

APPLIED ISSUES

# Selective predation on an introduced zooplankter (*Bythotrephes cederstroemi*) by lake herring (*Coregonus artedii*) in Harp Lake, Ontario

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## SUMMARY

1. *Bythotrephes cederstroemi* (Crustacea: Onychopoda: Cercopagidae) invaded Harp Lake, Ontario in 1993, since when the zooplankton community has shifted from dominance of small-bodied to large-bodied species. During 1995 diets of adult lake herring (*Coregonus artedii*), Harp Lake's primary planktivorous fish, were examined to determine the extent to which this conspicuous zooplankter has become integrated into the lake's foodweb and whether fish condition has been affected in consequence.
2. *Bythotrephes* and *Daphnia galeata mendotae* were strongly preferred prey, whilst *Holopedium gibberum* and calanoid and cyclopoid copepods were negatively selected by lake herring. Predation on *Bythotrephes* and *Holopedium* was not size-selective, although *D. galeata mendotae* and calanoid copepods (*Leptodiaptomus minutus* and *L. sicilis*) consumed by herring were significantly larger than co-occurring conspecifics in the lake.
3. Caudal spines of *Bythotrephes* may form boluses in lake herring stomachs. However, the number of caudal spines in fish digestive tracts did not differ significantly from the number of *Bythotrephes*' mandible pairs, indicating that the former were not differentially retained.
4. Lake herring weight-at-length relationships in lakes in Muskoka, Ontario, invaded by *Bythotrephes* did not differ from those in adjacent non-invaded lakes, indicating that *Bythotrephes* invasion of lakes apparently has not affected condition of lake herring.

## Introduction

Non-indigenous species have been introduced into ecosystems throughout the world. Species invasions are regarded as a serious conservation problem, although they provide ecologists with novel opportunities with which to assess altered trophic interactions in communities. The North American Great Lakes support a large number of non-indigenous species, many of which were introduced via discharges

of ballast water from ships (Mills *et al.*, 1993). The cladoceran *Bythotrephes cederstroemi* Schoedler was probably introduced to the Great Lakes in ballast water collected from the Neva River or Lake Ladoga, Russia (Sprules, Riessen & Jin, 1990; D. Berg, unpublished data). The species was first identified in Lake Ontario in 1982, and was established in all of the remaining Great Lakes by 1987 (Bur, Klarer & Krieger, 1986; Lehman, 1987; Cullis & Johnson, 1988; Johannsson, Mills & O'Gorman, 1991). The range of *Bythotrephes* has since expanded to include at least twenty inland lakes in Ontario, as well as others in

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Minnesota and Michigan (Yan *et al.*, 1992). *Bythotrephes* is an important exotic species because, when abundant, it can impact zooplankton communities. Lehman (1988) and Yan & Pawson (1997) reported that predation by *Bythotrephes* dramatically reduced populations of small- but not large-bodied zooplankton in Lake Michigan and Harp Lake, Ontario.

*Bythotrephes* is among the largest zooplankton species, and is easily detected by visually selecting planktivorous fish. European studies have revealed positive selection for *Bythotrephes* by many fish (Lindström, 1955; Nilsson, 1961, 1979; Grimas & Nilsson, 1965; Nilsson & Anderson, 1967; de Bernardi & Canali, 1975; Stenson, 1978, 1979; Garnås, 1983). Intense planktivory apparently limits the abundance of *Bythotrephes* in some arctic lakes in Sweden (Stenson, 1978). Studies on the Great Lakes have revealed predation of *Bythotrephes* by fish including alewife (*Alosa pseudoharengus* Wilson), rainbow smelt (*O. mordax* Mitchell), emerald shiner (*Notropis atherinoides* Rafinesque), spottail shiner (*N. hudsonius* Clinton), yellow perch (*P. flavescens*), white perch (*Morone americana* Gmelin) and walleye (*Stizostedion vitreum*) (Bur & Klarer, 1991; Hartman *et al.*, 1992; Mills *et al.*, 1992). However, fish feeding preferences on *Bythotrephes* relative to other taxa of zooplankton are poorly established for North American lakes. Predator-based limitation of *Bythotrephes* abundance is of fundamental importance considering the potential of this invader to alter zooplankton communities (Lehman, 1988; Yan & Pawson, 1997).

Effects of *Bythotrephes* ingestion on growth and condition of planktivorous fish have not been well studied. Fish may be positively affected by introduction of a new, highly visible food source. Alternatively, large boluses of caudal spines may be formed in the stomach of fish that consume *Bythotrephes* (Keilty 1990), thereby impeding food passage and reducing growth rate or condition. Giussani & de Bernardi (1977) reported that utilization efficiency by coregonid fish of *Bythotrephes* was apparently lower than for other zooplankton prey. *Bythotrephes* may also adversely affect planktivorous fish indirectly, by reducing availability of zooplankton prey or by altering size structure of zooplankton communities (Yan & Pawson, 1997).

In this study, predation on *Bythotrephes* by lake herring *Coregonus artedii* Lesueur in Harp Lake was examined (Fig. 1). Temporal patterns of predation by

lake herring on *Bythotrephes* relative to other zooplankton prey were assessed, and also whether lake herring fed on a size-selective basis on different zooplankton taxa. Relative passage rates of *Bythotrephes*' caudal spines and mandibles through lake herring stomachs were also assessed to determine whether caudal spine boluses are differentially retained. Finally, weight-at-length relationships for lake herring from lakes with and without *Bythotrephes* were compared to determine whether invasion by this cladoceran affects fish condition.

