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Non-Visual Feeding Behavior of the Mottled Sculpin Cottus bairdi: Ecological and Evolutionary Implications

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NON-VISUAL FEEDING BEHAVIOR OF THE MOTTLED SCULPIN

Cottus bairdi:

ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS

by

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A Thesis Submitted to the Faculty of the Graduate

School of Loyola University of Chicago in Partial

Fulfillment of the Requirements for the Degree of

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VITA

The author, Denise Maxine Denham Hoekstra, is the daughter of Margaret Cavell (Gardiner) Denham and John Courtenay Denham (1907-1983). She was born July 15, 1959, in Portage la Prairie, Manitoba, Canada.

Her elementary education was obtained in the public schools of Portage la prairie, Manitoba and was completed in 1977 at the Vernon Senior Secondary School, Vernon, British Columbia, Canada.

In September, 1977, Ms. Hoekstra entered Capilano College North Vancouver and received two years of academic schooling. In September 1979 Ms. Hoekstra entered the University of British Columbia receiving the degreee of Bachelor of Science in biology in May, 1981.

In September, 1983, Ms. Hoekstra was granted an assistantship in biology at Loyola University of Chicago, enabling her to complete the Master of Science in biology in 1984.

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CHAPTER I

INTRODUCTION

Sculpins, demersal fish of the Cottidae family, can be found from shallow stream water (<1m) to the extreme depths (322m) of Lake Superior (McPhail and Lindsay 1970). The four Lake Michigan sculpin species are segregated according to depth. The deepwater sculpin, Myoxocephalus thompsoni, is found at depths greater than 82m while the more shallow dwelling slimy sculpin, Cottus cognatus, is most abundant at depths of 27 to 80m. The spoonhead sculpin, Cottus ricei, is commonly found near 80m (McPhail and Lindsay 1970). Cottus bairdi is the shallowest of the four species, it being found at <1 to 10m.

Field evidence suggests that Great Lakes sculpins can feed non visually. At 80m maximum light intensities are low (0.01 lx based on Beeton 1962) and close to the feeding threshold for the visually depen- dent Atlantic Herring, Clupea harengus, (Blaxter 1966). Herring have considerably larger eyes (i.e. than the cottids) and hence probably more sensitive eyes (Lythgoe 1979) for visual prey detection. The low light intensity at 80m and the small size of the cottid eye suggests nonvisual prey detecting capability. Kraft (1977) found that there was no diel feeding periodicity for the deepwater and slimy sculpin at 80 to 86m.

In this study the mottled sculpin, Cottus bairdi, (found at <1 to 10m) was used to test whether there are alternatives to vision for prey

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detection. Most investigation of the relationship between feeding and sensory systems in fish have been limited to studying vision (Zaret 1980). However, many fish have other sensory specializations such as chemosense (Bardach and Case 1965; Bardach et al. 1967; Todd et al. 1967), electroreception (Kalmijn 1974) and the lateral line (Bleckmann et al 1981; Bleckmann and Schwartz 1982).

The mottled sculpin has been used in this initial study of nonvisual feeding and prey detection as it is the species of Great Lake sculpin most easily collected and maintained. With regards to Great Lakes sculpins in general, this approach is conservative as this species is least likely to require a nonvisual feeding mode. Hence, if a sense other than vision is used in the species found in an area where visual detection is possible, one can be reasonably sure that this alternative sense(s) can be used in other deeper dwelling species where light levels are low. The present study demonstrates nocturnal feeding in Lake Michigan. Emery (1973) also observed feeding at night by this sculpin but used diving lights for observation so visual detection cannot be excluded. My laboratory experiments show that blinded sculpins feed readily and prey detection is mechanosensory, via the lateral line system. Chemical cues are not necessary and are ignored without mechanical stimulus. Mapping the receptive field of the mottled sculpin's lateral line system and comparison with the morphology of the lateral lines of other sculpin species shows some possible ecological and evolutionary relationships.

MATERIALS AND METHODS

Laboratory Experiments

All fish were collected in hand nets from Lake Michigan while SCUBA diving 1-2km from the Chicago shoreline in 7-10m of water. Sizes ranged from 5 to 10cm standard length and 4 to 14 grams in weight.

I first conducted experiments to test for feeding in absence of light. Four sculpins in the first experiment, three in the second experiment and two in the third, were housed in a dark sealed tank. A 14 hour light 10 hour dark cycle was maintained. Each fish was fed Daphnia approximately one hour after darkness for 6 consecutive days and starved on the seventh. On the eighth day the fish were fed Daphnia as usual, allowed to feed for one hour after which they were pithed and guts removed and preserved in 10% formalin. The weight and standard length of each fish was measured. Gut contents were later counted and measured with the aid of a compound microscope and ocular micrometer. During experiment I the smallest of the four fish was eaten by another larger sculpin during darkness. Sculpin remains were found in the gut of the latter. Daphnia left in the tank were siphoned off and enumerated, 100 of which were measured. The tank temperature was 18C.

To observe nonvisual feeding activities I blinded 10 sculpins. Tricaine methane sulfonate (MS222) was used as anesthetic for eye

removal. A dry ice chilled probe was applied to the eye to restrict blood flow and the eye was then removed with forceps. The fish recovered (i.e. restored a normal breathing and swimming pattern) within 1 to 2 minutes. Trauma seemed minimal as all fed the next day or as early as 2 hours after eye removal. Blinded sculpins were fed live Daphnia, Asellus, Hyalella, Hydropsychidae larvae, and freeze-dried shrimp.

For prey detection experiments I used freeze-dried shrimp or amphipods (rehydrated), either tethered to a nylon line or scattered on the botton of the aquarium, and plastic beads (1-4mm diameter) tethered to a nylon line. Experiments were conducted either in still water (a 50 x 25 x 32cm aquarium with no aeration during experimentation) or an artificial stream (3m long constructed of 15cm inside diameter PVC pipe cut lengthwise so it has a hemicylindrical cross section; water flow averaged about 2 cm/sec). Tethered prey (shrimp or beads) were presented to fish at a variety of positions and moved by hand. For shrimp scattered on the bottom I watched to see if a searching fish would locate the prey.

To determine if the lateral line was needed for prey detection I covered sections of the lateral line system, including head and mandibular pores, with Orabase®, a nontoxic, nonanaesthetic paste used in dental work. I then presented the fish with moving beads to various locations and noted reactions.

The "receptive field" (i.e. area of the lateral line sensitive to prey movement) of four blind fish was mapped using two methods. In the first method each fish was videotaped while feeding on Daphnia magna

(1-2mm). Detection distance (i.e. distance and position of <u>Daphnia</u> with respect to the fish for a successful strike) was transposed from the video screen onto an acetate sheet and subsequently measured. One hundred or more strikes for each fish was measured. Zones (20-40°,40-60°,60-80°) were arbritarily marked (Figure 3 and 4) and a receptive field was mapped. A similar technique was used to determine the strike field of the fourth instar <u>Chaobrus trivittatus</u> (Giguere et al. 1982). In the second method a stationary prey, a bead suspended from a vibrator on a monofilament line (0.01mm), was used such that the experimentor controlled amplitude (2mm) and frequency (3Hz) of the stimulus. A false plexiglass stage was placed in the aquarium 8cm from the bottom (Figure 1). Four slits were cut in the stage through which a weighted nylon line was placed. The slits enabled each of these four lines to be moved horizontally across the aquarium. Rewards were attached to two lines by means of silicone vacuum grease while the remaining two had beads. Four blind fish were videotaped and detection distance was mapped as in the first method with the exception that distances marking unsuccessful attempts were also measured.

