

Indirect food web effects of *Bythotrephes* invasion: responses by the rotifer *Conochilus* in Harp Lake, Canada

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Abstract As a recent invader of North American lakes, *Bythotrephes longimanus* has induced large changes in crustacean zooplankton communities through direct predation effects. Here we demonstrate that *Bythotrephes* can also have indirect food web effects, specifically on rotifer fauna. In historical time series data, the densities of the colonial rotifer *Conochilus unicornis* significantly increased after *Bythotrephes* invasion in Harp Lake, Ontario. No such changes were observed in a non-invaded reference lake, the nearby Red Chalk Lake. Evidence for two mechanisms explaining the *Conochilus* increase was examined based on changes to the crustacean

zooplankton community over time. Rapid and severe declines in several herbivorous species of cladoceran zooplankton after *Bythotrephes* detection indicated a decrease in exploitative competition pressure on *Conochilus*. Secondly, a later and significant decline to virtual extinction of native invertebrate predators (*Mesocyclops* and *Leptodora*) could account for the observed *Conochilus* increase which also began 1–2 years after invasion by *Bythotrephes*. Ultimately, it appears that both reduced competition followed by a loss of native invertebrate predators were necessary to lead to the large *Conochilus* densities observed following invader establishment. From this analysis of long-term community data, it appears that *Bythotrephes* has important indirect, as well as direct, food web effects in newly invaded North American lakes with implications for trophic relationships.

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Introduction

Bythotrephes longimanus, a recent invader into Canadian lake food webs, is a predatory cladoceran, native to the northern Palaearctic (Sprules et al. 1990). Since its arrival, *Bythotrephes* has

rapidly spread across central North America and in a recent census inhabits over 70 lakes in Ontario (Therriault et al. 2002). *Bythotrephes* has been linked to changes in the crustacean zooplankton community via direct predatory effects (Yan and Pawson 1997; Yan et al. 2002; Boudreau and Yan 2003). The appearance of *Bythotrephes* has resulted in a significant decrease in cladoceran species richness, with several historically prevalent species of Cladocera (e.g. *Daphnia pulicaria*, *Daphnia retrocurva*) disappearing altogether in invaded lakes (Lehman and Caceres 1993; Yan and Pawson 1997; Schulz and Yurista 1998). These changes to zooplankton epilimnetic communities have been reported both in the Great Lakes as well as in smaller inland Canadian Shield lakes.

Among the inland Canadian Shield lakes, Harp Lake has been monitored by the Ontario Ministry of the Environment (MOE) since the mid-1970's. These long-term data provide an excellent opportunity to study changes in the zooplankton community associated with an invasion by *Bythotrephes* in 1993. After invasion, a 17% decline in zooplankton species richness was observed, with severe declines in, or disappearance of, medium-sized cladocerans, (e.g. *Bosmina longirostris*, *Diaphanosoma birgei*, and *Bosmina tubicen*) (Yan and Pawson 1997; Yan et al. 2002). In the Great Lakes, *Bythotrephes* has also been implicated in declines of the macrozooplankton predator *Leptodora*, through exploitative competition and predation (Branstrator and Lehman 1991; Branstrator 1995). Yan and Pawson (1997) noted a similar decrease in *Leptodora* populations in Harp L., especially during the months of July and August, when *Bythotrephes* was most abundant in the lake.

While the effects of *Bythotrephes* on the macrozooplankton epilimnetic communities are well documented within the Great Lakes and Canadian Shield lakes, few studies have determined whether *Bythotrephes* has indirect effects on other species in the pelagic community (see Hovius et al. 2006). One group of pelagic organisms that should be affected, given the changes in the macrozooplankton community, is the microzooplankton group, the rotifers, since they are usually in competition with cladoceran species

and are consumed by most pelagic invertebrate predators. Rotifers are an important food web link to the microbial loop in lakes and therefore to issues of water quality.

