

Food of the Alewife (*Alosa pseudoharengus*) in Lake Ontario before and after the Establishment of *Bythotrephes cederstroemi*

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Diets and length-weight relationships of Lake Ontario alewife (*Alosa pseudoharengus*) in 1972 differed from those in 1988; the large cladoceran *Bythotrephes cederstroemi* colonized the lake during the mid-1980's. Microcrustacean zooplankton were the dominant prey of alewife during April-October in 1972 and 1988. Although *Bythotrephes* was not found in 1988 net samples, it replaced other zooplankters in the alewife's diet. Typically, tailspines were the only part of *Bythotrephes* in alewife stomachs; their frequency was high in April-May, diminished rapidly in summer, and was very low by fall. In spring 1988, alewife 3165 mm were in better condition than in spring 1972, and this may have been due to larger fish feeding more heavily on *Bythotrephes*. Variation in diet among widely separated sampling sites was due to differences in alewife abundance, stability of thermal structure, progress of zooplankton community development, and distance to the mouth of the Niagara River (through which *Bythotrephes* probably enter the lake in summer and fall). In the Great Lakes, inter- and intralake differences in diet clearly exist, and these must be incorporated into models of alewife planktivory to gain an accurate understanding of energy flow between trophic levels.

Étant donné que le régime alimentaire et les relations longueur-poids du gaspéreau (*Alosa pseudoharengus*) du lac Ontario ont changé entre 1972 et 1988, on a tenté de déterminer si la colonisation du lac par le gros cladocère *Bythotrephes cederstroemi* vers le milieu des années 1980 était un facteur responsable. D'avril à octobre en 1972 et 1988, les microcrustacés zooplanctoniques étaient la principale proie du gaspéreau. Bien que *Bythotrephes* n'était pas présent dans les échantillons recueillis au filet en 1988, il a remplacé d'autres espèces de zooplancton dans le régime alimentaire du gaspéreau. Généralement, seules les épines de la queue de *Bythotrephes* étaient retrouvées dans l'estomac des poissons; leur fréquence était élevée en avril et mai, chutait au cours de l'été et était très faible en automne. Au printemps de 1988, les gaspareaux de 165 mm ou plus de longueur étaient en meilleure condition qu'au printemps de 1972; ceci peut être dû au fait que les gros poissons consommaient de plus grandes quantités de *Bythotrephes*. La variation du régime alimentaire entre les sites d'échantillonnage très éloignés l'un de l'autre était le résultat de différences entre l'abondance du gaspéreau, la stabilité de la structure thermique, le niveau d'évolution de la communauté zooplanctonique et la distance de l'embouchure de la rivière Niagara (par où *Bythotrephes* entre probablement dans le lac en été et en automne). Il existe manifestement dans les Grands Lacs des différences intralacustres et interlacustres du régime alimentaire, différences qui doivent être incluses dans les modèles de la planctivorie du gaspéreau si l'on veut comprendre le transfert d'énergie entre les niveaux trophiques.

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Lake Ontario was the first of the Laurentian Great Lakes invaded by the alewife (*Alosa pseudoharengus*). Alewife apparently entered Lake Ontario in the 1860's and have

been the dominant fish species there since the 1870's (Smith 1970; Christie and Thomas 1981). They are now an important food of introduced salmonines in Lakes Ontario (Brandt 1986; Elrod and O'Gorman 1991), Huron (Diana 1990), and Michigan (Eck and Brown 1985), and they are the basis of fisheries of considerable economic importance (Talhelm 1987).

In lacustrine systems, alewife are planktivores that readily supplement their diet of zooplankton with other foods such as

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fish eggs and larvae, insects, and amphipods (Ode11 1934; Hutchinson 1971; Kohler and Ney 1980; Wells 1980). In Lake Michigan, Hewett and Stewart (1989) considered about 65% of the diet (wet weight) of adult alewife to be zooplankton during April-October and the rest to be mostly *Mysis* and amphipods. In Lake Ontario, alewife food habits are well documented only for the Bay of Quinte (Hurley 1986); in the main lake, information on alewife food habits is scant (Pritchard 1929), although the fish's diet should be similar to that in Lake Michigan because the invertebrate fauna of the two lakes is similar. The colonization of the Great Lakes by the cladoceran *Bythotrephes cederstroemi* in the 1980's (Bur et al. 1986; Lange and Cap 1986; Sprules et al. 1990; Johannsson et al. 1991), however, has undoubtedly influenced the diet of the alewife. Because this exotic cladoceran is larger than endemic zooplankters, it is highly visible to predators, and because alewife are size-selective planktivores (Wells 1970; Warshaw 1972), *Bythotrephes cederstroemi* should be an important food for them. In central Lake Erie, consumption of zooplankton by yellow perch (*Perca flavescens*) nearly doubled after *Bythotrephes* became abundant (Bur and Klarer 1991). If the diet of alewife in the Great Lakes shifts similarly, predation on benthic macroinvertebrates would decline whereas predation on zooplankton would increase. This might influence productivity of alewife populations because a switch to more pelagic feeding would change the fish's daily temperature regime and thus food consumption and conversion efficiency (Stewart and Binkowski 1986). Such a shift in distribution might also alter the availability of alewife to predators.

The objective of this study was to determine if food habits and body condition of alewife changed with the colonization of Lake Ontario by *Bythotrephes cederstroemi*. We did this by comparing the diet and length-weight relationship of alewife in 1988 with that in 1972, prior to the establishment of *Bythotrephes* in Lake Ontario. Length-weight relationships can be influenced by fish abundance, so we also compared the magnitude and size structure of alewife populations in the two years. Because any effect of *Bythotrephes* on diet probably varies with season and lake region, we sampled alewife food habits over a broad range of depths at three widely spaced locations from spring through fall to compare spatial and seasonal patterns of alewife planktivory. To determine whether seasonal diet shifts were related to the occurrence of *Bythotrephes*, we attempted to track its abundance by periodically sampling zooplankton in south-central Lake Ontario.

Methods

Collecting Alewife for Food Habits

From May to October 1972, 490 alewife were collected for diet analysis by bottom trawling from the R/V *Kaho*. The fish were subsamples of catches at 33 stations, total depth 9-146 m, along three transects off Hamilton, Ontario, and Rochester and Oswego, New York (Fig. 1). In 1988, 761 alewife were collected for analysis by bottom trawling from the R/V *Kaho* along transects off Olcott, Rochester, and Oswego, New York. Catches were subsampled at 29 stations, total depth 15-110 m, from April to October. In 1972, only adult alewife (≥ 108 mm) were collected whereas in 1988, adult and subadult alewife (≤ 107 mm) were collected. The whole fish was preserved in 10% formalin after either injecting 10% formalin into the coelomic cavity (1972) or puncturing the coelomic cavity (1988).

