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## The role of prey detection in the selection of prey by pinfish *Lagodon rhomboides* (Linnaeus)

Joseph J. Luczkovich

*Department of Biological Sciences, Florida State University, Tallahassee, Florida, U.S.A.*

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**Abstract:** Selective feeding by fishes may be due in part to the conspicuousness of particular prey types; certain prey may be disproportionately detected by fish and thus could be subject to a greater risk of predation. In laboratory experiments designed to test the relative importance of chemoreception, vision, and prey activity in the process of prey detection, I allowed pinfish *Lagodon rhomboides* (Linnaeus) to choose among various seagrass-meadow-associated infaunal and epifaunal prey [*Melita*, *Cerapus*, *Caprella* (amphipods); *Hippolyte* (shrimp); *Americanuphis*, *Nereis* (polychaetes); and *Clytia*, *Sertularia* (hydroids)]. In laboratory trials, pinfish approached individual prey enclosed in clear glass tubes with an open end (covered with 50- $\mu$ m mesh Nitex screen to allow water exchange) that were provided with sand and seagrass blade substrata. Within each trial, one prey species was offered in an array consisting of an unaltered tube and tubes that had been manipulated to prevent detection of the enclosed prey using vision (opaque sides), olfaction (sealed tops), or both senses (opaque sides and sealed top). Pinfish most frequently approached prey in the clear-sided, screen-topped tubes and least frequently approached tubes with opaque sides and sealed tops; the tubes with sealed tops and clear sides or screened tops and opaque sides were approached with intermediate frequency. Approach frequencies were similar for all prey types tested. It appears that vision and chemoreception were used jointly by pinfish to locate the enclosed prey. In a second series of prey choice experiments, pinfish were offered four prey types (amphipods, shrimp, polychaetes, and hydroids), either live or freshly killed, in clear glass tubes with screen tops to determine if inactive, but otherwise similar prey, were approached as frequently as active prey. All prey types tested were approached with similar frequency; however, live prey were approached more frequently than dead prey (although not significantly more frequently). Small, mobile epifaunal prey (i.e., amphipods and other microcrustaceans) should be disproportionately detected on the seagrass blades by pinfish in the field and thus may be subject to a greater risk of predation than sessile prey.

**Key words:** Foraging behavior; Prey detection; Prey motion; Prey selection; Seagrass epifauna; Sparidae

### INTRODUCTION

Foraging fishes are known to be selective in the foods they consume (Brooks & Dodson, 1965; Stein *et al.*, 1975; O'Brien *et al.*, 1976; Vince *et al.*, 1976; Stein, 1977; Vinyard, 1980; Zaret, 1980; Bohl, 1982; Schmitt & Holbrook, 1984). The degree of selectivity may depend upon how fishes perceive prey availability. The relative pro-

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Correspondence address: J.J. Luczkovich, Harbor Branch Institution, 5600 Old Dixie Highway, Fort Pierce, FL 34946, U.S.A.

portions of prey species may not be perceived by fishes in proportion to their abundance in the environment as determined by ecological sampling. Certain characteristics of prey influence their detection by predators; in particular, prey items differ in their appearance, behavior, and size. Some potential prey appear or behave cryptically, thereby avoiding detection and capture (Stein & Magnuson, 1976; Sih, 1982; Main, 1987). Prey that are active and moving may be more susceptible to attack than prey that are relatively inactive (Kislalioglu & Gibson, 1976; Zaret, 1980; Magnhagen & Wiederholm, 1982; Main, 1987). The size of a potential prey item may influence a predator's ability to detect and capture it (Kislalioglu & Gibson, 1975; Zaret & Kerfoot, 1975; O'Brien *et al.*, 1976; Main, 1985). The availability of prey from a predator's perspective is a combination of the prey's detectability as well as its abundance relative to other prey.