Field and Digestion Experiments

Fish were collected in 7m of water off the Chicago shoreline of Lake Michigan. Two series of four SCUBA dives (presunset(I), postsunset(II), presunrise(III), postsunrise(IV)) were done [series 1: July 26/27, 1982 (18:38, 21:28, 3:25, 5:36 CDT); series 2 August 2/3 1982 (18:45, 21:10, 3:00, 6:45 CDT)] in which 11 to 17 mottled sculpin were collected during each dive. Water temperature was 15 and 21C for series

1 and 2 respectively. Each dive lasted 25 to 90 minutes. For series 1, the moonphase was first quarter with moonrise and moonset being 12:13 and 23:24 July 26. For series 2, the moon was almost full (August 4) with moonrise and moonset being 18:56 and 4:19 August 3. For both series of dives it was heavily overcast so moonlight had little effect on feeding. After spearing, each fish was immediately pithed and injected in the coelom with 10% formalin. At the end of each dive all fish were preserved in 10% buffered formalin. Weight and standard length were measured for each fish. Number of intact prey in each gut was recorded, measured and then dried at 55C for 24 and 48 hours. At each time one weighing was taken. Longer drying showed no decrease in weight. Nonintact gut contents were dried and weighed in the same manner. The weights were added to produce total weights. Gammarus, isopods, and crayfish were measured from the tip of the telson to the tip of the head. Eurycercus were measured with the aid of a calibrated ocular micrometer and a compound microscope.

The August 2/3 field experiment required a digestion experiment to confirm continuous feeding. In the laboratory three mottled sculpin were fed 7 to 11 amphipods (Hyallela). Four hours after the beginning of feeding (which took up to 45 minutes) fish were pithed and the gut contents examined. Tank water temperature was 18C.

CHAPTER III

RESULTS

Laboratory Experiments

In the laboratory all sculpins fed in total darkness and five ate 13 to 27 _Daphnia_ in one hour (Table 1 and Figure 2). In addition to finding _Daphnia_ in the fish guts, measurements showed that in all five guts _Daphnia_ were larger than _Daphnia_ remaining in the tank; significantly so in three out of five fish (Mann-Whitney U test p<.05 Table 1). (Note; One fish in experiment I and 2 in II were not included in Table 1 since only 2 to 4 prey were found in each gut, however, these fish are included in the histograms in Figure 2). In experiment I four fish were originally used but during the darkness period on the day of the experiment the smallest of the four was eaten by another larger sculpin. Sculpin remains were found in the latter. The bias towards large _Daphnia_ may be due to an increased encounter rate with the more active larger size prey, or the increased hydromechanical signal they create.

Blinded _C_. _bairdi_ feed successfully on live moving Isopods, _Daphnia_, _Hyalella_ and Hydropsychidae larvae always within 24 hours and in several cases within 2 hours after surgery. Blinded sculpins showed no response to dead shrimp lying on the bottom of the aquarium even if they touched the shrimp with the head or elsewhere. Fish did respond readily to moving tethered beads and dead shrimp (described in detail below).

Covering sections of the lateral line system with Orabase® produced site-specific effects. For example, a fish with the pores on its left side of its head covered would respond to moving beads and shrimp on the right side of its head or either side of its body, but not stimuli to the left side of the head. Covering the lateral line on the right side of the body eliminates response only to stimuli presented to the right side of the body. Orabase® can be easily rinsed off with the result that fish then respond to stimuli of the previously covered region.

Responses of the fish to prey (inert, dead, or live) are stereotyped (Table 2). The responses (Table 2) indicate considerable versatility: the prey may be above the fish, on the sand surface, or buried beneath the sand. It may be to its front or side (except in a stream). The fish can respond to prey upstream, in which case the prey need move only once, locating it presumably by the distortion of the stream current. In all cases when the prey is first detected the fish freezes its opercles in a partially open position, a reaction that eliminates water movements caused by its own respiration. A fish moving from position to position in an aquarium also freezes its opercles momentarily each time it stops.

Results from the receptive field mapping using free roaming Daphnia, and a vibrating bead are illustrated in Figure 3 and 4 respectively. For free roaming a two factor ANOVA (with fish and zone as factors) indicated a significant zone effect ($p < 0.001$) and nonsignificant fish and fish and zone interaction ($p > 0.2$). Subsequent multiple comparison tests indicated that response distance for the zone immediately in

front of the snout (central zone $0-20^{\circ}$) was significantly shorter than for the zones to the side of the head ($20-40^{\circ}$, $40-60^{\circ}$, $60-80^{\circ}$) ($p<0.001$ Tukey test). The three size zones were not significantly different ($p>0.03$). Qualitatively similar results were obtained using the vibrating bead (Figure 4). Data from all four blind fish were pooled (x^2 heterogeneity test was not significant). In the central zone ($0-20^{\circ}$), the bead was significantly less likely to be detected than in the other zones (x^2 test $p<.001$).

Field and Digestion Experiments

During day dives we saw sculpins only under rocks whereas at night sculpins were fully exposed on flat silt beds or perched on large rocks (>20 cm). On October 2, 1982, and August 15, 1983, a dive during sunset (19:05 and 20:01) respectively indicated that between 40 and 50 minutes after sunset there was a "crucial" period during which sculpins emerged from under rocks.

Analysis of gut contents revealed that major sculpin prey items included Gammarus, Asellus, and Eurycercus lamellatus. Other prey items included Chironomus sp. fourth instar larvae, juvenile crayfish, oligochaetes, and Stenonema. Size of major prey captured ranged from 1.2mm to 2.24mm for Eurycercus and 2.0mm to 14.7mm for Gammarus. Prey type did not vary with time. Since sculpins ambush moving prey, gut contents were presumably a result of what was in the immediate area. There was no specialization on certain prey types.

Results from the two dive series show an increase in the total weight of gut contents from presunset to the postsunset dives (Figure

5). This increase is also seen in the number of intact prey found in each gut (Figure 6). Weights of intact and nonintact prey showed the same trend (not shown). The presunrise and postsunrise dives, however show no particular trend. Kruskal-Wallis tests (a nonparametric ANOVA), comparing all 4 dives in each series, showed a significant difference in the number of prey and weight of gut contents (p <.001 in all cases except 0.025>p>0.01 for number of intact prey on August 2/3 dives). A posteriori Mann-Whitney U tests showed that for both series the number of intact prey and weight of gut contents of dive I was signficantly less than that of dives II, III and IV. There was no significant difference (p>0.05) among dives II, III, and IV on August 2/3 dives; however there was a significant increase in prey weight from dive II to dives III, III to IV and II to IV on July 26/27 dives (p<0.001). Thus the July 26/27 data show continuous feeding through the night. The August 2/3 data do not demonstrate this as clearly. Laboratory digestion experiments showed that most amphipods eaten 3 to 4 hours earlier were fragmented and hard to identify. Only one or two prey out of 7-11 were still intact after 4 hours. Actual feeding and digestion times were 45 and 3 hours 35 minutes respectively therefore, amphipods still intact were most likely taken at the end of the feeding period. Since the time between dives II and III for August 2/3 was longer than the digestion experiments (about 5 vs 4 hours) and since the digestion experiments were performed in cooler water (18 vs 21C), I conclude feeding was continuous during the night for the August dives.

