

Thermal Habitat Partitioning by Fishes in Lake Michigan

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Thermal distribution of Lake Michigan fishes were determined by aimed bottom trawling ($n = 68$) along temperature isotherms (3-20°C) in a region where the thermocline intersected the bottom off Grand Haven, Michigan, during September. Alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), spottail shiner (*Notropis hudsonius*), and trout-perch (*Percopsis omiscomaycus*) comprised 94% of the catch by numbers. Species segregated along temperature gradients. Patterns of thermal habitat partitioning were maintained despite rapid oscillations in thermocline location. Alewife, rainbow trout, and yellow perch (*Perca flavescens*) showed intraspecific differences in thermal distribution of size-classes. Thermal niche shifts of some fishes on the bottom apparently occur at dawn and dusk. Patterns of thermal resource use are considered in relation to competition, predation, and thermal ecology of the more common species.

Key words: competition, fishes, habitat partitioning, Lake Michigan, predation, temperature

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La distribution, en fonction de la température, des poissons du lac Michigan a été étudiée par chalutage sur le fond ($n = 68$) dirigé le long des isothermes (3-20°C) dans une région où la thermocline touche le fond au large de Grand Haven, au Michigan, en septembre. Le gaspereaue (*Alosa pseudoharengus*), l'éperlan arc-en-ciel (*Osmerus mordax*), le queue à tache noire (*Notropis hudsonius*) et l'omisco (*Percopsis omiscomaycus*) constituent 94% des prises en nombre. Les espèces se répartissent séparément le long des gradients de températures. Ce compartimentage de l'habitat thermique se maintient en dépit des rapides oscillations de la thermocline. Le gaspereaue, l'éperlan arc-en-ciel et la perchaude (*Perca flavescens*) montrent des différences intraspécifiques dans la distribution thermique des classes de taille. Des déplacements de niches thermiques de certains poissons sur le fond semblent se produire au lever et à la tombée du jour. Nous analysons l'utilisation des ressources thermiques en fonction de la concurrence, la prédation et l'écologie thermique des espèces les plus communes.

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SYMPATRIC species often use different resources. This pattern of resource subdivision has often been attributed to competition (Larkin 1956; Schoener 1974), though predation and other interactions influence resource use. Habitat partitioning is common in fish communities (Nilsson 1967; Keast 1970, 1978; Zaret and Rand 1971; Moyle 1973; Mendelson 1975; MacLean and Magnuson 1977; Ross 1977; Werner et al. 1977; Gorman and Karr 1978). Partitioning of food resources within the same habitat, though less common, also occurs in fish communities (MacLean and Magnuson 1977; Ross 1977; Werner 1977; Werner et al. 1977). Partitioning resources by use of different times of day may allow coexistence (MacLean and Magnuson 1977; Svenson 1977).

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As Moermond (1979) has recently pointed out, most resource partitioning studies of freshwater fish communities have involved small streams and lakes in which physical structure of the habitat may provide a template for habitat partitioning. But what about the fish communities of large lakes which have reasonably uniform bottom habitat? On which axes might resource partitioning occur?

Within larger-scale, more pelagic systems, temperature provides structure in a seemingly homogeneous habitat. Temperature also functions importantly as a determinant of physiological and biochemical rates (Fry 1971) and small-scale changes in temperature can have important consequences to an organism's survival, growth, and/or reproductive success (e.g. Kitchell et al. 1977). Behavioral thermoregulation of fish is well documented (Ferguson 1958; Brett 1971; Neill and Magnuson 1974; Beitinger 1975; Coutant 1977). If species within a system inhabit and forage in different thermal zones, potential predator-prey and

competitive interactions may be minimized (MacLean and Magnuson 1977). Of course, only manipulative experimentation can directly verify competition (MacLean and Magnuson 1977). Our purpose here is to examine the thermal distribution of fishes within Lake Michigan to determine if evidence exists for thermal habitat segregation among species.

