

Alewife planktivory controls the abundance of two invasive predatory cladocerans in Lake Michigan

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SUMMARY

1. We sampled along a nearshore transect (10-m bathymetric contour) in Lake Michigan to determine diet, 24-h feeding periodicity, daily ration and food requirements of an invasive fish, the alewife, *Alosa pseudoharengus*, relative to zooplankton abundance and production. Our objective was to determine whether the alewife controls the abundance of two invasive, predatory cladocerans, *Bythotrephes longimanus* and *Cercopagis pengoi*.
2. Bosminidae was the most abundant prey taxon and Chydoridae, *Leptodora*, Chironomidae and *Bythotrephes* were the least abundant. Neither *Bythotrephes* nor *Cercopagis* were important prey for small alewives (≤ 100 mm). *Bythotrephes* was eaten by over 50% of large alewives (>100 mm) and accounted for 10–27% of the diet weight. *Cercopagis* was eaten by about 30% of the large alewives but only accounted 1% of the diet weight.
3. Food weight in stomachs was highest early in the night for small alewives and lowest at night for large alewives. Chironomidae and large Chydoridae were the preferred prey of small alewives. *Bythotrephes* and large Chydoridae were the preferred prey for large alewives.
4. Food requirements of alewife were much less than production for most prey taxa, although the consumption of *Bythotrephes* greatly exceeded production on both dates. Alewives consumed only 3% of *Cercopagis* production. High selectivity and food requirements of alewife for *Bythotrephes*, and low selectivity and food requirements for *Cercopagis*, probably explain the difference in abundance between these two invasive cladocerans at our nearshore site in Lake Michigan.

Keywords: alewife, *Bythotrephes longimanus*, *Cercopagis pengoi*, daily ration, planktivory

Introduction

Invasive species have altered the ecology of the Great Lakes, including Lake Michigan (Wells & McClain, 1973; Madenjian *et al.*, 2002; Mills *et al.*, 2003). In order for a new species to become established in an ecosystem, there must be functional vector(s) to

introduce the species into the system, the species must be adapted to the environment or adapt quickly, and conditions must be favourable for the species to persist. Once a species is introduced and successfully colonises a new system, it redefines the food web dynamics of the system and ultimately affects the success of future invasive species (Vanderploeg *et al.*, 2002). The alewife, *Alosa pseudoharengus* Wilson, is an invasive fish that continues to influence the food web dynamics of Lake Michigan. Alewives were found in Lake Michigan in 1949 and their numbers rose rapidly in the 1950s (Wells & McClain, 1973). The success of

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the alewife was probably due in part to the loss of lake trout, *Salvelinus namaycush* Walbaum, the dominant piscivore in the Great Lakes prior to the invasion of the sea lamprey, *Petromyzon marinus* Linnaeus (Smith, 1970).

The alewife was linked to major disruptions for both planktivorous fish and zooplankton populations in Lake Michigan (Wells, 1970; Madenjian *et al.*, 2002). Alewives not only reduced the number of large zooplankton, but also consumed small zooplankton more effectively than native fishes, because of their ability to switch between particulate and filter feeding modes (Wells, 1970; Janssen, 1976; Crowder, 1980). Thus, alewives have been implicated in declines and habitat changes for various native fish including yellow perch (*Perca flavescens* Mitchell), bloater (*Coregonus hoyi* Gill) and emerald shiner (*Notropis atherinoides* Rafinesque) (Crowder, 1980; Jude & Tesar, 1985; Mason & Brandt, 1996; Shroyer & McComish, 2000). In turn, alewives now comprise the major food of stocked lake trout and non-native stocked Pacific salmon (*Oncorhynchus tshawytscha* Walbaum and *Oncorhynchus kisutch* Walbaum) in Lake Michigan (Madenjian *et al.*, 2002).

Heavy stocking of salmonines in Lake Michigan probably reduced alewife abundance in the 1980s (Jude & Tesar, 1985; Madenjian *et al.*, 2002) and may have aided the successful establishment of the large predatory cladoceran *Bythotrephes longimanus* Leydig (hereafter *Bythotrephes*) in 1986 (Evans, 1988; Makarewicz *et al.*, 1995). Although *Bythotrephes* has a long-tail spine that serves as a deterrent to small fish (Barnhisel, 1991), it is ineffective against non-gape limited predators, such as large alewives, that selectively prey on the species (Branstrator & Lehman, 1996; Pothoven, Fahnenstiel & Vanderploeg, 2001; Pothoven & Vanderploeg, 2004). Both the size structure and species composition of *Daphnia* spp. in Lake Michigan changed following the arrival of *Bythotrephes* (Lehman & Caceres, 1993; Makarewicz *et al.*, 1995). Following their establishment, *Bythotrephes* was more abundant offshore than nearshore, where fish predation may limit its abundance (Lehman & Caceres, 1993; Pothoven *et al.*, 2001; Pothoven, Fahnenstiel & Vanderploeg, 2003). The scarcity of *Bythotrephes* near the shore may have provided an opportunity for another predatory cladoceran, *Cercopagis pengoi* Ostroumov (hereafter *Cercopagis*) to become established in the lake in 1999 (Vanderploeg

et al., 2002). *Bythotrephes* is capable of eating *Cercopagis* (Witt & Caceres, 2004) and, although *Cercopagis* is eaten by fish, including the alewife (Charlebois, Raffenberg & Dettmers, 2001; Bushnoe *et al.*, 2003; Thompson, Makarewicz & Lewis, 2005), it is unclear whether it is a preferred prey in Lake Michigan because it is much smaller than *Bythotrephes* (Vanderploeg *et al.*, 2002).