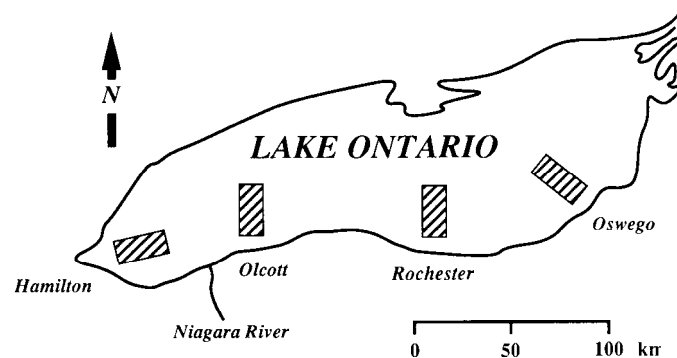


FIG. 1. Locations of sites where alewife were collected from Lake Ontario in 1972 and 1988. The Olcott site was not sampled in 1972, and the Hamilton site was omitted in 1988.

Assessing Alewife Abundance, Size, and Condition

Bottom-trawl nets towed by the R/V *Kaho* to collect alewife in 1972 and in 1988 were similar in dimensions and mesh sizes. Trawl doors differed between years, but the towing vessel and all trawling procedures (e.g. towing speed, warp to depth ratio) were virtually identical. Handling of the catch was also similar; adults and subadults were sorted on the basis of length and then counted separately. Therefore, we assumed that if the alewife catch rate in 1972 differed from that in 1988 ($P < 0.05$), it was due solely to a change in abundance. Catches were transformed by $\log_e(\text{catch} + 1)$ to help stabilize the variance and to normalize the data before comparing mean catches by using the general linear model program of SAS Institute (1988) to perform an analysis of variance (ANOVA). For this analysis, we used data from April-May only when alewife are closest to bottom (Elrod and O'Gorman 1991) and from only those depths and lake areas (Olcott, Rochester, and Oswego) that were fished in both years. Trawl tows that fit these criteria totaled 12 in 1972 and 23 in 1988.

In each sampling period in 1988, from 13 to 27 bottom-trawl tows were made in each of the three lake areas from which alewife were collected for diet analysis. The depth range fished varied among seasons but was always similar in the three areas in each season. To determine if adult alewife abundance differed between areas, the catches were \log_e transformed and the mean catches in each season were compared with ANOVA performed with a general linear model, followed by the Tukey-Kramer multiple comparison test (SAS Institute 1988). We could not determine if alewife abundance along the south shore of Lake Ontario differed among sampling periods because the availability of alewife to the bottom trawl changed with season (Elrod and O'Gorman 1991).

We measured (total length, nearest millimetre) a random sample of adult and subadult alewife from most trawl hauls in April-May in 1972 and 1988. Length samples from those depths and lake areas fished in both years were used to construct length-frequency distributions of adults ($n = 1352$ in 1972 and 860 in 1988) and subadults ($n = 32$ and 628). The distributions were compared by use of a Kolmogorov-Smirnov test (SAS Institute 1988).

A small sample of adult alewife from most trawl hauls was measured and weighed (nearest gram) at Olcott, Rochester, and Oswego in April-May and October in 1972 and 1988. Depth ranges fished in spring were 18-110 m in 1972 and 8-150 m in 1988, and depths fished in fall were 9-146 m and 8-150 m. We measured and weighed adults 125-200 mm in spring

($n = 230$ in 1972 and 321 in 1988) but only fish 150-179 mm in fall ($n = 174$ and 303). Fish were placed on ice soon after capture and weighed and measured within 30 h of capture. Lengths and weights were transformed by \log_{10} before calculating length-weight relationships. We used the homogeneity-of-slopes model of the general linear model program of SAS Institute (1988) to perform an analysis of covariance (ANCOVA) for each season. When the F value indicated that the slopes were not significantly different ($P > 0.05$), we used the ANCOVA model of the general linear model program (SAS Institute 1988) to determine if the intercepts differed.

Sampling Zooplankton

Zooplankton collections were made 2 and 20 km from shore at Smoky Point (20 km east of Rochester) and Oak Orchard (51 km west of Rochester) (Fig. 1). Collections were made in April, June, July, September, and October in 1987 and 1988 to document when *Bythotrephes cederstroemi* was abundant. Bottom depths were 22 and 206 m off Oak Orchard and 25 and 196 m off Smoky Point. Zooplankton abundance and composition were determined from vertical hauls with a 0.5-m-diameter, 153- μ m-mesh nylon net. Before each plankton haul, we determined temperatures in the water column with a mechanical bathythermograph. At the 2-km sites, the net was lowered to the lake bottom except when thermal stratification was strong, in which case the net was lowered to the top of the thermocline. For sites 20 km offshore, sampling was to a depth of 50 m or to the top of the thermocline if one was formed. Zooplankton were preserved in a sugar-formalin solution (Haney and Hall 1973).

Individual zooplankters were identified to species in all samples (Edmondson 1963; Balcer et al. 1984) and enumerated in one to three 1-mL subsamples. Immature zooplankters (neonates and copepodites) were also counted and measured in all subsamples. Because of their low density and high visibility, all *Bythotrephes* in each sample were counted.

Examining Alewife Stomach Contents

1972

Alewife total length (TL) was measured to the nearest millimetre, and contents of alewife stomachs were identified and counted at 15-30X. For some fish, all organisms in the stomach were counted, but for most fish, a subsample was counted. Water was added to the entire contents of an individual stomach to bring the total volume to 20-40 mL. After thorough mixing, a Hensen-Stemple pipette was used to withdraw 1-mL aliquots. The volume of the subsample examined was typically 2.5-20% of the total sample, and total numbers of organisms in the stomach were estimated from the subsample by direct proportion.

1988

Alewife were measured to the nearest millimetre (TL) as in 1972, but we followed a different procedure to estimate total stomach contents. Stomachs were removed and dissected into anterior and posterior segments. We counted only the contents of the anterior (dorsal) limb of the stomach because the contents of the posterior (ventral) limb were digested. Contents of the anterior stomach section were sorted; all microinvertebrates were removed, counted, and, when possible, measured at 20X. The remaining microinvertebrate fraction was subsampled as in 1972. At least two to three 1-mL aliquots were withdrawn from a known-volume dilution of the microinvertebrates. We identified (Balcer et al. 1984), counted, and measured all zooplankton in these subsamples by use of an electronic caliper

interfaced with a microcomputer (Mills and Confer 1986). Zooplankters were measured from the anterior margin of the helmet to either the base of the tailspine (cladocerans) or the base of the caudal setae (copepods). For macro- and microinvertebrates that were not intact, we found the number of organisms by counting characteristic body parts. For example, the only recognizable body part of *Bythotrephes* in alewife stomachs was the tailspine. *Bythotrephes* has a characteristic kink in its tailspine, and the number of *Bythotrephes* in alewife stomachs was based on counts of spines with the tailspine kink. The approach was similar for *Mysis relicta*; the number eaten was based on counts of characteristic paired eyes.

Contents of the anterior and posterior portions of each alewife stomach were dried separately at 60°C for 48 h and weighed to the nearest 0.01 mg on a Cahn electrobalance. We used the ratio of the dry weight to the number of organisms in the anterior limb to convert dry weight of the posterior limb to number of organisms. Numbers of organisms in the anterior and posterior limbs were combined to determine the total number of prey in an alewife stomach.