A recent cross-lake survey of 14 Canadian Shield lakes provided evidence that *Bythotrephes* invasion is leading to large increases in rotifer densities, particularly in *Conochilus unicornis* (Hovius et al. 2006). *Conochilus* is a pelagic rotifer, living in large spherical colonies, forming a major component of rotifer communities in Canadian Shield lakes (Dieguez and Balseiro 1998). It is an important organism within the food web, both as a dominant filter feeders in the productive epilimnetic zone of lakes (Armengol et al. 2001), and as a source of food for larval fish and insects (Guma'a 1978; Williamson 1983). Here we determine whether there is evidence for increases similar to those observed in the cross-lake study (Hovius et al. 2006) in time series data from Harp Lake, a lake which has been well-studied both before and following, *Bythotrephes* invasion. We hypothesize that competition and predation pressure on *Conochilus* populations is greatly reduced after the arrival of *Bythotrephes*, leading to an indirect food web effect. With time series data encompassing both pre and post invasion densities, we hope to better identify potential food web changes leading to the large increases in *Conochilus* observed in our cross-lake survey (Hovius et al. 2006). Losses of Cladocera species and abundances could reduce competition for food resources for rotifers, as daphnid species have been shown to out-compete rotifers through exploitative and interference competition (Gilbert 1988a; Gilbert 1989). Of the two types of competition, *Conochilus* in particular, is likely to suffer from exploitative competition with crustacean zooplankton owing to their generalist feeding strategies and to a large size overlap in preferred planktonic food resources with crustacean zooplankton (reviewed in Arndt 1993, Walz 1995). Rotifer populations could also benefit from a reduction in macrozooplankton predators, including *Leptodora* and *Mesocyclops*, with *Bythotrephes* invasion. Juvenile *Leptodora* rely on the rotifer *Conochilus* sp. as a primary source of food (Branstrator 1995), and may control their population dynamics (Edmondson and

Litt 1987). *Mesocyclops* preys upon several rotifer species including *Conochilus* (Barbiero and Tuchman 2004). Thus, a reduction over time in *Leptodora* owing to *Bythotrephes*, might act as a release in population control for *Conochilus*.

To evaluate the effects of *Bythotrephes* on dynamics of *C. unicornis* in Harp L., densities of the rotifer were assessed before and after the 1993 invasion. Red Chalk Lake, a nearby non-invaded lake with similar limnological characteristics, was used as a control over the same time period. Using environmental and other zooplankton time series data, we attempt to determine the proximate mechanisms, or the series of direct links, that led to the indirect effects on *Conochilus* of *Bythotrephes*. To date, long-term time series data that encompass periods before and after *Bythotrephes* invasion are rare for North American lakes and this forcibly restricts our analyses to comparison of these two intensively sampled lakes that were part of a long-term monitoring program.

Materials and methods

Study site

Harp Lake is an oligotrophic, single-basin lake located in south-central Ontario (latitude 45°23', longitude 79°07'). It has a surface area of 71 ha, with a deep point of 37.5 m. The physical and chemical properties (Table 1) are similar to lakes of the same size within the region (Yan and

Pawson 1997). A description of its crustacean zooplankton and fish communities can be found in Yan and Pawson (1997). *Bythotrephes* was first observed in Harp L. during the summer sampling of 1993 although the invasion may have actually occurred a few years earlier and remained undetected until this year.

Red Chalk Lake is a nearby non-invaded lake (latitude 45°11', longitude 78°56'). Red Chalk L. is similar to Harp L., being oligotrophic, non-acidic, and dimictic with a surface area of 57 ha and a maximum depth of 38 m (Yan et al. 2001). The lakes are limnologically similar (Table 1), making them ideal for a comparative study. A detailed description of the crustacean zooplankton community in Red Chalk L. is given in Yan et al. (1996).

Sample collection

All zooplankton samples used during the study were collected by the Ontario Ministry of the Environment (MOE), from 1986 to 1998, every 3–4 weeks during the months of July and August. The samples were collected at the deep point in each lake using an 80 µm conical net, with a diameter of 0.125 m and a length of 0.75 m. Sequential vertical hauls were taken from different depths, 6, 13, 21 and 30 m in Harp L., and 8, 16, 24 and 32 m in Red Chalk L. The contents of these hauls were combined to form a single composite sample, which reflected the diminution of lake volume with depth. Samples were preserved immediately in 5.5% buffered sucrose formalin. For a detailed description of the sampling procedures, see Yan and Pawson (1997). The samples were originally collected for macrozooplankton assessment and not for rotifer analysis, and thus, a mesh aperture of 80 µm was used. Nets of this size will collect only half of the rotifers that are slightly smaller in length than the mesh (Yan and Geiling 1985) and can therefore not be relied upon for accurate solitary rotifer counts. However, the larger mesh size does accommodate a study on the colonial rotifer genus, *Conochilus*. Mature *Conochilus* colonies are >>80 µm in diameter (Dieguez and Balseiro 1998) and will have been accurately sampled in the MOE surveys.

