-

invaded lakes. Even though low-productivity lakes, such as those in our study, are predicted to be influenced more by bottom-up, rather than top-down, forces (Jeppesen and others 2003), significant effects of zooplankton on phytoplankton biomass have been observed in other oligotrophic lakes (Sarnelle and Knapp 2005). The weak overall effects of zooplankton on phytoplankton echo the experimental results of Sommer and others (2001), where increased abundance of zooplankton functional groups had no effect on total phytoplankton biomass. Pérez-Fuentetaja and others (2000) also found that zooplankton had a weak influence on chlorophyll in oligo- and meso-trophic lakes. Thus, it appears that the invasion of *Bythotrephes* will probably not have a large cascading effect on phytoplankton biomass in lower productivity lakes, despite large reductions in epilimnetic zooplankton biomass (>70%). However, more productive lakes may be more likely to respond to top-down changes (Jeppesen and others 2003), and although *Bythotrephes* seems to prefer oligotrophic lakes, it has been found in some mesotrophic systems (Jarnagin and others 2000), suggesting that the invader may have the potential to instigate increases in algal biomass in lakes of moderate productivity.

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