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DISTRIBUTION, ABUNDANCE, AND BIOLOGY OF THE ALEWIFE IN U.S. WATERS OF LAKE SUPERIOR

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Abstract. Alewives (Alosa pseudoharengus) were first reported in Lake Superior in 1954 and gradually increased in abundance in the late 1950s. In the 1960s and early 1970s, the fish were widespread in the lake but scarce. We determined the more recent abundance and distribution of alewives by cross-contour trawling in the spring in 1978-1988. Alewives were scarce lake-wide; the mean catch rate was only 23 fish per 100 h of trawling and represented a density of 0.003 kg per hectare in the area swept by the trawls. Fish of six age groups were caught in trawls in spring and gill nets in fall in 1983-1987. Total annual mortality was 64%, a high natural rate in the absence of fishing. Alewives in Lake Superior were small at the end of their first growing season but later grew faster than those in the other Great Lakes. Fecundity, estimated to be 64,000 eggs (mean total length = 187 mm) was higher than in other freshwater stocks. Zooplankton was the major food of alewives < 100 mm long and Mysis was the main food of larger fish. Exposure to water temperatures below lethal minimums for overwintering fish and for developing eggs limits the success of this species in Lake Superior.

INDEX WORDS: Alewife, Lake Superior, fish growth, fish diet, fish establishment.

Introduction

The biology of alewives *(Alosa pseudoharengus)* in the Great Lakes and the ecological effects of this species on the lake ecosystems have been widely documented. Selective predation by alewives altered the species and size composition of Lake Michigan zooplankton (Wells 1970). Large and expanding alewife populations in Lake Michigan, Huron, and Ontario have been implicated in the decline of several native fish species (Smith 1970, Crowder 1980, Eck and Wells 1987). Massive summer die-offs of alewives that fouled Lake Michigan beaches during the mid-1960s required costly removal and reduced the lake-based tourist trade (Brown 1972).

In Lake Superior, alewives were first collected in 1954 (Miller 1957). The initial collections were made independently in Whitefish Bay and the Apostle Islands, two areas widely separated geographically (Fig. 1), and indicated that the species probably entered the lake much earlier. However, in contrast to their abundanced in the other Great Lakes, alewives remained scarce in Lake Superior and did not become an important member of the fish community. Consequently, little is known about their biology and distribution. We here provide the first compilation of information on the life history of alewives in Lake Superior.

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Methods

Information on the abundance and distribution of alewives in 1954-1971 was determined from published and unpublished records of commercial and experimental fishing conducted by federal, state, and provincial natural resource agencies. Data on the biology, relative abundance, and distribution of alewives in 1978-1988 were obtained from cross-contour bottom trawling as part of the forage stock assessment program of the National Fisheries Research Center —Great Lakes.

Trawling was done in May and June from 1978 to 1988 at 53 stations spaced about 25 km apart along the U.S. shore from Grand Portage, Minnesota, to Sault Saint Marie (Fig. 1). In 1982, no trawling was done from Whitefish Bay to Keweenaw Point, Michigan. Tows were made with semi-balloon bottom trawls (11.9-m headrope, 15.6-m footrope, 12.7-mm stretched mesh cod end) towed at a speed of 4.3 km/h. Three cross-contour replicate tows were made at each station. At each station the tows began at the 15-m depth contour and ended after reaching the maximum depth obtainable within 1 h of towing. Because of the variation of the depth and slope of the near-shore zone, maximum ending depths ranged from 35 to 142 m and averaged about 66 m. All alewives captured were counted and measured (total length in mm), and in 1983-1987 all specimens were frozen for later determination of age, diet, and maturity. Catches at individual sampling stations in seven distinct geographic areas were combined and expressed as the mean number of alewives per 100 h of trawling. Biomass (kg/ha) was estimated by dividing the weight of alewives caught by the area swept by the trawls. Additional alewives for diet, maturity, and age determination were obtained from catches in graduated mesh gill nets (25, 51, 57, 64, 76, and 88-mm stretched measure) fished in September 1983, October 1984, and September 1986 in western Wisconsin waters from the Apostle Islands to Duluth, Minnesota (Fig. 1).

