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# Feeding Ecology and Vertical Migration of Adult Alewives (*Alosa pseudoharengus*) in Lake Michigan<sup>1</sup>

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JANSSEN, J., AND S. B. BRANDT. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. Can. J. Fish. Aquat. Sci. 37: 177-184.

Vertical distributions of adult alewife (135-216 mm long) and *Mysis relicta* were measured acoustically on a 24 h basis during July, September, and October 1975 and June 1976 at a station 8 km northeast of Milwaukee, Wisconsin in 50 m of water. Both *Mysis* and adult alewife concentrated on the bottom during day and migrated upwards to the base of the thermocline at night. Extent and timing of vertical migrations of *Mysis* and alewife coincided. During bright moonlight *Mysis* concentrated at depths well below the thermocline and larger adult alewives concentrated within this *Mysis* layer while smaller adult alewives migrated to the base of the thermocline. An examination of stomach contents indicated that vertical migrations were mechanistically linked to feeding behavior. Adult alewives fed extensively on *Mysis* at night. Total lengths of *Mysis* in alewife stomachs were significantly longer than total lengths of *Mysis* captured in vertical plankton tows. *Pontoporeia hoyi* occurred in alewife stomachs in late afternoon (September) and early evening (June, October). Microcrustacean zooplankton were eaten mostly during day (June) or early morning (October). As *Mysis* was the most important food, the vertical migration of alewives is interpreted as an adaptation for feeding on vertically migrating *Mysis*.

**Key words:** alewives, Lake Michigan, *Mysis*, *Pontoporeia hoyi*, vertical migration, feeding ecology, light

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Des méthodes acoustiques ont été utilisées pour mesurer la distribution verticale de gaspareaux adultes (135-216 mm de long) et de *Mysis relicta* sur base de 24 h en juillet, septembre et octobre 1975 et en juin 1976 à une station située à 8 km au nord-est de Milwaukee, dans le Wisconsin, à une profondeur d'eau de 50 m. *Mysis* et gaspareaux adultes se concentrent, les uns et les autres, sur le fond durant la journée et remontent à la base de la thermocline la nuit. L'étendue et la chronologie des migrations verticales de *Mysis* et du gaspareau coincident. Par nuits de clair de lune brillant, les *Mysis* se concentrent à des profondeurs bien au-dessous de la thermocline, et les grands gaspareaux adultes se trouvent parmi cette couche de *Mysis*, alors que les gaspareaux adultes plus petits émigrent vers la base de la thermocline. Un examen des contenus stomacaux indique un lien mécanique entre migrations verticales et comportement alimentaire. Les gaspareaux adultes se nourrissent intensivement de *Mysis* la nuit. La longueur totale des *Mysis* présents dans les estomacs de gaspareaux est nettement plus grande que celle des *Mysis* capturés dans des prises de plancton verticales. *Pontoporeia hoyi* est présent dans les estomacs de gaspareaux en fin d'après-midi (septembre) et début de soirée (juin, octobre). Les microcrustacés planctoniques sont mangés surtout de jour (juin) ou tôt le matin (octobre). Comme *Mysis* est la plus importante nourriture des gaspareaux, la migration verticale de ces derniers est interprétée comme adaptation à une alimentation à même des *Mysis* se déplaçant verticalement.

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THE alewife (*Alosa pseudoharengus*) is an exotic fish species in Lake Michigan. Since their first recorded appearance in 1949 (Miller 1957), they spread throughout the lake to become the most abundant species (Brown 1968, 1972; Wells and McLain 1973). The invading alewife undoubtedly affected native fish stocks and the size distribution of zooplankton in Lake Michigan (Smith 1968, 1970; Wells and McLain 1973; Wells 1970). Although mechanisms of these effects are still largely undetermined, we suspect that they may be primarily mediated through the feeding ecology of alewives.