Methods

SAMPLING STRATEGY

The intersection of the thermocline with the bottom provides a natural experiment on fish distribution because gradients of temperature along the bottom are dynamic. Particular temperatures are found at different geographic or bathymetric positions on different days because of wind and seiche effects, and temperatures at a single point vary with time. Our sampling strategy was to measure by bottom trawling the distribution of fishes across a region where the thermocline intersected the bottom (hereafter referred to as the front).

From September 7 to 13, 1977, we sampled a frontal region (3–20°C) off Grand Haven, Michigan. The sampling scheme employed strata based on isotherms. Temperatures, taken at each station, were used to determine the position of subsequent stations such that sampling effort would be evenly allocated to various temperature strata both day and night.

DATA COLLECTION AND PROCESSING

At every station vertical temperature profiles were determined with a shallow-water 60-m bathythermograph (BT). Surface temperatures were recorded continuously between stations and during trawls. Additionally, at each station we measured temperature at the surface (surface bucket sample) and 1 m above the bottom (8-L Niskin water bottle sample) with a mercury thermometer.

Fish were collected with 15-min (range 12–17 min) bottom tows with a semiballoon otter trawl from the RV *Laurentian*. This bottom trawl had a 7.6-m headrope and body of 2-cm-stretch mesh nylon; the cod end was lined with 0.6-cm-stretch mesh.

We mounted a thermistor to the headrope of the trawl to aim the trawl to fish along isotherms. The thermistor was connected to an onboard graphic recorder (Montedoro Whitney model TC-10-5) via a cable. The continuous thermal record enabled us to trawl along relatively constant isotherms even though temperature changed up to 8°C horizontally across the bottom in less than 500 m. Often a constant trawling temperature was maintained easily by following depth contours. Temperatures along the 68 hauls were read at 1-min intervals to the nearest 0.1°C and means calculated for each tow. Maximum and minimum temperatures of each tow were taken from the entire record.

All fish were counted and identified to species. Within a species, all individuals up to 50 per trawl haul were preserved. If more than 50 were caught, a random subsample of at least 50 individuals was preserved. A few of the larger individuals, including lake trout (*Salvelinus namaycush*), yellow perch (*Perca flavescens*), and carp (*Cyprinus carpio*) were measured immediately to the nearest millimetre and released. For preservation, fish were immediately put en masse into a plastic bag, placed between two slabs of dry ice, and then stored in a freezer. At the laboratory, thawed fish were measured (fork length, mm).

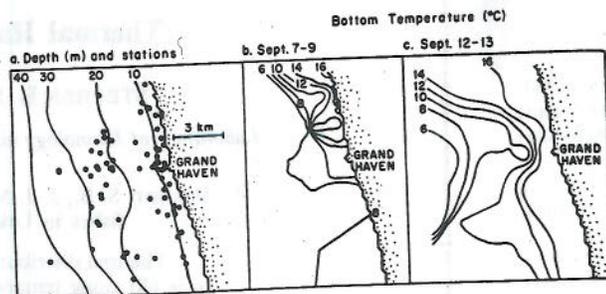


FIG. 1. Station locations and depth (a) and bottom temperatures for September 7–9 (b) and September 12–13 (c). Some stations were sampled more than once during the cruise. Note that thermal structure is highly dynamic (From Brandt 1980).

Day and night trawl catch data were categorized into 2°C thermal strata based on mean trawl temperature (mean temperature range per trawl = 1.3°C). Geometric mean of catch per unit effort (15-min bottom time) was calculated for each species for each 2°C interval. All statistical comparisons between trawl catches were nonparametric (Dunn 1964; Zar 1974; Gibbons 1976). Comparisons among fish catches at different thermal strata were made using the Kruskal-Wallis analysis of variance and, subsequently, Dunn's (1964) multiple comparison test ($\alpha = 0.1$). Comparisons between day and night catches of fish were made using the Mann-Whitney *U* test. Other statistical comparisons are given with the results. A $P \leq 0.05$ was considered significant.