To understand the impact of invasive species on ecosystems, we need to understand their interactions with native and other invasive species (Witt & Caceres, 2004). We sampled a nearshore area in Lake Michigan during August 2004 to collect information on the interactions of the alewife with two predatory cladocerans, *Bythotrephes* and *Cercopagis*. All three species co-occur in the nearshore in the summer in Lake Michigan. The goals were to: (i) describe the diet composition and feeding periodicity of alewives; (ii) evaluate its prey selectivity; and (iii) estimate its daily ration and consumption relative to the biomass and daily production of *Bythotrephes*, *Cercopagis* and other prey.

Methods

Field sampling

Sampling occurred at approximately 4-h intervals over 24–28 h along a 2.5 km contour transect at a depth of 10 m in Lake Michigan, approximately 0.6 km offshore of Muskegon, Michigan during 2–3 and 16–17 August 2004. These sampling dates coincided with the full and new moon periods, respectively.

Alewives and other planktivorous fish were collected using a 7.6-m semi-balloon 4-seam Skate model bottom trawl (13-mm stretched-mesh cod-liner) (Innovative Net Systems, Milton, LA U.S.A.). The bottom trawl was towed along the transect for approximately 15–20 min and all fish were immediately frozen and stored at -30°C . A midwater trawl was also used, but few fish were captured and all the data presented are for fish taken in the bottom trawl.

Immediately following each bottom trawl, the transect was sampled using fishery acoustics with a Biosonics DT6000 129 kHz split beam echosounder (BioSonics Inc, Seattle, WA, U.S.A.) (ping rate of 3 pings s^{-1} , a pulse width of 0.4 ms and a target acquisition threshold of -70 dB). Boat speed was approximately 7.5 km h^{-1} .

Upon completion of the acoustics sampling, zooplankton were collected at the midpoint of the transect from an anchored ship, with whole water column tows using a 1-m diameter, 153- μm mesh conical plankton net. The net was pulled vertically through the water column at a speed of 0.5 m s⁻¹ from 1 to 2-m above the bottom up to the surface. The net was washed thoroughly and the contents were transferred to a sample bottle, narcotised with Alka-Seltzer and preserved with sugar formaldehyde to form a 2% solution (Haney & Hall, 1973). Water temperature profiles were recorded during each time interval using a Seabird Conductivity, Temperature, Depth profiler (Sea-Bird Electronics Inc, Bellevue, WA, U.S.A.).

Sample analysis

We used Echoview 3.3 (Sonar Data, <http://www.sonardata.com>) software to analyse the acoustic data. Only acoustic transects completed during the night were used to estimate alewife density because fish disaggregate at night and variation is lower (Brandt *et al.*, 1991). Before processing, raw acoustic files were inspected for bottom intrusion and noise. Density was calculated using the backscattering coefficient and mean backscattering coefficient of all targets between -50 to -39 dB for the echo-squared integration. Bounds of -50 to -39 dB were chosen to restrict density estimates to alewife-sized targets, based on the length of alewives collected in trawls (60–190 mm) and target strength to length equations for this species (Warner, Rudstam & Klumb, 2002). All midwater targets were assumed to be alewives based on day and night bottom trawls and night midwater trawls where the alewife was the only pelagic species collected. Alewives were allocated to small (≤ 100 mm total length; young of the year) and large (> 100 mm total length; yearlings and adults) size categories. The density of small and large alewives was determined by multiplying the total density of pelagic fish determined with acoustics, by the numerical proportion of each alewife size group captured in trawls for each sample interval.

To determine zooplankton abundance and composition, an aliquot was taken from a known sample volume with a Hensen–Stempel pipette, so that a minimum 550 zooplankters were identified for each sample. To count large predatory cladocerans and other large rare prey (Chironomidae larvae, pupae

and adults; and large Chydoridae) that were found in lower densities than the other zooplankton, the whole sample was rinsed through a 600- μm mesh sieve and large taxa were identified and counted.

To determine zooplankton biomass, length measurements were made on a sub-sample of individuals of the taxa (10 adult copepods and 25 copepodites or cladocerans) that accounted for over 10% of the total density, using Image Pro Plus image analysis software (Media Cybernetics, Silver Spring, MD, U.S.A.). Up to 100 individual large predatory cladocerans were measured for each sample. Biomass was determined using published weight–length regressions (Smock, 1980; Sprung, 1984; Culver *et al.*, 1985; Malley *et al.*, 1989; Shea & Makarewicz, 1989; Makarewicz & Jones, 1990; Grigorovich *et al.*, 2000). For zooplankton taxa that were $< 10\%$ of the sample, a mean default weight was used from the literature (Hawkins & Evans, 1979).

Diet and ration analyses were carried out separately for small and large alewives. All fish captured during each sample interval were used for diet analysis, except for two intervals on 17 August (13:00 and 17:00 hours), when a random sample of approximately 30 small and 50 large alewives was taken from large catches. In the laboratory, fish were thawed, measured (nearest mm total length) and weighed (nearest g), stomach contents were removed and the entire fish (minus stomach contents) was dried at 70 °C to a constant weight. Stomach contents were dried at 70 °C to a constant weight after diet composition was determined. To examine feeding periodicity, the amount of food eaten (dry, mg food g⁻¹ fish) and the number of *Bythotrephes* or *Cercopagis* eaten was compared across time intervals on each date for each size class of alewife using a Kruskal–Wallis test. The mean length of *Bythotrephes* and *Cercopagis* was compared between the environment and fish diets (sample dates combined) using ANOVA. The proportion of each instar of *Bythotrephes* and *Cercopagis* was compared between the environment and fish diets (sample dates combined) using a chi-squared test.

