



Implications of an invertebrate predator's (*Bythotrephes cederstroemi*) atypical effects on a pelagic zooplankton community

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Abstract

The traditional view of predaceous zooplankton is that they prefer small-bodied prey, are hindered by morphological anti-predator defenses, and have a minor influence on zooplankton communities when fish are present. We performed a series of experiments with the large-bodied onychopod (cladoceran) *Bythotrephes cederstroemi*, in which we incubated this predator with known prey to determine prey preference and predation rates. We also performed an allozyme analysis of prey tissue in the gut of *B. cederstroemi* collected from several stations around Lake Michigan to determine what prey types are chosen in the field. We found that *B. cederstroemi* does not fit the standard invertebrate predator mold: adult *B. cederstroemi* prefer large (>2.0 mm) *Daphnia pulicaria* over smaller individuals; the elongated tailspine and helmet of *Daphnia galeata mendotae* are not effective deterrents to *B. cederstroemi* predation; and *B. cederstroemi* is a generalist predator with the potential to consume a significant portion of cladoceran production in Lake Michigan.

Introduction

Although the importance of fish in structuring aquatic communities has been well demonstrated (e.g., Brooks & Dodson, 1965; Galbraith, 1967; Hall et al., 1970; Langeland, 1982) and invertebrate predators have been known to eliminate zooplankton species from pelagic communities in the absence of planktivorous fish (e.g., Dodson, 1974a; Kerfoot, 1977), the impact of invertebrate predators on zooplankton community structure in the presence of planktivorous fish is less clear. Certainly invertebrate predators can reduce the abundance of their prey (e.g., Brandl & Fernando, 1981; de Bernardi & Giussani, 1975; McQueen, 1969), but several studies question whether invertebrate predation alone is a likely cause of local prey species extinction in systems with planktivorous fish (de Bernardi et al., 1987; Dodson, 1974a; Hall et al., 1976). Indeed little evidence supports the alternate hypothesis that inverte-

brate predators are capable of structuring zooplankton communities in lakes with planktivorous fish, although the opossum shrimp *Mysis relicta* has been implicated as a potential cause of cladoceran declines and local extinctions in Lake Tahoe, Flathead Lake and two Norwegian lakes (Goldman et al., 1979; Langeland, 1981; Richards et al., 1975; Spencer et al., 1991).

Bythotrephes cederstroemi Schödler, a predatory cladoceran native to northern Europe and Asia, invaded the Laurentian Great Lakes in the mid-1980's. *B. cederstroemi* was first found in Lake Huron in late 1984, and subsequently reached Lakes Erie (Bur et al., 1986) and Ontario in 1985 (Lange & Cap, 1986), Lake Michigan in 1986 (Evans, 1988; Lehman, 1987), and Lake Superior in 1987 (Cullis & Johnson, 1988). *B. cederstroemi* has also spread to several nearby inland lakes (Yan et al., 1992). Like many other exotic members of the Great Lakes biota, *B. cederstroemi* is thought to have arrived in the ballast water of ships

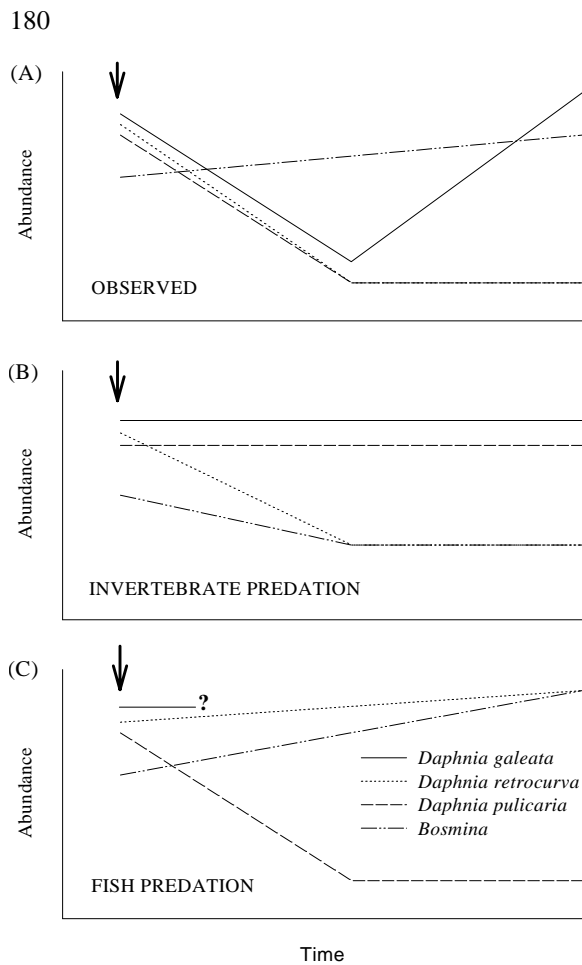


Figure 1. Stylized depiction of changes in the Lake Michigan cladoceran prey community. Arrow indicates introduction of *Bythotrephes cederstroemi* (A) or onset of increased predation (B and C). (A) Observed changes in the Lake Michigan cladoceran community following the introduction of *Bythotrephes cederstroemi* to the lake in the mid-1980's (after Lehman, 1991). (B) Hypothesized changes that would be observed in the Lake Michigan cladoceran community following an increase in traditional invertebrate predation. (C) Hypothesized changes that would be observed in the Lake Michigan cladoceran community following an increase in predation by planktivorous fish.

(Carlton & Geller, 1993; Sprules et al., 1990). Since its invasion a decade ago, *B. cederstroemi* has flourished and appears to be a permanent member of the Great Lakes plankton.

Concurrent with the invasion of *Bythotrephes cederstroemi* in Lake Michigan were dramatic changes in the zooplankton community (Lehman, 1991), and these changes have persisted through the early 1990's (Makarewicz et al., 1995). Specifically, prior to the *B. cederstroemi* invasion the daphnid assemblage was dominated by three species: the large-bodied *Daphnia pulicaria*, the moderate sized and helmeted *Daphnia*

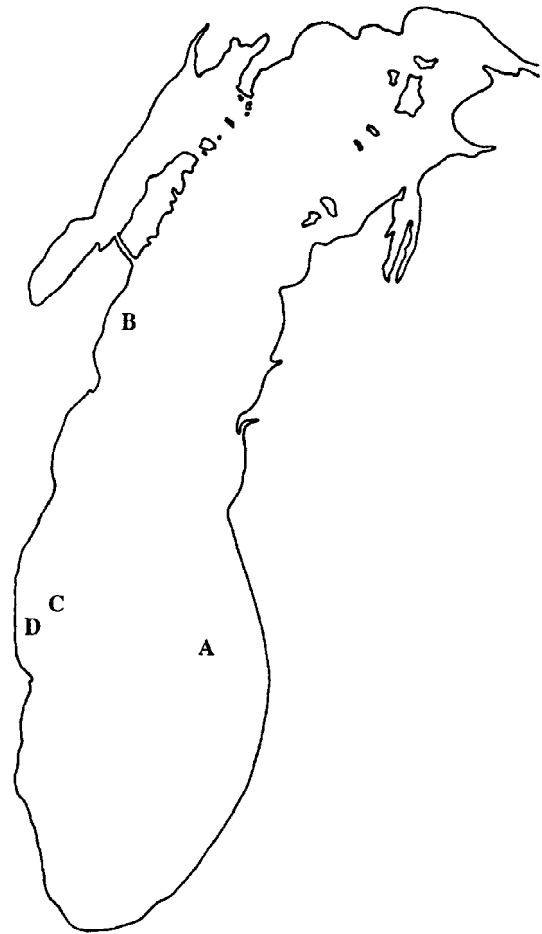


Figure 2. Location of the four stations around Lake Michigan where *Bythotrephes cederstroemi* and potential prey were collected for analysis of prey diet composition. Station A is the 100 m deep reference station (43°N, 86°40'W) where the zooplankton for the natural assemblage predation experiment were also collected. Station B (44°30'N, 87°25.8'W) is 40 m deep, Station C (43°15'N, 87°40.3'W) is 100 m deep and Station D (43°6'N, 87°48'W) is 40 m deep.

galeata mendotae, and the small, helmeted *Daphnia retrocurva*. After *B. cederstroemi* became established, all three daphnid populations collapsed, and by late 1987 only *D. galeata mendotae* remained in the offshore plankton assemblage of Lake Michigan. Additionally, abundances of the small herbivorous cladoceran *Bosmina longirostris* increased, and those of the native predatory cladoceran *Leptodora kindtii* declined (Figure 1A). Based on this correlative evidence, Lehman (1988, 1991) hypothesized that predation by *B. cederstroemi* was responsible for the decline of the daphnids and possibly for that of *Leptodora* (although he speculated that *Leptodora* might not be

preyed on directly by *B. cederstroemi*, but might suffer mortality by being caught on the long caudal spine of the invader). Lehman (1988, 1991) attributed the increased abundances of *Bosmina* to the decline of its predator *Leptodora*.

