Predation on the exotic spiny water flea
Bythotrephes cederstroemi by lake herring
Coregonus artedi in Harp Lake, Ontario.

Robert Andrew. Coulas
University of Windsor

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Predation on the exotic spiny water flea *Bythotrephes cederstroemi*
by lake herring *Coregonus artedi* in Harp Lake, Ontario

by
Robert Andrew Coulas

A Thesis
Submitted to the Faculty of Graduate Studies and Research
through the Department of Biological Sciences
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Windsor, Ontario, Canada

1996
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Abstract

The predaceous, spiny water flea Bythotrephes cederstroemi invaded the Great Lakes in the early 1980’s, and Harp Lake in 1993. Harp Lake, a small inland waterbody in central Ontario, provides an excellent opportunity with which to assess ecological perturbations involving this exotic species at a tractable spatial scale. Lake herring (Coregonus artedi) and zooplankton were sampled during summer and autumn 1995. Diets of lake herring were examined and compared with zooplankton taxa in the plankton. Fish demonstrated strong positive selection for Bythotrephes and Daphnia spp., and negative selection for Holopedium gibberum and calanoid and cyclopoid copepods.

An examination of the occurrence of Bythotrephes tailspines and mandibles in fish digestive tracts revealed that tailspines were not differentially retained, and that the formation of dense tailspines boluses appears to have no effect on their retention in the digestive tract. An assessment of lake herring weight at length relationships in invaded and noninvaded lakes in central Ontario revealed no significant differences in fish growth rates attributable to invasion by Bythotrephes.

Results from this study indicate that adult lake herring readily incorporate Bythotrephes into their diet in invaded lakes. However, it is not evident whether lake herring are beneficially or adversely affected by lake invasion of, and predation on, Bythotrephes.
For the patience, encouragement and guidance towards all that I have accomplished I dedicate this work to my fiancé, Lori-Ann Clancy.
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Introduction

Non-indigenous species have been introduced into ecosystems throughout the world. The Great Lakes support at least 139 exotic species, many of which were introduced via discharges of ballast water (Mills et al. 1993). Most species introductions appear to cause little ecological or economic damage, although approximately 10% of exotics have caused problems in the Great Lakes (Mills et al. 1993). While regarded as a conservation biology problem (Meffe and Carroll 1994), species invasions provide researchers with opportunities to assess novel trophic interactions in communities, including dynamic responses of native species to the presence of new predators, competitors, or food sources.

The large predaceous zooplankter **Bythotrephes cederstroemi** Schoedler was first identified in Lake Ontario in 1982 (Johannsson et al. 1991), followed by Lake Huron in 1984 (Bur et al. 1986), Lake Erie in 1985 (Bur et al. 1986), Lake Michigan in 1986 (Lehman 1987; Evans 1988), and Lake Superior in 1987 (Cullis and Johnson 1988; Garton and Berg 1990; Jin and Sprules 1990). The range of this species has expanded to include establishment in at least sixteen inland lakes in Ontario as well as others in Minnesota and Michigan (Yan et al. 1992, N. Yan and W. Dunlop, *pers. comm.*). Considerable debate has centred on the effects of **Bythotrephes** on plankton communities. Lehman (1988) and Lehman and Cáceres (1993) reported that populations of Lake Michigan **Daphnia** spp. and **Leptodora kindti** were eliminated or dramatically reduced subsequent to **Bythotrephes** invasion. Experiments by other researchers indicate, however, that low **Bythotrephes** population densities likely render it unimportant in structuring zooplankton communities in the Great Lakes, except possibly in areas with local predator accumulations (Ferro and Riessen 1990; Vanderploeg et al. 1993).

Considerably less is known about feeding behaviour, size limitations and seasonality of *Bythotrophes* predation by fishes in North American lakes. In the Great Lakes, alewife (*Alosa pseudoharengus*), rainbow smelt (*O. mordax*), emerald shiner (*Notropis atherinoides*), spottail shiner (*N. hudsonius*), yellow perch (*P. flavescens*) and white perch (*Morone americana*) are reported to consume *Bythotrophes* (Bur and Klarer 1991; Hartman et al. 1992; Kozuchowski et al. 1992; Mills et al. 1992). In both Europe and the Great Lakes, mature fish appear to preferentially select *Bythotrophes* over co-occurring zooplankton species, and may subsequently limit its abundance or preclude it from systems entirely (Bur and Klarer 1991; Stenson 1978). Predator-based limitations in abundance would be of fundamental importance if *Bythotrophes* is capable of exerting predation effects of the magnitude reported in Lake Michigan by Lehman (1988) and Lehman and Cáceres (1993).

This thesis examines the occurrence of *Bythotrophes* in the diet of lake herring (*Coregonus artedi*) in Harp Lake, a small lake in central Ontario. Research on *Bythotrophes* in the Great Lakes is encumbered by factors such as
large spatial scales and patchy occurrence of this invader and its prey. Accurate assessments of fish predation on *Bythotrehpes* in the Great Lakes is also confounded by these problems. My research on Harp Lake is conducted at a fraction of the spatial scale of the Great Lakes, thereby providing a tractable assessment of the importance of fish predation on *Bythotrehpes*. This study was undertaken in conjunction with assessments of *Bythotrehpes* utilization of zooplankton prey by Dr. Gary Sprules, University of Toronto.

The overall objective of this thesis was to assess consumption of *Bythotrehpes* by lake herring, including feeding preferences, size selectivity and growth rate implications. My first objective was to examine seasonal abundance of *Bythotrehpes* in plankton and in lake herring diets from Harp Lake. Two different electivity indices, calculated using each of zooplankton abundance and biomass, were used to determine whether this major planktivore exhibited positive or negative selection for *Bythotrehpes*. Electivity indices provide useful assessments of selective predation based on the occurrence of prey in the predator's diet relative to those in the environment (Pearre 1982; Chesson 1983; Lazzaro 1987).

A second objective of this thesis was to assess prey size selectivity by lake herring in Harp Lake. *Bythotrehpes* is much larger (4 - 8 times) in body size than other major zooplankton taxa (eg. cladocerans and copepods) in the lake, and should be a primary target of visually-orienting predators such as lake herring.

A third objective was to determine relative passage rates of tailspines and mandibles of *Bythotrehpes* through lake herring stomachs to see whether tailspines provide an unbiased estimate of lake herring consumption of spiny water fleas. Passage of tailspines through alewife is impeded by the formation of large tailspine boluses in the stomach (D. Branstrator, University of Michigan, *pers. comm.)*. A final, related objective assessed whether growth rates of lake
herring varied among Muskoka lakes that have or have not been invaded by *Bythotrephe*. Formation of boluses could potentially affect hunger level and, thus, subsequent feeding and growth rates of the fish.

**Methods**

**Site Description**

Harp Lake is located in the Moon/Go Home watershed in south-central Ontario at 45°23' latitude and 79°07' longitude (Fig. 1). This single basin lake has an area of 71.4 ha, a mean depth of 12.4 m and a maximum depth of 37.5 m (Fig. 2). Harp Lake is a relatively neutral (pH = 6.3), oligotrophic (total phosphorus = 8 mg L⁻¹) lake located on Precambrian Shield (Dillon et al. 1987). The lake stratifies to a depth of ~5m during summer. As with many lakes in this region, Harp Lake is surrounded by a large number (~80) of cottages.

Harp Lake has been studied as a reference basin by the Ministry of Environment and Energy (MOEE) since 1978 to assess effects of acid rain on zooplankton assemblages in Ontario lakes (Yan 1986). Until the invasion of *Bythotrephe* in 1993, the zooplankton community of the lake was relatively stable (Yan and Pawson 1996). The community was dominated numerically (> 10% abundance) by small cladocerans (eg. *Bosmina longirostris*, *Diaphanosoma birgei*, *Chydorus sphaericus*) and copepods (eg. *Epischura lacustris*, *Skistodiaptomus oregonensis*, *Leptodiaptomus minutus*) for a 15-year period. Large cladocerans (eg. *Daphnia galeata mendotae* and *Holopedium gibberum*) were not numerically important. Abundance of none of these species varied by more than ± 2 standard deviations of mean abundance during the period (1978 and 1993) prior to the invasion of *Bythotrephe*. 
For the past 30 to 50 years, Harp Lake has been stocked with juvenile lake trout (*Salvelinus namaycush*) and brook trout (*S. frontalis*). The littoral fish community consists of smallmouth bass (*Micropterus dolomieu*), various cyprinid minnows (*Notropis* spp.) and yellow perch (*Perca flavescens*) (*pers. obs.*). The pelagic fish community is dominated by planktivorous lake herring and piscivorous lake trout.