Analysis of Diet Data

We applied known length - dry weight regressions (Cornell University Biological Field Station, unpubl. data; Johannsson and O'Gorman 1991) to prey lengths to estimate the dry mass of prey items. When organisms were unmeasurable owing to breakage or digestion, we used average values for the same prey item from alewife examined in the same month at the same site. In 1972, prey organisms were not measured; we calculated the average biomass of individual prey for the various prey organisms at each transect in each month of 1988, and we applied these values to the 1972 organism counts to estimate prey biomass (for alewife collected at Hamilton in 1972, we used average biomass values from Olcott, the closest port).

When grouping fish for analysis, we used fish length (sub-adult: ≤ 107 mm, adult: ≥ 108 mm), month (April-May (April 20 - May 11), June (2-14), July (July 19 - August 1), September (8-22), October (16-31)) and trawl depth (shallow: 9-34 m, intermediate: 35-69 m, deep: 70-146 m).

The diet of alewife was characterized by numbers and biomass of prey in stomachs. Percent occurrence of prey types was calculated as the percentage of alewife with nonempty stomachs containing a prey type. For both years, we estimated wet weight (grams) of alewife in April-May and October by use of length-weight regressions. The regressions were calculated from lengths and weights obtained each spring and fall from alewife collected soon after capture or after they were held on ice overnight. Wet weights for June-September were estimated by linear extrapolation between spring and fall values. We calculated the relative prey biomass, defined as the prey mass eaten per gram of fish, by dividing dry prey mass by the estimated wet weight of the fish. In addition, for each individual, we calculated the percentage of the prey weight contributed by each prey type. To examine patterns of microcrustacean zooplankton consumption between sites, we included only fish for which microcrustaceans made up at least 75% of the prey biomass and only alewife captured at shallow and intermediate depths to avoid bias due to the lack of samples from deep trawls at Rochester and Oswego in 1972. To determine how alewife size affected macroinvertebrate consumption, we pooled trawls for which occurrence of the particular macroinvertebrate was highest.

Results

1972

Stomachs of 490 adult alewife (≥ 108 mm) were examined; 460 contained identifiable prey, 10 contained unidentifiable

TABLE 1. Functional groupings of the prey of alewife in Lake Ontario during April-October in 1972 and 1988. Organisms were identified to the taxonomic level indicated, and those that were numerically important are marked with an asterisk.

1972	1988
Microcrustacean zooplankton	
Small cladocerans	Small cladocerans
<i>Diaphanosoma</i> sp.	<i>Eubosmina coregoni</i> *
<i>Eubosmina coregoni</i> *	<i>Bosmina longirostris</i> *
<i>Bosmina longirostris</i> *	<i>Chydorus sphaericus</i>
<i>Chydorus sphaericus</i>	<i>Ceriodaphnia lacustris</i>
<i>Ceriodaphnia lacustris</i>	
Large cladocerans	Large cladocerans
<i>Daphnia</i> sp.*	<i>Daphnia galeata mendotae</i>
<i>Macrothricidae</i>	<i>Daphnia retrocurva</i> *
<i>Leptodora kindti</i> *	<i>Daphnia pulex</i>
<i>Holopedium gibberum</i>	<i>Leptodora kindti</i>
<i>Polyphemus pediculus</i>	<i>Holopedium gibberum</i>
<i>Ilyocryptus</i> sp.	<i>Polyphemus pediculus</i>
	<i>Bythotrephes cederstroemi</i> *
Calanoid/harpacticoid copepods	Calanoid/harpacticoid copepods
Harpacticoida*	Harpacticoida
Diaptomidae*	Diaptomidae*
<i>Limnocalanus macrurus</i> *	<i>Limnocalanus macrurus</i> *
<i>Eurytemora affinis</i> *	<i>Eurytemora affinis</i> *
Cyclopoid copepods	Cyclopoid copepods
<i>Diaicyclops thomasi</i> *	<i>Diaicyclops thomasi</i> *
<i>Mesocyclops edax</i>	<i>Acanthocyclops vernalis</i>
<i>Tropocyclops prasinus mexicanus</i>	<i>Mesocyclops edax</i>
	<i>Tropocyclops prasinus mexicanus</i>
Malacostracans	
<i>Mysis relicta</i> *	<i>Mysis relicta</i> *
Amphipoda*	Amphipoda*
Other prey	
Ostracoda	Ostracoda
<i>Pisidium</i> sp.	Rotifera
<i>Hydrocarina</i>	Coleoptera
Rotifera	Chironomidae*
<i>Ascellus</i>	Ephemeroptera
Bryozoa	
Mollusca	
Fish eggs	
Coleoptera	
Chironomidae*	
Ephemeroptera	

prey, and 20 were empty. Although we identified 31 food types in alewife stomachs (Table 1), only 12 items occurred frequently; they included nine species of microcrustacean zooplankton, *Mysis relicta*, amphipods, and chironomids.

Food habits of adult alewife

We grouped food of adult alewife into four prey types (zooplankton, mysids, amphipods, and other prey) and found that 73% of fish containing food consumed only one prey type (Table 2). Almost all alewife (91%) were eating one dominant prey type that contributed more than 75%, by weight, to their diet. Zooplankton and mysids were usually dominant prey types contributing the highest percentage of the weight in stomachs, amphipods were sometimes dominant but were more often sup-

TABLE 2. Numbers of adult alewife (out of 460 in 1972 and 611 in 1988) that ate mostly one prey type (100 or 75-99% of stomach contents by weight) in Lake Ontario during April-October in 1972 and 1988. Also shown is the mean percent of the weight in stomachs contributed by a prey type for alewife that ate that prey type.

Prey type	Weight in stomach		Mean percent of prey weight
	100%	75-99%	
1972			
Zooplankton	325	58	91
<i>Mysis</i>	4	16	86
Amphipods	4	8	42
Other ^a	2	2	18
Percent of all adults	73	18	
1988			
Zooplankton	338	42	77
<i>Bythotrephes</i>	14	58	62
<i>Mysis</i>	8	18	69
Amphipods	4	13	43
Other ^a	4	4	39
Percent of all adults	60	22	

^aInsects, ostracods, fish eggs, bryozoans, and mites.

