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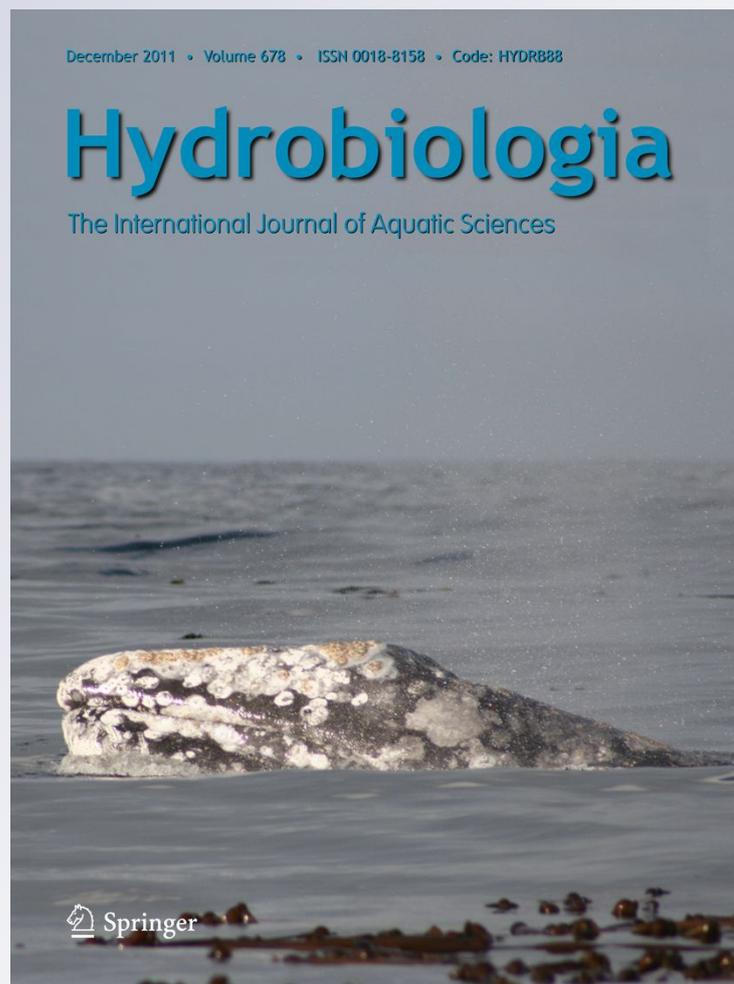
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# Effects of *Bythotrephes longimanus* (Crustacea, Cladocera) on the abundance, morphology, and prey community of *Leptodora kindtii* (Crustacea, Cladocera)

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**Abstract** We hypothesized that native *Leptodora kindtii* would be shorter and have smaller feeding baskets in central Ontario lakes with greater abundances of small-bodied zooplankton prey, and that differences in zooplankton size among lakes could be attributed to the invasive cladoceran *Bythotrephes longimanus*. We evaluated these conjectures by comparing size metrics of *Leptodora* and the size of their preferred cladoceran prey in lakes invaded or not by *Bythotrephes*. *Leptodora* was less abundant in invaded lakes, but were smaller bodied with smaller feeding

baskets only in lakes with long invasion histories. Small cladoceran abundance was greater in non-invaded lakes and was directly related to *Leptodora* abundance although not to *Leptodora* size. Mean *Leptodora* body size declined with increasing abundance of *Bythotrephes*. We evaluated three possible explanations for these patterns in *Leptodora*—(a) competition with *Bythotrephes* for zooplankton prey, (b) direct predation by *Bythotrephes*, and (c) size-selective predation by fish. While we were unable to unequivocally distinguish among these hypotheses, our observations are most consistent with predation by *Bythotrephes* changing zooplankton community composition and size structure in a manner that is detrimental to *Leptodora*. Our results indicate that *Bythotrephes* invasion may trigger more complex and subtle changes in food webs than previously thought.

**Keywords** *Leptodora* size · Feeding basket size · *Bythotrephes* invasion · Cladoceran size · Boreal lakes

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## Introduction

*Bythotrephes longimanus* Leydig (hereafter *Bythotrephes*) is a predatory cladoceran that was first detected in Lake Ontario in 1982 (Mills et al., 2003) and has since continued to spread to all of the Laurentian Great Lakes and more than 100 inland lakes in Ontario, Canada. Long-term zooplankton monitoring of Harp Lake, Ontario first detected *Bythotrephes* in 1993 and

it has continued to spread to nearby lakes in south-central Ontario, likely being transported via human vectors (MacIsaac et al., 2004).