In the seagrass meadows in the Northeast Gulf of Mexico, pinfish *Lagodon rhomboides* (Linnaeus) exhibit selective feeding on epifaunal prey, but the explanations for the patterns of selective feeding are uncertain. Pinfish consume a diversity of prey types during their ontogeny: whereas new recruits [ $< 20$  mm standard length (SL)] are planktivores, individuals 20–35 mm SL are predators on benthic invertebrates (amphipods and harpacticoid copepods), then enter an omnivorous stage (35–100 mm SL) during which algae, diatoms, amphipods, copepods, shrimp, polychaetes, hydroids, tunicates, and fishes may be consumed, and finally become herbivores that consume seagrass shoots at the largest sizes (100–150 mm SL) (Caldwell, 1957; Hansen, 1969; Carr & Adams, 1973; Stoner, 1980a; Livingston, 1982; Huh & Kitting, 1985; Luczkovich, 1987). Even though pinfish appear to be opportunistic, they are still somewhat selective about the foods they consume during the omnivorous stage: they consume amphipods, for example, in amounts disproportionate to their field abundances (Young *et al.*, 1976; Nelson, 1979; Stoner, 1979; Luczkovich, 1987). Stoner (1979) determined that certain amphipod species were over-represented in the diet of the pinfish and that the degree of selectivity was dependent on the amount of seagrass present in the habitat: pinfish are very “choosy” in high-density seagrass habitats and non-selective in sparsely vegetated areas. Because overall prey densities are greatest in high-density seagrass habitats (Stoner, 1980b; Lewis, 1984), the pinfish could have been relatively less hungry, and thus more selective, than in the sparsely vegetated seagrass meadow. However, this pattern of selectivity does not necessarily represent active choices by foraging pinfish, because other processes, chief among these being differential prey detection, could have produced the same results. In light of the influence of prey conspicuousness on selection of prey, I examined how pinfish detect prey and how activity levels of various prey types influence prey choice.

The mechanisms involved in the detection and selection of prey by pinfish have been incompletely studied. Most authors claim that pinfish locate their prey using vision alone (Nelson, 1979; Stoner, 1979; Main, 1985), yet pinfish are highly sensitive to chemical stimuli (Carr & Chaney, 1976; Carr *et al.*, 1976). The chemical stimuli used by these authors were prey extracts made from ground and filtered whole animals (shrimp, oysters, and fish), but such chemical extractions are not normally experienced

by pinfish searching for uninjured, live prey. Clearly, either vision, chemoreception, or both, are being employed by pinfish while foraging in natural situations.

I tested two hypotheses concerning the ability of pinfish to detect natural prey: (1) pinfish should use chemoreception as well as vision to detect prey; and (2) pinfish should detect active prey more frequently than inactive prey. As a test of the first hypothesis, natural prey items were enclosed in glass tubes and given portions of seagrass blades on which to rest; a natural background for cryptic prey was thus provided. The tubes were manipulated to prevent either the prey's visual or chemical cues, or both, from being detected by foraging pinfish. Variation in the number of attacks directed at each of the tubes measured whether vision, chemoreception, or both mechanisms were used by pinfish to detect prey. As a test of the second hypothesis, pinfish were given a choice of several prey types, either live or freshly killed, enclosed in glass tubes with seagrass blade substrata. Differences in the number of attacks directed at live or dead prey measured the importance of prey activity on preferences toward prey.

## MATERIALS AND METHODS

### ANIMAL COLLECTION AND MAINTENANCE

Pinfish were collected using a 5.5 m long otter trawl on the day prior to testing from a *Thalassia testudinum* König and *Syringodium filiforme* Kutz seagrass meadow adjacent

TABLE I  
Seawater conditions and mean pinfish lengths for the experiments.

Date	Temperature (°C)	Salinity (ppt)	Standard length (mm)	
			Mean	SD
Experiment 1 <sup>a</sup>				
3 Apr. 86	21.0	31.5	35.7	(4.74)
10 Apr. 86	20.0	31.0	34.8	(3.34)
17 Apr. 86	19.0	32.0	34.9	(1.88)
23 Apr. 86	17.0	34.0	35.4	(2.68)
6 May 86	22.5	30.0	46.7	(2.80)
22 May 86	22.0	30.0	— <sup>b</sup>	—
4 Jun. 86	26.0	30.0	44.1	(10.62)
4 Jul. 86	26.0	33.0	50.9	(12.96)
11 Jul. 86	27.0	32.0	59.4	(14.78)
Experiment 2 <sup>c</sup>				
17 Aug. 86	25.5	33.0	77.9	(4.08)
4 Sep. 86	26.0	30.0	77.8	(3.46)
18 Sep. 86	25.5	31.0	80.4	(4.25)

<sup>a</sup> Based on 18 fish for each date. <sup>b</sup> Fish were measured to ensure that they were between 40–50 mm, but the measurements were not recorded. <sup>c</sup> Based on 12 fish for each date.

to the Florida State University Marine Laboratory. Prey were collected using a modified epibenthic crab dredge [see Leber & Greening (1986) for a description] and 75 mm diameter core samplers. All organisms were held in the laboratory in flow-through seawater systems under ambient seawater temperature and salinities (Table I). Light was provided by overhead fluorescent bulbs which simulated natural daylight conditions (photoperiod of 14 h with an illuminance of  $421.4 \pm 40.25$  s.d. lux). In all experiments, fish were transferred to test aquaria on the evening prior to testing and allowed to acclimate overnight. This allowed a standard food deprivation period of 10–15 h, a time sufficient for gut clearance based on the natural feeding periodicities of pinfish in the field (Luczkovich, 1987). In addition, by using fish naive to the laboratory for each test and holding them for less than 24 h prior to testing, the fish did not become entrained to an artificial laboratory feeding schedule. In all experiments, fish were tested once then released.