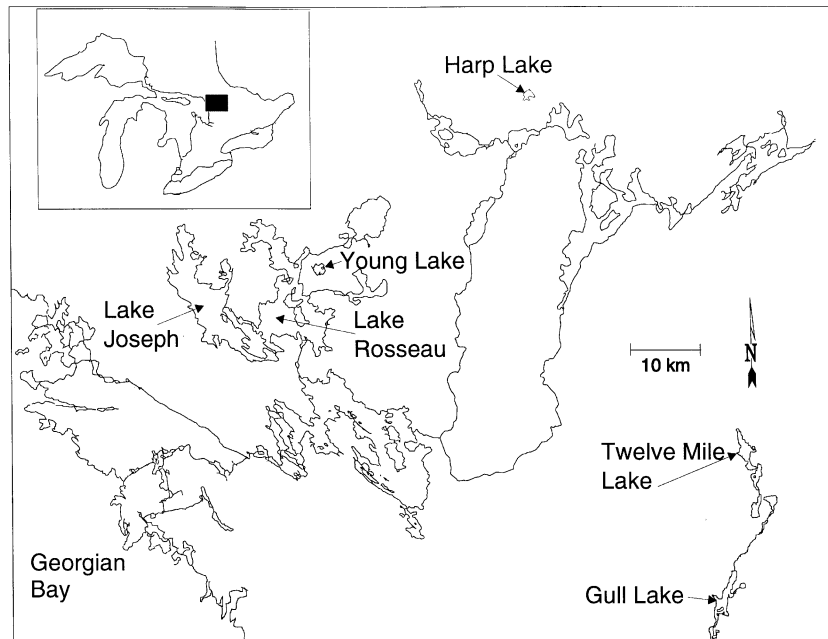
## Materials and methods

### Harp Lake site description

Harp Lake is located near Georgian Bay in the Moon/Go Home drainage basin (Fig. 1). Harp Lake is oligotrophic (total phosphorus =  $8 \mu\text{g L}^{-1}$ ), with an area of  $0.71 \text{ km}^2$  and mean and maximum depths of 12.4 and 37.5 m (Dillon, Reid & de Grosbois, 1987). The lake stratifies to a depth of about 5 m during summer (Fig. 2). The lake has been used as a reference basin since 1978 as part of an acid rain study by the Ontario Ministry of Environment and Energy (MOEE) (Yan, 1986). Until invasion of the lake in 1993 by *Bythotrephes*, the zooplankton community was dominated by small-bodied cladocerans [e.g. *Bosmina longirostris* (O.F.M.), *Diaphanosoma birgei* Korínek, *Chydorus sphaericus* (O.F.M.)] and copepods (e.g. *Epischura lacustris* S.A. Forbes, *Skistodiaptomus oregonensis* Lilljeborg, *L. minutus* Lilljeborg). Large cladocerans (e.g. *D. galeata mendotae* Birge and *H. gibberum* Zaddach) did not become numerically important in the lake until after *Bythotrephes* invaded the lake (Yan & Pawson, 1997).

Harp Lake has been stocked with juvenile lake trout *S. namaycush* Walbaum and brook trout *S. fontinalis* Mitchell for the past 50 years. The littoral fish community consists of smallmouth bass *Micropterus dolomieu* Lacépède, various cyprinid minnows (*Notropis* spp.) and yellow perch *P. flavescens* (R. Coulas, personal observation). The pelagic fish community is dominated by planktivorous lake herring and piscivorous lake trout (W. Dunlop, personal observation).

Water temperature and thermocline depth were monitored throughout this study using a YSI temperature meter (Model 33SCT).



**Fig. 1** Moon/Go Home drainage basin in south-central Ontario (inset). Lakes invaded by *Bythotrephes* include Joseph, Rosseau, Harp. Reference lakes not invaded by *Bythotrephes* include Young, Twelve Mile, Gull.

#### *Fish collections*

Fish and zooplankton were sampled from Harp Lake over seven sampling periods during summer and autumn 1995. All sampling was done between 07.00 and 09.00 h. Monofilament gill nets of 4 and 6 cm stretch were randomly set at three of six sampling locations in Harp Lake. At each sampling site, nets were set perpendicular to the shoreline, beginning at a depth of 10 m and extending for 90 m toward the middle of the lake. The outermost net-set depth ranged between 18 and 30 m. Additional fish samples were collected on 26 April and 19 May 1995, although corresponding plankton samples are lacking. Each net was removed within 40 min to prevent excessive catches of lake herring and to permit rapid preservation of fish stomach contents, thereby minimizing digestion of diet items. Fork length and fish weight were determined within 2 h of capture. Fork length (mm) was measured on a standard fish board, while body weight (g) was measured using a Pennsylvania Model 4050 T electronic balance ( $n = 355$ ). The first left gill arch of each fish was examined for morphological characteristics such as gill raker number, gill raker length and raker space ( $n = 25$ ). All gill measurements were recorded digitally  $\pm 0.1$  mm using a micro-computer adapted to a Wild–Leica dissecting microscope at  $6\times$  magnification.

Fish gastrointestinal tracts were removed and pre-

served in 10% buffered sugar-formalin (Windell, 1968). Digestive tract (stomach and foregut) contents of a minimum of six randomly selected fish from each sampling period were collected, identified and enumerated ( $n = 64$  total). Zooplankton were enumerated with a Wild–Leica dissecting microscope at  $12\times$  magnification. Prey were identified *in toto* to the lowest taxonomic level (Balcer, Korda & Dodson, 1984). Cladocerans were identified to genus because carapace integrity was typically good. Calanoid and cyclopoid copepods and aquatic insects were identified to order owing to poor body integrity in fish stomachs. Naupliar copepods were counted as a single group and later apportioned according to adult abundance. Likewise, calanoid and cyclopoid copepodids were initially identified into two groups, and later apportioned according to adult abundance. Numbers of left and right mandibles and caudal spines of *Bythotrephes* were recorded for all fish diet samples.

#### *Zooplankton collections*

Schindler–Patalas zooplankton samples (30 L with 53- $\mu$ m mesh) were collected from each of the shallowest and deepest depths where each gill net was set. An additional plankton sample was taken on each sampling date from a reference station in the middle of Harp Lake using a 50-cm mouth diameter, 53- $\mu$ m

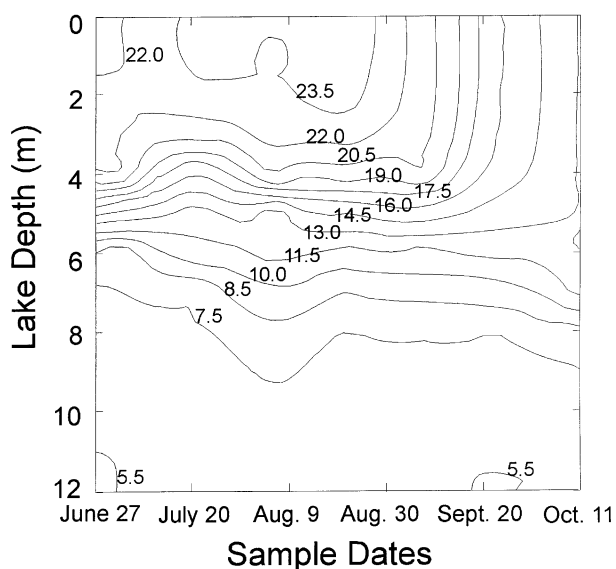


Fig. 2 Temperature profile of surface waters of Harp Lake during summer 1995 ( $^{\circ}\text{C}$  at < 12 m).