Results

The intersection of the thermocline with the bottom was marked by reasonably sharp thermal gradients across the sloping bottom (as steep as 1°C/50 m). At any one time, the isotherms paralleled the bathymetry. However, the front was quite dynamic. Throughout the sampling period the intersection of the front with the bottom shifted from depths of ~14 to 30 m (Fig. 1). Mean trawl temperatures ranged from 4.0°C to 19.5°C (see Brandt 1980).

COMPOSITION OF TRAWL CATCH

A total of 20 352 fish representing 16 species were captured (Table 1). Alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), spottail shiner (*Notropis hudsonius*), and trout-perch (*Percopsis omiscomaycus*) were the most abundant species and represented 94% of the total catch. To compare thermal differences within species, we subdivided catches of alewife, spottail shiner, trout-perch, rainbow smelt, and yellow perch into size (age) categories (Fig. 2). Young-of-the-year (YOY) alewives (<80 mm) represented nearly one-third of all fish caught and over 85% of all alewives (Table 1). Size distribution of spottail shiner was distinctly trimodal (<55 mm, 55–80 mm, >80 mm). Trout-perch were subdivided into two size-categories (<85 mm, >85 mm). Larval smelt (<60 mm) represented 10% of total fish

TABLE 1. Total catch of fish for day and night bottom trawls in Lake Michigan, listed in order of decreasing abundance. Data were collected from 68 tows during September 7-13, 1977.

Species	Life stage	Day	Night	Total	% total
Alewife	Adult	1083	35	1188	5.5
	YOY	6354	258	6612	32.5
	Total	7437	293	7730	38.0
Trout-perch		302	2095	3397	16.7
Rainbow smelt	Adult	891	384	1275	6.3
	Larval	510	1532	2042	10.0
	Total	1401	1916	3317	16.3
Spottail shiner		2532	2078	4610	11.7
Deepwater sculpin		0	427	427	2.1
Yellow perch		173	253	426	2.1
Slimy sculpin		3	199	202	1.0
Johnny darter		5	83	88	0.4
Ninespine stickleback		24	44	68	0.3
Bloater and cisco		19	43	62	0.3
White sucker		1	8	9	<0.1
Lake trout		0	8	8	<0.1
Longnose sucker		1	4	5	<0.1
Bluegill		2	0	2	<0.1
Carp		1	0	1	<0.1
Total		11901	8451	20352	99.9

catch and nearly two-thirds (61.6%) of all smelt. The catch of yellow perch was about equally divided between juveniles (<85 mm, 54.9%) and adults (>100 mm, 45.1%). Only four individuals 85-100

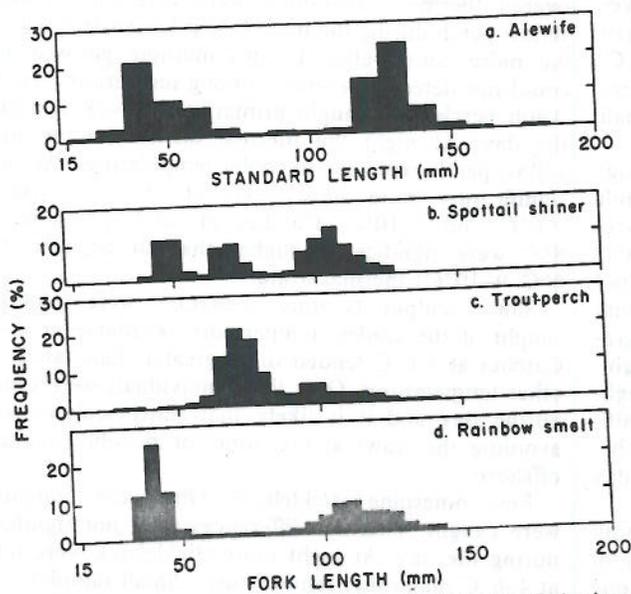


FIG. 2. Frequency distribution of standard length of alewives (a) and fork length of spottail shiner (b), trout-perch (c), and rainbow smelt (d) caught in bottom trawls during September. Samples are combined for day and night.

