Changes in zooplankton and the phenology of the spiny water flea, Bythotrephes, following its invasion of Harp Lake, Ontario, Canada

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Abstract: The crustacean zooplankton community of Harp Lake, Ontario, Canada, has changed appreciably since the invasion by the spiny water flea, Bythotrephes. Crustacean species richness has declined, large-bodied Cladocera have replaced small-bodied ones, and there has been a downward trend in the total abundance of zooplankton because copepod abundance has remained stable while Cladoceran abundance has declined. Although the zooplankton community has now been stable for 4 years (1995–1998), the biology of the invader has changed dramatically. In particular, there have been 10-fold differences in the mean annual abundance of Bythotrephes in this 5-year period and substantial changes in the timing of population maxima. We attribute these changes to two factors: (i) transition from a summer to a fall switch from parthenogenesis to gametogenesis and (ii) interannual differences in the thickness of a warm, dark stratum in the lake. We hypothesize that this stratum provides a refuge for Bythotrephes from predation by lake herring, Coregonus artedii.

Résumé: La communauté des crustacés du zooplancton du lac Harp, en Ontario, Canada, s’est modifiée de façon notable depuis l’invasion de la Puce d’eau épineuse, Bythotrephes. La richesse en espèces des crustacés a décliné. Les cladocères de grande taille ont remplacé ceux de petite taille et il y a une tendance à la baisse dans l’abondance totale du zooplancton, car, bien que la densité des copépodes soit demeurée constante, celle des cladocères a baissé. La communauté zooplanctonique est restée stable depuis 4 ans (1995–1998); néanmoins, la biologie de l’espèce envahissante a changé de façon spectaculaire. En particulier, il y a eu des variations par un facteur de 10 des densités annuelles moyennes de Bythotrephes pendant cette période de 5 ans et des changements importants dans la phénologie des maximums de densité. Nous attribuons ces changements à deux facteurs: (i) un déplacement de l’été à l’automne du passage de la parthénogenèse à la gamétogenèse et (ii) aux différences inter-annuelles de l’épaisseur d’une strate obscure et chaude dans le lac. Nous croyons que cette strate fournit un refuge à Bythotrephes contre la prédation exercée par le Cisco de lac, Coregonus artedii.

Introduction

The population dynamics of introduced species are difficult to predict. “Boom and bust” dynamics are common for both introduced plants (Creed and Sheldon 1995) and animals (Williamson and Fitter 1996), but monotonic increases to steady states (Ramcharan et al. 1992) are also common. The dynamics of particular invaders may be system-specific. For example, Ramcharan et al. (1992) noted both boom–bust dynamics and monotonic increases in abundances in invading zebra mussel populations. Hence, we cannot reliably predict the long-term demographics of introduced species in particular systems either from short-term studies in those systems or from longer-term studies in other invaded habitats.

The cladoceran Bythotrephes longimanus (Crustacea: Branchiopoda: Onychopoda), until recently termed B. cederstroemi (Grigorovich et al. 1998), invaded each of the Laurentian Great Lakes in the 1980s. The probable source was the Baltic Sea, a population originating in Lake Ladoga, upstream of St. Petersburg (Berg et al. 2001). Bythotrephes first appeared in Canadian Shield lakes in 1989 (Yan et al.
We predict that it will become an important member of the Shield lake plankton for three reasons. Firstly, the invader is spreading rapidly. Since 1989, *Bythotrephes* has colonized at least 34 inland lakes in Ontario (MacIsaac et al. 2000). Secondly, many Shield lakes have suitable *Bythotrephes* habitat, given its apparent preference for large, oligotrophic lakes in its native Eurasia (MacIsaac et al. 2000). Finally, *Bythotrephes* has had large impacts on the structure of zooplankton communities (Lehman and Caceres 1993; Yan and Pawson 1997) soon after its establishment. Unfortunately, the available North American *Bythotrephes* case studies are too brief to determine if the invader has characteristic demographics or if the effects of the invader are permanent. Both European (Manca and Ruggiu 1998) and North American Great Lakes’ studies (Johannsson et al. 1991) indicate that *Bythotrephes* populations are characterized both by large interannual variations in abundance and by flexible demographic and behavioural responses to predators (Bilkovic and Lehman 1997; Strale and Hälbich 2000). Hence, we should not assume that the patterns in zooplankton detected soon after North American *Bythotrephes* invasions will be stable.

