

# Shifting invertebrate zooplanktivores: watershed-level replacement of the native *Leptodora* by the non-indigenous *Bythotrephes* in Canadian Shield lakes

Erika J. Weisz · Norman D. Yan

Received: 15 September 2009 / Accepted: 25 May 2010  
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**Abstract** The abundance of the native, pelagic macroinvertebrate predator, *Leptodora kindtii*, is negatively correlated with the abundance of a new invasive competitor, *Bythotrephes longimanus*, in a small number of Canadian Shield lakes. However, we do not yet know if *Bythotrephes* is replacing *Leptodora* on a regional scale. We determined the distribution of both species in 166 lakes in the District of Muskoka, south-central Ontario, Canada—the watershed with the longest history and largest prevalence of *Bythotrephes* invasions in North America. The frequency of occurrence of *Leptodora* was substantially reduced (twofold) in the presence of *Bythotrephes*. We argue that *Bythotrephes* is responsible for this dramatic reduction in the frequency of occurrence of *Leptodora*. Lakes in which both species co-occurred could not be distinguished from invaded lakes without *Leptodora*, suggesting a pattern of species replacement at a watershed level. We believe this is the first account of the widespread replacement of a native, pelagic macroinvertebrate predator by *Bythotrephes* in North America, and it does not bode well for *Leptodora* given the rapid, ongoing spread of *Bythotrephes*.

**Keywords** Biological invasions · *Bythotrephes longimanus* · *Leptodora kindtii* · Macroinvertebrate predator · Regional distribution · Species replacement

## Introduction

Macroinvertebrate predators contribute significantly to the competitive and predatory forces that shape freshwater pelagic communities. When abundant, macroinvertebrate predators strongly influence food web interactions (Herzig and Auer 1990), even in the presence of planktivorous fish (Wissel and Benndorf 1998). Pelagic predatory macroinvertebrates occupy a species-poor niche in North American freshwaters, consisting mainly of a few species of mysids, the larvae of *Chaoborus*, mites, a non-indigenous jellyfish (*Craspedacusta sowerbii*), *Leptodora kindtii*, and a few onychopodid cladocerans, including two non-indigenous taxa—*Cercopagis* (MacIsaac et al. 1999) and *Bythotrephes*. *Bythotrephes longimanus* (Crustacea, Onychopoda) was first detected in the North America Great Lakes in the early 1980's (Johannsson et al. 1991), and spread to all of the Great Lakes by the end of that decade. By 1989, it had been detected in the inland lakes of the Great lakes basin (Yan et al. 1992), and since that time it has been spreading rapidly across the Canadian Shield (Therriault et al. 2002, Weisz and Yan 2010). *Bythotrephes* introductions have been followed by dramatic

E. J. Weisz (✉) · N. D. Yan  
Department of Biology, York University, 4700 Keele St.,  
Toronto, ON M3J 1P3, Canada  
e-mail: erikaweisz@gmail.com

N. D. Yan  
Dorset Environmental Science Centre, Dorset,  
ON P0A 1E0, Canada

reductions in the species richness and abundance of native zooplankton, particularly their Cladoceran prey (Boudreau and Yan 2003; Strecker et al. 2006; Yan et al. 2001). A small number of case studies have also suggested that *Bythotrephes* introductions may lead to reduced abundances of native macroinvertebrate predators, particularly *Leptodora kindtii* Focke (Crustacea, Haplopoda), a species that competes for the same prey as *Bythotrephes* (Branstrator 1995; Foster and Sprules 2009).