Table 1 Comparison of the limnological characteristics of Harp Lake and Red Chalk Lake

Characteristic	Harp Lake	Red Chalk Lake
Latitude	45°23'	45°11'
Longitude	79°07'	79°56'
Area (ha)	71.4	57.1
Mean depth (m)	13.3	14.2
Maximum depth (m)	37.5	38
pH	6.3	6.3
Secchi depth (m)	3.98	5.95

The pH and Secchi depth data are long term averages of data collected by the Ontario Ministry of Environment, Dorset, Ontario, Canada (Yan et al. 2001)

Bythotrephes were purposely sampled for in Harp L. using 10 vertical plankton hauls at 10 random locations on the same schedule as other zooplankton since 1994. Hauls were taken 3 m from the bottom of the lake to the surface, using a zooplankton net (0.75 m in diameter, 285 μm mesh, 2.5 m in length, with a 1 m cylindrical section above a 1.5 m conical section) (Yan and Pawson 1997). The same sampling technique was used on occasion to assess the presence of *Bythotrephes* in Red Chalk L., where *Bythotrephes* was never observed (Yan et al. 2001).

Sample processing

Conochilus densities were counted as individuals, not as number of colonies, since colonies dis-aggregate after preservation. Sub-samples from the original crustacean zooplankton samples from each lake were counted until a volume representing ≥ 20 l of actual lake volume was counted. Counts were performed using an Olympus CKX41 inverted microscope at 100 \times magnification. Data for crustacean zooplankton and *Bythotrephes* abundances were obtained from the MOE.

Densities of all July and August samples were averaged to obtain yearly summer mean densities for *Conochilus*, crustacean zooplankton (including the predators *Leptodora kindtii* and *Mesocyclops edax*) and *Bythotrephes* (averaged over 10 sites and 10 hauls). The *Bythotrephes* density reported for 1993 in Harp L. however, was obtained from a single sampling date in mid-August since this was just after initial detection of the species. Water chemistry and chlorophyll *a* (chl *a*) data were also obtained from the MOE.

Analyses

The comparison of *Conochilus* densities before and after invasion of *Bythotrephes* in Harp L. with the populations in the control Red Chalk L. is typical of a BACI (Before-After-Control-Intervention) design. As is customary for analysis of data from such designs, we calculated the difference in densities (ΔN) at each point in time between the impacted and control lakes and then compared the mean values before and after

invasion using a *t*-test (Stewart-Oaten et al. 1986). Unfortunately more rigorous forms of time series analysis were not possible on such short time series (12 years). In cases where replication is not possible (as with our observation type of data on whole-lakes), Murtaugh (2002) recommends that instead of statistical testing, graphical displays, as well as expert opinion and common sense be used in the interpretation of BACI design data.

In order to evaluate which indirect effect pathways potentially induced by *Bythotrephes*, were causing changes in *Conochilus* densities in Harp L., a stepwise multiple regression was carried out using the annual Harp L. data from 1986 to 1998. Temporal autocorrelation (first order) of the residuals of the multiple regression was tested for using standardized Moran's *I* (*Z*). The test was non-significant ($Z=-1.5$, $P=0.1310$) based on a permutation procedure (Lichstein et al. 2002), hence we did not adjust for temporal dependence in the regression model. Possible explanatory variables in the model included \log_{10} transformed values of annual chlorophyll *a*, as well as summer mean density of zooplankton for the following groupings: predators (*Leptodora kindtii* and *Mesocyclops edax*), increasing Cladocera (*Holopedium* sp. and *Daphnia galeata mendotae*) and decreasing Cladocera (*Bosmina* sp., *Daphnia retrocurva*, *Eubosmina tubicen*, *Diaphanosoma* sp., *Polyphemus pediculus* and *Chydorus sphaericus*). Forward stepwise regression was used to determine the indirect factors most related to observed changes in *Conochilus* density over time.