*Bythotrephes* first appeared in Harp Lake, Ontario, Canada, in 1993 (Hall and Yan 1997). By 1995, the crustacean zooplankton of the lake had changed in several ways. The abundance of two small taxa, *Bosmina longirostris* and *Tropocyclops extensus*, declined appreciably, and three small cladocerans, *Chydorus sphaericus*, *Diaphanosoma birgei*, and *Bosmina (Neobosmina) tabicen*, disappeared from our collections. In contrast, the abundance of a few larger taxa, *Holopedium gibberum* and especially *Daphnia mendotae* and *Leptodiaptomus sicilis*, increased to previously unrecorded levels (Yan and Pawson 1997). Eliminating competing hypotheses, Yan and Pawson (1997) suggested that *Bythotrephes* was responsible for these changes. Dumitru et al. (2000) provided supporting evidence, demonstrating that despite substantial predation from lake herring (Coulas et al. 1992), it first appeared in zooplankton samples in Harp Lake in the summer of 1993, having perhaps invaded a year or two earlier.

We compare the changes in the zooplankton of Harp Lake, associated with the arrival of *Bythotrephes*, with those in the neighboring Blue and Red Chalk lakes, which have not been colonized by *Bythotrephes*. Like Harp Lake, the two reference lakes are nonacidic, oligotrophic, clear-water, stratified lakes (Table 1) with characteristic demographics or if the effects of the invader are permanent. Both European (Manca and Ruggiu 1998) and North American Great Lakes’ studies (Johannsson et al. 1991) indicate that *Bythotrephes* populations are characterized both by large interannual variations in abundance and by flexible demographic and behavioural responses to predators (Bilkovic and Lehman 1997; Strale and Hälbich 2000). Hence, we should not assume that the patterns in zooplankton detected soon after North American *Bythotrephes* invasions will be stable.

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We now suspect that the interactions quantified by Dumitru et al. (2000) between *Bythotrephes* and its Harp Lake prey might have been short-lived. After all, *Bythotrephes* growth was unusual in 1995. *Bythotrephes* typically grow between each instar (e.g., Burkhhardt 1994; Strale and Hålbich 2000), but there was no growth between instars II and III in Harp Lake in the summer (Yan and Pawson 1998). The life history of *Bythotrephes* was also unusual. *Bythotrephes* normally switches from parthenogenetic to gametogenic reproduction in the fall (Strale and Hålbich 2000), but this switch happened in midsummer in Harp Lake in 1994 and 1995. Yan and Pawson (1998) hypothesized that these peculiarities in demographics were attributable to a scarcity of prey in midsummer, an observation supported by Dumitru et al. (2000). Here, our goal is to determine if the *Bythotrephes* population or its zooplankton prey changed after 1995. In particular, our objectives are to determine (i) if the short-term changes in the zooplankton community observed by Yan and Pawson (1997) have been maintained, if any new changes have developed, and if the Harp Lake changes are unusual in comparison with neighboring lakes that have not been invaded; (ii) if the unusual life-history characteristics of *Bythotrephes* observed by Yan and Pawson (1998) have been maintained; and (iii) if there is evidence that a refuge from lake herring predation is important in the demographics of *Bythotrephes* in Harp Lake, as suspected by Yan and Pawson (1998).

