Biol Invasions (2011) 13:2621–2634
DOI 10.1007/s10530-011-0081-0

ORIGINAL PAPER

# *Bythotrephes* invasion elevates trophic position of zooplankton and fish: implications for contaminant biomagnification

**Michael D. Rennie · Angela L. Strecker · Michelle E. Palmer**

Received: 18 June 2010 / Accepted: 31 January 2011 / Published online: 12 August 2011

**Abstract** We estimated the effects of *Bythotrephes longimanus* invasion on the trophic position (TP) of zooplankton communities and lake herring, *Coregonus artedi*. Temporal changes in lacustrine zooplankton communities following *Bythotrephes* invasion were contrasted with non-invaded reference lakes, and along with published information on zooplankton and herring diets, formed the basis of estimated changes in TP. The TP of zooplankton communities and lake herring increased significantly following the invasion of *Bythotrephes*, whereas TP in reference lakes decreased (zooplankton) or did not change significantly (lake herring) over a similar time frame. Elevated TP following *Bythotrephes* invasion was most prominent in lakes that also supported the glacial relict, *Mysis diluvania*, suggesting a possible synergistic interaction between these two species on zooplankton community composition. Our analysis indicated that elevated TPs of zooplankton communities and lake herring are not simply due to the presence of *Bythotrephes*, but rather reflect changes in the zooplankton community induced by *Bythotrephes*; namely, a major reduction in the proportion of herbivorous cladoceran biomass and a concomitant increase in the proportion of omnivorous and/or predatory copepod biomass in invaded lakes. We demonstrated that increases in TP of the magnitude reported here can lead to substantial increases in fish contaminant concentrations. In light of these results, we discuss potential mechanisms that may be responsible for the disconnect between empirical and theoretical evidence that mid-trophic level species invasions (e.g., *Bythotrephes*) elevate contaminant burdens of consumer species, and provide testable hypotheses to evaluate these mechanisms.

**Keywords** Cercopagidae · Mysis · Fish · Food web · Contaminants · Coregonidae

---

**Electronic supplementary material** The online version of this article (doi:10.1007/s10530-011-0081-0) contains supplementary material, which is available to authorized users.

M. D. Rennie (✉)
Environmental and Life Sciences Program,
Trent University, 2140 East Bank Drive, 2nd Floor
(DNA Building), Peterborough, ON K9J 7B8, Canada
e-mail: Michael.Rennie@dfo-mpo.gc.ca

*Present Address:*
M. D. Rennie
Fisheries and Oceans Canada, Freshwater Institute,
501 University Crescent, Winnipeg,
MB R3T 2N6, Canada

A. L. Strecker
School of Aquatic and Fishery Sciences, University
of Washington, 1122 NE Boat St., Seattle,
WA 98105, USA

M. E. Palmer
Department of Biology, York University,
4700 Keele St., Toronto, ON M3J 1P3, Canada

## Introduction

The trophic position (TP) of organisms has important consequences for the biomagnification and bioaccumulation of contaminants in consumers at higher trophic levels (Cabana and Rasmussen 1994). Comparative studies have shown that the presence of mid-trophic level consumer species results in longer food chains in lake ecosystems and elevated contaminant levels in top predators (e.g., Rasmussen et al. 1990; Vander Zanden and Rasmussen 1996). These observations have led to the hypothesis that invasions by mid-trophic level (mid-trophic hereafter) species that increase food chain length should also increase contaminant concentrations in consumer species. However, direct tests of this hypothesis are few, and largely inconclusive. Johnston et al. (2003) reported no significant effect of the invasion of rainbow smelt (*Osmerus mordax*, a planktivorous fish that tends to feed at a higher trophic level than native plantivores; Swanson et al. 2003) on mercury (Hg) concentrations in piscivorous fishes. In the Laurentian Great Lakes, the invasion of round goby (*Apollonia melanostomus*, which is elevated trophically relative to native littoral fish species; Campbell et al. 2009) has similarly led to concerns regarding elevated Hg in consumer species. However, Hogan et al. (2007) reported a decline in smallmouth bass (*Micropterus dolomieu*) Hg following the establishment of round goby. More recently, Hg concentrations of planktivorous coregonids (*Coregonus artedi* and *C. clupeaformis*) were found not to be related to the establishment of the invertebrate predator, *Bythotrephes longimanus* (Rennie et al. 2010); the authors concluded that these changes were more likely related to climate change as opposed to food web changes following invasion.

A major untested assumption of the aforementioned studies and others that have investigated the effects of mid-trophic species invasions on consumer contaminant levels is that the TP of higher order consumers will increase following invasion (e.g., Gorokhova et al. 2005). Despite the lack of evidence for elevated fish contaminant concentrations in lakes invaded by *Bythotrephes*, there is good reason to expect that their invasion and establishment should alter the TP of higher order consumers, via both direct and indirect mechanisms. *Bythotrephes* could elevate consumer TPs directly, as it commonly reaches abundances greater than those of native invertebrate predators (Foster and Sprules 2009), and is a common prey item of planktivorous fishes following invasion (Coulas et al. 1998; Mills et al. 1992; Parker Stetter et al. 2005). *Bythotrephes* may also elevate consumer TPs indirectly, as invasion has generally resulted in major changes in zooplankton community composition, characterized by declines in crustacean zooplankton abundance, richness, biomass, and productivity (Barbiero and Tuchman 2004; Boudreau and Yan 2003; Fernandez et al. 2009; Strecker and Arnott 2008; Yan et al. 2002). In most instances, zooplankton composition shifts to a more copepod dominated assemblage as *Bythotrephes* seems to have the greatest negative effect on cladoceran zooplankton (Strecker et al. 2006). Thus, a decline in the relative abundance of herbivorous (i.e., cladoceran) taxa could also lead to an overall increase in the TP of the zooplankton community, and therefore the TPs of planktivorous fishes.

Given this evidence, we set out to determine whether the expectation that *Bythotrephes* invasion should elevate the mean TP of the crustacean zooplankton community and their putative consumers (i.e., the lake herring, *C. artedi*) could be supported. We tested this expectation using published diet information for zooplankton and lake herring, and applied these to a trophic position estimation model. Further, we used this information to generate hypotheses to better understand why studies of mid-trophic invasions have so frequently failed to detect increased contaminant burdens in putative consumer species, in light of our findings.

## Methods

### Study area

Nineteen lakes for which zooplankton communities could be characterized both historically and contemporarily were selected for analysis (Table 1). We selected eleven lakes invaded by *Bythotrephes* and eight reference lakes that had not at the time of this study been invaded by *Bythotrephes*. Reference lakes were selected to reflect similar morphology and water chemistry to invaded lakes (Table 1). All selected lakes undergo thermal stratification during summer months. Eight invaded lakes included the glacial relict omnivore *Mysis diluvania* (formerly *M. relicta*,

**Table 1** Lakes from Ontario, Canada included in the study for which historical and contemporary data on zooplankton biomass were available