To help define the functional role of these clupeids in the Lake Michigan ecosystem, we examined changes in vertical distribution and food of adult alewives over 24-h periods. Alewives in Lake Michigan eat almost exclusively crustacea ranging in size from small copepods and cladocera to *Pontoporeia hoyi* and *Mysis relicta* (Morsell and Norden 1968; Rasmussen 1973; Webb and McComish 1974; Rhodes and McComish 1975). Other organisms such as fingernail clams, mites, aquatic insects, fish eggs, oligochaetes, leeches, and filamentous algae are also consumed, but only in small quantities. Many potential prey of alewives in Lake Michigan concentrate at certain depths, and their depth distribution changes with time of day and the thermal structure of the water column (Beeton 1960; Wells 1960; Bowers and Grossnickle 1978). The interactions of alewives with these organisms in the pelagic zone have not been described.

In this study we sought to determine if alewives vertically migrated, whether this correlated with vertical distribution of prey, particularly *Mysis*, and whether the migration was related to diel feeding activity.

## Materials and Methods

We measured the vertical distributions of fish and *Mysis* acoustically and analyzed the stomach contents of alewives caught in trawls at 4-h intervals or less during 24-h periods on July 22–23, 1975; September 15–16, 1975; October 14–15, 1975; and June 7–8, 1976. Samples were collected at a sampling station 8 km northeast of Milwaukee, Wisconsin at a depth of 50 m from the University of Wisconsin's R/V *Aquarius*. Thermal profiles were measured with a 60 m mechanical bathythermograph and temperatures were read at 1-m intervals to the nearest 0.1°C. In October at dawn and dusk, we measured the surface light intensity with a Whitney light meter (ca. 1960 model) every 2.5 min while pelagic fish distributions were recorded acoustically.

### FISH DISTRIBUTION

Fish samples were collected with a semiballoon otter trawl during 10–30 min bottom tows at speeds of approximately 1.5 m/s (3 knots). The trawl had a 7.6 m headrope, 2 cm bar mesh, and a 0.6 cm mesh liner in the cod end. All fish caught were identified and counted. Twenty or more (unless fewer were available) alewives were preserved for stomach analyses in 10% formalin after cutting the body wall. Catch per unit effort (CPUE) of alewives

is expressed as the number caught per 10 min towed on the bottom.

During October, the otter trawl was also fished in mid-water to identify pelagic fish targets recorded on the echo sounder. The midwater depth of the trawl was estimated from the length and angle of the cable that had been left out.

For quantitative analyses of midwater fish distributions in October and July, a high resolution Simrad EK-120 echo sounder was used for sound transmission and reception. This echo sounder operates at a frequency of 120 kHz and transmits sound pulses of 0.1 ms duration at a rate of 96 pulses/s. The short pulse length provides a theoretical vertical resolution of 0.075 m. The transducer beam angle for this instrument approximates 11° at -3 db points. We towed the transducer alongside the vessel within a hydrodynamically stable 1.2 m V-fin "fish" at a depth of 1 m.

Acoustic signals were bandshifted to 12 kHz, amplified, and then recorded on one channel of a magnetic tape recorder (Sony, model 277-4) during all trawl tows. The trigger signal, which initiates sound transmission at each acoustic pulse, was amplified and recorded on a second channel of the tape recorder. Later ashore, analog data from the tapes were high pass filtered, rectified, low pass filtered ("envelope detected"), and then input to a 24 K Datacraft (model 6024/5) computer. The high pass filter reduced 60 cycle noise. Signals from a time-mark generator were used to calibrate the filters and rectifier. Data were digitized by the computer and corrected for signal attenuation and spreading loss (Forbes and Nakken 1972; Clay and Medwin 1977). Data were then analyzed by echo-squared integration to provide measures of relative fish abundance for each 1 m depth stratum throughout the water column for each 2 min of transect time. Results from echo-squared integration are directly proportional to absolute fish densities (Thorne 1971). This entire analysis procedure is performed in real time and is fully described in Brandt (1975, 1978) and Peterson et al. (1976).

During September and June, echograms from a 50 kHz Furuno (model F-836) echo sounder were used to monitor vertical distributions of fish. The transducer for this echo sounder was mounted in the hull of the R/V *Aquarius*.

### Mysis DISTRIBUTION

We collected triplicate samples of *Mysis* at night towing a 0.5 m plankton net (#0 mesh = 0.571 mm) vertically from bottom to surface at a constant speed. All zooplankton were preserved in 10% formalin. All *Mysis* were counted and measured for total lengths.