*Bythotrephes* has been implicated in the decline and disappearance of several zooplankton species following its introduction to the Laurentian Great Lakes and inland lakes (Yan & Pawson, 1997; Barbiero & Tuchman, 2004). Changes in zooplankton body size have also been observed following the *Bythotrephes* invasion. In Harp Lake small-bodied cladocerans, such as *Bosmina longirostris* (O.F. Müller), *Chydorus sphaericus* (O.F. Müller), *Diaphanosoma birgei* Kořinek, and *B. tubicen* (Brehm) have declined or disappeared, and large-bodied cladocerans, such as *Holopedium gibberum* Zaddach and *Daphnia galeata mendotae* Birge, and the copepod *Leptodiaptomus sicilis* (Forbes), have increased in abundance following *Bythotrephes* invasion (Yan & Pawson, 1997). Strecker et al. (2006) found lower abundance of most zooplankton species—both small- and large-bodied—in inland lakes invaded by *Bythotrephes* compared to non-invaded reference lakes across a larger geographical range. Similarly both small-bodied zooplankton species, such as *Eubosmina coregoni* (Baird), and large-bodied species, such as *H. gibberum*, *D. retrocurva* Forbes, and *D. pulicaria* Forbes, declined in abundance from pre-invasion levels following invasion of *Bythotrephes* into the Great Lakes (Barbiero & Tuchman, 2004).

The invasion of *Bythotrephes* may also affect species within the same guild, such as the native invertebrate predator *Leptodora kindtii* (Focke) (hereafter *Leptodora*), either directly through predation or indirectly through changes to prey availability. *Leptodora* abundance declined in Harp Lake (Yan & Pawson, 1997) and in the Great Lakes (Barbiero & Tuchman, 2004) following the *Bythotrephes* invasion, and *Bythotrephes* appears to be replacing *Leptodora* on a watershed level (Weisz & Yan, 2010). *Leptodora* and *Bythotrephes* both prefer cladoceran prey (Lunte & Luecke, 1990; Foster, 2007) and the decline of cladocerans in invaded lakes may affect *Leptodora* populations. While zooplankton often respond to predation pressure from invertebrate predators by developing morphological defenses (Laforsch & Tollrian, 2004), the responses of invertebrate predators to changes in the body size of their prey are less well understood. The maximum-sized prey *Leptodora* can exploit is constrained by the size of its feeding

basket and smaller *Leptodora* have smaller feeding baskets (Herzig & Auer, 1990; Branstrator, 1995; Manca & Comoli, 1995). *Leptodora* body size and relative feeding basket size can vary seasonally with changes in prey size and density (Abrusán, 2003). Therefore, modifications to zooplankton community composition and size structure after *Bythotrephes* invasion may result in changes in *Leptodora* body and feeding basket size. We have previously demonstrated impacts of *Bythotrephes* on native macroinvertebrate abundances and seasonal consumption of zooplankton prey (Foster & Sprules, 2009) and on their trophic position (Foster & Sprules, 2010), but to our knowledge, no study has examined morphological differences in *Leptodora* in lakes invaded by *Bythotrephes*.

In this study, we hypothesize that differences in the body size and feeding basket size of *Leptodora* between central Ontario lakes invaded by *Bythotrephes* and non-invaded reference lakes will vary with differences in the body sizes of crustacean zooplankton in the same lakes.

In other words, *Leptodora* are shorter and have smaller feeding baskets in lakes with small-bodied zooplankton and vice versa. Given the variety of previous observations on effects of *Bythotrephes* on zooplankton communities, we had no a priori expectation as to whether zooplankton size would be larger or smaller in the invaded lakes we studied. As far as we are aware, such an impact of *Bythotrephes* on the morphology of a native macroinvertebrate predator has never been demonstrated and our work thus identifies a new dimension of the complex impacts this invader can have.

## Methods

Eight oligotrophic to meso-oligotrophic inland lakes located in the districts of Muskoka, Parry Sound, and Haliburton in south-central Ontario, Canada were sampled in the summers of 2003 and 2004 (Table 1). All lakes contained the glacial relict *Mysis relicta* Lovén, which is indicative of a common post-glacial history and similar zooplankton assemblages (Dadswell, 1974; Nero & Sprules, 1986). The lakes all supported planktivorous fish communities, including yellow perch (*Perca flavescens* (Mitchill)), and a combination of cisco (*Coregonus artedii* Lesueur), rainbow smelt (*Osmerus mordax* (Mitchill)), and lake whitefish (*C. clupeaformis* (Mitchill)) (Table 1). Six

lakes were sampled each summer, with the original design being to sample three invaded by *Bythotrephes* and three that were not invaded. One of the non-invaded lakes (Maple) remained so throughout our study and a second one (Boshkung) had no detectable *Bythotrephes* in 2001. The third, Mountain, is within about 13 km of these two in the same small drainage basin, and was thus assumed to be *Bythotrephes*-free. However, *Bythotrephes* were discovered in Boshkung and Mountain in 2003 and thus these lakes were likely invaded in about 2002. We characterized them as invaded and tested them with the remainder of the invaded lakes (Table 1). In 2004, four of the lakes were sampled again and two new non-invaded lakes were added. Therefore, we sampled five lakes with *Bythotrephes* and one lake without *Bythotrephes* in 2003 and three lakes with *Bythotrephes* and three without *Bythotrephes* in 2004 (Table 1). The four study lakes, indicating that were sampled in both study years, were averaged to give a total of eight lakes—five invaded and three not invaded.