| Lake | Location (dd° mm′) | Area (ha) | Max. depth (m) | DOC (mg/l) | Total *P* (ug/l) | Years sampled | Year *Bythotrephes* reported | *Mysis* present |
|---|---|---|---|---|---|---|---|---|
| Boshkung | 45° 04′ 78° 44′ | 717 | 71.0 | 4.3 | 3.93 | 1992[a], 2003[b] | 2003 | Yes[1,3] |
| Harp | 45° 23′ 79° 08′ | 71.7 | 37.5 | 6.7 | 7.2 | 1981–1989[c], 2003[b] | 1993[b] | Yes[2,3] |
| Gull | 44° 50′ 78° 47′ | 996 | 49.0 | 5.2 | 5.64 | 1992[a], 2003[b] | 2003 | Yes[1,3] |
| Lake of Bays | 45° 15′ 79° 04′ | 6,905 | 70.0 | 5.1 | 3.38 | 1992[a], 2003[b] | 1995 | Yes[1,3] |
| Leonard | 45° 04′ 79° 27′ | 195 | 15.2 | 4.21 | 6.88 | 1984[d], 2004[e] | 2001 | Yes[4] |
| Skeleton | 45° 15′ 79° 27′ | 2,157 | 65.0 | 2.6 | 3.82 | 1992[a], 2003[b] | 1998 | Yes[1,3] |
| Twelve mile | 45° 01′ 78° 43′ | 338 | 28.0 | 3.9 | 5.07 | 1992[a], 2003[b] | 2003 | Yes[1,3] |
| Vernon | 45° 20′ 79° 17′ | 1,505 | 37.2 | 7.1 | 7.9 | 1992[a], 2003[b] | 1991 | Yes[1,3] |
| Mean (SD) |  | 1,610.6 (2,252.2) | 46.6 (20.7) | 4.89 (1.48) | 5.48 (1.71) |  |  |  |
| Kimball | 45° 21′ 78° 41′ | 213 | 61.0 | 3.09 | 3.62 | 1983[d], 2004[e] | 2004 | No[3] |
| Nunikani | 45° 12′ 78° 44′ | 116 | 24.0 | 3.72 | 4.61 | 1984[d], 2005[e] | 2005 | No[3] |
| Sherborne | 45° 11′ 78° 47′ | 252 | 35.1 | 3.38 | 4.39 | 1984[d], 2005[e] | 2005 | No[3] |
| Mean (SD) |  | 193.7 (70.0) | 40.0 (19.0) | 3.40 (0.31) | 4.21 (0.52) |  |  |  |
| Big Porcupine | 45° 27′ 78° 37′ | 235 | 30.5 | 2.77 | 3.82 | 1983[d], 2005[e] | *n/p* | No[3] |
| Bigwind | 45° 03′ 79° 03′ | 111 | 32.0 | 3.76 | 6.04 | 1983[d], 2004[e] | *n/p* | No[4] |
| Clear | 45° 11′ 78° 43′ | 88.4 | 33.0 | 1.97 | 3.07 | 1983[d], 2005[e] | *n/p* | No[4] |
| Crown | 45° 26′ 78° 40′ | 136 | 30.0 | 2.74 | 4.81 | 1983[d], 2005[e] | *n/p* | No[4] |
| Louisa | 45° 28′ 78° 29′ | 531 | 61.0 | 3.87 | 3.74 | 1983[d], 2005[e] | *n/p* | No[3] |
| Maggie | 45° 30′ 78° 52′ | 138 | 31.0 | 2.41 | 4.48 | 1987[d], 2005[e] | *n/p* | No[4] |
| Smoke | 45° 31′ 78° 41′ | 679 | 55.0 | 3.69 | 4.95 | 1983[d], 2005[e] | *n/p* | No[3] |
| Solitaire | 45° 23′ 79° 01′ | 124 | 31.0 | 2.44 | 7.59 | 1983[d], 2004[e] | *n/p* | No[4] |
| Mean (SD) |  | 255.3 (223.6) | 37.9 (12.5) | 2.96 (0.72) | 4.81 (1.44) |  |  |  |

Data source: [a] Almond et al. (1996); [b] Strecker et al. (2006); [c] Girard et al. (2007); [d] Yan et al. (1996); [e] M. Palmer, *unpublished*

Data source of *Mysis* presence/absence: [1] Almond et al. (1996); [2] Yan and Pawson (1997); [3] Cabana et al. (1994); [4] presence/absence estimated from distribution maps on extent of glacial inundation (Martin and Chapman 1965; Prest and Douglas 1969)

*n/p* = not present in most recent survey year listed. Means and standard deviations are in italics. Max. depth = maximum depth. Total *P* = total phosphorous

Audzijonyte and Väinölä 2005) and three did not. *Mysis* were absent from our reference lakes, and we had no comparable data on reference lakes with *Mysis* in our study region. Based on evidence from the literature (Lasenby et al. 1986; Nero and Sprules 1986), it was anticipated that *Mysis* would have a large structuring force on zooplankton communities and might therefore also alter *Bythotrephes* effects on zooplankton communities, or alter fish feeding habits in lakes where they were present.

## Sampling

Sampling protocols for summer crustacean zooplankton differed slightly among studies from which data were obtained (Table 1): Strecker et al. (2006) sampled every 2 weeks from May to September with a 150-µm mesh net that was 0.5 m in diameter; Almond et al. (1996) sampled in May, July and September with a 200-µm mesh net that was 0.5-m in diameter; and the Ontario Ministry of the Environment (OMOE) sampling program (Girard et al. 2007; Yan et al. 1996) and M. Palmer (unpublished) sampled every 2 weeks (Harp Lake pre-invasion only) or monthly, typically from May/June to September/October, using an 80-µm mesh net that was 0.12 m in diameter. Larger mesh sizes are more efficient at filtering water; however, the OMOE nets are equipped with flow meters, and volumes have been corrected for inefficiency (Girard et al. 2007). All study protocols sampled the entire water column.

*Bythotrephes* was sampled separately from other crustacean zooplankton in the study of Strecker et al. (2006) with a 400-µm net, as larger mesh sizes are appropriate for capturing larger-bodied predators. With data from that study, a regression was developed comparing *Bythotrephes* abundance in larger mesh nets with that from smaller mesh size nets used for zooplankton community sampling (abundance in *Bythotrephes* net = 1.54*(abundance in zooplankton net) +5.34, $R^2 = 0.70$). This regression equation was applied to *Bythotrephes* abundance in seven lakes where *Bythotrephes* was sampled with smaller mesh-size nets to maintain consistency among sampling protocols. *Bythotrephes* abundance was converted to biomass using the formula of Yan and Pawson (1998).

### Estimating zooplankton trophic position

Zooplankton species in each lake were assigned a TP based on literature accounts of feeding for each species, or for closely related species where such data could not be identified (Supplementary Material 1). Trophic position ($\tau$) was estimated with a method used frequently in the literature (Adams et al. 1983; Post and Takimoto 2007; Vander Zanden and Rasmussen 1996):

$$\tau_i = \sum_{j \in L} w_{ij} \tau_j + 1 \tag{1}$$

where $\tau_i$ is the trophic position of species $i$, $\tau_j$ is the trophic position of species $j$, $w_{ij}$ is the proportion of species $j$ in the diet of species $i$ (where $0 \le w_{ij} \le 1$ and $\sum_{j \in L} w_{ij} = 1$ for all $i$) and $L$ is a set of species in a lake.

For each lake and in each time period (historical, contemporary), we reduced seasonal-scale data (monthly or fortnightly) on zooplankton biomass to one mean annual estimate of biomass for each taxa across all samples in a given year. For lakes where more than 1 year of either historical or contemporary data was available (e.g., Harp Lake), a single average over all years was estimated. Mean weighted TP of the zooplankton community in each time period was estimated as the TP of all zooplankton taxa weighted by their proportional contribution to annual average biomass estimates. Data on juvenile copepods were not available for all studies and were excluded from our analyses. It is unlikely that this exclusion influenced our results; using a subset of our available data, we determined that juvenile copepod biomass was not different between invaded and non-invaded lakes in either time period (M. Palmer, unpublished). Rare taxa that were found infrequently and poorly estimated by the sampling procedure used (e.g., *Leptodora kindtii*, *Polyphemus pediculus*, Supplementary Material 1) were also found to have no significant influence on our estimates of mean zooplankton TP and were therefore excluded.

### Estimation of lake herring diets, trophic position

Lake herring are one of the most common and widely distributed planktivorous fish in the current range occupied by *Bythotrephes* (as well as within their projected range of expansion, MacIsaac et al. 2004). We sought out literature that characterized the diets of lake herring exposed to various zooplankton communities (Coulas et al. 1998; Johnson et al. 2004; Trippel and Beamish 1993; Vander Zanden and Rasmussen 1996). These studies indicated some general trends: lake herring tended to select positively for large cladoceran species (e.g., *Daphnia, Holopedium, Bythotrephes*); small cladocerans (e.g., *Bosmina*) and copepods (both calanoids and cyclopoids) were typically negatively or neutrally selected; copepod nauplii were effectively absent from diets; and *Mysis* can represent a highly variable proportion of diets. No estimates of herring selectivity for *Mysis* currently exist in the literature.