To determine diet composition, all large prey (*Bythotrephes*, *Cercopagis*, *Leptodora kindtii* Focke, Chironomidae pupa, larvae and adults) from each stomach were identified and counted. Head capsules (Chironomidae) or bodies with eye-spots (*Bythotrephes*, *Cercopagis*, *Leptodora*) were used to count partial prey. Bodies only were used to provide a conservative

estimate of *Bythotrephes* and *Cercopagis*, because spines can accumulate in stomachs (Branstrator & Lehman, 1996). Meso-zooplankton (e.g. Copepoda, Cladocera) from each stomach were added to a known volume (10–25 mL) of water and sub-sampled with a 1 mL aliquot, so that approximately 100 individuals were counted. If stomachs contained fewer than 100 mesozooplankton, all individuals were counted. The mesozooplankton was classified as Bosminidae, Daphniidae, Sididae, small Chydoridae (≤ 0.50 mm), large Chydoridae (> 0.50 mm), Cyclopoida, Calanoida and nauplii. Prey lengths of at least five intact individuals of each prey group except nauplii from each stomach (if available) were measured using Image Pro image analysis software (Media Cybernetics, Silver Spring, MD, U.S.A.). Prey length was converted to dry weight using weight-length regressions (Hawkins & Evans, 1979; Smock, 1980; Culver *et al.*, 1985; Makarewicz & Jones, 1990; Grigorovich *et al.*, 2000). The average dry weight of an individual of each prey type was determined for each size class of alewife and multiplied by the number of each prey type in a stomach. Prey weights of each prey group were summed across all individual fish from a sample date and diet composition was determined as the per cent of the total calculated dry weight. This method of determining diet composition helps correct for different stages of digestion of different prey (Hyslop, 1980). Diet composition was also calculated on a numerical basis and as the frequency of occurrence for each size class of fish on each date.

Daily ration was estimated in terms of g food (dry) g^{-1} alewife (dry) d^{-1} using the model derived by Elliott & Persson (1978):

$$C_t = \frac{(S_t - S_0 e^{-Rt})}{1 - e^{-Rt}} Rt; \quad (1)$$

where C_t is the consumption over time interval t_0 – t_t , S_0 is the average amount of food in the stomach at time t_0 , S_t is the amount of food in the stomach at t_t , R is the instantaneous evacuation rate and t is the time interval between samples (h). The estimates of C_t are summed over all time intervals in a 24-h period to give the total daily ration. We assumed that the same group of fish was sampled over each 24-h period. On 16–17 August, an additional sample was taken following the 24-h period, but this sample was used only to examine feeding periodicity and not for calculations of the daily ration. The instantaneous gastric

evacuation rate R is a temperature dependent exponential function (Elliott, 1972) described by the relationship:

$$R = ae^{bT} \quad (2)$$

where T is the measured water temperature, and a and b are constants. The slope (b) is assumed constant for different prey types and fish species, but the intercept (a) changes with prey type (Durbin *et al.*, 1983). We used a slope of 0.115 and an intercept of 0.0406 (Durbin *et al.*, 1983). Both values have been used previously for anadromous alewife (Stone & Jessop, 1994). R was assumed to vary only with temperature and to remain unaffected by fish size, food size, meal size or feeding frequency (Durbin *et al.*, 1983). Persson (1979) found that R did not differ between various prey, including chironomids and zooplankton for perch (*Perca fluviatilis* Linnaeus).

Daily production for prey groups was determined using P/B relationships. Production for cladocerans and copepods was determined using the temperature based daily P/B relationships from Shuter & Ing (1997):

$$\log P/B_{\text{daily}} = \alpha + \beta T \quad (3)$$

where $\alpha = -1.725$ (Cladocera), -1.766 (Cyclopoida) or -2.458 (Calanoida), and $\beta = 0.044$ (Cladocera), 0.040 (Cyclopoida) or 0.050 (Calanoida). A P/B value of 4 was used for Chironomidae (Johnson & Brinkhurst, 1971). Water temperature (T) was measured directly in the field on each date. All production estimates for prey groups were determined on an areal ($\text{mg m}^{-2} \text{d}^{-1}$) basis to allow for comparison with fish consumption data. Production was determined for each time interval and averaged over all sample periods to obtain one estimate of production for each date.

Daily ration (dry, g food g^{-1} fish d^{-1}) of an individual alewife was multiplied by the average dry weight of alewives collected in bottom trawls. This was performed for each size class of alewife on each sample date to determine the food requirements of an average fish (g food $\text{fish}^{-1} \text{d}^{-1}$). The individual fish consumption estimate was multiplied by the density of fish determined from acoustics to produce an estimate of population food requirements ($\text{mg food m}^{-2} \text{d}^{-1}$). This population demand was

multiplied by the overall proportional diet composition (dry weight) to obtain daily food requirements of alewives for each prey group. Daily food requirements for both size classes of alewife were summed and compared with daily prey production for each sample date.

To determine the sensitivity of the population food requirement ($\text{mg food m}^{-2} \text{d}^{-1}$) and production estimates to variation in parameters, we varied 'a' and 'b' for the determination of evacuation (R), and 'α' and 'β' for the determination of production (P) separately by $\pm 20\%$. Food weights (S) and water temperatures (T) that are used to determine daily ration were not varied because they were measured directly in the laboratory and field.