CHAPTER IV

DISCUSSION

These results indicate a well developed use of the lateral line system for prey detection by the mottled sculpin. Reaction by eyeless sculpins to moving objects and lack of response to nonmoving food indicate that neither vision nor chemosense is required for prey detection. Obstructing the lateral line system with Orabase® which eliminates responses to moving stimuli, results in lack of response to moving prey indicating that the lateral line is needed for blinded sculpins to detect prey. Moving objects create water currents and it is known that the lateral line is sensitive to water displacements (Dikjgraaf 1962). The basic unit of the lateral line system is the hair cell. Neuromasts, groups of hair cells enclosed in a gelatinous cupula, are positioned in canals and are deflected by water currents (Figure 7). These deflections cause neurons to fire resulting in a behavioral response (Dikjgraaf 1962). This sensitivity accounts for the reactions seen by blind sculpins listed in Table 2. In the stream detection is probably based on the distortion in laminar flow created by the object (Vogel 1981). In this context it is probably significant that blind fish in the stream lowered their heads so placing the head pore system near the bottom where flow is more laminar (Vogel 1981).

The lateral line sensory system has been found to be an important

factor in other behavioral responses such as schooling (Partridge and Pitcher 1980; Denton and Gray 1983; Sand 1981), surface feeding (Bleckmann 1980; Bleckmann et al. 1981; Bleckmann and Schwartz 1982; Muller and Schwartz 1982) and in startle responses (Faber and Korn 1978; Blaxter et al. 1981). Both amphibians and fish use the lateral line sensory system to determine the distance and direction of a surface wave source (Elepfandt 1982; Schwartz 1967; Bleckmann 1980; Muller and Schwartz 1982). The lateral line systems of clupeids, which is mechanically linked to the inner ear in this group of fishes, has been implicated in localization of subsurface disturbances (Blaxter et al. 1981). While a precise quantitative examination of the direction and distance determining the capabilities of the sculpin's lateral line system has not been performed, it is clear that from these preliminary mapping results the sculpin can locate subsurface moving objects using the lateral line. Distance determination by the top minnow requires only one intact canal organ while determination of source direction depends on the spactial interaction of several organs (Bleckmann and Schwartz 1982). Site specific effects of lateral line organ canals obstructed with Orabase® suggest that the spatial integrity of organs is also necessary for correct directional responses in the sculpin.

Prey eaten in the field indicate that at least some modes of prey orientation listed in Table 2 are used. As mottled sculpin have small eyes situated dorsally and prey are mostly on or in the substratum, visual detection of prey, particularily at night, would be inefficient. Isopods and Eurycercus, found on the surface of sediments, indicate use

of mode I-A-2. Chironomus fourth instar larvae are buried in the sediment (Merritt and Cummins 1978), which indicates use of mode I-A-3. Whether any of the modes in II (moving water) is used is uncertain. I do note that currents (unmeasured) were present during the August 2/3 dives in the epilimnion but not during the July 26/27 dives at the thermo-cline.

Although I have shown in the laboratory that the lateral line is used for prey detection, whether or not this system is the sole method used in the field is unknown. Vision may be used along with the lateral line, especially at the "crucial" periods of sunrise and sunset when sculpin are emerging from rocks or searching for rocks for protection. Diurnal changes in sculpin location appear to be a result of conflicting requirements for feeding and avoiding predation. Hiding during the day is probably an antipredation strategy against yellow perch, Perca fla-vescens, as sculpins constitute a major prey (Wells 1980). Cottus bairdi were seen hiding beneath rocks during the day and fully exposed on silt beds or perched on top of rocks at night. Rarely were sculpins seen on sand beds, presumably because there is little food there (Jans-sen unpublished). Silt beds have an abundance of amphipods, Eurycercus and Chironomus larvae, and amphipods, isopods and Stenonema are associ-ated with rocks. Being in open space eliminates interference by obsta-cles of currents produced by moving prey.

Some sculpins are found at considerable depths where light levels and lake currents are extremely low. These species are likely to be able to use similar lateral line prey detection methods as mottled scul-

pins (Table 3). As light levels are low and as sculpins have small eyes it is highly unlikely that vision is used in prey detection. The lack of diel feeding periodicity in deepwater and slimy sculpins at 80m supports this view (Kraft 1977).

The mottled sculpin is primarily a stream dweller and the reduced detection of prey in front of the fish (Figure 3 and 4) may be a result of constraints inherent to detecting prey in streams. In streams the flow of water around the fish is such that a "stagnation point" is created upstream of the fish directly in front of the snout (Vogel 1981) (Figure 8A). Current distortion by the prey cannot penetrate this area (Figure 8C) and thus sensory capabilities (i.e a pore) placed at the tip of the snout are relatively useless. However, if the prey is situated in an area other than the stagnation point, (upstream and to the side) the current distortion is not blocked by the stagnation point and the prey is detected (Figure 8D).

The mandibular pore pattern of riverine and lake species differs, suggesting that streams and lakes impose different selective constraints on prey detection via lateral line system. Neither Cottus cognatus nor C. bairdi, both riverine species, possess a mandibular pore at the tip of the mandible. Examining the connectivity of the lateral line system (Figure 7B) shows a barrier (mandibular symphysis) immediately at the tip of the jaw which prevents interaction between the neuromasts on one side of the jaw with those on the other. This barrier (or "lack of pore") is situated at the site of the stagnation point formed by the natural flow of the stream and correlates with the zone of decreased

sensitivity to prey immediately in front of the snout. <u>Cottus</u> <u>ricei</u>, limited to lakes, possesses a particular canal arrangement that may have evolved to detect prey at very low current and light levels. All pores are enlarged (i.e. relative to those of <u>C</u>. <u>bairdi</u> and <u>C</u>. <u>cognatus</u>) and the two pores at the tip of the mandible are fused into one large pore (Figure 7A). The resultant canal is continuous along the whole range of the jaw. Canal neuromasts respond to flow in the canals caused by pressure differences (Figure 7). Flow in the canal connecting two pores is caused by pressure differences between the pores. In <u>C</u>. <u>bairdi</u> and <u>C</u>. <u>cognatus</u> there is no pore at the jaw tip to detect a pressure differential between the tip and another part of the jaw (Figure 7B). In <u>C</u>. <u>ricei</u> a pressure difference at the jaw tip pore relative to adjacent pores will cause flow in the canal and could therefore be detected by a neuromast (Figure 7A). The deepest of the lake sculpins, <u>Myoxocephalus</u> <u>thompsoni</u>, has replaced the canal system with freely exposed neuromasts (McAllister 1968). The neuromasts are situated on the top and side of the head and extend along the side of the body. Preliminary observations of the deepwater sculpin indicate that this fish is sensitive to moving prey primarily in the region above the head. Moreover there seems to be minimal response to a submerged probe or a stimulus placed under the jaw. This is expected since there appear to be no neuromasts in this area.

The anatomical variations in the lateral line system of cottids may be related to certain ecological constraints, such as low light levels or ambient water flow as has been found for amblyopsid (cavefish)

species (Poulson 1963). Given this, sculpins have evolved a lateral line system that best suits the ecological constraints for each specific situation. Shallow depths and fluctuating light levels (i.e. a day and night) results in periodic feeding in C. bairdi. Night feeding is used as an escape from day time predation. At greater depths where light levels are low and constant, feeding is nonperiodic. This absence of diel feeding periodicity may reflect the more continuous encounter frequency expected at depths where prey behavior is not strongly governed by diel light cycles. The low constant light levels are thought to offer a "release" from predation so feeding can occur continually as is seen in the case of C. cognatus and Myoxocephalus thompsoni (Kraft 1977). The evolution of the lateral line system appears to be intimately linked to the feeding ecology of the Great Lake cottids. Ultimately, precise quantitative receptive field mapping in terms of sensory processing capabilities will further define the functional significance of the morphological variation seen in all sculpin species.

TABLE 1. Prey Selectivity by the Mottled Sculpin Mann-Whitney U test
test comparisons of mean _Daphnia_ size in fish gut and in the
tank.