The idea that predation by *Bythotrephes cederstroemi* could be responsible for the observed zooplankton community changes in Lake Michigan was controversial (Sprules et al., 1990) for several reasons. First, the observed decrease in abundance of the large *Daphnia pulicaria*, and increase in abundance of the small *Bosmina longirostris* are not consistent with changes traditionally associated with invertebrate predators, and fish predation was hypothesized to be a more likely cause of the species changes in the Lake Michigan zooplankton community (Sprules et al., 1990). Invertebrate predators typically have been thought of as 'size-dependent', choosing relatively small prey over large (Zaret, 1980), and many studies have confirmed that most pelagic invertebrate predators select small prey or are unable to capture and consume large prey efficiently (e.g., Dodson, 1974a; Pastorok, 1981). Pelagic invertebrate predators also commonly are deterred by the presence of exuberant morphological defenses such as spines and helmets (e.g., Dodson, 1974b) like those of *D. galeata mendotae*. *Daphnia retrocurva* possesses only a small crest that has been shown to be an ineffective predator defense against another cladoceran predator, *Leptodora kindtii* (Havel, 1985). Although the decrease of the small-bodied *Daphnia retrocurva* and the persistence of helmeted *D. galeata mendotae* (after an initial decline) are consistent with the predicted effects of invertebrate predation, the decreased abundance of large *D. pulicaria* and increased abundance of small *B. longirostris* are consistent with the predicted effects of predation by planktivorous fish (Figure 1B).

It is difficult to predict the effect of hypothetical increased predation by planktivorous fish on the abundance of *Daphnia galeata mendotae*. *D. galeata mendotae* is smaller than *D. pulicaria*, and therefore should be less preferred; however, it reaches lengths greater than 2 mm and is large enough to be seen and consumed by fish. Some data suggest, however, that *D. galeata mendotae* is sometimes ignored by fish (Hall, 1964) or can survive fish predation, even without vertically migrating, due to its high growth rate and fecundity (Stich & Lampert, 1984).

A second reason *Bythotrephes cederstroemi* was thought to be an unlikely cause of the changes in the Lake Michigan zooplankton community is that

the autecology of *B. cederstroemi* was relatively unstudied prior to its invasion; thus its diet was not known. Mordukhai-Boltovskaia (1958) reported that *Bythotrephes* prefer small soft prey, such as *Polyphemus* and *Bosmina*, which would not be consistent with the observed decrease in abundance of the large-bodied *Daphnia pulicaria* and increase in *Bosmina longirostris*. This same study, however, describes *Bythotrephes* as smaller than *Leptodora*, and is therefore more likely to be describing the diet of the smaller congener of *B. cederstroemi*, *B. longimanus*. Because *B. cederstroemi* is a much larger zooplankton, sometimes reaching a total length of greater than 1.5 cm and a dry mass of over 1 mg (personal observation), one might predict that its diet would include larger prey than would that of *B. longimanus*. However, *B. cederstroemi* is much smaller than *Mysis* and not substantially larger than some other pelagic invertebrate predators, such as *Chaoborus americanus*, that prefer to feed on small or mid-sized prey.

A final line of evidence in opposition to the hypothesis that *Bythotrephes cederstroemi* predation was responsible for the decline of the daphnids came from several experiments in North America which suggested that *B. cederstroemi* consumes less than would be necessary to effect such large changes in its putative prey populations (Sprules et al., 1990; Vanderploeg et al., 1993). The feeding rates reported in these studies, however, are well below the amount of energy consumption needed to maintain *B. cederstroemi* growth and reproduction predicted by two bioenergetic models (Lehman & Cáceres, 1993; Yurista & Schulz, 1995). *B. cederstroemi* is very difficult to culture (Yurista, 1992) and is highly cannibalistic. The predation estimates of Sprules et al. (1990) and Vanderploeg et al. (1993) may have been confounded by abnormal predator behavior and a failure to include cannibalism estimates in predation rates, because multiple predators were incubated in a single container without an acclimation period.

Clearly the correlative zooplankton abundance data do not exclude either the hypothesis that the changes in Lake Michigan zooplankton composition were caused by an increase in predation by fish or that the changes were caused by an increase in predation by the introduced *Bythotrephes cederstroemi*. Without a more detailed knowledge of the autecology of *B. cederstroemi*, accurately assessing its impact on pelagic communities is impossible, and the possibility that fish predation caused the changes in zooplankton structure in Lake Michigan is equally likely. We performed a

series of experiments designed to determine the diet composition of *B. cederstroemi* in an effort to shed light on its predatory impact and its functional role in the Lake Michigan zooplankton community.

Methods

Common to all experiments

Because *Bythotrephes cederstroemi* is difficult to culture, we took several precautions to avoid abnormal predator behavior in our experiments. First, in preliminary experiments we found that *B. cederstroemi* fed at a very low rate during the first 24 h after capture, then fed at a higher, constant rate. A similar observation was made by Brandl & Fernando (1974) for *Acanthocyclops vernalis*. Furthermore, *B. cederstroemi* often had a high mortality rate during the first 24 h after capture, perhaps due to injuries incurred from the plankton net. Therefore, we incubated *Bythotrephes* at 16 °C in individual culture wells (2 ml) with *Artemia* provided for food during a 24-h acclimation period prior to laboratory experiments. Second, *B. cederstroemi* appears to be highly sensitive to lighting conditions, often repeatedly swimming into walls of containers if light is intense or unidirectional. We attempted to provide diffuse light simulating conditions at 15–20-m depths in Lake Michigan. In all experiments, light levels were adjusted to $<3 \mu\text{E m}^{-2} \text{s}^{-1}$ with green filters or screening. Light intensity was monitored with a LiCor quantum light meter with a 2Π sensor. Finally, we observed that *B. cederstroemi* is highly cannibalistic. To avoid complications from cannibalism, we used only a single *B. cederstroemi* in each replicate for all experiments.

All *Bythotrephes cederstroemi* were collected from the top 30 m of offshore Lake Michigan during the summers of 1990 and 1991 with a 1-m dia. 300 μm -mesh net. As the phototactic animals swam to the surface, they were grabbed by their tail spines with a jeweler's forceps and placed in culture wells filled with filtered lake water (Whatman GF/F). After the 24-h acclimation period described above, individual *B. cederstroemi* were moved to the larger experimental containers. Only actively swimming adult animals were used; in addition, we selected individuals without late stage embryos to prevent the hatching of neonates during the experimental incubation. We used 1.2-l wide mouth Nalgene bottles for all experiments to prevent wall effects from interfering

with predator behavior, although larger container sizes might have resulted in incrementally higher predation rates (O'Brien, 1988). Preliminary experiments with counted prey demonstrated that up to 45% of some hydrophobic prey, such as daphnid species, can be lost to adhesion onto wall surfaces in bags and contoured narrow mouth jars, even after careful rinsing; differential recovery rates of prey species would complicate the results of predation experiments. The use of wide mouth, cylindrical straight-sided containers filled to the top with lake water prevented adhesion to the walls and capture of hydrophobic prey in surface tension. This allowed almost full recovery of added prey (never $<97\%$). Because over 97% of the prey were always recovered, there was very little sampling error associated with the predation estimates.

During the experiments, each *Bythotrephes cederstroemi* was checked daily for mortality. Replicates in which the predator had died during incubation were excluded from analyses. For each predation experiment, controls with no *B. cederstroemi*, but with the same prey assemblages were maintained under identical conditions. The experimental containers were not incubated on a plankton wheel, and thus some concentration of contents at the bottom of the vessels may have occurred. Plankton wheels generally are used in experiments with herbivores, to avoid settling of phytoplankton. The zooplankton prey, of course, may follow settling algae to the bottom, but are not likely simply to settle out of the container. We did not visually observe such aggregations, but nonetheless it is possible that our predation rates may be slight overestimates because our bottles were not mixed during incubation. After the experimental incubations, *B. cederstroemi* were removed and frozen on Teflon disks with dry ice for later measurement of dry mass. The remaining contents of each container were poured through a 53 μm sieve, rinsed into sample bottles, and preserved with sugar-formalin for later counting. Statistical analyses were computed with SYSTAT version 5.0 (Wilkinson, 1990).

Prey selection on natural zooplankton assemblages

An experiment to determine prey preference from a natural zooplankton assemblage was conducted on board the R/V Laurentian from 12 to 15 August 1991. Zooplankton were collected from 30–0 m at Station A (Figure 2) with a 0.5-m dia. 63 μm mesh Puget Sound closing net. The contents of the net tow were then diluted to approximately natural density by first

placing them into a container filled with 50 l of 3.0 μm cartridge-filtered (Gelman) Lake Michigan water, and then mixing well and removing 100 ml subsamples from the container. These subsamples were added to the 1.2-l experimental containers which were then filled with filtered lake water to which 2 ml of *Chlamydomonas reinhardtii* culture were added as food for the herbivorous zooplankton. Initial 100 ml subsamples ($n = 20$) were preserved in sugar formalin. Controls ($n = 20$ for each incubation period), without *Bythotrephes cederstroemi*, and experimentals ($n = 28$ for each incubation period), each with a single *B. cederstroemi* collected from the same station as the prey, were incubated for 48 and 72 h in a water-filled tank on the deck of the Laurentian. Because of ship-time limitations, the *B. cederstroemi* were not acclimated to experimental conditions before incubation. Water temperature was maintained at 16 ± 1.0 °C by periodically refilling the tank with epilimnetic water from the appropriate depth.

