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Partitioning of food resources by sculpins in Lake Michigan

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Synopsis

Resource partitioning was studied in two benthic Lake Michigan fishes, the deepwater sculpin, *Myoxocephalus thompsoni*, and the slimy sculpin, *Cottus cognatus*, that exhibit nearly disjunct distributions along a hypolimnetic depth gradient. Fish were collected in an area of sympatry over two 24 h periods. These sculpins exhibited food segregation – slimy sculpins ate primarily *Pontoporeia affinis*, deepwater sculpins ate both *P. affinis* and *Mysis relicta* – and their depth segregation was associated with the reported abundance of these prey. Different feeding behaviors may be responsible for this association, since slimy sculpins consumed intermediate size ranges of *Pontoporeia* and deepwater sculpins consumed *Pontoporeia* in a pattern similar to the ambient size distribution. Neither fish showed a daily activity cycle, and both appear food-limited.

Introduction

Recent studies suggest mechanisms by which Lake Michigan fishes partition resources in a deep lake environment that provides little variation in physical structure (Brandt et al. 1980, Crowder et al. 1981). These studies have focused on highly mobile fishes that can rapidly change location in response to variations in temperature and prey abundance (Brandt et al. 1980, Janssen & Brandt 1980, Crowder et al. 1981, Crowder & Magnuson 1982).

In this study we explored resource partitioning in two benthic fishes, the deepwater sculpin, *Myoxocephalus thompsoni*, and the slimy sculpin, *Cottus cognatus*, that exhibit nearly disjunct distributions along a hypolimnetic depth gradient in Lake Michigan. Slimy sculpins have been reported to be most abundant at depths from 27 to 73 m, and deepwater sculpins have been reported most abundant at

depths greater than 82 m (Wells 1968). Wells observed an area of sympatric occurrence at depths between 73 and 92 m. The physical environment inhabited by these fishes is nearly constant: both bottom sediments and temperature are uniform throughout the year. The typical mid-summer thermocline depth in Lake Michigan is between 10 and 20 m, with hypolimnetic bottom temperatures ranging seasonally from 3 to 6° C. A modest change in light intensity is probably the sole physical feature that varies over the depth range inhabited by slimy and deepwater sculpins.

Our objective was to determine what factors influence the distribution of deepwater and slimy sculpins in the homogeneous profundal environment of a freshwater lake ecosystem. Differences in these species' feeding in response to diurnal fluctuations in light intensity and differences in feeding habits were examined as two potential ex-

planations for their distribution. Data concerning the type and timing of prey selection were collected with these questions in mind. The relationships of predator size to prey size and number, as well as prey size to ambient prey size distribution – relationships previously used to characterize the energetics and optimal foraging patterns of visual predators – were also examined.

Materials and methods

Fish were collected about 9 km northeast of the Milwaukee harbor entrance in 24 h field collections made by bottom trawling on June 7–8, and October 10–11, 1976, from the R/V *Aquarius* at a speed of 1.5 ms^{-1} (three knots). The 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. The study area and duration of trawling were chosen by making preliminary collections over a range of depths at which slimy and deepwater sculpins occur. A permanent sample depth was selected where both species occurred in approximately equal numbers. Trawls were alternately north-south in direction along the 80 and 86 m depth contours, respectively, in June and October. Echosounder readings were used to guide the vessel along the selected contour depth.

June trawls ran for 10 or 20 min; durations were chosen to obtain sample sizes of at least 10 fish per species. In October each trawl ran 20 min and at least 30 fish per trawl were obtained. Five sample collections were made during June, six during October.

Fishes were frozen on dry ice immediately after collection in the field, then thawed and measured (total length) in the laboratory. Stomachs were removed by dissection and the contents placed in distilled water. Only two prey types were common: *Pontoporeia affinis* (Crustacea, Amphipoda) and *Mysis relicta* (Crustacea, Mysidaceae). Intact food items were counted under a dissecting microscope, then measured with an ocular micrometer (second antennal segment to tip of uropod). Any prey item that had lost these appendages was not counted and measured. Various levels of digestion were ob-

served among intact prey organisms.