All experiments were conducted in rectangular glass aquaria (115 l) supplied with seawater filtered through a 150- $\mu$ m nylon mesh bag from a common head box via polyvinylchloride (PVC) piping (Fig. 1). The seawater was distributed to the tanks using

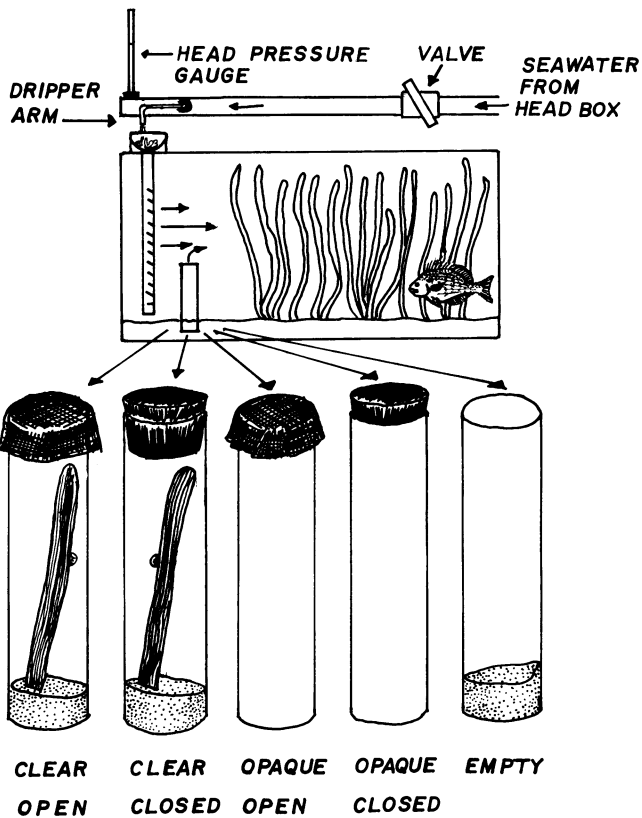


Fig. 1. Diagram of the experimental aquarium, the seawater delivery system, and the five tube types used in Experiment 1.

a modification of the apparatus described by Pearson *et al.* (1979). Seawater flowed to each aquarium through adjustable dripper arms made from rubber stoppers and glass tubing. By adjusting the head pressure (as measured by the height of a column of water in a gauge made from glass tubing) with a valve, these arms allowed seawater to flow at a constant rate into a trough positioned over each aquarium. Flow rates were monitored at each dripper arm with a stopwatch and graduated cylinder; rates were maintained at  $600 \text{ ml} \cdot \text{min}^{-1}$ . Seawater entered each aquarium through a PVC tube (12 mm inside diameter) that drained each trough and had slits cut into it at  $45^\circ$  angles. Water flowing from this tube served to create a flow of seawater throughout each aquarium. Dye studies indicated that the water entering the tanks reached the downstream end within 2–3 min. The bottom of each tank was covered with 25–30 mm of clean beach sand. Artificial seagrass shoots constructed from green fly-fishing line (to simulate *S. filiforme*) or 1 cm wide strips cut from green plastic sheeting (to simulate *T. testudinum*) were provided as shelter for the fish without introducing other potential foods that might have been present on natural seagrasses.

## EXPERIMENTAL PROCEDURES

### *Experiment 1*

Pinfish of a particular size that had been collected on a particular date were placed three per tank into five aquaria. I used three fish per tank because small pinfish are group foragers (Stanford, 1974; Luczkovich, 1987) and because preliminary tests showed that the highest approach rates (number of approaches per fish) were obtained with three fish in a tank, instead of one or two fish. Because the fish within an aquarium may influence one another, their responses were not considered to be independent observations; therefore, in the analyses to follow, the response variable (number of approaches per tube) was pooled for all fish within an aquarium.

