

Diet and Prey Selection of Alewives in Lake Michigan: Seasonal, Depth, and Interannual Patterns

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Abstract.—To evaluate the current diet of alewives *Alosa pseudoharengus* and interactions with their prey in light of recent changes in Lake Michigan, we determined the seasonal diet and prey selectivity of large (>100 mm total length) and small (<100 mm) alewives in southeastern Lake Michigan. Selectivity and diet were evaluated on a biomass basis for alewives collected near Muskegon, Michigan, during June, July–August, and October 1999–2001. Fish were sampled from three depth zones: shallow (15–25 m), transitional (35–55 m), and deep (65–90 m). Prey selectivity and diet patterns indicated that alewives had considerable flexibility in adjusting to prey availability, which varied by season, depth zone, and year. Although small copepods were an abundant prey item throughout the year and in all depth zones, they were mainly important in the diet (large and small alewives) in June and at the shallow stations, where many of the other prey types were not available. Despite declining numbers, *Diporeia* continued to be important for large alewives in spring, particularly at the transitional and deep stations, where their biomass was many times higher than that of other prey. During summer, large alewives selected either *Bythotrephes longimanus* or *Mysis relicta* in all depth zones and years. The diet of large alewives consisted mainly of *Mysis* in July 1999 and August 2001, whereas in August 2000 mainly *Bosmina* were eaten. During October, *Mysis* and *Bythotrephes*, along with large zooplankters (*Daphnia* spp. and large calanoid copepods), were selected and were most important in the diet of large alewives. In contrast, only the large zooplankton were selected and were important prey for the small alewives in fall. Annual, seasonal, and depth differences in prey biomass as well as differences in alewife size all influenced diet and selectivity patterns.

The alewife *Alosa pseudoharengus* has greatly altered the food web of Lake Michigan since its arrival in the 1940s. Alewives have been implicated in changes in zooplankton populations (Wells 1970; Evans and Jude 1986; Evans 1990) and in declines of some native fish species (Wells and McLain 1973). An aggressive salmonine stocking program that has provided a valuable recreational fishery brought alewives under control (Madenjian et al. 2002). Currently, alewives predominate the diet of stocked salmonines and trout in Lake Michigan (Stewart and Ibarra 1991; Madenjian et al. 1998).

Alewife diet and consumptive demands in Lake Michigan were studied extensively from their arrival in the 1940s through the late 1980s (Wells 1980; Crowder et al. 1981; Rand et al. 1995). However, there are few recent data on alewife diet, even

though the ecology of Lake Michigan is constantly changing. Zooplankton species composition has changed considerably since the early 1980s, although crustacean biomass has remained relatively constant (Makarewicz et al. 1995; Madenjian et al. 2002). *Bythotrephes longimanus*, a nonindigenous, predatory cladoceran, became established in the lake in 1986 (Evans 1988) and is both a competitor with alewives (Lehman and Caceres 1993; Vanderploeg et al. 1993; Schulz and Yurista 1999) as well as a potential food source (Mills et al. 1992; Rand et al. 1995; Rivier 1998). Finally, the burrowing amphipod *Diporeia* spp., a seasonally important prey item for alewives (Rand et al. 1995), has been declining in Lake Michigan since 1992 (Nalepa et al. 2000).

Few studies have examined alewife feeding preferences in the field even though size-selective feeding by alewives has been implicated in declines of large-bodied zooplankton in the Great Lakes (Wells 1970; Evans 1990). However, most

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diet studies have not been designed to simultaneously examine alewife diet relative to prey abundance. Collection of diet and prey abundance data allows calculations of prey selection necessary for predicting food consumption and diet under varying prey availability scenarios (Vanderploeg and Scavia 1979; Lechowicz 1982; Vanderploeg 1994) and provides insight into the feeding patterns of alewives, as well as how this species can alter the abundance or composition of invertebrate communities. Considering the influx of nonindigenous species and the dynamic nature of Lake Michigan, it is becoming increasingly important to understand the relationship between alewives and their prey as fishery managers take a more holistic approach to balancing salmonine stocking rates and alewife stocks.