**Materials and methods**

**Study lake descriptions**

Harp Lake is a single-basin, relatively small (71.4 ha), deep (\( z_{max} \) of 37.5 m) lake located in southcentral Ontario, Canada. Its waters are soft and nutrient-poor (Table 1), as is typical of the region. Before the arrival of *Bythotrephes*, an average of 16 crustacean zooplankton taxa was recorded each year in the lake (Yan and Pawson 1997). Copepods contributed roughly 80% of the biomass. Because the hypolimnion of the lake is both deep and well oxygenated, several of these were cold stenotherms and (or) glacial relics, including *Epischura lacustris*, *Leptodiaptomus sicilis*, and *Senecea calanoides*. *Coregonus artedi*, lake herring, is the dominant pelagic zooplanktivorous fish in the lake (Coulas et al. 1998). *Bythotrephes* first appeared in this region of Ontario in 1989 (Yan et al. 1992). It first appeared in zooplankton samples in Harp Lake in the summer of 1993, having perhaps invaded a year or two earlier.

We compare the changes in the zooplankton of Harp Lake, associated with the arrival of *Bythotrephes*, with those in the neighbouring Blue and Red Chalk lakes, which have not been colonized by *Bythotrephes*. Like Harp Lake, the two reference lakes are nonacidic, oligotrophic, clear-water, stratified lakes (Table 1) with largely forested catchments. Yan et al. (1996) describe their zooplankton communities.

**Sampling and sample enumeration**

Each time that we visited Harp Lake, we estimated the euphotic zone depth as twice the Secchi depth. We also quantified thermal stratification using a temperature profile taken at 1-m intervals at the deepest spot in the lake. We identified the top of the hypolimnion as the depth at which the decline of temperature with depth fell to <1°C·m\(^{-1}\). Yan and Pawson (1997) detail the methods used for locating the one sampling station for collecting, identifying, measuring, and counting crustacean zooplankton from Harp Lake between 1978 and 1995. We used identical methods between 1996 and 1998 in Harp Lake and in all years in Blue Chalk and Red Chalk lakes (Yan et al. 1996). Yan and Pawson (1998) detail the methods used for locating the 10 *Bythotrephes* sampling stations in Harp Lake and for collecting *Bythotrephes* in 1994 and 1995. They also detail methods that were used to assess the gender, developmental stage, fecundity, stage of brood development, and clutch size of parthenogenetic and gametogenic broods. We used identical methods for collecting and counting *Bythotrephes* from 1996 to 1998 with the following exceptions. The filtration efficiency of the *Bythotrephes* net (0.75 m diameter, 2.5 m long, 285 \( \mu \)m mesh) averaged 88% between 1995 and 1997. Efficiency was not measured in 1988; the 1995–1997 mean value was employed instead. Vertical hauls were taken from 2 to 3 m above bottom to the surface at all 10 stations in all years except 1996, when samples were collected only from the four stations within the 21-m contour and only from the bottom of the metalimnion.

Most samples were examined in their entirety for *Bythotrephes*. We examined 550, 1144, 30, 237, and 1641 *Bythotrephes* annually from 1994 to 1998, respectively. Gender was not assessed in 1996 or 1997.

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Hall and Yan (1997) noted that only 2% of the *Bythotrephes* population was located in the hypolimnion during the day in Harp Lake; hence, we report *Bythotrephes* abundance per unit volume of epilimnion + metalimnion. *Bythotrephes* abundance did not differ among the nine sampling strata when tested in 1994 and again in 1998; hence, we report the descriptive statistics of the population without correcting for the areas of the sampled strata.

### Analytical methods

We can be certain that *Bythotrephes* was in Harp Lake in 1993. Hence, for statistical comparisons, we treat 1993 to 1998 as the postinvasion period. All statistical analyses were performed on ice-free season averages. We used several univariate metrics, including total zooplankton abundance (log-transformed), average species richness, i.e., the average number of species recorded in our standardized counts of roughly 250 animals, and the size of all Cladocera measured in the year. To test if the community changed after the arrival of *Bythotrephes*, we calculated a $t$ statistic assuming unequal variances, given the unbalanced design (15 preinvasion and 6 postinvasion years). If significance levels were close to 0.05 in this conventional assessment, we retested the significance of the $t$ statistic using a randomization procedure, i.e., by reshuffing the time series 999 times and recalculating the difference between means of the last six shuffled data points in comparison with the mean of previous data points in the series. This approach was used because our time series of annual means should not be considered a random sample, and it is unbalanced, implying some risk of bias in the use of conventional statistical tables (Manly 1991). Because multivariate metrics may provide more sensitive indications of change in communities than do univariate ones (Yan et al. 1996), we also described changes in average community composition in the lake using the correspondence analysis routines in Statistica.