On the day of testing, glass test tubes with one opening ( $95 \times 25$  mm diameter; 35 ml volume) that contained the prey were placed into each aquarium. Prior to adding prey, all glass tubes were washed in hot water with detergent, then rinsed in freshwater, deionized water, and finally in filtered seawater. The tubes were prepared following this standard procedure for all tests. Substrata (an 80-mm portion of a blade of *S. filiforme*, 5–10 ml of sand), filtered seawater, and individual prey organisms were added to each tube.

I manipulated the five tubes within an aquarium in order to restrict the prey and to prevent visual stimuli, chemical stimuli, or both of these from reaching the fish. A 500- $\mu\text{m}$  screen top covered the opening of one tube creating a tube that was both clear and open to water exchange, thus allowing both visual and chemical stimuli to be released. Another tube was sealed with a rubber stopper creating a tube that was both clear and closed, thus allowing only visual stimuli to be released. A third tube was lined with opaque white paper and covered with a 500- $\mu\text{m}$  screen top creating a tube that was

both opaque and open, thus allowing only chemical stimuli to be released. The fourth tube was lined with opaque white paper and sealed with a rubber stopper to create an opaque and closed tube that allowed no visual or chemical stimuli to be released. These four tubes, along with a fifth empty tube that had no top or paper lining, were randomly placed across the upstream end of each aquarium with 3 cm between each tube and other tubes or the aquarium walls (Fig. 1). Dye studies showed that the rubber stoppers sealed completely for at least 24 h; water escaped from the open tubes upward into the current and flowed downstream, completely exchanging all water with aquarium water within 24 h at a seawater inflow rate of  $600 \text{ ml} \cdot \text{min}^{-1}$ .

While watching from behind a styrofoam blind, I counted the number of approaches toward each tube type made by the three fish during a 15-min observation period. An approach was defined as the orientation of a fish towards the tube within the region 1 cm from the surface of each tube. This usually occurred as the pinfish searched slowly over the tank bottom, much as they do in the field (Luczkovich, 1987).

The prey species tested occur naturally in pinfish diets at the field collection site (Luczkovich, 1987). They were the amphipods *Melita appendiculata* (Say), *Caprella penantis* Leach, and *Cerapus* sp. (*cf. tubularis* Say), the shrimp *Hippolyte zostericola* (Smith), and the polychaete *Americonuphis magna* (Andrews). While in the tubes, the crustaceans rested on the seagrass blades and the polychaetes buried in the sand. Within an aquarium, all tubes contained the same species of prey. Thus, in this experiment, the fish were not offered a choice of prey, but only a choice of tube type within an aquarium.

The experiment was repeated nine times, with one fish group tested per prey type per day, during a period from 3 April through 17 July 1986 (Table I). The pinfish at the study area grew during the test period, so that the average size of the fish tested progressively increased toward the end of the experiment. These temporally repeated trials are not true replicates, but are listed as a factor termed "fish size/time"; the effect of this factor on the number of approaches to tubes can be ascribed to the increase in the size of the fish tested or any of a number of seasonally dependent environmental factors (water temperature, salinity, photoperiod, food availability, etc.) that were experienced by the free-ranging fish prior to capture and testing. Water temperature, salinity and mean fish size measured during each trial are given in Table I.

### *Experiment 2*

During 36 replicate experimental trials, I simultaneously tested preferences for four prey types and determined the effect of prey activity on attack preferences by offering pinfish equal amounts of four types of prey enclosed in clear glass tubes. Prey activity was manipulated by offering freshly killed prey to pinfish in half of the trials. In addition, since prey activity was of interest, prey representing a range of activity levels, including highly mobile amphipods and polychaetes, relatively inactive shrimp, and sessile hydroids were offered in this design. The prey species tested were amphipods, *Melita appendiculata*, shrimp, *Hippolyte zostericola*, polychaetes, *Nereis falsa* Quatrefages, and

a *T. testudinum* blade covered with sessile epibionts, primarily colonies of the hydroids *Sertularia* sp. and *Clytia* sp. The polychaetes tested were different than those used in Experiment 1 because of my inability to obtain enough small *Americanuphis magna* individuals and the abundance of *N. falsa* in the prey collections during the time that this experiment was conducted. All prey types tested occur naturally in the diet of the pinfish (Luczkovich, 1987). Although the prey types tested differed in size (Table II), the amount of prey biomass provided in each tube in this experiment was similar so that choice of tubes could not be based on energetic differences among prey of different sizes. Thus, because I held prey weight per tube constant in these experiments, the density within a tube differed among prey types (Table II).