Stomachs from June samples were preserved in alcohol and the fish were discarded. All stomach samples and fish from the October cruise were dried at 55°C for 2 weeks. Stomach contents were desiccated separately from the remains of each fish to determine stomach content as a percentage of fish weight. Dry samples were weighed on an analytical balance. Replicate measurements were taken on consecutive days to ensure that samples were completely dried.

Results

Slimy sculpins predominated at depths less than 75 m in June and 81 m in October; deepwater sculpins predominated at depths greater than 85 m in June and 91 m in October. The area of greatest distributional overlap between the two species covered a 10 m depth range during both June (75–85 m) and October (81–91 m). These observations are consistent with those made in southeastern Lake Michigan by Wells (1968).

Pontoporeia affinis and *Mysis relicta* were the predominant prey items for deepwater and slimy sculpins in both June and October (Table 1). Chi-square tests (frequency of occurrence) showed that slimy sculpins consume significantly more *Pontoporeia* than deepwater sculpins in both June and October ($p < 0.01$). Deepwater sculpins consumed significantly more *Mysis* than did slimy sculpins in both June and October ($p < 0.01$). These data are consistent with Wells (1980). The only seasonal prey difference evident was the presence of fish eggs in October, of which slimy sculpins contained significantly more than deepwater sculpins. Less than 1% of the stomachs examined contained identifiable remains of sphaerid clams or oligochaetes. Fragments of filamentous algae and cinders were the only other identifiable stomach content.

No diel differences in feeding were found. To test for feeding periodicity associated with photoperiod we compared the number of fish with intact prey in day versus night samples collected in June. No significant differences were found for either sculpin species ($\chi^2 = 2.6$, deepwater; $\chi^2 =$

0.28, slimy). Tests for individual prey types also showed no significant differences ($\chi^2 = 0.56 - 2.1$).

Since the absence of periodicity in prey number was an unanticipated result of the June collections (see Discussion), weight of stomach contents was analyzed as an additional test of periodicity. Analysis of covariance (detailed in Kraft 1977), using weight of stomach contents as the dependent variable and fish weight as a covariate, showed no difference among October sample periods for either deepwater or slimy sculpins (Fig. 1). Night versus daylight differences were tested by contrasting the stomach weights of fish caught at 1530 and 0830 h against those caught at 1845, 2230, 0115 and 0330 h. No significant difference was found for either species.

For October samples, chi-square tests of day versus night differences in individual prey types were insignificant in all cases but one: slimy sculpins contained significantly more *Pontoporeia* at night than during the day ($p < 0.01$). However, since both stomach contents weight data and the June samples failed to confirm this pattern in slimy sculpins, we consider this observation anomalous.

The relationships between sculpin size and prey size, as well as number of prey, were tested using October samples (177 deepwater sculpins: 55–135 mm; 256 slimy sculpins: 43–99 mm). The hypothesis that larger fish ate larger prey items was tested in several ways. First, using regression analysis, no significant relationship between fish size and *Pontoporeia* or *Mysis* length was found for either sculpin species. Second, t-test comparisons demonstrated no significant difference in prey sizes among 10 mm sculpin size intervals. Finally, we plotted the largest prey item in each fish as a func-