**Physical and Chemical Measurements**

Corresponding with long-term sampling of zooplankton in Harp Lake by the MOEE, limnological water measurements were regularly monitored during this study. Water transparency was measured using a 20 cm Secchi disk at the deepest location in the lake. Water temperature and thermocline depth were measured using an YSI temperature meter (Model 33SCT). A temperature profile was established for the upper 14 m of the water column at the centre of the lake (Fig. 3).

**Fish Collections**

Fish and zooplankton were sampled from Harp Lake over seven sampling periods during 1995 that encompassed the emergent season of *Bythotrophes*. Monofilament gill nets of 4 cm and 6 cm stretch were randomly set at three of six possible 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. Each net was removed within 40 minutes after being set to prevent excessive catches of herring and to permit rapid preservation of fish stomach contents, thereby minimizing digestion of diet items. All fish were referenced to site and depth of capture, and placed on ice.
Additional fish samples collected on 26 April and 19 May were provided by the Ministry of Natural Resources (W. Dunlop), though corresponding plankton samples were lacking. Fish collection methods paralleled those described above.

Fork length, fish weight and sex were determined within two hours of capture at the Ministry of Natural Resources (Fisheries Assessment Unit) lab in Bracebridge, Ontario. Fork length (mm) was measured on a standard fish board, while body weight (g) was measured using an electronic balance (Pennsylvania Model 4050 - T). As well, the first left gill arch of each fish was examined for morphological characteristics such as gill raker number, gill raker length, and raker space. All measurements were recorded digitally ± 0.1 mm using a microcomputer adapted to a Wild-Leica dissecting microscope at 6x magnification.

Gastrointestinal tracts of all fish were removed and preserved in 10% buffered sugar-formalin, while the body of each fish was archived in a freezer for further reference (Windell 1968).

Plankton Collections

Upon collection of fish from each site, two Schindler-Patalas zooplankton samples (0.03 m³ with 53-µm mesh) were taken at the shallowest and deepest depths corresponding to where each gill net had been set. An additional plankton sample was taken from the middle of Harp Lake using a 53-µm nitex mesh Wisconsin plankton net with a 4:1 mouth-to-length ratio and a 50 cm mouth diameter. This sample was collected from a depth of 20 m to the surface (3.927 m³) at a fixed site for all collection periods. Zooplankton samples were narcotized with carbonated water and preserved with 4% buffered, sugar-formalin (Haney and Hall 1973).
Assessment of Fish Diet

Digestive tract contents of six randomly selected fish from each sampling period were flushed from stomach and foregut, identified and enumerated. All zooplankton taxa were enumerated with a Wild-Leica dissecting microscope at 12x magnification, with halogen bottom-illumination. Zooplankton samples were examined using a plankton wheel. Prey were identified to the lowest taxonomic level (Balcer et al. 1984). Cladocerans were identified to genus because carapace integrity was typically good, but calanoid and cyclopoid copepods and aquatic insects were identified to order only. Stomach contents were counted in toto for all taxa. In addition, mandibles of Bythotrephes were counted for comparison with tailspine number to test whether the two body structures passed through digestive tracts with equal efficiency.

Zooplankton Enumeration and Size Structure

Lake plankton samples were enumerated using the same equipment, procedures and taxonomic resolution as with fish stomach samples. Schindler-Patalas samples were processed in toto for all taxa. Owing to high densities of zooplankton in lake samples collected with the Wisconsin net, three replicate subsamples (with replacement) were counted per sample. Each 5 mL subsample was collected from a well-mixed sample using a wide bore pipette. For rare taxa (eg. Bythotrephes), the entire sample was processed to estimate density. Species’ abundance densities were estimated as:

\[ N = C * \frac{V_{sa}}{V_{su}} * \frac{1}{V_{ls}} \]  

Eqn. 1

where \( N \) is total abundance density (Ind. m\(^{-3}\)), \( C \) is mean plankton count, \( V_{sa} \) is sample volume, \( V_{su} \) is subsample volume and \( V_{ls} \) is volume (m\(^3\)) of lake water
sampled. Zooplankton abundance was estimated by averaging all plankton samples collected on that date.

Size structure of the five most numerically important zooplankton taxa was determined by measuring body length of ≥150 randomly selected individuals using a Wild-Leica dissecting microscope linked to a microcomputer. ZEBRA2 digitizing software was employed to digitize animal lengths and for later conversion to biomass (Allen et al. 1994). Body length measurements consisted of tip-of-head to base-of-tailspine (= carapace) for *Daphnia*, *Holopedium* and *Bythotrophes*, and of tip-of-head to base of caudal rami in copepods. Size measurements of the most abundant zooplankton species, (*Daphnia* and calanoid copepods), were made for each sampling date. Sufficient body length measures for three other zooplankton taxa (cyclopoid copepods, *Holopedium* and *Bythotrophes*) could only be made during periods of highest abundance. Size-structured abundance density within a species was calculated as:

\[ N_i = N_s s_i \]  

Eqn. 2

where \( N_i \) is abundance density (ind. m\(^{-3}\)) of animals of a particular size and \( s_i \) is the proportion of individuals counted of a particular size class.

**Zooplankton Biomass Estimate**

To account for large variation in body sizes among prey types and provide an alternative measure of prey abundance, size-structure abundance density data were used to estimate total biomass density for major zooplankton taxa. Biomasses of individual zooplankton were calculated using length-mass regressions as:

\[ Y_i = a x^b \]  

Eqn. 3
where $Y$ is body mass ($\mu$g) of an individual zooplankter, $a$ is a constant multiplier for body length $x$ (mm), and $b$ is an exponent. Algorithm values for constants $a$ and $b$ for most zooplankton were provided in ZEBRA2 software (Allen et al. 1994; Yan 1986), while those for *Bythotrophes* from Harp Lake were provided by Pawson et al. (1995) (Table 1). This procedure was conducted on at least 150 individuals of each taxon from both fish stomachs and lake samples. A correction factor for body shrinkage in formalin was applied to zooplankton length before conversion to individual biomass values (Giguère et al. 1987; N. Yan, pers. comm.) (Table 1). Biomass values were estimated only for planktonic zooplankton because some taxa (*Mysis relicta, Chaoborus punctipennis*) that were occasionally found in fish diets live primarily in the benthos and were not captured during plankton sampling. It was not possible to establish the original length of these prey, nor to convert abundance to biomass, because only fragments of these taxa were found in the digestive tract.