Results

The difference in *Conochilus* densities between the impacted Harp L. and the control Red Chalk L. were significantly affected by the *Bythotrephes* invasion (Fig. 1a). A *t*-test on the values of the differences (ΔN) demonstrated that a significant impact of *Bythotrephes* on *Conochilus* densities occurred, with higher densities of *Conochilus* post-invasion ($P=0.002$). *Conochilus* densities in Harp L. increased 5-fold from a mean of 4120 individuals m^{-3} , prior to the arrival of *Bythotrephes*, to a mean of 21 000 individuals m^{-3} post

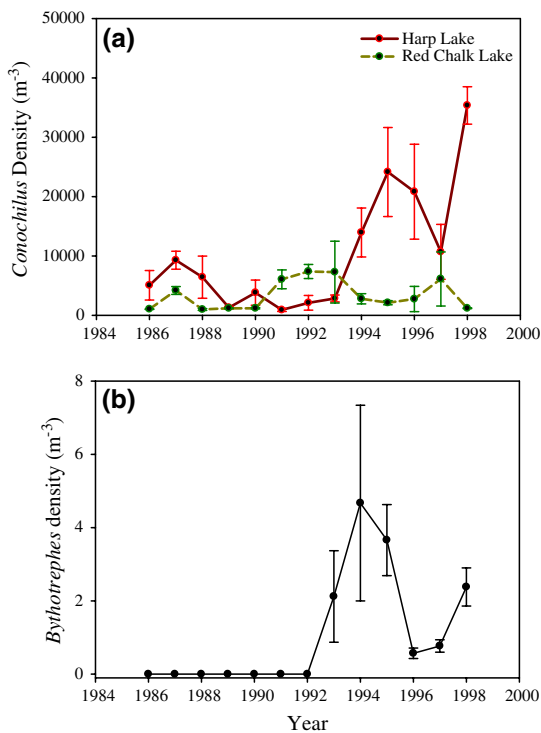


Fig. 1 Annual summer (July–August) mean (\pm standard error across sampling dates) (a) *Conochilus* densities (m^{-3}) for Harp L. and Red Chalk L. between 1986 and 1998 and (b) *Bythotrephes* densities between 1986 and 1998 in Harp Lake

invasion, but this only beginning in 1994, 1 year after *Bythotrephes* detection and probably one to two after actual invasion. No similar increase was observed after 1993 in Red Chalk L. We verified for an effect of density on the response observed in Harp L., which might be expected if the data were significantly temporally autocorrelated (i.e. higher densities of the rotifer prior to invasion pre-conditioning for an effect of higher densities post invasion, but in reality, unrelated to the invasion event). However, from Fig. 1a, it can be observed that densities of *Conochilus* were actually lower in Harp L. before the increase observed after 1993 and *Bythotrephes* invasion. This means that it is unlikely that we are making a type I error in concluding a significant effect from the *t*-test.

Large changes in the crustacean zooplankton community of Harp L. following *Bythotrephes* invasion were observed, and will be summarized here since they are important for explaining

potential mechanisms for indirect effects (but see Yan and Pawson 1997 for further details on macrozooplankton dynamics to 1995). After *Bythotrephes* colonized Harp L., yearly mean *Bythotrephes* densities ranged from 0.77 to 4.67 individuals m^{-3} (Fig. 1b). There were eight common cladoceran species present prior to *Bythotrephes* invasion (Fig. 2a, b). After 1993, six cladoceran species: *Bosmina* sp., *Chydorus sphaericus*, *Daphnia retrocurva*, *Eubosmina tubicen*, *Polphyemus pediculus*, and *Diaphanosoma* sp. disappeared (Fig. 2a), although most had already been depressed by 1993, when *Bythotrephes* was first detected. Other cladocerans, *Holopedium* sp. and *Daphnia galeata mendotae*, however, became more abundant after 1993 (Fig. 2b), indicating a compensatory food web response by larger cladoceran species. The net result for the cladoceran community over the entire water column was a lack of observable change in total biomass, even though densities declined (Fig. 2c). Analogous data for comparison with dynamics in Red Chalk L. are shown in Fig. 2d, e and f over the same time period. Extinctions of major cladoceran groups and increases in *D. galeata mendotae* after 1993 were not observed in Red Chalk L. In fact, total density and biomass as well as the densities of most cladoceran species increased after 1993.

Yearly mean total chl *a* levels were higher in Harp L. than in Red Chalk L. for all years in this study (Fig. 3). Chl *a* levels in Harp L. were elevated during the late 1980's, lowering to levels ranging from 0 to 2 $\mu\text{g l}^{-1}$ higher than those in Red Chalk L. in the 1990's. Most of the decrease in total chl *a* however, occurred a few years prior to the 1993 invasion by *Bythotrephes* (Fig. 3).