To further assess the diet breadth of *Bythotrephes cederstroemi* in Lake Michigan, *B. cederstroemi* were collected from 12 to 15 August 1991 at four stations around Lake Michigan (Figure 2) for allozyme analysis to determine prey diet composition. Because *B. cederstroemi* shreds its prey and ingests no identifiable hard parts, it is impossible to use morphological identification of prey remains in the gut to determine diet composition. We used cellulose acetate electrophoresis to identify soft tissue remains of prey from *B. cederstroemi* (Schulz & Yurista, 1995). At each station we collected *B. cederstroemi* and froze them on Teflon disks on dry ice for later allozyme analysis. At stations A, B and D we collected only adult *B. cederstroemi*, while at station C juveniles were common and we collected them. We collected potential prey items for allozyme analysis by pouring the contents of 0.5-m dia. 63 μm mesh Puget Sound closing net tows (0–20-m vertical tows) through 63 μm Nitex sieves and then freezing the sieves in plastic Petri dishes on dry ice for later sorting and analysis. In the laboratory, all frozen specimens were stored at -80 °C until analysis. Detailed methods are given in Schulz & Yurista (1995), along with the results from Station A. To determine the zooplankton composition at stations B, C and D we took one quarter of a frozen sieve containing the contents of the zooplankton tow from that station, and transferred the animals to sugar-formalin. We then enumerated the zooplankton in this sample. To determine the zooplankton composition at station A, we used the initial samples from the natural assemblage

Table 1. The number of *Bythotrephes cederstroemi* (n) analyzed at each station for prey allozymes (for station locations see Figure 2). Details of the analysis for each station are also provided – the number of *Bythotrephes* without any detectable prey allozymes; the number with identifiable prey allozymes; the number with prey allozymes that were ambiguous because the banding patterns were not unique to one prey type; the total number of prey allozyme bands; and the total number of allozyme bands found in predators which did not belong to any putative prey species surveyed

Station	n	n without any detectable prey allozymes	n with identifiable prey allozymes	n with ambiguous prey allozymes	Total number of prey allozyme bands	Number of unidentified prey allozyme bands
A	30	5	23	2	110	4
B	30	6	16	8	58	1
C	27*	16	10	1	16	1
D	30	4	22	4	71	8

* The *Bythotrephes* from Station C were juveniles.

experiment, which were collected at the same time as the frozen zooplankton for allozyme analysis.

The determination of diet composition from allozymes required analysis of both prey and predator allozymes at each station. We characterized the allozymes of all potential prey species that were abundant enough to obtain sufficient sample for assaying the allozyme profile of each population. At station A, the potential prey analyzed were calanoid copepods, cyclopoid copepods, *Daphnia galeata mendotae*, and *Epischura*. At station B, we analyzed the allozymes of calanoid copepods, cyclopoid copepods, *D. galeata mendotae*, *Epischura*, *Bosmina longirostris*, *Eubosmina*, and *Holopedium*. Calanoid copepods, cyclopoid copepods, *D. galeata mendotae*, *Epischura*, and *Bosmina* were analyzed at station C, and calanoid copepods, cyclopoid copepods, *D. galeata mendotae*, *Epischura*, *Bosmina*, and *Eubosmina* at station D. The number of *B. cederstroemi* at each station containing prey bands that could be identified unambiguously, the number with no detectable prey allozymes, and the number of unidentifiable prey bands are listed in Table 1.

Prey preference between calanoid copepods and Daphnia pulicaria

A laboratory experiment to determine if *Bythotrephes cederstroemi* prefer calanoid copepods or *Daphnia* species was conducted from 28 to 29 August 1990. *B. cederstroemi* were collected from Lake Michigan and transported in culture wells to Ann Arbor, Michi-

gan, where they were acclimated for 24 h. *Daphnia pulicaria* and *Diatomus* spp. collected from Third Sister Lake, Washtenaw County, Michigan, were used as prey. Because *D. pulicaria* was eliminated from Lake Michigan in 1987, we were forced to use animals from a different source, but we used *D. pulicaria* of a similar size to those in Lake Michigan at the time of the *B. cederstroemi* invasion. To prevent birth of neonates during the experimental period, only *D. pulicaria* without eggs or embryos were used as prey. Prey items were identified and sorted manually under a dissecting scope. They were then pipetted into the experimental containers and *Chlamydomonas reinhardtii* culture was added for food. Individual *B. cederstroemi* were incubated at 16 ± 0.5 °C with either 20 *D. pulicaria* ($n = 4$), 20 calanoid copepods ($n = 4$), or a mixed assemblage of 10 *D. pulicaria* and 10 calanoid copepods ($n = 4$). One set of controls ($n = 2$ per prey treatment) and experimentals was incubated for 24 h, another for 48 h.

Evaluation of the helmet of Daphnia galeata mendotae as a predator defense

A laboratory experiment to determine if the elongated helmet and tailspine of *Daphnia galeata mendotae* are effective deterrents to predation by *Bythotrephes cederstroemi* was performed from 26 to 28 September 1991. Helmeted *D. galeata mendotae* were isolated from Lake Michigan and cultured on a shaker table for two weeks prior to the experiment to maintain their elongated tailspines and helmets. A non-helmeted *D. galeata mendotae* clone was obtained from A. Tessier of Michigan State University. *B. cederstroemi* were collected from Lake Michigan and transported in culture wells to Ann Arbor, Michigan where they were acclimated for 24 h. Each *B. cederstroemi* was offered a choice between 15 helmeted and 15 non-helmeted *D. galeata mendotae*. The *D. galeata mendotae* were measured, sorted individually and pipetted into the experimental containers. Two ml of *Chlamydomonas reinhardtii* culture were added to each replicate for food. Again, only individuals without eggs or embryos were used as prey to avoid confounding effects of prey births during the experiment. The mean body length (measured from eye to base of tail spine; Bottrell et al., 1976) for both the helmeted and non-helmeted *D. galeata* selected for the experiment was 1.5 mm, ranging from 1.36 to 1.74 mm. The average helmet length (length from eyespot to top of head) was 0.184 mm (± 0.008 SE; $n = 28$) for the helmeted clone, and 0.079

mm (± 0.005 SE; $n = 28$) for the non-helmeted clone. The tailspines measured 0.529 mm (± 0.034 SE; $n = 28$) for the helmeted clone, and 0.374 mm (± 0.009 SE; $n = 28$) for the non-helmeted clone. Experimental ($n = 20$) and control ($n = 5$) treatments were incubated at 16 ± 0.5 °C for 48 h.

Prey size selection on Daphnia pulicaria

Two laboratory experiments were conducted from 22 to 26 July of 1991 to determine which size classes of *Daphnia pulicaria* are preferred by *Bythotrephes cederstroemi*. Immediately prior to the experiment *D. pulicaria* from a culture originally isolated from Lake Michigan were measured and sorted by hand into three size classes: small (0.8–1.0 mm), medium (1.4–1.6 mm) and large (>2.0 mm). Measurements of *D. pulicaria* lengths were made from the center of the eye to the base of the tail spine (Bottrell et al., 1976). In the first experiment, each *B. cederstroemi* was offered a choice between 10 small and 10 medium *D. pulicaria* ($n = 10$). One set of 10 experimental replicates was incubated for 48 h and another for 96 h. After 48 h an additional 4 small and 8 medium *D. pulicaria* were added to each of the 96-h incubation replicates to replace approximately the number which had been consumed in the 48-h incubation treatment. In the second experiment, *B. cederstroemi* were offered a choice between 10 small, 10 medium and 10 large *D. pulicaria* ($n = 10$). Again, one set of experimental replicates was incubated for 48 h and another for 96 h. After 48 h an additional 4 small, 6 medium and 8 large *D. pulicaria* were added to each of the 96-h incubation replicates to replace approximately the number that had been consumed in the 48-h incubation treatment, and to keep the number of available prey of each size relatively constant. Control replicates ($n = 5$) were incubated for 96 h. Two ml of *Chlamydomonas reinhardtii* culture were added to every container for food. A temperature of 16 ± 0.5 °C was maintained for all incubations.