If these case studies have broader predictability, the recent introduction of *Bythotrephes* into North America is a cause for concern as it may lead to the widespread disappearance of *Leptodora*. Decreased abundances of *Leptodora* that have been documented in Lake Michigan and a few Canadian Shield lakes have been attributed to competition with and/or predation by *Bythotrephes* (Barbiero and Tuchman 2004; Branstrator and Lehman 1991; Foster and Sprules 2009; Yan and Pawson 1997). In its native Europe, *Bythotrephes* often co-exists with *Leptodora* (Enz et al. 2001; Palmer et al. 2001). In Canada, we know neither the frequency of co-occurrence, nor the environmental conditions that might foster such co-existence. Although it has been predicted that co-existence of the two predators is unlikely in Canadian Shield lakes (Branstrator 1995; Foster and Sprules 2009), and classic theory suggests competitive exclusion (Hardin 1960), it has long been known that many plankton species with overlapping niches can co-exist (Hutchinson 1961). Nevertheless, if *Bythotrephes* is experiencing competitive and/or enemy release due to its change in locale (Elton 1958), increased prey consumption by *Bythotrephes* could negatively effect native *Leptodora* populations. In addition, *Leptodora* itself can fall prey to *Bythotrephes*, while the reverse does not seem to be the case, as even small *Bythotrephes* are too large for the grasping basket of *Leptodora* (Branstrator 1995; Herzig and Auer 1990).

Our objective was to determine if the frequency of occurrence (prevalence) of *Leptodora* is reduced in the presence of *Bythotrephes* on a watershed scale. To establish if there was indeed a reduction of *Leptodora* prevalence, the distribution of both species was surveyed across the most heavily invaded watershed in North America—the Muskoka region of Ontario, Canada. To determine if correlations of *Bythotrephes* presence with *Leptodora* frequency might have a

causal basis, we also had to determine what other factors might be correlated with *Leptodora* presence; hence, we amassed both physical and water quality data for each sampled lake. Physico-chemical data were compared between three pairs of lake sets: (a) those lakes with and without *Leptodora*; (b) those lakes with only *Leptodora* vs. those with both *Leptodora* and *Bythotrephes*; and (c) lakes invaded by *Bythotrephes* that do not support *Leptodora* vs. those that support both species. In this way, we were able to determine what conditions might foster the co-existence of these two competing predators.

## Methods

### Study area

We sampled 193 lakes within watershed 2 EB (Cox 1978), which contains approximately 1636 lakes >1 ha (Cairns et al. 2006), and encompasses the District of Muskoka and parts of the counties of Haliburton, Nipissing and Parry Sound (Ontario, Canada). This area is mostly underlain by the granitic rock that typifies the Canadian Precambrian shield. The watershed contains lakes both above and below elevations that led to post-glacial meltwater inundations, causing glacial relict taxa such as *Mysis relicta* to occur at lower but not higher regions (Carter et al. 1980). It is also a watershed that contains 46 lakes known to be invaded by *Bythotrephes* (Cairns et al. 2006; Weisz and Yan 2010), and is therefore an ideal region for comparing the distribution of the native *Leptodora* with the non-native *Bythotrephes*. The 193 study lakes were largely nutrient poor (4–17.4  $\mu\text{g L}^{-1}$  total phosphorus (TP)) and softwater (17.4–98  $\mu\text{S cm}^{-1}$  conductivity), but ranged widely in dissolved organic carbon concentrations (DOC) (2–33.4  $\text{mg L}^{-1}$ ) and area (6.6–155.5 ha), as is typical of Canadian Shield lakes.

### Survey design and lake selection methods

In 2005, 92 lakes were selected from a database of all lakes within the watershed, compiled from Landsat (TM) digital satellite data (Hélie et al. 1993). We used spatial location and lake size as strata in an equally stratified random sampling design (Hirzel and Guisan 2002). To effect this design, and to ensure

that the entire watershed was sampled, the study area was divided into a 12-cell grid. Within each cell, lakes were grouped into three size categories (1–10, 10.1–100 and >100 ha) and an equal number of lakes from each size category were randomly selected. This provided a set of lakes with a preset variation in size, and a wide but uncontrolled variation in chemistry (Neary et al. 1990). This allowed us to determine any differences in water quality between lakes with and without both *Leptodora* and *Bythotrephes*, as well as conditions that might foster only one species. In 2006, 101 lakes were selected along gradients of hydrological connection to lakes known to be invaded by *Bythotrephes* before 2004. Most study lakes (88%) were located upstream of an invaded lake, as the majority of known invaded lakes are located at the bottom of their respective watershed.