The first goal of this study was to evaluate the seasonal diet patterns of alewives in southeastern Lake Michigan during 1999–2001 along a near-shore-to-offshore transect. We expected that, compared with previous studies, *Bythotrephes* would now be an important part of alewife diet, although we did not expect major changes in the overall contribution of zooplankton. We also expected that alternative prey, such as *Mysis relicta* or zooplankton, would replace *Diporeia* in the diet. A second goal was to determine prey selectivity of alewives. We expected that large pelagic prey would be selected if they were available.

Methods

Field collections were made in southeast Lake Michigan near Muskegon, Michigan, during 1999–2001. We sampled in June and July 1999 and in June, August, and October 2000 and 2001. We sampled along a 15-km transect from nearshore to offshore at three depth zones: shallow (15–25 m), transitional (35–55 m), and deep (65–90 m). The transitional depth zone historically had the highest densities of *Diporeia* and is also the region where zebra mussels *Dreissena polymorpha* are expanding most rapidly (Nalepa et al. 2000, 2001).

Alewives were collected during daylight from each depth zone during each season with a 7.6-m semiballoon bottom trawl (13-mm stretch mesh cod liner). Subsamples of at least 30 alewives (if available) were immediately frozen upon capture. In the laboratory, alewives were measured (total length; mm) and their stomachs were removed and dissected. Diet analysis was done separately for small (<100 mm total length) and large (>100 mm) alewives. The size classifications generally

correspond with age-0 or yearling and adult alewives based on length frequency distributions.

All macroinvertebrate prey items (*Mysis* and *Diporeia*) and the large zooplankter *Bythotrephes* were removed from stomachs and counted, and the lengths of whole organisms were measured by means of a computer image-analysis system. Prey lengths of macroinvertebrates and *Bythotrephes* were converted to dry mass using weight–length regressions (Shea and Makarewicz 1989; Makarewicz and Jones 1990; T. Nalepa, Great Lakes Environmental Research Laboratory, personal communication). The dry weight of partially digested organisms that could not be measured was assumed to be equal to the mean weight of measured organisms. Paired eyes (*Mysis* and *Diporeia*) or bodies with eyespots (*Bythotrephes*) were used to enumerate partial prey items. All zooplankton in the diet other than *Bythotrephes* (e.g., Copepoda and Cladocera) were added to 10–25 mL of water and subsampled with a 1-mL Hensen–Stemple Pipette. Dilutions were chosen so that each subsample contained approximately 200 organisms. Zooplankton were classified as *Bosmina* spp., cyclopoid copepods, small calanoid copepods (<2 mm total length exclusive of caudal setae), *Daphnia* spp. (mostly *D. galeata mendotae*), other cladocerans, and large calanoid copepods (>2 mm). Mean individual weights for the most abundant taxa in each grouping were derived from Hawkins and Evans (1979) and multiplied by total counts to obtain the biomass of each zooplankton group in the diet of each fish. Biomass of each prey group was summed across all individual fish from each sample period and depth, and diet composition was estimated as the percent of the total calculated dry weight from each respective collection. Diet composition was compared across seasons, years, and depth zones using log-linear modeling. Alewife size within each size grouping was compared across seasons, years, and depth zones using a generalized linear model. All statistical analyses were performed using SYSTAT (SPSS 1998).

To evaluate prey availability, we collected zooplankton, *Mysis*, and *Diporeia* in conjunction with all fish collections. Invertebrates were sampled at a shallow (20 m), transitional (45 m), and deep (75 m) station to characterize prey biomass within each depth zone where fish were collected. Prey availability was expressed as biomass per unit area to allow comparisons of pelagic prey with *Diporeia* (a benthic prey) to provide for comparisons of prey biomass across depth zones and to account for the nonuniform distribution of animals through

the water column (Lehman 1991). Zooplankton were collected with triplicate vertical net tows at each station. Whole water column samples were taken from just above the bottom to the surface using a 0.5-m diameter plankton net (153- μ m mesh) during the day that fish were collected. Zooplankton were anesthetized with carbonated water and preserved in 4% sugar-buffered formalin. In the laboratory, zooplankton were added to 300–1,000 mL of water and subsampled with a 1-mL Hensen–Stemple Pipette so that at least 200 organisms were counted for each sample. Zooplankton were classified into the same categories used for diet analysis, and numbers were converted into biomass using the same mean individual weights that were used for diet analysis. All *Bythotrephes* in zooplankton samples were counted and measured (Pothoven et al. 2001), and was biomass determined using a weight–length regression (Makarewicz and Jones 1990).