TABLE II  
Densities and average wet and dry weights used in the experiments.

Prey species	Density	Wet weight (mg)	Dry weight (mg)	Mean length (mm)
<i>Hippolyte zostericola</i>	1	11.0	2.39	10.8
<i>Melita appendiculata</i>	7	13.4	1.38	3.3
<i>Nereis falsa</i>	5	9.5	2.67	10.0
Epibionts on <i>Thalassia</i>			7.96	–
Hydroid colonies ( <i>Clytia</i> sp. and <i>Sertularia</i> sp.)	92.9 <sup>a</sup>	– <sup>b</sup>	6.80	–
Serpulid polychaetes	7.8 <sup>a</sup>	–	0.65	–
<i>Melobesia</i> sp.	+ <sup>c</sup>	–	+	
<i>Diplosoma macdonaldi</i> Herdman	+	–	+	

<sup>a</sup> Average density. <sup>b</sup> Wet weight could not be measured without removing epiphytes. <sup>c</sup> A “+” indicates that these were present in small amounts.

The test apparatus was similar to that used in Experiment 1. An experimental trial consisted of the responses of an individual fish in an aquarium to the tubes presented; 12 fish, six using live prey and six using freshly killed prey, were tested on 3 days. Pinfish were collected on the day prior to testing and allowed to acclimate overnight in test aquaria. Because only large pinfish (> 70 mm SL) were available late in the season, I used one fish per aquarium; pinfish become solitary foragers as they get older (Caldwell & Caldwell, 1967; Luczkovich, 1987) and as their population density decreases late in the year (Adams, 1976).

The four prey types, either all alive or all freshly killed, were presented in separate tubes placed in a random order across the upstream end of each aquarium 3 cm apart from one another. There was an empty tube present in each aquarium as a control. Prey were enclosed in clear tubes with screen tops, each of which contained filtered seawater, 5–10 ml of sand substrate, and an 80-mm portion of a blade of *T. testudinum* scraped clean of all epifaunal organisms (unless epibionts were offered as prey). When unscraped blades with hydroid colonies were offered, mobile epifauna were removed by washing

the blades under a stream of filtered seawater. After live prey had been added to all tubes prior to an experimental run, prey were killed in half of the tubes of each prey type (selected at random) by partially immersing the tubes in an ice bath for 0.5 h. Tubes containing the freshly killed prey were then allowed to warm to room temperature and placed into the appropriate aquaria. Tubes containing the live prey were placed into the remaining aquaria. During the period immediately following tube introduction, I observed from behind a blind the number of approaches to each tube during a 5-min observation period. Comparisons were made between the number of approaches toward the five tubes in each aquarium and among aquaria that contained live (active) vs. freshly killed (inactive) prey.

#### STATISTICAL ANALYSIS

All statistics were done using the BMDP8V statistical package on the CDC Cyber 720 at Florida State University. All responses were transformed with a logarithmic (base 10 or natural) function after adding 1 to the number of approaches. This reduced the observed heterogeneity of variances and non-normality of the untransformed data.

Both experiments involved a multifactorial repeated measures design, since approaches by fish to tubes within an aquarium are not independent of one another and fish may approach more than one tube during a trial. The responses of each group of fish within an aquarium to different tube types (Experiment 1) or of each fish to different prey types (Experiment 2) were treated as repeated measures of approach preferences. For Experiment 1, there were two sources of variation that occurred among aquaria: prey type and fish size/time. For Experiment 2, there were two sources of variation that occurred among aquaria: prey activity level (live or dead) and block (week of repeated experiment).

#### RESULTS

The fish approached the tubes while searching in the aquaria in a manner consistent with their observed foraging behavior in both the laboratory and the field. I have previously described foraging behavior observed in the field in which pinfish approached and attacked the epifaunal organisms residing on seagrass blades (Luczkovich, 1987). In separate feeding observations made in laboratory aquaria, pinfish approached seagrass blades to which the epifaunal prey species used in these experiments were clinging; these approaches led directly to predatory attacks. In these observations, pinfish would approach each seagrass blade and bite at specific points where the epifaunal prey resided. The infaunal polychaetes were attacked after a similar approach to their tubes in the sand.