We used the same 17 zooplankton taxa previously used by Yan and Pawson (1997), with log-transformed, ice-free season mean abundances of these taxa as our input.

### Results

The zooplankton community of Harp Lake has changed dramatically since the arrival of *Bythotrephes* in 1993. However, there have been no substantial changes in the community since the 1995 field season, i.e., since Dumitrul et al. (2000) predicted transitions in the zooplankton community and (or) in the *Bythotrephes* population.

With only 3 years of postinvasion data (1993–1995), Yan and Pawson (1997) were not able to detect a change in the overall abundance of zooplankton in Harp Lake; however, this now appears to be changing. The geometric mean of the mean annual zooplankton abundances fell from 22.1 animals·L$^{-1}$ ($s^2 = 1.02, n = 13$) before the arrival of *Bythotrephes* to 18 animals·L$^{-1}$ ($s^2 = 1.02, n = 6$) between 1993 and 1998 (Fig. 1a). This change in mean total crustacean zooplankton abundance, while not significant at $p = 0.05$ ($t = 1.83, p = 0.096$ by conventional assessment, and $t = 1.86, P = 0.075$ with 999 randomizations, after log-transformation), does suggest a trend. This trend was entirely attributable to a significant decline in the mean abundance of Cladocera (log-transformed) after 1992 ($t = 5.6, p < 0.001$), not to any change in the abundance of Copepoda (Fig. 1a).

There is no doubt about the changes in overall crustacean species richness and size structure. Zooplankton richness has declined in Harp Lake since the arrival of *Bythotrephes* (Fig. 1b). The average number of species detected in our standard counting protocol was 9.92 species per count between 1980 and 1992. It fell by 18% to a mean of 8.1 species per count in the 6 years after *Bythotrephes* was detected ($t = 4.18, p < 0.001$ with 999 randomizations). The mean individual body length of Cladocera in our samples doubled from 0.43 mm before the invasion to 0.85 mm after the invasion (Fig. 1c, $t = 11.7, p < 0.001$ after 999 randomizations).

The change in mean Cladoceran size was principally attributable to a change in the relative abundances of different

### Table 1. Limnological comparison of Harp, Blue Chalk, and Red Chalk lakes.$^a$

<table>
<thead>
<tr>
<th></th>
<th>Harp Lake</th>
<th>Blue Chalk Lake</th>
<th>Red Chalk Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude</td>
<td>45°23'</td>
<td>45°12'</td>
<td>45°11'</td>
</tr>
<tr>
<td>Longitude</td>
<td>79°07'</td>
<td>78°56'</td>
<td>79°56'</td>
</tr>
<tr>
<td>Lake area (ha)</td>
<td>71.4</td>
<td>52.4</td>
<td>57.1</td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td>13.32</td>
<td>8.5</td>
<td>14.2</td>
</tr>
<tr>
<td>Maximum depth (m)</td>
<td>37.5</td>
<td>23</td>
<td>38</td>
</tr>
<tr>
<td>Total phosphorus (µg·L$^{-1}$)</td>
<td>6.78</td>
<td>5.97</td>
<td>5.27</td>
</tr>
<tr>
<td>pH</td>
<td>6.27</td>
<td>6.6</td>
<td>6.30</td>
</tr>
<tr>
<td>Secchi depth (m)</td>
<td>3.98</td>
<td>6.56</td>
<td>5.95</td>
</tr>
<tr>
<td>Conductivity (µS)</td>
<td>35.7</td>
<td>28.6</td>
<td>28.8</td>
</tr>
</tbody>
</table>