We also measured the vertical distribution of *Mysis* in the water column before starting each trawl tow and during additional periods at dawn and dusk with a Furuno 850-A echo sounder. This 200 kHz echo sounder can record targets as small as *Mysis* and was used successfully for studies of *Mysis* distribution by Teraguchi et al. (1972) and Bowers and Grossnickle (1978). Measurements were taken with the transducer suspended off the side of the ship while the ship drifted. Echograms were used to determine the depth of *Mysis* concentrations. Fish targets are also visible on the echogram but are distinct from those of the *Mysis*. Because we did not correct for differences in sampling volume that resulted from the spherical spreading of sound from the transducer with depth, the targets are disproportionately more numerous near the bottom of the echogram.

## FEEDING OF ALEWIVES

For each preserved alewife, all whole *Mysis*, *Pontoporeia*, and microcrustacean zooplankters in the cardiac region of the stomach were counted. Percent occurrence (percent of fish containing the item) and number of food items per stomach (median and upper and lower quartiles) were used as qualitative and quantitative indicators of alewife feeding habits. Total length (mm) of each alewife and all *Mysis* from each stomach sample were measured.

## Results

### VERTICAL MIGRATION OF ALEWIFE

Echosounding in July and October indicated a greater number of fish in the water column at night than during the day. This correlated inversely with a decrease in the number of adult alewives captured in night trawls relative to day trawls (Fig. 1). Significantly more fish were pelagic at night than during the day (Mann-Whitney *U*-test,  $n = 6$  night estimates, 7 day estimates,  $P < 0.05$ ). Echograms for June and September also indicated that substantially more fish were in the water column at night. During the daytime, fish were extremely scarce in the water column on all sampling

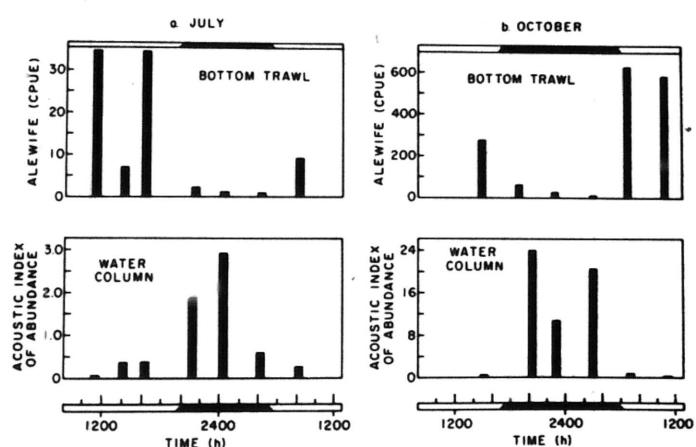


FIG. 1. Alewife catch per unit effort (CPUE) in bottom trawls and acoustic index of fish abundance in the water column (mean echo squared integration) over 24-h periods in July and October 1975 at a station approximately 8 km northeast of Milwaukee, Wisconsin.

dates, although some large schools were recorded from the epilimnion in July and September.

While the echo sounder can show fish depth distribution, it cannot indicate species. We believe that most

TABLE 1. Comparison of percent species composition of fishes caught in bottom trawls during day and night for July, September, and October 1975 and June 1976. The sampling station was 8 km northeast of Milwaukee, Wisconsin in Lake Michigan at a water depth of 50 m.

Dates	Total trawl length (min)	Beginning times	Percent of total numbers									Total number of fish	
			Alewife			Smelt	Bloater	Fourhorn sculpin	Ninespine stickleback	Lake trout			
			Adult	Juvenile	Slimy sculpin								
July 22–23, 1975	65 Day	1111											
		1358											
	50 Night	1606											
		0807	18	11	71	0	<1	<1	0	0	0	717	
Sept. 15–16, 1975	30 Day	2108											
		0013											
	30 Night	0410	1	<1	99	0	0	0	0	0	0	1686	
		1458											
Oct. 14–15, 1975	31 Day	0658											
		1108	39	0	37	21	2	0	1	0	0	346	
	40 Night	1928											
		0053	<1	0	99	<1	0	0	0	0	0	175	
June 7–8, 1976	40 Day	1513											
		0708											
	40 Night	1105	94	0	<1	5	<1	0	<1	<1	0	1694	
		1909											
		2308											
		0307	24	0	73	3	0	0	<1	0	0	418	
		1525											
		1936											
		0532											
		1119	35	53	7	5	<1	0	0	0	0	1742	
		2049											
		0211	14	0	85	<1	0	<1	0	0	0	857	