Total biomass density ($B; \mu$g m$^{-3}$) of each major zooplankton taxon was calculated for $c$ number of size classes for both lake and diet samples as:

$$B = \sum_{i=1}^{c} (N_i \times Y_i) \quad \text{Eqn. 4}$$

Data Analysis

Electivity Indices

Two indices for diet electivity were used to analyze lake herring feeding preference on zooplankton from Harp Lake. Indices were calculated using both prey density and biomass values. The first index Chesson’s $\alpha$, is derived from Ivlev’s forage ratio calculation, and provides a measure of the proportional abundance of a prey type in fish diet relative to its proportional abundance in the
lake. Chesson’s $\alpha$ values range between 0 (strong negative selection) and 1 (strong positive selection), with a value of 0.2 indicating neutral selection. Chesson’s $\alpha$ was used because its value is not dependent on the absolute abundance of a prey type (Chesson 1978, 1983). Chesson’s $\alpha$ is calculated as:

$$\alpha_i = \frac{\frac{r_i}{P_i}}{\sum_{i=1}^{n} \frac{r_i}{P_i}}$$  \hspace{1cm} \text{Eqn. 5}$$

where $r_i$ and $p_i$ are the proportions of prey type $i$ in the diet and in the environment, respectively, and $n$ is the number of prey types. Chesson’s $\alpha$ was calculated for each sampling date. In addition, an overall value was calculated by pooling feeding data across dates. The variance for the pooled $\alpha$ was estimated by Manly (1974) as:

$$\text{var} \alpha = \alpha^2 \left[ \left( \frac{1}{r_i} \right) - \left( \frac{2}{P_i * y} \right) + \left( \frac{x}{y^2} \right) \right]$$  \hspace{1cm} \text{Eqn. 6}$$

where $x$ is:

$$x = \sum_{i=1}^{n} \frac{r_i}{P_i^2}$$  \hspace{1cm} \text{Eqn. 7}$$

and where $y$ is:

$$y = \sum_{i=1}^{n} \frac{r_i}{P_i}$$  \hspace{1cm} \text{Eqn. 8}$$

Overall $\alpha$ values for each species were tested against the neutral selectivity value of $n^{-1}$ using Student’s $t$-test (Manly 1974; Barnhisel and Harvey 1995). Chesson’s $\alpha$ values were arcsine, square-root transformed prior to analysis to meet assumptions of normality (Sokal and Rohlf 1995). To preserve an experimentwise error rate of 0.05, individual $t$-tests for each plankton species
were assessed at Bonferroni-adjusted probability level of 0.01 (0.05/5; Sokal and Rohlf 1995).

The second index was developed by Pearre (1982). Pearre’s V index compares relative abundance of each prey species in diet and environment collections against all other prey items found in both samples. Pearre’s V index ranges between 1 (strong positive selection) and -1 (strong negative selection), with a value of zero indicating neutral selection. The index is calculated as:

$$V_a = \frac{a_d*b_e - a_e*b_d}{\sqrt{a*b*d*e}}$$  \hspace{1cm} \text{Eqn. 9}

where $V_a$ is Pearre’s index for lake herring selection of species $a$, $a_d$ is relative abundance of species $a$ in diet, $b_e$ is relative abundance of all other species in the environment, $a_e$ is relative abundance of species $a$ in the environment, and $b_d$ is relative abundance of all other species in the diet. Values without subscripts are expressed as follows: $a = a_d + a_e$, $b = b_d + b_e$, $d = a_d + b_d$, $e = a_e + b_e$, and $n = a_d + a_e + b_d + b_e$. This index is not sensitive to rare prey types and is statistically tested using the $\chi^2$ statistic:

$$\chi^2 = n*V^2$$  \hspace{1cm} \text{Eqn. 10}

Both electivity indices were used for comparative purposes to assess prey abundance and biomass selection by *Bythotrephes*.

**Size Selection of Zooplankton**

An analysis of zooplankton size selection by lake herring was made using prey size structure of lake and fish diet samples. Prey size distributions from plankton and fish diet were compared separately for each sampling period using Kolmogorov-Smirnov two-sample tests (Sokal and Rohlf 1995).
Mandible - tailspine retention efficiency

For all herring identified with Bythotrephes in the digestive tract, the number of tailspines was regressed on the higher of the right or left mandible number (Systat 1992). The regression coefficient was tested against a value of 1 using a t-test to determine whether tailspines passed through herring at the same rate as mandibles (Sokal and Rohlf 1995).

Lake Herring Growth Comparisons

A final analysis was conducted to assess the weight at length relationship for lake herring from six lakes in the Muskoka region. Lakes Joseph, Rosseau and Harp have all been invaded by Bythotrephes, while Young, Twelve Mile and Gull lakes have not been invaded (Fig. 1). All three invaded lakes contained Bythotrephes for at least three years prior to fish sampling, with Harp Lake being the most recently invaded system. Morphological descriptions of each lake are provided in Table 2. Sampling procedures for fish on these lakes are based on the spring, littoral-index survey protocol used by the Muskoka Lakes Aquatic Assessment Unit of the Ontario Ministry of Natural Resources (MacKay 1995), and are identical to methods and lab procedures employed on Harp Lake. Lake herring were frozen within 12 hr of collection and later measured for body weight and fork length. Lake herring were collected from all 6 lakes between mid-April and the end of May during 1995. Time of collection was standardized across lakes to minimize seasonal variability in food availability among lakes. Variation in weight of lake herring from invaded and noninvaded lakes was analyzed using analysis of covariance (ANCOVA) with length entered as a covariate and invasion history 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 (Minitab 1993).

Results

Zooplankton Abundance and Biomass in Lake Herring Diet

Lake herring stomach contents revealed a wide diversity of prey items (Fig. 4; Table 3). Diets were dominated numerically by aquatic insects (mainly Diptera and Hymenoptera) for the first two sampling periods during spring 1995. Five other taxa (Bythotrephes, Daphnia, Holopedium and calanoid and cyclopoid copepods) were the principal diet components for all other sampling dates. Bythotrephes was found in virtually all fish collected on or after May 19. It was a numerically important component of diet only on May 19 (Fig. 4), though it was a dominant (>10%) biomass contributor during June, July and October (Fig. 5). Relative biomass contribution of Bythotrephes to lake herring diet was highly variable, ranging between 1 and 64 % (Fig. 5). It is noteworthy that there was usually a ten-fold increase in relative biomass of Bythotrephes in diet of lake herring as compared to relative abundance owing to the tremendous size difference between Bythotrephes and most other zooplankton (Figs. 4, 5).

Daphnia was the most common (37 - 97%) prey in fish diet on all sample dates during the summer and autumn (Fig. 4; Table 3), and a dominant biomass contributor on all sample dates, though particularly during August and September (Fig. 5). Calanoid copepods were common diet items in both spring and fall (Figs. 4, 5). Holopedium was the only other common planktonic zooplankter in fish diet during spring (Figs. 4, 5).

The only other zooplankter that contributed substantially to lake herring diet was Mysis relicta. This species was found in fish diets mainly during June, August and September (Fig. 4). Mysis was likely an important biomass
contributor to diet during August, though it was not possible to estimate the magnitude of its contribution. Several other taxa that were rare in lake herring diet and in plankton samples included *Diaphanosoma bergei*, *Bosmina* spp., *Polyphemus pediculus* and *Chaoborus punctipennis*.

Zooplankton Abundance and Biomass in Harp Lake

Zooplankton abundance and biomass in Harp Lake were dominated by calanoid copepods (mainly *Leptodiaptomus minutus*, *Epischura lacustris*) during every sampling period (Figs. 6, 7). *Daphnia* was also a numerically important (12 - 47%) component of the plankton during the summer period (Fig. 6); however, because individuals were on average quite small (0.74 - 0.98 mm) at this time, and had correspondingly low individual biomasses, the total biomass contribution of *Daphnia* was less important (Fig. 7; Table 4).

The only other taxa that ever comprised >5% of plankton abundance and biomass were *Holopedium* and *Bosmina* spp., mainly during spring and early summer (Figs. 6, 7). While *Holopedium* was less important numerically than *Daphnia* during June, its higher individual mean biomass (7.13 and 12.94 µg ind.⁻¹) relative to that of *Daphnia* (3.45 and 3.54 µg ind.⁻¹) increased its total biomass contribution (see Table 4). Cyclopoid copepods (mainly *Tropocyclops extensus* and *Mesocyclops edax*) contributed marginally (<5%) to total biomass throughout the summer (Fig. 7).

*Bythotrehpes* was always rare, never comprising more than 0.01% and 1% of total zooplankton abundance and biomass, respectively. Despite its relative rarity in the plankton, fish closely tracked *Bythotrehpes* abundance in the lake (Fig. 8). For example, the product-moment (Pearson) correlation coefficient for mean abundance of *Bythotrehpes* in fish diet and lake plankton was 0.93. The highest incidence of *Bythotrehpes* in fish diet corresponded with the highest
density in the plankton (Fig. 8). However, the lowest density of *Bythotrehpes* in the plankton (September 20) corresponded with a relatively high frequency in the diet. *Bythotrehpes* density was highly variable in the lake at that time, however, possibly illustrating marked patchiness (Fig. 8).