zooplankton species in the lake rather than to a change in size of individual species. The abundance of mostly small Cladocera decreased by orders of magnitude (Fig. 2). These included *Chydorus sphaericus* (long-term mean length of 0.29 mm in Harp Lake), which declined in abundance in 1991, before we had actually detected *Bythotrephes* in the lake, *Daphnia retrocurva* (0.86 mm), *Diaphanosoma birgei* (0.65 mm), *Bosmina (Neobosmina) tubicen* (0.39 mm), and *Bosmina longirostris* (0.31 mm). In contrast, the abundance of the two larger Cladocerans, *Holopedium gibberum* (0.84 mm) and *Daphnia mendotae* (0.93 mm), has increased appreciably. There were no long-term changes in the mean sizes of individual cladoceran taxa if we ignore some recent artifactual increases in variability of the size of those species with plummeting populations (Fig. 3). Hence, it is clear that the cause of the overall increase in Cladoceran size in the lake (Fig. 1c) was the replacement of small taxa with larger taxa after 1993.

These enormous changes in the zooplankton community of Harp Lake were complete by 1995. There were no appearances, disappearances, or appreciable changes in the abundance of taxa between 1995 and 1998 (Fig. 2). Hence, there were no appreciable changes in abundance, richness, or
size structure of the community since 1995 (Fig. 1). Further, the correspondence analysis confirms that the community had two periods of compositional stability separated by a transition in the early 1990s (Fig. 4).

Although there have been no appreciable recent changes in the crustacean zooplankton assemblage in Harp Lake, the situation for *Bythotrephes* is quite different. Patterns of abundance, growth, and life history have changed both within and among years.

The abundance patterns of *Bythotrephes* have changed since 1995 in several ways. The mean abundance of *Bythotrephes* for the ice-free season was 2 animals·m⁻³ in 1994 and 3.2 m⁻³ in 1995. In both years, the population was very small in the spring, lagging well behind increases in water temperature and population increases of small Cladocera (Yan and Pawson 1998). The *Bythotrephes* population then reached a single maximum in July, after which it fell in response to a switch from parthenogenesis to gametogenesis and resting-egg production. The only similarity to this 1994–1995 pattern in recent years is the low population size in the spring (Fig. 5). All else has changed. In 1996 and 1997, the population was small at all times, averaging only 0.26 and 1.32 animals·m⁻³, respectively. At 5.14 m⁻³, the population was larger in 1998 than in any other year. The interannual changes in seasonality were dramatic. The summer maximum of 1994 and 1995 disappeared to be replaced by an unprecedented fall maximum in 1998.

The summer maximum failed to appear from 1996 to 1998 despite good aestival fecundity. During July and August, the average sizes of parthenogenic clutches were quite similar between 1994 and 1998 at around 3 embryos per clutch (Fig. 6). Further, the number of gravid animals was similar, so that the summer egg ratio was similar in 1995 (at 0.24 eggs-female⁻¹) and in 1998 (at 0.36). The persistence of the population into the fall of 1998 suggests a major change from the earlier life-history pattern in the lake. Indeed, in comparison with 1994 and 1995, there were far fewer males in midsummer in 1998 (Fig. 7a). Of greater importance, no females were producing clutches of resting eggs in July and early August of 1998, whereas most females had switched to resting-egg production in the summers of 1994 and 1995 (Fig. 7b).

Growth patterns of *Bythotrephes* also changed during our study. In 1995, there was very little growth between instars II and III in the summer, and body sizes actually fell through August (Fig. 8). In contrast, in 1998, mean lengths increased from instar II to III at all times, and the body size of each instar increased almost continuously throughout the year.