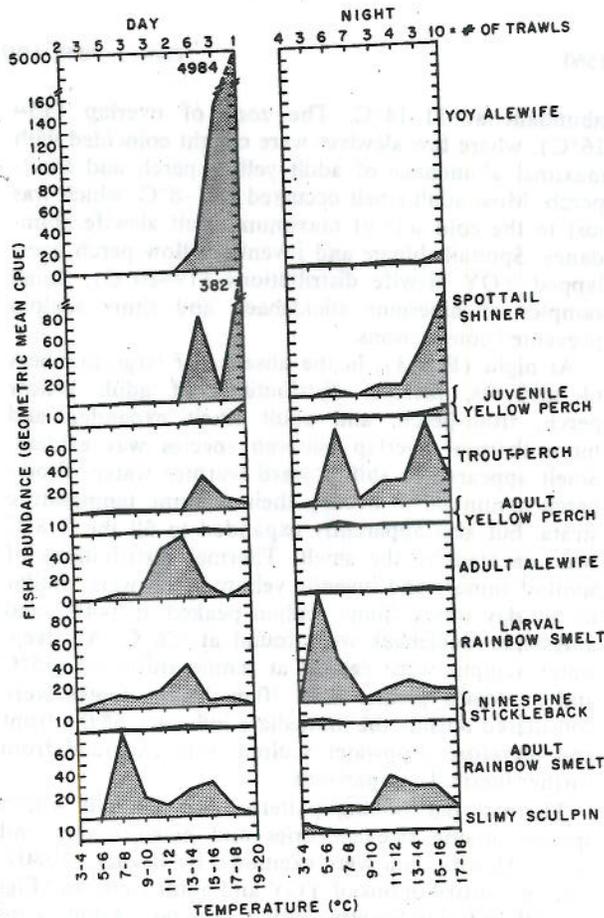


FIG. 3. Abundance of dominant fish species (geometric mean catch per unit effort (CPUE)) in Lake Michigan during day and night for each 2°C temperature strata. Fish were collected using a bottom trawl during September.

mm were caught; 95% of adults caught were 180-300 mm long.

THERMAL DISTRIBUTION OF FISH

The distribution of each of the six most abundant species (alewife, smelt, spottail shiner, trout-perch, deepwater sculpin, and yellow perch) differed significantly with temperature. Thermal distributions were maintained despite rapid changes in thermal structure. Differences in thermal distributions were often detected among species and among size-categories within species. Thermal distribution often varied day to night between and within species.

When we compare the thermal distributions among species in Lake Michigan, fish seem to be thermally segregated from each other, particularly during the day (Fig. 3). Different species reached maximum abundance at different temperatures. YOY alewives reached maximum abundance at temperatures greater than 17°C during the day. Adult alewives were most

abundant at 11–14°C. The zone of overlap (15–16°C), where few alewives were caught coincided with maximal abundance of adult yellow perch and trout-perch. Most adult smelt occurred at 7–8°C, which was just to the cold side of maximum adult alewife abundance. Spottail shiners and juvenile yellow perch overlapped YOY alewife distributions (19–20°C). Small samples of ninespine stickleback and slimy sculpin prevented comparisons.

At night (Fig. 3), in the absence of large numbers of alewives, thermal distributions of adult yellow perch, trout-perch, and adult smelt expanded and more thermal overlap between species was evident. Smelt appeared to shift toward warmer water. Trout-perch continued to occupy their daytime temperature strata, but also apparently expanded to fill the 7–8°C zone vacated by the smelt. Thermal distributions of spottail shiners and juvenile yellow perch were similar to the day series. Slimy sculpin peaked at 3–4°C and ninespine stickleback were found at <6°C. All deep-water sculpin were caught at temperatures of ≤5°C and at depths greater than 70 m. These depths were considered outside the immediate influence of the front and therefore deepwater sculpin were excluded from further thermal comparisons.