Each lake was visited every 2 weeks from June to September in 2003 and late May to late August in 2004. Water chemistry samples were taken the week of 14 July 2003 by Strecker et al. (2006) and Hovius et al. (2006). An integrated tube sampler (2.5 cm

diameter) was used to collect water from the epilimnion, which was filtered with 80- $\mu$ m mesh to remove large particles. Total phosphorus was analyzed following Ontario Ministry of Environment (1983) protocols. Epilimnetic chlorophyll *a* (chl *a*) samples were collected every 2 weeks by Strecker et al. (2006) and Hovius et al. (2006) in 2003 and by the authors in 2004, and averaged between study years. A known volume of water was filtered onto a 0.7- $\mu$ m glass fiber filter, the filtrate extracted for 24 h in methanol and analyzed with a TD 700 Fluorometer (Turner Designs, Sunnyvale, California, USA) (Welschmeyer, 1994).

*Leptodora* and *Bythotrephes* were collected every 2 weeks from 9 June to 15 September, 2003 and 27 May to 26 August, 2004 between dusk and dawn by hauling a large zooplankton net (0.75-m diameter, 5-m length, 285- $\mu$ m mesh) fitted with a flowmeter (Rigoshia & Company Ltd., Saitamao, Japan) from 5 m above bottom to the surface. *Leptodora* and *Bythotrephes* samples were collected in 2003 at nine stations during each sampling period, and in 2004 they were collected monthly at ten stations and at a representative subset of five stations on the intervening sampling dates. The multiple stations in each lake were subjectively located within depth contour intervals in each lake so that most depths and areas of a lake

**Table 1** Characteristics of study lakes, classified by invasion status

| Lake name                               | Invaded    |          |            |            |       | Not invaded        |           |       | Mann–Whitney tests <sup>b</sup> |         |
|-----------------------------------------|------------|----------|------------|------------|-------|--------------------|-----------|-------|---------------------------------|---------|
|                                         | Boshkung   | Mountain | Harp       | Peninsula  | Fairy | Maple <sup>a</sup> | Pickereel | Sand  | Z value                         | P value |
| Year of invasion                        | 2002       | 2002     | 1993       | 1991       | 1990  | –                  | –         | –     | –                               | –       |
| Years sampled                           | 2003, 2004 | 2003     | 2003, 2004 | 2003, 2004 | 2003  | 2003, 2004         | 2004      | 2004  | –                               | –       |
| Cisco                                   | P          | P        | P          | A          | A     | A                  | P         | P     | –                               | –       |
| Rainbow smelt                           | P          | P        | A          | P          | P     | P                  | A         | P     | –                               | –       |
| Lake whitefish                          | P          | P        | A          | A          | A     | P                  | A         | A     | –                               | –       |
| Yellow perch                            | P          | P        | P          | P          | P     | P                  | P         | P     | –                               | –       |
| Surface area (ha)                       | 715.8      | 319.4    | 71.7       | 864.8      | 711.5 | 335.3              | 513       | 568.2 | 0.45                            | 0.79    |
| Mean depth (m)                          | 23.1       | 13.5     | 11.6       | 9.7        | 22.1  | 12.7               | 8.6       | 22.8  | 0.45                            | 0.79    |
| Chlorophyll ( $\mu$ g l <sup>-1</sup> ) | 1.8        | 1.4      | 1.5        | 2.0        | 2.2   | 1.8                | 2.7       | 1.2   | 0.01                            | 0.99    |
| Total P ( $\mu$ g l <sup>-1</sup> )     | 3.93       | 4.50     | 7.22       | 9.00       | 4.50  | 9.80               | 8.10      | 7.10  | -1.35                           | 0.25    |

For fish species, P and A indicate presence and absence, respectively

<sup>a</sup> Although *Bythotrephes* was detected in Maple Lake in 2003, it is treated as a non-invaded lake because in 2 years of sampling only one individual *Bythotrephes* was detected

<sup>b</sup>  $n_{inv} = 5$  and  $n_{not} = 3$  for all tests

were represented. Samples were preserved in sugared, buffered formalin (Prepas, 1978). On each sampling date, composite samples were produced by combining into a single sample jar subsamples selected from each station and weighted according to the proportional surface area of the depth contour containing the station. Subsamples were selected from the composite samples until roughly 100 individuals were obtained (or as many as possible if fewer were in the sample). In each composite sample, we measured *Leptodora* total body length, from the front of the head to the telson bifurcation using Fowler® Ultra Cal Mark 111 calipers (Brantford, Ontario, Canada) that have a measurement resolution of 0.01 mm (Fig. 1). Mean *Leptodora* total body length was determined for each lake and sample date. In order to avoid imprecision from small sample sizes, these statistics were limited to dates for which at least ten individuals could be measured.