Wisconsin plankton net with a length-to-mouth ratio of 4 : 1. Samples were collected from 20 m depth to the surface ( $4\text{ m}^3$ ), treated with carbonated water, and preserved with 4% buffered, sugar-formalin (Haney & Hall, 1973).

Lake plankton samples were enumerated using the same equipment, procedures and taxonomic resolution as per fish stomach samples. Schindler–Patalas samples were processed *in toto* for all taxa. Three replicate subsamples (with replacement) were counted for each Wisconsin net sample (MacIsaac *et al.*, 1992). Entire Wisconsin net samples were examined to estimate densities of rare taxa (e.g. *Bythotrephes*). Zooplankton abundance was estimated by averaging all plankton samples collected on a particular date.

Size structure of the five numerically most important zooplankton groups was determined by measuring body length of at least 150 randomly selected individuals from each of plankton and fish diet using a Wild–Leica dissecting microscope linked to a micro-computer. Animal lengths were digitized for conversion to biomass (ZEBRA2 software; Allen, Yan & Geiling, 1994). Body length measurements consisted of tip-of-head to base-of-carapace for *D. galeata mendotae* and *H. gibberum* (exclusive of gelatinous mantle), and of tip-of-head to base of caudal rami in calanoid copepods. *Bythotrephes* was measured from the base of the caudal process (i.e. anterior to the first caudal spike) to the middle of the eye spot. Abundant

zooplankton taxa (*D. galeata mendotae* and calanoid copepods) were measured on each sampling date. Measurements for less abundant zooplankton (*H. gibberum* and *Bythotrephes*) were limited to periods of highest abundance. Size-structured zooplankton abundance was calculated as:

$$N_i = N * s_i \quad (1)$$

where  $N_i$  is abundance (individuals  $\text{m}^{-3}$ ) of animals of size class  $i$ ,  $N$  is species density (individuals  $\text{m}^{-3}$ ) and  $s_i$  is the proportion of individuals counted of size class  $i$ .

Size-structured abundance data were used to estimate total dry biomass for major zooplankton taxa. Biomasses of individual zooplankters were calculated using length–mass regressions in ZEBRA2 software (Yan, 1986; Allen *et al.*, 1994; N. Yan, unpublished data). Biomass values were corrected for loss of weight in formalin (Giguère *et al.*, 1987; N. Yan, unpublished data). Biomass values were estimated only for planktonic zooplankton because some prey items, including *Mysis relicta* (Loven) and *Chaoborus punctipennis* (Say), live primarily in the benthos during daylight hours and were never captured in plankton samples. It was not possible to establish the original lengths of these prey nor to convert abundance to biomass because only fragments of these taxa were found in the digestive tract.

Total dry biomass ( $B$ ;  $\mu\text{g m}^{-3}$ ) of major zooplankton taxa was estimated for both lake and diet samples as:

$$B = \sum_{i=1}^c (N_i * Y_i) \quad (2)$$

where  $Y_i$  is dry biomass ( $\mu\text{g m}^{-3}$ ) of individuals of size class  $i$  and  $c$  is the number of size classes.

#### Lake herring feeding

Two indices were used to analyse lake herring feeding preference in Harp Lake using the five most abundant zooplankton taxa from plankton and fish diet assessments. Chesson's  $\alpha$  index provides a measure of the proportional abundance of a prey type in fish diet relative to its proportional abundance in the lake (Chesson, 1983). Chesson's index is commonly used in fish diet research, and is considered one of the most reliable for field-based observations (Lechowicz, 1982). Chesson's  $\alpha$  ranges between 0 (strong negative selection) and 1 (strong positive selection), with a value of

**Table 1** Morphometric characteristics of six lakes in central Ontario that were sampled for lake herring. Lakes were selected on the basis of presence or absence of *Bythotrephes*. Fish characteristics provided for each basin sampled are mean (SD) values

Lake	Surface area (ha)	Mean depth (m)	Maximum depth (m)	<i>Bythotrephes</i> present?	Lake Herring		
					N	Fork length (mm)	Wet mass (g)
Rosseau	6295	23.2	90	Yes	52	246.9 (21.3)	168.2 (43.1)
Joseph	5375	24.7	93	Yes	22	253.2 (24.7)	201.2 (61.2)
Harp	72	11.6	34	Yes	57	214.5 (15.2)	103.6 (23.7)
Young	109	11.9	22	No	173	220.3 (25.3)	111.9 (46.6)
12 Mile	463	10.6	24	No	52	222.1 (18.8)	114.4 (25.7)
Gull	996	16.5	49	No	66	243.2 (22.3)	180.9 (54.5)

0.2 indicating non-selective feeding for five prey classes. An overall Chesson's  $\alpha$  value was calculated by pooling mean  $\alpha$  values across dates; variance for the pooled  $\alpha$  value was estimated using the method of Manly (1974). Overall  $\alpha$  values for each species were tested against the neutral selectivity value using Student's *t*-test (Manly, 1974). Chesson's  $\alpha$  values met the assumption of normality following arcsine, square-root transformation. Individual *t*-tests for each plankton species were assessed at an adjusted probability level of 0.01 (0.05/5).

Chesson's index is sensitive to rare prey types. A second index of feeding preference, developed by Pearre (1982), was employed to compare relative abundance of each prey species in diet and environment collections against all other prey items found in both samples. Thus Pearre's index is not biased by rare prey types. Pearre's *V* index ranges between 1 (strong positive selection) and -1 (strong negative selection), with a value of zero indicating neutral selection. Pearre's index follows the  $\chi^2$  distribution.