Thermal partitioning patterns also differed within species among size-categories and between day and night. Alewife data were examined by Brandt (1980). Thermal distributions of YOY and adult alewives (Fig. 3) differed significantly during the day. Adults captured on or near the bottom were most abundant at temperatures of 11–14°C ($P < 0.1$). YOY alewives were captured mainly at temperatures greater than 15°C ($P < 0.1$) and the majority were at 17–20°C. Night catches of both YOY and adult alewives were significantly less than day catches and were too small to discern nocturnal thermal distributions.

Thermal distributions of adult smelt differed significantly between day and night. During day, adult smelt were widely distributed between 7 and 18°C ($P < 0.1$) with maximum abundance at 7–8°C (Fig. 3). At night, modal smelt distributions shifted to warmer water (11–16°C). The shift in the thermal distribution may have resulted from a vertical migration of smelt at 7–10°C into the water column at night. Total bottom catch of adult smelt was lower at night (Table 1) but day and night catches were not significantly different. No differences could be detected between the size-distributions of adults taken during day and night ($P > 0.05$, Median test).

Larval smelt were caught at all temperatures both day and night (Fig. 3). During the day catches of larval smelt were not significantly different among thermal strata although the mode occurred at 13–14°C. At night there were significant differences in the overall thermal distribution of larval smelt ($P < 0.05$, Kruskal-Wallis) although pairwise differences could not be detected with the conservative Dunn's (1964) test. Maximum occurrence was at 5–6°C. Larval smelt

were believed to be predominantly pelagic (Jude et al. 1978) and were often caught in midwater by the ascending or descending trawl. Thus, their broad thermal distribution may only represent an epilimnetic distribution.

Spottail shiners were concentrated in the warmest water available (Fig. 3). No differences in thermal distributions were detected among the three size-categories or between day and night. Significantly more spottail shiners were captured at 15–20°C than at all other temperatures.

Both total catch and thermal distribution of trout-perch differed significantly between day and night (Fig. 3). Data suggest that either trout-perch were avoiding the bottom trawl during the day or that extensive onshore-offshore migrations were occurring. During the day, trout-perch concentrated at temperatures greater than 15°C. The thermal distribution of trout-perch expanded at night to 7–18°C. The thermal distribution appeared bimodal at night but no significant differences among temperatures could be ascertained. Night catches were significantly greater than day catches at 7–8°C but not at 15–20°C (Mann-Whitney U , $P < 0.05$). No significant differences between thermal distributions of size-groups could be demonstrated.

The distribution of juvenile and adult yellow perch differed significantly with temperature (Fig. 3). No day-night differences could be detected for juveniles. Catches at 15–20°C were significantly larger than catches at cooler temperatures. Although differences in overall thermal distribution were detected for adult yellow perch during the day ($P \leq 0.1$, Kruskal-Wallis), the more conservative Dunn's multiple pairwise test could not detect differences among temperature strata. Adult perch were caught primarily at 15–18°C during the day. At night the thermal distribution of adult yellow perch expanded to cooler temperatures. At night significantly more adults were at 15–18°C than at <6°C and 9–10°C. Catches of adult perch at 7–8°C were significantly higher than at adjacent (5–6°C, 9–10°C) thermal strata.

Slimy sculpin (*Cottus cognatus*) were generally caught at the coldest temperatures available at night. Catches at <6°C tended to be greater than catches at other temperatures. Only three individuals were caught during day and it is likely that slimy sculpins were avoiding the trawl at this time, or possibly migrated offshore.