**Electivity Indices**

Examination of diet abundance and plankton abundance samples for the five primary zooplankton taxa revealed marked selection by lake herring. Chesson’s α values were very similar irrespective of whether they were calculated with abundance (Fig. 9a) or biomass (Fig. 10a) data. Overall, lake herring demonstrated significant (P < 0.01, t-test) positive selection for *Bythotrehpes* (Fig. 9b). The highest selection values for *Bythotrehpes* corresponded with its peak density in the lake (Table 4).

Chesson’s α revealed no other instances of significant positive prey selection by lake herring based on prey abundance or biomass (t-tests; Figs 9b, 10b). *Daphnia* appeared to be positively selected on three sampling dates, though it was negatively selected on four other dates. Overall, however considering biomass, selection for *Daphnia* did not differ significantly from random feeding (Fig. 10b). All other zooplankton groups exhibited negative selection by lake herring on all dates except for slight positive selection of *Holopedium* biomass on 8 June (Figs. 9a, 10a). For example, α values for calanoid and cyclopoid copepods and *Holopedium* were always less than the neutral selection value of 0.2, and all three species were significantly negatively-selected by lake herring (P < 0.01, t-tests; Figs. 9b, 10b).

In general, Pearre’s V index provided similar results to Chesson’s index. For example, *Bythotrehpes* was positively selected by lake herring on all sampling dates regardless of whether abundance (Fig. 11a) or biomass (Fig. 12a) data were
examined. As with Chesson’s α, overall selection of *Bythotrephe* was significant ($P = 0.001$, $\chi^2$-test). In contrast to Chesson’s α, however, *Daphnia* was consistently and significantly positively selected by lake herring ($P = 0.001$, $\chi^2$-test; Figs. 11b, 12b). In addition, selection for *Daphnia* individuals exceeded that for *Bythotrephe* on six of seven sampling dates. Biomass data yielded slightly different results, with *Bythotrephe* being selected slightly more strongly on three of seven sampling dates.

*Holopedium* abundance and biomass was positively selected by lake herring on the earliest sampling date (June 8), though the species was strongly avoided thereafter (Figs. 11a, 12a). Cyclopoid and especially calanoid copepods were strongly negatively selected by lake herring on all sampling dates ($P < 0.001$, $\chi^2$-test; Figs. 11b, 12b).

**Prey Size Selection**

Lake herring exhibited significant size selection within a taxon in addition to marked predation differences among taxa. Overall size selection was greatest for the two taxa that dominated the zooplankton numerically. For example, prey size selection was most dramatic and consistent for *Daphnia*. *Daphnia* 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. 13a). This difference was significant on all sample dates. Similarly, calanoid copepods consumed by lake herring were significantly larger (by an average of 0.15 mm) than those in the lake on six of the seven dates (Fig. 13a). Cyclopoid copepods consumed by herring were significantly larger than those in the lake on 8 June, though the size distributions of the groups did not differ on 28 June (Fig. 13b).
Zooplankton species that possess morphological deterrents to fish predation were not consumed in a size-selective manner. For example, for each of the individual dates when sufficient numbers of individuals were present to permit examination, size distributions of neither *Bythotrehpes* nor *Holopedium* varied among fish diet and lake plankton samples (P > 0.05, Fig. 13b).

Size selection of prey by lake herring is consistent with anatomical features of the fish (Table 5). For example, herring gill raker space averaged 0.5 mm, indicating that potential prey smaller than this value would likely not be retained and ingested. The prey types that most strongly exhibited size selective predation (*Daphnia*, calanoid and cyclopoid copepods) were among the smaller zooplankton studied. Even though *Holopedium* is among the smallest zooplankton examined for size selection, its 'effective' size in the lake was substantially larger than the measurements described in Fig. 13b owing to the presence of a gelatinous mantle coating the body.

Mandible and Tailspine Passage Through Herring

*Bythotrehpes* tailspine number was regressed on the highest mandible number (left or right) to assesses whether the larger body part was differentially retained relative to smaller prey components (Fig. 14). Numbers of the two body parts were highly correlated (product-moment r = 0.99) in fish stomachs. There was no evidence that tailspines were retained differentially, as the regression coefficient (1.03) did not vary significantly from one (two-sided t=1.37, df=38, P > 0.10). Though both variables increased at the same rate it was noted that the regression intercept was significantly higher for tailspine number than mandible number. (two-sided t=3.06, df=38, P < 0.01)
Lake Herring Weight-Length Relationships

Lake herring weight at length relationships for three invaded and non-invaded lakes in central Ontario are shown in Fig. 15. Lake herring weight was strongly related to fish length ($P < 0.001$), but not to lake invasion status ($P = 0.748$)(Table 6). Similarly, the effect of length on fish weight did not vary by lake invasion status ($P = 0.714$). However, weight varied significantly within lake types ($P < 0.001$)(Table 6). Thus, while growth rates 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 (Case 1987; Pimm 1989). Establishment of a viable population requires that an invader successfully compete for resources and avoid predators and pathogens. The proficiency with which an invader achieves these requirements determines, in part, its potential abundance and ecological impact on the community it has invaded. The most troublesome invasions typically involve exotic species that experience minimal competition and predation with native species, and which develop large population sizes in consequence. Some classic examples of troublesome invasions to North America include purple loosestrife *Lythrum salicaria*, European starling *Sturnus vulgaris*, and, more recently, the zebra mussel *Dreissena polymorpha* (Elton 1958; Mills et al. 1993; MacIsaac 1996). Particularly aggressive invaders have been attributed with massive disruptions of ecosystems and with extirpation and even extinction of native species (e.g. see reviews in Groves and Burdon 1986; MacDonald et al. 1986; Mooney and Drake 1986; Lodge 1993). Generalist predators are known to minimize or extinguish the invasion process (Elton 1958). However, Bythotrephes invasion of lakes in central Ontario, and Harp
Lake in particular, provides an opportunity to examine the success of an invading zooplankter in systems dominated by obligate planktivores.

**Lake Herring Feeding Behaviour**

Lake herring is the dominant zooplanktivorous fish in Harp Lake's pelagic food chain. Very little research has addressed feeding behaviour of lake herring, possibly because they are inconspicuous and sensitive to environmental conditions including temperature changes and human handling.

In a series of laboratory experiments, Janssen (1978, 1980) contrasted the feeding behaviour of lake herring with that of alewife. Whereas the former species exhibited active visual foraging behaviour, the latter fed principally by filter-straining. Lake herring were observed to feed in the dark and to seek out specific zooplankton prey. Recent research has documented capture probabilities for zooplankton subject to predation by lake herring (Link 1996). Lake herring had much lower capture probabilities on copepods, which are strong swimmers capable of active evasive behaviour, than on slow-swimming cladocerans (Link 1996).

Additional information regarding feeding behaviour of lake herring has been derived from *in situ* observations of feeding electivity (Engel 1976) and diel habitat preference (Emery 1973). Engel (1976) demonstrated positive feeding selection by lake herring for cladocerans (e.g. *Leptodora kindti*, *Daphnia* spp., *Chydorus sphaericus*, *Bosmina longirostris*) and negative selection for copepods (*Cyclops bicuspidatus thomasi*, *Diaptomus minutus*). In Harp Lake, lake herring also exhibited positive selection for *Daphnia* and *Bythotrephes*, though *Bosmina* was rarely encountered in the diet. *Bosmina* spp. should be too small (≤ 400 µm) to be effectively retained by lake herring in Harp Lake based on first gill arch
distances (~0.5 mm)(Table 5). Lake herring did, however, exhibit strong negative selection for calanoid and cyclopoid copepods in Harp Lake (Table 9 - 12).

An investigation of temporal activity of lake herring documented that feeding activity occurs primarily during crepuscular or night-time periods (Emery 1973). As well, lake herring move from the pelagic zone during the day to inshore at night.