To determine prey selectivity, we used Vanderploeg & Scavia's (1979) selectivity coefficient, W calculated as:

$$W'_i = (r_i/p_i)/(r_i/p_i)_{pref} \quad (4)$$

where relative prey abundance in the environment (P) and diet (r) were expressed in numbers and $(r_i/p_i)_{pref}$ was the maximum value of (r_i/p_i) . Prey abundances were calculated based on the number of each prey in the environment or diet across all time periods on each respective date. The selectivity coefficient, W varies between 0 for no ingestion of a prey type to 1, the W value for the most preferred prey type(s), i.e. the prey type(s) with the maximum value of (r_i/p_i) . We speak of selectivity being high when is near 1 and low when it is near 0. The selectivity coefficient, W , is unaffected by prey abundance and is easily understood as the relative mortality imposed by the predator on different prey types (Vanderploeg & Scavia, 1979; Vanderploeg, Scavia & Liebig, 1984; Vanderploeg, 1994). It has been especially useful for relating food selection to foraging strategy and feeding mechanisms and for models predicting prey consumption under various prey abundance scenarios (e.g. Vanderploeg, 1981, 1994; Vanderploeg *et al.*, 1984; Pothoven & Vanderploeg, 2004). Selectivity was also calculated for each individual alewife and the percentage of fish that preferred a particular prey item above all other prey, i.e. the number of times for that prey type, was determined. The average prey abundance across all time periods for each date was used to determine relative prey abundance available to individual alewives.

Results

Prey abundance and production

Bosminidae was the most abundant prey taxon on both sampling dates, with average abundances of 7367 and 28 083 m^{-3} on 2 and 16 August, respectively (Table 1). The abundance of Bosminidae and small Chydoridae was higher on 16 August than 2 August, whereas the abundance of other prey decreased or remained generally constant over the same period. The least abundant prey taxa were large Chydoridae, *Leptodora*, Chironomidae and *Bythotrephes*. The average abundance of *Bythotrephes* was 0.25 and 0.32 m^{-3} on 2 and 16 August, respectively, whereas that of *Cercopagis* was 82 and 13 m^{-3} . Estimates of daily production were highest for Bosminidae (20.0 and

Table 1 Average prey abundance across sample periods (number m^{-3}) (1 SE), prey production ($\text{mg m}^{-2} \text{d}^{-1}$) and food requirements (consumption) ($\text{mg m}^{-2} \text{d}^{-1}$) of the alewife population on 2–3 and 16–17 August at a nearshore site in southeastern Lake Michigan

	Abundance	Production	Consumption
August 2			
Nauplii	7367 (1431)	NA	<0.001
Small Chydoridae	316 (97)	0.396	0.031
Bosminidae	13120 (2478)	20.010	0.369
Cyclopoida	465 (125)	0.612	0.049
Sididae	40 (18)	0.099	0.003
Cercopagis	82 (36)	0.502	0.011
Daphniidae	132 (41)	0.451	0.255
Leptodora	2 (1)	0.039	0.001
Calanoida	3119 (358)	0.757	0.047
Large Chydoridae	8 (6)	0.213	0.121
Bythotrephes	0.25 (0.22)	0.039	0.590
Chironomidae	1 (0.3)	2.579	0.912
August 16			
Nauplii	1156 (211)	NA	<0.001
Small Chydoridae	881 (348)	0.922	0.046
Bosminidae	28083 (8876)	39.257	1.640
Cyclopoida	300 (55)	0.366	0.110
Sididae	15 (24)	0.030	0.013
Cercopagis	13 (3)	0.064	0.002
Daphniidae	83 (24)	0.257	0.087
Leptodora	2 (1)	0.029	0.003
Calanoida	356 (48)	0.186	0.048
Large Chydoridae	0.42 (0.42)	0.008	0.942
Bythotrephes	0.32 (0.10)	0.053	0.329
Chironomidae	3 (1)	121.727	1.751

NA, not applicable.

Chydoridae are separated into small (≤ 0.5 mm) and large (> 0.5 mm) categories. Prey listed in order of increasing average weight.

39.3 mg m⁻² d⁻¹) and Chironomidae (2.6 and 121.7 mg m⁻² d⁻¹) and were typically lowest for *Leptodora* and *Bythotrephes*, ≤0.053 mg m⁻² d⁻¹ (Table 1). Water temperature was 20.9 and 18.8 °C, throughout the water column, on 2 and 16 August, respectively.

Alewife diet

A total of 224 small alewives and 397 large alewives were examined to determine diet and ration. About 3% of stomachs were empty. For small alewives, Bosminidae was the most important item by weight (45–50%) along with Chironomidae (17–30%) and large Chydoridae (8–25%) (Table 2). Neither *Bythotrephes* nor *Cercopagis* were important prey (<1%) on a weight basis for small alewives. For large alewives, Chironomidae were the largest component of the diet by weight (39–45%) along with *Bythotrephes* (10–27%) and Bosminidae (11–24%) (Table 2). Daphniidae accounted for 12% of the diet on 2 August and Chydoridae for 15% on 16 August, respectively. *Cercopagis* never accounted for more than 1% of large alewife diet by weight. Nearly all Chironomidae found in stomachs were larvae (56%) or pupae (43%).

By number, Bosminidae was the dominant item (>67%) for both small and large alewives (Table 2). Prey taxa that were a large part of the diet by weight, such as Chironomidae and *Bythotrephes*, were a small part of the diet on a numerical basis (<3%).

Bosminidae, Cyclopoida and small Chydoridae were each eaten by over 70% of small alewives on each date (Table 2). *Bythotrephes* was eaten by 2 and 16% of small alewives on 2 and 16 August, respectively, and *Cercopagis* was eaten by 6 and 9% of fish on the same dates. For large alewives, only *Bythotrephes* and Bosminidae were eaten by over 50% of fish on each date (Table 2). *Cercopagis* was eaten by about 30% of the large alewives on both dates. Small Chydoridae and Chironomidae were eaten by over 50% of large alewives on 16 August.