### Sampling protocol

Weisz and Yan (2010) provide a full description of the sampling methods. Lakes were sampled using a standard Ontario Federation of Anglers and Hunters (OFAH) *Bythotrephes* conical tow net (30 cm aperture, 65  $\mu\text{m}$  mesh). To improve detection of small populations, two hauls were taken and subsequently combined into a composite sample at each of 5 sites along the longest fetch of each lake. A sixth oblique tow was taken at the downwind area of each lake to account for potential spatial irregularity of *Bythotrephes* and *Leptodora* due to wind-induced patch formation and movement (Petruniak 2009; Zozulya 1978). Samples were preserved in 5.5% sucrose-formalin and examined in their entirety for the presence and numbers of *Leptodora* and *Bythotrephes*.

Vertical temperature, oxygen profiles and Secchi disc depths were measured at every lake at the deepest site along the sampled fetch. Composite (epilimnetic + metalimnetic) water samples were collected at the deepest site for subsequent analysis at the Ontario Ministry of the Environment's Dorset Environmental Science Centre chemistry lab. The samples were analyzed for pH, alkalinity, total phosphorus (TP), calcium, conductivity, and dissolved organic carbon (DOC) following the methods of the Ontario Ministry of the Environment (1983).

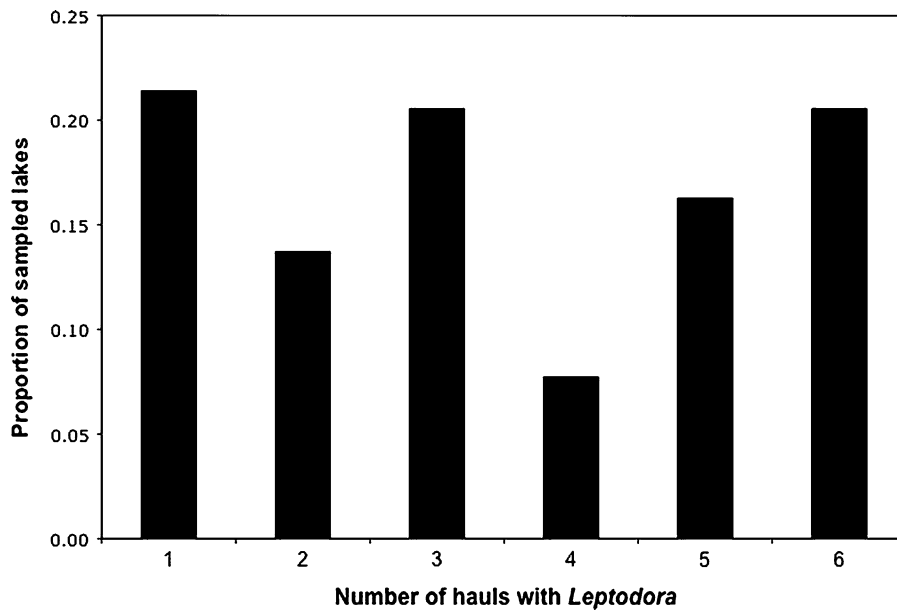
Despite visiting each lake only once, we are confident in the quality of both our *Bythotrephes* and *Leptodora* presence/absence data. We visited all

lakes between June and August, a time period during which Foster and Sprules (2010) confirmed the presence of a sufficient density of *Leptodora* and *Bythotrephes* to be detected by our sampling protocol. In addition, Boudreau and Yan (2004) confirmed that 3 samples taken at different sites on a lake, each a pooled composite of 2 hauls, detect *Bythotrephes* 100% of the time at typical summer abundances ( $4 \text{ m}^{-3}$ ), but protocols that collect *Bythotrephes* at 5 stations detect *Bythotrephes* 100% of the time when abundances were low ( $0.9 \text{ m}^{-3}$ ). Our addition of a 6th station at the downwind area of each lake provided extra assurance in the unlikely case that 5 stations happened to miss *Bythotrephes* because of particularly low abundances or very heterogeneous distributions. Consistent with Boudreau and Yan's observation for *Bythotrephes*, our results indicate that our protocol was very effective at detecting *Leptodora*, as they were found in at least 3 or more hauls in over 65% of the lakes sampled, with an average of 3.4 hauls containing *Leptodora* (Fig. 1).