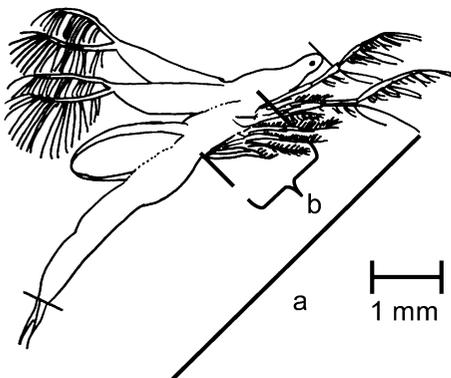
In 2004, we also measured the size of the feeding basket, from the base of the first to the base of the sixth appendages (Fig. 1) of 10–100 females when *Leptodora* were abundant. This measurement has been used in previous studies and has been shown to correlate with average prey size (Herzig & Auer, 1990; Abrusán, 2003). We did not measure external dimensions (Branstrator, 1995; Manca & Comoli, 1995) which are unduly affected by feeding appendage orientation during measurement.

Zooplankton were sampled in all eight study lakes in 2003 during the day with a 110- $\mu$ m mesh conical closing net of 0.5-m diameter (Strecker et al., 2006). Samples were taken from the entire water column every 2 weeks from May to September, and equal volumes from each date were pooled for subsequent

enumeration. No zooplankton samples were taken in 2004, thus, we use values from 2003 as representative of general crustacean abundance within each lake. All zooplankton samples were preserved in sugared, buffered formalin (Prepas, 1978). Zooplankton were enumerated using a protocol designed to insure reasonable representation of rare species (Strecker et al., 2006). Subsamples were generated with a Folsom plankton splitter, and a mean of 336 individuals (minimum = 199, SD = 109) were enumerated and the remainder of the sample was scanned for rare species. Cladocerans were further partitioned into small and large groups using an average body length cutoff of 0.5 mm. This breaking point correlates to the maximum-sized prey that *Leptodora* in invaded lakes can likely consume based on the average feeding basket length (S. Foster, unpublished), and is therefore representative of food availability. *Holopedium gibberum* were excluded from this analysis because their gelatinous sheath may provide them with some protection from invertebrate predation. Although there is some evidence that *Bythotrephes* may eat *Holopedium* (Wahlström & Westman, 1999; Barbiero & Tuchman, 2004), we are aware of no study indicating that *Leptodora* do so.

#### Statistical analysis

Our study design uses invasion status (invaded or not by *Bythotrephes*) as a fixed treatment, the lakes within each treatment as replicates, and seasonal averages of the dependent variables (except *Leptodora* basket size, see below). The design is unbalanced with small numbers of replicates so we have elected to use non-parametric statistical analyses when contrasting variables between treatments, but we have used parametric tests when evaluating linear trends between variables. We used rank-based Mann–Whitney non-parametric tests to examine differences between invaded and non-invaded lakes in (a) physical and chemical characteristics (5 invaded and 3 non-invaded lakes), (b) *Leptodora* abundance (5 invaded and 3 non-invaded lakes), (c) *Leptodora* body length (4 invaded and 3 non-invaded lakes because *Leptodora* were too rare in invaded Harp lake for reliable measurements), and (d) small cladoceran abundance (5 invaded and 3 non-invaded lakes) using R Version 2.12 (R Development Core Team, 2010). We used linear regression to examine relationships across all lakes between



**Fig. 1** Diagram showing measurements of *Leptodora* (a) total body length and (b) feeding basket. Redrawn from Rivier (1998)

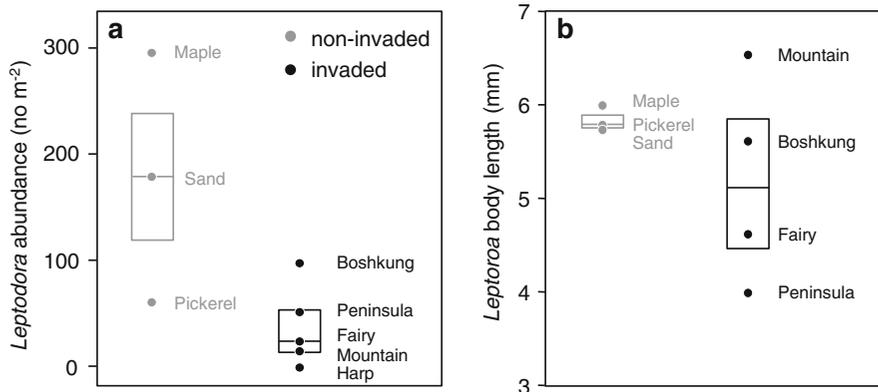
small cladoceran abundance and each of *Leptodora* body length ( $n = 7$ ) and abundance ( $n = 8$ ), and between *Leptodora* body length and *Bythotrephes* abundance ( $n = 7$ ) in R Version 2.12 (R Development Core Team, 2010). Variables were log-transformed as needed to linearize relationships. Although an analysis of *Leptodora* and *Bythotrephes* abundances in these lakes was part of a study focused on seasonal prey consumption by a number of macroinvertebrate species (Foster & Sprules, 2009), we present some summary abundance data in this study for completeness.