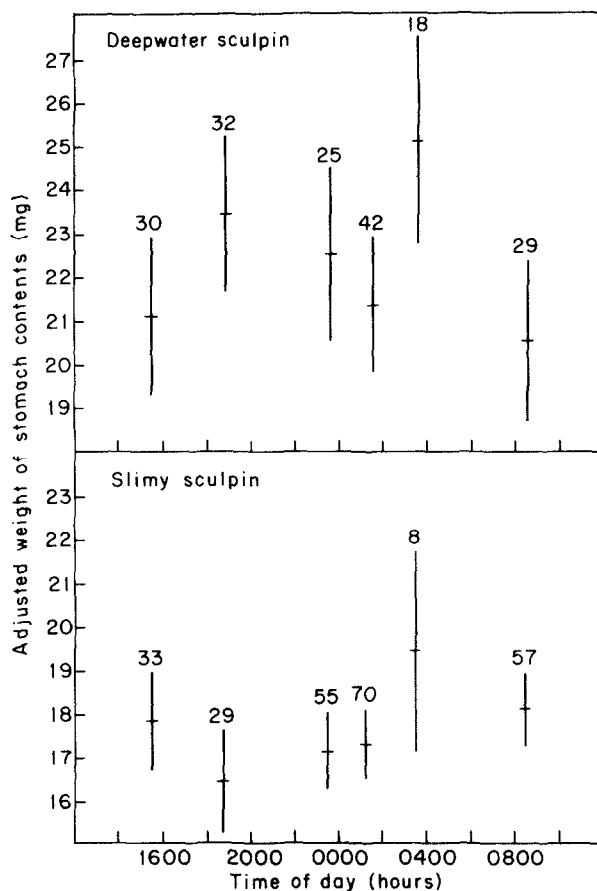


Fig. 1. Weight of sculpin stomach contents (mg) adjusted for covariance in fish size. The mean + 1 SE of the weight of material in stomachs is shown for each sample period. The number of fish in a sample is given at the top of each bar.

tion of fish size to determine whether prey size became limiting below a given predator length (e.g. due to handling time). No such relationship was evident over the size ranges examined.

Chi-square tests of independence did not reject the null hypothesis that the number of *Pontoporeia*

Table 1. Frequency of occurrence of intact food items in deepwater sculpin and slimy sculpin stomachs.

	Mysis		Pontoporeia		Eggs		Misc.		Number of stomachs	
	June	Oct.	June	Oct.	June	Oct.	June	Oct.	June	Oct.
Deepwater sculpins	32	42	33	22	—	10	1	1	73	177
Slimy sculpins	2	8	74	74	—	48	1	1	121	256

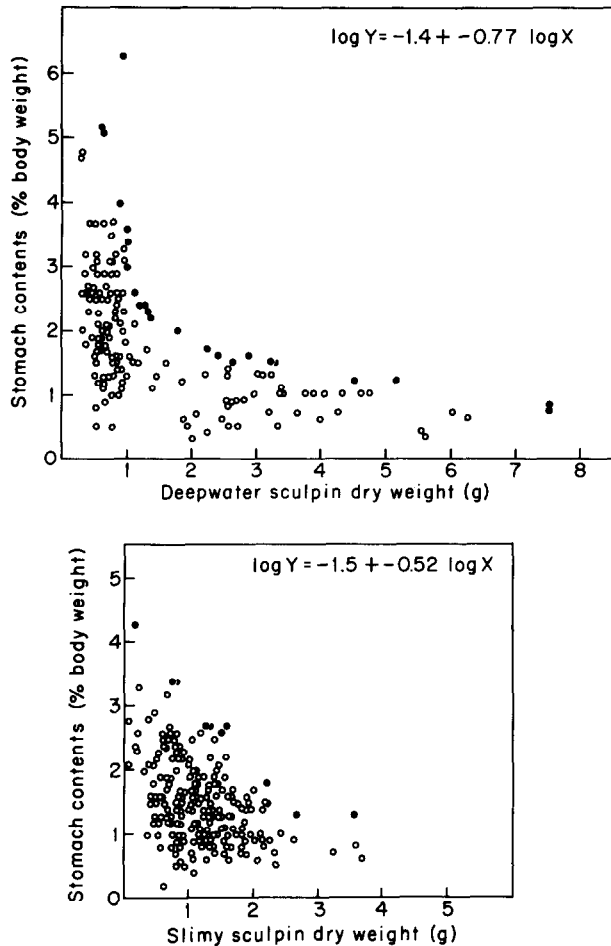


Fig. 2. Sculpin stomach contents (% body weight) as a function of fish weight. Solid circles are maximum observed stomach fullness, as described by the equations in the figure.

and *Mysis* in stomachs was independent of predator size when comparing sculpins smaller than 100 mm with fish larger than 100 mm TL.

To test for size-related changes in predator success, we plotted the relation between observed stomach fullness and fish weight for each individual. Maximum values of stomach contents as percent body weight were then selected (Fig. 2). These points are described by power functions ($Y = aX^b$) which had similar constants (a) but different exponents (b) of -0.77 and -0.52 for deepwater and slimy sculpins, respectively.

