

Variation in the response of crustacean zooplankton species richness and composition to the invasive predator *Bythotrephes longimanus*

Angela L. Strecker, Shelley E. Arnott, Norman D. Yan, and Robert Girard

Abstract: The predacious invertebrate *Bythotrephes longimanus* has now invaded >90 freshwater lakes in North America. There is some evidence that *B. longimanus* has a negative effect on summer zooplankton species richness; however, no study has examined the effect of *B. longimanus* throughout the ice-free season in more than one lake. We visited 10 invaded and 4 reference lakes every 2 weeks from May to September, collecting *B. longimanus*, crustacean zooplankton, and water chemistry samples. Composite samples were pooled across the study season for each lake. *Bythotrephes longimanus* significantly reduced cladoceran species richness, diversity, and abundance, and the total zooplankton community also exhibited decreased richness, diversity, and abundance. Seasonal sampling was better than synoptic surveys at detecting changes in abundance, but richness estimates were similar. As *B. longimanus* continues to spread across lake landscapes, we expect it will have profound impacts on local and regional richness and species distribution patterns.

Résumé : L'invertébré prédateur *Bythotrephes longimanus* a maintenant envahi >90 lacs d'eau douce en Amérique du Nord. Il y a des indications que *B. longimanus* a un effet négatif sur la richesse spécifique du zooplancton d'été; cependant, aucune étude n'a examiné les effets de *B. longimanus* au cours de la période sans glace dans plus d'un seul lac à la fois. Nous avons visité 10 lacs envahis par le prédateur et 4 lacs témoins à toutes les 2 semaines de mai à septembre et prélevé des *B. longimanus*, des crustacés zooplanctoniques et des échantillons d'eau pour analyse chimique. Nous avons amalgamé les échantillons de toute la période pour chacun des lacs. *Bythotrephes longimanus* réduit significativement la richesse spécifique, la diversité et l'abondance des cladocères; la communauté totale du zooplancton subit aussi une réduction de richesse, de diversité et d'abondance. L'échantillonnage saisonnier permet mieux que les inventaires synoptiques de détecter les changements d'abondance, mais les estimations de richesse sont semblables par les deux méthodes. À mesure que *B. longimanus* continue de se répandre dans les paysages lacustres, nous prévoyons qu'il aura des répercussions importantes sur les patrons de richesse et de répartition d'espèces aux échelles locale et régionale.

[Traduit par la Rédaction]

Introduction

Bythotrephes longimanus Leydig (Crustacea, Onychopoda) is a predatory zooplankton species that has invaded numerous lakes in North America. First detected in Lake Ontario in 1982 (Mills et al. 2003), *B. longimanus* has spread to all of the Laurentian Great Lakes and >90 inland lakes in Ontario (C. Gamble, Ontario Federation of Anglers and Hunters, 4601 Guthrie Dr., Peterborough, ON K9J 8L5, Canada, unpublished data), Minnesota (M. Brown, Department of Biology, University of Minnesota–Duluth, Duluth, MN 55812, USA, unpublished data), and Michigan (Jarnagin et al. 2000) and reservoirs in Ohio (Ferry and Wright 2002). *Bythotrephes longimanus* occupies lakes that

span a gradient of temperature, salinity, pH, and depth within its native range in Eurasia (Grigorovich et al. 1998). Humans are an important dispersal vector for *B. longimanus*, and with its broad tolerance of environmental conditions, it appears to have the potential to invade a large number of lakes in North America (MacIsaac et al. 2000, 2004).

Our understanding of the impacts of *B. longimanus* on inland aquatic communities in North America is incomplete. Invasion events are unpredictable, thus little empirical data documenting the effects of invasion on recipient communities exists. However, a single case study of long-term bi-weekly records of both pre- and post-invasion planktonic communities from Harp Lake, Ontario, has revealed evidence of negative effects of *B. longimanus* on crustacean

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A.L. Strecker¹ and S.E. Arnott. Department of Biology, Queen's University, Kingston, ON K7L 3N6, Canada.

N.D. Yan. Biology Department, York University, Toronto, ON M3J 1P3, Canada, and Dorset Environmental Science Centre, Ontario Ministry of the Environment, Dorset, ON P0A 1E0, Canada.

R. Girard. Dorset Environmental Science Centre, Ontario Ministry of the Environment, Dorset, ON P0A 1E0, Canada.

¹Corresponding author (e-mail: strecker@biology.queensu.ca).

zooplankton species richness and cladoceran zooplankton abundance since its invasion in 1993 (Yan et al. 2001, 2002).

Although trends seen in Harp Lake suggest that the invasion of *B. longimanus* will have important consequences for zooplankton communities, effects of predation can be site-specific (Posey and Hines 1991). Broader spatial surveys are necessary to determine how universal the impacts of *B. longimanus* are in temperate lakes. A study comparing 17 invaded boreal shield lakes to 13 uninvaded reference lakes provided strong evidence that the patterns of invasion observed in Harp Lake were also expressed in other lakes of differing water chemistry, morphometry, and species assemblages (Boudreau and Yan 2003). However, sampling for this study was limited to a single midsummer vertical zooplankton haul, which can underestimate the annual species pool by 50% (Arnott et al. 1998). As well, *B. longimanus* abundances generally peak in midsummer in boreal lakes (J. Young and E. Parrott, Department of Biology, York University, Toronto, ON M3J 1P3, Canada, unpublished data); however, they tend to be absent from the pelagic zone in the early and latter months of the ice-free season. If some zooplankton species are able to take advantage of vernal and autumnal temporal refuges that exist when *B. longimanus* are rare or absent from the water column, then Boudreau and Yan (2003) may have overestimated the effect of *B. longimanus* on annual zooplankton species pools. For example, some copepods may change the timing of reproduction in order to reduce overlap with predators that peak later in the summer (Hairston, Jr., and Walton 1986), and *Daphnia* clones have exhibited earlier age at maturation in the presence of fish kairomones (Sakwińska 2002).

The primary objective of this study was to examine the effects of *B. longimanus* on ice-free season averages of species richness, diversity, evenness, and abundance of crustacean zooplankton in boreal shield lakes. We expected that *B. longimanus* would cause declines in all these indices of community structure. However, because of the inclusion of time periods when *B. longimanus* was absent from the water column, there may be temporal refuges available for some species, during which time they might prosper. We used the persistence of *B. longimanus* in the water column of our study lakes as a way to assess the availability of a temporal refuge for zooplankton. Therefore, high persistence would suggest that there is a short time available for zooplankton to avoid *B. longimanus* and we would expect to see greater negative effects compared with times of low persistence of the invader, when zooplankton would have an opportunity to survive in the absence of predation by this invertebrate. Hence, our seasonal purview might actually detect reduced effects in comparison with those observed during peak *B. longimanus* abundance (Boudreau and Yan 2003; Barbiero and Tuchman 2004), or indeed no effects at all.