The mean total length of *Bythotrephes* (including the spine) eaten (9.86 mm) was similar to that in the environment (10.06 mm) ($F = 0.52$; d.f. = 1,85; $P = 0.47$). Most *Bythotrephes* in stomachs were stage-2 instars (84%) and the remainder were stage 3 (12%) or stage 1 (4%), a distribution similar to that in the environment, where instars 1, 2 and 3 accounted for

Table 2 Diet composition (per cent) for small (≤100 mm) and large (>100 mm) alewives on 2–3 and 16–17 August in the nearshore of southeastern Lake Michigan

	August 2			August 16		
	%W	%N	%F	%W	%N	%F
Small						
Nauplii	<0.1	0.5	10.3	<0.1	<0.1	6.9
Small Chydoridae	4.9	9.4	78.2	1.4	3.1	76.3
Bosminidae	49.9	84.3	95.4	45.1	84.1	94.7
Cyclopoida	2.6	2.1	70.1	4.1	3.8	72.5
Sididae	0.2	0.1	10.3	0.4	0.3	24.4
Cercopagis	<0.1	<0.1	5.8	<0.1	<0.1	9.2
Daphniidae	1.5	0.7	29.9	4.1	2	31.3
Leptodora	<0.1	<0.1	1.2	0.1	<0.1	7.6
Calanoida	1.9	0.5	27.6	2.1	0.6	25.2
Large Chydoridae	8.0	1.6	25.3	24.6	5.5	36.6
Bythotrephes	0.2	<0.1	2.3	0.4	<0.1	16.0
Chironomidae	30.5	0.6	28.9	16.9	0.3	45.8
<i>n</i>	87			131		
Large						
Nauplii	<0.1	<0.1	1.4	<0.1	0.1	1.8
Small Chydoridae	0.8	5.6	24.1	0.6	2.3	62.4
Bosminidae	11.3	66.8	53.2	24.5	88.8	70.6
Cyclopoida	2.0	5.6	29.2	1.0	1.7	40.0
Sididae	0.1	0.3	3.2	0.1	0.2	9.4
Cercopagis	0.5	1.1	30.6	<0.1	0.1	27.1
Daphniidae	11.7	12.0	22.7	0.3	0.2	7.1
Leptodora	0.1	0.1	5.1	<0.1	<0.1	5.3
Calanoida	1.9	1.8	12.9	0.2	0.1	4.7
Large Chydoridae	4.7	2.7	26.8	14.8	5.2	31.8
Bythotrephes	27.4	2.7	65.3	10.0	0.6	71.2
Chironomidae	38.8	1.0	42.6	44.6	0.5	55.3
<i>n</i>	216			170		

%W, per cent of total dry weight; %N, per cent of total prey items; %F, frequency occurrence; *n*, number of fish with food in stomachs.

Prey items are listed in order of increasing average weight. Chydoridae are separated into small (≤0.5 mm) and large (>0.5 mm) categories.

Minor prey such as fish, Mollusca, Nematoda, Acarina not included in above proportions.

4%, 74% and 22% of the *Bythotrephes*, respectively ($\chi^2 = 1.4$; d.f. = 2; $P = 0.49$). In contrast, the mean body length of *Cercopagis* in the environment (1.26 mm) was smaller than that eaten by alewife (1.45 mm) ($F = 6.8$; d.f. = 1,981; $P = 0.009$). Only *Cercopagis* bodies were measured because tail spines were rarely intact. The proportion of each *Cercopagis* instar differed between the environment, where instars 1, 2 and 3 accounted for 19, 52 and 28% of the population, respectively, and alewife diet, where each respective instar accounted for 6, 81 and 12% of the *Cercopagis* ($\chi^2 = 10.7$; d.f. = 2; $P = 0.005$).

Alewife feeding periodicity

Food weight (dry, mg food g⁻¹ fish) differed over time for both small ($\chi^2 > 14$; d.f. = 6–7; $P < 0.03$) and large alewives ($\chi^2 > 27$; d.f. = 6–7; $P < 0.001$) on both sample dates (Kruskal–Wallis test, $P < 0.05$) (Table 3). For small alewives, food weight in stomachs was highest early in the night (21:00-hours sample), decreased through the night and was lowest early in the morning (05:00-hours sample). At the peak feeding period, the diet of small alewives was dominated by Chironomidae on 2 August, and by Daphniidae and Bosminidae or Chironomidae on 16 August.

Table 3 Average food weight (dry, mg food g⁻¹ fish) (1 SE), average number of *Bythotrephes* per stomach and average number of *Cercopagis* per alewife stomach for each 4-h sample interval on 2–3 and 16–17 August for small (<100 mm) and large (>100 mm) alewives at a nearshore site in southeastern Lake Michigan

	Time	Food weight (1 SE)	n	<i>Bythotrephes</i>	<i>Cercopagis</i>
2 August					
Small	09:00	11.5 (1.4)	2	0	0
	13:00	11.7 (1.0)	28	0.04	0
	17:00	13.8 (3.7)	5	0	0
	21:00	20.5 (3.7)	9	0.56	0.67
	01:00	17.3 (1.9)	6	0	0.67
	05:00	9.8 (1.9)	15	0	0.13
	09:00	12.9 (1.2)	23	0	0
Large	09:00	8.7 (1.0)	67	6.79	1.54
	13:00	9.1 (0.9)	53	6.21	4.64
	17:00	9.4 (1.7)	20	4.60	0.20
	21:00	5.6 (0.7)	29	1.10	1.55
	01:00	4.2 (0.8)	42	1.14	0.14
	05:00	0	1	0	0.00
	09:00	4.4 (1.2)	9	0	0.22
16 August					
Small	17:00	41.9 (3.0)	18	0.06	0.28
	21:00	67.0	1	0	0
	01:00	23.3 (7.3)	12	0.58	0
	05:00	7.0 (1.5)	24	1.79	0.04
	09:00	19.1 (13.6)	3	2.67	0
	13:00	30.8 (2.1)	30	0.27	0.20
	17:00	17.5 (1.4)	31	0	0
	21:00	38.4 (12.2)	17	0	0
Large	17:00	4.6 (0.7)	12	0.50	2.50
	21:00	1.5	1	3.00	0
	01:00	5.8 (0.7)	25	6.56	0.24
	05:00	10.5 (1.9)	31	3.87	0.13
	09:00	8.8 (2.1)	4	23.75	1.00
	13:00	12.1 (2.0)	51	6.69	1.02
	17:00	9.6 (1.0)	49	4.10	0.31
	21:00	10.5 (0.9)	3	0.33	0