Two main *Conochilus* predators, the cladoceran *Leptodora kindtii* and the copepod *Mesocyclops edax*, which were both more common in Harp L. prior to the arrival of *Bythotrephes*, declined to essential biological extinction after invasion (Fig. 4a). Interestingly, both native predator populations (and especially *Leptodora*) showed large peaks in densities in 1992 (when *Bythotrephes* was likely present but undetected) and in 1993 (when *Bythotrephes* densities were still low). It was only in 1994 that truly severe

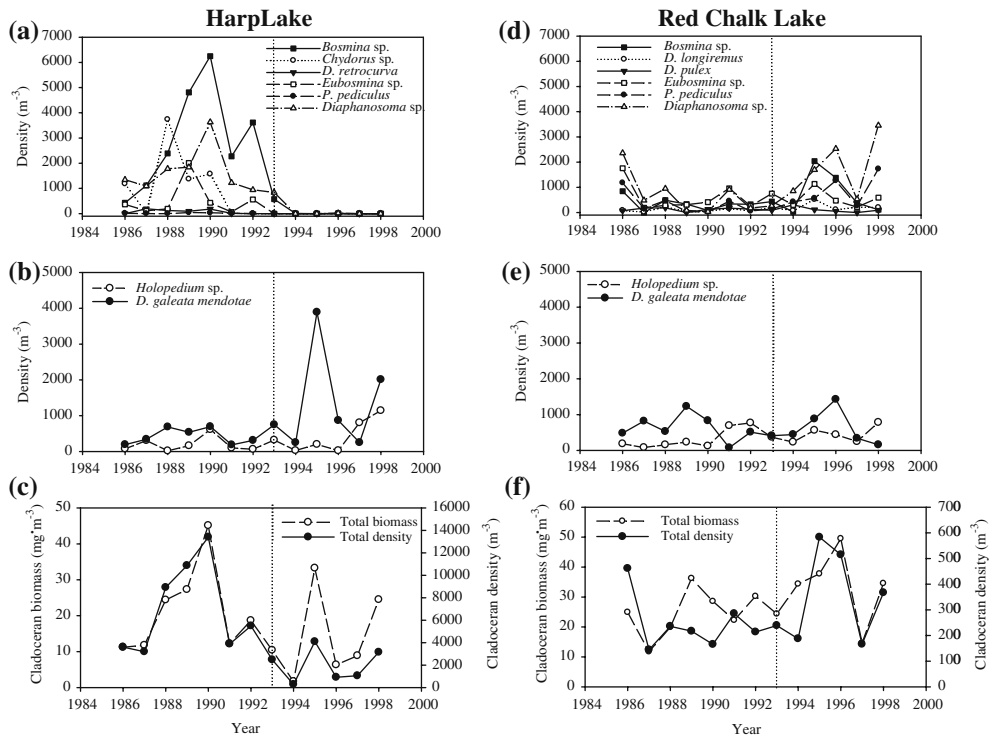


Fig. 2 Annual summer (July–August) mean cladoceran densities and total biomass for (a) six cladoceran species that displayed reduced densities after 1993 in Harp L., (b) two cladoceran species that increased in density after 1993 in Harp L., (c) mean total cladoceran biomass (dry weight) and density in Harp L., (d) the dominant

cladoceran species in Red Chalk L., (e) *Daphnia galeata mendotae* and *Holopedium* sp. in Red Chalk L., and (f) mean total cladoceran biomass (dry weight) and density in Red Chalk L. The date of *Bythotrephes* detection in Harp L. is indicated with a dotted vertical line on all graphs

declines in these two populations were observed. In Red Chalk L. (Fig. 4b), declines in *Leptodora* were also observed starting in 1990, but in

contrast to Harp L, there were very large increases in *Mesocyclops* after 1993.