A secondary objective of this study was to assess the relationship between species richness and several environmental factors that are typically related to the number of crustacean zooplankton species in a lake. In general, species richness is positively related to lake area (Dodson 1992) and has a hump-shaped relationship with lake productivity (Dodson et al. 2000). In addition, invertebrate predators have been

shown to be important in structuring zooplankton communities. In a survey of 60 lakes on the Precambrian Shield, Keller and Conlon (1994) found that a number of zooplankton species common to the region, such as *Daphnia galeata mendotae* and *Diaphanosoma birgei*, were completely absent from fishless lakes containing the phantom midge larvae, *Chaoborus americanus*, a factor attributed to invertebrate predation. Although our lakes were not chosen to span large gradients of area or productivity, we believe that *B. longimanus* may alter these conventional relationships and will be an important driver of ecosystem change.

Materials and methods

Twenty lakes in the districts of Muskoka, Haliburton, and Parry Sound in southcentral Ontario, Canada, were chosen for the survey. The lakes are oligo- to meso-trophic and circumneutral in pH, as is typical of many boreal shield lakes (Table 1). All of the study lakes have forested catchments (mixed deciduous and coniferous) and small littoral zones and are used primarily for recreation. Cisco (*Coregonus artedii*), rainbow smelt (*Osmerus mordax*), lake whitefish (*Coregonus clupeaformis*), and yellow perch (*Perca flavescens*) are the primary planktivorous fish in these lakes (Ontario Ministry of Natural Resources: S. Scholten and E. McIntyre, District of Parry Sound, Parry Sound, ON P2A 1S4, Canada, and S. Sandstrom, District of Muskoka, Bracebridge, ON P1L 1W9, Canada, unpublished data). All the study lakes were chosen to have a similar glacial history, and therefore, there were equal probabilities of including zooplankton species dispersed by glacial retreat. Although our intention was to have equal numbers of invaded and reference lakes, *B. longimanus* was detected in six of our planned reference lakes, reducing their number to four. Hence, we reported results from 14 study lakes, 10 invaded and 4 reference.

Crustacean zooplankton were sampled every 2 weeks from May to September 2003 ($n = 9$) at a deep hole in each lake, located each time using GPS (global positioning system). Sample volume varied slightly among dates because of small differences in station depth (Table 1). A single zooplankton sample was taken by pulling a conical net (mesh size 110 μm , 0.5 m diameter) through the water column, starting 5 m off the lake bottom. Samples were preserved in 5.5% sugared and buffered formalin, and following preservation, a seasonal composite sample was obtained by combining equal proportions from each of the nine biweekly zooplankton samples. Rotifers were sampled from the epilimnion in a concurrent study with an integrated tube sampler (2.5 cm inner diameter) (Hovius et al. 2006). On each sampling date, *B. longimanus* was sampled at five stations in each lake, including the deep hole, with a conical net (mesh size 400 μm , 0.5 m diameter). The stations were <1 km apart. A single haul was taken at each station from 5 m off the lake bottom to the water surface. Mean ice-free *B. longimanus* abundance in the 10 invaded lakes was estimated by averaging *B. longimanus* abundance in the five replicate hauls in each lake over eight sampling dates from June to September 2003. Only eight dates were used, as *B. longimanus* samples were not taken in May. The number of sampling dates when *B. longimanus* was present and its

Table 1. Physical and chemical characteristics of study lakes.

Lake	Latitude (N), longitude (W)	Z _{max} (m)	Composite sample mean depth (m)	Area (ha)	Calcium (mg·L ⁻¹)	DOC (mg·L ⁻¹)	Conductivity (µmhos·cm ⁻¹)	pH	TP (µg·L ⁻¹)
Reference									
Buck	45°25', 79°23'	23.0	20.6 (1.7)	656.0	2.6	10.7	25.6	6.33	13.30
Doe	45°32', 79°25'	23.0	12.6 (1.5)	1 187.0	3.6	7.0	46.0	7.08	12.00
Pickernel	45°41', 79°18'	38.0	26.7 (1.1)	513.0	2.8	6.7	32.4	6.82	8.10
Sand	45°37', 79°10'	59.0	37.4 (5.3)	568.2	3.5	6.0	37.2	6.78	7.10
Mean		35.8	24.3*	731.1	3.1	7.6	35.3	6.75	10.13*
Invaded									
Kashagawigamog	44°59', 78°36'	39.7	31.1 (0.8)	817.9	10.8	6.9	95.4	7.56	7.41
Skeleton	45°15', 79°27'	64.7	53.6 (3.3)	2 155.5	3.8	2.6	44.0	6.94	3.82
Fairy	45°20', 79°11'	69.5	50.8 (3.6)	711.5	3.5	5.9	49.6	6.95	6.98
Mary	45°15', 79°15'	56.4	48.9 (1.4)	1 065.4	3.4	6.6	51.0	6.96	7.21
Lake Muskoka	45°03', 79°28'	66.5	40.4 (0.9)	12 206.0	3.6	5.5	54.4	7.02	5.50
Lake of Bays	45°15', 79°04'	70.1	39.3 (3.9)	6 904.1	2.9	5.1	36.4	6.97	3.38
Harp	45°23', 79°07'	37.5	31.2 (1.2)	71.7	3.0	6.7	38.0	6.98	7.22
Vernon	45°20', 79°17'	37.2	28.8 (3.7)	1 505.1	3.0	7.1	36.8	6.75	7.90
Bernard	45°45', 79°23'	47.9	40.3 (0.7)	2 057.7	4.1	3.4	65.2	7.13	9.56
Peninsula	45°20', 79°06'	34.1	21.9 (0.8)	864.8	4.4	6.1	70.6	7.14	9.00
Mean		52.4	38.6*	2 836.0	4.3	5.6	54.1	7.04	6.80*

Note: Standard deviation of mean depth of the composite sample is indicated in parentheses. A *t* test was performed to contrast values in reference and invaded lakes, where an asterisk (*) indicates $p < 0.05$. Lakes are sorted by increasing *B. longimanus* abundance. Z_{max}, maximum depth; DOC, dissolved organic carbon; TP, total phosphorus.

Table 2. Biotic characteristics of study lakes.