**Fish Electivity on Bythotrophes**

Lake herring in Harp Lake demonstrated strong selection for *Bythotrophes* (Figs. 9 - 12). These findings agree with earlier studies conducted in Europe with other fish species, including coregonids. For example, *Bythotrophes* spp. was consumed by brown trout (*Salmo trutta*) and arctic char (*Salvelinus alpinus*) (Lindström 1955; Nilsson 1955, 1961; Nilsson and Pejler 1973). More recent studies demonstrated strong positive selection by perch (*Perca fluviatilis*), smelt (*Osmerus eperlanus*), roach (*Rutilus rutilus*), brown trout (*S. trutta*) and lake whitefish (*Coregonus albula*) in lakes throughout northern Europe (Hakkari 1978; Fitzmaurice 1979; Garnâs 1983; Næsje et al. 1987; Jachner 1991). It is instructive to note that with the exception of *O. eperlanus*, all of these studies involved adult fishes. In North America, juvenile rainbow smelt (*O. mordax*) and lake herring avoid *Bythotrophes* (Barnhisel and Harvey 1995).

Lazzaro (1987) evaluated electivity indices and expressed two concerns regarding their ability to estimate feeding preference. First, electivity measures depend critically on how well plankton sampling devices replicate the food environment experienced by the predator. Highly biased estimates of prey abundance may be arrived at if sampling gear is not selected with careful regard to the size-spectrum of foods consumed by the predator, or if plankton are collected from areas other than where the predator forages. In this study, this
problem was minimized by collecting samples from sites where lake herring occurred using fine-mesh plankton collecting devices. Second, electivity measures depend on equal digestion and passage rates of prey in the fish gut (Lazzaro 1987). Easily digested prey will be underestimated in fish diets and thus appear to be negatively selected when analyzed with an electivity index (Gannon 1976). To minimize digestion of stomach contents and gut evacuation, short time intervals were employed between the time of capture and the removal and preservation of the gastrointestinal tract.

Different views of feeding preference may also be arrived at depending on which electivity index is employed. Lechowicz (1982) compared findings of different electivity indices to assess fundamental mathematical and biological principles (Table 7). Chesson’s $\alpha$ index received a favourable rating because it accounted for variation of prey items by comparing the relative abundance of other prey items in each sample (Lechowicz 1982). However, Chesson’s $\alpha$ is sensitive to rare prey items found in the diet (see Table 7). This limitation is relevant to this study because *Bythotrephes* was rare relative to other zooplankton in the lake (Figs. 6, 7). By contrast, Pearre’s $V$ electivity index is not biased for rare prey items (Pearre 1982). A limitation of this index is that it is nonlinear and unstable for prey types that change in relative abundance between sampling periods (Table 7; Pearre 1982).

Features of prey also require consideration when assessments of lake herring diet electivity are explored. Prey pigmentation, transparency and conspicuousness play an important role in affecting the ‘apparent’ size of prey to visually-orienting predators (Kerfoot 1980). In addition to its large size, *Bythotrephes* has blue-shaded appendages, a reddish colour around the brood pouch, and a very large dark eye (*pers. obs.*). While the ecological significance of
this colouration pattern is not known, it could alter Bythotrephes's conspicuousness to fish predators.

Prey avoidance behaviours may also affect zooplankton vulnerability to fish predators. Fish electivity in a zooplankton assemblage consisting of cladocerans, cyclopoid copepods and calanoid copepods was lower for prey that possessed pronounced escape behaviour (Drenner and McComas 1980). Cladocerans including Daphnia and Ceriodaphnia were captured at twice the rate of copepods (Drenner and McComas 1980). In this study, Daphnia and Bythotrephes were positively selected and calanoid and cyclopoid copepods negatively selected by lake herring (Figs. 11, 12). Fish predation appears to structure the taxonomic composition of Harp Lake. Harp Lake is dominated by calanoid copepods (Fig. 5), not unlike the lakes surveyed by Brooks (1968) that contained large numbers of planktivorous fishes.

Morphological features that impede the capture, killing or ingestion of prey may also serve to reduce predation. For example, the gelatinous mantle enveloping the carapace of Holopedium and the long, chitinous tailspine of Bythotrephes may be effective at reducing fish predation. Stenson (1985) noted that the relative size of the gelatinous sheath around Holopedium gibberum was proportional to predation pressure exerted by fish. Juvenile fish attempt but are unable to ingest Bythotrephes owing to its tailspine; eventually these fish develop an aversion to Bythotrephes (Barnhisel 1991a, 1991b). Above a certain mouth (gape) size, fishes positively select Bythotrephes. Bloater chub (C. hoyi) in Lake Michigan that were as small as 30 mm ate Bythotrephes (Branstrator and Lehman 1995). Juvenile rainbow smelt, lake herring and lake whitefish between 8-12 cm all consumed Bythotrephes in Lake Michigan, though the former two species avoid spiny water fleas (Barnhisel and Harvey 1995).
Barnhisel and Harvey (1995) also demonstrated that the proportion of Bythotrephes in fish diet increased with body length of juvenile lake herring. In my study with adult lake herring, no relationship was found between fish size and importance of Bythotrephes as a food item (see Table 3).

Size Selectivity of Lake Herring

Lake herring in Harp Lake fed on specific size classes of prey for common but not for rare plankton species. For example, calanoid copepods and Daphnia ingested by lake herring were significantly larger than plankton in the lake (Fig. 13a), though neither Bythotrephes, Holopedium, nor cyclopoid copepods were fed upon in this manner (Fig. 13b). Galbraith (1967) previously reported that rainbow trout and yellow perch fed preferentially on large Daphnia. Brooks and Dodson (1965) demonstrated that introduced alewife altered species composition and size structure in some Connecticut lakes as a result of size-selective predation. Indeed, size-selective planktivory is one of the best documented phenomena in ecology.

Bythotrephes Coexistence with Lake Herring Predators

Lake herring quickly incorporated Bythotrephes into its diet as the spiny water flea population increased during May in Harp Lake (Fig. 8). Bythotrephes was never an important component of the zooplankton in the lake, never accounting for more than 0.01% of total abundance, 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, though catch rate data suggest the population is large. For example, ~20 fish were captured per gill net with 30 minute set periods, though 200 individuals were captured during
one period. Given the relatively high density of lake herring in this small lake, and the fish's strong selection for *Bythotrephes*, it seems reasonable to assume that lake herring could strongly affect *Bythotrephes* abundance and possibly even its presence in Harp Lake. Harp Lake's thermal regime may, however, provide *Bythotrephes* with a spatial refuge from lake herring, thereby reducing predator-prey contact and spiny water flea mortality. During summer 1995, a thermocline established at ~5m depth in Harp Lake between June 8 and June 27 and persisted until autumn turnover in early September (Fig. 3; C. Charron, *pers. comm.*). Spatial distributions of *Bythotrephes* and lake herring exhibit little overlap. For example, efforts to capture lake herring in the epilimnion of Harp Lake using gill nets were unsuccessful (*pers. obs.*). Emery (1973) reported that lake herring were found primarily along the bottom of lakes in Algonquin Park, Ontario. These finding are consistent with limited laboratory and synoptic survey data that suggest that the species strongly prefers cold (4 - 12º C) water (Janssen 1978; W. Dunlop, *pers. comm.*). By contrast, an intensive survey of diel vertical distribution revealed that *Bythotrephes* spent approximately 80% of a 24 hr period in the epilimnion of Harp Lake during July 1995 (C. Charron, *pers. comm.*). Lake herring feeding on *Bythotrephes* may be limited to the period between 4 and 8 am when *Bythotrephes* is homogenously distributed throughout the epilimnion and hypolimnion (C. Charron, *pers. comm.*). Predation on *Bythotrephes* appears to depend not on temporary excursions by lake herring into the epilimnion, but on movement into the hypolimnion by *Bythotrephes* during early morning hours. Potential predation rate is, however, greatly reduced by the spatial refuge afforded *Bythotrephes* by the thermal structure of the lake.