Large alewives exhibited less periodicity in feeding, but food weight tended to be lowest at night (01:00-hours sample). The number of *Bythotrephes* and *Cercopagis* per alewife stomach differed over time for small and large fish on both dates (Kruskal–Wallis test, $P < 0.05$), except that the number of *Bythotrephes* per small alewife did not differ over sampling intervals on 2 August (Table 3).

Selectivity

Overall, Chironomidae and large Chydoridae were the preferred prey of small alewives, *Bythotrephes* and large Chydoridae of large alewives (Fig. 1). For individual fish, large Chydoridae were selected by 25% of small alewives, while Chironomidae, small Chydoridae, Bosminidae and Daphniidae were each selected by at least 10% of the small fish (Fig. 2). *Bythotrephes* was the preferred prey of 58% of the large alewives, while large Chydoridae and Chironomidae were preferred by about 15% of fish (Fig. 2). *Cercopagis* was rarely preferred by any individual fish in either size class.

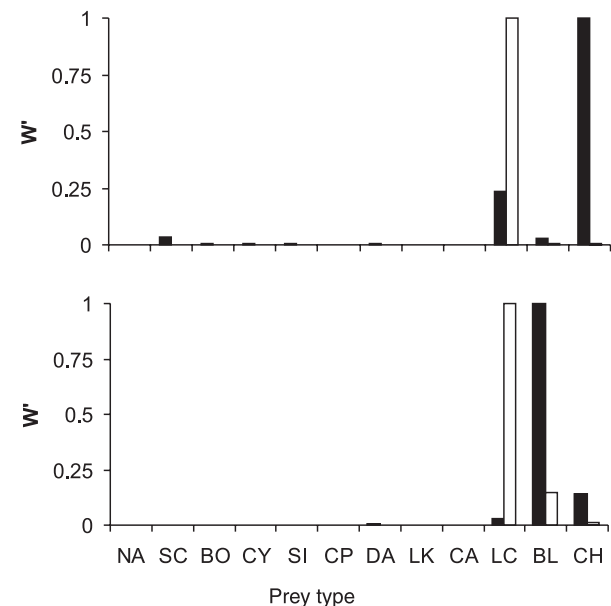


Fig. 1 Overall prey selectivity (W') of small (≤ 100 mm, top panel) and large (> 100 mm, bottom panel) alewives on 2–3 (black bars) and 16–17 (open bars) August at a nearshore site in southeastern Lake Michigan. NA = nauplii, SC = small Chydoridae (≤ 0.5 mm), BO = Bosminidae, CY = Cyclopoida, SI = Sididae, CP = *Cercopagis*, DA = Daphniidae, LK = *Leptodora*, CA = Calanoida, LC = Large Chydoridae (≥ 0.5 mm), BL = *Bythotrephes*, CH = Chironomidae.

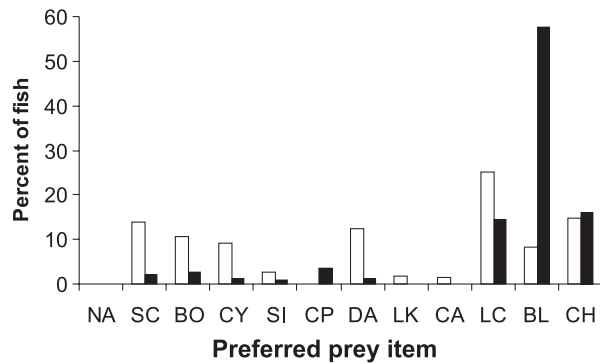


Fig. 2 Per cent of the number of individual small (≤ 100 mm, open bars) and large (> 100 mm, black bars) alewives that preferred a particular prey item above all other prey, i.e. the number of times for that prey type, for both sample dates combined. See Fig. 1 for prey abbreviations.

Table 4 Average total length (mm), wet weight (g), individual daily ration (dry, $\text{g food g}^{-1} \text{ fish d}^{-1}$), individual food consumption (dry, $\text{g food fish}^{-1} \text{ d}^{-1}$), and density (number ha^{-1}) for small (≤ 100 mm) and large (> 100 mm) alewives on 2–3 and 16–17 August at a nearshore site in southeastern Lake Michigan

	Length	Weight	Ration	Consumption	Density
Small					
8/2/04	85	4.5	0.157	0.163	15.48
8/16/04	82	4.3	0.222	0.216	87.82
Large					
8/2/04	145	21.6	0.056	0.291	74.07
8/16/04	128	15.9	0.073	0.286	111.86

Alewife density and daily ration

Hydroacoustic estimates of fish density at night were 15.48 and 87.82 ha^{-1} for small alewives on 2 and 16 August, respectively, and 74.07 and 111.86 ha^{-1} for large alewives (Table 4). The benthic spottail shiner, *Notropis hudsonius* Clinton, was the only fish species besides the alewife that was caught in significant numbers. Spottail shiners were only caught at night and mainly ate large Chydoridae (83% by weight) and Chironomidae (15%).