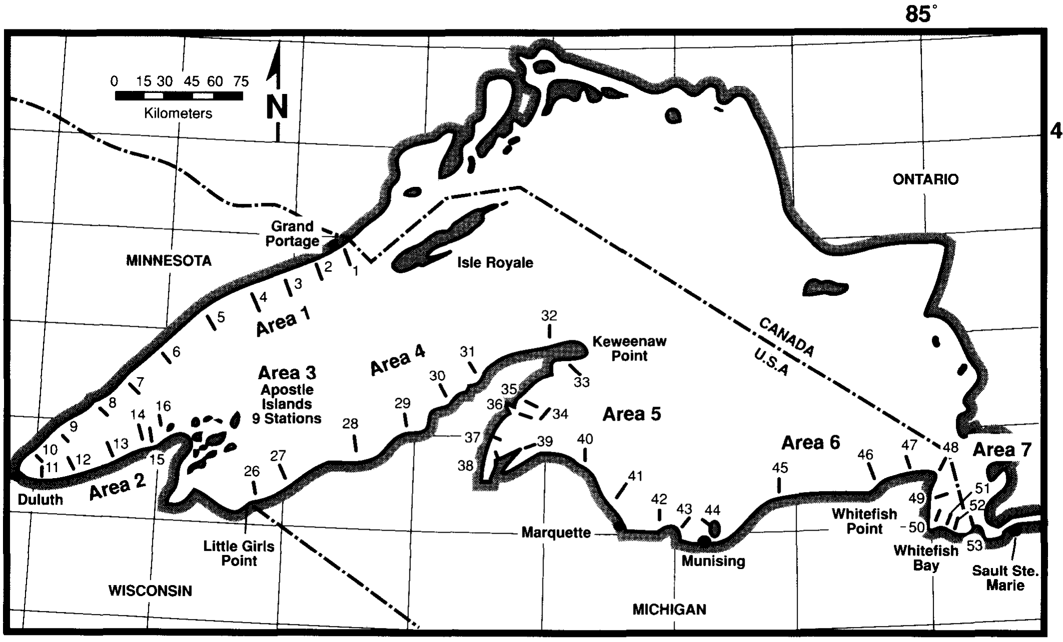

FIG. 1. Locations of annual cross-contour trawling stations in seven geographic areas of Lake Superior. Geographic areas are: Area 1. Grand Portage to Duluth; Area 2. Duluth to Apostle Islands; Area 3. Apostle Islands; Area 4. Little Girls Point to Keweenaw Point; Area 5. Keweenaw Point to Marquette; Area 6. Marquette to Whitefish Point; Area 7. Whitefish Bay.

In the laboratory, frozen specimens were thawed and total length (mm) and weight (g) were recorded. Sex and stage of gonad development were determined by visual examination. Sagittal otoliths for age determination and stomachs for diet analysis were collected from a 141-fish subsample.

Otoliths were prepared for direct examination as described by Libby (1982) and aged according to O'Gorman *et al.* (1987). For some of the larger fish, the otoliths were nearly opaque and annuli were sometimes faint and difficult to interpret. Scales were not used for aging because they were shown to be unreliable for alewives from other Great Lakes (O'Gorman *et al.* 1987).

Fecundity was estimated for 17 mature females collected in June and October. Fall collections were included to increase sample size because the number of pre-spawning specimens was limited. To estimate total egg numbers by direct proportion, we used the mean count of three 1 % subsamples of the total ovary weight taken from the anterior, medial, and posterior portions of one ovary. Egg diameters were measured randomly to the nearest 0.01 mm with an ocular micrometer at 450x.