Few ninespine stickleback (*Pungitius pungitius*) were caught. Thermal differences were not significant during the day. At night more stickleback were taken at 4–6°C than other temperatures. Small samples of all other species (johnny darter, *Etheostoma nigrum*; longnose sucker, *Catostomus catostomus*; white sucker, *Catostomus commersoni*; lake trout; lake herring, *Coregonus artedii*; bloater, *Coregonus hoyi*; bluegill, *Lepomis macrochirus*; carp) prevent conclusions about thermal distributions.

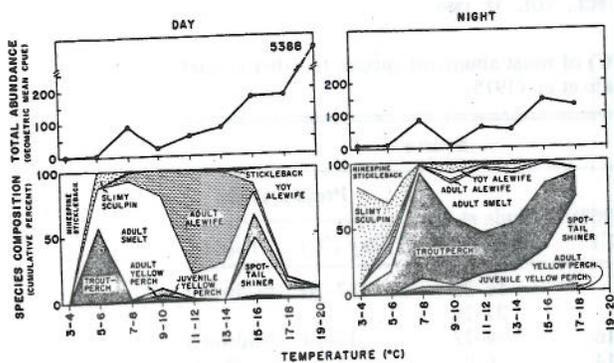


FIG. 4. Total abundance (geometric mean CPUE) and species composition (cumulative percentage) of trawl catches at each 2°C temperature stratum for day and night.

Trawl catch tended to increase with temperature both day and night (Fig. 4). The composition of day trawl catch was dominated by different species or size-classes at different temperatures (Fig. 4) though alewife and smelt predominate. A somewhat different pattern was evident at night when alewife vertically migrate and are seldom caught on the bottom (Janssen and Brandt 1980). Trout-perch, spottail shiner, and smelt are most common in night catches.

Discussion

Our data document that the most abundant fish species in Lake Michigan occur at different temperatures. One interpretation of these results is that fish are partitioning thermal resources (MacLean and Magnuson 1977; Magnuson et al. 1979). Habitat segregation by temperature could be an effective means of reducing potential competition for food and/or predation. By occupying different thermal zones, these fish (or age-groups within species) may effectively isolate themselves from other fish species. Adults of these species share many common prey including *Mysis relicta*, *Pontoporeia hoyi*, and larger zooplankton species (Smith and Kramer 1964; Morsell and Norden 1968; Lackey 1969; Anderson and Smith 1971; Rasmussen 1973; Brandt 1978; Janssen and Brandt 1980). Small fishes may have even larger diet overlaps, since most species probably feed on small copepods, cladocerans, and rotifers (Norden 1968; Siefert 1972). Availability of prey taxa, size spectrum, and abundance may also differ at different temperatures (Wells 1960; Lane 1975).

Adult yellow perch and trout-perch reach peak abundance, and spottail shiners occur in large numbers at the narrow temperature zone where alewife size-groups overlap (15–16°C) and neither are particularly abundant. Adult smelt, however, are most abundant just to the cold side of alewife thermal distributions. Whether these temperatures are preferred or whether fish have shifted their thermal distributions in response to the abundant alewives is a matter of conjecture.

Detailed information on the thermal distributions of fish in Lake Michigan before the alewife invasion is not available.

Fish and other taxa shift niches in response to presence of potential competitors (for other examples see reviews by Nilsson 1967; Schoener 1974; Colwell and Fuentes 1975; Werner and Hall 1976, 1979; Diamond 1978; Sale 1979). Observations that fish have thermal niche widths of about 4°C (Neill and Magnuson 1974; Magnuson et al. 1979) suggest that fish have some flexibility in thermal selection and may be able to shift distributions in thermal space. Although preferred temperatures of centrarchids in laboratory experiments are relatively unaffected by abiotic variables (Magnuson and Beiting 1978), social interactions (Beiting and Magnuson 1975; Medvick et al. 1981) and prey availability (Neill and Magnuson 1974) can alter thermoregulatory behavior. Partial evidence of niche shifts is provided by the apparent expansion of thermal habitats of trout-perch, smelt, and adult perch at night when alewife vacate the bottom.