Zooplankton dry biomass was utilized with both selection indices, although statistical tests based on plankton abundance yielded the same results even for taxa that were subject to size-selective predation by lake herring (e.g. *D. galeata mendotae*; Coulas, 1996).

Product-moment (Pearson's) correlation coefficients were computed to assess the relationship between proportional abundance of a prey type (*D. galeata mendotae*, *Bythotrephes*) in the plankton and in fish diet. This measure provides an estimate of how closely predators were assessing or tracking abundance of these prey types in the lake, and thus whether the fish modified diet according to changes in the plankton community.

Size-selective predation by lake herring on

zooplankton was assessed using size structure of lake and fish diet samples for the four most abundant prey types (*D. galeata mendotae*, *Bythotrephes*, calanoid copepods, *H. gibberum*). Size distributions were compared separately for each sampling period using Kolmogorov-Smirnov two-sample tests.

The number of *Bythotrephes* caudal spines in lake herring stomachs was regressed on the higher of the right or left *Bythotrephes* mandible number to assess whether the former were retained longer in the digestive tract than typical food items. The mandibles of *Bythotrephes* are only slightly smaller (0.4–0.5 mm; Martin & Cash-Clark, 1995) than zooplankton prey of lake herring. Thus the number of caudal spines (6–8.5 mm; R. Coulas, unpublished data) relative to that of mandibles provides an assessment of caudal spine retention. The slope was tested against a value of 1 using a *t*-test to determine whether caudal spines passed through herring stomachs at the same rate as mandibles.

#### Lake herring condition

The weight-at-length relationships for lake herring from Lakes Joseph, Rosseau and Harp were compared to those of Lakes Young, Twelve Mile and Gull (Fig. 1). The first three lakes were invaded by *Bythotrephes* at least 3 years prior to fish sampling, while the last three lakes have not been invaded (Table 1). Sampling procedures for fish on these lakes are identical to methods and laboratory procedures employed on Harp Lake (see also MacKay, 1995). Lake herring were collected from all six lakes between mid-April and the end of May 1995. Time of collection was standardized across lakes to minimize seasonal variability in food availability among lakes. Variation in weight of lake

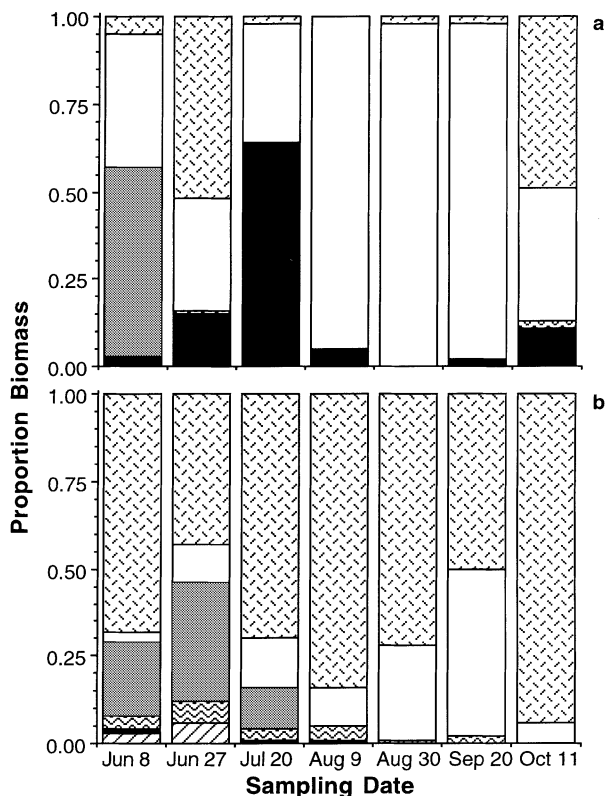


Fig. 3 Proportional biomass of various species of zooplankton in (a) lake herring stomach samples and (b) in Harp Lake. Zooplankton taxa: calanoid copepods (cross stippled), *Daphnia galeata mendotae* (open), *Holopedium gibberum* (dark stippled), cyclopoid copepods (wave), *Bosmina* spp. (diagonal lines) and *Bythotrephes* (solid).

herring from invaded and non-invaded lakes was analysed using analysis of covariance (ANCOVA), with length entered as a covariate and invasion status as a factor variable. This analysis was performed on log-transformed length and weight data using the GLM procedure of MINITAB 9.0 for Windows.

## Results

Lake herring consumed a wide variety of prey items in Harp Lake. Diets were dominated by aquatic insects (mainly Diptera and Hymenoptera) for two sampling periods during spring 1995. Five other taxa (*Bythotrephes*, *D. galeata mendotae*, *H. gibberum* and calanoid and cyclopoid copepods) were the principal biomass components of lake herring diet during summer sampling dates (Fig. 3a). *Bythotrephes* was found in virtually all fish collected on or after May 19. It was a dominant (> 10%) biomass contributor during June,

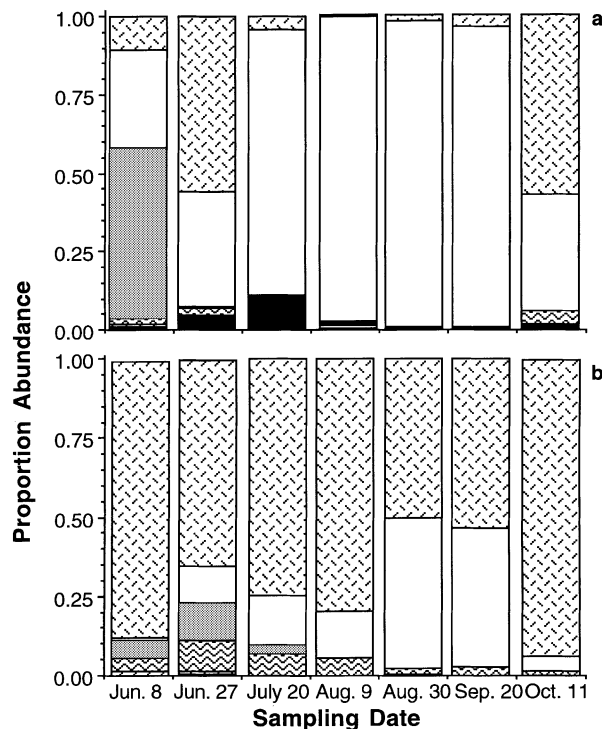


Fig. 4 Proportional abundance of various species of zooplankton in (a) lake herring stomach samples and (b) in Harp Lake. Species key as per Fig. 3. *Chaoborus punctipennis* and *Mysis relicta* represented 1.01% of fish diet items on 8 August, and less than 0.50% on all other dates. These species were never encountered in lake plankton samples.