Stomach contents were examined microscopically to determine diet components. Large invertebrates and rare smaller zooplankters were separated and counted directly. Stomachs with large numbers of small zooplankton were diluted to 20 times the initial volume and estimates of total numbers were made from counts of two 1-mL sub-samples expanded to the total volume. Food items were identified only to the generic level. Weights were assigned to each invertebrate taxon by multiplying numerical data by average weights from Hawkins and Evans (1979) and unpublished data from the Ashland Biological Station. Due to the small numbers of specimens available, we combined data from fish collected in spring and fall.

RESULTS AND DISCUSSION

Distribution and Abundance

Alewives were captured incidentally at many locations in 1954-1971 (Table 1) and catches generally increased in frequency and magnitude during the period. By the mid 1960s, alewives were found along the entire shoreline and in 1971 were present even at Isle Royale, an isolated island 33 km from the mainland. In the Apostle Islands, where sampling was fairly intensive each year, the catches of alewives fluctuated substantially in 1959-1972, with little or no trend (Table 2).

Catches of alewives in spring trawling in 1978-1988 were small in all areas of the lake (Table 3). Lake-wide, the annual catch per 100 h of trawling ranged from 2 fish in 1982 to 32 fish in 1984. Alewife abundance was highest in the area from the Apostle Islands to Duluth (mean 1978-1988 catch rate 39 fish per 100 h) and lowest in Minnesota waters and Whitefish Bay (mean 1978-1988 catch rate < 10 fish per 100 h). Reproductive success generally appeared low. In 6 of 11 years, no yearling alewives were collected and when yearlings were taken, their numbers rarely exceeded the numbers of adults caught.

Mean alewife biomass in 1978-1988 was 0.003 kg/ha, which is less than 1 % of the estimated levels in other Great Lakes. O'Gorman and Schneider (1986) reported that the mean spring standing stock was 84.4 kg/ha in southern Lake Ontario (1978-1982), 14.9 kg/ha in western Lake Huron (1973-1983), and the fall standing stock in Lake Michigan averaged 15.3 kg/ha (1967-1982).

In Lake Superior, alewife abundance was inversely related to water depth. Reigle (1969) reported that Lake Superior alewives rarely occupied depths greater than 75 m in spring. We found that a regression, forced through the origin, of the 1978-88 mean alewife abundance (fish per 100 h) versus the percentage of the total water area less than 75 m deep (arcsine transformed) in each of the seven lake areas showed a strong inverse relation between water depth and alewife abundance ($r^2 = 0.78$, $P < 0.01$).

Age, Mortality, and Growth

Fish from age 0 to age 6 were represented in the combined fall and spring samples but some larger fish that were captured but not aged may have been older. On the basis of this age composition, we estimated total annual mortality, calculated from the descending limb of a catch curve (Ricker 1975) that included all samples combined, to be 64% ($r^2 = 0.99$, $P < 0.003$) for age groups 3-6. Mortality of males ($A = 67\%$, $r^2 = 0.99$, $P < 0.007$) was significantly higher ($p < 0.005$) than that of females ($A = 62\%$, $r^2 = 1.00$, $P < 0.0001$). Among fish of ages 0-4 taken in fall, annual mortality was 69% ($r^2 = 0.68$; $P < 0.08$).

Inasmuch as there is no fishing for alewives in Lake Superior and few are found in the stomachs of predators, these values suggest a high natural mortality rate due to physical factors. Reported mortalities of alewives for the other Great Lakes are based on age compositions using scales and are therefore not comparable.

Growth in length was fastest during the first 2 years of life and weight gain was greatest in the second year (Fig. 2). Growth rates decreased sharply after age 1. Although female alewives were slightly longer and heavier at age than males, these differences were not statistically significant ($P < 0.08$).

TABLE 1. Numbers and locations of alewives collected or reported by commercial fishermen, management agencies, and USFWS, Lake Superior, 1954–1971.