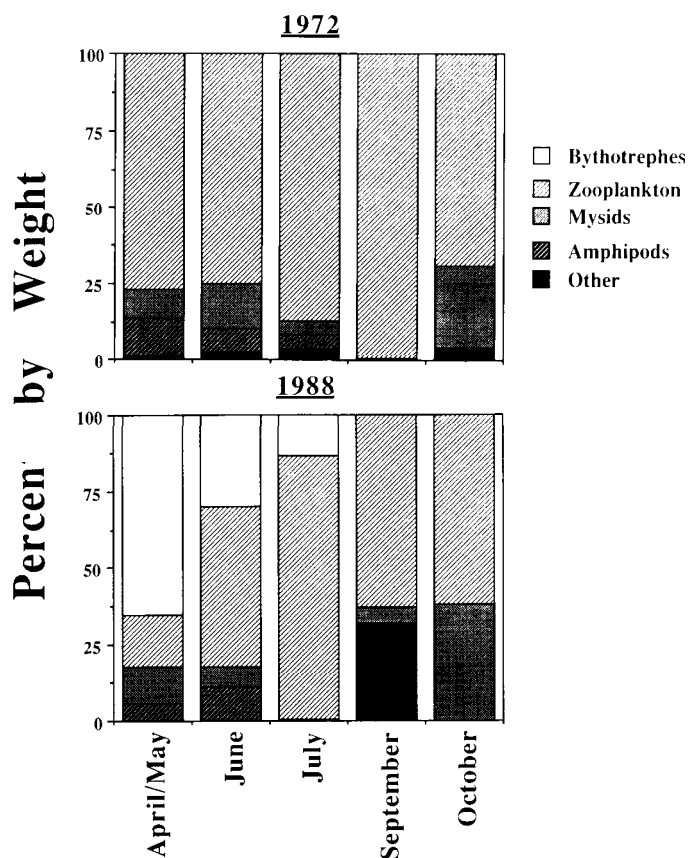


FIG. 2. Mean percent composition by weight contributed by *Bythotrephes* and other prey types to the diet of adult alewife in Lake Ontario, during April-October in 1972 and 1988 (one sample on August 1 included with July). Fish from all trawl hauls were pooled for each season; alewife in 1972 were captured off Hamilton, Rochester, and Oswego; alewife in 1988 were captured off Olcott, Rochester, and Oswego. The "other" category includes insects, ostracods, fish eggs, chironomids, bryozoans, and mites.

TABLE 3. Mean dry weight (mg) of prey eaten per gram wet weight of fish for adult alewife caught from Lake Ontario with bottom trawls in three depth ranges during April-October in 1972 and 1988. Also shown are the number of trawl hauls from which fish were examined and the number and mean total length of fish with identifiable prey in their stomachs.

Month	Trawl hauls <i>(N)</i>	Fish		Zooplankton		<i>Mysis</i>	Amphipods	Other”	Total
		<i>n</i>	mm	<i>Bythotrephes</i>	Other				
1972, <i>shallow (9-34 m)</i>									
April-May	3	18	162	0	0.05	0	0.01	<0.01	0.06
June	7	78	143	0	0.50	0	0	0.02	0.52
July	5	57	153	0	1.01	0	0.03	0.04	1.08
September	5	50	155	0	0.66	0	0.01	<0.01	0.67
October	3	27	153	0	0.28	0	<0.01	<0.01	0.28
1972, <i>intermediate (35-69 m)</i>									
April-May	3	31	153	0	0.07	0	0.01	<0.01	0.08
June	4	33	150	0	0.39	0.01	0	<0.01	0.40
July	3	17	148	0	0.70	0.02	0.01	0.03	0.76
September	3	16	162	0	0.47	0	0	0	0.47
October	4	39	159	0	0.26	0	<0.01	<0.01	0.26
1972, <i>deep (70-146 m)</i>									
April-May	3	22	155	0	0.01	0.58	0.09	0	0.68
June	2	15	171	0	0.11	1.44	0.25	0	1.82
July	1	9	144	0	0.27	0.05	<0.01	<0.01	0.32
September	2	20	144	0	1.00	0	0	0	1.00
October	1	10	173	0	0.05	1.01	<0.01	0	1.06
1988, <i>shallow (9-34 m)</i>									
April-May	0	0	-	-					
June	3	32	156	0.66	0.71	0	0	0	1.37
July	4	77	159	0.14	0.78	0	0	0	0.92
September	1	18	135	0	0.03	0	0	0.04	0.07
October	0	0	-	-			-		
1988, <i>intermediate (35-69 m)</i>									
April-May	3	38	156	0.84	0.42	0.12	0.01	<0.01	1.39
June	5	60	159	0.40	0.92	0.06	0.69	<0.01	2.09
July	5	85	160	0.09	0.75	0	0.01	<0.01	0.85
September	1	14	150	0	0.45	0.05	0.01	0.01	0.51
October	6	93	151	<0.01	0.79	0.01	<0.01	<0.01	0.80
1988, <i>deep (70-146 m)</i>									
April-May	6	82	151	1.07	0.06	0.21	0.20	0.01	1.54
June	1	13	160	0.47	1.23	0.39	<0.01	<0.01	2.09
July	0	0	-				-		
September	0	0	-	-			-	-	
October	3	50	149	<0.01	0.38	1.14	<0.01	<0.01	1.52

"Insects, ostracods, fish eggs, bryozoans, and mites.

plemental food, and other prey types were almost always supplemental.

Microcrustacean zooplankton dominated the diet of adult alewife during April-October, averaging 70% to nearly 100% of the mean percent composition of stomach contents by weight (Fig. 2). Nearly 30% of the diet of adult alewife by weight was *Mysis* in October, and 5-13% of the diet during April-August was amphipods.

Factors affecting alewife food habits

Depth-The most frequently observed prey items at shallow and intermediate depths from April through October were (in descending order) cyclopoid and calanoid copepods, small cladocerans, large cladocerans, and amphipods. Nearly 94% of all fish fed on cyclopoids during April-September, while calanoids

were more frequent in the diet during April-July at shallow and intermediate depths. In contrast, large and small cladocerans became more important in the diet in late summer and fall. In terms of dry weight of prey eaten per gram of alewife, zooplankton dominated all other groups at shallow and intermediate depths (Table 3). The mean percent composition by weight of each prey type showed similar results, with zooplankton making up 80-100% of the diet (Fig. 2). For adults collected in deep water, the prey biomass consumed per gram of alewife was predominantly *Mysis* (April-June and October) and microcrustacean zooplankton (July and September).

Transect location - Zooplankton biomass consumed by adult alewife differed among sites (Table 4). Through July, cyclopoid copepods (mostly *Diaptomus thomasi*) were gener-

TABLE 4. Mean dry weight (mg) of zooplankton eaten per gram wet weight of adult alewife (>75% of stomach contents by weight) at bottom depths <70 m at different locations in Lake Ontario during April-October in 1972 and 1988.