Determination of maximum predation rates on Daphnia pulicaria

Maximum prey consumption rate for *Bythotrephes cederstroemi* on *Daphnia pulicaria* was assessed in a laboratory experiment from 17 to 20 August 1991. We assessed maximal predation rate in a separate experiment, rather than using predation rates from the selectivity experiments, because in the selectivity experiments prey were not saturating and they were not

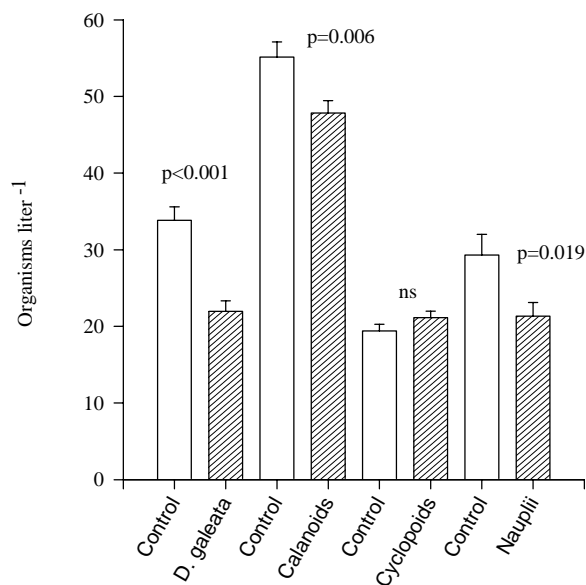


Figure 3. Predation by *Bythotrephes cederstroemi* on a natural zooplankton assemblage from an offshore station in Lake Michigan (Station A); the most abundant zooplankton taxa are shown. Hollow bars show the number of each taxon present after incubation in a predator-free control container. Hatched bars show the number of each taxon present after incubation with a single *B. cederstroemi*. The difference between control and predator container abundances is the amount of *B. cederstroemi* predation during the experiment. During a 72-h incubation with the zooplankton assemblage, *Bythotrephes cederstroemi* consumed significant numbers of *Daphnia galeata mendotae*, calanoid copepods, and copepod nauplii, but did not consume cyclopoid copepods (Student's *t*-test; $\alpha = 0.05$). Error bars are standard error of the mean.

maintained at a constant density. Each *B. cederstroemi* that had been collected from Lake Michigan, transported in culture wells to Ann Arbor, Michigan, and acclimated for 24 h was allowed to feed on 40 *Daphnia pulex*. This is a high prey density (33.3 *D. pulex* l⁻¹), but within the range that occurs naturally. The *Daphnia pulex* were sorted from the same culture originally isolated from Lake Michigan that was used in the size selection experiments. Only barren prey > 1.4 mm were used. Containers were incubated for either 48 h ($n = 5$) or 72 h ($n = 15$) at 16 ± 0.5 °C. No control replicates were used for this experiment because we had already determined in the previous experiment that recovery and survival of *D. pulex* was >97%.

Results

Prey selection on natural zooplankton assemblages

The natural zooplankton assemblage collected from Station A on 12 August 1991 consisted primarily of cyclopoid and calanoid copepods, copepod nauplii, and *Daphnia galeata mendotae*. *Bosmina longirostris* and *Asplanchna* were also present, but in low densities (<5 individuals / liter). The number of prey per day consumed by *B. cederstroemi* in the 48-h treatment was less than that consumed in the 72-h treatment, perhaps because the research cruise was too short to permit an acclimation period for the *B. cederstroemi* used in this experiment. The 72-h treatment therefore was used to determine predation rates in the natural assemblage. When allowed to feed on this assemblage, *Bythotrephes cederstroemi* consumed significant numbers of *Daphnia galeata mendotae* ($p < 0.001$), copepod nauplii ($p = 0.019$) and calanoid copepods ($p = 0.006$) compared with the controls (independent samples *t*-test, $\alpha = 0.05$; Figure 3). There were no significant differences in the numbers of *Asplanchna* or *Bosmina* present in control and experimental treatments, but this is partly a reflection of the low number of individuals present. The number of cyclopoid copepods in the experimental replicates also did not differ significantly from that in the controls ($p > 0.05$). On average, *B. cederstroemi* consumed approximately 12 *D. galeata mendotae*, 8 nauplii, and 7 calanoid copepods over the 72-h incubation period.

At each site, the number of times each prey type's allozymes were detected in a *Bythotrephes cederstroemi* as a percent of the total number of prey identified from their allozymes as having been consumed at that site was compared with the percent of each prey type in the total zooplankton assemblage (Figure 4). In descending order of the number of individual predators that were found to contain each prey taxon, at station A calanoid and cyclopoid copepods, *Epischura*, and *Daphnia galeata mendotae* were consumed by *B. cederstroemi*. At station B, *Bosmina*, *Daphnia galeata mendotae*, calanoid and cyclopoid copepods, and *Epischura* were consumed. At station C, the juvenile *B. cederstroemi* consumed calanoid copepods and *Epischura*. At station D, cyclopoid copepods, calanoid copepods, *D. galeata mendotae*, and *Bosmina* were consumed.

% ZOOPLANKTON COMPOSITION

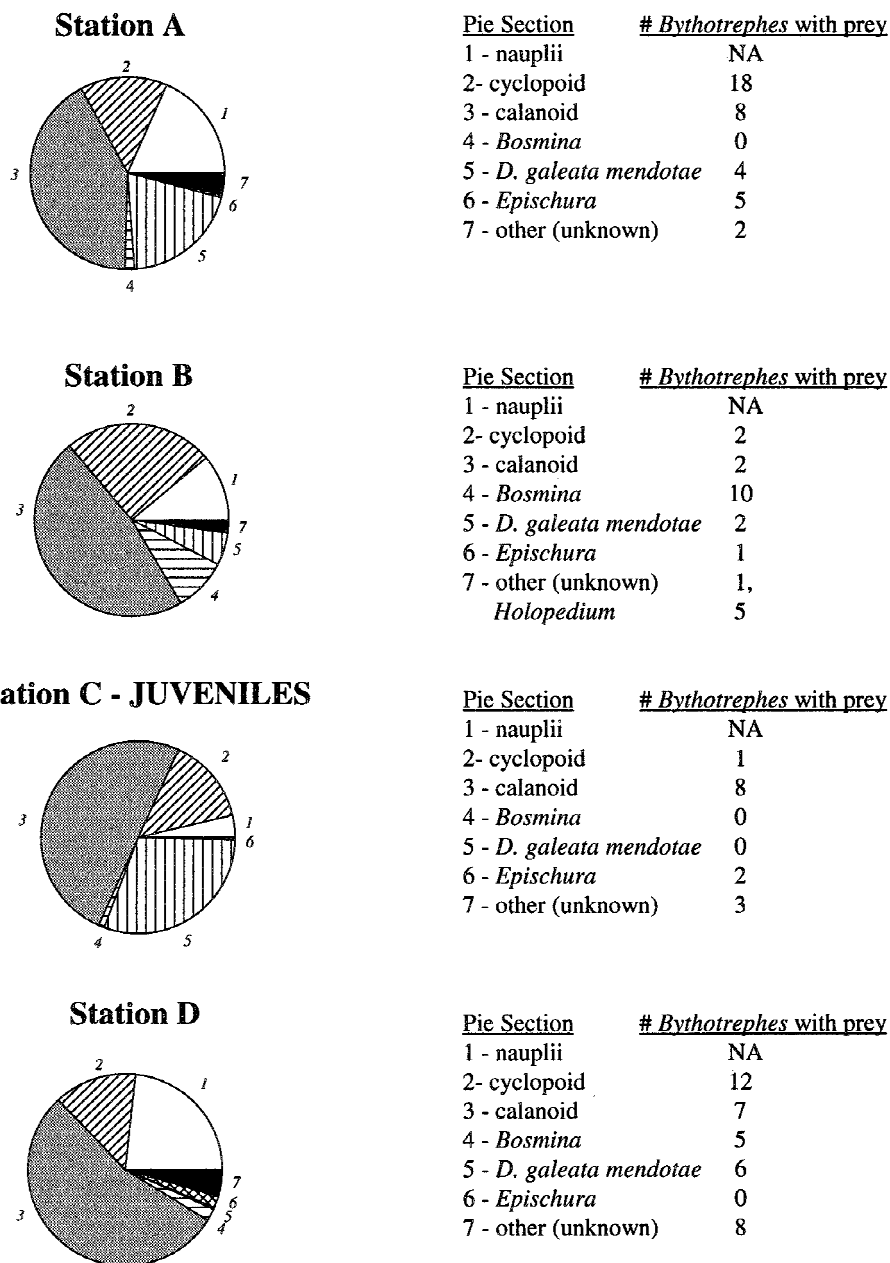


Figure 4. Comparison of the % zooplankton composition at each of 4 stations in Lake Michigan with the total number of *Bythotrephes cederstroemi* collected at each site that contained each prey type as identified by allozymes (see Figure 2 for station locations). The *B. cederstroemi* collected from stations A, B and D were adults, while those collected from station C were juveniles. In the zooplankton composition column 'other' indicates a summation of the numbers of rare, <1%, taxa; in the *B. cederstroemi* diet column 'other' signifies an unknown prey type that could not be identified from the prey taxa surveyed.

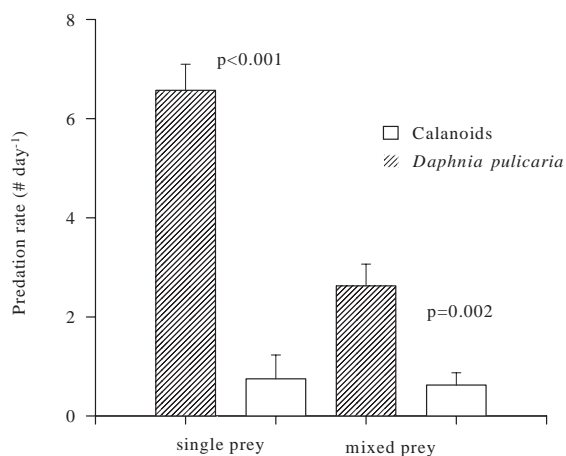


Figure 5. Predation by *Bythotrephes cederstroemi* when offered either *Daphnia pulex* or calanoid copepods alone, or a choice between the two prey types. Data from the 24- and 48-h incubations were pooled. *B. cederstroemi* consumed significantly more *D. pulex* than calanoid copepods, both when offered as the single available prey and as a mixed prey assemblage. Error bars are standard error of the mean.