Lake	Mean chl <i>a</i> (µg·L ⁻¹)	Sample dates <i>Bythotrephes</i> present	Persistence of <i>Bythotrephes</i>	Lake herring	Rainbow smelt	Lake whitefish	Yellow perch
Reference							
Buck	2.8	0	0	A/P	A	A	P
Doe	3.4	0	0	L	A	L	P
Pickernel	4.4	0	0	L	A/P	A	P
Sand	2.0	0	0	L	H	A	P
Mean	3.1*	0	0				
Invaded							
Kashaga-wigamog	2.0	5	0	M/H	L/M	A/P	P
Skeleton	0.7	6	0	L	L/M	M	P
Fairy	2.2	7	0	A	M	A	P
Mary	2.5	8	0	A	M	A	P
Lake Muskoka	2.9	8	1	VL	N/A	VL	P
Lake of Bays	1.7	7	1	L/M	M	M/H	P
Harp	1.7	7	2	H	A	A	P
Vernon	2.8	7	4	L	M	A/P	P
Bernard	2.8	7	2	A/P	L/M	H	P
Peninsula	2.6	8	6	A	M	A	P
Mean	2.2*	7	1.6				

Note: Persistence is defined as number of consecutive sampling dates that *B. longimanus* abundance was >5 individuals·m⁻³. Categorical abundance of planktivorous fish provided by Ontario Ministry of Natural Resources (S. Taylor, District of Parry Sound, Parry Sound, ON P2A 1S4, Canada, and S. Sandstrom, District of Muskoka, Bracebridge, ON P1L 1W9, Canada, unpublished data). A *t* test was performed on chlorophyll *a* (chl *a*) concentrations in reference and invaded lakes, where an asterisk (*) indicates $p < 0.05$. Lakes are sorted by increasing *B. longimanus* abundance. A, absent; A/P, absent, but detected in the past; VL, very low; L, low; M, medium; H, high; N/A, not available; P, present.

persistence in invaded lakes are described (Table 2). Persistence was defined as the number of consecutive sampling dates that *B. longimanus* abundance in the lake was >5 individuals·m⁻³. It has been suggested that there may be

an effect threshold of *B. longimanus* at abundances of 3–5 individuals·m⁻³, especially with regards to their main prey, cladocerans (Boudreau and Yan 2003). The higher threshold value (5 individuals·m⁻³) was chosen, as it is a more conser-

vative estimation of *B. longimanus* effects on the zooplankton community.

Zooplankton were enumerated using a protocol designed to ensure reasonable representation of rare species (Girard and Reid 1990). Subsamples were generated with a Folsom plankton splitter, and a mean of 336 individuals (standard deviation = 109) was enumerated. The remainder of the sample was scanned for rare species. Juvenile copepods were excluded from all analyses, except total abundance. Zooplankton were identified and counted on a Leica MZ 12.5 dissecting microscope. Because of uncertainty in identification, *Bosmina (Bosmina) freyi* and *Bosmina (Bosmina) lieferi* (Taylor et al. 2002) were pooled, as were *Chydorus sphaericus* and *C. brevilabris* (Frey 1980). Species presence or absence and taxonomic revisions are listed in Table S1.²

Water chemistry samples were taken the week of 14 July 2003. An integrated tube sampler (2.5 cm inner diameter) was used to collect water from the epilimnion, which was filtered through 80 µm mesh to remove large particles, especially zooplankton. Calcium, dissolved organic carbon (DOC), conductivity, pH, and total phosphorus (TP) were analyzed following Ontario Ministry of the Environment (1983) protocols (Table 1). Chlorophyll *a* (chl *a*) samples were collected every 2 weeks by concentrating a known volume of epilimnetic water onto a 0.7 µm glass fibre filter, extracting for 24 h in methanol, and analyzing with a fluorometer (Table 2) (TD 700; Turner Designs, Sunnyvale, California) (Welschmeyer 1994).

We used two methods to assess the adequacy of our zooplankton richness estimates. First, we compared observed species richness, the number of species found in the composite sample, with Chao's index (S_{Chao1}), a nonparametric measure recommended for estimating species richness, because it does not require knowledge of the species abundance distribution (Magurran 2004). S_{Chao1} was calculated by

$$(1) \quad S_{\text{Chao1}} = S_{\text{obs}} + \frac{F_1^2}{2F_2}$$

where S_{obs} is the number of species observed in the sample, F_1 is the number of species in the sample that are represented by a single individual, and F_2 is the number of species that are represented by two individuals (Chao 1984). This estimator will exceed observed species richness as the relative frequency of singletons increases, providing an estimate of total richness based on the chance that some rare species might be missed (Magurran 2004). The second approach to assessing our richness estimates was to determine if our counting effort was sufficient to sample all species present by examining the relationship between number of individuals counted and richness. The difference in species richness using Chao's index was negligible ($t = -0.05$, $p = 0.96$), as was the relationship between number of individuals counted and richness ($r^2 = 0.10$, $p = 0.29$), suggesting that our observed richness is probably representative of the number of crustacean zooplankton species in the pelagic region

of the lakes. *Bythotrephes longimanus* was not included in richness estimates.

Species diversity and evenness were assessed using the Shannon–Wiener diversity index and Smith and Wilson's (1996) evenness index, E_{var} , respectively. The values of E_{var} fall between 0 (minimum evenness) and 1 (maximum evenness),

$$(2) \quad E_{\text{var}} = \frac{2}{\pi \arctan \left\{ \frac{\sum_{i=1}^S (\ln n_i - \sum_{j=1}^S (\ln n_j)/S)^2}{S} \right\}}$$

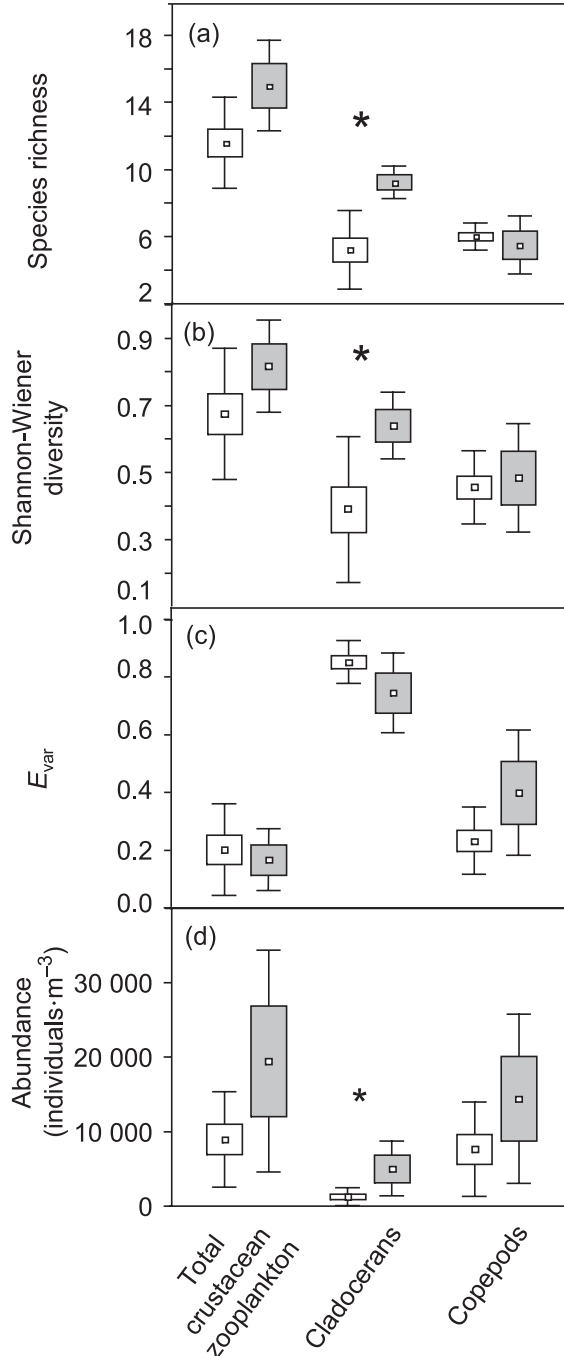
where n_i is the number of individuals of species i , n_j is the number of individuals of species j , and S is the total number of species. E_{var} is recommended as the best evenness measure for general use (Smith and Wilson 1996).