A multiple regression was performed to determine which of the annual changes in zooplankton populations (increasing Cladocera, declining Cladocera, total predator density) and resource supply (chl *a*) of the lake were most related to the increase in *Conochilus* densities through time. All values were log₁₀ transformed before analysis to stabilize the variances. The best indicators of rotifer densities were total densities of declining Cladocera (the species in Fig. 2a) and chlorophyll *a*. Overall, the best fitting model in explaining *Conochilus* density was ($N=13$, $R^2_{adj}=0.79$, $P=0.0002$):

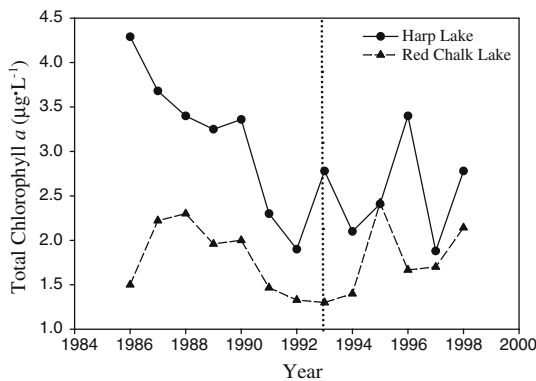


Fig. 3 Mean annual total chlorophyll *a* (µg l⁻¹) for Harp L. and Red Chalk L., from 1986 to 1998. The first year of detection of *Bythotrephes* in Harp L. is indicated with a dotted vertical line

$$\log \text{Conochilus}(l^{-1}) = 3.6 - 0.3 \log(\text{Declining Cladocera}) + 2.1(\log \text{chl } a)$$

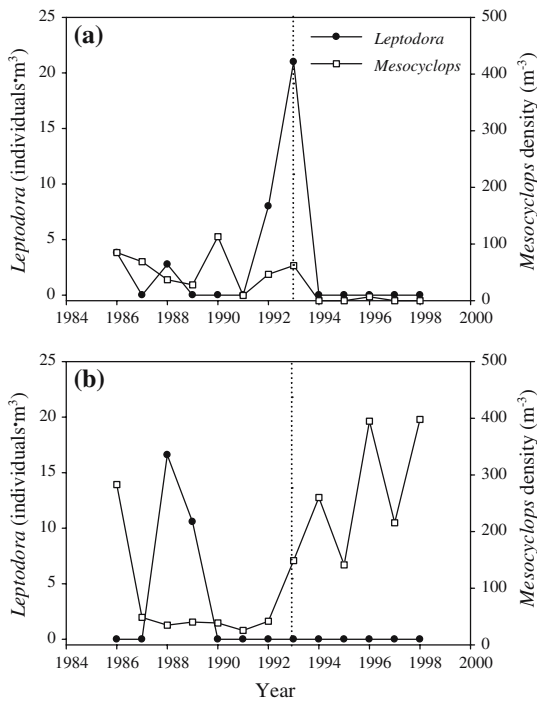


Fig. 4 Annual summer (July–August) mean densities of *Leptodora kindtii* and *Mesocyclops edax*, rotifer predators, between 1986 and 1998 in (a) Harp L. and (b) Red Chalk Lake. The first year of detection of *Bythotrephes* in Harp L. is indicated with a dotted vertical line

Discussion

Conochilus populations in Harp L. increased significantly after the 1993 invasion of *Bythotrephes*. Mean *Conochilus* density increased 5-fold, an increase not observed in the reference lake over the same time period. These observations, although purely correlational, suggest that *Bythotrephes* likely induced large increases in the colonial rotifer after establishment in Harp L. The mechanisms for the increase remain to be explored. The two main mechanisms by which an increase in *Conochilus* populations could have been induced are: reduced predation and/or reduced competition. We explore the evidence for both from these time series data.

Based on the multiple regression analysis, reduced competition appears to be a key factor responsible for the increase in *Conochilus* following invasion by *Bythotrephes*. Six clado-

ceran species disappeared from the food web after invasion and these were negatively related to *Conochilus* density in the model. It is generally acknowledged that cladocerans are better competitors than rotifers, negatively affecting rotifer numbers through both exploitative and interference competition (Yan and Geiling 1985; Gilbert 1988a, 1989). However, *Conochilus* may be less susceptible to interference competition than other rotifer species. Owing to its large colonial structure, it may be less sensitive to damage from larger *Daphnia* species (Gilbert 1988b). In terms of exploitative competition, *Conochilus* has been classified as a generalist herbivore (Walz 1995), as are many crustacean zooplankton, because it is able to consume both small bacteria and aflagellate algae, feeding unselectively on larger algae up to 20 μm in size (reviewed in Arndt 1993, Walz 1995). The overlap in food size preference suggests that a reduction in the presence of cladoceran species should lead to decreased competitive pressure for *Conochilus*.