Prey preference between calanoid copepods and *Daphnia pulex*

Data from the 24-h and 48-h incubation treatments in which *Bythotrephes cederstroemi* was offered either *Daphnia pulex* or calanoid copepods alone, or a choice between the two prey types, were converted to number of individuals consumed per day and pooled for analysis. *B. cederstroemi* consumed significantly fewer calanoid copepods than it consumed *D. pulex*, both when offered as single ($p < 0.001$) and mixed prey ($p = 0.008$) (Kruskal–Wallis one-way ANOVA, $\alpha = 0.05$; Figure 5). On average, *B. cederstroemi* consumed 0.8 ± 1.4 (SD) calanoids and 6.6 ± 1.4 (SD) *D. pulex* when these prey were present alone, and 0.6 ± 0.7 (SD) calanoids and 2.5 ± 1.2 (SD) *D. pulex* in the mixed assemblage.

Evaluation of the helmet of *Daphnia galeata mendotae* as a predator defense

There was no significant difference ($p = 0.286$) between the numbers of helmeted and unhelmeted *Daphnia galeata mendotae* consumed by *Bythotrephes cederstroemi* when offered both morphs in a mixed prey assemblage (Kruskal–Wallis ANOVA, $\alpha = 0.05$; Figure 6). On average, *B. cederstroemi* consumed 2.5 ± 1.7 (SD) helmeted and 1.9 ± 1.4 (SD) unhelmeted *D. galeata mendotae* per day. The average dry mass of the

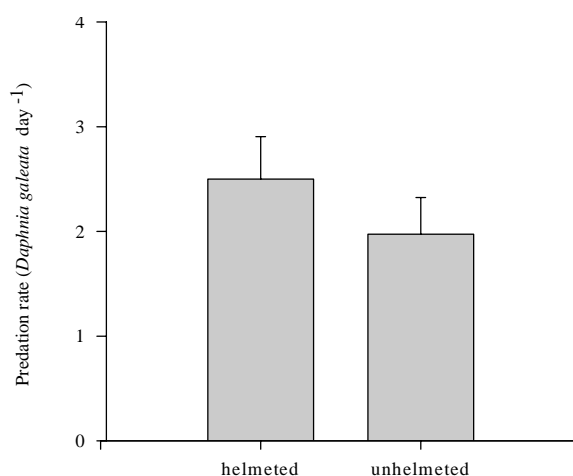


Figure 6. Predation by *Bythotrephes cederstroemi* when offered a choice between helmeted and unhelmeted *Daphnia galeata mendotae*. There was no significant difference between the number consumed of each morph. Error bars are standard error of the mean.

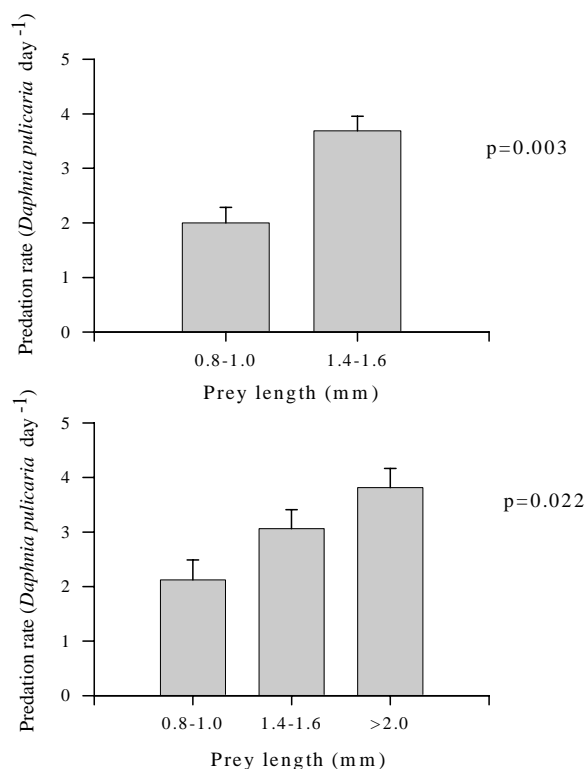


Figure 7. Predation by *Bythotrephes cederstroemi* when offered a choice between either 10 small (0.8–1.0 mm) and 10 medium (1.4–1.6 mm) *Daphnia pulex* (panel A), or between 10 small, 10 medium and 10 large (>2.0 mm) *D. pulex* (panel B). Error bars are standard error of the mean.

Table 2. Comparison of the daily prey consumption rate of *Bythotrephes cederstroemi* predicted from a bioenergetics model of Lake Michigan *B. cederstroemi* at 16 °C (Yurista & Schulz, 1995) and determined experimentally during feeding on *Daphnia pulex* from Lake Michigan at 16 °C in the laboratory. Consumption estimates are expressed both in terms of dry mass per day and percent of total body mass per day

Life history stage	Model prediction		Experimental result	
	Consumption rate ($\mu\text{g day}^{-1}$)	% Body mass	Consumption rate ($\mu\text{g day}^{-1}$)	% Body mass
First instar	96 \pm 1.4	143	–	–
Second instar	244 \pm 4.2	166	–	–
Third instar (adult)	374 \pm 5.5	105	308 \pm 2.1	98

B. cederstroemi in this experiment was $192.3 \pm 12.5 \mu\text{g}$.

Prey size selection on *Daphnia pulex*

When offered a choice between 10 small (0.8–1.0 mm) and 10 medium (1.4–1.6 mm) *Daphnia pulex*, *Bythotrephes cederstroemi* consumed significantly more ($p = 0.003$) medium than small prey (Kruskal–Wallis ANOVA, $\alpha = 0.05$; Figure 7). On average, *B. cederstroemi* consumed 2.0 ± 0.8 (SD) small and 3.7 ± 0.8 (SD) medium *D. pulex* per day. When offered a choice between 10 small (0.8–1.0 mm) and 10 medium (1.4–1.6 mm) and 10 large (>2.0 mm) *D. pulex*, *B. cederstroemi* exhibited a significant ($p = 0.022$) size preference for larger *D. pulex* (Kruskal–Wallis ANOVA, $\alpha = 0.05$; Figure 7). On average, *B. cederstroemi* consumed 2.1 ± 1.0 (SD) small, 3.1 ± 0.9 (SD) medium and 3.8 ± 1.0 (SD) large *D. pulex* per day. The average dry mass of the *B. cederstroemi* in this experiment was $400.3 \pm 20.4 \mu\text{g}$.

Determination of maximum predation rates on *Daphnia pulex*

When allowed to feed on 40 *Daphnia pulex* of lengths >1.4 mm, *B. cederstroemi* consumed an average of 7.1 ± 1.1 (SE) *D. pulex* per day in the 48-h incubation and 6.7 ± 0.9 (SE) *D. pulex* per day in the 72-h incubation for an overall average of 6.8 ± 0.7 (SE) *D. pulex* per day consumption rate. The average length of the *D. pulex* added was used to convert the predation rate to dry mass consumed per day using the regression of Bottrell et al. (1976) for *D. pulex*, with a correction for log transformation

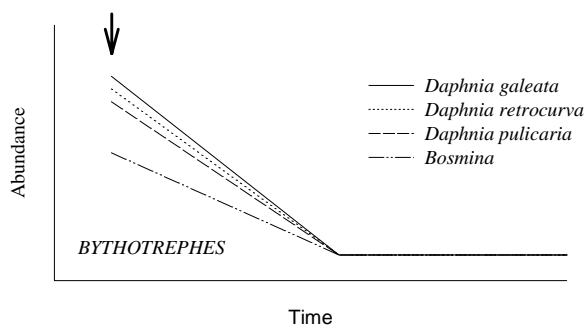


Figure 8. Predictions, based on our experimental results, of the effects of *Bythotrephes cederstroemi* predation alone on a zooplankton community similar to that existing in Lake Michigan prior to *B. cederstroemi* invasion. Arrow indicates introduction of *B. cederstroemi*.

(Bird & Prairie, 1985). This calculated predation rate (98% of body mass per day) is similar to, but slightly less than the consumption rate predicted by the bioenergetics model (105% of body mass per day; Yurista & Schulz 1995) for *B. cederstroemi* in Lake Michigan (Table 2). The average dry mass of the *B. cederstroemi* in this experiment was 314.8 ± 23.0 (SE) μg .

Discussion

The results indicate that *Bythotrephes cederstroemi* is a voracious generalist predator; it prefers large over small *Daphnia pulex* prey and is not deterred by the helmets of *D. galeata mendotae*. These characteristics are atypical of invertebrate zooplankton predators and will influence the functional role of *B. cederstroemi* in the Lake Michigan community.

The offshore zooplankton assemblage used in the predation experiment to determine which prey were consumed by *Bythotrephes cederstroemi* did not contain a diverse cladoceran community. Cyclopoid and calanoid copepods and nauplii, along with *Daphnia galeata mendotae*, were the only available prey. Our results indicate that the only abundant cladoceran in the assemblage, *Daphnia galeata mendotae*, was consumed, as were copepod nauplii and calanoid copepod adults (Figure 3). Of the abundant taxa, only cyclopoid copepod adults were not part of the diet of *B. cederstroemi* in this experiment.