We are also confident in our ability to distinguish the water quality of our lakes despite visiting each lake only once. We compared the coefficient of variation between the six chemical parameters from June to August 2006 from Red Chalk Lake (data courtesy of A. Paterson, Dorset Environmental Science Centre)—a typical, non-acidic, low DOC lake in the region that has good habitat for both *Bythotrephes* and *Leptodora*—to the variance from our entire lake dataset from 2006. The magnitude of variability in chemistry among lakes in our spatial dataset was much greater (coefficient of variation was much higher) when compared to seasonal data from Red Chalk lake, i.e. the coefficient of variation for Red Chalk lake in 2006 varied from 1 to 7% among parameters, much less than the 9–98% for our entire 2006 dataset (Table 1).

### Data analysis

Except where otherwise indicated, all data were analyzed using Sigmapstat (v 3.11, Systat Software 2004). A relatively small number of outlier lakes were removed in order to reduce the influence of very atypical lakes on subsequent analyses, and permitting the analyses to reflect the main environmental gradients among lakes. It was outliers in the chemistry data that were of most concern, as the chemistry



**Fig. 1** Frequency histogram of *Leptodora* detection at the 6 sampling stations in each lake ( $n = 166$ )

**Table 1** Coefficients of variation of six chemical parameters compared between the spatial lake set used in this study ( $n = 166$ ) to those of Red Chalk Lake (data courtesy of A. Paterson, Dorset Environmental Science Centre). Both datasets were taken from June–August of 2006

| Parameter  | Red Chalk Lake | Spatial Lakes |
|--|----------------|---------------|
| pH   | 0.03           | 0.08          |
| Dissolved organic carbon ( $\text{mg L}^{-1}$ )      | 0.07           | 0.39          |
| Total phosphorus ( $\mu\text{g L}^{-1}$ )            | 0.02           | 0.71          |
| Alkalinity ( $\text{mg L}^{-1}$ as $\text{CaCO}_3$ ) | 0.04           | 0.79          |
| Conductivity ( $\mu\text{S cm}^{-1}$ )               | 0.01           | 0.80          |
| Calcium ( $\text{mg L}^{-1}$ )                       | 0.01           | 0.53          |

variables exhibited the highest deviation from normality. The outliers that were removed all had very high conductivity values when compared to the rest of the dataset (Mann–Whitney U-test,  $P < 0.001$ ). In total, 24 lakes were removed, as well as 3 lakes from 2005 that were re-sampled in 2006, which reduced the final lake set from 193 to 166 lakes.

To establish whether the number of lakes in which *Leptodora* was observed differed in the presence and absence of *Bythotrephes*, we employed a 2\*2 contingency table of observed and expected frequencies using a chi-squared test.

To determine the combination of environmental variables that best predicted the presence of

*Leptodora*, a Principal Components Analysis (PCA) was performed using Canoco (v 4.1, ter Braak and Smilauer 1998) on the correlation matrix of the ranks of dissolved organic carbon (DOC), pH, calcium, TP, alkalinity, conductivity, lake area, surface temperature, Secchi depth, and maximum sampling depth (ter Braak and Smilauer 1998). The sample scores from the first three axes of the PCA were then used in a stepwise logistic regression model with *Leptodora* presence as the dependent variable. The logistic regression model was generated in SAS (v 9.1, SAS Institute 2002–2003). To verify if environmental conditions differed in lakes with and without *Leptodora*, we used either *t*-tests or Mann–Whitney U-tests on all 10 environmental variables. Finally, to determine the conditions in which *Leptodora* and *Bythotrephes* coexisted, *t*-tests and Mann–Whitney U-tests were used to compare physicochemical variables between uninvaded and invaded lakes containing *Leptodora*; and, between invaded lakes with *Leptodora* and invaded lakes without *Leptodora*.