Year	Number	Location	Source of Record[a]
1954	1	Whitefish Bay, MI	fisherman (Miller 1957)
1954	1	Apostle Islands, WI	WDNR (Miller 1957)
1955	5	Whitefish Bay, MI	commercial pound net MIDNR, OMNR (Miller 1957)
1956	8	MN north shore, Keweenaw Bay, Black Bay	MNDNR, MIDNR, OMNR (Miller 1957)
1957	2	Apostle Islands, WI	commercial gill net (WDNR)
1958	40	Apostle Islands, WI	commercial pound net (WDNR)
1958	24	Marquette, MI	dead on beach (USFWS)
1959	47	Apostle Islands, WI	commercial pound net (WDNR)
1959	4	Marquette, MI	USFWS trawl
1960	332	Apostle Islands, WI	commercial pound nets (WDNR)
1961	263	Apostle Islands, WI	commercial pound nets (WDNR)
1961	4	Split Rock River, MN	electrofishing (MNDNR)
1962	84	Black Bay, ON	commercial pound net (OMNR)
1963	8	Batchawana and Black Bays, ON	commercial gill net and trawl, (OMNR)
1963	16	Huron Bay, MI	MIDNR gill net
1963	2,600[b]	Whitefish Bay, MI	USFWS trawl (Reigle 1969)
1964	?	Black Bay, ON	commercial gill net (OMNR)
1964	2,600[b]	Keweenaw Pt. to Sault Ste. Marie, MI	USFWS trawl (Reigle 1969)
1965	212	Various south shore locations, MI	USFWS trawl (Reigle 1969)
1966	19	Keweenaw Bay, MI	MIDNR gill net
1969	30	Whitefish Bay, MI	commercial gill nets (MIDNR)
1969	8	Munising, MI	commercial gill nets (MIDNR)
1970	5	Mouth of Jackpine River, ON	OMNR gill net
1970	30	Whitefish Bay, MI	commercial gill net (MIDNR)
1970	585	Portage Canal, MI	USFWS trawl
1970	8	Hovland to Silver Bay, MN	MNDNR gill nets
1971	38	Grand Marais to Grand Portage, MN	MNDNR gill nets
1971	3	Isle Royale, MI	lake trout stomach (USFWS)

[a] MIDNR - Michigan Department of Natural Resources; MNDNR - Minnesota Department of Natural Resources; OMNR - Ontario Ministry of Natural Resources; USFWS - U.S. Fish and Wildlife Service; WDNR - Wisconsin Department of Natural Resources.

[b] number estimated from weights landed.

Lake Superior alewives appeared to grow faster than those in Lake Ontario and similar to those in Lakes Huron and Michigan. Estimated mean lengths-at-age in the fall for Lake Superior ale-wives were compared to that of fish in other Great Lakes populations by using a one-way ANOVA to test for differences. Fall length-age data for alewives from the other Great Lakes were from O'Gorman *et al.* (1987). Because these data were from samples stratified by 10 mm length groups, we selected a subsample of our data stratified in the same manner for the comparisons. In all stocks compared, ages were determined with otoliths. Although the mean lengths-at-age derived are not representative of the actual growth increments, the comparison of these means is useful in determining differences in growth among alewives from other lakes. After age 0, Lake Superior fish generally had the greatest length (Table 4). Alewives from Lakes Michigan and Huron were similar to each other in length and Lake Ontario fish were significantly smaller. The low densities of alewives and other planktivores and the resultant lack of competition for food might explain the rapid growth of Lake Superior alewives. Alternatively, only the faster growing fish may survive over winter in Lake Superior as has been suggested for other Great Lakes stocks (Brown 1972, Argyle 1982, O'Gorman and Schneider 1986). In Lake Superior, the length of age-0 fish was among the shortest for the four stocks compared, whereas length at age 1 was the largest. This may be the result of extreme size selective mortality during the first winter when only the largest fish survived.