The allozyme technique for determining prey diet composition establishes whether or not the allozymes of a particular zooplankton taxon are present in the gut of the *Bythotrephes cederstroemi* at the time of collection. This technique is not quantitative, but only

indicates what prey types have been consumed. The fact that one type of prey's allozymes are found in a greater number of predators may not indicate that this prey is consumed in greater numbers than are other prey. The increased presence of the prey allozymes instead may be due to a greater mass of prey consumed at one time, which would leave a greater allozyme signal in the gut and cause it to be detected more frequently. Because the allozyme technique is qualitative, one must use caution when comparing the percent of each prey type found in the predator to the abundances of prey in the lake (Figure 4). The presence of a few allozyme bands that did not match those from the prey standards we assayed (Table 1) indicates that *B. cederstroemi* may have consumed prey that we could not assay because they were rare or small, for example the rotifer *Asplanchna*. Alternatively these bands could be from prey that we did survey, but are uncommon allozyme banding patterns in the prey population and so were not represented in our standard analysis. Because the number of unknown bands was small (~5%), their identification would not significantly alter our results.

The allozyme method is also limited to identifying the taxa of the prey consumed, not the life history stage of those prey. At three of the four stations in Lake Michigan, the allozymes of cyclopoid copepods were found in *Bythotrephes cederstroemi*. Because adult cyclopoid copepods were not consumed in the natural assemblage predation experiment, the discovery of their allozymes in the gut of *B. cederstroemi* might appear problematic. However, the predation experiment also indicated that *B. cederstroemi* consumes a significant number of copepod nauplii, suggesting that the presence of cyclopoid allozymes can be attributed to the consumption of cyclopoid nauplii. Vanderploeg et al. (1993) also reported that *B. cederstroemi* consumed copepod nauplii in Lake Huron. Thus, despite the fact that *B. cederstroemi* may not consume adult cyclopoids, it may still have an impact on the cyclopoid population by the consumption of nauplii. Only calanoid and cyclopoid copepod allozymes were detected in the juvenile *B. cederstroemi* collected at station C, despite the presence of a large population of *Daphnia galeata mendotae* and a small number of *Bosmina longirostris* at this location. Juvenile *B. cederstroemi* in Lake Michigan are considerably smaller than adults; first instars average 67 μg dry mass and second instars average 146.4 μg dry mass, compared with an average 355 μg dry mass for adults (Yurista & Schulz, 1995). Perhaps nauplii constitute a greater proportion of the diet for these smaller juveniles, re-

sulting in the prevalence of calanoid and cyclopoid copepod allozymes in their guts.

Both the allozyme data and the results of the natural assemblage experiment indicate that adult *Bythotrephes cederstroemi* are generalist predators. In addition to the adult calanoid copepods, copepod nauplii, and *Daphnia galeata mendotae* that were consumed in the predation experiment, the allozymes of the cladocerans *Bosmina longirostris*, *Holopedium*, and *Eubosmina* were also detected in *B. cederstroemi*. Although *Bythotrephes cederstroemi* can capture and ingest many different types of prey, *Daphnia pulex* was by far the prey of choice when compared to calanoid copepods (Figure 5). Furthermore, *D. galeata mendotae* was consumed by adults at all stations around Lake Michigan, and *Bosmina longirostris* was also a major diet component at two stations (Figure 4). Thus, despite the observation that *B. cederstroemi* is a generalist predator, these results suggest that cladocerans are preferred prey.

Originally, we hypothesized that *Daphnia galeata mendotae* might have survived *Bythotrephes cederstroemi* predation because their long helmets and tailspines were effective morphological defenses. Clearly, this is not the case. Not only were helmeted *D. galeata mendotae* consumed in the natural assemblage experiment (Figure 3), but also the helmeted *D. galeata mendotae* were just as likely to be captured and consumed as were the non-helmeted individuals when *B. cederstroemi* were given a choice between the two (Figure 6). Additional evidence suggests that other morphological defenses may not provide protection from *B. cederstroemi* predation. At station B (Figure 4), *Holopedium* allozymes were found in the guts of several *B. cederstroemi*. *Holopedium* is enclosed in a gelatinous sheath that has been shown to be effective in reducing predation by *Chaoborus* (Allan, 1973). Apparently, the sheath of *Holopedium* does not completely inhibit predation by *B. cederstroemi*, although additional experiments would be necessary to determine if it provides any protection at all. A recent study indicates that *Holopedium* population abundances in Lake Michigan declined drastically after the appearance of *B. cederstroemi*, adding further correlative support to the lack of protection from *B. cederstroemi* provided by the gelatinous sheath (Makarewicz et al., 1995). However, after *B. cederstroemi* invaded an inland lake, *Holopedium* greatly increased in abundance over pre-invasion levels (Yan & Pawson, 1997). The effectiveness of *Holopedium*'s gelatinous sheath

for deterring *B. cederstroemi* predation requires future direct evaluation.

This lack of deterrence of predation by some morphological defenses is a departure from the behavior of a typical pelagic invertebrate predator. For example, long helmets on *Daphnia retrocurva* reduced predation by the copepod *Acanthocyclops vernalis* (Havel, 1985), long mucrones and antennules on *Bosmina* hindered predation by the copepod *Epischura* (Kerfoot, 1975; Wong, 1981b), large crests on *Daphnia carinata* decreased predation by notonectids (Grant & Bayly, 1981), spines on the rotifers *Keratella* and *Brachionus* made them less susceptible to predation by the rotifer *Asplanchna* (Gilbert, 1966; Stemberger & Gilbert, 1984, 1987), and *Daphnia pulex* with spined dorsal crests were more likely to escape from *Chaoborus* predators than those without crests (Havel & Dodson, 1984).

The repeated preference shown by *Bythotrephes cederstroemi* for large prey items (Figure 7) also is atypical of pelagic invertebrate predators (Zaret, 1980). Most zooplankton predators are incapable of handling large prey efficiently (e.g., for copepod predators, Anderson, 1970; Brandl & Fernando, 1974; Dodson, 1974a; Wong, 1981a; for cladoceran predators, de Bernardi & Giussani, 1975; Herzig & Auer, 1990; for *Chaoborus* species, Fedorenko, 1975; Pastorok, 1981; and for *Neomysis mercedis*, Chigbu & Sibley, 1994). *B. cederstroemi*, however, was not only able to capture and consume *Daphnia pulicaria* greater than 2.0 mm in length, but also preferred these large prey. This preference demonstrates that *B. cederstroemi* was capable of consuming the large *D. pulicaria* present in Lake Michigan during the mid 1980's, and should not be eliminated as a potential cause of mortality for these daphnids merely because it is an invertebrate predator. Unlike another predatory cladoceran, *Leptodora kindtii*, *B. cederstroemi* does not have a trap basket for potential prey; it instead grasps a prey item with long feeding appendages and shreds it, ingesting only soft parts (personal observation). Because it is not restricted by the capacity of a trap basket, *B. cederstroemi* is able to feed successfully on the large prey it captures. Both the selection of large prey and the sensitivity to light exhibited by *Bythotrephes cederstroemi* may be explained by the hypothesis that this cladoceran is a visual predator. Brooks (1959) reported that *Polyphemus pediculus*, a close relative of *B. cederstroemi*, can use its eye to form a distinct image that is used to locate prey. Studies have demonstrated that chases by *P. pediculus*

cease in the absence of light, and that its eye can be seen tracking a moving target (Young, 1988; Young & Taylor, 1988). Earlier studies on another *B. cederstroemi* relative, *Podon polyphemoides*, also suggest that its predation, which depends on light, stops after sunset (Bosch & Taylor, 1973a, b). *B. cederstroemi* has an eye similar in appearance to that of *P. pediculus*. Larger prey may be more visible to *B. cederstroemi* and pursued preferentially. Alternatively, *B. cederstroemi* may locate prey by mechanical disturbance, and the larger prey may create more disturbance and therefore be more detectable than small prey.

The predation rate determined during feeding by *Bythotrephes cederstroemi* on large *Daphnia pulicaria* is slightly less than that predicted by a bioenergetic model based on measures of ingestion, assimilation, respiration and estimated growth and reproduction (Table 2). The bioenergetics model predicted that a consumption rate of 105% of body mass per day would be required, and our study found a 98% of body mass per day consumption rate. The model assumes ad lib. food, but in our experiment food was constantly decreasing, and may have been below saturation; a slightly reduced consumption value is therefore expected. The measured consumption rate of 98% of body mass per day is comparable to that found for several other invertebrate predators, such as *Polyphemus* (86% d⁻¹; Monakov & Sorokin, 1972), *Mesocyclops edax* (103–110% d⁻¹; Brandl & Fernando, 1975), and *Macrocyclops albidus* (86% d⁻¹; Monakov, 1972), but higher than the consumption rate of other pelagic predators, for example *Leptodora kindtii* (50% d⁻¹; Karabin, 1974) and *Mysis* (39% d⁻¹; Cooper & Goldman, 1980). Both our measured and predicted consumption rates are almost double those observed by Vanderploeg et al. (1993) for Lake Huron *B. cederstroemi* (55% d⁻¹). This discrepancy may be attributable both to our use of an acclimation period and to our prevention of cannibalism. Consumption rates on the order of those measured in our experiment would approximately equal the average daily replacement values for herbivorous zooplankton in Lake Michigan (Yurista & Schulz, 1995).