## Results

The frequency of occurrence of *Leptodora* decreased significantly in the presence of *Bythotrephes*. There were only 8 lakes where both *Bythotrephes* and

*Leptodora* co-occurred, much lower than the expected 15 lakes (Table 2). In contrast, the number of lakes that supported *Bythotrephes* and did not support *Leptodora* (16 lakes) was much higher than expected (9 lakes). Put most simply, *Leptodora* occurred in 2/3 of lakes without *Bythotrephes*, but only 1/3 of lakes with *Bythotrephes*

*Leptodora* did not have narrow environmental requirements in our survey. The distribution of lakes with *Leptodora* within the PCA ordination scatterplot indicated that lakes with very large differences in physical and chemical attributes can support *Leptodora* populations (Fig. 2). Indeed, none of the three axes from the PCA on lake morphometry and chemistry met the significance requirements for entry into the stepwise logistic regression model predicting *Leptodora* presence/absence. The *t*-tests and Mann–Whitney U-tests confirmed that lake size was the only variable that differed significantly between lakes that contained *Leptodora* vs. lakes that did not (Table 3). Logistic regression analysis also determined that lake size was a significant predictor of *Leptodora* presence ( $P = 0.026$ ); however, the range of sizes of lakes that contained *Leptodora* was vast (1.43–834.30 ha), indicating that lake size is not a limiting factor in its distribution.

Lakes in which *Leptodora* and *Bythotrephes* co-occurred were significantly larger, had more circumneutral pH, lower DOC levels, and greater conductivity levels than lakes containing *Leptodora* alone (Table 4). Among the 10 physico-chemical variables, only lake size differed ( $P = 0.030$ ) between invaded lakes that did support *Leptodora* vs. those that did not—invaded lakes with *Leptodora* tended to be larger than those without.

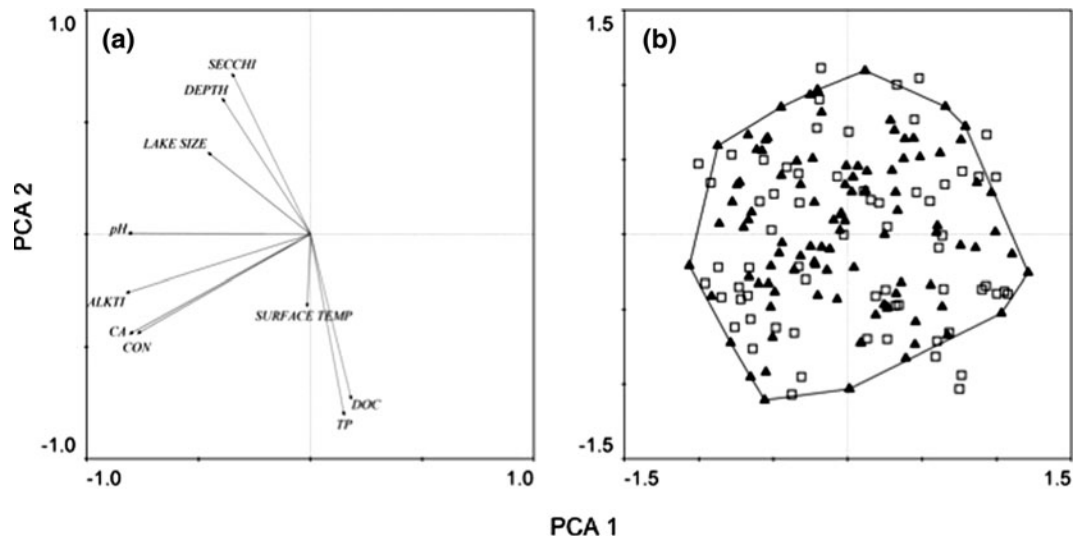
**Table 2** Contingency table and chi-squared test results of the separate occurrences and co-occurrences of *Leptodora* and *Bythotrephes* for 166 lakes in the Muskoka region in 2005 and 2006. Of particular interest was the frequency of occurrence of *Leptodora* in the presence and absence of *Bythotrephes*