Total cladoceran density declined following *Bythotrephes* invasion, which would support the argument that competitive pressure from herbivorous cladoceran declined after invasion. On the other hand, the total biomass of cladocerans remained fairly constant, owing to compensatory density increases by *Holopedium* and the large cladoceran *D. galeata mendotae*. However, there are important biological traits of these two cladoceran species that lead to the conclusion that the compensatory biomass increases may not equate with an increase in competitive pressure for *Conochilus*. *Holopedium* is a generally poor competitor that has low clearance rates (Allan 1973; Hessen et al. 1993; Brett and Goldman 1994). *D. galeata mendotae* uses vertical migration to avoid predation (Stirling et al. 1990; Lehman and Caceres 1993; Schulz and Yurista 1998), which could effectively result in a vertical separation of resource use between *Conochilus* and *D. galeata mendotae*. Dumitru et al. (2001) reported that owing to vertical migration, there is only weak overlap between *Bythotrephes* and *D. galeata mendotae* in Harp L., as *D. galeata mendotae* remains in deep waters for large portions of the day. *Conochilus*, which likely remains in the epilimnion or the metalimnion, as observed in

other lakes (Galkovskaya and Mityanina 2005), would perhaps therefore not be in direct competition with migrating *D. galeata mendotae* at least during the productive daylight hours. Thus, competitive release induced by *Bythotrephes* predation, is a likely candidate to explain the observed release of *Conochilus* in Harp L after invasion.

The relationship between resource (chlorophyll *a*) and *Conochilus* density dynamics also changed following *Bythotrephes* invasion in Harp L. Chl *a* emerged as an important variable explaining *Conochilus* changes in the multiple regression analysis. Interpretation of the results are complicated somewhat by the fact that chl *a* levels in Harp L. declined steadily through the late 1980's and early 1990's owing to declining phosphorus levels in this lake (Dillon and Molot 2005). In Harp L. however, peak abundances of *Conochilus* after *Bythotrephes* invasion coincided with peak years of chl *a* (in years 1995, 1996 and 1998). Such a correspondence of *Conochilus* peaks (although much smaller) with chl *a* peaks were not observed in Red Chalk L. where no *Bythotrephes* invasion occurred. These results suggest a release of grazer community control over phytoplankton biomass when *Bythotrephes* was added as a strong top-down force in the food web. If this were the case, it is possible that *Conochilus* was then able to take advantage of the extra resources in high chlorophyll years. However, not knowing the size structure of the phytoplankton community is a severe limitation to interpretation. Grazing by *Conochilus* can exceed grazing rates of crustacean zooplankton on smaller phytoplankton (<23 μm) in oligotrophic lakes (Armengol et al. 2001) and therefore feeding predominantly by such size-limited herbivores should favor the growth of less edible phytoplankton (i.e. large size classes) (Grover 1995). Thus, whether coincident increases in total chlorophyll in years of peak *Conochilus* density was the cause of *Conochilus* population growth or a consequence of *Conochilus* feeding (i.e. releasing larger phytoplankton from competition which leads to high measured chl *a*), remains unknown. Correspondence between the dynamics of *Conochilus* and their phytoplankton prey biomass and size structure should be examined in greater detail in future studies to determine why peaks

should be coincident when *Bythotrephes* suppresses cladoceran herbivore density.

Release from predation by native invertebrates is another potential mechanism for the large increases in *Conochilus* in Harp L. following *Bythotrephes* establishment. Previous work has shown that *Conochilus* is not vulnerable to predation by *Bythotrephes* (Hovius et al. 2006) despite being very vulnerable to *Leptodora* (Lunte and Luecke 1990). *Leptodora* is a large predacious cladoceran that relies on *Conochilus* as its primary food source, and is the primary predator of *Conochilus* in most lakes (Lunte and Luecke 1990; Branstrator and Lehman 1991). *Leptodora* populations, declined to extinction shortly after the *Bythotrephes* invasion in Harp L. but they were also at undetectable levels in Red Chalk L. in July and August starting in 1990 for unknown reasons. However, *Mesocyclops*, the other major predator of *Conochilus* in these lakes had densities reduced to virtual extinction after *Bythotrephes* invasion in Harp L. even while densities of *Mesocyclops* increased to unprecedented levels over the same period in Red Chalk L. Interestingly, *Mesocyclops* and *Leptodora* dynamics responded similarly in Harp L. with increases in the early years of invasion followed by large declines, suggesting these native predator species may both be secondary prey choices for *Bythotrephes*, only being consumed once preferred and smaller crustacean prey resources are exhausted. Suppression of both predator species has been observed in previous studies following *Bythotrephes* invasion. *Leptodora* declined in Lake Michigan (Branstrator and Lehman 1991; Branstrator 1995) likely because *Bythotrephes* both out-competed *Leptodora* for shared resources, and attacked and fed directly on *Leptodora* (Branstrator 1995). *Mesocyclops edax* populations were suppressed after the arrival of *Bythotrephes* in other North American lakes, possibly as a result of *Bythotrephes* feeding on copepod nauplii (Vanderploeg et al. 1993; Barbiero and Tuchman 2004).