Conclusion

Based on the results of our predation experiments and diet composition survey, we can predict *a posteriori* the effects an invading population of *Bythotrephes cederstroemi* should have had on the Lake Michi-

gan zooplankton assemblage (Figure 8). Some of the changes in the Lake Michigan biota that coincided with the introduction of *Bythotrephes cederstroemi* may well be attributable to predation by the invader. The decline of the daphnid species, in particular, seems likely to have been due at least in part to *B. cederstroemi* predation. Not only have we demonstrated that *B. cederstroemi* can capture and consume large numbers of *Daphnia pulicaria*, but Vanderploeg et al. (1993) have shown that it can consume *Daphnia retrocurva* as well. Both the decline in *Daphnia pulicaria*, which could be explained by fish predation, but not by traditional invertebrate predation, and the decline in *D. retrocurva*, which could be explained by traditional invertebrate predation, but not by fish predation, are consistent with predation by *B. cederstroemi*.

Other changes in the Lake Michigan zooplankton assemblage remain unexplained. For example, why *Daphnia galeata mendotae* has survived is not clear. Perhaps, as in other studies, its high reproduction rates keep pace with *B. cederstroemi* predation (Stich & Lampert, 1984). Another possibility is that *D. galeata mendotae* is vertically migrating to reduce overlap with the predator, as suggested by Lehman & Cáceres (1993). If *B. cederstroemi* is a visual predator, vertical migration into deeper waters during the day may allow *D. galeata mendotae* to escape predation, even if overlap is not reduced. The initial decline in *D. galeata mendotae* abundance may have been due to *B. cederstroemi* predation on a population dominated by a non-migrating clone. Selection may have resulted in clonal succession and dominance by a migrating clone, thus allowing the survival and recovery of the *D. galeata mendotae* population.

Also, the initial increase in *Bosmina* population sizes would not be a predicted result of *B. cederstroemi* invasion, because *Bosmina* was found to be consumed by this predator. Our knowledge of the diet of juvenile *B. cederstroemi* is still incomplete. Because consumption as a juvenile is estimated to be 44% of the total lifetime consumption of *B. cederstroemi* (Yurista & Schulz, 1995), we would predict that the impact of juvenile predation on smaller prey such as *Bosmina* should be considerable. If *Bosmina* is not a preferred prey of *B. cederstroemi*, the decline of *Leptodora kindtii* – whether due to direct predation by *B. cederstroemi*, competition, or other factors – may have reduced predation pressure sufficiently for *Bosmina* population sizes to increase. Alternatively, predation by *B. cederstroemi* on the daphnids may

have released *Bosmina* from competition. Recent evidence (Makarewicz et al., 1995), however, indicates that *Bosmina* abundances did decrease precipitously in 1991 and 1992, six years after the appearance of *B. cederstroemi* in Lake Michigan. Perhaps this delayed decline was due to increased predation by *B. cederstroemi* on *Bosmina* in the absence of alternate cladoceran prey.

One additional factor that may have contributed to the apparently large impact of *Bythotrephes cederstroemi* predation on the Lake Michigan zooplankton community is that *B. cederstroemi* is a new invader to the lake. The Lake Michigan zooplankton community and this invader have no history of coexistence and therefore have had no time in which to co-evolve prey defenses and countermeasures. The Lake Michigan zooplanktons' defenses, such as the long helmet and tailspine of *Daphnia galeata mendotae*, evolved as protection against native predators such as *Leptodora kindtii*, and clearly did not deter *B. cederstroemi* predation. Some fish species have been shown to have little effect on their native zooplankton communities, but dramatic effects on newly invaded communities (Kalas, 1995; Pont et al., 1991). Invading plants tend to be more vigorous and better competitors in their new habitats than in their native ones, perhaps due to differential allocation of resources in the new environment, where they are released from natural enemies (Blossey & Notzold, 1995). Perhaps as more time passes, the North American zooplankton will be selected for defenses or behaviors that will make them less susceptible to devastation by *B. cederstroemi*, just as *Daphnia galeata mendotae* now coexists with *B. cederstroemi* after an initial precipitous decline.

The example of *Bythotrephes cederstroemi* predation in Lake Michigan illustrates another exception to the strict separation between invertebrate and vertebrate predators, which has traditionally been made in aquatic ecology. Our results indicate that *Bythotrephes cederstroemi* is an atypical invertebrate predator. Adult *B. cederstroemi* are not deterred by such morphological defenses as helmets and gelatinous sheaths; they choose large prey over small; they have the potential to consume a significant proportion of cladoceran production in Lake Michigan and alter the zooplankton community. The morphology of *B. cederstroemi* – its lack of a prey-size restricting trap basket and the possibility that it is a visual predator – seem to make *B. cederstroemi* more functionally equivalent to a planktivorous larval fish than to an 'invertebrate' size-dependent predator in the classical

sense. As animals and plants continue to invade new ecosystems and concerns about the homogenizing of faunas grow (Kinzelbach, 1995), determining the impact of these exotics becomes increasingly important. As in the case of *B. cederstroemi*, not all invaders will fit our expectations. We may be more successful in predicting the results of invasions and other community disturbances if we do not adhere to taxonomic generalizations, but instead examine each new species' functional role in the community.

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References

- Allan, J. D., 1973. Competition and the relative abundances of two cladocerans. *Ecology* 54: 484–498.
- Anderson, R. S., 1970. Predator-prey relationships and predation rates for crustacean zooplankters from some lakes in western Canada. *Can. J. Zool.* 48: 1229–1240.
- Bird, D. F. & Y. T. -Prarie, 1985. Practical guidelines for the use of zooplankton length-weight regression equations. *J. Plankton Res.* 7: 955–960.
- Blossey, R. & R. Notzold, 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *J. Ecol.* 83: 887–889.
- Bosch, H. F. & W. R. Taylor, 1973a. Distribution of the Cladoceran *Podon polyphemoides* in the Chesapeake Bay. *Mar. Biol.* 19: 161–171.
- Bosch, H. F. & W. R. Taylor, 1973b. Diurnal vertical migration of an estuarine cladoceran, *Podon polyphemoides*, in the Chesapeake Bay. *Mar. Biol.* 19: 172–182.
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson & T. A. Weglenska, 1976. A review of some problems in zooplankton production studies. *Norw. J. Zool.* 24: 419–456.
- Brandl, Z. & C. H. Fernando, 1974. Feeding of the copepod *Acanthocyclops vernalis* on the cladoceran *Ceriodaphnia reticulata* under laboratory conditions. *Can. J. Zool.* 52: 99–105.
- Brandl, Z. & C. H. Fernando, 1975. Investigations on the feeding of carnivorous cyclopoids. *Verh. int. Ver. Limnol.* 19: 2959–2965.
- Brandl, Z. & C. H. Fernando, 1981. The impact of predation by cyclopoid copepods on zooplankton. *Verh. int. Ver. Limnol.* 21: 1573–1577.
- Brooks, J. L., 1959. Cladocera. In W.T. Edmondson (ed.), *Freshwater Biology*. John Wiley, New York: 587–656.
- Brooks, J. L. & S. L. Dodson, 1965. Predation, body size and composition of the plankton. *Science* 150: 28–35.
- Bur, M. T., D. M. Klarer, & K. A. Krieger, 1986. Note: first records of a European Cladoceran, *Bythotrephes cederstroemi*, in Lakes Erie and Huron. *J. Great Lakes Res.* 12: 144–146.
- Carlton, J. T. & J. B. Geller, 1993. Ecological Roulette: the global transport of nonindigenous marine organisms. *Science* 261: 78–82.
- Chigbu, P. & T. H. Sibley, 1994. Predation by *Neomysis mercedis*: effects of temperature, *Daphnia magna* size and prey density on ingestion rate and size selectivity. *Freshwat. Biol.* 32: 39–48.
- Cooper, S. D. & C. R. Goldman, 1980. Opossum shrimp (*Mysis relicta*) predation on zooplankton. *Can. J. Fish. aquat. Sci.* 37: 909–919.
- Cullis, K. I. & G. E. Johnson, 1988. Note: first evidence of the cladoceran *Bythotrephes cederstroemi* Schoedler in Lake Superior. *J. Great Lakes Res.* 14: 524–525.
- de Bernardi, R. & G. Giussani, 1975. Population dynamics of three cladocerans of Lago Maggiore related to predation pressure by a planktophagous fish. *Verh. int. Ver. Limnol.* 19: 2906–2912.
- de Bernardi, R., G. Giussani & M. Manca, 1987. Cladocera: predators and prey. *Hydrobiologia* 145: 225–243.
- Dodson, S. I., 1974a. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. *Ecology* 55: 605–613.
- Dodson, S. I., 1974b. Adaptive change in plankton morphology in response to size-selective predation: A new hypothesis of cyclomorphosis. *Limnol. Oceanogr.* 19: 721–729.
- Evans, M. S., 1988. *Bythotrephes cederstroemi*: its new appearance in Lake Michigan. *J. Great Lakes Res.* 14: 234–240.
- Fedorenko, A. Y., 1975. Instar and species-specific diets in two species of *Chaoborus*. *Limnol. Oceanogr.* 20: 238–249.
- Galbraith, M. G., Jr., 1967. Size-selective predation on *Daphnia* by rainbow trout and yellow perch. *Trans. am. Fish. Soc.* 96: 1–10.
- Gilbert, J. J., 1966. Rotifer ecology and embryological induction. *Science* 151: 1234–1237.
- Goldman, C. R., M. D. Morgan, S. T. Threlkeld & N. Angeli, 1979. A population dynamics analysis of the cladoceran disappearance from Lake Tahoe, California-Nevada. *Limnol. Oceanogr.* 24: 289–297.
- Grant, J. W. G. & I. A. E. Bayly, 1981. Predator induction of crests in morphs of the *Daphnia carinata* King complex. *Limnol. Oceanogr.* 26: 201–218.
- Hall, D. J., 1964. An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. *Ecology* 45: 94–112.
- Hall, D. J., W. E. Cooper & E. E. Werner, 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.* 15: 839–928.