The slope of the length-weight regression of log transformed data (all fish combined) indicated that

$$\mathrm{LOG}\ W = -5.210 + 3.090\ \mathrm{LOG}\ L$$

Analysis of covariance indicated no significant differences between the length-weight regressions of male and female fish ($P < 0.60$).

TABLE 2. Numbers of adult and young-of-the-year alewives collected by the U.S. Fish and Wildlife Service in the Apostle Islands region of Lake Superior, 1959–1972.

Year	Number of 15-min Trawl Tows	Gill Net Fished (Thousands of Meters)	Alewives Caught	
			Age 0	Adult
1959	50	10.7	–	1
1960	64	26.8	2	1
1961	77	4.6	52	–
1962	157	3.0	2	2
1963	135	34.1	1	33
1964	83	53.0	–	43
1965	124	53.6	5	70
1966	158	53.3	3	1
1967	180	18.6	4	1
1968	155	18.0	3	–
1969	173	27.4	–	–
1970	128	26.8	98	1
1971	164	27.4	9	12
1972	21	20.7	1	7

Maturity and Fecundity

Female alewives matured as early as age 2 (140 mm, Table 5) and although the proportion mature increased with age, full cohort maturity was not reached until age 5. Peak maturity for males was observed at age 3 (150 mm) and the proportion mature declined at older ages. Because maturity was determined for fish collected in the fall, gonad development may have been misclassified. In males, length at maturity was extremely variable and no clear pattern was discernible. Immature fish ranged from 70 to 241 mm but all fish less than 140 mm were immature.

Egg size was small and variable. Egg diameters averaged 0.23 mm and ranged from 0.07 to 0.46 mm. Although egg size varied among individuals it was not related to the size of the fish. Egg sizes from other Great Lakes populations are unknown, but alewives from marine environments have eggs that average 0.9 mm in diameter (Scott and Cross-man 1973).

TABLE 3. Numbers of yearling and adult alewives captured per 100 h of cross-contour trawling in seven geographic areas of Lake Superior, 1978–1988.

	Year										
Life Stage	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
Grand Portage, MN, to Duluth, MN - 10 Stations											
Yearling	0	21	0	0	0	0	41	0	0	0	0
Adult	0	0	0	0	0	41	0	0	0	0	0
Duluth to Apostle Islands, WI - 6 Stations											
Yearling	0	0	86	58	0	0	14	0	0	0	16
Adult	0	7	43	101	7	14	58	7	14	0	9
Apostle Islands, WI - 9 Stations											
Yearling	0	0	0	0	0	27	27	0	0	0	0
Adult	0	0	27	0	0	0	0	0	108	27	0
Little Girls Point, MI, to Keweenaw Point, MI - 7 Stations											
Yearling	0	0	0	0	0	0	9	0	0	0	2
Adult	0	0	5	0	0	14	2	5	0	0	6
Keweenaw Point to Marquette, MI - 9 Stations											
Yearling	0	0	2	0	–	0	0	0	0	0	0
Adult	40	60	20	0	–	0	20	20	40	30	0
Marquette to Whitefish Point, MI - 6 Stations											
Yearling	0	0	0	0	–	0	0	0	0	0	0
Adult	0	0	0	0	–	0	0	15	15	0	0
Whitefish Bay, MI - 6 Stations											
Yearling	0	0	0	0	–	0	0	0	0	0	0
Adult	0	17	17	0	–	17	9	17	9	0	0