Our data cannot separate the effects of competition and predation (MacLean and Magnuson 1977). Distributions of predators or prey could strongly affect thermal distributions of fish. For example, segregation of size-groups within a species could be a mechanism to reduce potential cannibalism. The adults of smelt, yellow perch, and alewives have been observed to feed on their young (Rhodes et al. 1974; Jude et al. 1975). Both smelt (O'Gorman 1974) and alewives (Rasmussen 1973; Webb and McComish 1974) feed on larval fish of other species in Lake Michigan. Unpublished laboratory studies (T. Edsall, U.S. Fish and Wildlife Service, personal communication) indicated that smelt larvae are rapidly digested by alewives and would be unlikely to appear in alewife stomachs from field collections.

Conclusions from this study must be considered in light of the assumptions made. Comparisons of thermal distributions assumed that species or size-categories within a species have equal catchability at different temperatures (if they occur there). This assumption was evidently not true for larger species (lake trout, carp, suckers), pelagic species (alewives at night), or for fish that may avoid the trawl. We also assumed that trawl efficiency and operation was constant for each tow. Statistical differences among thermal strata with small sample sizes (no. of trawls) could have resulted from malfunctioning of the trawl. This was unlikely, however, since trawls were taken randomly with respect to temperature, and thermal distributions were consistent. Trawl catches of adult fishes in mid-water by the ascending or descending trawl were likely small.

That fishes were indeed responding to temperature is evidenced by the fact that the actual temperatures at which fish were caught coincided with previous studies of the thermal distributions of these species in

TABLE 2. Comparison of thermal distribution (°C) of most abundant species to other studies in Lake Michigan. Data from Wells (1968) and Jude et al. (1975).

Species	Life stage	Source			
		Wells (1968) day (°C)	Jude et al. (1975) (°C)	Present study	
				Day (°C)	Night
Alewife	YOY	—	16–20 24–28	17–20	Midwater
	Adult	11–16	16–22	11–14	Midwater
Smelt	Adult	6–14	6–8	7–8	11–16
Spottail shiner		>13	11–16	17–20	17–20
Trout perch		10–16	16–18	15–16	7–16
Yellow perch	Juvenile	>11	20–24	>15	>17
		>11	16–22	>15	7–8
					11–17
Slimy sculpin		4–5	6–8	—	4–6
Deepwater sculpin		<5	—	—	<5

Lake Michigan (Wells 1968; Jude et al. 1975) (Table 2) and with temperature preferences determined in the laboratory. For example, peak abundance of adult smelt at 7–8°C was nearly identical with laboratory determined temperature preferences of 6–8°C (Ferguson 1965; Hart and Ferguson 1966). Similarly yellow perch usually prefer temperatures of ~20–22°C and juveniles tend to prefer higher temperatures than adults (McCauley and Read 1973; Reutter and Herdendorf 1974; Jude et al. 1975; Coutant 1977). Young-of-the-year alewives prefer 25°C while adults prefer 16°C (Otto et al. 1976). Thermal distributions were maintained throughout the sampling period despite rapid changes in the configuration of the thermal structure. Responses of fishes to temperature may have been more precise than indicated by the data since bottom trawls occasionally sampled across thermal strata. (For trawl temperature ranges see Brandt 1980.)

During summer, when higher temperatures prevail, physiological rates, demand for resources, and the intensity of interspecific interactions are likely to be at a maximum (MacLean and Magnuson 1977). While Wells' (1968) data on the seasonal distribution of fish species in Lake Michigan (for 1964) indicate extensive overlap in bathymetric distributions in summer, it is now apparent that these species are more finely segregated in temperature-space. Since shifts in thermal structure (due to wind stress and internal seiches) are common and often rapid events in Lake Michigan (Mortimer 1971; Mortimer and Csanady 1975), a further element of predictability may be added to ecological studies of fish by considering temperature. Taking temperature into closer account should allow us to unravel some of the details of species interactions among Great Lakes fishes.

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