The size of small alewives was similar between dates, but large alewives were longer and weighed more on 2 than 16 August (Table 4). Daily ration was similar between dates for each size class of alewife. Daily ration (dry, $\text{g food g}^{-1} \text{ fish d}^{-1}$) was higher for small fish, but individual food requirements (dry, $\text{g food fish}^{-1} \text{ d}^{-1}$) were higher for large fish (Table 4).

Table 5 Per cent change in population food requirements ($\text{mg m}^{-2} \text{ d}^{-1}$) and prey production ($\text{mg m}^{-2} \text{ d}^{-1}$) of *Bythotrephes* as reported in Table 1 following a $\pm 20\%$ change in the various parameters used to determine consumption and production. See text for explanation of procedures

Parameter	Parameter change			
	2 August		16 August	
	+20%	-20%	+20%	-20%
Food requirements				
a	21	-21	19	-19
b	65	-41	51	-33
Production				
α	-54	121	-54	121
β	53	-34	46	-32

In general, food requirements of alewife were much less ($< 25\%$) than estimates of production for most prey taxa on both sample dates (Table 1). However, food requirements greatly exceeded estimates of *Bythotrephes* production on both dates. Alewife food requirements also exceeded production for large Chydoridae on 16 August and on average were 45% of daphniid production. Alewife food requirements were never more than 3% of *Cercopagis* production.

The population food requirement estimate was fairly sensitive to errors in the parameter ' b ' used to determine evacuation (R), and production (P) was sensitive to errors in the parameters ' α ' and ' β ' (Table 5). Nonetheless, even if the errors resulting in the highest estimate of production ($\alpha - 20\%$) and the lowest estimate of food requirements ($b - 20\%$) were combined, food requirements still exceeded *Bythotrephes* production on both dates.

Discussion

Overall, *Bythotrephes* was the preferred, as well as the most frequently selected, prey of large alewives at our nearshore station during August 2004. Our selection estimates are conservative because the other most selected prey (Chironomidae, large Chydoridae) are generally benthic and their abundance in the environment might have been underestimated, thus leading to overestimates of selection. In contrast to large alewives, small individuals preferred large zooplankton and Chironomidae overall, although *Bythotrephes* was selected by about 6% of individuals. Strong selection for *Bythotrephes* in the nearshore of Lake

Michigan is not surprising, because *Bythotrephes* is relatively conspicuous regardless of instar. *Bythotrephes* is relatively large compared with other zooplankton, and has a prominent eye-spot, heavy yellowish pigmentation and a large brood (Barnhisel & Harvey, 1995; Coulas, MacIsaac & Dunlop, 1998; Vanderploeg *et al.*, 2002). Moreover, *Bythotrephes* is known to be a preferred prey for large alewives in the offshore waters of Lake Michigan, where *Bythotrephes* is abundant (Pothoven & Vanderploeg, 2004).

In addition to being a preferred prey, *Bythotrephes* was also eaten by most large alewives (65–71%) and accounted for 10–27% of their diet by weight. The average number of *Bythotrephes* per large alewife stomach (including fish that did not eat *Bythotrephes*) was only five, but the maximum was 78, indicating that large alewives can eat large numbers of this prey. *Bythotrephes* was eaten less frequently (2–16%), and contributed less (<1% by weight) to the diet weight, for small alewives. Adult, yearling and age-0 alewives began eating *Bythotrephes* soon after its arrival in Lake Michigan (Rand *et al.*, 1995; Branstrator & Lehman, 1996) and this invasive zooplankton has remained an important prey for large alewives (Pothoven & Vanderploeg, 2004). After they were introduced into Lake Ontario, *Bythotrephes* quickly became a major prey item for alewives (Mills *et al.*, 1992) and never became abundant in the lake (Mills *et al.*, 2003). In Harp Lake, Ontario, lake herring *Coregonus artedii* Lesueur quickly incorporated *Bythotrephes* as a main component of the diet after its introduction (Coulas *et al.*, 1998). In Lake Erie, yellow perch and white perch *Morone americana* Gmelin became more reliant on zooplankton, particularly *Bythotrephes*, after its arrival in the lake (Bur & Klarer, 1991).

The daily food requirements of the alewife across both dates greatly exceeded the daily production of *Bythotrephes* on both dates. In contrast, daily food requirements were <25% of daily production of all other species except large Chydoridae, the only other prey taxon for which consumption exceeded production, and Daphniidae. Although there are potential problems with our estimates of consumption and production, consumption by the alewife certainly has a major impact on *Bythotrephes* in nearshore areas of Lake Michigan. First, estimates of daily ration were similar between dates for both small and large alewives, despite some sample intervals when fish sample size was low. In addition, our estimates of

consumption are well below maximum consumption values for the alewife. Based on data from Stewart & Binkowski (1986), maximum consumption would be around 33–34% of body weight (dry) for small fish, and 20–23% for large fish, much higher than the 16–22% and 6–7%, respectively, that we calculated. Abundance estimates can also have a major impact on overall consumption estimates (Rand *et al.*, 1995). We only used acoustic estimates of fish density at night because they are more accurate than daytime estimates (Brandt *et al.*, 1991.). Both production and consumption estimates are sensitive to errors in parameter measurements, although our sensitivity analyses suggested that these errors were unlikely to change our main conclusion that alewives were controlling the abundance of *Bythotrephes*, but not of *Cercopagis*. There are also potential differences in production estimates depending on the equations used (Stockwell & Johannsson, 1997), but the choice of equations would probably not change our overall conclusions. Finally, the argument that alewives control *Bythotrephes* abundance in the nearshore is strengthened by the consistency of their importance in the diet, high overall and individual selection and high consumption of *Bythotrephes*.