Multivariate ordination techniques were used to evaluate species abundances in relation to environmental variables and the presence of *B. longimanus*. A preliminary examination using correspondence analysis suggested that linear ordination analysis was appropriate, thus redundancy analysis (RDA) was performed using Canoco 4.5 (ter Braak and Šmilauer 2002). *Bythotrephes longimanus* was entered as a categorical variable to maximize differences between the levels of the treatments. Environmental variables were assessed for collinearity if the variance inflation factor was >10 (Quinn and Keough 2002). All of the significant predictors were independent. All species represented by adults were included in the analysis, and abundances were log-transformed to reduce the influence of dominant species. Forward selection identified the variables that explained the most variance in species data, which were then tested for significance using a Monte Carlo permutation test (499 permutations).

Multiple regression analyses were performed to determine what proportion of the variation in species richness data could be explained by *B. longimanus* abundance and persistence, presence or absence of dominant planktivorous fish species, and environmental variables (i.e., TP, pH, maximum depth, and lake area), using the best subsets procedure (StatSoft Inc. 2001). Planktivorous fish data were provided from sampling by the Ontario Ministry of Natural Resources, but because of uncertainty in quantifying fish abundance, the major planktivores were placed in categories of abundance (Table 2). For the multiple regression analysis, abundances were converted to categorical numerical values (absent = 0, absent but detected in the past = 0, very low = 1, low = 2, medium = 3, high = 4) and averaged for each lake to create an index of fish density. Yellow perch could only be classed as present or absent, and as they were present in all lakes, they were excluded from analyses. Collinearity of environmental predictor variables was detected if the variance inflation factor of any predictors was >10 (Quinn and Keough 2002). Chl *a* was removed from the analysis because of

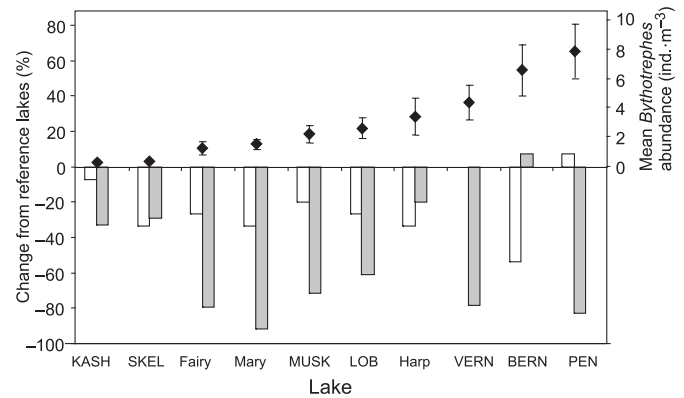
²Supplementary data for this article are available on the journal Web site (<http://cjfas.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5070. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Fig. 1. Box-and-whisker plots of (a) species richness, (b) Shannon–Wiener diversity, (c) E_{var} , and (d) abundance (individuals·m⁻³) for total crustacean zooplankton, cladocerans, and copepods in invaded (open boxes; $n = 10$) and reference (shaded boxes; $n = 4$) lakes. The centre is the mean, the box is the standard error, the whiskers are the standard deviation, and the asterisk (*) is $p < 0.05$.



collinearity with TP. Assumptions of normality, heterogeneity of variance, and independence were also assessed. The best models were chosen by using several criteria: adjusted r^2 , Mallow's C_p , and Akaike's information criterion (AIC) (Quinn and Keough 2002). When evaluating the models, smaller values of Mallow's C_p and AIC indicate the best fit.

Fig. 2. On the left axis, percent change in invaded lakes richness (open bars) and abundance (shaded bars) from the average of the reference lakes, contrasted with mean *B. longimanus* abundance (◆; individuals (ind.)·m⁻³) on the right axis. Vertical error bars represent \pm standard error. Abbreviated lake names: BERN, Bernard; KASH, Kashagawigamog; LOB, Lake of Bays; MUSK, Lake Muskoka; PEN, Peninsula; SKEL, Skeleton; VERN, Vernon.