In order to characterize the proportion of zooplankton diet items in putative lake herring diets, we used estimates of selectivity indices (Chesson's $\alpha$, Table 2) from Coulas et al. (1998) who derived estimates for lake herring in Harp Lake, included in this study. Coulas et al. (1998) provide the most comprehensive and detailed account of lake herring feeding patterns currently in the published literature. Chesson's $\alpha$ was selected due to the availability of data, as well as the reported robustness of this index in cases where diet items may be absent (Chesson 1978). Thus, lacking information of similar detail for lake herring from uninvaded lakes, we felt confident in applying these same selectivity coefficients to herring in all lakes. We used the "overall" selectivity estimates from Coulas et al. (1998), which integrate seasonal selectivity estimates over the growing season, similar to the time frame captured by our mean annual estimates of zooplankton biomass. While there was generally overlap between zooplankton collections (typically May to October) with

**Table 2** Selectivity indices for lake herring diets used to determine the proportional contribution of herring diet items in the current study

| Zooplankton taxa | Selectivity index |
|---|---|
| Large cladocerans | 0.1 |
| Small cladocerans | 0.001 |
| *Bythotrephes* | 0.85 |
| *Holopedium* | 0.03 |
| Calanoids | 0.004 |
| Cyclopoids | 0.015 |

Selectivity indices were estimated from means over all seasons reported in Coulas et al. (1998), Fig. 6a. Taxonomic definitions in Coulas et al. (1998) correspond to those above in the following manner: *Daphnia* = large cladocerans; *Bosmina* = small cladocerans. All other taxa correspond directly

lake herring collections (June to October) reported in Coulas et al. (1998), differences in the frequency of sampling and temporal overlap among zooplankton collections from the various data sources and estimates of lake herring feeding from our single lake study (Coulas et al. 1998) did not permit lake herring diet estimates on a seasonal basis within each lake and time period.

Assuming that depletion of resources in the environment does not occur (a reasonable assumption in the case of fish foraging on zooplankton in a lake), Chesson's $\alpha$ can be described as:

$$\alpha_i = \frac{w_i/n_i}{\sum_{k=1}^{L} w_k/n_k} \tag{2}$$

where $i = 1, \ldots, L$, such that

$$\sum_{i=1}^{L} \alpha_i = 1 \tag{3}$$

where $\alpha_i$ is the selectivity index of a consumer for prey type $i$, $w_i$ is the quantity of prey $i$ in the consumers diet, $n_i$ is the quantity of prey $i$ in the environment, with $L$ prey types of interest (Chesson 1978, 1983; Vanderploeg and Scavia 1979; note that notation has been changed from the original sources so as to be consistent with Eq. 1). Similarly, $\alpha_i$ can be obtained where $w_i$ and $n_i$ represent proportions (rather than quantities) of prey type $i$ in the diet and environment, respectively (Chesson, 1978); proportions are used in the current study. Selectivity indices used are assumed to be constant and similar among lakes.

From Eq. 2, it can be shown that the ratio of the proportions in the diet of a consumer for two prey species, $j$ and $m$, can be expressed as:

$$w_j/w_m = (\alpha_j/\alpha_m)(n_j/n_m) \tag{4}$$

where all estimates besides $w$ are known quantities; $\alpha$ from Table 2, and $n$ from lake sampling data. Eq. 4, combined with the constraint from Eq. 1 that:

$$w_1 + w_2 + \cdots + w_L = 1 \tag{5}$$

permits the estimation of any $w$, by expressing each of the remaining $w_i$ in terms of the $w$ of interest. Thus, for $w_I$:

$$w_1 = 1 - \{[(\alpha_2/\alpha_1)\cdot(n_2/n_1)]\cdot w_1\} - \cdots - \{[(\alpha_L/\alpha_1)\cdot(n_L/n_1)]\cdot w_1\} \tag{6}$$

From Eq. 6, $w_1$ can be easily obtained, where all $\alpha$ and $n$ are known. The value for $w_1$ is then included in Eq. 5 for the estimation of the next $w_i$, and so on, until all $w_i$ are determined. Lake herring diet proportions for all prey items in a particular lake and time period were solved in this manner. Estimated diet proportions of zooplankton in lake herring diets and zooplankton TP (Supplementary Material 1) were then applied to Eq. 1 to estimate lake herring trophic position.

To address variability in the importance of *Mysis* in lake herring diets, and lacking lake herring selectivity indices for *Mysis* or methodologically comparable *Mysis* abundance data for most of our lakes and time periods, we modelled lake herring TP under two alternative scenarios; one where *Mysis* contributed a significant proportion of herring diets (30%, Table 2) and one where *Mysis* were of little importance to herring diets (5%). These were chosen as reasonable estimates of *Mysis* contributions to lake herring diets based on literature values reported elsewhere (Johnson et al. 2004; Trippel and Beamish 1993; Vander Zanden and Rasmussen 1996). In these cases, the appropriate proportion in the diet for *Mysis* (0.05 or 0.3) was inserted into equation 5, prior to the estimation of all other $w_i$. Lake herring TP was then estimated from each scenario of these diet proportions using Eq. 1 (Supplementary Material 2).

## Statistical analysis

To assess how changes in zooplankton community composition influenced observed changes in zooplankton TP, we applied principal coordinates analysis (PCoA) on chord distances (Orlóci 1967) of both historical and contemporary zooplankton communities. Chord distance was selected because it reflects differences in relative abundance of the various taxa being compared (Legendre and Legendre 1998). Zooplankton species were assigned to functional groups following Sprules 1984; (Supplementary Material 1). As with estimates of mean zooplankton TP, rare taxa and juveniles were excluded. We standardized functional group biomass to *Z*-scores to account for differences among study protocols. We used PCoA to generate biplots showing temporal changes in the positions of zooplankton communities among lakes where *Bythotrephes* invaded and *Mysis* were present, lakes where *Bythotrephes* invaded and *Mysis* were absent, and non-invaded reference lakes. Temporal changes were represented on biplots by arrows, which indicate the direction that zooplankton communities in each lake shifted between historical and contemporary samples. Biplots generated from PCoA were nearly identical to those generated using an alternative method (non-metric multidimensional scaling on the first 5 dimensions), but because the former is based on eigenanalysis, it can provide additional information on correlations between species and sites that were not available through other methods of determination. Thus, results from the PCoA are presented here. Further, we compared distance measures of zooplankton communities between time periods (i.e., distances in multidimensional taxonomic space between historical and contemporary scores for each lake) among the three classifications of lakes using one-way analysis of variance (ANOVA).

Mean change in zooplankton TPs and putative lake herring TPs (contemporary − historical) among lake types were compared using two-sample *t* tests (using a Welch correction for degrees of freedom where appropriate, two-tailed hypotheses) and one-way ANOVA followed by Tukey's Highly Significant Difference (HSD) test. Single-factor *t*-tests were also used to determine if changes in TP were different from zero. Where appropriate, assumptions regarding normality and homogeneous variance were evaluated. In cases where these assumptions were violated (ANOVAs comparing changes in lake herring TP), we used a nonparametric Kruskal–Wallis (KW) test followed by a Tukey-type multiple comparison test on the mean rank sums (Zar 1999, eq 11.26, 11.27).

Lake morphology and water chemistry was compared among lake types using a nonparametric Kruskal-Walis (KW) test. All analyses were performed using R (R Development Core Team 2008). Chord distance was estimated using the R library *vegan* and ordination was performed using the R library *BiodiversityR*.

## Results

### Zooplankton community trophic position

The mean temporal change in TP of zooplankton communities from *Bythotrephes*-invaded lakes was significantly greater and in the opposite direction compared to non-invaded reference communities (mean increase in invaded lakes, 0.18; reference lakes, −0.06; $t_{14.9} = 5.31$, $P < 0.0001$). While the mean TP of all invaded zooplankton communities increased (*t* test of mean TP change = 0: $t_{10} = 4.60$, $P = 0.001$), TP of reference communities decreased over the same time period (*t* test of mean TP change = 0: $t_7 = -2.65$, $P = 0.03$). This pattern was not due solely to the inclusion of *Bythotrephes* in invaded zooplankton communities, but rather reflected changes in the zooplankton community as a whole following *Bythotrephes* invasion; excluding *Bythotrephes* from TP estimates, the pattern of significantly greater TP in invaded communities persisted (difference between invaded and reference lakes: $t_{14.2} = 4.60$, $P = 0.0004$; *t* test of mean TP change in invaded lakes excluding *Bythotrephes* = 0: $t_{10} = 3.82$, $P = 0.003$; mean increase = 0.16).