|  | <i>Leptodora</i><br>present<br>( $n = 101$ ) | <i>Leptodora</i><br>absent<br>( $n = 65$ ) |
|--|--|--|
| <i>Bythotrephes</i> present ( $n = 24$ ) | 8  | 16   |
| <i>Bythotrephes</i> absent ( $n = 142$ ) | 93   | 49   |
| Chi-squared test                         | $\chi^2 = 7.614$                             | $P = 0.006$                                |

## Discussion

We conclude that the non-native predator, *Bythotrephes*, is commonly eliminating *Leptodora* within the Muskoka region, or reducing their population size below the detection limits of our multi-station sampling protocol. Such replacement has been previously observed in a few inland lakes (Foster and Sprules 2009; Yan and Pawson 1997), but here we provide the first evidence that this replacement is occurring on a watershed level. In the past, *Leptodora* distribution in Canada has been shown to be fairly ubiquitous, occurring across the Canadian Shield in lakes with a large physico-chemical ranges, with a trend towards larger, clearer lakes (Carter et al. 1980; McNaught 1993; Patalas 1975). This pattern is similar to Eurasia, where *Leptodora* is widely distributed across the continents in lakes of varying types, from the subarctic to the subtropics (Fernando and Kanduru 1984; Vekhov 1982). Similar to McNaught's (1993) and Patalas' (1975) surveys of Canadian Shield lakes, we determined that *Leptodora*, like *Bythotrephes* (MacIsaac et al. 2000), tends to be found more frequently in large lakes, although the range of sizes of lakes *Leptodora* inhabits is quite broad. The current distribution ranges of both species overlap substantially in the Muskoka region, with both occurring broadly across the watershed; however, the number of lakes where these two predators coexist is significantly lower than expected from their individual occurrences, and the instances where *Leptodora* is absent in the presence of *Bythotrephes* is very high. Similar to Foster (2007)'s smaller data set, these findings support the idea of species replacement occurring in many Canadian Shield lakes, or at least that abundances of *Leptodora* are highly suppressed in the presence of *Bythotrephes*. As this replacement or suppression appears to be widespread, the effect on lake food webs could be severe as *Bythotrephes* has a greater consumption impact, and has been shown to increase total invertebrate predator consumption of prey by over 25% (Foster and Sprules 2009).

It is quite possible that summer populations of *Leptodora* have actually disappeared in many cases after the arrival of *Bythotrephes*. However, a second possible interpretation of the unexpectedly low frequency of *Leptodora* in invaded lakes is that *Bythotrephes* is simply better at invading lakes that do not contain *Leptodora*. This explanation is not supported



**Fig. 2** (a) Directional plot and (b) scatter plot of 166 sampled lakes within watershed 2 EB, Muskoka region, Ontario, based on Axis 1 and 2 of a PCA run on 10 ranked limnological characteristics. Variables are lake size (LAKE SIZE), maximum sampling depth (DEPTH), Secchi depth (SECCHI), pH (pH), total inflection point alkalinity, or Gran alkalinity (ALKTI), calcium (CA), conductivity (CON), surface temperature

(SURFACE TEMP), total phosphorus (TP), and dissolved organic carbon (DOC). Triangles represent lakes containing *Leptodora*, and the outlining polygon represents the environmental limits of lakes supporting *Leptodora*. The large size of the polygon indicates that *Leptodora* are found very broadly along environmental gradients within the watershed