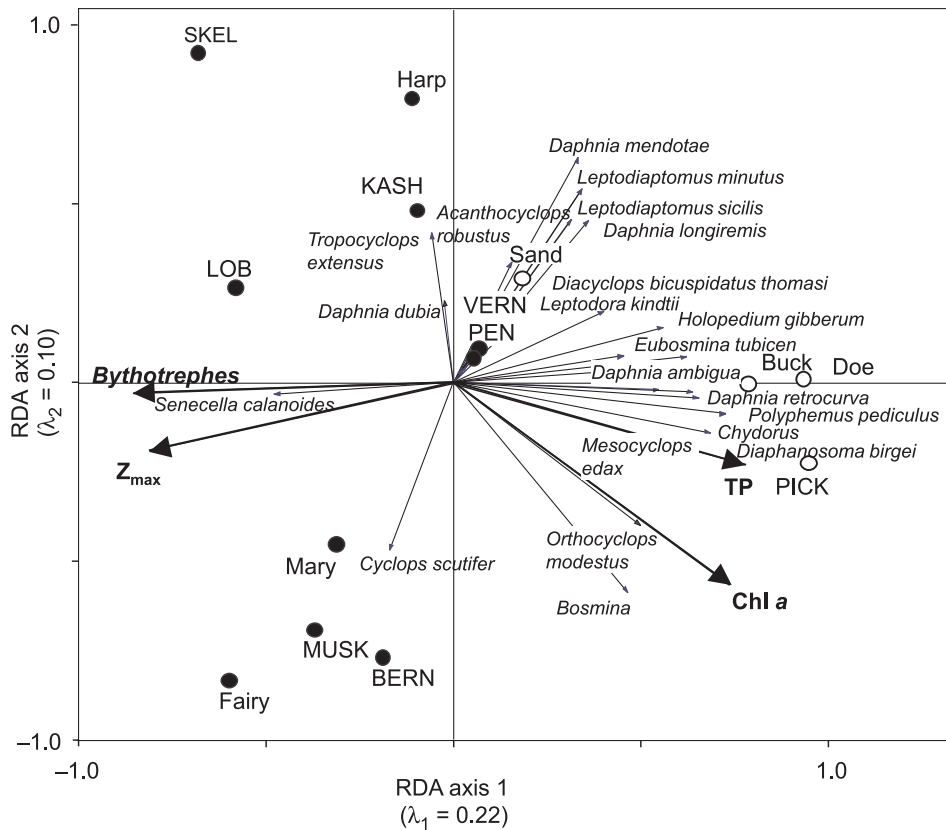


Results

Physical and chemical characteristics did not differ between invaded and uninvaded lakes, with the exception of total phosphorus and chl *a*, which were, on average, 3.33 $\mu\text{g}\cdot\text{L}^{-1}$ and 0.94 $\mu\text{g}\cdot\text{L}^{-1}$ greater in the uninvaded lakes, respectively (TP, $t = -2.45$, $p = 0.03$; chl *a*, $t = -4.83$, $p < 0.01$) (Tables 1, 2). There were no significant differences between invaded and uninvaded lake calcium ($\log(x + 1)$ -transformed), DOC, conductivity, and pH (Table 1). There was also no difference in general lake morphometry, as both maximum depth (Z_{max}) and surface area ($\log(x + 1)$ -transformed) were similar between lake categories (Table 1).

In comparisons of invaded and noninvaded lakes, we found that there was a large reduction in observed species richness of zooplankton taxa in invaded lakes, from an average of 15.0 in uninvaded lakes down to 11.6 species in invaded lakes ($t = -2.12$, $p = 0.06$) (Fig. 1). This decline was largely due to changes in cladoceran zooplankton, which decreased on average by four species in invaded lakes ($t = -3.28$, $p < 0.01$) (Fig. 1). Copepod richness was similar in invaded and reference lakes ($t = 0.76$, $p = 0.46$) (Fig. 1). There was no difference in Shannon–Wiener diversity in total zooplankton ($t = -1.31$, $p = 0.22$) and copepods ($t = -0.40$, $p = 0.70$) in invaded lakes compared with uninvaded lakes, but there was a significant reduction in the diversity of cladoceran zooplankton ($t = -2.17$, $p = 0.05$) (Fig. 1). Evenness of the total zooplankton community ($t = 0.40$, $p = 0.70$) was unaffected by *B. longimanus* invasion, whereas cladocerans experienced a slight increase with invasion ($t = 1.89$, $p = 0.08$), and copepods showed a slight decrease in the *B. longimanus* lakes ($t = -1.89$, $p = 0.08$) (Fig. 1). Invasion had a negative effect on overall zooplankton ($t = -1.91$, $p = 0.08$) and copepod abundance ($t = -1.91$, $p = 0.08$), resulting in a twofold difference for both groups. In addition, there was a decline in cladoceran abundance in invaded lakes ($t = -2.86$, $p = 0.01$), where an almost fourfold difference was observed (Fig. 1).

Fig. 3. Redundancy analysis of zooplankton species abundances and environmental conditions. Environmental variables are represented by the large arrows and species are represented by the small arrows. Species with short arrows were removed to reduce crowding. Circles are site scores for invaded (●) and reference (○) lakes. Species names are italicized. Abbreviated lake names: BERN, Bernard; KASH, Kashagawigamog; LOB, Lake of Bays; MUSK, Lake Muskoka; PEN, Peninsula; PICK, Pickerel; SKEL, Skeleton; VERN, Vernon. Environmental variables: TP, total phosphorus; Z_{max} , maximum depth; chl *a*, chlorophyll *a*.



The relationship between *B. longimanus* abundance and zooplankton species richness and abundance was inconsistent across the invaded study lakes (Fig. 2). The deviations in species richness and abundance from the reference lake condition generally increased with higher abundance of *B. longimanus*, but some invaded lakes actually had greater richness and abundance than uninvaded lakes. When we explicitly considered changes in zooplankton communities relative to the abundance of *B. longimanus* in the lakes using linear regression, we found that crustacean zooplankton species richness ($r^2 = 0.04$, $p = 0.52$), diversity ($r^2 < 0.01$, $p = 0.93$), and abundance ($r^2 = 0.06$, $p = 0.42$) were not related to the mean abundance of *B. longimanus*. Likewise, cladoceran species richness ($r^2 = 0.13$, $p = 0.20$), diversity ($r^2 = 0.11$, $p = 0.26$), and abundance ($r^2 = 0.15$, $p = 0.14$) were not related to mean *B. longimanus* abundance.

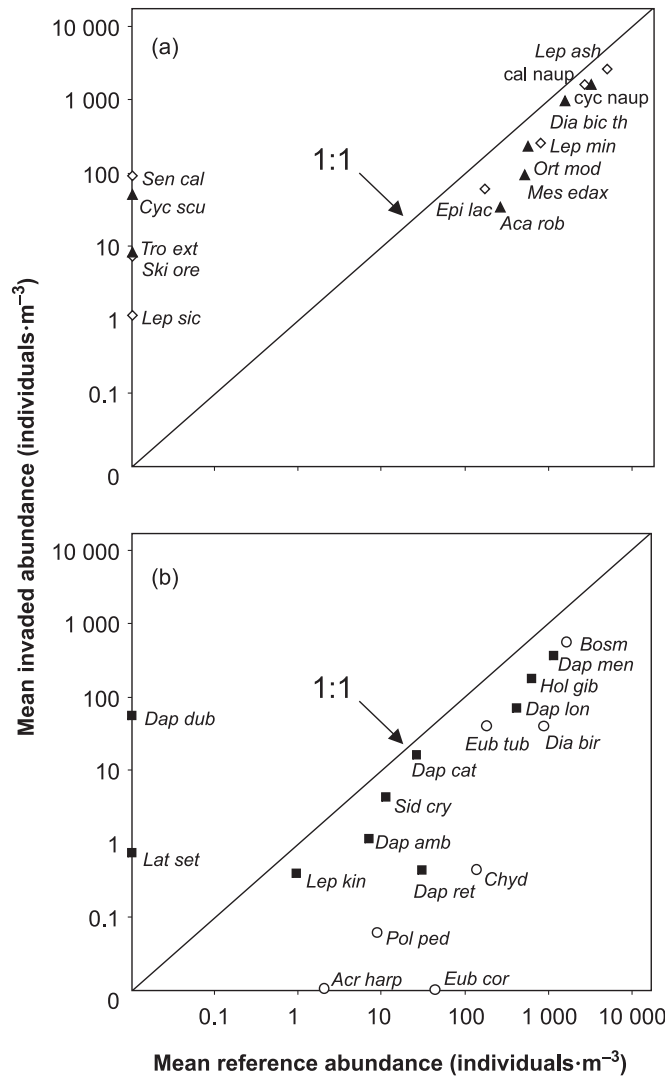
RDA captured a significant amount of variance ($p < 0.01$) in zooplankton species abundances, with *B. longimanus* presence or absence explaining 43% of total species variation, and Z_{max} (22%), chl *a* (20%), and TP (15%) contributing to the remainder of species abundance variation (Fig. 3). The first axis ($\lambda_1 = 0.22$, $p = 0.03$) contrasts the presence with the absence of *B. longimanus*, as most of the invaded lakes fall on the same side as the *B. longimanus* vector, and all of the reference lakes are on the opposite side of the gradient. A number of species were negatively associated with