of the night pelagic targets are adult alewives based on abundances of fish species caught and other factors as outlined below.

We caught a total of 7635 fish representing seven species (Table 1). Alewife and slimy sculpin (*Cottus cognatus*) were the most abundant fishes caught in all seasons. Adult alewives almost always dominated the daytime catches but were rarely caught at night in bottom trawls. Slimy sculpins dominated the catches at night and fewer of them were caught during the day than at night. Rainbow smelt (*Osmerus mordax*) were the third most abundant species. Occasionally fourhorn sculpin (*Myoxocephalus quadricornis*), bloaters (*Coregonus hoyi*), ninespine stickleback (*Pungitius pungitius*), and lake trout (*Salvelinus namaycush*) were also caught. Most alewives in the catch were age II or older, ranging in length from 135 to 216 mm for all dates and times combined. The absence of juvenile alewives in bottom trawls is consistent with reports that the juveniles are predominantly pelagic (Wells 1968a; Brown 1972; Brandt 1978).

We concluded that the pelagic fish in the water column at night were mainly adult alewives because (1) the adults were the most abundant fish on the bottom during the day (Table 1), (2) the reduction of adult alewives on the bottom at night corresponded with an increase of fish in the water column (Fig. 1), (3) the only fish we captured in midwater trawling at night were adult alewives, and (4) the only other abundant species, the slimy sculpin, was most abundant in bottom trawl catches at night (Table 1), and having no swim bladder, is less likely than the alewife to be in midwater or to register on an echo sounder.

Vertical migration of adult alewives is further corroborated by the progressive shifts in vertical distribution of fish at dawn and dusk, coinciding with changes in surface light intensity. For example, during October, fish began to migrate toward the bottom at surface light intensities of less than 10 lx (Fig. 2), and the migrations were complete at surface light intensities of approximately 400 lx. The rate of downward migration was estimated to be 0.85 m/min. Similar migration patterns were observed during other months.

#### VERTICAL DISTRIBUTION OF MYSIS AND FISH

The night vertical plankton tows yielded *Mysis* abundance estimates of 522/m<sup>2</sup> in July, 190/m<sup>2</sup> in September, 230/m<sup>2</sup> in October, and 165/m<sup>2</sup> in June.

The extent and timing of vertical migrations of fish were closely linked to thermal structure and *Mysis* distribution. Regardless of date or habitat conditions, the night time fish targets were always concentrated in the *Mysis* layer (Fig. 3) as determined with the 200 kHz Furuno 850-A echo sounder. On dark nights (i.e. new moon) with a thermocline present (Fig. 3b), both fish and *Mysis* were at the base of the thermocline. On moonlit nights (Fig. 3a, b) *Mysis* did not rise as high in the water column and all or a portion of the

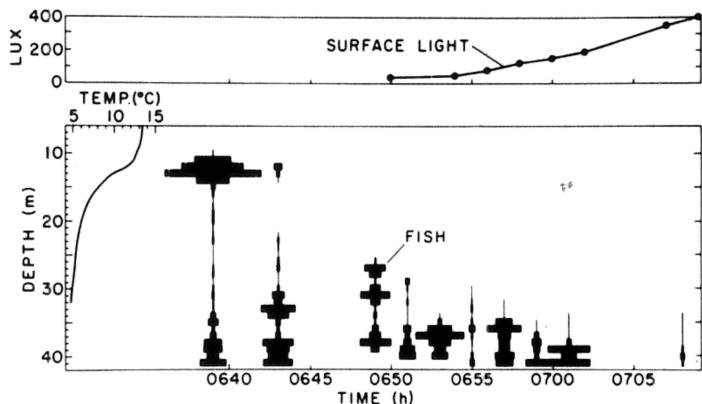


FIG. 2. Relative abundance of fish throughout the water column and corresponding surface light intensities during dawn on October 15, 1975. Horizontal bars represent relative fish abundance as measured by echo squared integration. Fish are believed to be predominantly adult alewife.