Triplicate samples of *Mysis*, which can only be captured effectively at night, were sampled at each station during the night of the fish collections using a 1-m-diameter plankton net (1,000- μ m mesh) towed vertically from near the bottom to the surface at speeds of 0.5 m/s. *Mysis* were anesthetized with carbonated water and preserved in 4% sugar-buffered formalin. In the laboratory all mysids were counted and measured (Pothoven et al. 2000), and their biomass was determined using a weight–length regression (Shea and Makarewicz 1989). *Mysis* were assumed to be absent at the shallow station in 2000–2001, based on data collected in 1999, and because of limiting water temperatures at the bottom at the station (Shea and Makarewicz 1989). *Diporeia* were collected in triplicate at each station with a Ponar grab and washed through a 0.5-mm Nitex mesh net. Retained material was preserved in 5% formalin containing rose bengal stain. *Diporeia* were measured and their biomass was determined using weight-length regressions (T. Nalepa, Great Lakes Environmental Research Laboratory, personal communication). Biomass for each prey group was compared across seasons, years, and depth zones using a generalized linear model. A Bonferroni adjustment was used to account for the testing of multiple prey types that might not be independent, so *P*-values less than 0.006 were considered significant for prey biomass tests.

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

$$W'_i = (r_i/p_i)/(r_i/p_i)_{\text{pref}},$$

where relative prey abundance in the environment (p) and diet (r) were expressed in biomass units and $(r_i/p_i)_{\text{pref}}$ was the maximum value of r_i/p_i . 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 W' is near 1 and low when it is near 0. The selectivity coefficient, W' , is unaffected by prey abundance or whether abundance is expressed as numbers or biomass and is easily understood as the relative mortality imposed by the predator on different prey types (Vanderploeg and Scavia 1979; Vanderploeg et al. 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).

Results

Prey Biomass

In general, *Diporeia* had the highest available biomass in the environment, followed by small calanoid and cyclopoid copepods (Figure 1). The biomass of *Mysis* ($F = 6.5$; $df = 2, 34$; $P = 0.004$) and *Bythotrephes*, cyclopoid copepods, *Bosmina*, and *Daphnia* ($F > 13.8$; $df = 2, 56$; $P < 0.001$) differed across seasons but did not for *Diporeia*, other cladocerans, and large and small calanoid copepods. The biomass of *Mysis*, *Bythotrephes*, *Daphnia*, and *Bosmina* was highest in the summer or fall but was highest in the spring for cyclopoid copepods. The biomass of *Mysis* ($F = 7.1$; $df = 2, 34$; $P = 0.003$) and *Bythotrephes*, cyclopoid copepods, and *Bosmina* ($F > 7.1$; $df = 2, 56$; $P < 0.002$) differed across years, but that of all other prey groups did not. The availability of *Mysis* generally increased from 1999 to 2001 but decreased for cyclopoid copepods and *Bythotrephes* during the same period. The biomass of *Bosmina* was high in 2000 relative to 1999 and 2001. That of *Diporeia* ($F = 42.7$; $df = 2, 59$; $P < 0.001$), *Mysis* ($F = 15.6$; $df = 1, 34$; $P < 0.001$), cyclopoid copepods, small calanoid copepods, and *Daphnia* ($F > 18.6$; $df = 2, 56$; $P < 0.001$) differed across depth zones ($F > 4.74$, $df = 1$, $P < 0.01$), but biomass of other cladocerans, *Bythotrephes*, large calanoid copepods, and *Bosmina* did not. The biomass of *Diporeia*, *Mysis*, and *Daphnia* was highest at the deep station, and small calanoid and cyclopoid copepod