the invader (e.g., *D. birgei*, *Mesocyclops edax*, *Holopedium gibberum*), and only one species, the glacial relict *Senecella calanoides*, was positively correlated with *B. longimanus* presence. The second axis ($\lambda_2 = 0.10$) seems to be related to lake productivity, as some cladoceran taxa (*Bosmina* (*Bosmina*) spp., *Daphnia retrocurva*, and *D. birgei*) and omnivorous cyclopoids (*M. edax* and *Orthocyclops modestus*) were positively associated with the TP and chl *a* vectors.

The majority of zooplankton taxa were, on average, in lower abundance in invaded lakes than in reference lakes (Fig. 4). The cladoceran taxa tended to fall further below the 1:1 line than did the copepods, especially smaller-bodied taxa such as *Chydorus* spp. and *Eubosmina coregoni*. A few larger taxa, such as *S. calanoides*, *Cyclops scutifer*, and *Daphnia dubia*, were more abundant in invaded lakes than reference lakes, on average, but for the most part, both large- and small-bodied zooplankton were less abundant in *B. longimanus* invaded lakes.

Species richness tended to increase with longer persistence times of *B. longimanus* populations throughout the summer ($r^2 = 0.31$, $p = 0.09$), suggesting that there is no temporal refuge available to zooplankton. Using multiple regression analysis, we found that all of the most parsimonious models to explain species richness had negative associations of species richness with mean *B. longimanus* abundance, but that zooplankton richness was positively re-

Fig. 4. Mean abundance (individuals·m⁻³) of (a) calanoid (◇) and cyclopoid (▲) copepods and (b) large (■; >1 mm) and small (○; <1 mm) cladocerans in reference lakes plotted against corresponding abundance in invaded lakes. Abbreviations of zooplankton taxa: (a) *Aca rob*, *Acanthocyclops robustus*; *cal naup*, calanoid nauplii; *cyc naup*, cyclopoid nauplii; *Cyc scu*, *Cyclops scutifer*; *Dia bic th*, *Dia cyclops bicuspidatus thomasi*; *Epi lac*, *Epischura lacustris*; *Lep ash*, *Leptodiptomus ashlandi*; *Lep min*, *Leptodiptomus minutus*; *Lep sic*, *Leptodiptomus sicilis*; *Mes edax*, *Mesocyclops edax*; *Ort mod*, *Orthocyclops modestus*; *Sen cal*, *Senecella calanoides*; *Ski ore*, *Skistodiptomus oregonensis*; *Tro ext*, *Tropocyclops extensus*; (b) *Acr har*, *Acroperus harpae*; *Bosm*, *Bosmina (Bosmina) spp.*; *Chyd*, *Chydorus spp.*; *Dap amb*, *Daphnia ambigua*; *Dap cat*, *Daphnia catawba*; *Dap dub*, *Daphnia dubia*; *Dap lon*, *Daphnia longiremis*; *Dap men*, *Daphnia mendotae*; *Dap ret*, *Daphnia retrocurva*; *Dia bir*, *Diaphanosoma birgei*; *Eub cor*, *Eubosmina coregoni*; *Eub tub*, *Eubosmina tubicen*; *Hol gib*, *Holopedium gibberum*; *Lat set*, *Latona setifera*; *Lep kin*, *Leptodora kindtii*; *Pol ped*, *Polyphemus pediculus*; *Sid cry*, *Sida crystallina*.



lated to *B. longimanus* persistence in high abundances in the lake (Table 3). In both models, species richness was positively related to duration of *B. longimanus* persistence and

TP and negatively related to mean *B. longimanus* abundance. In addition, the best model selected by AIC had positive associations of zooplankton richness with area and pH. The presence of fish planktivore species had no effect on zooplankton species richness.

Discussion

Our study has demonstrated that *B. longimanus* can have negative effects on zooplankton communities through parts of the ice-free season, reducing species richness, diversity, and abundance throughout the ice-free season. This negative effect was exacerbated in the cladocerans, which showed significant declines in richness (on average, four less species in invaded lakes), abundance (a fourfold decline), and diversity. These results are in agreement with the declines in zooplankton richness observed in Harp Lake (Yan et al. 2002), Muskoka lakes (Boudreau and Yan 2003), and Lakes Michigan, Erie, and Huron (Barbiero and Tuchman 2004) (Table 4). Reductions in the abundance of zooplankton have been shown experimentally (Strecker and Arnott 2005) and in Harp Lake (Yan et al. 2001); however, some recent studies have failed to detect changes in total zooplankton community abundance (Boudreau and Yan 2003; Barbiero and Tuchman 2004) (Table 4). The samples in Boudreau and Yan’s (2003) study were taken on a single sampling date, and this snapshot approach does not take into account seasonal dynamics, as was done in our study and Yan et al. (2001). Barbiero and Tuchman’s (2004) samples were only taken for 1 month starting 1 August and, thus, do not reflect zooplankton abundance in late spring, early summer, and fall. A comparison of our study with others over a shorter period of time suggests that short-term synoptic surveys may adequately document changes in some measures of zooplankton community structure associated with *B. longimanus* invasion. For example, the effect of *B. longimanus* on species richness seems to be consistent between different sampling routines, but longer studies, especially in smaller inland lakes, that encompass the entire season seem to capture changes in total abundance better than single sampling dates (Table 4).

Several zooplankton taxa showed steep declines in *B. longimanus* invaded lakes. As past studies have documented the general negative effect that *B. longimanus* has on many cladoceran taxa (Boudreau and Yan 2003), we expected to observe this in our study as well. As expected, the abundances of a number of common cladoceran species, such as *Bosmina (Bosmina) spp.*, and *D. birgei*, were severely reduced: on average, a decrease of greater than four times in invaded lakes. The larger species *Daphnia longiremis*, *Daphnia mendotae*, and *H. gibberum* also had lower abundances in invaded lakes, suggesting that body size alone does not provide refuge from predation. As well, it appears as though some hypolimnetic species, such as *D. longiremis* (Keller and Conlon 1994), do not escape predation. These patterns are generally in agreement with Boudreau and Yan (2003), Yan et al. (2001), and Barbiero and Tuchman (2004), although there seem to be some system-specific differences. For example, *D. mendotae* has remained unaffected by *B. longimanus* in Harp Lake (Yan et al. 2001; Boudreau and Yan 2003; this study) but has declined in other lakes (Barbiero and Tuchman 2004). Unexpectedly,

Table 3. Multiple regression of crustacean zooplankton species richness with predictor variables in all study lakes (invaded: $n = 10$; reference: $n = 4$).

