LETTER

An introduced invertebrate predator (*Bythotrephes*) reduces zooplankton species richness

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Abstract

Rarely do ecologists have the data needed to assess the impacts of invading species on biodiversity, i.e. pre- and post-invasion census information from both invaded and control sites. Using a 21-year time series, we demonstrate that the invasion of Harp Lake, Ontario, Canada, by the Eurasian spiny water flea, *Bythotrephes longimanus*, a zooplanktivore, was accompanied by a rapid and long-lasting reduction in the average species richness of crustacean zooplankton, particularly of cladoceran taxa. No such reduction was observed in seven nearby un-invaded lakes over the same two decades. If the Harp Lake results are typical, we predict a widespread reduction in crustacean zooplankton richness on the Canadian Shield for three reasons. Shield lakes provide the invader with good habitat. Its dispersal rates and colonization success are high. Zooplankton richness in Harp Lake is now unusually low for a Shield Lake of its size and acidity.

Keywords


INTRODUCTION

It is widely believed that freshwater biodiversity is more seriously threatened by the introduction of non-indigenous species than by global climate or land use change, or by atmospheric pollutants (Sala *et al*. 2000). Unfortunately, we rarely have the data needed to test this belief, i.e. pre- and post-invasion biodiversity assessments in invaded lakes and otherwise similar, un-invaded or control lakes (Mack *et al*. 2000). The predatory Eurasian spiny water flea, *Bythotrephes longimanus* (Crustacea, Onychopoda, Grigorovich *et al*. 1998) was introduced into the North American Great Lakes in the 1980s (MacIsaac *et al*. 2000), and since 1989, it has been spreading among Canadian Shield lakes in the Great Lakes watershed (Yan *et al*. 1992; MacIsaac *et al*. 2000). To determine if *Bythotrephes* might have widespread impacts on the species richness of its zooplankton prey on the Shield we must answer three questions. Do Shield lakes provide the invader with suitable habitat? Are the invader’s dispersal rates and colonization success high? Does zooplankton species richness fall after *Bythotrephes* invasions? In its native Eurasia, *Bythotrephes* occupies large, clear-water lakes (MacIsaac *et al*. 2000), and there are many thousands of such lakes on the Shield. In 1989, less than a decade after its North American appearance, *Bythotrephes* colonized the Shield (Yan *et al*. 1992). Since then, the number of invaded Shield lakes has swelled to 50 (Therriault *et al*. 2002, MacIsaac and Yan, unpub. data). Hence, the spread of *Bythotrephes* is not greatly limited by habitat availability, low colonist vagility, or poor colonization success on the Shield. Here we address the third question. Does zooplankton species richness fall in a Shield lake after a *Bythotrephes* introduction?

MATERIALS AND METHODS

*Bythotrephes* appeared in Harp Lake, Ontario, Canada in 1993 (Yan & Pawson 1997). To determine if zooplankton species richness changed thereafter we compare means of annual richness estimates for the pre-introduction (1980–92) and post-introduction (1993–2000) periods in Harp Lake. To determine if *Bythotrephes* might be responsible for the change, we compare Harp Lake with seven limnologically similar, un-invaded lakes, sampled over the same two decades. To determine if the Harp Lake community is now unusual, we employ 47 nearby lakes representing the range of limnological conditions typical of the region (Yan *et al*. 1996). Hence, following Chapman (1998/9), we employ the Harp Lake introduction as the “experiment”, comparing it with seven “experimental controls”, and with 47 lakes that identify the regional norm (“the regional reference set”).

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Harp Lake (pH 6.3) and the seven control lakes are all small (lake areas of 21–94 ha), slightly acidic (pH 5.6–6.7), and nutrient-poor (total phosphorus of 4.9–10.5 µg/L), with water qualities typical of the Shield (Dillon et al. 1993). The 47 regional reference lakes have similar characteristics, and 22 of them have a pH > 6 (Yan et al. 1996). Above this pH, crustacean zooplankton are largely unaffected by lake acidification (Havens et al. 1993).

Zooplankton were collected in volume-weighted composite samples at a single mid-lake station on a monthly or fortnightly basis during the ice-free seasons of 1980–2000 from Harp and the control lakes, and on a monthly basis in 1 year from the regional reference lakes. Sample collection, preservation, and processing methods have been identical since 1980 (Yan et al. 1996). Yan et al. (1996) and Arnott et al. (1998) provide general descriptions of the zooplankton communities. Annual species counts increase with sample size (Arnott et al. 1998). Because we employed both monthly and fortnightly sampling frequencies, we report annual average not annual total species richness estimates. This was calculated as the annual average of the numbers of crustacean species detected in standard counts of a minimum of 250 individuals in each sample. This parameter stabilizes rapidly, generally after two samples, with increases in sample size (Keller & Yan 1991).