Expt.	Fish	Fish length (total)(cm)	#prey/l	#prey eaten	Median prey size (mm)	Median prey size in gut (mm)	p
I	A	9.9	20.7	16	1.24	1.73	.20
	B	7.1	20.7	20	1.24	2.07	<.001
II	A	6.2	7.5	13	1.79	2.38	<.001
III	A	7.0	22.4	27	2.37	2.52	.10
	B	7.3	22.4	17	2.37	2.76	<.02

TABLE 2. Qualitative Responses of the Mottled Sculpin to Prey in Still

or Moving Water with the Prey and Fish in Various Positions

I. Still water (prey must be moving)

A. Prey in front of snout

1. Prey above eye level. Fish elevates its head by erecting

its pelvic fins. When the prey is in line with the mouth

the fish strikes

2. Prey on the bottom. The head is lowered so the mandible

touches the bottom. Tilting the head down is facilitated by

erecting the anal fin. When the prey is in line with the

mouth the fish strikes.

3. Prey buried. As in I.A.2 except during the strike where the

fish swims hard so that the head penetrates the sand at least

as far as the eye socket.

B. Prey to side of head. Fish flips its body so the head comes to

rest near the stimulus, then proceeds as in I.A.1, 2 or 3. On

some occasions the fish takes prey during the flip except when

the prey is buried.

II.Moving water (2-3 cm/sec, midstream, prey need not move after

initial detection).

A. Fish facing upstream, prey to front of snout.

1. Prey above eye level. Usually no response; a response is

more likely when the prey is nearer the bottom.

2. Prey on bottom. Once prey moves the fish lowers its head

as in I.A.2 and proceeds to move upstream to the prey in short

hops, stopping to detect the prey after each hop.

   3. Prey buried (prey must continue to move). Fish proceeds as

in II.A.2. When it reaches the prey is swims so the head

penetrates the sand to bite at the prey.

B. Fish facing upstream with prey to side of head or body. No

response except when prey is within a few millimeters of

the fish.

C. Fish with body perpendiclular to flow. (This is an uncommon and

transient position).

   1. Prey upstream on bottom. Fish flips head to upstream position

and proceeds as in I.A.2 or 3.

   2. Prey downstream-no response.

Table 3. Depth distribution, pore pattern and habitat of the four Lake
        Michigan Cottids. Pore patterns taken from McAllister 1968.
        Light intensity at 80 m is 0.01 lx, taken from Beeton 1962.

Species	Depth found(m)	Pore pattern	Habitat
C. bairdi	<1 - 10	4 - 0 - 4	Rivers and lakes
C. cognatus	10 - 73	4 - 0 - 4	Rivers and lakes
C. ricei	80	3 - 1 - 3	Lakes
M. thompsoni	82 - 183	pores absent	Lakes

FIGURE 1. Illustration of experimental set-up to map the receptive field of the mottled sculpin using a vibrating bead. In the case of free roaming prey the vibrator and false stage is removed. All movements were videotaped and measured off a TV monitor.
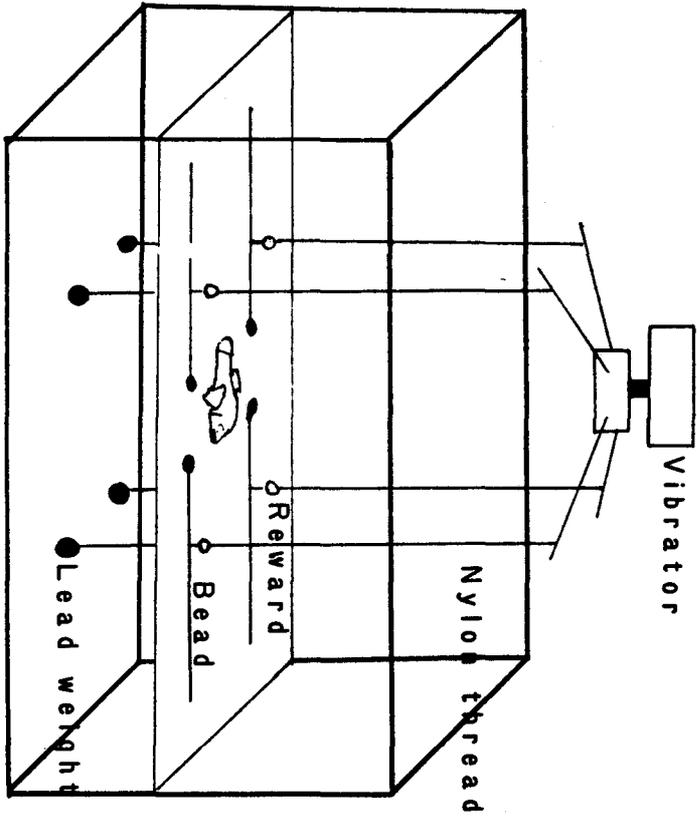
FIGURE 2. Relative frequency of <u>Daphnia</u> size classes (mm) found in the gut after feeding in total darkness for three separate experiments. Three fish were used in the first and second experiment; 2 in the third. Arrows represent average size of <u>Daphnia</u> used in the experiment as well as the average size found in the sculpin stomach.

Figure showing six histograms of relative frequency versus Daphnia size (mm). Top row labeled "TOTAL # OF PREY USED"; bottom row labeled "IN SCULPIN STOMACHS". Y-axis: RELATIVE FREQUENCY. X-axis: DAPHNIA mm.
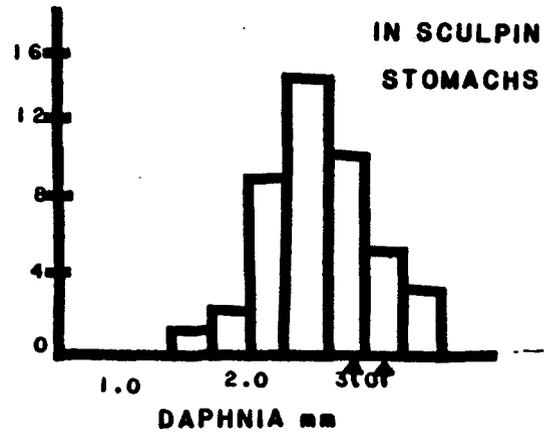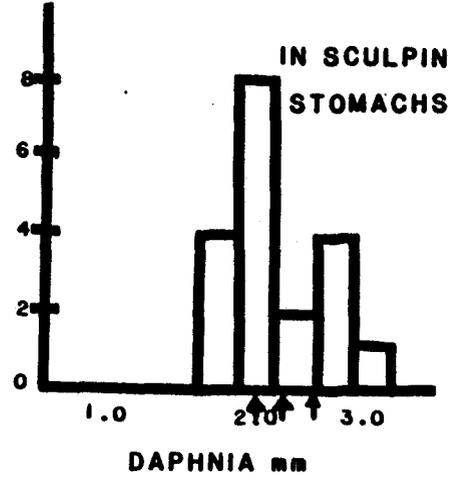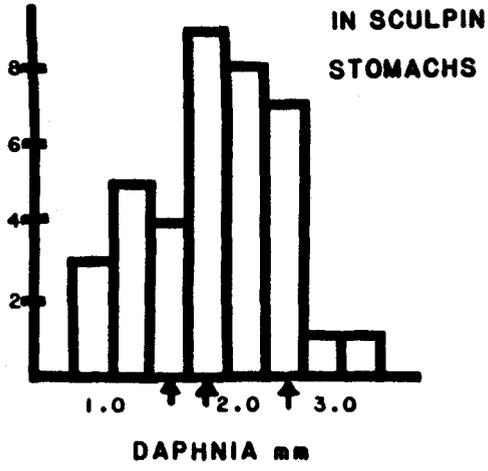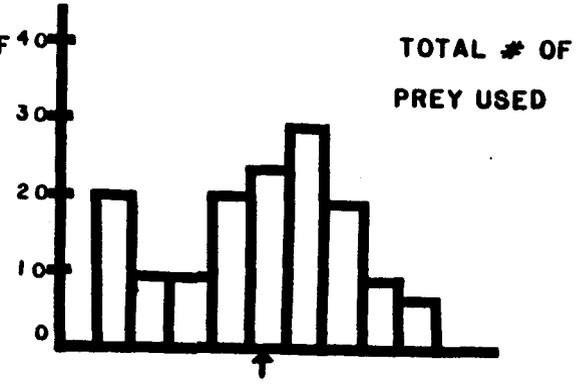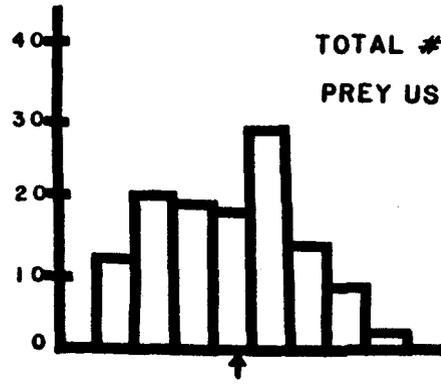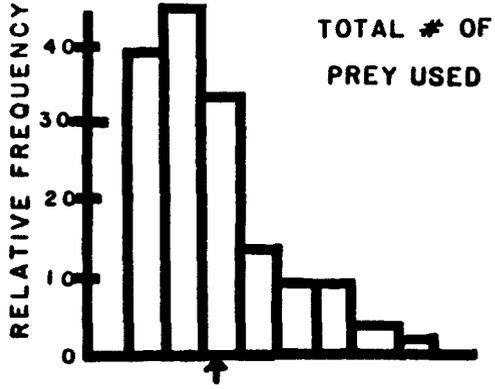
FIGURE 3. Receptive field of the mottled sculpin using 2mm <u>Daphnia</u> <u>magnus</u> as a stimulus. The curved bar in each zone represents the mean detection distance from fish to detected and caught stimulus. Maximal detection distances range from 4.0mm to 21.00mm. Results based on > 100 strikes per fish for 4 fish.