	Adjusted R^2	Mallows C_p	AIC	F ratio	p value	Variable	Coefficient	Partial correlation coefficient	t value	p value
Model 1	0.73	4.59	16.37	12.57	<0.01	<i>B. longimanus</i> abundance	-1.32	-0.84	-4.87	<0.01
						<i>B. longimanus</i> persistence	1.23	0.83	4.77	<0.01
						TP	-0.47	0.70	3.12	0.01
Model 2	0.77	5.10	14.77	9.79	<0.01	Area	0.24	0.49	1.57	0.15
						<i>B. longimanus</i> abundance	-1.78	-0.89	-5.65	<0.01
						<i>B. longimanus</i> persistence	1.70	0.89	5.52	<0.01
						pH	0.20	0.43	1.36	0.21
						TP	0.62	0.81	3.93	<0.01

Note: Persistence is defined as number of consecutive sampling dates that *B. longimanus* abundance was >5 individuals·m⁻³. AIC, Akaike's information criterion; TP, total phosphorus.

Table 4. Summary of effects of *B. longimanus* on several zooplankton community attributes in different types of sampling regimes.

Variable	Long-term study of Harp Lake, ^{a,b} Great Lakes ^c	Synoptic survey ^d	Seasonal survey ^e	Field experiment ^f
Richness				
Total zooplankton	— ^{a,c}	—	—	0
Cladocerans	— ^a	—	—	0 ^g
Copepods	0 ^a	0	0	0 ^g
Abundance				
Total zooplankton	- ^b , 0 ^c	0	—	—
Cladocerans	- ^b , 0 ^c	—	—	— (small); 0 (large)
Copepods	0 ^{b,c}	0	—	— (calanoids); 0 (cyclopoids)
Diversity				
Total zooplankton	N/A	N/A	0	0
Cladocerans	N/A	N/A	—	0 ^g
Copepods	N/A	N/A	0	+ ^g

Note: Symbols: +, positive effect ($p < 0.05$); —, negative effect ($p < 0.05$); -, negative effect ($p < 0.1$); 0, no effect.

^aYan et al. (2002); biweekly or monthly collections (1980–2000).

^bYan et al. (2001); biweekly or monthly collections (1980–1998).

^cBarbiero and Tuchman (2004); multiple stations in Lakes Michigan, Huron, and Erie (1983–1999).

^dBoudreau and Yan (2003); single midsummer sampling date (2001).

^eThis study.

^fStrecker and Arnott (2005); 30-day enclosure experiment.

^gA. Strecker, unpublished data.

several common copepod taxa (*Leptodiatomus minutus*, *Diacyclops bicuspidatus thomasi*, and *M. edax*) in our study were also negatively affected by *B. longimanus*. Previously, only *M. edax* was thought to be affected by invasion (Boudreau and Yan 2003; Barbiero and Tuchman 2004). Given that copepods are in high abundance in the late spring in these lakes, before *B. longimanus* emerges from resting eggs and rapidly builds up populations through parthenogenic reproduction (A. Strecker, unpublished data), it is especially surprising that they declined, as their earlier dominance in lakes would suggest that they should be able to use a temporal refuge from *B. longimanus* predation. However, longer-lived slow-reproducing copepods may actually be more susceptible to predation by *B. longimanus* because they are unable to reproduce as quickly as cladocerans. Thus, the copepods are less able to respond to low predator abundances, as *B. longimanus* is known to have extremely patchy spatial and temporal dynamics (J. Young and E. Parrott, Department of Biology, York University, To-

ronto, ON M3J 1P3, Canada, unpublished data) and, therefore, cannot take advantage of this window of opportunity. This further supports the notion that to adequately assess changes in total and individual zooplankton abundances resulting from *B. longimanus* invasion, longer-term surveys are necessary.

Our study suggests that most species are not able to take advantage of a temporal refuge from *B. longimanus* predation. We found that longer persistence times of *B. longimanus* resulted in higher species richness, the opposite of what we would expect to see if a temporal refuge was indeed available. *Bythotrephes longimanus* was detected in invaded lakes on an average of seven sampling dates, or about 14 weeks during the summer. This is likely a conservative estimate, as *B. longimanus* was present in 90% of invaded lakes on the final sampling date in September and has shown the ability to persist into late fall in some lakes (J. Young, Department of Biology, York University, Toronto, ON M3J 1P3, Canada, personal communication). Thus, in most lakes, the only op-

portunity for a temporal refuge is in the spring, and our evidence suggests that this window of opportunity is not being used by zooplankton, perhaps because water temperatures are cool and food availability is low in these oligo-mesotrophic lakes. If zooplankton were indeed using this temporal refuge, we would expect to see no effect of *B. longimanus* on zooplankton richness and abundance, especially on copepods, which are typically in high numbers in these lakes in late spring, thus having reduced temporal overlap with the invader. However, this was not the case: overall zooplankton abundance and richness were reduced, and several copepod taxa were also negatively affected by *B. longimanus*. Another potential explanation is that there are competitive interactions occurring between *B. longimanus* and its predators. *Mysis relicta* and other zooplanktivores may benefit from longer *B. longimanus* persistence times by switching from smaller zooplankton to the larger invader, thus freeing the zooplankton from intense predation. Gut content analysis of *M. relicta* collected from several of our study lakes has revealed the presence of *B. longimanus* body parts, thus it seems that the invader can also be a prey item for other invertebrate predators (Nordin 2005).