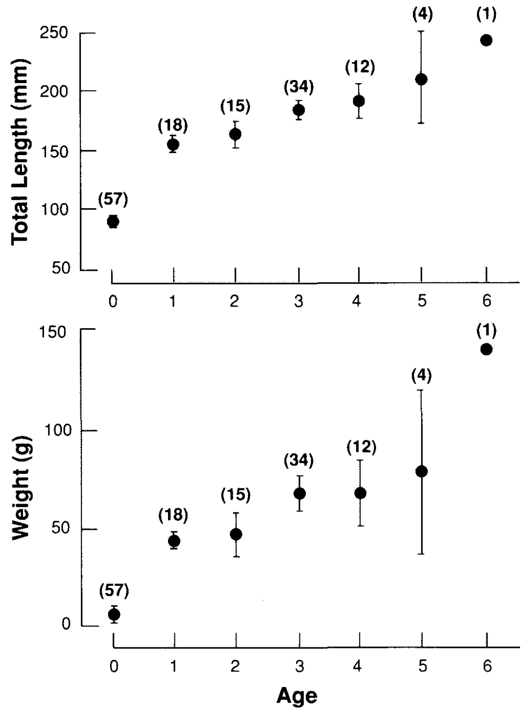

FIG. 2. Mean length (mm) and weight (g) at age with 95% confidence intervals, Lake Superior alewives, 1983-1987. Sample sizes are in parentheses.

Fecundity estimates for Lake Superior alewives ranged from 29,894 to 159,366 with a mean of 63,559 ± 1,624 (mean total length = 187 mm). No differences were found between fecundity estimates of spring and fall females (Students t-test, $P < 0.70$). A linear equation best described the relation between fecundity and total length ($P < 0.006$, $r^2 = 0.52$, Fig. 3). Fecundity in other freshwater populations ranged from 11,147 to 22,407 in Lake Michigan (mean total length = 169 mm, Norden 1967); from 8,190 to 10,011 in Cayuga Lake, New York (mean total length - 123 mm, Rothchild 1966); and from 10,000 to 12,000 in Seneca Lake, New York (mean standard length = 145 mm, Odell 1934). Lower fecundity estimates in these stocks may be related to the smaller size of the females examined, but even our smallest females (140-160 mm) had more eggs than the maximum reported for the other stocks. Fecundity of Lake Superior alewives is similar to that of marine populations where from 60,000 to 100,000 eggs have been reported (mean total length = 273 mm; Rounsefell and Stringer 1945). The high fecundity of Lake Superior alewives may be a response to their low density, fast growth, or high natural mortality (Nikolsky 1978).

TABLE 4. Comparisons of mean length-at-age (mm) of length-statified samples of alewives collected in fall in Lakes Superior, Michigan, Huron, and Ontario. Lengths with the same key symbol positions within an age group are not significantly different at the 0.05 level. Numbers in parentheses indicate sample size.

	Age				
Lake	0	1	2	3	4
Superior	89 (54)*	156 (16)*	176 (8)*	189 (21)*	188 (3)*
Michigan	110 (6)**	140 (15)*	163 (1)*	174 (26)*	181 (18)*
Huron	117 (2)*	146 (17)**	155 (20)*	174 (13)*	178 (17)**
Ontario	87 (12)*	137 (12)*	155 (1)*	157 (10)*	167 (15)*
P value =	0.0007	0.0001	0.0379	0.0001	0.0015

Diet

Numerically, zooplankton made up 75% of the diet of Lake Superior alewives. *Daphnia* spp. and *Diaptomus* spp. represented 28% and 27%, followed by *Cyclops* (9%) and *Limnocalanus* (7%). The importance of *Diaptomus* and *Limnocalanus* declined as fish length increased, whereas that of *Daphnia* increased. *Epischura Mesocyclops, Bosmina, Diaphanosoma, Polyphemus,* and *Leptodora* were also eaten but none of these genera composed more than 1% of the diet.

TABLE 5. Maturity schedule for Lake Superior alewives, 1983-1987.

Age	Number Examined	Percent Mature		
		Males	Females	Combined
0	57	0	0	0
1	17	50	0	12
2	15	0	44	27
3	34	89	88	44
4	12	60	71	67
5	4	50	100	50

Mysis was second to zooplankton in numerical abundance and composed 22% of the diet. Although *Mysis* was rare in the diet of fish less than 100 mm long (Fig. 4), it became increasingly important in fish of larger sizes. Similar increases with size have been reported for Lake Michigan alewives (Morsell and Norden 1968, Wells 1980) except that *Pontoporeia* was the dominant crustacean there. Other food items eaten by alewives in Lake Superior in smaller amounts were *Pontoporeia,* ostracods, and various insects such as chironomid pupae and larvae, beetles, and caddisflies.