It is possible that the reduction in these two predator species led to a reduction of predation pressure allowing *Conochilus* populations to increase in Harp L since large declines in overall native predator densities were not also observed in Red Chalk L. (where no increase in rotifers was

observed). In Harp L., *Bythotrephes* were first detected in 1993 but it was likely present in the lake before then at lower densities since declines in crustacean zooplankton began in the early 1990's. *Conochilus* densities however, did not increase significantly before 1994 which suggests they were still limited by some factor until then. Since *Leptodora* and *Mesocyclops* were both very abundant in 1992 and 1993, predation is the likely explanation for delayed increases in the rotifer populations. In addition, dynamics of *Conochilus* and predators in Red Chalk L. showed an inverse correspondence with years of high predator abundance coinciding with years of very low rotifer densities (e.g. 1986, 1988–1990 and 1994–1998). *Mesocyclops* preys upon several rotifer species, including *Conochilus* (Barbiero and Tuchman 2004). Increases in *Conochilus* were observed in Lake Michigan following the suppression of *Leptodora* by *Bythotrephes* (Branstrator 1995). Edmondson and Litt (1987) found evidence for *Leptodora* controls of *Conochilus* populations in a long-term study of Lake Washington, Seattle. In mesocosm experiments, high *Leptodora* densities reduced *Conochilus* densities by >40%, (Lunte and Luecke 1990). However, despite observed declines in native predator abundances in Harp L., *Leptodora* and *Mesocyclops* densities did not emerge as a significant explanatory factor for changes in *Conochilus* density in the multiple regression. This is not surprising since the densities of native predators were extremely low, but highly variable in Harp L. (which suggests that a non-linear model may better explain predators than does stepwise multiple regression which assumes linearity). However, one can not ignore the biological significance of a complete loss of predators as a factor that releases prey populations, as well as the delayed increase in *Conochilus* even after the sharp declines in several cladoceran competitors with *Bythotrephes* invasion. Thus we cannot exclude the possibility that release from predation for *Conochilus* occurred in Harp L.

In summary, *Conochilus* populations increased in Harp L. following invasion of *Bythotrephes*. There is evidence for multiple indirect effects of *Bythotrephes* leading to these increases and we propose the following hypothesis: initially a

decrease in competitive pressure from crustacean zooplankton species allowed for increased production by *Conochilus* populations (but not realized densities because of the presence of native predators), followed by a reduction in predation pressure from native macrozooplankton predators after depletion of *Bythotrephes*' preferred crustacean zooplankton prey. Sharp declines in competitors alone in 1993 were not enough to lead to large *Conochilus* increases because of a dynamic response by the invertebrate predators, which may have been in turn, a response to increased *Conochilus* productivity. Predation by native invertebrate species may limit *Conochilus* in these lakes because no increase in *Conochilus* populations were observed until 1–2 years after *Bythotrephes*, by which time the native invertebrate predator populations likely became *Bythotrephes* prey. Ultimately, it appears that there were several indirect food web pathways that led to large increases in the rotifer *Conochilus* in Harp Lake. By using time series data and experimental approaches in the future, we will better be able to determine better the mechanisms by which indirect effects of *Bythotrephes* in newly invaded lakes arise, if more detailed data on food web changes are collected such as changes in phytoplankton community composition. With time, as more lakes are invaded in North America with both pre and post-invasion data, a clearer and more mechanistic picture will evolve as to the food web pathways of indirect effects of this invasive species.

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