The distributions of prey sizes in October sculpin stomachs are shown in Figure 3. Figure 3A also shows the size distribution of *Pontoporeia* collected

by Lubner (unpublished data) three days prior to our October collection. Lubner's samples were taken at a similar depth (89 m) and same general location as our study.

A Kolmogorov-Smirnov Two-Sample Test was used to examine differences between the distribution of *Pontoporeia* in sculpin stomachs and the sediment, excluding prey below 2.9 mm length (see Discussion) from the ambient distribution. No significant difference was found between deepwater sculpin prey and the environment; slimy sculpins were found to contain a significantly different prey distribution ($P < 0.001$).

Discussion

Timing of feeding

Our observations indicate that sculpins at 80–86 m depth in Lake Michigan feed at a constant rate and presumably maintain a constant level of activity throughout the day (Fig. 1). This contrasts with other observations of these and closely related cottid fishes that have been observed to feed or be most active at night: *Myoxocephalus thompsoni*, *Cottus cognatus*, *C. ricei* in Lake Superior (Selgeby, personal communication), *Myoxocephalus quadricornis* in Baltic Sea (Westin 1971), *C. bairdi* in Lake Michigan (Hoekstra & Janssen 1985), *C. asper* in California (Broadway & Moyle 1981), and *C. bairdi* in Ontario lakes (Emery 1973). These observations of nocturnal activity in sculpins have been made at depths shallower than our sample depths, where photoperiod effects are more likely.

We recognize the problem of determining feeding periodicity by examining stomach contents of fish with slow evacuation rates. Therefore we compared both numbers of intact prey and weight of stomach contents as indicators of periodicity. A peak in intact prey, though not necessarily reflective of the exact timing of feeding, should have been observed if feeding periodicity was evident (Eggers 1977).

Field observations, supported by laboratory observations of feeding by blinded *C. bairdi*, indicate

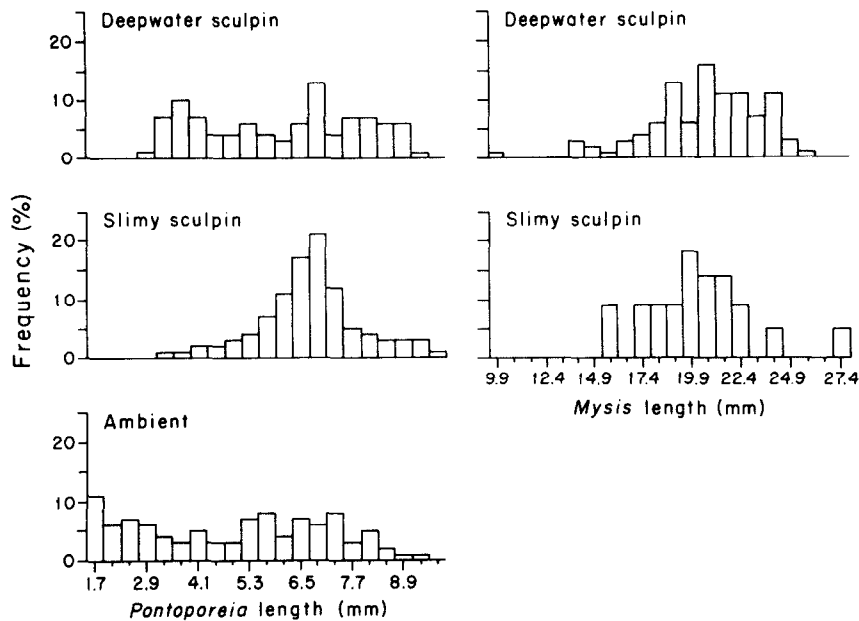


Fig. 3. Frequency distribution of *Pontoporeia* (n = 65, deepwater; n = 618, slimy) and *Mysis* (n = 108, deepwater; n = 24, slimy) lengths (mm) in deepwater and slimy sculpin stomachs. Ambient *Pontoporeia* distribution (n = 147) from Lubner (unpublished data).

that sculpins do not rely on vision for prey detection. Rather, they act as proprioceptive predators, responding to mechanical stimuli (Hoekstra & Janssen 1985).