A closer examination of the data revealed a significant impact of the presence of *Mysis* on temporal patterns in mean zooplankton TP ($F_{2,16} = 23.9$, $P < 0.0001$; Fig. 1). Mean zooplankton TP was higher in invaded *Mysis* lakes than either reference lakes (Tukey's HSD, $P < 0.0001$) or invaded non-*Mysis* lakes (Tukey's HSD, $P < 0.01$), but invaded non-*Mysis* lakes and reference lakes were not significantly different (Tukey's HSD, $P > 0.05$; Fig. 1). In *Bythotrephes* invaded lakes, mean zooplankton TP increased in the presence of *Mysis* (*t* test of mean TP change = 0: $t_7 = 6.10$, $P = 0.0004$, mean increase = 0.23), but did not change when *Mysis* were absent (*t* test of mean TP change = 0: $t_2 = 1.19$, $P > 0.05$; mean increase = 0.04; Fig. 1).

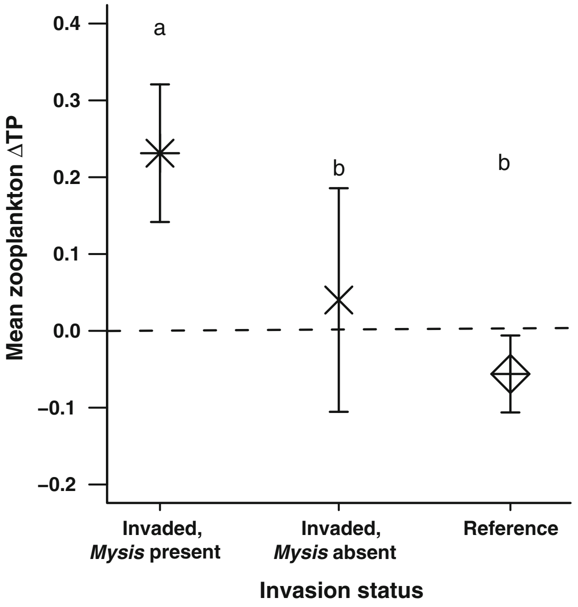

**Fig. 1** Mean (±95% CI's) temporal change in zooplankton community-wide trophic position (TP) in lakes invaded by *Bythotrephes* with and without *Mysis*, relative to non-invaded reference lakes. *Common letters* indicate that means are not significantly different (Tukey's Honestly Significant Difference test)

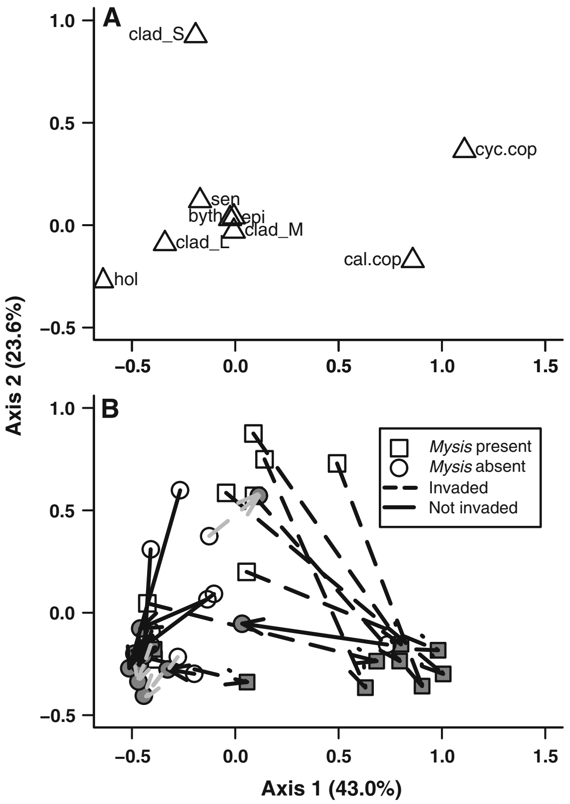

**Fig. 2** Biplot of site and functional group scores on the first two axes from principal coordinates analysis of chord distances among historical and contemporary zooplankton communities. Percentages next to axis labels indicate % variance explained on each. *Open symbols* are historical zooplankton communities, *shaded symbols* are contemporary. *Arrows* indicate directional change of zooplankton community position in taxonomic multidimensional space from historical to contemporary time periods for each lake examined (one *arrow* per lake). Panel **a** shows functional group scores, and panel **b** shows temporal patterns of change among sites (information in panels **a** and **b** separated for clarity). *Grey-shaded arrows* in Panel **b** are *Bythotrephes* invaded lakes without *Mysis*. *Abbreviations: clad_S* = small cladocerans, *clad_M* = mid-sized cladocerans, *clad_L* = large cladocerans, *cyc.cop* = cyclopoid copepods, *cal.cop* = calanoid copepods, *sen* = *Senecella calanoides* (grazer calanoid copepod), *epi* = *Epischura lacustris* (predatory calanoid copepod), *hol* = *Holopedium glacialis* (large gelatinous cladoceran), and *byth* = *Bythotrephes longimanus* (predatory cladoceran)

Principal coordinates analysis explained 66.6% of the total variation in zooplankton communities on the first two axes (Fig. 2). Following *Bythotrephes* invasion, lakes with *Mysis* shifted dramatically along the first two axes, away from cladoceran functional groups and towards communities where calanoid copepods were a greater proportion of the biomass (Fig. 2). On average, cladoceran biomass in *Mysis* lakes declined by 47% following *Bythotrephes* invasion (±1 standard error = 7%; $t$ test, mean = 0: $t_7 = -6.50$, $P = 0.0003$; 49% ± 7% excluding *Bythotrephes*). In contrast, reference lakes showed very little movement on the first axis between historical and contemporary communities, instead shifting along axis 2 towards a greater biomass of large cladocerans and *Holopedium* (Fig. 2). Cladoceran biomass increased in reference lakes on average by 10% (±4%; $t$ test, mean = 0: $t_7 = 2.60$, $P = 0.035$). Invaded lakes without *Mysis* were less consistent; following *Bythotrephes* invasion, zooplankton communities in two lakes shifted in the same direction as reference lakes, while one shifted along axis 1 and 2 towards cyclopoid copepods (Fig. 2). Temporal changes in the proportion of cladoceran biomass from invaded lakes without *Mysis* were not different from zero ($t$ test: $t_2 = 0.76$, $P > 0.05$).

An examination of the mean chord distances from historical to contemporary zooplankton community site scores revealed differences among invaded and non-invaded lakes (ANOVA: $F_{2,16} = 22.8$, $P < 0.0001$,

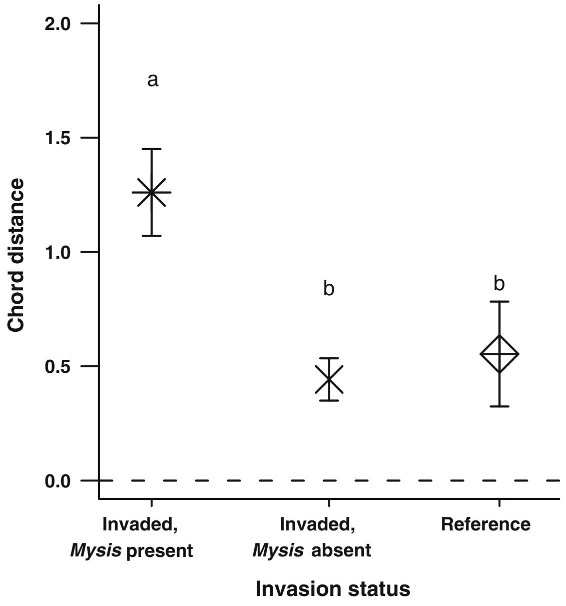

**Fig. 3** Comparison of mean chord distances (±95% CI's) paired by time for zooplankton communities in lakes invaded by *Bythotrephes* with and without *Mysis*, relative to non-invaded reference lakes. *Common letters* indicate that means are not significantly different (Tukey's Honestly Significant Difference test)

Fig. 3). The greatest shift in zooplankton community structure occurred among *Mysis* lakes that were also invaded by *Bythotrephes*, which were significantly different from reference lakes (Tukey's HSD: $P = 0.0002$) and invaded non-*Mysis* lakes (Tukey's HSD: $P < 0.0001$). The degree of temporal change in zooplankton communities (measured via chord distance) in reference lakes was not different from invaded lakes without *Mysis* (Tukey's HSD: $P > 0.05$; Fig. 3). The zooplankton communities in all lakes changed significantly over time, as 95% confidence intervals around mean estimates of chord distance did not include 0 (0 indicating no community change over time; Fig. 3).