*Bythotrephes* has been sampled in Harp Lake since 1994 in vertical hauls from 3 m above bottom to the surface using a 0.75-m diameter, 285-µm mesh, 2.5 m long net at 10 randomly located stations (Yan & Pawson 1997). In the summer of 2001, we employed this sampling design to look for *Bythotrephes* in the seven control lakes. To determine if the Harp Lake *Bythotrephes* population was unusual, we also employed this sampling design in 16 other invaded Shield lakes. These samples were examined in their entirety for *Bythotrephes*.

**RESULTS**

The median *Bythotrephes* abundance in the 17 invaded lakes was 2.96 animals m$^{-3}$ (range of 0–12.6) averaged over the water column. The Harp Lake population was of typical size at 4.17 animals m$^{-3}$. *Bythotrephes* was not detected in any of the control lakes.

Crustacean zooplankton species richness has fallen in Harp Lake, but not in the control lakes. From 1980 to 1992, i.e. prior to the invasion, we recorded an ice-free season average of 9.98 species of crustacean zooplankton in our standard counts in Harp Lake. Since the invasion, the average has fallen by 17% to 8.25 species (Fig. 1), a significant change ($P < 0.001$, $t$-test assuming unequal variances). Comparing the same two time periods in the control lakes, there was no change in richness in Blue Chalk, Chub, Crosson, Dickie, and Heney lakes, while richness actually increased in Plastic and Red Chalk lakes (Fig. 1).
The species richness in Harp Lake is now unusually low for a shield lake in most years. In the regional reference lakes, richness increases with pH and with lake size (Fig. 3). It ranged from 8 to 12 species/standard count in the 22 lakes with pH > 6. Prior to the Bythotrephes introduction, the richness of the Harp Lake zooplankton community was always within this normal range for non-acidic lakes (Fig. 3). After the introduction, the Harp Lake value approached the minimum, and in 4 of 7 years, fell below the minimum richness observed in all 22 non-acidic reference lakes.

**Discussion**

The unique difference between Harp and the seven control lakes is the recent invasion of Harp Lake by Bythotrephes; hence, we conclude that Bythotrephes is responsible for the decline in zooplankton species richness in Harp Lake. This conclusion is supported by three factors: a comparison of zooplankton production with Bythotrephes predation in Harp Lake, indicating that predation by Bythotrephes is directly responsible for crashes in its prey populations (Dumitru et al. 2000); a consideration and rejection of several alternative explanations for changes in zooplankton, namely changes in lake acidity, stratification, UV irradiance, nutrient status and fish management practices (Yan & Pawson 1997); and the identity of the missing species — Chydorus sphaericus, Daphnia retrocurva, Diaphanosoma bergii, Mesocyclops edax, Bosmina tubicen, and Bosmina longirostris (Yan et al. 2001). All are vulnerable to Bythotrephes predation (Grigorovich et al. 1998; Dumitru et al. 2000).

Others have noted that Bythotrephes can reduce abundances of particular zooplankton. For example, Bythotrephes has been implicated in reductions in abundance of Leptodora (Branstrom 1995) in Lake Michigan, and some Daphnia species in large (Lehman & Caceres 1993; Mackarewicz et al. 1995) and small lakes (Hoffman et al. 2001, Manca et al. 2000) and reservoirs (Ketelaars & van Breemen 1993). Further, both mesocosm experiments (Wahlstrom & Westman 1999) and comparisons of prey production with Bythotrephes consumption (Hoffman et al. 2001) confirm that Bythotrephes may at times be responsible for reductions in the abundance of its prey. However, Harp Lake provides the first evidence of a long-lasting reduction in zooplankton species richness, which, because of our control lake data, we can clearly associate with a Bythotrephes introduction.

Zooplankton species richness in temperate lakes is normally controlled by their location with respect to postglacial invasion corridors (Carter et al. 1980; Stemberger 1995), by lake size (Dodson 1992; Allen et al. 1999), which controls habitat availability, and by the productivity of their food base (Dodson et al. 2000; Jeppesen et al. 2000). Superimposed on these natural regulators are the impacts...
of man (e.g. Yan et al. 1996). We must now include *Bythotrephes* introductions to the list of regulators.

We have only one case study of a *Bythotrephes* introduction on the Canadian Shield – Harp Lake. Hence, we must be cautious in extrapolating the results. Nonetheless we have no a priori reason for assuming that the Harp Lake results are unique. The *Bythotrephes* population in the lake is not unusual in size, and the lake has typical water quality (Dillon et al. 1993), invertebrate predators (*Chaoborus, Leptodora* and *Mysis*), and dominant fish species (Coulas et al. 1998) for Shield lakes of its elevation and glacial history. Should these results prove to be the norm, we predict that there will be a reduction in crustacean zooplankton species richness, particularly cladocerans, on the Canadian Shield in response to the spread of *Bythotrephes*. Of course, we have only a seven-year post-invasion time series, and dispersal and colonization events may act at long time scales to invalidate this prediction (Leibold et al. 1997).

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**REFERENCES**


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