July and October (Fig. 3a). Relative biomass contribution of *Bythotrephes* to lake herring diet was highly variable, ranging between 1 and 64% (Fig. 3a). It is noteworthy that there was usually a tenfold increase in relative biomass of *Bythotrephes* in diet of lake herring as compared to relative abundance (Fig. 4a,b) because of the tremendous size difference between *Bythotrephes* and most other zooplankton.

*Daphnia galeata mendotae* was a dominant biomass contributor to fish diet on all sample dates, particularly in August and September (Fig. 3a). Calanoid copepods were common diet items in both spring and autumn (Fig. 3a). *Holopedium gibberum* was a common component of fish diet only on 8 June (Fig. 3a). *Mysis relicta* and *Chaoborus punctipennis* were found in fish diets during the June to October period, but collectively represented less than 1% of prey abundance (Fig. 4a). Several other taxa that were rare in lake herring diet and in plankton samples included *D. bergei*, *Bosmina longirostris*, *B. (Neobosmina) tubicen* Brehm and *Polyphemus pediculus* L.

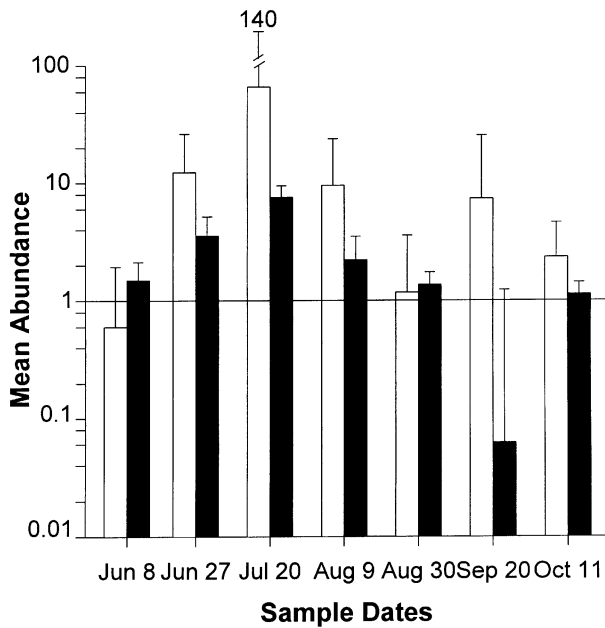


Fig. 5 Mean (+ 1 SD) abundance of *Bythotrephes* in lake herring diet (individuals per fish; white bar) and in Harp Lake plankton (individuals  $m^{-3}$ ; black bar).

In contrast to fish diet, zooplankton biomass and abundance in Harp Lake were dominated by calanoid copepods (*L. minutus*, *E. lacustris*) during every sampling period (Figs 3b, 4b). While *D. galeata mendotae* was a numerically important component of the plankton during the summer period (12–47%; Fig. 4b), individuals were quite small (0.74–0.98 mm) and its biomass contribution was generally low (Fig. 3b). The only other taxa that ever constituted more than 5% of plankton biomass were *H. gibberum* and *Bosmina* spp., mainly during spring and early summer (Fig. 3b). Cyclopoid copepods, mainly *Tropocyclops extensus* (Kiefer) and *Mesocyclops edax* (S. A. Forbes), contributed only marginally (< 5%) to plankton biomass and abundance during summer (Figs 3b, 4b).

*Bythotrephes* was always rare and never constituted more than 1% and 0.01% of total zooplankton biomass and abundance, respectively (Figs 3b, 4b). Despite its relative rarity in the plankton, biomass of *Bythotrephes* in fish stomachs was highly correlated with its abundance in the lake (Pearson's  $r = 0.93$ ; Fig. 5).

Examination of fish diet and lake plankton biomass for the five primary zooplankton groups revealed marked selection by lake herring (Fig. 6a,b). Both Chesson's  $\alpha$  and Pearre's  $V$  selectivity indices revealed significant positive selection by lake herring for *Bythotrephes* ( $P \leq 0.01$ ; Fig. 6a,b). The highest selection

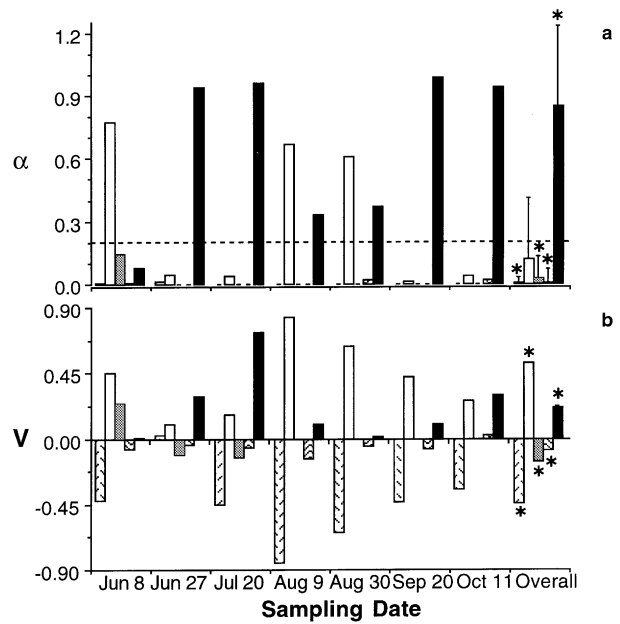


Fig. 6 Mean seasonal and overall (+ 1 SD) values for (a) Chesson's  $\alpha$  and (b) Pearre's  $V$  for lake herring feeding on zooplankton biomass. Neutral selection values are 0.2 (dotted line) and 0 for Chesson's and Pearre's indices, respectively. \* $P < 0.01$ . Symbols as per Fig. 3.

values for *Bythotrephes* corresponded with its peak density in the lake (Fig. 5).