## Lake herring trophic position

Estimated change in lake herring TP following *Bythotrephes* invasion differed between invaded and reference lakes, and patterns were similar for both low (5%) and high (30%) estimates of importance of *Mysis* in the diet (low *Mysis* KW test: $X_2^2 = 8.86$, $P = 0.01$; high *Mysis* KW test: $X_2^2 = 10.92$, $P = 0.004$, Fig. 4). Increases in lake herring TP were significant (low *Mysis*, *t* test, mean = 0: $t_7 = 3.4$, $P = 0.01$, mean increase = 0.31; high *Mysis*, *t*-test, mean = 0: $t_7 = 3.6$, $P = 0.009$, mean increase = 0.24), and lake herring TP was significantly higher in *Mysis* lakes relative to reference

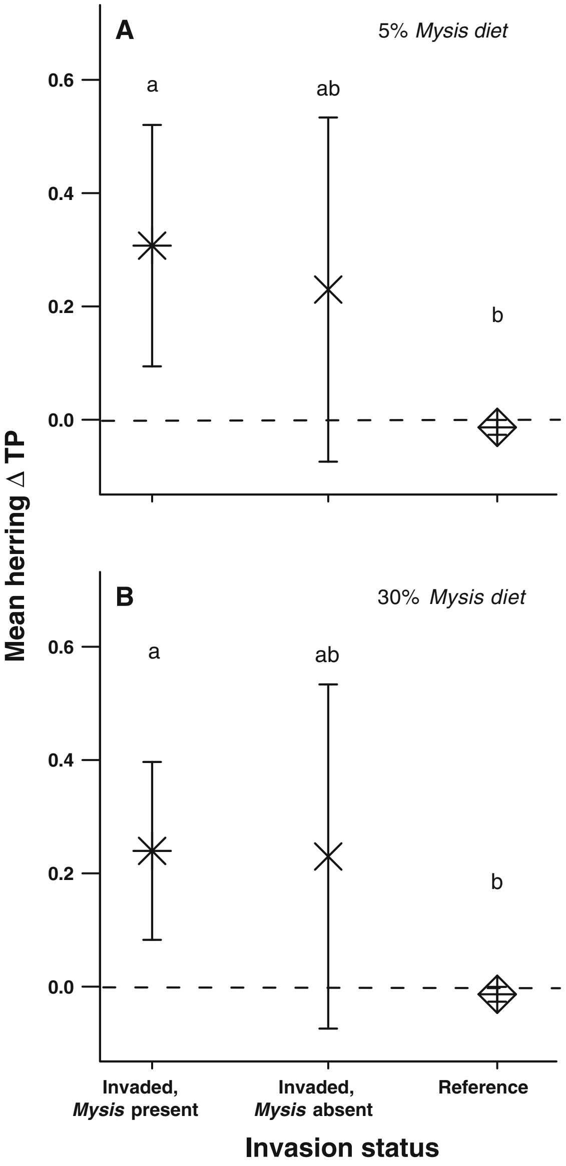

**Fig. 4** Mean (±95% CI's) temporal change in lake herring trophic position (TP) in lakes invaded by *Bythotrephes* with and without *Mysis*, relative to non-invaded reference lakes.**a** shows herring TP estimates where *Mysis* are a small proportion of the diet (5%).**b** shows lake herring TP estimates where *Mysis* are a large proportion of the diet (30%). *Common letters* indicate that means are not significantly different (Tukey-type comparisons of mean ranks, see text for details)

lakes (low *Mysis*, $Q = 2.71$, $Q_{0.05,3} = 2.394$, Fig. 4a; high *Mysis*, $Q = 3.02$, $Q_{0.05,3} = 2.394$, Fig. 4b). Increases in lake herring TP for invaded lakes without *Mysis* were only marginally non-significant ($t$ test, mean = 0: $t_2 = 3.25$; $P = 0.08$, mean increase = 0.23) and were intermediate to those with *Mysis* (low *Mysis*, $Q = 0.14$; high *Mysis*, $Q = 0.13$) and reference lakes (low *Mysis*, $Q = 2.14$; high *Mysis*, $Q = 2.36$, Fig. 4a,b). Estimated change in herring TP from reference lakes was significantly different from zero, and in the opposite direction of invaded lakes ($t$ test, mean = 0: $t_7 = -2.45$, $P = 0.04$, mean decrease = −0.014; Fig. 4). Interestingly, the mean increase in estimated lake herring TP was significantly lower when the importance of *Mysis* in diets was high compared to when it was low (paired $t$ test: $t_7 = 2.9$, $P = 0.02$).

### Lake attributes

Lake morphology was not different for most measures of physical and chemical descriptors (lake area, maximum depth, total phosphorous; Table 1, all $P > 0.05$). DOC tended to be very slightly higher in lakes with *Mysis* compared with reference lakes, though differences were small, on the order of 1–2 mg/l (Table 1; $P = 0.01$).

## Discussion

*Bythotrephes* invasion increased the mean estimated TP of zooplankton communities and an important planktivore, lake herring. Our analysis clearly demonstrated that this increase in TP was not due solely to the inclusion of a novel invertebrate predator (i.e., *Bythotrephes*). Rather, the decline in cladoceran biomass (typically herbivorous) and increase in copepod biomass (more typically omnivorous/predatory) associated with *Bythotrephes* invasion resulted in an overall increase in TP among the zooplankton. This is consistent with other studies that have reported a significant increase in the TP of fish (young of the year Baltic herring, *Clupea harengus*) following the invasion of a mid-trophic predator (*Cercopagis pengoi*; Gorokhova et al. 2005).

While significant statistically, the temporal changes in TP associated with invasion were on the order of 1/4–1/5 of a trophic level, on average, for either the zooplankton community or lake herring. This is relatively small compared to estimates of trophic elevation resulting from cercopagid invasion reported elsewhere (4/5 of a trophic level, Gorokhova et al. 2005). Because of its correlation with TP, isotopic signatures of nitrogen ($\delta^{15}$N) are often employed in relationships to predict contaminants in fish (e.g., Cabana and Rasmussen 1994). To determine the effects that such a change might have on lake herring contaminant concentrations, we translated the changes in TP we observed into changes in $\delta^{15}$N (assuming a fractionation of 3.4‰ for one trophic level), and estimated the effects this would have on the Hg concentrations of lake herring based on a relationship of tissue Hg and $\delta^{15}$N for Lake Simcoe lake herring ($\mathrm{Hg} = 0.0324 * \delta^{15}\mathrm{N} - 0.3812$; $n = 24$, $R^2 = 0.25$; M. Rennie, *unpublished*). Using the mean lake herring $\delta^{15}$N signature of 14.4‰ as a point for comparison, an increase of 0.7–0.85‰ resulted in a 30% increase in herring Hg from 0.08 μg/g to 0.11 μg/g. As lake herring are a forage species not commonly sought after, we estimated putative Hg increases in lake trout (*Salvelinus namaycush*), a fish popular with anglers that also consumes lake herring. Using biomagnification factors of 2.0 (Cabana and Rasmussen 1994) and 4.0 (Vander Zanden and Rasmussen 1996), an increase of 0.03 μg/g in a forage fish species (lake herring) translates into an increase of 0.06–0.12 μg/g in their predators (lake trout). Based on a mean mercury concentration for lake trout of 0.65 μg/g (mean from "Class 3" lakes, Cabana et al. 1994), an increase between 0.06 and 0.12 μg/g represents an increase in the daily Hg intake of an adult consumer of these fish from 0.24 μg $\mathrm{kg}^{-1}$ to between 0.26 and 0.28 μg $\mathrm{kg}^{-1}$, representing a 5–10% increase relative to the Provisional Tolerable Daily Intake (PTDI = 0.47 μg $\mathrm{kg}^{-1}$ $\mathrm{day}^{-1}$, daily intake based on 22 g/day mean daily intake for a 60 kg individual; Health Canada 2007). Thus, cause for concern regarding the effects of these invaders on fish contaminant concentrations is warranted.