*Leptodora* feeding basket length was only measured in 2004 when six lakes were sampled (Table 1). However, *Leptodora* were too rare in invaded Harp Lake for reliable basket length estimates, and so our design comprised only two invaded and three non-invaded lakes. Thus, we elected to use sample dates (on which more than ten *Leptodora* were present) rather than lakes as independent replicates, having first confirmed that average basket lengths for these dates were not autocorrelated for either invaded or non-invaded lakes (Durbin–Watson test,  $P > 0.05$ , in the library *car* in R; R Development Core Team, 2010) and hence are independent of one another. We used a Mann–Whitney non-parametric rank test in R Version 2.12 (R Development Core Team, 2010) to test for differences in average basket length between invaded and non-invaded lakes ( $n_{inv} = 5$  and  $n_{not} = 13$ ). We used these same data, and comparable data for

*Leptodora* body length, to test for allometric differences in *Leptodora* feeding basket length between invaded and non-invaded lakes after controlling for *Leptodora* body length using an analysis of covariance (ANCOVA) in STATISTICA 6 (StatSoft, 2001). Invasion status was a fixed treatment, body size a covariate, and average basket lengths for each sampling date the dependent variable ( $n_{inv} = 5$  and  $n_{not} = 13$ ).

## Results

Physical and chemical characteristics showed no statistically discernible differences between invaded and non-invaded lakes (Table 1). In contrast, the biological characteristics of interest showed important differences. Average seasonal *Leptodora* abundance was greater in non-invaded than invaded lakes (Mann–Whitney:  $Z = -1.937$ ,  $P = 0.053$ ,  $n_{inv} = 5$ ,  $n_{not} = 3$ ) (Fig. 2a). Abundance was variable among individual lakes with some overlap among invasion categories (Fig. 2a). *Leptodora* body length was not significantly different in invaded lakes compared to non-invaded lakes (Mann–Whitney:  $Z = -1.414$ ,  $P = 0.157$ ,  $n_{inv} = 4$ ,  $n_{not} = 3$ ) (Fig. 2b). Harp Lake was not included in the size analysis because of the small sample size collected in both years (<5 individuals total). There is substantial variation in mean length of *Leptodora* in invaded lakes: when we exclude the two



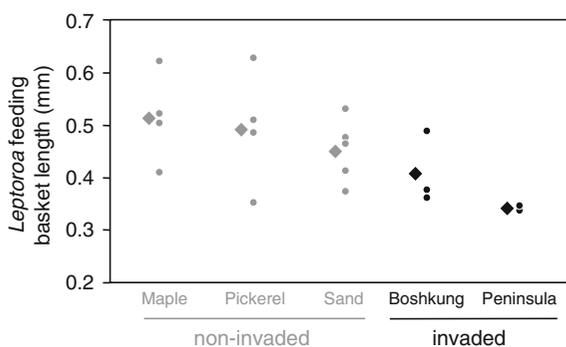
**Fig. 2** Mean seasonal *Leptodora* **a** abundance (no m<sup>-2</sup>) and **b** total body length (mm) in invaded (*black*) and non-invaded (*gray*) lakes ( $n_{inv} = 5$ ,  $n_{not} = 3$  in **(a)**,  $n_{inv} = 4$ ,  $n_{not} = 3$  in **(b)**). Note that sample sizes in **(a)** and **(b)** differ because Harp Lake is not included in **(b)** because too few *Leptodora* were captured to

get reliable estimates of average body size. *Boxes top and bottom* are the 75th and 25th percentiles of each category, respectively, *bar* is the median, and individual lake means are represented by *circles*, with the lake name indicated adjacent to the *symbol*

lakes invaded <3 years (Boshkung and Mountain), it is clear that *Leptodora* in invaded lakes are uniformly smaller than in non-invaded lakes (mean length invaded = 4.32 mm  $\pm$  0.43 SD.; mean length non-invaded = 5.85 mm  $\pm$  0.04 SD) (Fig. 2b).

We examined average *Leptodora* feeding basket size in a subset of our lakes on all sampling dates for which there were sufficient body size measures and found that feeding basket size in invaded lakes was significantly smaller than in non-invaded lakes (Mann–Whitney:  $Z = 2.22$ ,  $P = 0.026$ ,  $n_{\text{inv}} = 5$ ,  $n_{\text{not}} = 13$ , Fig. 3). Feeding basket size is strongly related to body size (Fig. 4) and hence the similar patterns we have documented for these two metrics in relation to *Bythotrephes* invasion are to be expected. There was no evidence for allometric changes in basket size independently of body size between invaded and non-invaded lakes in our study lakes (ANCOVA,  $F(\text{common slope})_{1,14} = 0.58$ ,  $P = 0.46$ ;  $F(\text{adjusted means})_{1,15} = 0.12$ ,  $P = 0.73$ ) (Fig. 4). *Leptodora* becomes sexually mature at approximately 5.3 mm (Branstrator, 2005), and some individual animals exceeded 10 mm in all study lakes indicating that both immature and mature animals were present.