*Daphnia galeata mendotae* was always a more common biomass component of fish diet than lake plankton. Despite this pattern, Chesson's  $\alpha$  indicated positive selection for *D. galeata mendotae* on three sampling dates and negative selection on four others (Fig. 6a). Overall selection for *D. galeata mendotae* did not differ significantly from non-selective feeding (Fig. 6a). Pearre's index indicated positive selection for *D. galeata mendotae* by lake herring on all dates ( $P = 0.001$ ; Fig. 6b). Moreover, selection for *D. galeata mendotae* exceeded that for *Bythotrephes* on three of seven sampling dates (Fig. 6b).

All other zooplankton groups examined were negatively selected by lake herring on all dates except for *H. gibberum* on 8 June (Fig. 6a,b); for example,  $\alpha$  values for calanoid and cyclopoid copepods and *H. gibberum* were always less than the neutral selection value (0.2), and all three species were significantly negatively selected by lake herring ( $P < 0.01$ ,  $t$ -tests).

Fish diet appeared to 'track' abundance of plankton availability for preferred taxa. Product-moment correlation coefficients for *D. galeata mendotae* (0.58) and particularly for *Bythotrephes* (0.70) indicate greater

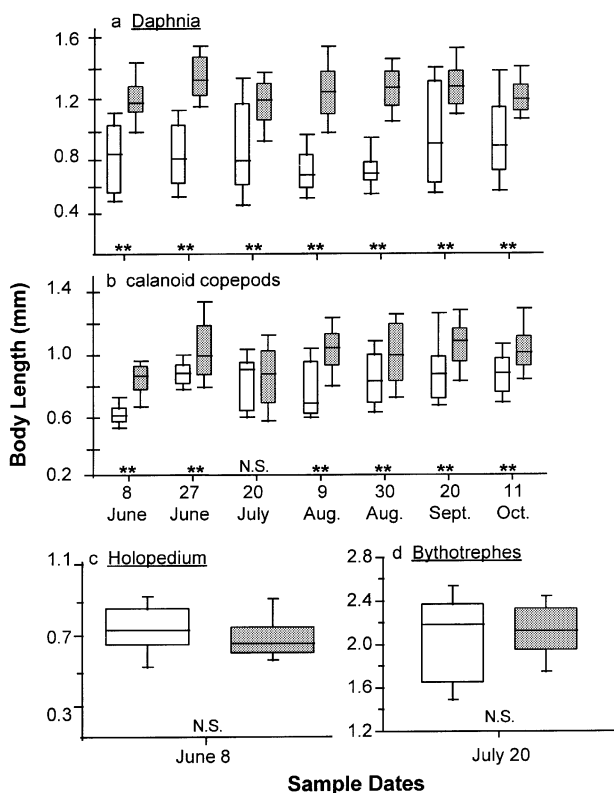


Fig. 7 Boxplots of zooplankton body length (mm) in plankton samples (open) and fish diet (stippled). Comparisons between lake and diet samples were made with a Kolmogorov–Smirnov two-sample test.  $N = 50$ . \*\* $P < 0.01$ , N.S.:  $P > 0.05$ .

representation of these species in fish diet when they were most abundant in the lake.

Lake herring also exhibited size selective predation for some prey taxa. Prey size selection was most dramatic and consistent for *D. galeata mendotae*. *Daphnia galeata mendotae* in lake herring diet were significantly larger, by an average of 0.39 mm, than individuals collected concurrently from the lake ( $\alpha = 0.05$ , Kolmogorov–Smirnov test; Fig. 7). Calanoid copepods consumed by lake herring were also significantly larger, by an average of 0.15 mm, than those in the lake on six of the seven dates (Fig. 7). By contrast, zooplankton species that possess morphological deterrents to fish predation were not consumed in a size-selective manner; for example, size distributions of neither *Bythotrephes* nor *H. gibberum* varied among fish diet and lake plankton samples ( $P > 0.05$ , Fig. 7).

Size selection of prey by lake herring is consistent with anatomical features of the fish. Inner gill raker space, measured at the base of the arch, averaged 0.5 mm (SD = 0.06 mm; maximum 0.58), suggesting

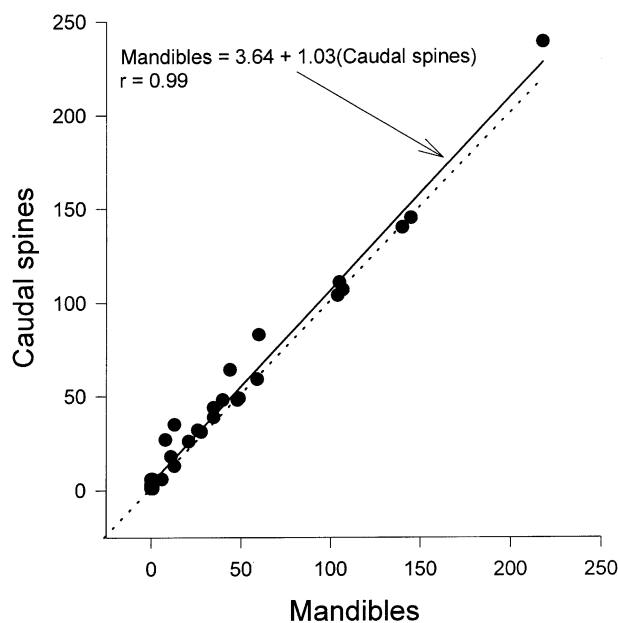


Fig. 8 *Bythotrephes* caudal spine number regressed on mandible number in lake herring diet from Harp Lake (solid line). The regression coefficient ( $\beta$ ) did not differ significantly ( $P > 0.10$ ) from a slope of 1 (dotted line).  $N = 38$ .

that potential prey smaller than this value would probably not be retained. The prey types that lake herring selected most strongly on the basis of size (*D. galeata mendotae*, calanoid copepods) were also among the smallest zooplankton taxa studied.