Hypotheses of elevated consumer contaminant concentrations resulting from mid-trophic species invasions are based on and supported by comparative studies (e.g., Vander Zanden and Rasmussen 1996), which can be subject to any number of uncontrolled variables representing differences in the systems being compared. In contrast, direct temporal evaluations of ecosystems invaded by mid-trophic species have failed to find evidence of elevated consumer contaminants following invasion. Johnston et al. (2003) show a non-significant trend of greater declines in predatory fish Hg from non-invaded lakes compared to those invaded by rainbow smelt. Two other studies have also reported declines or no significant change in consumer Hg following the invasion of mid-trophic species (Hogan et al. 2007; Rennie et al. 2010). Two of the aforementioned studies have invoked the concept of "growth dilution" as a possible explanation of their results (Hogan et al. 2007; Johnston et al. 2003), but without consideration to the mechanism behind this phenomenon, and without explicitly testing growth dilution as an explanation of their observations. Mechanistically, the concept of growth dilution can be thought of as a reduction in energy expenditures towards foraging that permits more growth in mass per unit of contaminant ingested (versus other prey that are foraged less efficiently). Of the aforementioned studies, only Hogan et al. (2007) documented increased consumer growth rates following invasion.

Changes in foraging efficiency of consumer species following mid-trophic invasion that reduce contaminant biomagnification rates (i.e., growth dilution) can provide an explanation for studies reporting no significant increase in consumer contaminants following invader establishment. Invasive mid-trophic species often have a higher $\delta^{15}$N or TP than traditional prey (Campbell et al. 2009; Swanson et al. 2003; Vander Zanden and Rasmussen 1996). Additionally, invasive mid-trophic species that achieve relatively high densities (like *Bythotrephes*) may be disproportionately favoured as prey by consumers (Coulas et al. 1998). The combined effect of more efficient foraging (resulting in "diluted" consumer contaminant concentrations) on abundant novel prey that have higher than average TP (and therefore $\delta^{15}$N) would act to make the slope of the relationship between Hg concentrations and TP ($\delta^{15}$N) in consumer species more shallow following invasion, thereby reducing estimates of contaminant biomagnification. Thus, a reasonable test of growth dilution would be to compare slopes of consumer contaminant and TP relationships and/or biomagnification factors before and after invasion; a decline in either following invasion supports a growth dilution hypothesis.

An increase in foraging efficiency may resolve the apparent conflict between the results of our study and that of recent work which found no significant difference in Hg concentrations of lake herring following *Bythotrephes* invasion, and further reported that temporal patterns in herring Hg from invaded lakes did not differ from those in reference lakes (Rennie et al. 2010). Other recent work has reported that growth rates of lake herring large enough to consume *Bythotrephes* are elevated in lakes where *Bythotrephes* have established (James 2010). This suggests that changes in the zooplankton community following *Bythotrephes* invasion may allow lake herring to forage more efficiently, thereby reducing biomagnification rates from prey to consumers (and therefore consumer Hg concentrations). Although *Bythotrephes* are a large prey item that may be foraged more efficiently by lake herring, the associated reduction in large-bodied cladocerans that has occurred following *Bythotrephes* invasion would be expected to have a negative impact on lake herring foraging efficiencies. Both *Bythotrephes* and large-bodied cladocerans are positively selected for by lake herring (Coulas et al. 1998; Johnson et al. 2004). How these two patterns (high abundance of *Bythotrephes*, reduction of other large-bodied cladocerans) ultimately interact to adjust lake herring foraging efficiency and growth is not immediately clear. More detailed work on lake herring feeding, growth patterns and biomagnification rates before and after *Bythotrephes* invasion (as outlined above) could help to resolve this issue.

*Bythotrephes* invasion had the most significant effects on lakes with *Mysis*. Comparable changes in the community structure and TP of zooplankton communities (and TP of lake herring) were less pronounced in the absence of *Mysis*. Based on our data alone, it is difficult to assess whether this is suggestive of a synergistic interaction between *Bythotrephes* and *Mysis* on zooplankton communities, or simply a reflection of a small sample size and resulting lack of statistical power. Studies have shown that lakes with *Mysis* typically have a reduced proportional biomass of cladoceran species compared to lakes without *Mysis* (Almond et al. 1996; Nero and Sprules 1986). *Bythotrephes* preferentially feed on cladocerans (Schulz and Yurista 1998), and their invasion has frequently been observed to lead to dramatic reductions in cladoceran biomass when *Mysis* are also present (e.g., Barbiero and Tuchman

2004). Nordin et al. (2007) found evidence of significant competition between *Mysis* and *Bythotrephes* for zooplankton prey in invaded lakes. However, *Bythotrephes* is primarily an epilimnetic predator in the geographic region under study (Young and Yan 2008). Therefore, the absence of the hypolimnetic predator *Mysis* may allow crustacean zooplankton to use the hypolimnion as a refuge from predation. In contrast, prey refuge may be highly limited in lakes where *Bythotrephes* and *Mysis* coexist. Experimental observations have demonstrated that *Bythotrephes* can induce migration of zooplankton away from warmer epilimnetic to colder, darker hypolimnetic waters (Pangle and Peacor 2006), which can ultimately lead to reduced population growth rates (Pangle et al. 2007). Our observations warrant further investigation into how the existing macrozooplankton community structure can affect *Bythotrephes* invasion impacts on zooplankton communities.

Time since invasion can be an important determinant of the ecosystem effects of non-indigenous species like *Bythotrephes*. For all three of our invaded lakes without *Mysis*, the first report of *Bythotrephes* is from the post-invasion survey data used in this study; these lakes are not subject to regular monitoring, and the post-invasion surveys reported here represent the first time these lakes had been sampled since the pre-invasion survey. However, this was also the case for nearly half of our invaded lakes with *Mysis* (Table 1). If the *Bythotrephes* invasion in our non-*Mysis* lakes was very recent compared to our invaded lakes with *Mysis*, then the minor changes in invaded non-*Mysis* lakes relative to invaded *Mysis* lakes might be due more to a lag in response to invasion, rather than of minor effects of *Bythotrephes* on zooplankton communities without *Mysis*. This scenario is impossible to verify due to a lack of regular monitoring data. However, large lakes that are subject to more regular monitoring, and in close proximity to our invaded non-*Mysis* lakes were reported as invaded 4–5 years prior to these surveys. Canoe traffic is high between these larger lakes and these invaded lakes (M. Palmer, *personal observation*). It is therefore likely that our invaded non-*Mysis* lakes have been invaded for up to 4 or 5 years. This is comparable to the mean time between reported invasion and post-invasion surveys from our invaded lakes with *Mysis* (5 years).

A greater importance of *Mysis* in lake herring diets may mitigate the impact of *Bythotrephes* invasion on the degree of change in lake herring trophic position. Overall, an increase in the proportion of *Mysis* in lake herring diets from 5% to 30% in either time period resulted in an increase of 1/5 of a trophic position for lake herring (Supplementary Material 2). However, the average temporal increase in trophic position following *Bythotrephes* invasion was actually lower by 0.06 of a trophic level under a scenario of high *Mysis* consumption by herring (30%) compared to low *Mysis* consumption (5%). While significant statistically, this small difference may not be biologically meaningful. When converted to units of $\delta^{15}$N, this translates into 0.2‰, which is below typical analytical error (0.3‰) for most mass spectrometers analyzing nitrogen isotopes and would likely go undetected using isotopic methods of evaluating TP.

Our study does not account for potential changes in zooplankton diets or feeding preference functions for lake herring resulting from ecosystem change associated with *Bythotrephes* establishment. Other experimental studies have reported that *Bythotrephes* introductions may cause a weak trophic cascade, reducing zooplankton biomass and increasing phytoplankton production (Strecker and Arnott 2008). Reduced zooplankton and increased algal production could lead to omnivorous copepods and *Mysis* relying more on algal production, reducing their TP. Thus, actual changes in zooplankton community and lake herring TP might be more conservative than those estimated here. This could be evaluated directly by examining stability in $\delta^{15}$N signatures of omnivorous zooplankton before and after invasion.