Small cladocerans were significantly more abundant in non-invaded than invaded lakes (Mann–Whitney:  $Z = 2.236$ ,  $P = 0.025$ ,  $n_{\text{inv}} = 5$ ,  $n_{\text{not}} = 3$ ). The average seasonal abundance of small cladocerans was not a significant predictor of mean *Leptodora* body size ( $r^2 = 0.104$ ,  $P = 0.481$ ,  $n = 7$  lakes; Fig. 5a), but *Leptodora* abundance increased significantly with

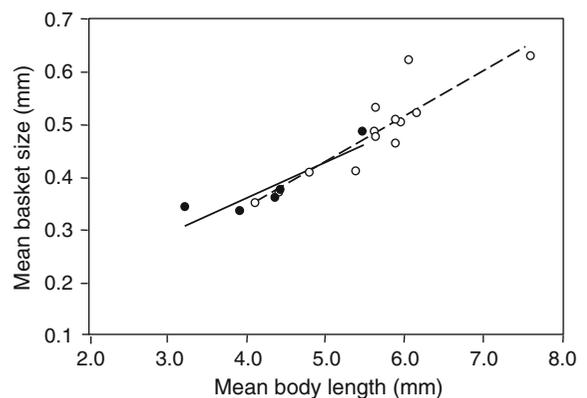


**Fig. 3** Average *Leptodora* feeding basket length (mm) in invaded (black) and non-invaded (gray) lakes on all lake-dates in 2004 when there were >10 *Leptodora* present ( $n_{\text{inv}} = 5$ ,  $n_{\text{not}} = 13$ ). Small circles represent sampling period mean for each lake, whereas large diamonds represent lake means across all sampling dates

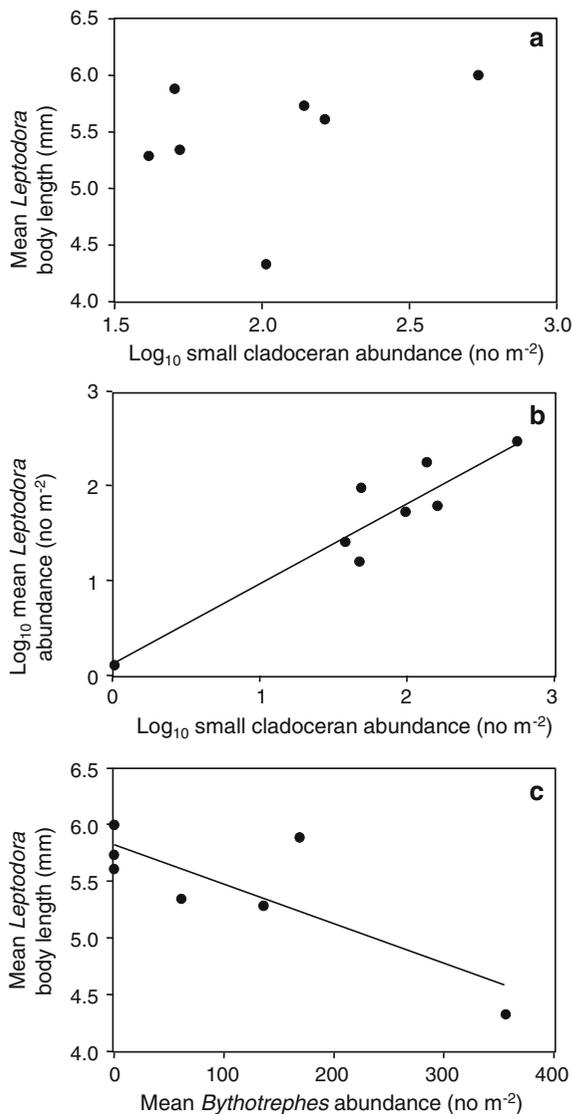
greater abundance of small cladocerans ( $r^2 = 0.880$ ,  $P < 0.001$ ,  $n = 8$  lakes; Fig. 5b). In contrast, mean *Leptodora* body size declined significantly with increases in average *Bythotrephes* abundance ( $r^2 = 0.658$ ,  $P = 0.027$ ,  $n = 7$  lakes; Fig. 5c), as did *Leptodora* abundance (Fig. 4 in Foster & Sprules, 2009). Note that the differences in sample size between analyses are the result of too few *Leptodora* individuals in Harp Lake to attain an accurate average body length. These trends are based on relatively few data with some gaps and thus must be considered with caution, but the observations falling outside the main cluster of points in Fig. 5b and c are for Harp and Peninsula lakes, respectively, which consistently showed these values over the 2 years they were sampled, and thus we have no reason to exclude them.