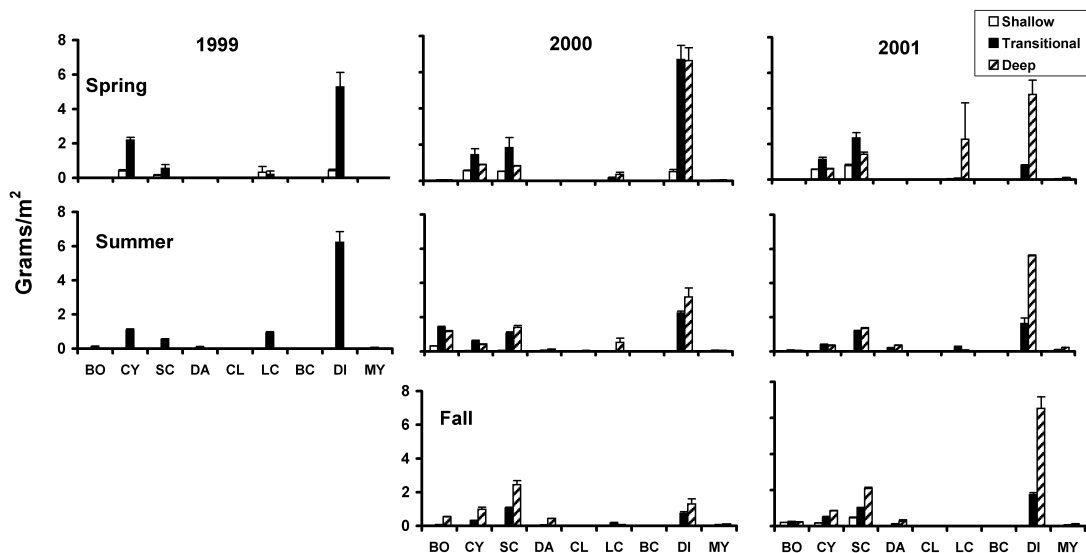


FIGURE 1.—Abundance (g/m^2) of prey groups consumed by alewives in southeastern Lake Michigan, by three depth zones (shallow [15–25 m], transitional [35–55 m], and deep [65–90 m]) in spring, summer, and fall 1999–2001. Prey types are ordered in increasing size from left to right, where B0 = *Bosmina*, CY = cyclopoid copepods, SC = small calanoid copepods, DA = *Daphnia*, CL = other cladocerans, LC = large calanoid copepods, BC = *Bythotrephes*, DI = *Diporeia*, and MY = *Mysis*. The thin vertical lines represent SEs.

biomass was higher at the transitional and deep stations than at the shallow station.

Alewife Diet

A total of 622 large and 172 small alewives that had food in their stomachs were used for diet analysis (Table 1). The size of large alewives varied across years ($F = 177$; $\text{df} = 2$, 685; $P < 0.01$), seasons ($F = 22$; $\text{df} = 2$, 685; $P < 0.01$), and depth zones ($F = 9$; $\text{df} = 2$, 685; $P < 0.01$). Large alewives were longer in 1999 and 2001 than in 2000. Alewives were also longer in the summer and at the deeper station. The size of small alewives also differed among years ($F = 9$; $\text{df} = 2$, 178; $P < 0.01$) and seasons ($F = 18$; $\text{df} = 1$, 178; $P < 0.01$) but not depth zones ($F = 2$; $\text{df} = 2$, 178; $P = 0.20$). Small alewives were longer in the spring than in the fall and in 1999 than in 2001.

Log-linear modeling indicated that year, season, and depth zone were all required to describe the variation in diet composition for both large and small alewives ($\chi^2 > 17$, $\text{df} = 2$, $P < 0.01$). During June, cyclopoid and small calanoid copepods contributed most to the diet of large alewives in the shallow zone each year, although *Diporeia* also contributed to the diet in 2001 (Table 1). In the transitional and deep zones, *Diporeia* were consistently a major part of large alewife diet each year during June; small zooplankters and *Mysis*

made substantial contributions in some instances. In the summer, small copepods and *Diporeia* made only minor contributions to large alewife diet, and *Mysis* were mainly eaten in summer 1999 and 2001 and *Bosmina* in 2000. *Bythotrephes* accounted for about a quarter of the diet in the transitional zone in August 2000. During October, large alewife diet consisted mainly of small zooplankters and *Daphnia* in the shallow zone (2001). In the transitional and deep zones, the diet was more varied, mainly consisting of large calanoid copepods, *Mysis* and *Daphnia* in 2000 and *Mysis* in 2001. The diet of small alewives was somewhat similar to that of large alewives in the June, when the diet consisted mainly of cyclopoid copepods and *Diporeia* (1999) or small calanoid copepods (2000; Table 1). Large calanoid copepods in 2000 and *Daphnia* in 2001 predominated the diet of small alewives in the October, but in contrast to large alewife, *Mysis* were rarely eaten.