To evaluate this possibility, and lacking data on the plasticity of our omnivorous zooplankters to increases in algal densities, we arbitrarily adjusted the algal fraction of contemporary zooplankton diets from invaded lakes (reported in Supplementary Material 1) to increase up to 20% with an equal associated decrease in heterotrophs (e.g., prey with TP $\geq$ 1). Under this scenario, the mean TP of the zooplankton community still increased significantly following *Bythotrephes* invasion, but only slightly (mean TP increase = 0.016 overall; $t_{17.0} = 2.18$, $P = 0.04$; 0.033 in *Mysis* lakes). In contrast to the assumption of fixed zooplankton diets following *Bythotrephes* invasion, the increase in herring TP we observed was significant only when the proportion of *Mysis* in herring diets was low (KW test, 5% *Mysis* in diets, $P = 0.018$; 30% *Mysis*, $P = 0.1$). Thus, an increase of up to 20% in the algal fractions of omnivorous zooplankton diets did mitigate TP increases in herring when the proportion of *Mysis* in herring diets was high, but not enough to cause a *decline* in herring TP. No change in TP would explain the failure to detect changes in Hg concentrations following mid-trophic invasions (e.g. Rennie et al. 2010). However, no change in TP combined with a decline in Hg concentrations following a mid-trophic invasion (e.g., Hogan et al. 2007) still requires explanation through some additional variable such as increased foraging efficiency of consumers.

We had no information available for zooplankton communities in *Mysis* lakes not invaded by *Bythotrephes* from our area of study to include as a second reference group. However, we do not believe that the absence of *Mysis* from our control lakes eliminates their utility as a reference for changes due to *Bythotrephes* invasion. The magnitude of change for both TP and community composition in our reference lakes was small, and in the opposite direction of those invaded by *Bythotrephes*, with or without *Mysis*. Published data from other lakes on the Canadian Shield in Ontario show that the crustacean zooplankton communities in unmanipulated lakes with *Mysis* have been stable over a similar time period. Unmanipulated reference lakes (Lakes 239, 373 and 442) at the Experimental Lakes Area support *Mysis,* and have shown no remarkable deviations from the long-term record in community composition over time like the 50% declines in cladoceran abundance observed in our invaded *Mysis* lakes (Findlay et al. 2005; Paterson et al. 2010). An examination of the data from Table 1 in Findlay et al. (2005) suggests at most a 10% decline in total cladoceran abundance in Lake 239, well shy of the trends observed in our *Mysis* lakes invaded with *Bythotrephes*. Community composition appears to have been comparatively more stable in lakes 373 and 442 (Paterson et al. 2010). Furthermore, a broad examination of unmanipulated North American lakes (with and without *Mysis*) demonstrated that regional variance far outweighed within-lake temporal variance (Rusak et al. 2002). More widespread regional changes that have been shown to affect zooplankton communities (specifically cladocerans) include lakes with and without *Mysis*; recent studies examining calcium declines (Jeziorski et al. 2008) and recovery from acidification (Yan et al. 2008) show no indication that lakes that support *Mysis* have responded any differently to these changes than lakes without *Mysis*. Furthermore, the lakes in our study were not significantly different among treatments with regards to lake area, maximum depth or total phosphorous concentrations. While we did detect significant differences in DOC, those differences were small, on the order of 2 mg/l. Higher DOC concentrations could potentially mitigate increased negative effects of ultraviolet radiation (Rautio and Tartarotti 2010; Williamson et al. 2001), assuming that UVR was increasing in our study region. However, such an effect would be opposite our results; our invaded lakes with *Mysis* had the highest DOC concentrations, which would make them least susceptible to UVR, and our reference lakes most susceptible. While it is clear that the presence of *Mysis* had an amplifying effect on changes in our invaded lakes, we believe the sum of the evidence presented here suggests that it was the effect of *Bythotrephes* on plankton communities that was amplified, rather than some independent factor.

In conclusion, we have provided strong evidence that the invasion of mid-trophic species, like *Bythotrephes*, has the capacity to increase the TPs of zooplankton communities and the fishes that prey upon them. Further, we showed that an increase of only 1/5 of a trophic level in lake herring (estimated as a result of *Bythotrephes* invasion) has the capacity to sufficiently increase contaminant burdens of consumer fish, to the point that daily intake limits of game fish for human consumption are affected. Based on these findings, we believe that the failure of previous studies to detect significant increases in consumer contaminant burdens following mid-trophic species invasions suggests two possible mechanisms at work: (1) increased foraging and growth efficiencies of consumers following mid-trophic species invasion, resulting in a decrease in contaminant biomagnification following invader establishment, or (2) changes in the feeding habits of omnivorous prey towards a greater degree of autotrophy following mid-trophic species invasion. The identification of these potential mechanisms regulating contaminant concentrations in invaded freshwater ecosystems provides testable hypotheses for future empirical study.

**Acknowledgments** We thank Bill Taylor for providing zooplankton biomass estimates from Jane Almond's thesis. Jake La Rose and the Lake Simcoe Fisheries Assessment Unit

(Ontario Ministry of Natural Resources) provided herring collections and funding for Hg and isotope determinations. Thanks also to Norm Yan for early discussions around this work and for organizing the workshops that ultimately led to this study, Bill Keller for providing access to the historical zooplankton data and Shelley Arnott for financial support and guidance. Scott Peacor and two anonymous reviewers provided helpful and constructive feedback on earlier drafts that improved the manuscript. This work was supported in part by Natural Sciences and Engineering Research Council of Canada (NSERC) Graduate scholarships to MDR, ALS and MEP, and by Ontario Graduate and York University graduate scholarships to MEP.

## References

Adams SM, Kimmel BL, Ploskey GR (1983) Sources of organic-matter for reservoir fish production: a trophic-dynamics analysis. Can J Fish Aquat Sci 40:1480–1495

Almond MJR, Bentzen E, Taylor WD (1996) Size structure and species composition of plankton communities in deep Ontario lakes with and without *Mysis relicta* and planktivorous fish. Can J Fish Aquat Sci 53:315–325

Audzijonyte A, Väinölä R (2005) Diversity and distributions of circumpolar fresh- and brackish-water *Mysis* (Crustacea : Mysida): descriptions of *M. relicta* Loven, 1862, *M. salemaai* n. sp., *M. segerstralei* n. sp and *M. diluviana* n. sp., based on molecular and morphological characters. Hydrobiologia 544:89–141

Barbiero RP, Tuchman ML (2004) Changes in the crustacean communities of Lakes Michigan, Huron and Erie following the invasion of the predatory cladoceran Bythotrephes longimanus. Can J Fish Aquat Sci 61:2111–2125

Boudreau SA, Yan ND (2003) The differing crustacean zooplankton communities of Canadian Shield lakes with and without the nonindigenous zooplanktivore Bythotrephes longimanus. Can J Fish Aquat Sci 60:1307–1313

Cabana G, Rasmussen JB (1994) Modeling food-chain structure and contaminant bioaccumulation using stable nitrogen isotopes. Nature 372:255–257

Cabana G, Tremblay A, Kalff J, Rasmussen JB (1994) Pelagic food-chain structure in Ontario lakes: a determinant of mercury levels in lake trout (*Salvelinus namaycush*). Can J Fish Aquat Sci 51:381–389

Campbell LM, Thacker R, Barton D, Muir DCG, Greenwood D, Hecky RE (2009) Re-engineering the eastern Lake Erie littoral food web: the trophic function of non-indigenous Ponto-Caspian species. J Great Lakes Res 35:224–231

Chesson J (1978) Measuring preference in selective predation. Ecology 59:211–215

Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. Ecology 64: 1297–1304

Coulas RA, MacIsaac HJ, Dunlop W (1998) Selective predation on an introduced zooplankter (*Bythotrephes cederstroemi*) by lake herring (*Coregonus artedii*) in Harp Lake, Ontario. Freshwat Biol 40:343–355

Fernandez RJ, Rennie MD, Sprules WG (2009) Changes in nearshore zooplankton associated with species invasions and potential effects on larval lake whitefish (*Coregonus clupeaformis*). Int Rev Hydrobiol 94:226–243

Findlay DL, Vanni MJ, Paterson M, Mills KH, Kasian SEM, Findlay WJ, Salki AG (2005) Dynamics of a boreal lake ecosystem during a long-term manipulation of top predators. Ecosystems 8:603–618

Foster SE, Sprules WG (2009) Effects of the *Bythotrephes* invasion on native predatory invertebrates. Limnol Oceanogr 54:757–769