## Discussion

Substantial differences in the abundance and size structure of *Leptodora* populations exist among our study lakes differing in the invasion status of *Bythotrephes*. Although decreased abundance of *Leptodora* following the *Bythotrephes* invasion has been previously demonstrated in a small number of lakes studied over time (Yan & Pawson, 1997; Barbiero &



**Fig. 4** Relationship between *Leptodora* basket and body sizes for invaded (solid symbols and line  $y = 0.066x + 0.087$ ) and non-invaded (open symbols and dashed line  $y = 0.078x + 0.046$ ) lakes where  $y$  is basket size and  $x$  is body size. Points represent the average measurements obtained on each lake-date in 2004 for which there were >10 *Leptodora* present ( $n_{\text{inv}} = 5$ ,  $n_{\text{not}} = 13$ ). Fitted lines are least squares linear regressions



**Fig. 5** Scatter plots of  $\log_{10}$ -small cladoceran seasonal mean abundance (no  $m^{-2}$ ) versus **a** mean *Leptodora* body length (mm) ( $n = 7$  lakes) and **b**  $\log_{10}$  mean *Leptodora* abundance (no  $m^{-2}$ ) ( $n = 8$  lakes), as well as **c** mean *Bythotrephes* abundance (no  $m^{-2}$ ) versus mean *Leptodora* body length (mm) ( $n = 7$  lakes). The equation of the linear regression in **(b)** is  $y = 0.856x + 0.092$  ( $r^2 = 0.880$ ,  $P < 0.001$ ) and in **(c)** is  $y = -0.004x + 5.819$  ( $r^2 = 0.658$ ,  $P = 0.028$ ), whereas the regression in **(a)** is not significant (see text). Note that the  $x$ -axes in **(a)** and **(b)** differ because Harp Lake is not included in **(a)** because too few *Leptodora* were captured for reliable estimates of average body size

Tuchman, 2004), our study and other recent studies (e.g., Weisz & Yan, 2011) suggest that declining *Leptodora* populations may be a widespread consequence of *Bythotrephes* invasion. In addition, our

study has demonstrated that these declines in *Leptodora* may be mediated by reduced abundance of small cladoceran prey. We have also shown that morphological responses of *Leptodora* to *Bythotrephes* invasion are not as clear. When we considered *Bythotrephes* invasion as a categorical variable (i.e., presence/absence), there was no difference in *Leptodora* body size in invaded lakes. However, when we treated *Bythotrephes* as a continuous variable (i.e., abundance), we observed significant declines in *Leptodora* body size with increased *Bythotrephes* abundance, suggesting that morphological differences in *Leptodora* may be a more sensitive response to invasion. In a subset of our lakes, we also observed smaller *Leptodora* feeding baskets in *Bythotrephes*-invaded lakes compared to non-invaded lakes, indicative of a morphological response of *Leptodora* in some invaded lakes. The relatively large body size of *Leptodora* in recently invaded lakes could be an indication that there has not been sufficient time for body length to respond to *Bythotrephes* invasion. As we chose our lakes to be as similar as possible in physical, chemical, and other biological aspects, here we present several possible food web explanations for the observed patterns, including: (a) competition for prey with *Bythotrephes*, (b) direct predation by *Bythotrephes*, and (c) size-selective predation by fish.

The first possibility is that predation by *Bythotrephes* changes zooplankton community composition and size structure in a manner that is detrimental to *Leptodora*. Although *Bythotrephes* effects on zooplankton appear to vary among studies (Yan & Pawson, 1997; Barbiero & Tuchman, 2004), we found that small cladocerans are significantly less abundant in invaded lakes in our study. *Leptodora* abundance increased significantly with small cladoceran abundance; however, we failed to observe a significant relationship between small cladocerans and *Leptodora* body size (Fig. 5), which may be attributable to the lack of morphological change in *Leptodora* in recently invaded lakes (Fig. 2). Since *Bythotrephes* and *Leptodora* overlap spatially (Foster & Sprules, 2009), and both feed on a similar size range of prey and prefer cladocerans (Lunte & Luecke, 1990; Vanderploeg et al., 1993), there is substantial potential for competition between them. *Leptodora* ingestion rate (Branstrator, 1998) and maximum prey size (Herzig & Auer, 1990) increase with feeding basket size (and body size with which it is strongly correlated), and thus

one would expect *Leptodora* to be as large as possible regardless of the zooplankton size distribution. However, Abrusán (2003) found that feeding basket size (corrected for body size) varied directly with seasonal changes in the size of their zooplankton prey. While this is an interesting possibility, it does not appear to be the mechanism at work in our study lakes: we would expect *Leptodora* to be comparatively larger (not smaller) in invaded lakes if they were responding to a paucity of small cladoceran prey.