The absence of diel periodicity in our samples may reflect the fact that sculpins continuously encounter prey at depths where prey activity is not governed by diel light cycles. The maximum light intensity at 80 m is 0.01 lux (based on Beeton 1962). Both *Mysis* and *Pontoporeia* in Lake Michigan are nocturnally active at shallow depths with increasing diurnal activity at greater depths (Beeton 1960, Wells 1968, Robertson et al. 1968). *Mysis* become planktonic and *Pontoporeia* semiplanktonic during periods of darkness. In addition, avoidance of potential predators undoubtedly affects sculpin activity and feeding patterns. For example, Hoekstra & Janssen (1985) observed *C. bairdi* at 7 m depth under rocks only during the day, whereas at night they were fully exposed, which was also the only time they had food in their stomachs. Continuous darkness at greater depths may 'release' sculpins from such predator-avoidance behavior, allowing them to feed continuously throughout the diel period.

Distribution and prey selection

The food and depth segregation exhibited by deepwater and slimy sculpins is consistent with the observation that other native Lake Michigan fishes segregate according to food taxon or have only moderate overlaps in food and habitat (Crowder et al. 1981). Slimy sculpins inhabit shallower depths and eat primarily *Pontoporeia*. Deepwater sculpins inhabit greater depths and eat both *Mysis* and *Pontoporeia*.

We cannot attribute depth segregation to any known physical factor since: (1) temperature is constant at these depths (Brooks & Torke 1977), (2) the substrate consists of silt and clayey-silt for kilometers on either side of the study area (Powers & Robertson 1968), and (3) the lack of feeding activity cycles indicates that light fluctuations did not affect feeding by sculpins.

We believe, however, that differences in the ability of these fishes to feed upon *Mysis* and *Pontoporeia* – along with a change in relative prey abundance at greater depths – is responsible for sculpin depth-habitat segregation. Different behaviors by these prey affect their ability to be cap-

tured by fish predators. *Mysis* is easily swallowed but difficult to catch, whereas *Pontoporeia* is easily captured but difficult to swallow (Janssen 1978).

Although estimates of *Pontoporeia* and *Mysis* abundance in Lake Michigan differ according to sampling methods and time of year, consistent trends occur correlating relative abundance with depth. Lubner (1974, 1979) found *Pontoporeia* abundance, biomass and production to be greatest at 65 m, moderate (and not significantly different) at 90 m and 115 m, and lowest at 140 m. His sample transects covered the same location and time period as our study. Sell (1982) concluded that *Mysis* abundance, and probably production, increases with depth in Lake Michigan.

Johnson (1975) found a direct relationship between deepwater and slimy sculpin distribution and the abundance of *Pontoporeia* and *Mysis* in Great Bear Lake. He observed slimy sculpins at depths up to 3 m, and deepwater sculpins at all depths greater than 3 m. *Pontoporeia* were most abundant at 3 m and nearly absent at depths exceeding 20 m; *Mysis* were first collected at 3 m and their densities peaked at 57 m.

The prey size distribution in sculpin stomachs also provides insight into differences in the ability of these fish to feed upon their primary prey items. It is apparent from Figure 3A and our results that: (1) slimy sculpins selectively consumed certain sizes of *Pontoporeia* resulting in a normal distribution indicative of greater predation on prey of intermediate sizes, (2) deepwater sculpins consumed *Pontoporeia* of all size ranges above 2.9 mm in approximately equal amounts, and (3) neither sculpin species consumed *Pontoporeia* smaller than 2.9 mm length. The size distribution of *Pontoporeia* consumed by deepwater sculpins resembles the ambient distribution collected by Lubner (unpublished data), except for a lack of the lowest size categories. The small number of *Mysis* consumed by slimy sculpins ($n = 21$) and the lack of a comparable estimate of the ambient *Mysis* distribution renders us unable to make similar comparisons for *Mysis*.