Prior to the introduction of *Bythotrephes*, Evans (1990) argued that size-selective predation by fish limited the abundance of large-bodied zooplankton like *Daphnia* in nearshore areas. Water exchange between offshore and nearshore may explain why large zooplankton persist in nearshore areas during summer when fish predation is intense (Evans, 1990). Other studies also suggest that planktivory limits *Bythotrephes* numbers in the nearshore of Lake Michigan and may encourage earlier reproduction and increased production of resting eggs (Lehman & Caceres, 1993; Pothoven *et al.*, 2001, 2003).

In contrast to *Bythotrephes*, neither size class of alewives showed any preference for *Cercopagis* on an overall or individual basis. Vanderploeg *et al.* (2002) proposed that alewives would prefer *Bythotrephes* to *Cercopagis* because of the size difference between the two prey types and the heavier pigmentation of *Bythotrephes*; *Cercopagis* is quite transparent. *Cercopagis* was also a fairly minor part of the diet for alewives by weight and number, although it was eaten by about 30% of the large alewives. Recent diet studies in southeastern Lake Michigan indicated that *Cercopagis* is not a major prey item for alewives in Lake

Michigan, despite its high abundance in nearshore areas (Pothoven & Vanderploeg, 2004; Hondorp, Pothoven & Brandt, 2005). In Lake Ontario, *Cercopagis* became, and remains abundant despite being eaten by a large percentage of alewives (Bushnoe *et al.*, 2003). Furthermore, *Cercopagis* is generally not a preferred prey of alewives in Lake Ontario, as few were eaten despite their high abundance in summer (Thompson *et al.*, 2005). On the other hand, Antsulevich & Välipakka (2000) showed that *Cercopagis* was a preferred prey of 8–14-cm long Baltic herring (*Clupea harengus membras* Linnaeus) in the Gulf of Finland (eastern Baltic Sea), and Gorokhova, Fagerberg & Hansson (2004) showed that *Cercopagis* was a preferred prey of Baltic herring >5 cm and sprat (*Sprattus sprattus* Linnaeus) >10 cm in a western Baltic Sea bay.

The different predator impacts on *Bythotrephes* and *Cercopagis* may explain differences in the abundance of these two invasive zooplankton species in nearshore areas of Lake Michigan. Alternatively, *Cercopagis* could have higher birth rates than *Bythotrephes*, as suggested by higher parthenogenic brood sizes (seven versus four) in our sampling area (J. Cavaletto, unpublished). However, differences in birth rates do not explain the nearshore to offshore difference in the abundance of *Cercopagis* and *Bythotrephes*. *Cercopagis* is abundant in the shallow nearshore areas but not in deep-water further offshore (Vanderploeg *et al.*, 2002). In contrast, *Bythotrephes* abundance increases from nearshore to offshore (Pothoven *et al.*, 2001, 2003). *Bythotrephes* is capable of eating *Cercopagis* and could directly influence its distribution if encounter rate was high enough (Witt & Caceres, 2004). The two species could also compete for at least some of the same food resources (Vanderploeg, Liebig & Omair, 1993; Vanderploeg *et al.*, 2002; Laxson *et al.*, 2003). Therefore, the disproportionate predation of the alewife on *Bythotrephes* could have facilitated the success of *Cercopagis* in the nearshore of Lake Michigan. Further offshore, where *Bythotrephes* remains abundant, fish are less abundant (Brandt *et al.*, 1991) and other large-bodied prey, such as *Mysis relicta* Loven, are available to fish (Pothoven & Vanderploeg, 2004). Thermal stratification in the deeper water may also provide *Bythotrephes* with a refuge from fish (Coulas *et al.*, 1998).

If alewife numbers decreased dramatically, *Bythotrephes* abundance, particularly nearshore, might be expected to increase. However, previous declines in

the abundance of the alewife did not reduce predation demands on large zooplankton because the abundance of other fish species such as yellow perch increased (Evans & Jude, 1986; Evans, 1990). Yellow perch are capable of eating *Bythotrephes* once they are large enough to handle the spine (Baker, Tolentino & McComish, 1992). As a particulate feeder, yellow perch might be even more size-selective for large zooplankton than the alewife because the latter can also filter feed (Janssen, 1976; Evans & Jude, 1986). Therefore, fewer alewives might not necessarily lead to more *Bythotrephes* in nearshore areas (Evans, 1990).

Large prey taxa were preferred by both size classes of the alewife, and selectivity for Bosminidae, a small and by far the most abundant prey item, was extremely low. However, because of its enormous abundance, Bosminidae were eaten by nearly all of the small alewives and over half the large alewives and contributed substantially to the diet of both size classes of fish. Other studies have indicated that Bosminidae are eaten by alewives in Lake Michigan (Wells, 1970; Crowder, Magnuson & Brandt, 1981; Pothoven & Vanderploeg, 2004). Alewives may have used both their ability to particulate feed on large prey and to filter feed on a slow moving, abundant, and small prey like Bosminidae (Janssen, 1976, 1980; Drenner, Strickler & O'Brien, 1978).

The alewife invasion was been one of the most influential changes affecting Lake Michigan fish and zooplankton communities (Wells, 1970; Madenjian *et al.*, 2002). Our study indicates that the impact of the alewife is not limited to native species and that they can control the abundance of newly invasive species of zooplankton. The ability to use different feeding tactics may help explain the success of alewives in the Great Lakes and as long as they remain abundant in Lake Michigan, they will probably continue to structure the zooplankton community and affect the success of future zooplankton invasions.

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