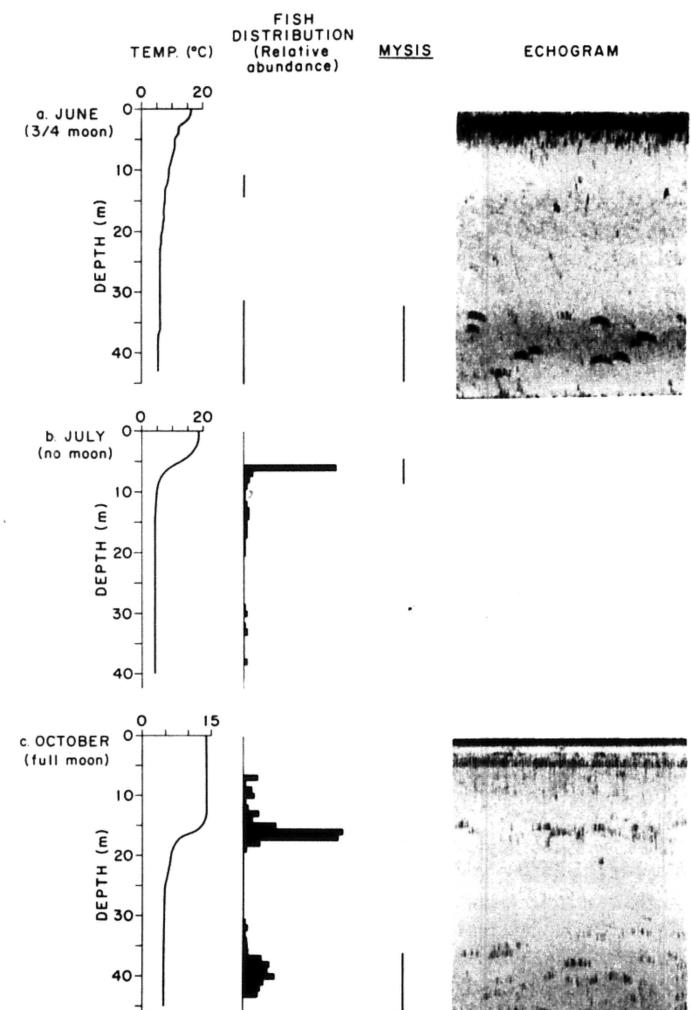


FIG. 3. Nocturnal vertical distributions of water temperature, relative fish abundance from echo squared integration, and *Mysis* from echograms from a 200 kHz Furuno 850-A echo sounder in Lake Michigan on (a) June 8, 1976 (03:30), (b) July 22, 1975 (21:22), and (c) October 14, 1975 (23:08).

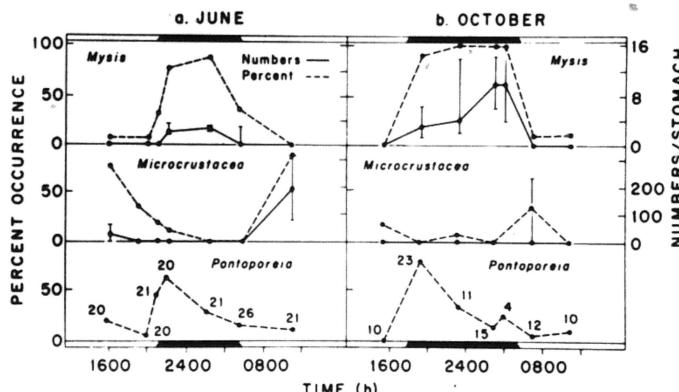


FIG. 4. Numbers per stomach and percent occurrence of *Mysis*, *Pontoporeia*, and microcrustacean zooplankton in alewife stomachs for (a) June 1976 and (b) October 1975 over 24-h periods. Alewives were collected with a bottom trawl 8 km northeast of Milwaukee in Lake Michigan in 50 m of water. Number of stomachs examined are indicated in the bottom panel.