*Bythotrephes* abundance declined rapidly during late summer, and was very low by the time the lake destratified (Figs. 3, 8). Destratification would eliminate
the spatial refuge, potentially increasing encounter rates of predators and prey. The low density of _Bythotrephes_ on 20 September, after the lake had destratified, appears related more to food limitation and increasing egg development time than to fish predation (C. Charron, _pers. comm._).

**Bythotrephes** Tailspine Passage Through Lake Herring Stomachs

Differential retention of _Bythotrephes_ tailspines relative to other prey items in fish stomachs could potentially affect fish hunger level and subsequent feeding. Keilty (1990) found that stomachs of alewife from Lake Michigan were 'solidly packed' with _Bythotrephes_. Some lake herring from Harp Lake and other invaded lakes in the Muskoka region were also found to contain stomachs filled with _Bythotrephes_ tailspines. By contrast, bloater chub eat but apparently do not retain the tailspines of _Bythotrephes_ (D. Branstrator _pers. comm._). Feeding on _Bythotrephes_ by lake herring did not result in differential retention of tailspines as evidenced by the relative passage rates of tailspines and _Bythotrephes_ mandibles (Fig. 14). This finding should be interpreted with caution, however, because most of the fish contained less than 100 _Bythotrephes_. If large numbers of _Bythotrephes_ are ingested, it is possible that tailspines may tangle together to form a bolus sufficiently large as to impede passage through the digestive tract.

**Lake Herring Growth**

The final objective of this thesis was to explore whether lake herring growth rates, as estimated by weight at length relationships, varied in relation to _Bythotrephes_ invasion status for 6 lakes in central Ontario. I found no differences in growth rate patterns for fish in invaded and noninvaded lakes.
This finding is consistent with the view that *Bythotrephes* tailspines pass through digestive tracts of lake herring at the same rate as other food items. Moreover, it is also possible that *Bythotrephes* is an important supplemental food for fishes in invaded lakes.

Additional study is needed before it can be conclusively stated that invasion by *Bythotrephes* has no impact on fish growth. Fish growth can be affected over the long term in a manner that would not be perceptible in this study. First, *Bythotrephes* is capable of dramatic alterations of zooplankton community structure, the results of which could adversely affect juvenile fishes. Small zooplankton species (e.g. *Bosmina longirostris*, *B. tubicen*, *Tropocyclops extensus*, *Chydorus sphaericus*, *Diaphanosoma birgei*) have either been eliminated from or greatly reduced in population abundance in Harp Lake since invasion of the basin by *Bythotrephes* (Yan and Pawson 1996). Larger zooplankton that are either too large for *Bythotrephes* to ingest (*Daphnia galeata mendotae*) or are negatively selected by lake herring (*Holopedium gibberum*, *Leptodiaptomus sicilis*) have all increased significantly in abundance during the same time period (Yan and Pawson 1996). Loss of small zooplankton could cause a recruitment bottleneck for small fishes that depend on these prey items when their gape limits them to small foods only (see Neill and Peacock 1980). These effects would not be manifest unless assessments of fish population size structure are made, and even then the effects may take years to become discernible.

Second, my assessments of fish growth considered adult fishes that ranged in age from ~4 to ~17 years (*W. Dunlop, pers. comm.*). Thus, even if *Bythotrephes* does affect fish growth, this survey may have underestimated the effect because the survey used fish from invaded lakes that potentially experienced up to 9 years of growth prior to establishment of *Bythotrephes* in the basins. This
study's limitation could be overcome by comparing otolith growth patterns in small fishes in invaded and noninvaded lakes, and limiting growth assessments to post-\textit{Bythotrephes} invasion years only. Alternatively, growth for the initial 3 or 5 years could be assessed in lakes in which \textit{Bythotrephes} has recently established. This procedure would be conducted on old fish (= pre-\textit{Bythotrephes}) and newer recruits (= post-\textit{Bythotrephes}), and replicated across lakes.

\textbf{Community Responses to \textit{Bythotrephes} Invasion}

\textit{Bythotrephes} has become well established in Harp Lake since its invasion in 1993. Though lake herring exhibited strong positive selection for \textit{Bythotrephes}, it has persisted in the lake for the past three years. Within this short time span, \textit{Bythotrephes} has had a dramatic effect on the native zooplankton density (Yan and Pawson 1996). Long term ecological impacts of \textit{Bythotrephes} in invaded systems remain unknown, though it is interesting to note that this species invaded Harp Lake despite its very high diversity of native crustacean zooplankton. Harp Lake's zooplankton fauna consisted of an average of 16 taxa prior to \textit{Bythotrephes} invasion, among the highest of any lakes in the Muskoka region (Yan and Pawson 1996; N. Yan, \textit{pers. comm.}). Invasion theory predicts that invasions are most likely to succeed in systems with low native species diversity (Elton 1958; Lodge 1993) and in which potent predators are lacking. Harp Lake satisfied neither of these requirements. Because much invasion theory was developed with plant communities in mind (e.g. Drake and Mooney 1986), it would be instructive if the events unfolding in Harp Lake could serve as an impetus for a full re-assessment of biological invasions theory.
Summary

*Bythotrephes cederstroemi* invaded the Great Lakes in 1984, and Harp Lake in 1993. The species has rapidly become incorporated in the Harp Lake food web, and together with *Daphnia*, is the most preferred food of the lake's major planktivore, lake herring. Lake herring negatively select other zooplankters in the lake including *Holopedium* and calanoid and cyclopoid copepods. Predation on *Daphnia* and calanoid copepods by lake herring is strongly size-selective, though the fish do not select *Bythotrephes*, cyclopoid copepods nor *Holopedium* based on size.

While tailspines of *Bythotrephes* form loose boluses in lake herring stomachs, they are not differentially retained relative to *Bythotrephes* mandibles. As well, fish growth rates in lakes invaded by *Bythotrephes* do not differ significantly from rates in noninvaded lakes. It remains unclear what, if any, long-term consequences *Bythotrephes* invasion has on fish recruitment and growth patterns.

The invasion of *Bythotrephes* into Harp Lake is inconsistent with current biological invasions theory; it would be highly desirable if this small lake in central Ontario could foster theoretical developments in this emerging field of conservation biology.
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Hall, London.

Emery, A. R. 1973. Preliminary comparisons of day and night habits of
freshwater fish in Ontario lakes. Journal of Fisheries Research Board of
Canada 30:761-774.


Table 1. Constants used to convert zooplankton length (x) to mass (Y) using the equation $Y = ax^b$ (Allen et al. 1994).

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Mass exponent $b$</th>
<th>Mass constant $a$</th>
<th>Shrinkage factor*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daphnia spp.</td>
<td>2.84</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Calanoid copepods</td>
<td>2.46</td>
<td>5.5</td>
<td>1.06</td>
</tr>
<tr>
<td>Cyclopoid copepods</td>
<td>2.46</td>
<td>5.5</td>
<td>1.06</td>
</tr>
<tr>
<td>Holopedium gibberum</td>
<td>3.04</td>
<td>11.21</td>
<td>1.39</td>
</tr>
<tr>
<td>Bythotrephes cederstroemi</td>
<td>3.066</td>
<td>8.688</td>
<td>1.167</td>
</tr>
</tbody>
</table>

* this factor accounts for zooplankton body shrinkage in 4% concentrated formalin (Giguère et al. 1987).
Table 2. Six lakes in central Ontario from which lake herring were sampled for the presence or absence of Bythotrephes. Three variables: area (hectares), mean depth (m) and maximum depth (m) are shown for all six lakes. As well, mean length (mm) and body weight (g) are shown with standard deviations (s.d.) values for lake herring caught in each lake. Data courtesy of W. Dunlop (Ontario Ministry of Natural Resources).