12mm

0mm

0°

20°

40°

60°
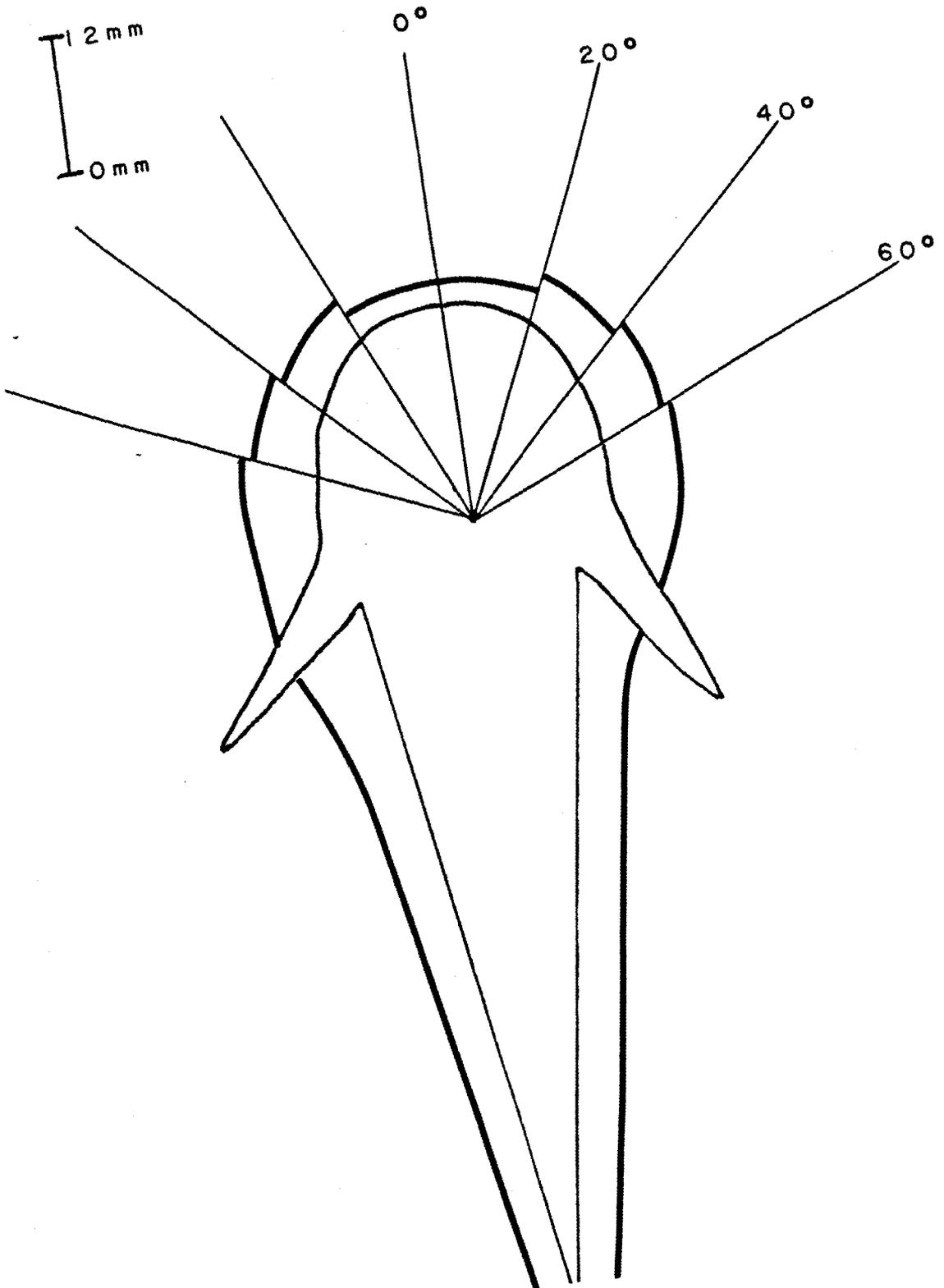
FIGURE 4. Receptive field of the mottled sculpin using a 3 Hz vibrating bead as the stimulus. In the stippled zone 2 out of 26 strikes results in a successful catch. In the clear zone 36 out of 91 strikes results in a successful catch. The zone marked around the perimeter of the fish represents a distance of .5 to 1.0cm from the body of the fish. This area was arbritarily marked and the number of hits and misses by the fish was recorded for each zone. Note zones 20 to 40^0 and 40 to 60^0 were pooled.