fish population remained with the *Mysis* deep in the water column. In October, however (Fig. 3c), the smaller adult alewives apparently migrated past the *Mysis* layer up to the base of the thermocline. Mean length of alewives caught near the bottom in the *Mysis* layer at night was significantly longer than that of alewives caught during the day when all fish were near the bottom ( $P < 0.05$  median test,  $n = 48$  fish at night, 42 during day). This indicates that smaller alewives migrated higher in the water column than did larger alewives.

Both fish and *Mysis* migrated to the bottom at dawn, and the vertical migration of the fish coincided with that of the *Mysis*. The downward rate of migration for *Mysis* in September, for example, was 0.7 m/min, similar to that of the fish.

#### FEEDING OF ALEWIVES

Adult alewives fed intensively on *Mysis* at night (Fig. 4). Both numbers of *Mysis* per stomach (Kruskal-Wallis analysis of variance by ranks and Dunn's (1964) multiple comparison tests,  $P < 0.1$ ) and percent occurrence of *Mysis* in alewife stomachs ( $\chi^2$  and Fisher exact test) were significantly higher at night than during day in June, September, and October. Day-night stomach comparisons were not made for July because too few alewives were caught in trawls at night.

*Mysis* were present in the stomachs of an average of 13% of the alewives sampled during the day and 85% at night in June, and 9% sampled during the day and 96% at night in October. Median numbers per stomach were near zero during the day but increased at night to 2 in June and 10 in October. In September, many alewives (77%) contained *Mysis* during the day but the number per stomach was higher at night (maximum 8/stomach) and in early morning (7/stomach) than later in the day (one to two/stomach). Although few

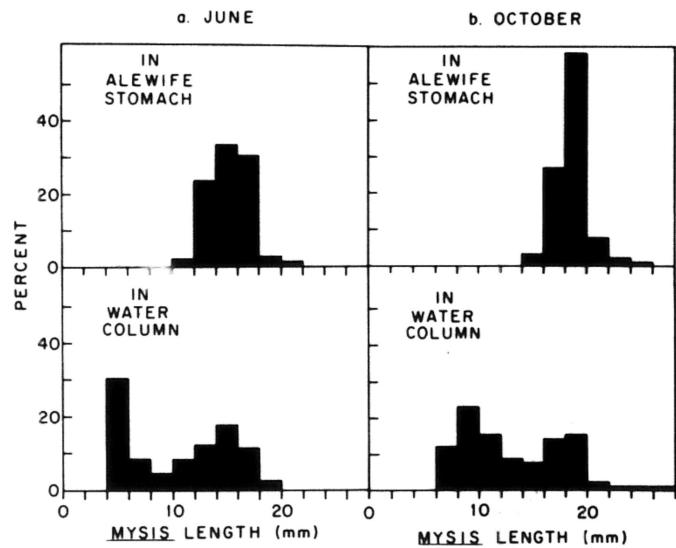


FIG. 5. Length frequency (percent) distributions of *Mysis* from stomachs of adult alewife and from the water column for (a) June 1976 and (b) October 1975 at a station 8 km northeast of Milwaukee in Lake Michigan in 50 m of water.

alewives were actually caught in midwater, four taken during a 37 min midwater-trawl tow at night in October contained 4–19 *Mysis*. These values are similar to those from alewives caught in bottom trawls at night.

The number of *Mysis* per stomach was extremely variable within trawl samples as indicated by the breadth of the quartiles (Fig. 4). Variance to mean ratios for June, September, and October night samples ( $n = 9$ ) ranged from 1.33 to 6.47 (median = 3.89). In eight samples the variance was significantly greater than the mean ( $P < 0.05$ ,  $\chi^2$  test on index of dispersion; Elliot 1971). The possible importance of this observation is considered in the discussion.

Body lengths of *Mysis* in alewife stomachs were longer than body lengths of *Mysis* in the water column in June and October (Fig. 5) and also in September (median test,  $n = 272$ –341 *Mysis* in sample, 115–269 in stomachs,  $P < 0.05$ ).