<table>
<thead>
<tr>
<th>Lake</th>
<th>Presence of Bythotrephes</th>
<th>Area</th>
<th>Mean Depth</th>
<th>Max. Depth</th>
<th>N</th>
<th>Fork Length (mm) Mean (s.d.)</th>
<th>Wet Weight (g) Mean (s.d.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rosseau</td>
<td>Yes</td>
<td>6295</td>
<td>23.2</td>
<td>90</td>
<td>52</td>
<td>246.9 (21.3)</td>
<td>168.2 (43.1)</td>
</tr>
<tr>
<td>Joseph</td>
<td>Yes</td>
<td>5375</td>
<td>24.7</td>
<td>93</td>
<td>22</td>
<td>253.2 (24.7)</td>
<td>201.2 (61.2)</td>
</tr>
<tr>
<td>Harp</td>
<td>Yes</td>
<td>72</td>
<td>11.6</td>
<td>34</td>
<td>57</td>
<td>214.5 (15.2)</td>
<td>103.6 (23.7)</td>
</tr>
<tr>
<td>Young</td>
<td>No</td>
<td>109</td>
<td>11.9</td>
<td>22</td>
<td>173</td>
<td>220.3 (25.3)</td>
<td>111.9 (46.6)</td>
</tr>
<tr>
<td>12 Mile</td>
<td>No</td>
<td>463</td>
<td>10.6</td>
<td>24</td>
<td>52</td>
<td>222.1 (18.8)</td>
<td>114.4 (25.7)</td>
</tr>
<tr>
<td>Gull</td>
<td>No</td>
<td>996</td>
<td>16.5</td>
<td>49</td>
<td>66</td>
<td>243.2 (22.3)</td>
<td>180.9 (54.5)</td>
</tr>
</tbody>
</table>
Table 3. Lake herring fork length (mm), weight (g) and mean abundance of zooplankton in stomachs for seven sampling periods. All mean values are followed with a standard deviation (s.d.). Samples sizes (N) of examined herring are provided.

<table>
<thead>
<tr>
<th>Sample Date</th>
<th>N</th>
<th>Mean (s.d.) Fork length (mm)</th>
<th>Mean (s.d.) Weight</th>
<th>Copepoda</th>
<th>Stomach contents (mean no. per fish (s.d.))</th>
<th>Bythotrephes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Daphnia</td>
<td>Holopedium</td>
</tr>
<tr>
<td>June 8</td>
<td>5</td>
<td>211.6 (12.8)</td>
<td>99.2 (23.5)</td>
<td>40.8 (86.8)</td>
<td>3.2 (6.6)</td>
<td>122.0 (144.3)</td>
</tr>
<tr>
<td>June 27</td>
<td>6</td>
<td>220.8 (9.9)</td>
<td>110.8 (9.9)</td>
<td>231.8 (308.8)</td>
<td>9.5 (6.9)</td>
<td>157.0 (138.1)</td>
</tr>
<tr>
<td>July 20</td>
<td>12</td>
<td>226.9 (8.8)</td>
<td>125.8 (11.9)</td>
<td>31.8 (55.6)</td>
<td>4.9 (8.0)</td>
<td>606.8 (536.7)</td>
</tr>
<tr>
<td>Aug. 9</td>
<td>6</td>
<td>231.2 (15.2)</td>
<td>132.0 (28.3)</td>
<td>16.8 (27.2)</td>
<td>4.7 (7.7)</td>
<td>2612.5 (2978.4)</td>
</tr>
<tr>
<td>Aug. 30</td>
<td>6</td>
<td>230.5 (5.2)</td>
<td>150.1 (13.3)</td>
<td>81.3 (75.0)</td>
<td>14.5 (12.6)</td>
<td>4433.8 (1634.1)</td>
</tr>
<tr>
<td>Sept. 20</td>
<td>6</td>
<td>233.5 (11.2)</td>
<td>156.0 (20.4)</td>
<td>248.3 (397.6)</td>
<td>12.5 (19.4)</td>
<td>6607.3 (6867.9)</td>
</tr>
<tr>
<td>Oct. 11</td>
<td>6</td>
<td>232.2 (5.0)</td>
<td>153.1 (12.0)</td>
<td>195.0 (277.8)</td>
<td>15.7 (14.4)</td>
<td>130.2 (77.3)</td>
</tr>
</tbody>
</table>
Table 4. Mean abundance (ind. x 1000 * m\(^{-3}\)) and mass (μg x 1000 * m\(^{-3}\)) densities of zooplankton in Harp Lake during 1995.

<table>
<thead>
<tr>
<th>Sample Date</th>
<th>Copepods</th>
<th>Density</th>
<th>Mass</th>
<th>Daphnia</th>
<th>Density</th>
<th>Mass</th>
<th>Holopedium</th>
<th>Density</th>
<th>Mass</th>
<th>Bythotrephes</th>
<th>Density</th>
<th>Mass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>calanoida</td>
<td>Density</td>
<td>Mass</td>
<td>cyclooida</td>
<td>Density</td>
<td>Mass</td>
<td></td>
<td>Density</td>
<td>Mass</td>
<td></td>
<td>Density</td>
<td>Mass</td>
</tr>
<tr>
<td>June 8</td>
<td></td>
<td>8.00</td>
<td>15.14</td>
<td>0.36</td>
<td>0.98</td>
<td></td>
<td></td>
<td>0.12</td>
<td>0.61</td>
<td>0.53</td>
<td>4.70</td>
<td>0.001</td>
</tr>
<tr>
<td>June 27</td>
<td></td>
<td>27.12</td>
<td>118.15</td>
<td>4.35</td>
<td>17.39</td>
<td></td>
<td></td>
<td>5.13</td>
<td>28</td>
<td>4.90</td>
<td>92.13</td>
<td>0.001</td>
</tr>
<tr>
<td>July 20</td>
<td></td>
<td>10.28</td>
<td>92.11</td>
<td>0.95</td>
<td>4.08</td>
<td></td>
<td></td>
<td>2.19</td>
<td>19.14</td>
<td>0.37</td>
<td>15.17</td>
<td>0.001</td>
</tr>
<tr>
<td>Aug. 9</td>
<td></td>
<td>6.55</td>
<td>28.22</td>
<td>0.44</td>
<td>1.24</td>
<td></td>
<td></td>
<td>1.23</td>
<td>3.72</td>
<td>0.00</td>
<td>0.00</td>
<td>0.002</td>
</tr>
<tr>
<td>Aug. 30</td>
<td></td>
<td>12.32</td>
<td>96.85</td>
<td>0.45</td>
<td>1.22</td>
<td></td>
<td></td>
<td>11.46</td>
<td>36.16</td>
<td>0.00</td>
<td>0.00</td>
<td>0.001</td>
</tr>
<tr>
<td>Sept. 20</td>
<td></td>
<td>12.84</td>
<td>113.79</td>
<td>0.68</td>
<td>3.78</td>
<td></td>
<td></td>
<td>10.58</td>
<td>111.21</td>
<td>0.00</td>
<td>0.00</td>
<td>0.001</td>
</tr>
<tr>
<td>Oct. 11</td>
<td></td>
<td>10.15</td>
<td>69.92</td>
<td>0.16</td>
<td>0.36</td>
<td></td>
<td></td>
<td>0.46</td>
<td>3.97</td>
<td>0.00</td>
<td>0.00</td>
<td>0.001</td>
</tr>
</tbody>
</table>
Table 5. Measures of lake herring first gill arch morphology.

<table>
<thead>
<tr>
<th>Measurements</th>
<th>Mean</th>
<th>s.d.</th>
<th>Min.</th>
<th>Max.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herring Length (cm)</td>
<td>21.61</td>
<td>1.05</td>
<td>20.40</td>
<td>23.80</td>
</tr>
<tr>
<td>Herring Weight (g)</td>
<td>110.75</td>
<td>16.91</td>
<td>94.30</td>
<td>147.60</td>
</tr>
<tr>
<td>Raker Number</td>
<td>38.70</td>
<td>3.09</td>
<td>32.00</td>
<td>43.00</td>
</tr>
<tr>
<td>Raker Length (mm)</td>
<td>8.52</td>
<td>0.92</td>
<td>7.50</td>
<td>10.30</td>
</tr>
<tr>
<td>Raker Space (mm)</td>
<td>0.50</td>
<td>0.06</td>
<td>0.40</td>
<td>0.58</td>
</tr>
</tbody>
</table>
Table 6. Analysis of covariance for lake herring weight-at-length relationships for six lakes in central Ontario.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length</td>
<td>1</td>
<td>4344.8</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Invaded</td>
<td>1</td>
<td>0.1</td>
<td>0.748</td>
</tr>
<tr>
<td>Length*Invaded</td>
<td>1</td>
<td>0.1</td>
<td>0.714</td>
</tr>
<tr>
<td>Lake{Invaded}</td>
<td>4</td>
<td>66.7</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Error</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>442</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 7. Seven criteria used to evaluate Chesson’s α index and Pearre’s V index (Lechowicz 1982).