**Table 3** Comparison of means of 10 limnological characteristics of lakes that contained *Leptodora* ( $n = 101$ ) with lakes that did not contain *Leptodora* ( $n = 65$ ). Range is indicated in brackets below the mean

| Variable   | <i>Leptodora</i> mean (range) | No <i>Leptodora</i> mean (range) | Test type             | <i>P</i> -value* |
|--|-------------------------------|----------------------------------|-----------------------|------------------|
| Lake size (ha)                                       | 45.2 (1.4–834.3)              | 20.3 (1.0–378.2)                 | Mann–Whitney Rank Sum | <b>0.008</b>     |
| Maximum sampling depth (m)                           | 9.6 (1.5–40.5)                | 8.5 (0.5–29.0)                   | Mann–Whitney Rank Sum | 0.423            |
| Secchi depth (m)                                     | 3.9 (1.0–8.0)                 | 4.0 (0.4–9.1)                    | <i>t</i> -test        | 0.572            |
| Surface temperature (°C)                             | 24.1 (18.2–28.5)              | 23.7 (16.8–28.2)                 | <i>t</i> -test        | 0.947            |
| pH   | 6.4 (5.1–8.0)                 | 6.3 (5.0–7.4)                    | Mann–Whitney Rank Sum | 0.134            |
| Dissolved organic carbon ( $\text{mg L}^{-1}$ )      | 4.7 (2.0–11.9)                | 5.3 (2.3–33.4)                   | Mann–Whitney Rank Sum | 0.253            |
| Total phosphorus ( $\mu\text{g L}^{-1}$ )            | 7.6 (2.7–41.6)                | 8.0 (1.2–59.0)                   | Mann–Whitney Rank Sum | 0.458            |
| Alkalinity ( $\text{mg L}^{-1}$ as $\text{CaCO}_3$ ) | 3.5 (−0.2–16.1)               | 3.1 (−0.1–17.8)                  | Mann–Whitney Rank Sum | 0.678            |
| Conductivity ( $\mu\text{S cm}^{-1}$ )               | 25.6 (12.4–150.0)             | 25.8 (13.2–147.0)                | Mann–Whitney Rank Sum | 0.559            |
| Calcium ( $\text{mg L}^{-1}$ )                       | 2.3 (1.0–7.6)                 | 2.3 (1.0–12.3)                   | Mann–Whitney Rank Sum | 0.609            |

\* Significant values after Benjamini-Hochberg false detection rate post-hoc correction are indicated in bold

by previous studies, as *Bythotrephes* has successfully invaded several lakes that had been previously known to support populations of *Leptodora*, including Lake Michigan (Branstrator 1995), Lake Erie (Garton et al. 1990), Harp Lake (Yan and Pawson 1997), and several inland Canadian Shield lakes (Foster and Sprules 2009). Within Lake Michigan, there was a strong reciprocal relationship between the abundances of *Bythotrephes* and *Leptodora* (Lehman 1991), and following the *Bythotrephes* invasion *Leptodora* fell

below detectable limits at several stations just 1 year after high abundances of the native species had been recorded (Branstrator 1995). Foster and Sprules (2009) also found this reciprocal relationship occurring in several inland lakes, with *Leptodora* abundances falling right after peak *Bythotrephes* abundances in August. Although it is unclear whether competition or predation causes these population reductions of *Leptodora*, it is obvious that *Bythotrephes* is outperforming *Leptodora* in lakes where *Leptodora* has been long

**Table 4** Comparison of 10 physical and chemical parameters in lakes with only *Leptodora* and lakes supporting both *Leptodora* and *Bythotrephes*, sampled in 2005 and 2006 ( $n = 166$ ). Means for lakes containing both species are in brackets below means for lakes with only *Leptodora*. *T*-tests

were carried out for the variables of pH, Secchi depth, and surface temperature, and Mann–Whitney Rank sum tests were carried out for all other variables due to their non-normal distributions