*Leptodora* are not always large-bodied, which implies there is an associated disadvantage possibly due to increased energetic costs associated with the building, maintenance and drag associated with larger structures (Abrusán, 2003). One possible explanation is that *Leptodora* in long-term invaded lakes (with higher *Bythotrephes* abundance) have reduced overall growth efficiency as a result of the absence of appropriate prey, leading to smaller maximum body sizes compared to non-invaded lakes (e.g., Sherwood et al., 2002). In contrast to *Bythotrephes*, which use their mandibles to shred prey and are effective predators on a wide range of prey, *Leptodora* are constrained by the size of their feeding basket to consume a narrow size range of prey. If prey populations are depleted, *Bythotrephes* will be better able to switch food items, particularly to alternative prey at the upper end of the size spectrum, whereas *Leptodora* basket and/or body size must change to exploit the full range of available prey sizes. With a small number of study lakes, we are limited in our interpretation; however, these patterns highlight the need for greater understanding of morphological responses to invasion.

A second possible explanation for the trend toward smaller bodied *Leptodora* in lakes with higher densities of the invader is direct size-selective predation by *Bythotrephes*. In laboratory conditions, *Bythotrephes* instars 1–3 consumed adult *Leptodora* from 7.6 to 8.6 mm long (Branstrator, 1995); however, their ability to detect *Leptodora* in the field remains unknown. Furthermore many *Leptodora* in non-invaded lakes exceed 8.6 mm and are as large as 12 mm; it is not known whether *Bythotrephes* could have consumed these large animals that presumably existed when lakes were first invaded. Field observations on these predation interactions are necessary before the importance of direct *Bythotrephes* predation as a cause of changes in *Leptodora* size can be assessed.

Finally, it is possible that smaller body sizes of *Leptodora* in high *Bythotrephes* density lakes is due to size-selective predation by fish. For this to be likely, it is logically necessary that the intensity of fish predation is greater in our invaded than non-invaded study lakes or that invasion by *Bythotrephes* changes the fish community of lakes. Our presence–absence fish data indicate broad similarity between invaded and non-invaded lakes with yellow perch present in all lakes and no clear patterns for planktivorous rainbow smelt and cisco or the benthivorous lake whitefish. Given the predominant impact of the obligately planktivorous cisco on macroinvertebrates (e.g., *Bythotrephes*; Young & Yan, 2008) and zooplankton (Milne et al. 2005), if fish predation were the main cause of the patterns we have observed, we would expect *Leptodora* to be most abundant and largest in lakes without cisco (Peninsula, Fairy, and Maple, Table 1). By contrast, abundances are very low in Peninsula and Fairy Lakes (although they are high in Maple Lake; Fig. 2a), and similarly the smallest *Leptodora* found in any lake occur in Fairy and Peninsula (but they are larger in Maple Lake; Fig. 2b).

The other possible explanation related to fish predation is that *Bythotrephes* alters the feeding behavior of the fish community. Recent studies have suggested that *Bythotrephes* can consume large portions of zooplankton productivity (Strecker & Arnott, 2008; Bunnell et al., 2011), yet a number of planktivorous fish may avoid consuming *Bythotrephes* (Barnhisel & Kerfoot, 2004) or experience lower net growth because *Bythotrephes* spines occupy gut space but have no nutritional value (Parker Stetter et al., 2005), resulting in an overall loss of food available to planktivores. This reduced availability of energy may drive planktivores to forage on other resources, such as large-bodied *Leptodora*. We know of no study documenting *Bythotrephes* effects on fish community assemblages or shifts in fish foraging, and our data are insufficient to assess this complex food web interaction. On balance these observations do not support a strong role of fish predation on *Leptodora* in our study, but we cannot rule it out entirely and suggest that assessing food web interactions related to invasion should be a research priority.

The design of our study was to contrast zooplankton communities in lakes that had been invaded by *Bythotrephes* to those in non-invaded reference lakes. Although the lakes were chosen to be as similar as possible, there will inevitably be some physical and

biological differences among them. These differences, and the observational nature of our study, make it difficult to assign exact causes to the patterns we have observed. Nevertheless, we can offer alternative explanations, which remain to be tested with mechanistic studies, and feel that any loss of causative detail is made up for by the fact that our observations have been made in the natural settings in which the organisms exist.

In this study, we demonstrated that the abundance and size structure of *Leptodora* differed between lakes invaded or not by *Bythotrephes*, but that recently invaded systems may show lagged responses to invasion, possibly due to lower abundances of the invader. Although mechanisms for the negative association between *Leptodora* and *Bythotrephes* remain unclear, the abundance of *Bythotrephes* in lakes may be mediating changes in *Leptodora* morphology via changes in the abundance of small cladoceran prey. Direct predation by *Bythotrephes* or effects of planktivorous fish mediated by energetic changes in lake food webs may also be involved. Regardless of what is driving the changes in *Leptodora* populations, these results indicate that *Bythotrephes* invasion may trigger more complex and subtle changes in food webs than previously thought.

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