Alewife Selectivity

During June in the shallow zone, large alewives selected small zooplankton each year (*Bosmina*, cyclopoid or small calanoid copepods; Figure 2). Diet selectivity varied at the transitional and deep zones during spring (e.g., large alewives strongly selected the largest prey, *Mysis*, in 1999 and 2001 and the smallest prey, *Bosmina*, in 2000). During

TABLE 1.—Diet of small (<100 mm total length) and large (>100 mm) alewives (percent dry weight) for three depth zones (shallow [15–25 m], transitional [35–55 m; trans.], deep [65–90 m]) and three sampling periods (spring, summer, fall) in Lake Michigan during 1999–2001; *N* = number of fish with food in their stomachs; TL = average length of alewives for each period.

Date	Depth zone	<i>N</i>	TL (mm)	<i>Bosmina</i>	Cyclopoids	Small calanoids
Small						
Jun 1999	Shallow	61	76	1	97	1
Jun 1999	Trans.	36	79	<1	44	<1
Jun 2000	Shallow	8	95	6	16	78
Oct 2000	Trans.	29	76	8	<1	1
Oct 2000	Deep	21	71	2	0	1
Oct 2001	Shallow	17	70	<1	18	29
Large						
Jun 1999	Shallow	17	160	<1	73	21
Jun 1999	Trans.	56	162	<1	45	5
Jun 2000	Shallow	23	119	15	39	46
Jun 2000	Trans.	7	118	15	9	19
Jun 2000	Deep	56	121	8	12	21
Jun 2001	Shallow	29	144	<1	13	31
Jun 2001	Trans.	28	136	<1	1	5
Jun 2001	Deep	28	145	<1	<1	<1
Jul 1999	Trans.	26	185	<1	<1	<1
Aug 2000	Shallow	39	116	73	<1	<1
Aug 2000	Trans.	103	132	58	2	5
Aug 2000	Deep	60	143	70	<1	<1
Aug 2001	Trans.	6	164	<1	0	<1
Aug 2001	Deep	8	151	<1	1	<1
Oct 2000	Trans.	30	129	<1	<1	<1
Oct 2000	Deep	32	132	1	0	1
Oct 2001	Shallow	8	123	9	16	41
Oct 2001	Trans.	36	140	<1	5	12
Oct 2001	Deep	30	140	<1	<1	<1

summer, large alewives strongly selected either *Bythotrephes* or *Mysis* across all depth zones and years. *Daphnia* were selected during October in the shallow zone (2001), whereas in the transitional and deep zones (2000 and 2001), *Mysis*, large calanoid copepods, and *Bythotrephes* were all selected. Small alewives selected small zooplankton (*Bosmina*, cyclopoid and small calanoid copepods) in the spring and large zooplankton (large calanoid copepods or *Daphnia*) in the fall (Figure 3).

Discussion

The diet of alewives in 1999–2001 was fairly similar to the diet that has been observed since the 1960s (Wells 1980; Crowder et al. 1981; Hewett and Stewart 1989; Rand et al. 1995). Specifically, the diet was predominated by small copepods in the spring, larger cladocerans becoming more important in late summer and fall. *Diporeia* continued to be an important prey item for large alewives into late spring. There was some evidence that the importance of *Mysis* in the diet in summer may have increased over time (Hewett and Stewart 1989; Rand et al. 1995), but other factors, such as

alewife size, can affect the importance of *Mysis* as a prey.

One important change in alewife diet over time was the increasing importance and selection of the invasive zooplankton *Bythotrephes*, which was first found in Lake Michigan in 1986 and whose numbers have remained fairly stable through 2001 (Pothoven et al. 2001) even though adult, yearling, and young-of-year alewives began eating this new prey soon after its arrival (Rand et al. 1995; Branstrator and Lehman 1996). Currently, *Bythotrephes* appears to be strongly selected by adult alewives but not juveniles. The long tail spine of *Bythotrephes* prevents ingestion by very small fishes (about 4 cm), and the aversion to ingestion of *Bythotrephes* decreases with increasing fish size (Barnhisel and Harvey 1995; Branstrator and Lehman 1996). The selection of *Bythotrephes* by large alewives is not surprising because *Bythotrephes* is also an important food source for fish in its native environments (Coulas et al. 1998; Rivier 1998).