Month	F i s h (n)	Cladocerans ^a		Copepods		<i>Bythorephes</i>	Total
		Large	Small	Calanoid	Cyclopoid		
1972, Hamilton							
April-May	22	0	0	0.02	0.05	0	0.06
June	41	<0.01	<0.01	0.12	0.28	0	0.40
July	26	<0.01	0.01	0.10	0.96	0	1.07
September	20	0.55	0.05	0.01	0.45	0	1.06
October	29	0.27	0.01	0.05	0.15	0	0.48
1972, Rochester							
April-May	0						
June	39	0	<0.01	0.05	0.32	0	0.37
July	8	<0.01	0.01	<0.01	0.27	0	0.28
September	15	0.19	0.02	0.01	0.25	0	0.47
October	23	0.03	0.01	0.01	0.02	0	0.07
1972, Oswego							
April-May	22	<0.01	<0.01	<0.01	0.05	0	0.06
June	21	<0.01	0.01	<0.01	1.29	0	1.30
July	30	0.03	0.11	0.03	0.99	0	1.16
September	30	0.30	0.01	0.01	0.08	0	0.39
October	9	0.10	0.06	<0.01	0.06	0	0.22
1988, Olcott							
April-May	9	<0.01	<0.01	0.18	0.01	1.69	1.87
June	16	<0.01	0.01	0.03	0.44	0.48	0.97
July	59	0.01	0.02	0.01	0.60	0.25	0.89
September	0		-				
October	37	1.32	0 . 0 1	0 . 0 8	0.17	<0.01	1.59
1988, Rochester							
April-May	12	0	<0.01	0.04	0.11	0.38	0.53
June	34	<0.01	0.02	0.27	0.60	0.73	1.62
July	46	0.12	0.10	0.01	0.65	0.03	0.91
September	8	0.02	<0.01	0	<0.01	0	0.03
October	30	0.23	0.01	0.05	0.11	<0.01	0.39
1988, Oswego							
April-May	14	<0.01	<0.01	0.31	0.56	0.72	1.60
June	29	<0.01	0.18	0.01	1.06	0.39	1.64
July	56	0.24	0.12	0.05	0.38	0.05	0.84
September	13	0.11	0.01	0.15	0.16	0	0.44
October	23	0.08	0.01	0.01	0.02	<0.01	0.11

^aSpecies listed in Table 1.

ally the dominant zooplankton in alewife stomachs at depths <70 m at all sites. Small cladocerans (mostly bosminids) and large cladocerans (daphnids and *Leptodora kindti*) first became important in the diet at Oswego in July and at Rochester and Hamilton in September. At Oswego, microzooplankton biomass eaten was highest in June and declined steadily through October; at Hamilton, the contribution was highest in July and September, and at Rochester there was no clear peak and the microcrustacean biomass consumed per gram of fish was lower than at other transects.

Alewife size - To determine if larger adult alewife preyed more heavily on large cladocerans than did smaller adult alewife, we summarized *Leptodora kindti* consumption for three trawls (18, 27, and 46 m) made at Oswego on September 7, 1972. *Leptodora kindti* were eaten by 31 of 32 adult alewife

examined from these trawls. The 31 alewife ranged in length from 140 to 185 mm. They were grouped into five 10-mm length groups, and mean number of *Leptodora* eaten increased with fish length ($r = 0.88$, $n = 31$, $P = 0.001$). On average, alewife 140-149 mm had eaten 300 *Leptodora* whereas those 180-189 mm had eaten nearly 600.

1988

Twenty-six food items were identified in alewife stomachs in 1988, 11 of which were numerically important, including *Bythotrephes cederstroemi* (Table 1). Prey that were numerically important in 1972 were usually also numerically important in 1988. Zooplankters netted from the lake in 1988, however, did not include *Bythotrephes*. Exclusive of nauplii, 80-87% of the Lake Ontario zooplankton community during

April-October was *Diacyclops thomasi*, *Leptodiaptomus minutus*, *Acanthocyclops vernalis*, *Daphnia retrocurva*, and *Bosmina longirostris*. In 1987, *Bythotrephes* was found only in those zooplankton samples taken in October (densities at inshore and offshore sites were <1/L).

Food habits of adult and subadult alewife

Of 611 adult alewife examined, three contained unidentifiable prey and 46 were empty. Adult alewife usually ate only one prey type and almost always (82%) ate one dominant food type that contributed at least 75% of the fish's prey by weight (Table 2). As in 1972, zooplankton and *Mysis* were the dominant foods that contributed the highest percentage of the weight in stomachs. The third-highest contributor was *Bythotrephes*. Amphipods and other prey remained of secondary importance.

In 1988, *Bythotrephes* dominated the food of adult alewife by weight in April-May and declined after August (Fig. 2). This large cladoceran was no longer in alewife guts in September and October, at which time 30% or more of the diet of these fish was mysids and chironomids. Apparently alewife were able to find *Bythotrephes* in Lake Ontario in 1988, even though they were not abundant enough to be in our zooplankton samples.

Subadult alewife (150 examined) fed almost exclusively on microcrustacean zooplankton (Table 5). Of 125 subadult alewife with identifiable food, only one had eaten an amphipod and six had eaten chironomid larvae or pupae. *Bythotrephes* occurred in 8 of 31 subadult alewife in April-May and 5 of 56 subadults in June. The smallest alewife that ate *Bythotrephes* was 75 mm; all others were ≥ 91 mm.

Factors affecting alewife food habits

Depth - Microcrustacean zooplankton (cyclopoid and calanoid copepods, small and large cladocerans, and *Bythotrephes*, in that order) were numerically dominant in the diet of adult alewife collected at shallow and intermediate depths throughout 1988. An exception was the alewife from a single

trawl made in shallow waters in September, when the main food item was chironomids. For fish taken from deep water, cyclopoid and calanoid copepods, small cladocerans, *Bythotrephes*, and other large cladocerans occurred most often in alewife stomachs, in that order.

Microzooplankton, including *Bythotrephes*, dominated the biomass eaten per gram of alewife at all depths during April-June (Table 3). Thereafter, zooplankton other than *Bythotrephes* usually dominated at shallow and intermediate depths; *Bythotrephes* was a minor part of the biomass eaten in July and contributed virtually nothing in September-October. In deep water, *Mysis* accounted for most of the dry weight of prey eaten in October (Table 3), even though more fish ate microzooplankton.

To examine how *Bythotrephes* was incorporated into adult alewife diets, we performed chi-square tests on pooled data from 12 trawls (April-May and June, intermediate and deep trawls). *Mysis* and non-*Bythotrephes* zooplankton were usually not found together in the same fish ($P < 0.01$) possibly because the feeding modes for fish eating macro- and microzooplankton are different. Alewife were probably particulate-feeding on *Bythotrephes* because the presence of *Bythotrephes* in alewife stomachs was independent of the presence of *Mysis* ($P = 0.97$) and of the presence of non-*Bythotrephes* microzooplankton ($P = 0.52$).

Transect location - As in 1972, zooplankton biomass consumed per gram of alewife differed seasonally among sites (Tables 4 and 5). Considering only non-*Bythotrephes* biomass eaten by adult alewife, zooplanktivory at Oswego peaked in June and declined through October. At Rochester, zooplanktivory was highest in June and July whereas at Olcott, it was highest in October. Cyclopoid copepods were the dominant non-*Bythotrephes* microcrustaceans eaten by adults and subadults at all sites through June and at Rochester in July; small cladocer-

TABLE 5. Mean dry weight (mg) of prey eaten per gram wet weight of fish for subadult alewife caught from Lake Ontario with bottom trawls at three locations during April-October 1988. Also shown are the number of trawl hauls from which fish were examined and the number and mean total length of fish with identifiable prey in their stomachs.