Girard RE, Clark BJ, Yan ND, Reid RA, David SM, Ingram RG and Findeis JG (2007) History of chemical, physical and biological methods, sample locations and lake morphometry for the Dorset Environmental Science Centre (1973–2006). Ontario ministry of the environment technical report

Gorokhova E, Hansson S, Hoglander H, Andersen CM (2005) Stable isotopes show food web changes after invasion by the predatory cladoceran *Cercopagis pengoi* in a Baltic Sea bay. Oecologia 143:251–259

Health Canada (2007) Human health risk assessment of mercury in fish and health benefits of fish consumption. Available from http://hc-sc.gc.ca/fn-an/pubs/mercur/merc_fish_poisson_e.html. Accessed June 2010

Hogan LS, Marschall E, Folt C, Stein RA (2007) How non-native species in Lake Erie influence trophic transfer of mercury and lead to top predators. J Great Lakes Res 33:46–61

James LAH (2010) The effect of the invasive macroinvertebrate, *Bythotrephes longimanus*, on cisco (*Coregonus artedii*) in Ontario shield lakes, Queen's University, Kingston

Jeziorski A, Yan ND, Paterson AM, DeSellas AM, Turner MA, Jeffries DS, Keller B, Weeber RC, McNicol DK, Palmer ME, McIver K, Arseneau K, Ginn BK, Cumming BF, Smol JP (2008) The widespread threat of calcium decline in fresh waters. Science 322:1374–1377

Johnson TB, Brown WP, Corry TD, Hoff MH, Scharold JV, Trebitz AS (2004) Lake herring (*Coregonus artedi*) and rainbow smelt (*Osmerus mordax*) diets in western Lake Superior. J Great Lakes Res 30:407–413

Johnston TA, Leggett WC, Bodaly RA, Swanson HK (2003) Temporal changes in mercury bioaccumulation by predatory fishes of boreal lakes following the invasion of an exotic forage fish. Environ Toxicol Chem 22:2057–2062

Lasenby DC, Northcote TG, Furst M (1986) Theory, practice, and effects of *Mysis relicta* introductions to north-american and Scandinavian lakes. Can J Fish Aquat Sci 43: 1277–1284

Legendre P, Legendre L (1998) Numerical ecology. Elsevier Science B. V, Amsterdam

MacIsaac HJ, Borbely JVM, Muirhead JR, Graniero PA (2004) Backcasting and forecasting biological invasions of inland lakes. Ecol Appl 14:773–783

Martin NV, Chapman LJ (1965) Distribution of certain crustaceans and fishes in region of Algonquin Park, Ontario. J Fish Res Board Can 22:969–976

Mills EL, Ogorman R, Degisi J, Heberger RF, House RA (1992) Food of the alewife (*Alosa pseudoharengus*) in Lake Ontario before and after the establishment of

*Bythotrephes cederstroemi*. Can J Fish Aquat Sci 49: 2009–2019

Nero RW, Sprules WG (1986) Zooplankton species abundance and biomass in relation to occurrence of *Mysis relicta* (malacostraca, mysidacea). Can J Fish Aquat Sci 43: 420–434

Orlóci L (1967) An agglomerative method for classification of plant communities. J Ecol 55:193

Pangle KL, Peacor SD (2006) Non-lethal effect of the invasive predator *Bythotrephes longimanus* on *Daphnia mendotae*. Freshwat Biol 51:1070–1078

Pangle KL, Peacor SD, Johannsson OE (2007) Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. Ecology 88:402–412

Parker Stetter SL, Witzel LD, Rudstam LG, Einhouse DW, Mills EL (2005) Energetic consequences of diet shifts in Lake Erie rainbow smelt (*Osmerus mordax*). Can J Fish Aquat Sci 62:145–152

Paterson MJ, Podemski CL, Findlay WJ, Findlay DL, Salki AG (2010) The response of zooplankton in a whole-lake experiment on the effects of a cage aquaculture operation for rainbow trout (*Oncorhynchus mykiss*). Can J Fish Aquat Sci 67:1852–1861

Post DM, Takimoto G (2007) Proximate structural mechanisms for variation in food-chain length. Oikos 116:775–782

Prest VK, Douglas RJW (1969) Quaternary geology of Canada. Geology and economic minerals of Canada. Queen's Printer, Geological Survey of Canada, Ottawa, pp 676–764

Rasmussen JB, Rowan DJ, Lean DRS, Carey JH (1990) Food-chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. Can J Fish Aquat Sci 47:2030–2038

Rautio M, Tartarotti B (2010) UV radiation and freshwater zooplankton: damage, protection and recovery. Freshwater Rev 3:105–131

R Development Core Team (2008) R: a language and environment for statistical computing. Retrieved from http://www.R-project.org on May 21 2010

Rennie MD, Sprules WG, Vaillancourt A (2010) Changes in fish condition and mercury vary by region, not *Bythotrephes* invasion: a result of climate change? Ecography 33:471–482

Rusak JA, Yan ND, Somers KM, Cottingham KL, Micheli F, Carpenter SR, Frost TM, Paterson MJ, McQueen DJ (2002) Temporal, spatial and taxonomic patterns of crustacean zooplankton variability in unmanipulated north-temperate lakes. Limnol Oceanogr 47:613–625

Schulz KL, Yurista PM (1998) Implications of an invertebrate predator's (*Bythotrephes cederstroemi*) atypical effects on a pelagic zooplankton community. Hydrobiologia 380: 179–193

Sprules WG (1984) Towards an optimal classification of zooplankton for lake ecosystem studies. Verh Internat Verein Limnol 22:320–325

Strecker AL, Arnott SE (2008) Invasive predator, *Bythotrephes*, has varied effects on ecosystem function in freshwater lakes. Ecosystems 11:490–503

Strecker AL, Arnott SE, Yan ND, Girard R (2006) Variation in the response of crustacean zooplankton species richness and composition to the invasive predator Bythotrephes longimanus. Can J Fish Aquat Sci 63:2126–2136

Swanson HK, Johnston TA, Leggett WC, Bodaly RA, Doucett RR, Cunjak RA (2003) Trophic positions and mercury bioaccumulation in rainbow smelt (*Osmerus mordax*) and native forage fishes in northwestern Ontario lakes. Ecosystems 6:289–299

Trippel EA, Beamish FWH (1993) Multiple trophic level structuring in salvelinus coregonus assemblages in boreal forest lakes. Can J Fish Aquat Sci 50:1442–1455

Vander Zanden MJ, Rasmussen JB (1996) A trophic position model of pelagic food webs: Impact on contaminant bioaccumulation in lake trout. Ecol Monogr 66:451–477

Vanderploeg HA, Scavia D (1979) Two electivity indices for feeding with special reference to zooplankton grazing. J Fish Res Board Can 36:362–365

Williamson CE, Olson OG, Lott SE, Walker ND, Engstrom DR, Hargreaves BR (2001) Ultraviolet radiation and zooplankton community structure following deglaciation in Glacier Bay, Alaska. Ecology 82:1748–1760

Yan ND, Pawson TW (1997) Changes in the crustacean zooplankton community of Harp Lake, Canada, following invasion by Bythotrephes cederstroemi. Freshwat Biol 37:409–425

Yan ND, Pawson TW (1998) Seasonal variation in the size and abundance of the invading Bythotrephes in Harp Lake, Ontario, Canada. Hydrobiologia 361:157–168

Yan ND, Keller W, Somers KM, Pawson TW, Girard RE (1996) Recovery of crustacean zooplankton communities from acid and metal contamination: comparing manipulated and reference lakes. Can J Fish Aquat Sci 53:1301–1327

Yan ND, Girard R, Boudreau S (2002) An introduced invertebrate predator (*Bythotrephes*) reduces zooplankton species richness. Ecol Lett 5:481–485

Yan ND, Somers KM, Girard RE, Paterson AM, Keller W, Ramcharan CW, Rusak JA, Ingram R, Morgan GE, Gunn JM (2008) Long-term trends in zooplankton of Dorset, Ontario, lakes: the probable interactive effects of changes in pH, total phosphorus, dissolved organic carbon, and predators. Can J Fish Aquat Sci 65:862–877

Young JD, Yan ND (2008) Modification of the diel vertical migration of *Bythotrephes longimanus* by the cold-water planktivore, *Coregonus artedi*. Freshwat Biol 53:981–995

Zar JH (1999) Biostatistical analysis. Prentice Hall Inc., Toronto