*Bythotrephes* caudal spine number was regressed on mandible number to assess whether the larger body part was differentially retained (Fig. 8). While numbers of the two body parts were highly correlated in fish stomachs (Pearson's  $r = 0.99$ ), there was no evidence that caudal spines were differentially retained, as the regression coefficient (1.03) did not vary significantly from 1 ( $P > 0.10$ ; Fig. 8). However, the regression intercept was significantly greater than 0, indicating that caudal spines were found more often than mandibles when few *Bythotrephes* were present in the stomach (Fig. 8).

Lake herring weight-at-length relationships were explored for three invaded and non-invaded lakes in central Ontario (Figs 1, 9). Lake herring weight was strongly related to fish length ( $P < 0.001$ ), but not to *Bythotrephes* invasion status ( $P = 0.748$ ) nor to an interaction between fish length and invasion status ( $P = 0.714$ ). Lake herring weight-at-length relationships also varied within lake types ( $P < 0.001$ ; Fig. 9).



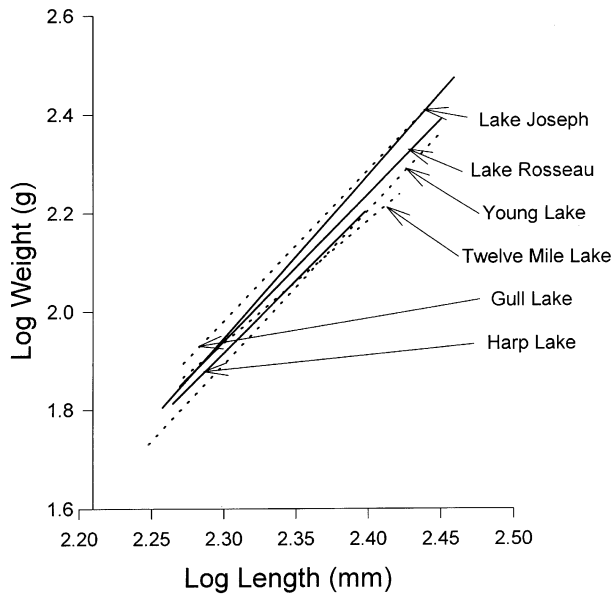


Fig. 9 Weight-at-length regressions for lake herring from Lakes Joseph, Rosseau and Harp (*Bythotrephes*-invaded lakes) and Lakes Young, Twelve Mile, and Gull (non-invaded lakes).

Thus while condition of fish varied among lakes, differences were not related to the presence of *Bythotrephes*.

## Discussion

The success of exotic species depends on their ability to establish and reproduce in invaded communities (Elton, 1958). The proficiency with which an invader avoids predators, pathogens and competitors determines, in part, its abundance and potential ecological impact on the community it has invaded. Exotic invertebrate predators may thrive and have profound impacts on lake ecosystems; for example, introduction of the opossum shrimp *Mysis relicta* into Flathead Lake, Montana, set off a trophic cascade in which reduced zooplankton abundance resulted in reduced food supply to and abundance of planktivorous fish, birds and mammals (Spencer, McClelland & Stanford, 1991). Similarly, during the short period that *Bythotrephes* has been resident in Harp Lake, it has dramatically reduced population densities of small-bodied zooplankton that previously dominated in the lake (Yan & Pawson, 1997). *Bythotrephes* successfully invaded and established in Harp Lake despite intense, selective predation by the lake's principal planktivorous fish. It is interesting to note that *Bythotrephes* invaded Harp Lake despite the lake's very high divers-

ity of native crustacean zooplankton (sixteen taxa) relative to other lakes in the region (Yan & Pawson, 1997). Invasion theory predicts that invasions are most likely to succeed in systems that lack potent predators and in which native species diversity is low (Elton, 1958; Lodge, 1993). Harp Lake seemingly satisfies neither of these requirements.

The present study indicates that adult lake herring preferentially select *Bythotrephes* even though the species has been resident in the lake for only a short period and never achieves high population densities. The large size of *Bythotrephes* relative to most zooplankton in North American lakes enhances its vulnerability to active planktivores like lake herring that locate prey visually (Janssen, 1978, 1980). This vulnerability is further enhanced by *Bythotrephes*' conspicuousness. *Bythotrephes* in Harp Lake have blue-tinged antennae and thoracopods, a red brood pouch, and a very large dark eye.

The feeding preference findings reported here closely parallel European studies that established predation on and preference for *Bythotrephes* spp. by many fish species. As examples, *Bythotrephes* is consumed by brown trout (*Salmo trutta* L.), arctic char [*Salvelinus alpinus* (L.)], lake whitefish (*Coregonus* spp.), smelt (*Osmerus eperlanus* L.), roach [*Rutilus rutilus* (L.)], and perch (*Perca fluviatilis* L.) (Lindström, 1955; Nilsson, 1955, 1961; Nilsson & Pejler, 1973; Giussani & de Bernardi, 1977; Hakkari, 1978; Fitzmaurice, 1979; Garnås, 1983; Næsje *et al.*, 1987; Jachner, 1991). It is instructive that with the exception of smelt, roach and perch, these studies involved adult fish. Small fish may attempt to consume *Bythotrephes*, although these attempts may be thwarted by physical limitations imposed by the caudal appendage and its barbs or by the mouth gape of the fish.

Engel (1976) demonstrated positive selection by lake herring for cladocerans including *Leptodora kindtii* Focke, *Daphnia* spp., *Chydorus sphaericus* and *B. longirostris*, and negative selection for copepods including *Cyclops bicuspidatus thomasi* S.A. Forbes and *Diaptomus minutus*. Lake herring in Harp Lake exhibited positive selection for *D. galeata mendotae* and *Bythotrephes* (although *Bosmina* was rarely encountered in the diet). These feeding preferences correspond with swimming abilities of different zooplankton species; for example, Link (1996) determined that lake herring had much lower capture probabilities for copepods than for slow-swimming cladocerans. Diet

of lake herring in Harp Lake has changed dramatically in recent years, with selection now strongest for species that were either absent (*Bythotrephes*) or much less common (*D. galeata mendotae*) prior to 1993. It seems likely that negative selection of *D. galeata mendotae* by lake herring, as indicated by some Chesson's  $\alpha$  values, may have resulted from sensitivity of the index to rare prey types; disproportionately greater selection by fish for *Bythotrephes* on these dates resulted in diminution of selection for *Daphnia* even though it was more common in fish diets than in the lake. It is, however, possible, that selection changed seasonally in relation to absolute abundance or size structure of the *Daphnia* population.