Month	Trawl hauls (n)	Fish			Cladocerans ^a		Copepods			Other ^b
		n	mm	<i>Bythotrephes</i>	Small	Large	Cyclopoid	Calanoid	Harpacticoid	
<i>Olcott</i>										
April-May	3	5	89	0.33	0	0	0.05	0	0	0
June	3	27	92	0.09	<0.01	0.01	0.32	0.03	<0.01	<0.01
July	0	0	-	-	-	-	-	-	-	-
September	0	0	-	-	-	-	-	-	-	-
October	2	2	98	0	<0.01	0.41	0.02	0.19	0	0
Rochester										
April-May	3	10	82	0.02	0	0	0.27	0.07	0	0
June	3	17	89	0.06	0.01	<0.01	1.58	0.46	0	0.10
July	1	12	99	0	0.23	0.09	0.59	<0.01	0	0
September	0	0	-	-	-	-	-	-	-	-
October	2	7	91	0	0.01	0.50	0.37	0.12	0	0
Oswego										
April-May	3	16	89	0.46	<0.01	0	0.93	0.50	0	0
June	3	12	92	0.12	0.19	0.01	1.60	0.04	<0.01	0
July	1	2	92	0	0.23	0.13	0.27	<0.01	0	0
September	1	2	85	0	<0.01	0.05	0.05	<0.01	0	0.02
October	3	13	78	0	0.10	0.32	0.23	0.06	0	0

^aSpecies listed in Table 1.

^bAmphipods and chironomids.

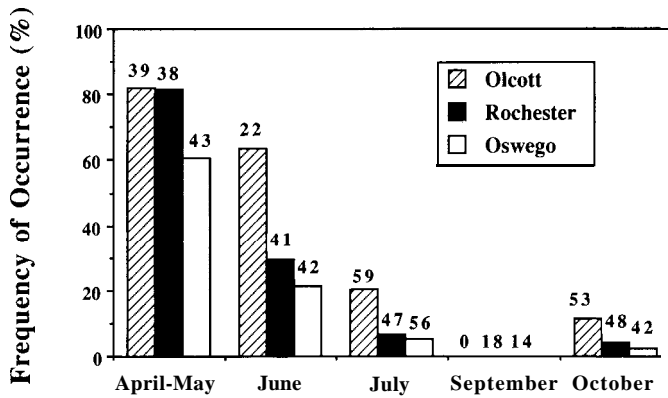


FIG. 3. Frequency of occurrence of *Bythotrephes cederstroemi* in stomachs of adult alewife at three locations in Lake Ontario during April-October 1988. Number of fish examined is above each bar.

ans became secondarily important at Oswego in June and at Rochester in July (Tables 4 and 5). Large cladocerans were the dominant prey of subadult fish at all sites in October.

Percent frequency of occurrence of *Bythotrephes* in adult alewife stomachs was consistently highest at Olcott, intermediate at Rochester, and lowest at Oswego (Fig. 3). However, the relative biomass of *Bythotrephes* eaten by alewife did not follow this site-to-site pattern through the season (Table 4). It was usually highest at Olcott, but the ranking differed by date at Rochester and Oswego.

Alewife size - To determine if alewife size was an important factor in the consumption of *Mysis*, amphipods, and *Bythotrephes*, we examined data from trawls where they were frequently eaten (Fig. 4). For seven deep trawls in April where *Mysis* were common prey, fish < 130 mm did not eat *Mysis*. Amphipods were consumed by 44 of 74 fish taken from five trawls (June) where their percent occurrence in fish stomachs was 50% or greater. Fish < 130 mm rarely ate amphipods; occurrence and median number consumed increased with fish length and were highest for the largest fish examined (160-169 mm). For *Bythotrephes*, we pooled 18 trawls made in April-May and June and found that this organism occurred in 50% of fish 90-109 mm (subadults) and in about 70% of fish > 110 mm. In general, the number of *Mysis* and *Bythotrephes* eaten increased with fish size and *Bythotrephes* was eaten by fish as small as 75 mm.

Alewife Abundance, Size, and Condition in 1972 and 1988

Abundance of adult alewife in 1972 was similar to that in 1988 (ANOVA of log_e-transformed trawl catches, $P = 0.33$) whereas abundance of subadult alewife in 1972 was lower than in 1988 ($P = 0.03$). Although adult alewife numbers were similar in both years, the fish were smaller in 1972 (Kolmogorov-Smirnov test, $P < 0.01$). The modal length group in 1972 was 140-149 mm, and 15% of the adults were ≥ 165 mm whereas in 1988 the modal group was 160-169 mm, and 21% of the adults were ≥ 165 mm. Lengths of subadults were not different ($P = 0.75$), although the small number measured in 1972 (32) precluded detection of all but the grossest of differences.

In 1988, abundance of adult alewife differed in the three lake areas we sampled. During April-June, catches of adults increased from Olcott eastward to Oswego (Table 6). After June, the west-to-east gradient in abundance disappeared, and the fish were equally abundant at Olcott and Oswego. At Rochester, adult abundance was variable after June and not similar to that in the other two lake areas.

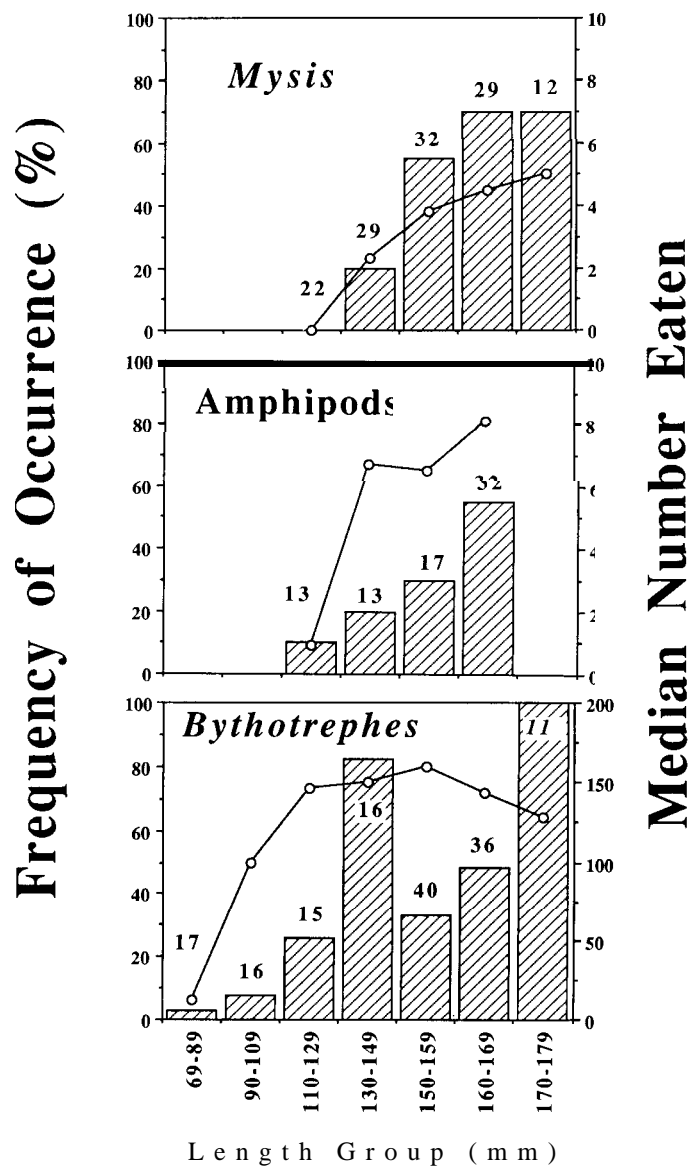


FIG. 4. For alewife caught where *Bythotrephes cederstroemi*, *Mysis relicta*, and amphipods were frequently eaten, the frequency of occurrence (line) of the three prey in alewife stomachs and the median number eaten (bar) by alewife in various length groups in Lake Ontario during April-October 1988. Number of fish examined is above each bar.