**Discussion**

Yan and Pawson (1997) detected a change in the richness of the zooplankton community of Harp Lake after the *Bythotrephes* invasion but did not report a change in mean Cladoceran size or abundance. Our addition of 3 years to the time series confirms that the richness of the community has indeed fallen. We supplement the previous work with our evidence that total abundance of zooplankton appears to be declining in the lake in response to a large drop in Cladoceran abundance.

Although reductions in total zooplankton abundance have been observed in mesocosm experiments with *Bythotrephes* (Wahlström and Westman 1999), our observation of a reduction in the abundance of an entire natural zooplankton community appears to be novel. There certainly have been reports of dramatic alterations in the daphniid component of
the Cladoceran assemblage (Manca and Ruggiu 1998; Lehman and Caceres 1993) but apparently not for the total zooplankton assemblage. If we are to attribute this change in Harp Lake to the arrival of *Bythotrephes*, we must, as a minimum, prove both that the observed changes are unusual in magnitude for the region and that synchronous changes have not occurred in nearby uninvaded lakes. Such interlake synchrony has been observed for some zooplankton species, e.g., *Leptodiaptomus minutus*, in other lakes in the region (Rusak et al. 1999) and attributed to annual variations in climate. Hence, it is possible that the decline in zooplankton abundance detected in Harp Lake, although real, may have had nothing to do with the arrival of *Bythotrephes*.

The decline in species richness observed is unprecedented in nonacidifying lakes on the Shield (Arnott et al. 1999); however, we have no readily available published data to compare with the changes in mean Cladoceran size and total zooplankton abundance. Hence, we compared these long-term changes in Harp Lake with those in Blue Chalk and Red Chalk lakes. The reference lake comparisons support our conclusion that Cladoceran size and total zooplankton abundance have changed in Harp Lake as a result of the invasion, not as a result of a regional climatic anomaly. Although mean zooplankton abundance in Harp Lake declined after 1992, there was no change in mean annual abundance in Blue Chalk Lake (*t* = 0.66, *p* = 0.52, tested on log-transformed data) or in Red Chalk Lake (*t* = −1.53, *p* = 0.16) after 1992 (Fig. 9a). Hence, the decrease in mean zooplankton abundance observed in Harp Lake was not a pattern found across the region. No formal analysis is required to determine that the increase in Cladoceran body size observed after 1992 in Harp Lake was unusual in comparison with the reference lakes (Fig. 9b). Hence, we conclude that the zooplankton community of Harp Lake changed after 1992 for reasons peculiar to the lake. We hypothesize that the arrival of *Bythotrephes* is this peculiarity.

Although the zooplankton community has not changed appreciably since 1995, the *Bythotrephes* population certainly has. The change in seasonality cannot be explained by exam-
Fig. 7. Seasonal changes in 1994 (○), 1995 (■), and 1998 (▲) of (a) males, as percent of the total *Bythotrephes* population, and (b) the percent of the total broods produced by *Bythotrephes* that were resting-egg broods. Too few animals were caught in 1996 for the sex ratio assessment, and gender was not recorded in 1997. The small, late-June peak in 1998 in Fig. 7a represents only one animal.

Fig. 8. Seasonal changes in the body + head length of female *Bythotrephes* (± standard error (SE)) in Harp Lake in (a) 1995 and (b) 1998. These years were selected given their large sample size. Instar IV animals are present only in the spring. Very few were captured; hence, their estimates are poor. Instars: I (■), II (○), III (◆), IV (▲).

Fig. 9. Comparison of long-term changes in (a) the total crustacean abundance and (b) Cladoceran body length of zooplankton in Harp Lake (▲) with two noninvaded reference lakes, Blue Chalk Lake (□), and the main basin of Red Chalk Lake (○).

Yan et al.

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difference between the depth at the top of hypolimnion and the euphotic zone depth (estimated as twice the Secchi depth, see their fig. 8). Where the euphotic zone includes some of the hypolimnion, the metric is negative, the mixed waters of the lake are well illuminated, and the risk of predation by the hypolimnetic lake herring was assumed to be high.