In terms of weight of prey consumed, zooplankton was a significant component of the diets of alewives < 100 mm (age 0) that may have been unable to eat *Mysis.* For alewives longer than 100 mm, *Mysis* constituted at least 98% of the diet by weight and all other organisms were of little importance.

Reasons for the Limited Success of Alewives in Lake Superior

Both predation and unfavorable water temperatures have been offered as possible explanations for the low abundance of alewives in Lake Superior. Because lake trout had not yet been reduced by the sea lamprey *(Petromyzon marinus)* when alewives began to colonize Lake Superior, Smith (1970) speculated that alewives did not increase dramatically as they had in the other Great Lakes because of predation by lake trout *(Salvelinus namaycush).* Dryer *et al.* (1965) examined 1,492 lake trout stomachs collected in 1950-1953 and in 1963 and found no alewives. More recent (1981-1987) data indicate that alewives are only rarely eaten by native and introduced salmonines in Lake Superior (unpublished data —Ashland Biological Station). Although the reduced abundance of predators may have allowed alewife population expansions in the other Great Lakes, we consider it extremely unlikely that predation was a significant factor limiting their success in Lake Superior. We believe that adverse environmental conditions are more likely responsible.

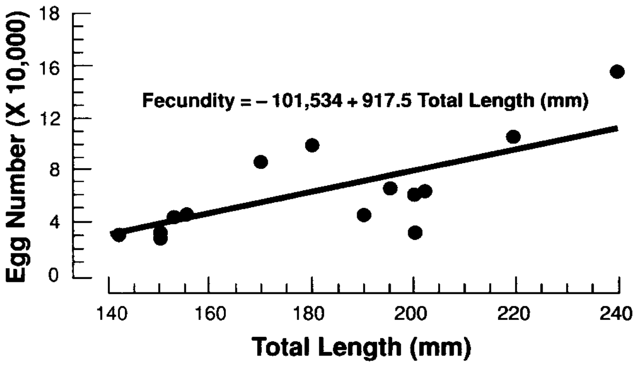

FIG. 3. Relationship between fecundity and total length of Lake Superior alewives, 1983-1987.

During most of the year, water temperatures in Lake Superior are near the lower tolerance threshold for alewives. Temperature has been shown to affect the growth and recruitment of alewives (Henderson and Brown 1985, Eck and Wells 1987), and their over winter survival (Brown 1972, Kohler and Ney 1981, O'Gorman and Schneider 1986). In the laboratory, mortality of alewives that were exposed to short- and long-term temperature declines increased as the temperatures approached 3.4°C (Colby 1973). Osmoregulatory failure in alewives from acute exposure to temperatures at or below 3.0°C has also been demonstrated (Stanley and Colby 1971). In Lake Superior, temperatures are below 3.0°C for at least 3 months during winter and early spring. Beeton *et al.* (1959) recorded isothermic conditions in May 1955 at various locations in Lake Superior where water temperatures were below 3.0°C from the surface to 200 m. During May 1978-1988, similar low temperatures were recorded by us at many locations lake-wide. Even if warmer water was present in the deepest portions of the lake, alewives probably do not descend to these greater depths as was found in Lake Ontario (Bergstedt and O'Gorman 1989). Severe and prolonged exposure to low temperatures during winter and early spring could reduce the survival of alewives which are adapted to warmer and less variable conditions (Colby 1973). Alewives that do survive in Lake Superior may overwinter in small thermal refugia, such as stream mouths, where temperature extremes may not reach the critical minima.