The slope of the length-weight relationship for adult alewife in spring 1972 was not as steep as the slope of the length-weight relationship in spring 1988 (ANCOVA, test for homogeneity of slopes, $P < 0.01$). The two regression lines intersected when alewife length exceeded 164 mm, so, on average, fish ≤ 165 mm were heavier in 1972, and those ≥ 165 mm were heavier in 1988. In fall, slopes of length-weight relationships for alewife 150-179 mm were similar ($P = 0.78$), but a significantly higher intercept in 1972 (ANCOVA, $P < 0.01$) indicated that the condition of the fish that fall was better than in fall 1988.

Discussion

Our findings indicate that colonization of Lake Ontario by *Bythotrephes* has led to a shift in the feeding ecology of the

TABLE 6. Mean numbers of adult alewife (antilogged means of the average \log_{10} -transformed catches) caught per 10-min tow with a bottom trawl in three areas of Lake Ontario during four sampling periods in 1988. For each sampling period, P values are from ANOVA performed with a general linear model on the \log_{10} -transformed catches, and means followed by the same letter are not significantly different (Tukey-Kramer multiple comparison test, $P < 0.05$).

Area	Sampling period			
	April-May	June	July	October
Olcott	148 z	134z	57 z	49 z
(n)	(23)	(17)	(19)	(17)
Rochester	484z	409 z y	11	249
(n)	(23)	(18)	(13)	(15)
Oswego	901 z	748 y	70 z	16 z
(n)	(27)	(14)	(17)	(20)
P	0.074	0.056	0.022	0.002

alewife. The shift, however, was not as we expected from macrozoobenthos to zooplankton, but rather the shift was within the zooplankton community. Benthic macroinvertebrates were as important in the April-October diet of alewife in Lake Ontario in 1988 as they were in 1972. *Mysis* and amphipods combined made up about 25% of the diet (wet weight) in spring and fall but < 10% in summer. Zooplankton made up the bulk of the diet in both years, but in spring 1988, the exotic cladoceran *Bythotrephes cederstroemi* was the most frequently eaten microcrustacean, contributing >60% of the food by weight. *Bythotrephes*, most likely because of its large size and visibility, was actively preyed on by adult and larger subadult alewife, and if it becomes premanently abundant in Lake Ontario, alewife would have a greater reliance on this organism than we demonstrated in this study.

Although *Bythotrephes* was first reported from the southwestern region of Lake Ontario in 1985, it was absent from plankton samples collected in other lake areas until fall 1987 (Makarewicz and Jones 1990; Johannsson and O'Gorman 1991; Johannsson et al. 1991; this study). *Bythotrephes* was not in plankton collections in 1988, yet we found them in abundance in the stomachs of alewife, leading us to conclude that alewife seek out these prey even if densities and encounter rates are low. Johannsson et al. (1991) attributed the abundance of *Bythotrephes* in 1987 to reduced alewife predation because numbers of adult alewife in spring 1987 were the lowest of any spring during 1985-88. But in spring 1990, adult abundance was equally low, and *Bythotrephes* failed to reappear (E. L. Mills and R. O'Gorman, pers. obs.). Perhaps a reduction in predation pressure for more than one summer is needed for substantial *Bythotrephes* recruitment to develop. (There is some evidence that the decline in alewife numbers noted in spring 1987 began in late summer 1986 whereas the downturn noted in spring 1990 most likely occurred in winter 1989-90.) Or perhaps unusually rapid warming of the lake in 1987 (Johannsson et al. 1991) worked in concert with reduced predation pressure and allowed a population to develop. In any event, if alewife numbers in Lake Ontario decline well below 1985-88 levels, *Bythotrephes* could redevelop, and alewife again would shift to feeding on it.

In Lake Ontario, tailspines were typically the only body part of *Bythotrephes* in alewife stomachs, and they were frequently found in a large bolus. Retention time for tailspines is unknown, but if it is longer than that for the body parts of other plankters, our estimates of importance of *Bythotrephes* to the diet of ale-

wife may be exaggerated (Gannon 1976). For example, the seasonal cycle of *Bythotrephes* in European lakes indicates that, in general, this zooplankter is rare in early spring (Sprules et al. 1990), yet we encountered the most spines in stomachs in April-May. We doubt that the spines were retained for months in alewife stomachs, even at the low water temperatures of winter, but we cannot completely eliminate that possibility. Alewife may also have been feeding on the spines of dead *Bythotrephes* that had settled to near bottom, or perhaps this organism concentrated near bottom. Evans (1988) found tailspines in the stomachs of deepwater sculpin (*Myoxocephalus thompsoni*) collected with bottom trawls at 91 m in Lake Michigan, and she hypothesized that the benthic sculpins were eating dead (and dying) *Bythotrephes*.

Incidence of *Bythotrephes* in alewife stomachs and its occurrence in the diet indicated a west-to-east gradient along the south shore of Lake Ontario during 1988. Its contribution to the alewife's diet declined from Olcott (nearest the Niagara River) to Oswego, indicating that abundance was highest in areas closest to the Niagara River. During April-June, this was probably due to differences in predation pressure as alewife numbers increased from Olcott eastward to Oswego. O'Gorman et al. (1991) demonstrated that spatial concentration of alewife in Lake Ontario can reduce the abundance of the largest zooplankters in a lake area. During July-October, there was no gradient in alewife numbers along the south shore, and we suspect that the gradient in *Bythotrephes* abundance was due to considerable numbers of them entering Lake Ontario from Lake Erie via the Niagara River. Of all the Great Lakes, Lake Erie appears to have the highest lakewide population of *Bythotrephes* (Jin and Sprules 1990), and abundance there usually peaks in summer and fall (J. H. Leach, OMNR, R.R. 2, Wheatley, Ont. NOP 2P0, pers. comm.).

As alewife grow longer, they eat larger prey items such as *Leptodora* and *Bythotrephes* more frequently and in greater numbers. Therefore, despite similar numbers of adults in 1972 and 1988, predation pressure on large zooplankters was greater in 1988 because adult alewife were longer in 1988 than in 1972. If the size structure of adult alewife in 1988 had been similar to that in 1972, *Bythotrephes* would have persisted longer in the lake and in the fish's diet. The notion that alewife size structure is one of the important determinants for establishment of populations of large cladocerans in Lake Ontario was first suggested by Johannsson et al. (1991). They showed that the dates when four species of large cladocerans first appeared in midlake during 1981-88 were more strongly correlated with the abundance of alewife ≥ 165 mm ($r = 0.84$) than they were with cumulative epilimnetic temperature ($r = -0.63$).