0° 20° 40° 60°

2/26

36/91
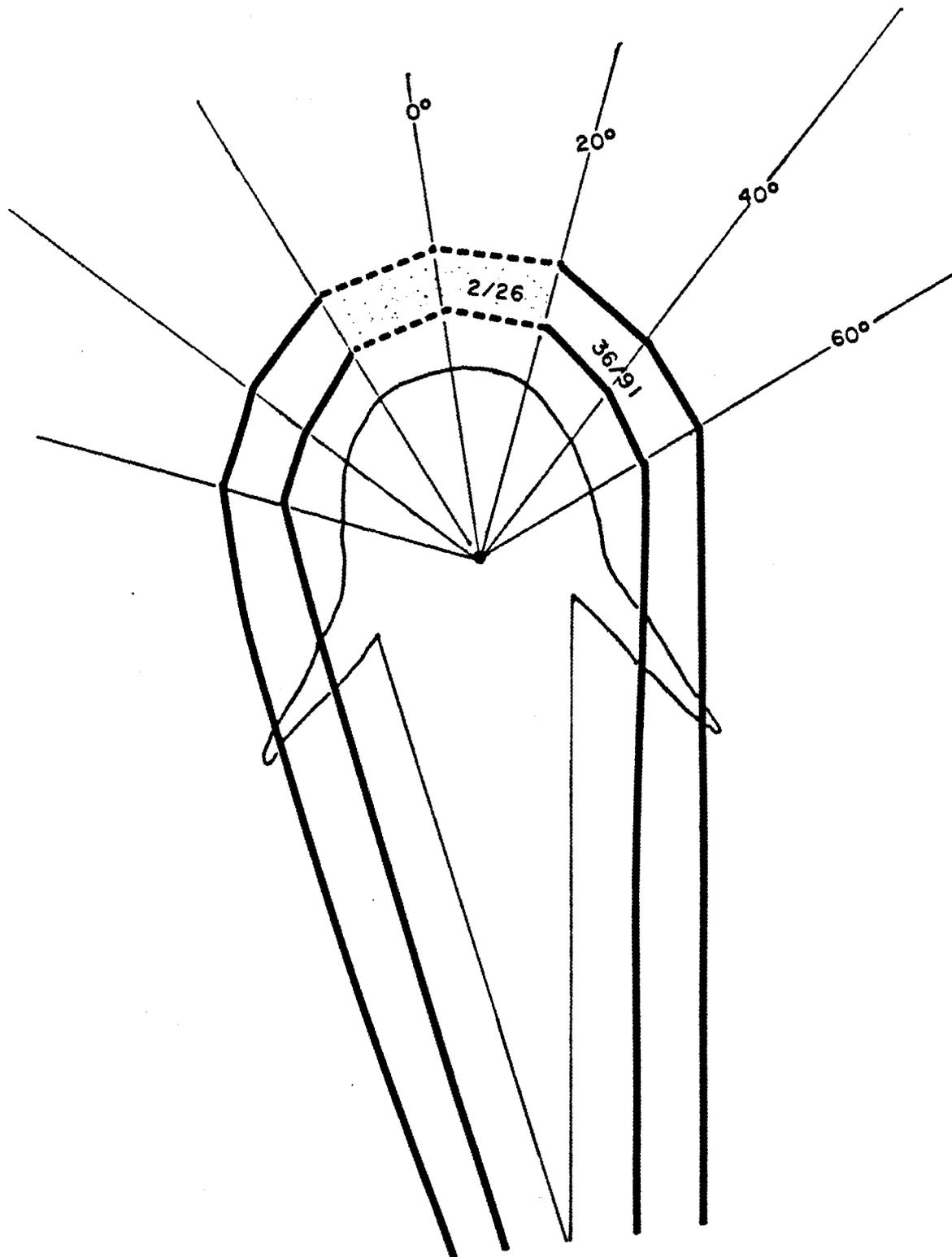
FIGURE 5.   Dry weight of gut contents (mg) as a function of time of day for the two sampling dates, July 26-27 and August 2-3, 1982. Points represent medians while bars represent quartiles. Number of fish in each sample: series 1; Dive I, II, III, IV; 11, 15, 14, 14 respectively: series 2; Dive I, II, III, IV; 14, 15, 14, 17 respectively.
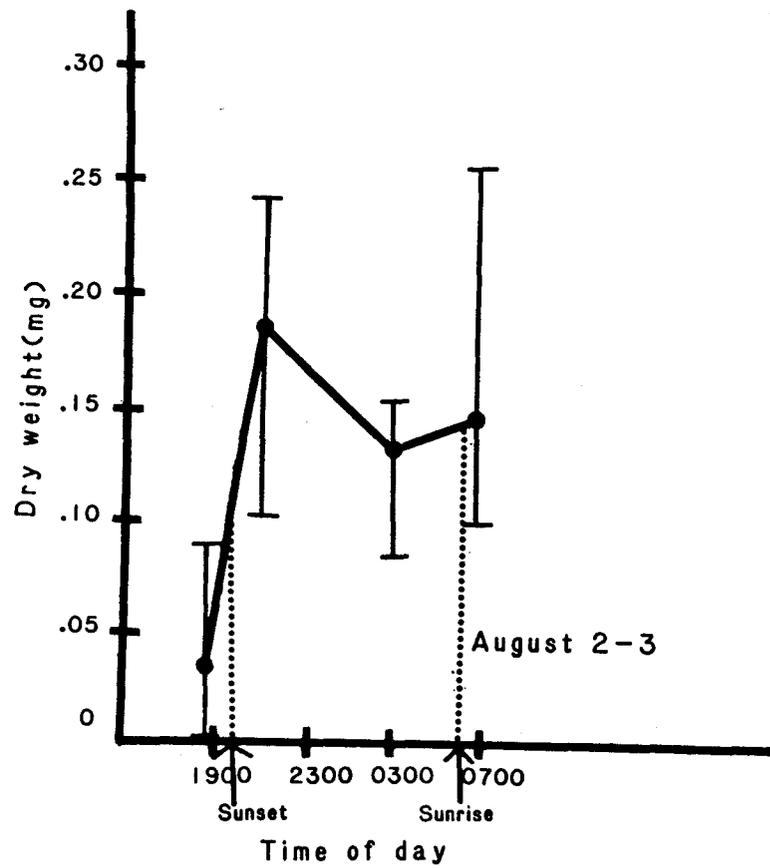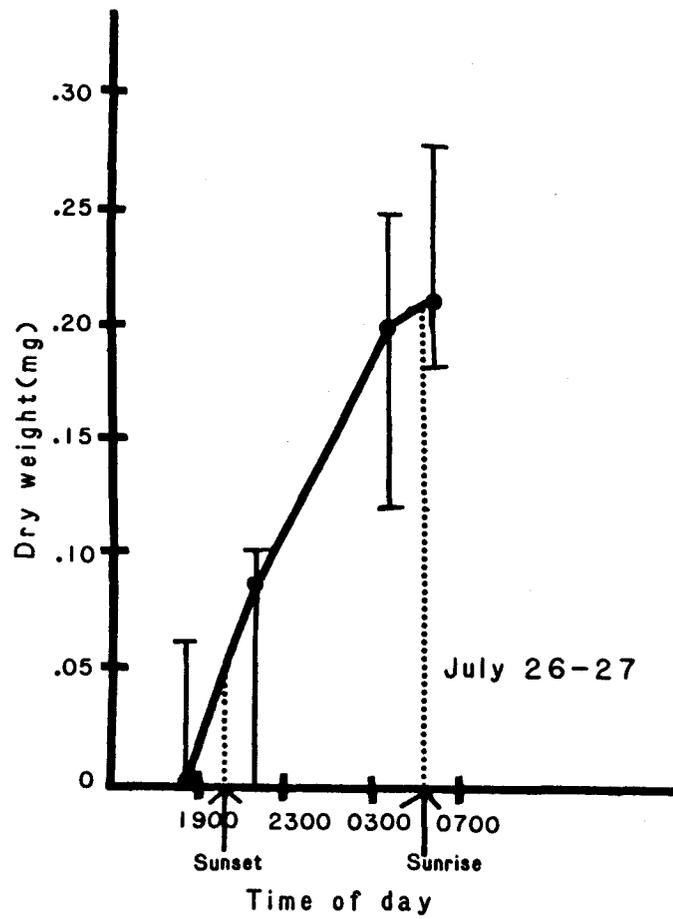
July 26-27

August 2-3

FIGURE 6. Number of prey found in the guts as a function of time of day
for the two sampling dates, July 26-27 and August 2-3, 1982.
Points represent medians while bars represent quartiles. The
number of fish caught in each sample is indicated in Figure
5.