*Pontoporeia* were less common prey of alewives than were *Mysis* (Fig. 4). The median number of *Pontoporeia* per stomach was always zero and total numbers ranged from 0 to 9. The highest percentage of *Pontoporeia* occurred in the stomachs sampled during the afternoon in September (60%) as compared to early evening in October (78%) and June (65%). Few alewives contained *Pontoporeia* during the day.

Microcrustacean zooplankton found in the alewife stomachs were mainly cyclopoid and calanoid copepods and *Daphnia* and *Bosmina* sp. These organisms were relatively uncommon in the stomachs of the adult alewives but did appear in moderate numbers in those of fish from certain trawls in June and October (Fig. 4). The greatest number per stomach was generally observed during the day.

The high numbers of microcrustaceans in stomachs

of fish caught in midwater in October suggests that alewives in the thermocline were feeding on zooplankton at night. In fact, the four fish caught near the thermocline in midwater at night all contained zooplankton (median 60.5 zooplankters per stomach, range 23–75) and had significantly higher numbers of zooplankters than fish caught at all other times except early morning (07:08). Midwater fish also contained numerous *Mysis*. Those alewives caught in bottom trawls in the early morning that contained zooplankton had probably fed in the thermocline during the night and then migrated to the bottom at dawn.

The relative importance of *Mysis* in the alewife diet can be estimated using the dry weights of prey measured by Morsell and Norden (1968). Their results state that dry weight on 1 *Mysis* is roughly equivalent to that of 1000 zooplankters. The maximum number of zooplankters (580) taken from an alewife's stomach in our study approximated 0.6 *Mysis* in weight.

## Discussion

Adult alewives migrate vertically in Lake Michigan. They concentrated near bottom during the day and in midwater at night. The upper limit to vertical migration was closely linked to the vertical distribution of *Mysis* and the position of the thermocline. When *Mysis* migrated to the base of the thermocline, as they do if moonlight is not great (Beeton 1960; Bowers and Grossnickle 1978), alewives also migrated to the base of the thermocline and remained there throughout the night. If, on the other hand, the upward migration of *Mysis* was limited to a region well below the thermocline, as it was on a moonlight night in October of our study, longer adult alewives still concentrated in the *Mysis* layer. Shorter adults, however, apparently passed through the *Mysis* layer and concentrated at the base of the thermocline where *Mysis* are scarce, presumably to feed on microcrustacea. Differences in vertical distribution of different size-classes of fish have been documented in marine systems (Clarke 1973, 1974; Clarke and Wagner 1976), but the adaptive significance is unclear.

We suggest that the extent of the vertical migration by alewives is mechanistically linked to their feeding behavior. Similar vertical distributions and migration rates of both adult alewives and *Mysis* suggest that alewives actually follow *Mysis*. It is unlikely, however, that both alewives and *Mysis* have identical thermal and light preferences and are merely responding similarly to abiotic physical stimuli. During all months except October pelagic alewives were concentrated in the *Mysis* layer. The bimodal distribution of fish during October coincided with the bimodal distribution of their prey, that is, large adult alewives were in the *Mysis* layer whereas smaller adults concentrated with the microcrustaceans at the base of the thermocline (Wells 1960; Lane 1975). It is difficult to explain on the basis of temperature and light characteristics alone, why

alewives should have two optima on one data and only one on another.

Our Lake Michigan data depict *Mysis* as the major constituent in the diet of adult alewives at the offshore station in 50 m of water. Alewives fed on *Mysis* almost exclusively at night. Previous studies of food habits of hypolimnetic alewives (Morsell and Norden 1968; Rasmussen 1973) suggested that *Pontoporeia* were the most important prey, but those fish were sampled mainly during daylight hours. Apparently *Mysis* are more vulnerable to alewife predation in the water column than near bottom. Alewives in the laboratory have difficulty feeding from the bottom and *Mysis* visually avoid them (Janssen 1978a). Thus, although both *Mysis* and alewives are most concentrated when on the bottom during the day, the *Mysis* are apparently unavailable then as prey.