- Hall, D. J., S. T. Threlkeld, C. W. Burns, & P. H. Crowley, 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. *Ann. Rev. Ecol. Syst.* 7: 177–208.
- Havel, J. E., 1985. Predation of common invertebrate predators on long- and short-feathered *Daphnia retrocurva*. *Hydrobiologia* 124: 141–149.
- Havel, J. E. & S. I. Dodson, 1984. *Chaoborus* predation on typical and spined morphs of *Daphnia pulex*: behavioral observations. *Limnol. Oceanogr.* 29: 487–494.
- Herzig, A. & B. Auer, 1990. The feeding behaviour of *Leptodora kindtii* and its impact on the zooplankton community of Neusiedler See (Austria). *Hydrobiologia* 198: 107–117.
- Kalas, S., 1995. The ecology of ruffe, *Gymnocephalus cernuus* (Pisces: Percidae) introduced to Mildevatn, western Norway. *Envir. Biol. Fishes* 42: 219–232.
- Karabin, A., 1974. Studies on the predatory role of the cladoceran, *Leptodora kindtii* (Focke), in secondary production of two lakes with different trophy. *Ekol. pol.* 22: 295–310.
- Kerfoot, W. C., 1975. The divergence of adjacent populations. *Ecology* 56: 1298–1313.
- Kerfoot, W. C., 1977. Implications of copepod predation. *Limnol. Oceanogr.* 22: 316–325.
- Kinzelbach, R., 1995. Neozoans in European waters – exemplifying the worldwide process of invasion and species mixing. *Experientia* 51: 526–538.
- Lange, C. & R. Cap, 1986. Note: *Bythotrephes cederstroemi* (Schodler) (Cercopagidae: Cladocera): a new record for Lake Ontario. *J. Great Lakes Res.* 12: 142–143.
- Langeland, A., 1981. Decreased zooplankton density in two Norwegian lakes caused by predation of recently introduced *Mysis relicta*. *Verh. int. Ver. Limnol.* 21: 926–937.
- Langeland, A., 1982. Interactions between zooplankton and fish in a fertilized lake. *Holarct. Ecol.* 5: 273–310.
- Lehman, J. T., 1987. Palearctic predator invades North American Great Lakes. *Oecologia* 74: 478–480.
- Lehman, J. T., 1988. Algal biomass unaltered by food-web changes in Lake Michigan. *Nature* 332: 537–538.
- Lehman, J. T., 1991. Causes and consequences of cladoceran dynamics in Lake Michigan: implications of species invasion by *Bythotrephes*. *J. Great Lakes Res.* 17: 437–445.
- Lehman, J. T., & C. E. Cáceres, 1993. Food-web responses to species invasion by a predatory invertebrate: *Bythotrephes* in Lake Michigan. *Limnol. Oceanogr.* 38: 879–891.
- Makarewicz, J. C., P. Bertram, T. Lewis & E. H. Brown, Jr., 1995. A decade of predatory control of zooplankton species composition of Lake Michigan. *J. Great Lakes Res.* 21: 620–640.
- McQueen, D. J., 1969. Reduction of zooplankton standing stocks by predaceous *Cyclops bicuspidatus thomasi* in Marion Lake, British Columbia. *J. Fish Res. Bd Can.* 26: 1605–1618.
- Monakov, A. V., 1972. Review of studies on feeding of aquatic invertebrates conducted at the Institute of Biology of Inland Waters, Academy of Science, USSR. *J. Fish Res. Bd Can.* 29: 363–383.
- Monakov, A. V. & Y. I. Sorokin, 1972. Some results on investigations on nutrition of water animals. In Z. Kajak & A. Hillbricht-Ilkowska (eds), *Productivity Problems of Freshwaters*. Polish Scientific Publishers, Krakow: 765–773.
- Mordukhai-Boltovskaia, E. D., 1958. Preliminary notes on the feeding of the carnivorous cladocerans *Leptodora kindtii* and *Bythotrephes*. *Dokl. Akad. Nauk SSSR* 122: 828–830.
- O'Brien, W. J., 1988. The effect of container size on the feeding rate of *Heterocope septentrionales*, a freshwater predaceous copepod. *J. Plankton Res.* 10: 313–317.
- Pastorok, R. A., 1981. Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology* 62: 1311–1324.
- Pont, D., A. J. Crivelli & F. Guillot, 1991. The impact of three-spined sticklebacks on the zooplankton of a previously fish-free pool. *Freshwat. Biol.* 26: 149–163.
- Richards, R. C., C. R. Goldman, T. C. Frantz & R. Wickwire, 1975. Where have all the *Daphnia* gone? The decline of a major cladoceran in Lake Tahoe, California-Nevada. *Verh. int. Ver. Limnol.* 19: 835–842.
- Schulz, K. L. & P. M. Yurista, 1995. Diet composition from allozyme analysis in the predatory cladoceran *Bythotrephes cederstroemi*. *Limnol. Oceanogr.* 40: 821–826.
- Spencer, C. N., B. R. McClelland & J. A. Stanford, 1991. Shrimp stocking, salmon collapse and eagle displacement: cascading interactions in the food web of a large aquatic ecosystem. *Bioscience* 41: 14–21.
- Sprules, W. G., H. P. Riessen & E. H. Jin, 1990. Dynamics of the *Bythotrephes* invasion of the St. Lawrence Great Lakes. *J. Great Lakes Res.* 16: 346–351.
- Stemberger, R. S. & J. J. Gilbert, 1984. Spine development in the rotifer *Keratella cochlearis*: induction by cyclopoid copepods and *Asplanchna*. *Freshwat. Biol.* 14: 639–647.
- Stemberger, R. S. & J. J. Gilbert, 1987. Multiple-species induction of morphological defenses in the rotifer *Keratella testudo*. *Ecology* 68: 370–378.
- Stich, H.-B. & W. Lampert, 1984. Growth and reproduction of migrating and non-migrating *Daphnia* species under simulated food and temperature conditions of diurnal vertical migration. *Oecologia* 61: 192–196.
- Vanderploeg, H. A., J. R. Liebig & M. Omair, 1993. *Bythotrephes* predation on Great Lakes' zooplankton measured by an *in situ* method: implications for zooplankton community structure. *Arch. Hydrobiol.* 127: 1–8.
- Wilkinson, L., 1990. SYSTAT: the system for statistics, SYSTAT, Inc., Evanston, IL.
- Wong, C.K., 1981a. Predatory feeding behavior of *Epischura lacustris* (Copepoda, Calanoida) and prey defense. *Can. J. Fish. aquat. Sci.* 38: 275–279.
- Wong, C. K., 1981b. Cyclomorphosis in *Bosmina* and copepod predation. *Can. J. Zool.* 59: 2049–2052.
- Yan, N. D. and T. W. Pawson, 1997. Changes in the crustacean zooplankton community of Harp Lake, Canada, following invasion by *Bythotrephes cederstroemi*. *Freshwat. Biol.* 37: 409–425.
- Yan, N. D., W. I. Dunlop, T. W. Pawson & L. E. MacKay, 1992. *Bythotrephes cederstroemi* (Schodler) in Muskoka Lakes: first records of the European invader in inland lakes in Canada. *Can. J. Fish. aquat. Sci.* 49: 422–426.
- Young, S., 1988. Chasing with a model eye. *J. exp. Biol.* 137: 399–409.
- Young, S. & V. A. Taylor, 1988. Visually guided chases in *Polyphe-mus pediculus*. *J. exp. Biol.* 137: 387–398.
- Yurista, P. M., 1992. Embryonic and post-embryonic development in *Bythotrephes cederstroemi*. *Can. J. Fish. aquat. Sci.* 49: 1118–1125.
- Yurista, P. M. & K. L. Schulz, 1995. Bioenergetic analysis of prey consumption by *Bythotrephes cederstroemi* in Lake Michigan. *Can. J. Fish. aquat. Sci.* 52: 141–150.
- Zaret, T. M., 1980. *Predation and Freshwater Communities*. Yale University Press, New Haven, 187 pp.