33
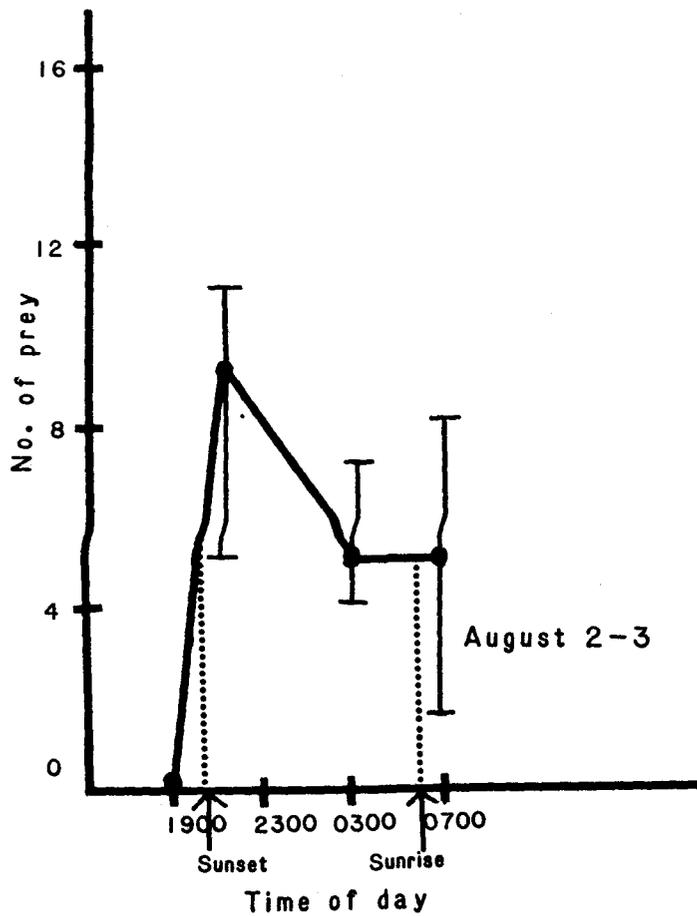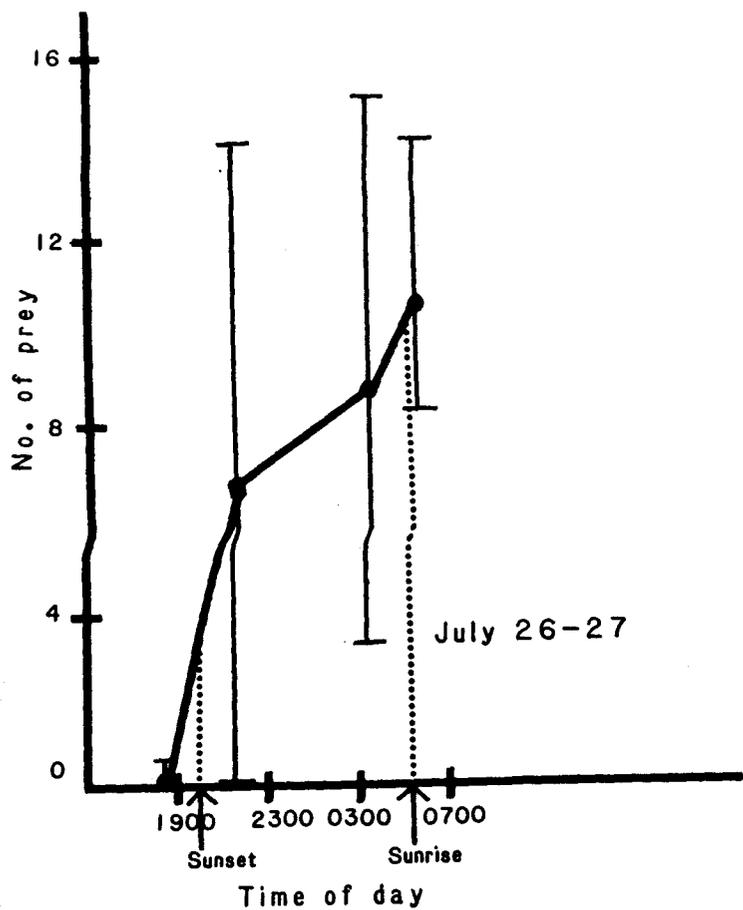
FIGURE 7. A representation of mandibular pore system of riverine and lake species of Cottids. (A1) Ventral view of lake species 3-1-3 mandibular pore pattern. (A2) Linear representation of 3-1-3 pore pattern. The straight line from A1 indicate corresponding pores in A2. (B1) Ventral view of riverine 4-0-4 mandibular pore pattern. (B2) Linear representation of 4-0-4 mandibular pore pattern. Straight lines in B1 indicate corresponding pores in B2. The neuromasts sit in canals between pores and are deflected by water currents (shown by arrow in A2). Deflection causes neurons to fire and a behavioral response is elicited. In A there is, due to fusion of the pores at the tip of the mandible, a large pore. A pressure difference between the tip pore and an adjacent pore can be detected as a current through the connecting canal. In A, the high pressure (H) at the tip pore causes flow due to the low pressure (L) at adjacent pores. In B, the mandibular symphysis separates the left and right mandibular canals. Because there is no pore at the tip, there is no way to detect a flow created by pressure difference between the jaw tip and adjacent pores.

Lake species

Riverine species
(may also occur in lakes)