The different *Pontoporeia* size distributions in the two sculpins probably reflect different feeding behaviors. Slimy sculpins exhibit prey size selec-

tion similar to another proprioceptive predator, *Chaoborus*, preying on *Daphnia* (Pastorok 1982). *Chaoborus* feeds upon larger prey sizes as a function of encounter frequency – which increases with the greater relative activity of larger prey but decreases due to their lesser numbers – until some size at which strike efficiency begins to decrease due to handling problems or reduced capture efficiency with larger prey.

Slimy sculpins' failure to feed upon large *Pontoporeia* may reflect handling constraints with larger prey. The failure of slimy sculpins to feed upon *Mysis*, however, is probably due to a combination of prey behavior, predator sensory abilities and predator behavior. Larger slimy sculpins were no more successful than smaller ones at capturing *Mysis*.

Prey selection by the Piute sculpin, *Cottus beldingi*, has been observed in the laboratory to be determined by encounter probability and capture success (Kratz & Vinyard 1981). Size-selective predation observed in stream-dwelling *C. cognatus* (Newman & Waters personal communication) and *C. bairdi* (Gilson & Benson 1979) may be explained in a similar fashion.

It is unclear why neither species consumed *Pontoporeia* smaller than 2.9 mm length. Whether this is due to an inability to detect items less than that size is uncertain, since eggs of less than 1 mm length were consumed. These could have been an incidental catch or a result of some other (e.g. chemosensory) predation mode. In another study of sculpin feeding it was noted that prey are prevented from escaping into the branchial cavity by gill rakers which project across the gill slits of the pharyngeal wall (Western 1969). Perhaps *Pontoporeia* below 2.9 mm length are able to crawl through the gill rakers.

Neither mean nor maximum prey sizes were correlated with predator size in these samples. Broadway & Moyle (1978) reported a similar result for *Cottus asper*. These observations contrast with other studies of benthic predators (Keast 1965, Cadwallader 1975, Kislalioglu & Gibson 1976). In addition, deepwater sculpins in our study contradict the observation that size-selective predation in bottom foraging fishes 'appears to be a general phe-

nomena' (Ringler 1979). Since similar observations have supported attempts to explain fish foraging behavior according to an optimal foraging theory, it would be fruitful to test these postulates on cottid fishes which may, like the proprioceptive predator *Chaoborus* (Pastorok 1982), yield spurious evidence of optimization due to the interactions of encounter frequency, size-limited capture success and size-biased ingestion probability.

Food limitation

The allometric relation between stomach volume and body volume is a power function ($Y = aX^b$), similar to the relation between maximum daily ration and body weight. The exponent of the relation between weight-specific maximum daily ration and body weight has been determined to be about -0.3 in several fish species (Kitchell et al. 1977).

The slopes of this function for deepwater and slimy sculpins were much greater than the value of -0.3 commonly observed for maximum daily ration (see Fig. 2). If the allometric relation between stomach volume and body volume is similar for a wide variety of fishes, then the highly negative slope found for deepwater and slimy sculpins suggests that food limitation increases rapidly with increasing fish size. Larger sculpins in our study ate a smaller percentage of their body weight than would be expected under ideal conditions of food availability. This is consistent with the hypothesis that predation rate is highly dependent on encounter rate and relatively independent of fish size.

In conclusion, our data suggest that the disjunct distribution of deepwater and slimy sculpins is related to differences in prey selection that result from different feeding behaviors, in conjunction with differences in the distribution of *Mysis* and *Pontoporeia*. This conclusion is supported by evidence that: (1) these are proprioceptive predators, (2) the distribution of slimy and deepwater sculpins coincides with areas of maximum *Pontoporeia* and *Mysis* abundance, respectively, (3) slimy and deepwater sculpins consume different size-frequencies of prey items, and (4) both appear food-limited.

Our observations show that deepwater and slimy sculpins provide a different perspective on many

commonly held assumptions regarding fish predation and energetics (O'Brien 1979, Werner 1979, Dill 1983). Because their prey detection systems are proprioceptive, cottid fishes should provide excellent experimental organisms for further studies of these mechanisms.

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