There was a substantial amount of among-lake variation in the responses of the zooplankton communities to *B. longimanus* invasion. This variability appears to be unrelated to the actual abundance of *B. longimanus*, which was not a strong predictor of zooplankton richness or abundance in invaded lakes. There is some evidence that zooplankton can adapt their morphologies in the presence of *B. longimanus* (Bungartz and Branstrator 2003), suggesting that the abundance of the invader may play a role in eliciting behavioural and morphological responses in the zooplankton community and thus increasing species survival. Two of the invaded lakes, Peninsula and Vernon, had zooplankton communities that more closely resembled communities in non-invaded reference lakes. Both lakes had relatively high mean *B. longimanus* abundance (7.8 and 4.3 individuals·m⁻³, respectively) and had richness values that fell more into the range of uninvaded lakes. When these lakes were excluded from regression analyses, mean *B. longimanus* abundance had a significant negative effect on species richness ($r^2 = 0.53$, $p < 0.01$). The redundancy analysis also suggests that Peninsula and Vernon lakes have species compositions that are more similar to those of reference lakes than invaded lakes. We are unsure why the zooplankton community composition of these two lakes is seemingly unaffected by invasion. One possibility is that *B. longimanus* is feeding in a density-dependent manner, reducing the abundances of certain preferred species to low densities, and then switching to higher-density prey items that can be caught more easily. Thus, *B. longimanus* is not reducing any species to the point where it can no longer be detected. Consistent with this hypothesis, the evenness of Peninsula and Vernon lakes was higher than the average of the invaded lakes, and the diversity was greater than the average diversity of the uninvaded lakes. The abundances of the zooplankton communities of both of these lakes are below the average of other invaded lakes, so although it seems that *B. longimanus* is reducing zooplankton abundance, species richness remains unaffected. However, if *B. longimanus* feeding is indeed density-dependent in these lakes, then why is this not occurring in

all of the invaded lakes? It is possible that zooplankton reproduction in these lakes was high enough to fend off the loss of species richness. Yan et al. (1991) showed that for the rotifer *Keratella taurocephala*, high rates of production could be maintained, even under intense predation by species of the invertebrate *Chaoborus*. Vernon Lake had high secondary production relative to *B. longimanus* consumption (A. Strecker, unpublished data), so this may, in part, explain the lack of effect on species richness.

Other potential explanations for the high levels of species richness observed in Peninsula and Vernon lakes are that they had different morphological, biotic, and chemical conditions than the rest of the invaded lakes, and thus, there existed some advantage that allowed coexistence. For instance, a deep-water spatial refuge in the lake can afford some species a certain amount of protection from predation. However, Peninsula and Vernon lakes were the two shallowest invaded lakes, suggesting that they, in fact, had a smaller spatial refuge than other invaded lakes. Another possibility is that Peninsula and Vernon lakes were less clear than other invaded lakes, thus offering zooplankton a dark-water refuge. This may be the case for Vernon Lake, which had higher DOC and lower Secchi disc values than did other invaded lakes, but not for Peninsula Lake, which had values that were within the range of the other invaded lakes. Thus, this variability that we observed between study lakes in response to an invasion of *B. longimanus* may be due to a combination of factors related to characteristics of the invader, i.e., feeding strategy, and to characteristics of the lakes, such as productivity and lake clarity.

The importance of lake area and productivity in determining crustacean zooplankton species richness in temperate freshwater lakes has been well established (Dodson 1992; Dodson et al. 2000). Surface area had little predictive power in our analysis of factors influencing species richness in lakes invaded by *B. longimanus*, but other variables related to the invader were much better predictors of zooplankton richness. Although we did not measure primary productivity, TP can be used as a surrogate for productivity (see Leibold 1999). A caveat of our study is that uninvaded lakes had slightly higher levels of TP and chl *a* than did the invaded lakes, but in our oligo-mesotrophic systems, these differences are small and are unlikely to lead to the observed differences in species richness. In addition, our multiple regression analyses suggest that although TP is an important predictor, *B. longimanus* explains far more variation in species richness. Although *B. longimanus* abundance by itself was a poor predictor of species richness, when combined with persistence of the invader in multiple regression analysis, the explanatory power of the two variables was much greater. It is possible that the result from the linear regression was being influenced by the two outlier values, Vernon and Peninsula lakes, while these values became less important with more predictive variables. In fact, neither of these values had an exceptionally large influence on the final multiple regression models, as measured by Cook's distance statistic (Quinn and Keough 2002).

The composition of the fish community can also have substantial effects on the structure of the zooplankton community (Brooks and Dodson 1965). Although there appear to be some differences in the abundance of planktivores present in

invaded versus reference lakes, our data suggest that *B. longimanus* is still having a substantial negative effect. If fish were in fact responsible for the effects that we observed, then we would expect larger zooplankton species to be more negatively affected than small taxa. However, reductions in species richness were proportionately greater for small species (28%) than for large-bodied zooplankton (14%), which supports our assertion that *B. longimanus* is largely responsible for the observed reduction in zooplankton species richness. Other variables, such as pH (Keller and Pitblado 1984), calcium (Schell et al. 2001; Wærvågen et al. 2002), and postglacial history of the lake (Dadswell 1974; Carter et al. 1980), can be important predictors of zooplankton richness. However, neither pH nor calcium were significantly different in *B. longimanus* lakes compared with reference lakes, and all of our study lakes have a similar postglacial history because of the presence of *M. relicta*. Thus, these factors did not influence our results.

There is now a significant body of evidence to suggest that *B. longimanus* invasions cause changes to the zooplankton communities of freshwater lakes. This is especially true of cladoceran taxa, which seem to take the brunt of *B. longimanus* predation, as our study has exhibited striking declines in their richness, abundance, and diversity in invaded lakes. A concurrent study of the rotifer composition and abundance of the same 14 lakes showed a positive relationship between rotifer and *B. longimanus* abundance, perhaps as a result of reduced competition with herbivorous cladocerans for zooplankton prey (Hovius et al. 2006). These results are somewhat surprising, as *B. longimanus* is an invertebrate predator that has several native functional analogues in these boreal lakes, including *M. relicta*, *Leptodora kindtii*, *Chaoborus* spp., and water mites (Arachnida, Hydrachnidia). It could be argued that *B. longimanus* occupies a unique feeding niche; however, this seems unlikely as its dietary overlap with other invertebrate predators is high (McNaught et al. 2004; Young and Riessen 2005). *Bythotrephes longimanus* employs several effective strategies to maintain high feeding rates in these boreal lakes: (i) although it is consumed by some fish species, presumably the long tail spine of *B. longimanus* decreases predation impact; (ii) it lacks large amplitude migrations (Yan and Pawson 1997), unlike many other invertebrate predators (*Chaoborus*, *Mysis*, *Leptodora*), so it is continuously in regions of high prey density; (iii) it reproduces parthenogenically, unlike mites, which are sexual and have slower reproductive times, so it can quickly respond to increases in food resources; and (iv) its neonates are larger, allowing them to exploit a larger range of prey sizes, unlike the small-bodied clutches of *Leptodora* (Branstrator 2005). What is clear is that not all lakes respond to *B. longimanus* invasion in the same way. Our study has highlighted that there are substantial among-lake differences in the effect of the invader on richness, abundance, and diversity of zooplankton communities.

As *B. longimanus* continues to spread across the landscape of North America, it seems likely that it will be an important new factor in determining the zooplankton composition of freshwater lakes. This is certain to have implications for regional species richness, as our results suggest that certain species, such as the ubiquitous taxa *D. birgei* and *M. edax*, have reduced abundances in invaded

lakes across the landscape, leaving few populations that may act as sources to disperse to new locales.

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