<table>
<thead>
<tr>
<th>Criteria</th>
<th>Chesson’s Alpha</th>
<th>Pearre’s Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Random model: zero value for equal occurrence</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>2. Symmetrical deviations from random electivity</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>3. Possible range of index values (ie. -1 to +1)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>4. Linear relationship for changes in prey utilization</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5. Sensitivity of index to sampling errors (ie. sample size)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>6. Statistical testability of the electivity</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>7. Stability of the electivity value (ie. relative abundance)</td>
<td>+</td>
<td>-</td>
</tr>
</tbody>
</table>

Key: + = yes; - = no.
Figure 1. Moon/Go Home watershed within shaded area of inset figure.

Lakes labelled in large roman numerals have been invaded by

**Bythotrephes:** I - Georgian Bay, II - Lake Muskoka, III - Lake Joseph, IV - Lake Rosseau, V - Lake Vernon, VI - Mary Lake, VII - Fairy Lake, VIII - Penninsula Lake, IX - Harp Lake, X - Lake of Bays. Lakes labelled in small roman numerals are reference lakes not invaded by **Bythotrephes:** i - Young Lake, ii - Twelve Mile Lake, iii - Gull Lake.
Figure 2. Bathymetry of Harp Lake. Contour lines are three meter increments.
Figure 3. Temperature-depth profile of Harp Lake between June 27 and October 11, 1995.
Figure 3

Lake Depth (m)

Sample Dates
Figure 4. Proportion abundance of lake herring diet items from April 26 to October 11, 1995. Lake herring stomach samples for April 26 and May 19 were provided by the Ontario Ministry of Natural Resources.
Figure 5. Proportion biomass estimates of lake herring diet for five major zooplankton taxa from June 8 to October 11, 1995.
Figure 6. Proportion abundance of major zooplankton taxa sampled from Harp Lake between June 8 and October 11, 1995.
Figure 6

Proportional Abundance

Jun 8   Jun 27   Jul 20   Aug 9   Aug 30   Sep 20   Oct 11

Sample Dates

- Calanoids
- Daphnia
- Holopedium
- Cyclopoids
- Bythotrephes
- Bosmina
Figure 7. Proportion biomass estimates of five major zooplankton taxa sampled from Harp Lake between June 8 and October 11, 1995.
Figure 8. Mean abundance of *Bythotrephes* in plankton and diet samples from June 8 to October 11, 1995. Error bars represent the range of two standard deviations on each sample date.
Figure 9a. Chesson's $\alpha$ values for abundance data between June 8 and October 11. Values range from 0 (strong negative selection) to 1 (strong positive selection) and a neutral selection value of 0.2.
Figure 9a

![Bar chart showing changes in population of different species over sample dates from June 8 to October 11. The x-axis represents sample dates, and the y-axis represents the population level (α). The chart includes different species:

- **Calanoids**
- **Daphnia**
- **Holopedium**
- **Cyclopoids**
- **Bythotrephes**

The population levels are measured on a scale from 0.0 to 1.0.
Figure 9b. Overall mean Chesson's $\alpha$ values for abundance data. Error bars are standard deviation estimates calculated from Manly (1974). * $P < 0.01$. 
Figure 9b

* - P < 0.01

**G**

- calanoids
- Daphnia
- Holopodium
- cyclopoids
- Bythotrophes

**A**

- 1.4
- 1.2
- 1.0
- 0.8
- 0.6
- 0.4
- 0.2
- 0.0

**T**

- Taxa

64
Figure 10a. Chesson’s $\alpha$ values for biomass estimates between June 8 and October 11. Values range from 0 (strong negative selection) to 1 (strong positive selection) and a neutral selection value of 0.2.
Figure 10b. Overall mean Chesson's $\alpha$ values for biomass estimates. Error bars are standard deviation estimates calculated from Manly (1974). * $P < 0.01$. 
Figure 10b

* - $P < 0.01$

$\alpha$

calanoids  Daphnia  Holopedium  cyclopoids  Bythotrephes

Taxa
Figure 11a. Pearre’s V values for abundance data between June 8 and October 11. Values range from -1 (strong negative selection) to 1 (strong positive selection) with neutral selection equaling 0.
Figure 11b. Overall mean Pearre's V values for abundance data. Error bars are standard deviation estimates calculated from Pearre (1982). * P < 0.01.
Figure 11b

- * P < 0.01

Taxa

- calanoids
- Daphnia
- Holopedium
- cyclopoids
- Bythotrephes
Figure 12a. Pearre's V values for biomass estimates between June 8 and October 11. Values range from -1 (strong negative selection) to 1 (strong positive selection) with neutral selection equaling 0.
Figure 12a

Sample Dates

- June 8
- June 27
- July 20
- Aug. 9
- Aug. 30
- Sept. 20
- Oct. 11

Types of planktonic organisms:
- calanoids
- Daphnia
- Holopedium
- cyclopoids
- Bythotrephes
Figure 12b. Overall mean Pearre's V values for biomass estimates. Error bars are standard deviation estimates calculated from Pearre (1982). * P < 0.01.
Figure 12b

* - P < 0.01

Taxa

- calanoids
- Daphnia
- Holopedium
- cyclopoids
- Bythotrephes
Figure 13a. Boxplots of two zooplankton taxa subject to size-selective predation. Each boxplot represents the variability in body length (mm). Within each box are the 25th and 75th percentiles, while and the 50th percentile (middle line). Error bars below and above indicate the 5th and 95th percentiles, respectively. Comparisons between lake and diet samples for each date were made with a Kolmogorov-Smirnov two-sample test.

** P < 0.01, N.S. P > 0.05.
Figure 13a

Daphnia

Body Length (mm)

** ** ** ** ** ** **
8 27 20 9 30 20 11

Sample Dates

calanoid copepods

** ** N.S. ** ** ** **
0.2 0.6 1.0 1.4

diet

lake
Figure 13b. Boxplots for three other major zooplankton taxa. Boxplots and statistical comparisons were the same as in Figure 13a.
Figure 13b

cyclopoid copepods

**
8 June

N.S.
27 June

Body Length (mm)

Holopedium

N.S.
June 8

Bythotrephes

N.S.
July 20

Sample Date

diet
lake

80
Figure 14. *Bythotrephes* tailspine number regressed on mandible number in lake herring diet from Harp Lake. Dotted lines are 95% confidence intervals for the regression line (solid). The regression coefficient (β) was not significantly different from a slope of 1 (labelled as 1:1 ratio line).
Figure 14

Spines = 3.64 + 1.03(Mandibles) (95% C.I.) $r = 0.99$

$H_0: \beta = 1$
$P > 0.10$

1:1 ratio
Figure 15. Lake herring weight-at-length regressions with reference to *Bythotrephes* invasion status for six lakes in central Ontario. Three lakes were invaded (Lake Joseph, Lake Rosseau, Harp Lake), while three others were not invaded (Young Lake, Twelve Mile Lake, Gull Lake).
Figure 15

- Invaded lakes
- Noninvaded lakes

Lake Joseph
Lake Rosseau
Young Lake
Twelve Mile Lake
Gull Lake
Harp Lake

Log weight (g)

Log Length (mm)
VITA AUCTORIS

NAME: Robert Andrew Coulas
DATE OF BIRTH: May 10, 1970
PLACE OF BIRTH: Deep River, Ontario
EDUCATION:
Paul Dwyer Catholic High School
Oshawa, Ontario
1984-1989

University of Western Ontario
London, Ontario
1989-1993
Hons. B. Sc.

University of Windsor
Windsor, Ontario
1994-1996
M. Sc.