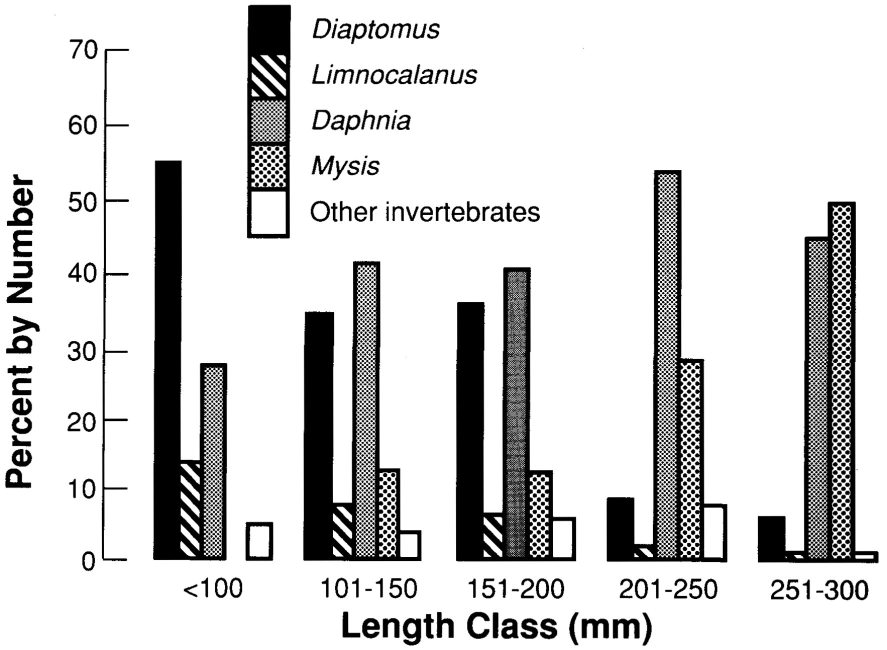

FIG. 4. Diet composition of Lake Superior alewives by 50-mm length classes, expressed as the percentage of the total number of identified food items, 1983-1987.

Low water temperatures during egg incubation may also contribute to the poor success of alewives in Lake Superior. In the lower Great Lakes and in smaller inland waters, alewives move from deep water to shallow, nearshore areas to spawn from April to August, when water temperatures are 10-16°C (Rothchild 1966, Norden 1967, Brown 1972). No observations of spawning alewives were made during the present study. However, based on the mean temperatures of surface water nearshore during 1967-1975 (Grumlatt 1976), spawning probably occurs in late June to July in Lake Superior when temperatures first exceed 10°C. The average length of young-of-the-year alewives collected on 30 August and 6 September 1989 in the Apostle Islands region was 38 mm; judging by that length they were probably 4 to 6 weeks old (hatched in mid to late July). Mean nearshore water temperatures in Lake Superior are generally 9 to 13°C in June and increase to 17°C in late July. Edsall (1970) reported that at temperatures below 10.6°C, alewife hatching success was less than 15% with 67% of the larvae deformed and unable to survive after yolk absorption.

In Lake Superior, nearshore water temperatures are generally not suitable for incubation until July and even then rarely reach 17°C, the optimal temperature for egg incubation in alewives (Edsall 1970).

Additionally, the growing season between the time of hatching and the onset of winter may be too short to allow most age-0 alewives to reach a size large enough to overwinter in Lake Superior. In Lake Michigan, September and October are critical months for alewife growth, and food consumption rates are highest (Stewart and Binkowski 1986). Average length of age-0 alewives in Lake Superior was the shortest among the Great Lakes stocks compared. A late spawning season in conjunction with lower water temperatures creates a short growing season that probably results in poor first-year survival. Successful alewife year classes are probably produced only in warm years when incubation and adequate growth are possible. For the few fish that survive through the first year, natural mortality throughout the rest of their lives is high because the fish are living at the extreme edge of their temperature range.

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