Vision may well be the mode by which alewives detect *Mysis* at night. The selection of large *Mysis* by alewives is consistent with the idea that large *Mysis* should be more visible and thus more vulnerable than small *Mysis* to alewife predation. *Mysis* in Lake Michigan prefer light intensities of about 0.1 lx when migrating (McNaught and Hasler 1966), but they were often found at depths with less light. Light intensities of 0.1 lx are well within the visual ability of clupeid. The Atlantic herring (*Clupea harengus harengus*) has a feeding threshold near 0.01 lx (Blaxter 1966). At such low light intensities, the Atlantic herring silhouettes its prey against downwelling light and approaches the prey from beneath. The alewife also approaches individual prey from beneath (Janssen 1978a), and its eye seems to be better adapted than the herring's eye for silhouetting prey, because the concentration of receptors in the ventral part of the retina is higher than that observed in the Atlantic herring (Ali and Anctil 1976). Alewives are also capable of feeding nonselectively in the dark, presumably by filtering (Janssen 1978b). But if alewives were filter feeding at night we would expect them also to pick up microcrustaceans. Indeed, the four alewives captured at night near the thermocline in October did contain substantial numbers of microcrustaceans. However, zooplankters were uncommon in alewife stomachs from samples taken on bottom at night. Perhaps filter feeding is only rewarding in high concentrations of zooplankton such as occur in the thermocline. Age-II and older alewives fed on zooplankton mainly at night during July and August in Echo Lake, Maine (Gately 1978).

Differences in the vertical distribution of large and small *Mysis* may contribute to the apparent "size selective" feeding by alewife at night. Smaller *Mysis* are often higher in the water column than large *Mysis* (Beeton 1960). If alewives fed primarily in the lower part of the *Mysis* layer, stomach samples would be biased toward larger prey.

Numbers of *Mysis* in fish stomachs varied greatly. If alewives were random sampling devices, a large variance/mean ratio in stomach contents would imply

that *Mysis* were distributed in patches. Clearly the *Mysis* are patchily distributed in that they are layered vertically. Night vertical hauls of *Mysis* are reported by N. E. Grossnickle (Harbor Branch Institution, Fort Pierce, FL 33450, USA, personal communication) indicate that they are also distributed horizontally in patches. For 12 out of 15 series of samples collected by Grossnickle at a 50 m station from July 1975 to June 1976, the variance was significantly greater than the mean ( $P < 0.05$ ,  $\chi^2$  test on the index of dispersion; Elliot 1971).

As noted earlier, *Pontoporeia* were less important than *Mysis* as alewife prey. *Pontoporeia* are usually buried in the sediments (Wells 1968b) and thus unavailable to alewives. Occasionally, and particularly at night, *Pontoporeia* make short sojourns in the water column (Marzolf 1965), however, and become vulnerable to alewife predation. Our sampling indicated that adult alewives feed on *Pontoporeia* primarily during late afternoon and early evening, apparently during the initial stages of their migration off the bottom. But, alewives are usually above most of the *Pontoporeia* later during the night.

*Mysis* and *Pontoporeia* are important prey for bloaters (Wells and Beeton 1963), slimy sculpin and deep-water sculpin (Kraft 1977). Foltz and Norden (1977) found that smelt fed largely on *Mysis*. Similarities among the diets of deepwater fishes in Lake Michigan suggest that competition for food may be important; however, we do not actually know if prey are ever in short supply for any of these species.

Spatially, the thermocline represents only a small percentage of the lake, yet recent studies have depicted this zone as a site of intensive interactions between nutrient, phytoplankton, and microcrustacean zooplankters (Mortonson 1977; Brooks and Torke 1977; Wells 1960; Lane 1975). These interactions are obviously highly significant to the productivity of the pelagic waters of Lake Michigan. Bowers and Grossnickle (1978) and Grossnickle (1978) have since added *Mysis* to this dynamic region in Lake Michigan with the observation that *Mysis* migrate to the base of the thermocline at night, if moonlight is not great, and feed on concentrations of diatoms and microcrustaceans. Our data on alewives add one higher trophic level to this complex system.

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