The ability of the longest alewife to eat large quantities of *Bythotrephes* and the availability of *Bythotrephes* from fall 1987 through spring 1988 may have been the reasons, in part, that the slope of the length-weight relationship for adult alewife in spring 1988 differed from that in spring 1972. In Lake Ontario, the slope of the length-weight relationship for adult alewife in spring is correlated with the number of adults caught (for 1978-90, excluding 1988: $r = -0.82$, $P < 0.01$; R. O'Gorman, unpubl. data). Yet, even though adult catches were similar in 1972 and 1988, the slopes of the length-weight relationships differed because alewife ≥ 165 mm were heavier in 1988. Furthermore, they were heavier even though they were more abundant, which indicates that the longest adults had access to more food resources in 1988 than they did in 1972. After spring, the contribution of *Bythotrephes* to the diet declined rapidly, and in fall, the slopes of the length-weight

relationships were similar, although the fish were lighter in 1988. This disparity was probably due to the much greater abundance of yearling alewife in 1988 and the resultant heavier predation pressure they exerted on the zooplankton community in summer and fall 1988.

Previous studies of alewife feeding have indicated that the diet is strongly influenced by lake thermal structure (Brandt 1980; Brandt et al. 1980; Janssen and Brandt 1980). Adult alewife are adept pelagic planktivores, particle-feeding on macrozooplankton as well as filter-feeding on microzooplankton, but are poor benthic feeders (Janssen 1976, 1978, 1980). Availability of benthic macroinvertebrates is seasonally variable and dependent on temporal and spatial overlap of predator and prey. Amphipods become active off bottom primarily during spring (Wells 1968). *Mysis relicta* prefers temperatures <6°C; it migrates inshore during winter and, as summer warming progresses, moves offshore, where it makes diurnal migrations from the lake bottom to the base of the thermocline (Beeton 1960; McNaught and Hasler 1966; Robertson et al. 1968; Carpenter et al. 1974; Balcer et al. 1984). In 1972 and 1988 in southern Lake Ontario, some alewife ate macroinvertebrates in spring, before a thermocline was firmly established, and in fall, as the thermocline underwent erosion. During the period of strong thermal stratification, the majority of alewife are epilimnetic (Olson et al. 1988; Elrod and O'Gorman 1991; Johannsson and O'Gorman 1991) and during this period, adult and subadult alewife in southern Lake Ontario fed on microcrustacean zooplankton.

Feeding habits of alewife appear to differ among Great Lakes populations. Modeling of alewife planktivory in Lake Michigan by Hewett and Stewart (1989) assumed that *Mysis* and *Pontoporeia* combined made up 25-45% of the adult diet (by weight) in summer and 0-25% of the yearling diet. Our results indicate that alewife use of high-energy macroinvertebrate prey is much lower in Lake Ontario, especially during thermal stratification. Predation pressure on the microzooplankton community, as well as consumption of microzooplankton by different age-classes of alewife and other fishes, is much higher in southern Lake Ontario than that predicted in Lake Michigan. In western Lake Ontario, however, where upwelling of cold bottom water is common and the thermocline is less firmly established, larger alewife may not always be separated from macrozooplankton by a strong thermal barrier during summer and fall. Alewife collected at Hamilton (western Lake Ontario) in 1972 seem to support this notion; they consumed *Mysis* as late as July. Consequently, because inter- and intralake differences in diet clearly exist, they must be incorporated into models of alewife planktivory to gain an accurate understanding of energy flow between trophic levels in each of the Great Lakes.

Microcrustacean zooplankton are low in caloric density relative to amphipods and mysids (Stewart and Binkowski 1986), but particle size is an important determinant of passage rate and digestibility; small particles such as microzooplankton have a much greater surface-to-volume ratio, so they digest rapidly. Bioenergetic models of alewife feeding have neglected the effect of particle size (e.g. Stewart and Binkowski 1986; Hewett and Stewart 1989), but this factor may provide a mechanism for optimizing foraging efficiency in order to maximize digestible-energy intake. If true, increased surface-to-volume ratio and passage rate of microzooplankton may allow alewife to compensate for their relatively lower energy content.

The patchy distribution of alewife and the fact that alewife were not collected synoptically could influence interpretation of site-to-site differences in planktivory. For example, fall col-

lections in 1988 were made first at the westernmost sites and up to 2 wk later at Oswego. Zooplankton abundance in Lake Ontario can change rapidly (Johannsson 1987), and spatially concentrated alewife can change the size structure of the zooplankton community (O'Gorman et al. 1991). During our study, however, some of the seasonal site-to-site differences, in microzooplanktivory appear to reflect different rates of zooplankton community development that are due to east-to-west temperature gradients in Lake Ontario (Patalas 1969, 1972; Johannsson 1987). In late spring or early summer, after the disappearance of the thermal bar (Rodgers 1965, 1987) prevailing northwesterly winds push warm surface water to the east, resulting in the earlier appearance of most species in the east, and a higher density of zooplankton in the eastern part of the lake in early to midsummer, declining by fall (Patalas 1969). Alewife zooplanktivory at Oswego reflected this seasonal pattern in 1972 and 1988. Czaika (1974) studied the nearshore zooplankton community in southwestern Lake Ontario from Port Weller to Rochester in 1972 and found that the density of most species peaked in September and October. In this study, alewife microzooplanktivory at Hamilton was higher than at Rochester or Oswego in September and October 1972 whereas in October 1988, microzooplanktivory was highest at Olcott. Differences in alewife abundance in different areas of the lake might also be expected to influence zooplankton density and thus zooplanktivory as reflected in the stomach contents. But in 1988 at least, alewife were not consistently concentrated in any lake area after spring, so site-to-site differences in microzooplanktivory were probably due to varying rates of zooplankton community development along the south shore.

Our results indicate that during summer and early fall, adult alewife prey wholly on microzooplankton, thus competing with subadults during the growing season. Although larger alewife are more likely to consume larger species of zooplankton such as *Leptodora kindti* and to retain larger plankters in general (MacNeill and Brandt 1990), there is considerable overlap in the sizes of zooplankton that are consumed by different life stages (O'Gorman et al. 1991). Competition for zooplankton food resources among adult, yearling, and young-of-year alewife is a strong possibility and probably influences alewife population dynamics (O'Gorman et al. 1987). Recent studies have indicated that the Lake Ontario zooplankton community has remained stable from the late 1960's to the mid-1980's (Johannsson 1987) despite decreased nutrient loading (Stevens and Neilson 1987) and increased stocking of salmonine predators (O'Gorman et al. 1987). Given the demonstrated dependence of all ages of alewife on microcrustacean zooplankton, continued reductions in nutrient loading and other factors that lower phytoplankton and zooplankton production will have a significant effect on both the alewife community and the salmonine population it supports.

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