Bythotrephes is only available as a food source during midsummer through late fall, but during that period they may alleviate some predation pressure on other preferred prey such as *Mysis*. *Bytho-*

TABLE 1.—Extended.

Date	<i>Daphnia</i>	Other cladocerans	Large calanoids	<i>Bythotrephes</i>	<i>Diporeia</i>	<i>Mysis</i>
Small						
Jun 1999	0	0	0	0	0	0
Jun 1999	0	0	5	0	49	1
Jun 2000	0	0	0	0	0	0
Oct 2000	4	0	87	0	0	0
Oct 2000	4	0	93	0	0	0
Oct 2001	52	0	0	<1	0	0
Large						
Jun 1999	0	0	2	0	4	0
Jun 1999	<1	0	28	0	18	4
Jun 2000	0	0	0	0	0	0
Jun 2000	0	0	0	0	57	0
Jun 2000	<1	0	12	0	47	<1
Jun 2001	6	0	<1	0	49	0
Jun 2001	2	0	10	0	32	50
Jun 2001	<1	0	0	0	67	32
Jul 1999	1	0	1	6	6	85
Aug 2000	<1	3	0	9	1	13
Aug 2000	2	2	0	26	3	2
Aug 2000	5	0	1	7	15	2
Aug 2001	1	0	0	<1	2	96
Aug 2001	5	0	0	12	7	74
Oct 2000	7	0	51	2	1	38
Oct 2000	25	0	43	2	2	26
Oct 2001	33	0	0	0	0	0
Oct 2001	3	0	0	2	0	78
Oct 2001	<1	0	0	<1	1	99

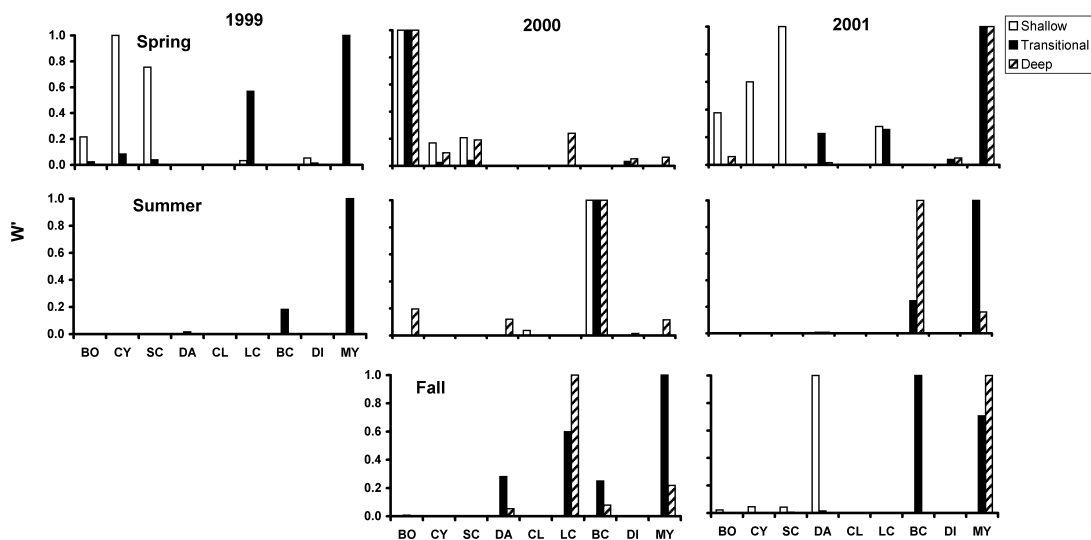


FIGURE 2.—Prey selectivity (W') by large alewives (>100 mm total length) captured from three depth zones (shallow [15–25 m], transitional [35–55 m], and deep [65–90 m]) of southeastern Lake Michigan in spring, summer, and fall 1999–2001. See Figure 1 for abbreviations.