Lake herring in Harp Lake fed on specific size classes of common plankton species. Calanoid copepods and *D. galeata mendotae* ingested by lake herring were significantly larger than corresponding plankton in the lake. This pattern did not extend to less common taxa, as neither *Bythotrephes* nor *H. gibberum* were consumed on a size-selective basis. *Bythotrephes* is such a conspicuous organism that even relatively small individuals may be perceptible to planktivores (Zaret, 1972).

#### *Bythotrephes coexistence with lake herring*

Lake herring quickly incorporated *Bythotrephes* into its diet as its population increased in Harp Lake. *Bythotrephes* was never a numerically important component of the zooplankton community in the lake, yet it was a highly preferred prey item of lake herring. Handling mortality precludes mark-recapture studies to ascertain the size of the lake herring population in Harp Lake, although catch rate data suggest the population is large; for example, about twenty fish were captured per gill net during each 30-min period, although 200 individuals were captured on one occasion. Based on the incidence of broken caudal spines in lake sediments, Hall & Yan (1997) suggested that up to 40% of deposited *Bythotrephes* had been consumed by fish in Harp Lake. Given the relatively high density of lake herring, and its strong selection for *Bythotrephes*, it seems reasonable to conclude that lake herring could strongly affect *Bythotrephes* abundance and possibly even its existence in Harp Lake. However, the lake's thermal regime appears to provide *Bythotrephes* with a spatial refuge from lake herring, thereby reducing predator-prey contact. During summer 1995,

a thermocline established at about 5 m depth in Harp Lake between 8 June and 27 June and persisted until autumn turnover in early September (C. Charron, University of Toronto, Mississauga, Ontario, personal communication). Spatial distributions of *Bythotrephes* and lake herring exhibited little overlap; for example, efforts to capture lake herring in the epilimnion of Harp Lake using gill nets were unsuccessful on three occasions. Emery (1973) reported that lake herring were found primarily along the bottom in lakes in Algonquin Park, Ontario. These findings are consistent with limited laboratory and synoptic survey data which suggest that the species strongly prefers cold water (4–12 °C, Janssen, 1978). By contrast, an intensive survey of diel vertical distribution revealed that *Bythotrephes* spent  $\approx$  80% of a 24-h period in the epilimnion of Harp Lake during July 1995 (C. Charron, personal communication). Lake herring feeding on *Bythotrephes* may be limited to the period between 04.00 and 08.00 h when *Bythotrephes* is much more homogeneously distributed throughout the water column. Predation on *Bythotrephes* appears to depend on its movement into the hypolimnion during the early morning hours. Nevertheless, the spatial refuge afforded to *Bythotrephes* by the thermal structure of the lake probably reduces predation by the lake's primary planktivore very considerably. Vertical distributions of coregonid planktivores and *Bythotrephes* in Harp Lake are exactly opposite to patterns observed in Lake Lucerne, Switzerland (C. Heller, personal communication) and other European lakes, although in all cases they serve to limit predator contact with prey. It remains unclear why *Bythotrephes* exhibits nocturnal migrations below the thermocline where its primary predators reside.

*Bythotrephes* abundance declined rapidly during late summer, and was very low when the lake destratified. Destratification would eliminate the spatial refuge and potentially increase encounter rates of predators and prey. However, the low density of *Bythotrephes* on 20 September, after the lake had destratified, may have resulted from a combination of increased death rate and reduced birth rate.

#### *Lake herring diet and condition*

Differential retention of *Bythotrephes* caudal spines relative to other prey items in fish stomachs could potentially affect fish hunger and subsequent feeding. Keilty (1990) found that stomachs of alewife from

Lake Michigan were solidly packed with *Bythotrephes*. Stomachs of some lake herring from Harp Lake and other invaded lakes in the Muskoka region were also filled with caudal spines from *Bythotrephes*. Feeding on *Bythotrephes* by lake herring did not result in differential retention of caudal spines as evidenced by the relative passage rates of caudal spines and mandibles. This finding should be interpreted with caution, however, as most of the fish contained fewer than 100 *Bythotrephes*.

No differences in condition of fish in invaded and non-invaded lakes were found. This is consistent with the view that *Bythotrephes* is processed through digestive tracts of lake herring at the same rate and with the same efficiency as other, smaller foods. However, this is inconsistent with the available evidence regarding utilization efficiency (i.e. ratio of utilized to total calories ingested) of coregonid fish preying on *Bythotrephes* and other zooplankton prey (Giussani & de Bernardi, 1977). Giussani & de Bernardi (1977) questioned preferential ingestion of *Bythotrephes* by coregonids considering the low population density of the former in Lake Maggiore, Italy, and low utilization efficiency of the latter on this prey type relative to *Daphnia*. Even if lake herring had low utilization efficiency when feeding on *Bythotrephes*, overall fish growth could be neutrally or even positively affected owing to enhanced availability of other preferred prey (i.e. *D. galeata mendotae*) in invaded lakes.

Additional study is required before it can be concluded that invasion by *Bythotrephes* has no adverse effects on fish condition. Condition or growth could be reduced in a density-dependent manner that would not be obvious in this study; for example, *Bythotrephes*-induced alterations of zooplankton community structure (Yan & Pawson, 1997) could reduce availability of small prey to larval fish and cause a bottleneck in juvenile recruitment. If realized, this effect could take years to detect, depending on the severity of food limitation. Moreover, because the present study considered only adult fish it may have underestimated the effects of *Bythotrephes* on fish condition. Fish in Lakes Joseph, Rosseau and Harp experienced up to 9 years of growth prior to establishment of *Bythotrephes*. This limitation could be overcome by comparing otolith growth patterns in small fish in invaded and non-invaded lakes, and by limiting assessments to years subsequent to *Bythotrephes* invasion. Although weight-at-length relationships were used to assess fish

condition differences in invaded and non-invaded lakes, use of size-at-age relationships would provide more conclusive information.

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