| Variable  | Mean– <i>Leptodora</i> only<br>( <i>Leptodora</i> and <i>Bythotrephes</i> ) | <i>P</i> -value* |
|---|---|------------------|
| Lake size (ha)  | 34.2 (163.9)  | < <b>0.001</b>   |
| Maximum sampling depth (m)                            | 9.3 (15.9)  | 0.174            |
| Secchi depth (m)                                      | 3.9 (4.5)   | 0.115            |
| Surface temperature (°C)                              | 24.1 (23.8)   | 0.722            |
| pH  | 6.3 (6.7)   | <b>0.032</b>     |
| Dissolved organic carbon (mg L <sup>-1</sup> )        | 4.8 (4.0)   | <b>0.035</b>     |
| Total phosphorus (µg L <sup>-1</sup> )                | 7.7 (5.4)   | 0.091            |
| Alkalinity (mg L <sup>-1</sup> as CaCO <sub>3</sub> ) | 3.3 (4.7)   | 0.235            |
| Conductivity (µS cm <sup>-1</sup> )                   | 25.0 (31.3)   | <b>0.030</b>     |
| Calcium (mg L <sup>-1</sup> )                         | 2.3 (2.5)   | 0.119            |

\* Significant values after Benjamini-Hochberg false detection rate post-hoc correction are indicated in bold

established. Unfortunately, we visited each lake only once, so we cannot provide additional insight into the relative importance of competitive or predatory forcing, as both production and consumption estimates require frequent sampling.

*Bythotrephes* and *Leptodora* co-occur more frequently in several European lakes than in our survey. In Lake Constance and Lake Lucerne, for example, *Bythotrephes* was observed to occur primarily below 20 m, leaving *Leptodora* to dominate the overlying epilimnion (Enz et al. 2001; Palmer et al. 2001). However, in several invaded Canadian Shield lakes, *Bythotrephes* are present throughout the metalimnion and epilimnion (Foster and Sprules 2009; Young and Yan 2008), which suggests that *Bythotrephes* and *Leptodora* most likely overlap spatially. Within our study, large surface area was the only variable that differentiated lakes in which the two predators coexisted and lakes that only supported *Bythotrephes*. Increased pH, conductivity, and DOC differentiated lakes with both species and lakes with *Leptodora* alone; however, these variables would be expected to differentiate the two groups as they were also found to be significant predictors of *Bythotrephes* presence (Weisz and Yan 2010). The strong similarities between invaded lakes and lakes that supported both species indicate that as the range of *Bythotrephes* continues to expand, the replacement or suppression of the native *Leptodora* will likely continue.

Given our observation of widespread reduced *Leptodora* frequency of occurrence in Muskoka lakes invaded by *Bythotrephes*, we predict widespread losses of *Leptodora* as *Bythotrephes* continues to spread across the Canadian Shield. As the *Bythotrephes* invasion is still at an early stage, it is important that lake monitoring be continued to test this prediction. Foster and Sprules (2009) suggest that *Bythotrephes* are effective competitors with juvenile and planktivorous fish, consuming herbivorous zooplankton that would otherwise become prey for higher trophic levels along conventional pathways within the food web. Therefore, the spread of *Bythotrephes* may have broader implications than its well-known impacts on zooplankton richness and the widespread impacts on competing macroinvertebrates that we have documented here. Fish production on the Shield might also be at risk, or at least the component that is dependent on pelagic production. Considering the widespread and ongoing nature of the *Bythotrephes* invasion, and its replacement of *Leptodora*, we consider *Bythotrephes* to be a damaging invader on the Canadian Shield, deserving of both study and management.

**Acknowledgments** Support for this research was provided by the Canadian Aquatic Invasive Species Network, Natural Sciences and Engineering Research Council of Canada Discovery Grant to NDY, the Ontario Ministry of the Environment, the Ontario Ministry of Natural Resources

(OMNR) and the Ontario Federation of Anglers and Hunters (OFAH). Extensive technical and field assistance was provided by Allegra Cairns, Jennifer Hoare, Crystal Hyatt, Jennifer Petruniak and Brady Yu. Many thanks to the staff at the Dorset Environmental Science Centre, particularly Robert Girard and Keith Somers. Finally, thanks to Michelle Palmer, Roberto Quinlan and Joelle Young for their suggestions on this manuscript.

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