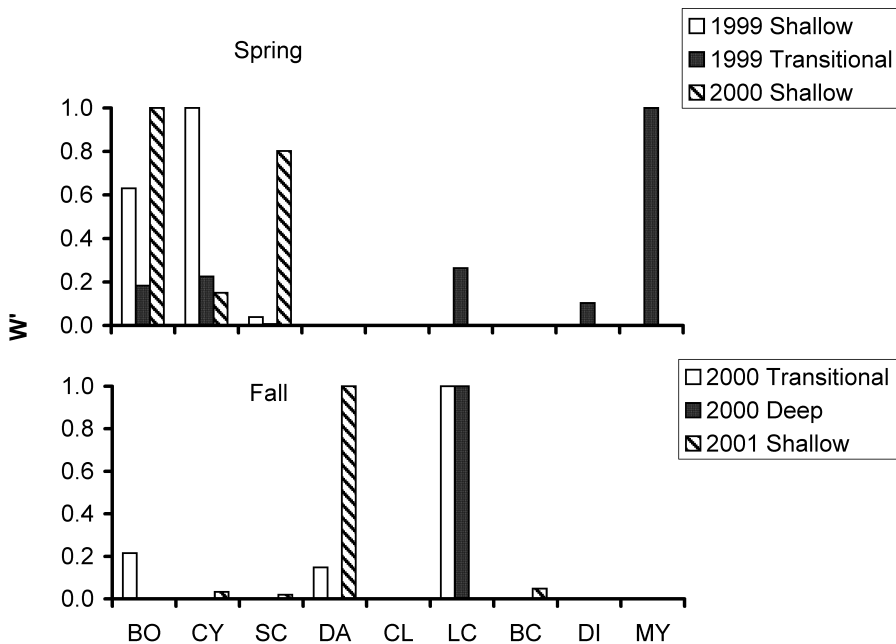


FIGURE 3.—Prey selectivity (W') by small alewives (<100 mm total length) captured from three depth zones (shallow [15–25 m], transitional [35–55 m], and deep [65–90 m]) of southeastern Lake Michigan in spring and fall 1999–2001. See Figure 1 for abbreviations.

*trephe*s may also provide an alternative to large-bodied zooplankters as a food source until alewives are large enough to consume *Mysis*, approximately age 3 for alewives in Lake Michigan (Hewett and Stewart 1989). For example, *Bythotrephes* were strongly selected and most important as a diet item in August 2000 when age 2 alewives predominated the population (S. Pothoven, unpublished data). In 1999 and 2001, when adult alewives were larger, *Mysis* were generally a more important prey type. Alewife predation on *Bythotrephes* may also indirectly reduce predation by *Bythotrephes* on small and large cladocerans (Vanderploeg et al. 1993). Most studies in the Great Lakes suggest that alewives play an important role in controlling abundance of *Bythotrephes* (Makarewicz and Jones 1990; Makarewicz et al. 1995; Vanderploeg et al. 2002), which is consistent with the strong selection we noted for *Bythotrephes*. This latter effect may be very important because Lehman and Branstrator (1995) estimated that 75% of the secondary production of daphnids was lost by adding *Bythotrephes* to the food web.

Alewives are a behaviorally flexible species that can switch feeding tactics to match the available prey resources and prey preferences (Janssen 1980; Janssen et al. 1995). For example, during

spring in the shallow zone, both small and large alewives tended to focus on small copepods, and the change in the environment from predominantly cyclopoid to calanoid copepods was also reflected in diet and selectivity patterns. However, the consumption of small copepods that we observed may have been related at least partly to the low abundance or absence of the other prey that were often preferred by alewives. For example, both size-classes of alewives were farther offshore in the springs of 1999 and 2000, and generally had strong selection for *Mysis* or large zooplankton, despite higher biomass of small copepods at the deeper sites. After June, selectivity for small copepods was low, and they were not a major diet item for either size-class of alewives. The change from copepods to other prey during the year and at deeper sites may reflect higher abundance of more preferred prey at the deeper sites and during the summer and fall. However, the change cannot entirely be separated from the fact that cyclopoid abundance decreased over the year, although small calanoid abundance did not vary seasonally. It seems unlikely that the change in high selectivity from copepods to other prey types is related to escape ability because *Mysis* and large copepods have more rapid escape responses than small copepods

(Drenner et al. 1978; Link 1996; H. Vanderploeg, unpublished data). Other factors may include a general preference for larger prey types or differences in energy content of the prey.