When the top of the hypolimnion was deeper than twice the Secchi depth, a warm, dark layer existed which was hypothesized to offer *Bythotrephes* a refuge from predation on the assumption that lake herring would only leave their preferred hypolimnetic habitat (Coulas et al. 1998) if epilimnetic prey were visible.

We suggest that the long-term changes in summer population size of *Bythotrephes* in Harp Lake can be explained by two factors: changes in the availability of the refuge from lake herring predation and changes in *Bythotrephes* life history. This refuge was both thick and long-lasting in 1993, the first year that *Bythotrephes* appeared in our zooplankton samples (Fig. 10). We suggest that this presented an ideal situation for the new colonists to prosper in the lake. As noted by Yan and Pawson (1998), the refuge did not exist in the spring of 1994 or 1995. It was available in July and August of 1994 and 1995 but not in the summers of 1996 through 1998. The mean abundance of *Bythotrephes* in July and August was correlated with the thickness of refuge between 1994 and 1997 (Fig. 11), the thicker the warm dark layer, the more abundant the *Bythotrephes* ($r = 0.97$, $n = 4$, $p < 0.05$) in the summer. However, 1998 does not fit the pattern. In comparison with the previous 4 years, there are too many *Bythotrephes* given the absence of the hypothesized predation refuge. We suggest that the risk of predation fails to predict summer *Bythotrephes* population size in 1998 because the invader’s life history changed in that year. Clutch sizes and egg ratios were similar in the summer, but unlike in earlier years, all of the summer clutches were parthenogenetic in 1998.

Changes in body size are consistent with the hypothesis that predatory mortality varies among years. Instar II and III animals were smaller in the summer of 1998 than in 1995, suggesting increased size-selective predation by lake herring (Bilkovic and Lehman 1997; Coulas et al. 1998).

We cannot explain the change from aestival to autumnal resting-egg production in the lake. However, it is worth not-
ing that the current pattern, the autumnal switch, is the typical one in Eurasia. It was the aestival switch of 1994 and 1995 that was the unusual pattern. It is possible that one strategy of the invader for coping with the multiple, novel cues in a new environment is early resting-egg production. Certainly, aestival resting-egg production has been interpreted as a stress response in other Cladocera (Arts and Sprules 1987), and Panov et al. (2000) recorded aestival resting-egg production in the invading fish-hook water flea, *Cercopagis pengoi*, in the Neva Estuary of the Baltic Sea.

It is clear that short data series collected soon after colonization are not adequate to quantify *Bythotrephes* abundance or typify *Bythotrephes* demographies. There was a great deal of interannual variability in demographics in Harp Lake. Similarly, *Bythotrephes* peak in Lake Ontario only in poor aede wave years (Johannsson et al. 1991). We should not be surprised if single stable endpoints between *Bythotrephes* and their predators or prey do not develop.

There has been a substantial recent increase in interest in the study of nonindigenous species. We now know that the economic cost of such species is enormous (Pimental et al. 2000) and that they can fundamentally change the structure and functioning of food webs (Vander Zanden et al. 1999). Furthermore, more invasions will certainly occur. Major invasion corridors remain open and transport mechanisms remain active (Carlton and Geller 1993). Intentional introductions are still being planned (Ewel et al. 1999; Dextrase and Coscarelli 2000). Finally, a changing climate (Dukes and Mooney 1999) and the increased internationalization of trade (Buckingham 1998) foster the global spread of species.

Given the magnitude of this issue, our lack of understanding of the current impacts and the future risks of nonindigenous species is alarming. We must re-evaluate long-held notions about the factors that render habitats vulnerable to invasions (Lozon and MacIsaac 1997). We must build tools that can be used to predict the capacity of biota to survive transport, successfully colonize, and, finally, alter their new communities to the point that they become “nuisances” (Ricciardi et al. 1998). If we exclude the zebra mussel (Strayer et al. 2000) and consider the increased internationalization of trade (Buckingham 1998) foster the global spread of species.

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