Canal

Mandibular symphysis

Neuromast

Pore

Pore
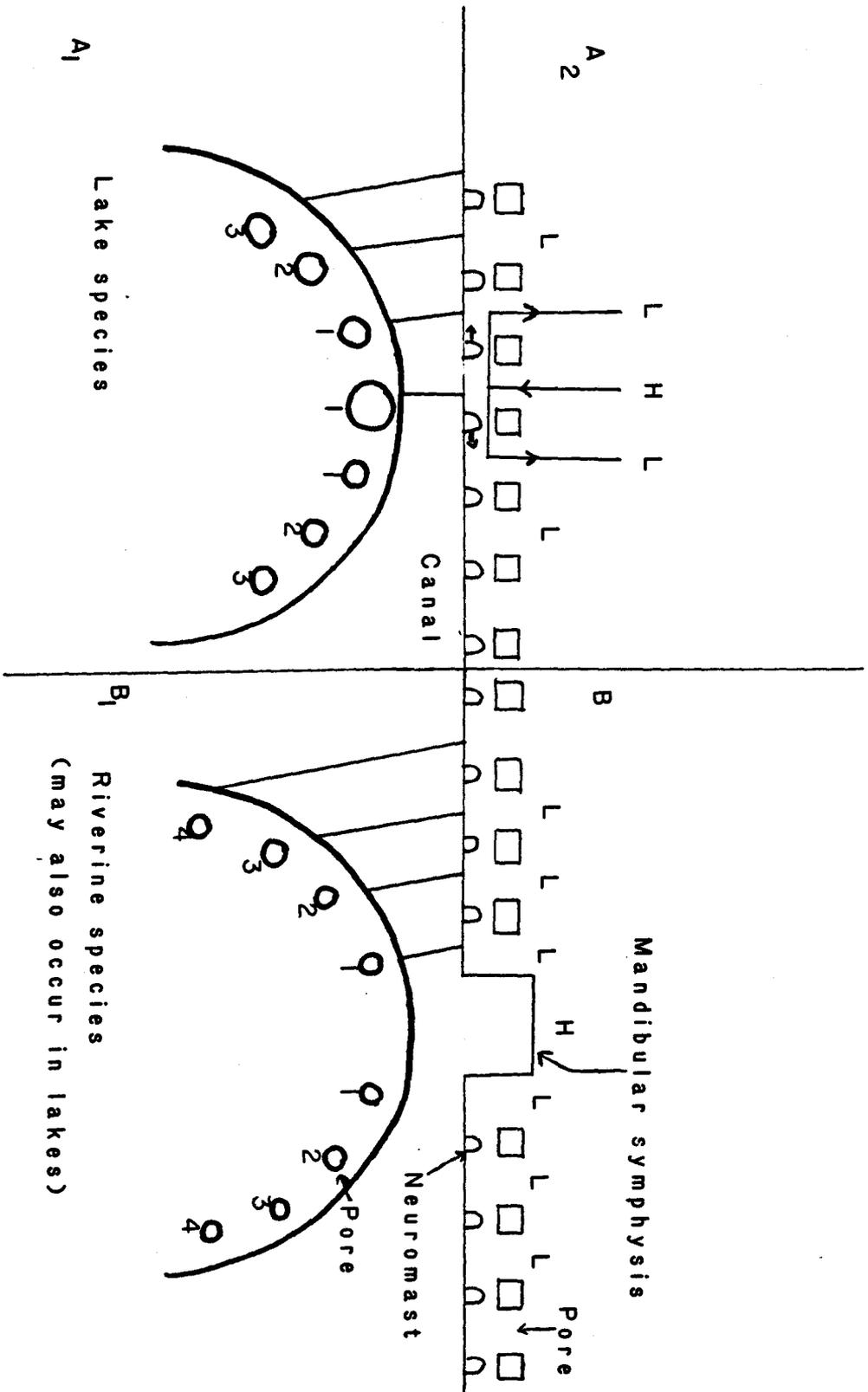
FIGURE 8. A representation of the manner in which prey distorts a
stream current; (A) stagnation point at the tip of the snout
(B) distortion of a stream current by prey (C) prey
distortion of current if prey is located in the area of the
stagnation point (prey is not detected) (D) distortion of
current if prey is located "outside" stagnation point (prey
is detected).

A

Stagnation point

B

Prey

C

D
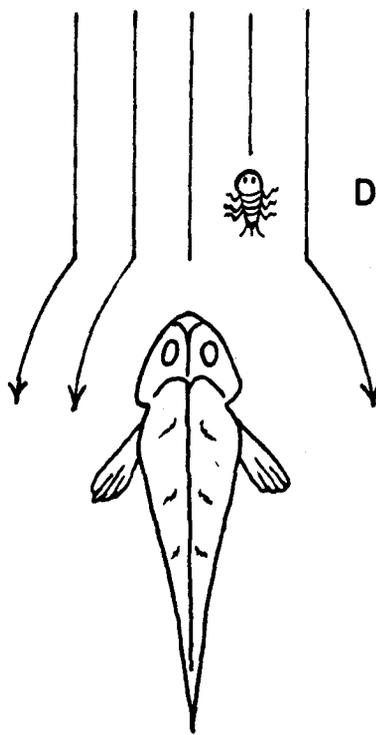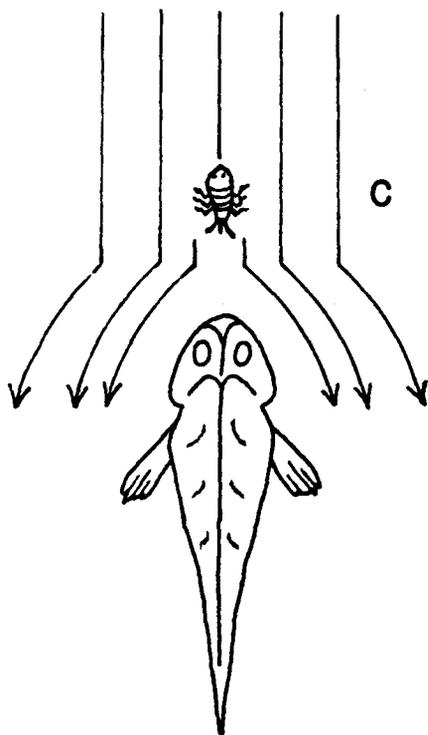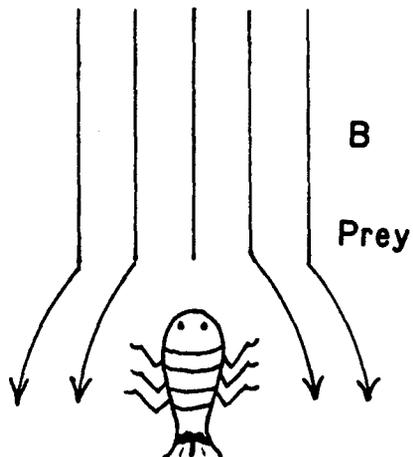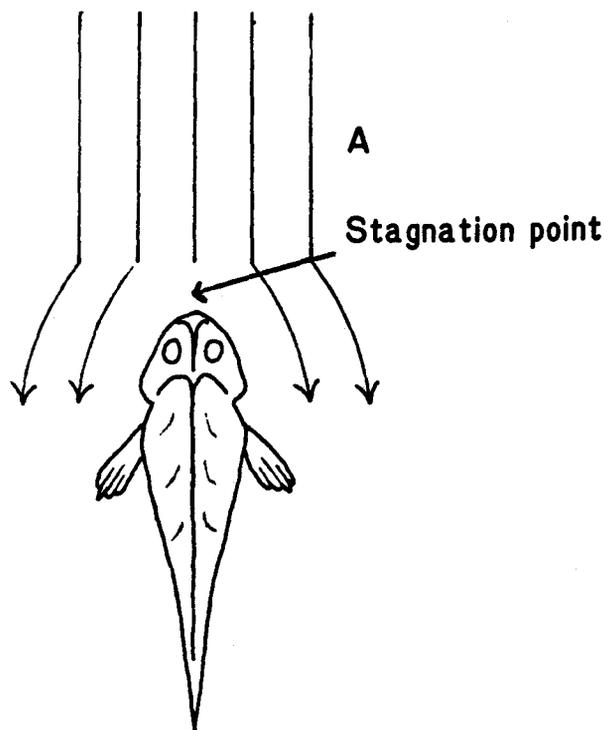
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APPENDIX A

RECEPTIVE FIELD MAPPING DATA

Two-way ANOVA: log transform data using <u>Daphnia</u> as the stimulus

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR F
MODEL	19	56.65662217	2.98192748	6.57	0.0001
ERROR	382	173.35641528	0.45381261		
CORRECTED	401	230.01303745	ROOT MSE	R-SQUARE	C.V.
TOTAL			0.67365615	0.246319	19.4321

LRD MEAN

3.46672595

SOURCE	DF	SS	F VALUE	PR F
FISH	3	2.03636735	1.50	0.2138
ZONE	16	41.00937851	5.65	0.0001

MEAN DETECTION DISTANCE FOR EACH ZONE (<u>Daphnia</u> as the stimulus)

0-20	2.2mm	60 to pectoral fin	5.3mm
20-40	4.3mm	side of body (pectoral	4.0mm
40-60	5.0mm	fin to tail fin)	

APPROVAL SHEET

The thesis submitted by Denise Maxine Denham Hoekstra has been read and approved by the following committee:

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The final copies have been examined by the director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the thesis is now given final approval by the Committee with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Science.

March 29, 1984
Date

John Janssen
Director's Signature