Although large alewives often tended to select less abundant, large prey types, the smallest prey type, *Bosmina*, was selected (June) and contributed a large fraction of the diet (August) in all depth zones in 2000. *Bosmina* are less motile than small copepods (Drenner et al. 1978; Link 1996), so alewives might be more likely to utilize the abundant *Bosmina* rather than small copepods. *Bosmina* have historically been eaten by alewives in Lake Michigan (Wells 1970; Crowder et al. 1981) and were selected by alewives in inland Adirondack lakes (Hutchinson 1971). However, a study in Lake Ontario found that alewives avoided *Bosmina* (Strus and Hurley 1992). The importance of *Bosmina* as a prey type in 2000 appears related to their high abundance, although the smaller overall size of adult alewives in 2000 may have also been a factor.

Alewives have been implicated in declines of *Daphnia* spp. and large calanoid copepods in Lake Michigan (Wells 1970; Evans and Jude 1986; Evans 1990). Size-selective predation by juvenile alewives during late summer and early fall may be the main factor behind planktivory-driven changes in zooplankton populations (Crowder et al. 1987; Hewett and Stewart 1989). This is consistent with our finding that small alewives selected large zooplankters (*Daphnia* and large calanoid copepods) in the fall, even though other prey types were more abundant. Although in some instances large alewives selected large zooplankters in the fall, they also selected other large-bodied prey (*Bythotrephes* and *Mysis*) that small alewives did not.

Although most prey of alewives are pelagic, the benthic amphipod *Diporeia* was an important part of the diet of adult alewives in June. Alewives do not feed efficiently on the lake bottom (Janssen et al. 1995) and they mainly consume *Diporeia* in the spring when the species is in the water column (Mills et al. 1992). Recently, *Diporeia* populations began to decline dramatically in Lake Michigan (Nalepa et al. 2000). However, we did not see any consistent decrease in the importance of *Diporeia* as a diet item over the course of this study, even though during this period *Diporeia* declined by 100% in the shallow zone (none found) and by 85% in the transitional zone. If *Diporeia* completely disappear, alewives will probably be forced to increase consumption of *Mysis* or subsist on diets composed of small copepods during winter

and spring (Hewett and Stewart 1989; Rand et al. 1995), which could affect growth, condition, and recruitment. Recent declines in condition of alewives may be linked to declines of *Diporeia* in Lake Michigan (Madenjian et al. 2002).

A potential problem with selectivity results is that fish and zooplankton are spatially patchy. As a result, what is observed in a zooplankton sample is not necessarily what is available to fish (Janssen 1980). However, the fairly consistent selectivity patterns across years provide some measure of power to our observations. Another potential problem is that differential gut passage rates could bias selectivity calculations (Gannon 1976). However, doubling the biomass of zooplankton eaten, which would simulate the effects of higher consumption of smaller prey due to faster digestion rates, did little to affect selectivity patterns. A related potential problem is that *Bythotrephes* spines may accumulate in fish stomachs (Branstrator and Lehman 1996). Because we only counted intact individuals or bodies, we used a conservative approach to evaluate the importance of *Bythotrephes* in the diet. Size-selective feeding within a prey group (Hutchinson 1971) could also affect our calculations somewhat because there could be differences in selectivity for the smallest and largest prey within our relatively broad prey categories. Finally, our diet results are biased toward daytime feeding patterns. However, because adult alewives feed heavily on *Mysis* at night (Wells 1980; Janssen and Brandt 1980), nighttime diet results would probably only corroborate our daytime results indicating the importance of *Mysis* in the diet.

The ability of alewives to use multiple feeding tactics may explain why this species has persisted in the changing environment of the Great Lakes since its arrival in the 1940s. Our results indicate that annual, seasonal, and depth zone differences in prey biomass and composition influence alewife diet. Additionally, differences in alewife size and age-structure affect diet and selectivity patterns. Changes in prey availability over time or water depths and alewife population structure need to be considered to accurately describe alewives in a food web context.

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