In both of the experiments, after the glass tubes with prey were introduced, the fish would swim slowly along the sand substratum, their heads directed downward and slowly moving from side to side. When the clear tubes were encountered, the fish would



orient toward the enclosed seagrass blade, occasionally swimming up the glass tube to its top. The open top tubes were frequently approached around the top, an area where water exchange between the tube and the aquarium was occurring. Occasionally, the fish directed bites at the tube sides and top. However, this did not occur during every trial; biting was usually observed only following a bout of activity by the prey. One or two fish in an aquarium would repeatedly approach and attack the same tube and sometimes switch to a nearby tube. Aquaria containing such unusual individuals were not dropped from the analyses, however. Most of the time of fish were inactive and hiding in the artificial seagrass provided.

### Experiment 1

The fish approached the tube relatively infrequently during the observations, but most approaches were observed during the first few minutes following introduction. I observed an average of 6.2 approaches per aquarium (range: 0–41) during trials in this experiment. Most approaches occurred around the clear-open tubes for all prey types and fish sizes.

There were significant effects of tube type, but not of fish size/time or of prey type, on the number of approaches to tubes by pinfish (ANOVA, Table III). The average number of approaches occurring around the clear-open tubes was significantly greater than around the control tubes (90% greater than around opaque-closed tubes and 47% greater than around empty tubes, Duncan's multiple range test,  $P < 0.05$ ) (Fig. 2). There were 34% more approaches around the clear-open tube type than around the opaque-open tube type and 32% more than around the clear-closed tube, although these differences were not significant (Duncan's multiple range test,  $P > 0.05$ ). The next highest mean number of approaches occurred around the clear-closed and opaque-open tubes, which allowed visual and chemical prey stimuli to be detected, respectively. The

TABLE III

ANOVA for Experiment 1. The response variable is the logarithm (base e) of the number of approaches to tubes + 1.0.

Source	df	SS	MS	F	P
Fish size/time	8	1.1399	0.14249	0.108	0.75
Prey type	4	7.1636	1.79089	1.352	0.25
Tube type	4	10.4277	2.60692	7.702	0.001
Fish size/time × prey type	32	42.3888	1.32465	—	—
Fish size/time × tube type	32	10.1122	0.31601	0.934	0.50
Prey type × tube type	16	3.5669	0.22293	0.695	0.75
Fish size/time × prey type × tube type	128	43.3267	0.33849	—	—

mean number of approaches to these two tube types were very similar to each other and to the empty tube control. No significant differences were found among these three tube types (Duncan's multiple range test,  $P > 0.05$ ). The fish approached the opaque-closed tubes least frequently, and the mean number of approaches was significantly lower than all other means (Duncan's multiple range test,  $P < 0.05$ ).

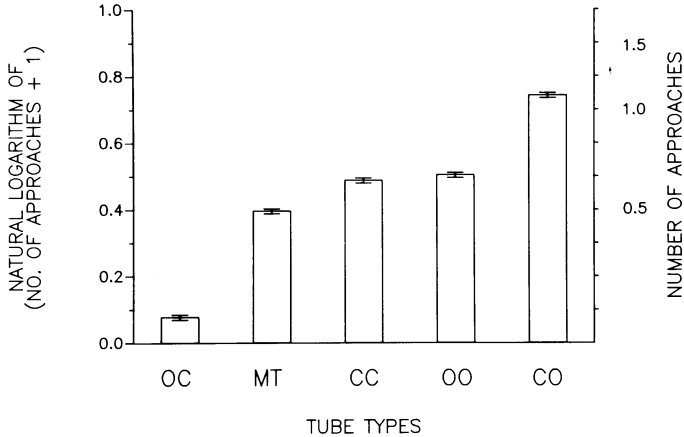


Fig. 2. The mean number of approaches ( $\pm 1$  SE) by pinfish *Lagodon rhomboides* to the five tube types containing live prey in Experiment 1: opaque and closed (OC), empty (MT), clear and closed (CC), opaque and open (OO), clear and open (CO) ( $n = 45$  for each tube type). The responses are pooled from five prey types that were offered in separate aquaria. Prior to analysis, data were transformed by adding 1.0 and taking the natural logarithm of each observation.

These results indicate that pinfish most frequently used both chemoreception and vision to detect prey in these tests. Pinfish may detect prey as frequently using either vision or chemoreception alone, however. Prey contained in the opaque-closed tubes were undetectable, judging from the infrequent approaches by pinfish. Empty tubes were approached more frequently than might be expected. Approaches to empty tubes may have been due to fish mistaking the nearly invisible tube for a gap in the line of tubes; such fish were scored as approaching the tubes, even though they could not have detected any prey in these tubes.

### Experiment 2

Pinfish approached the tubes infrequently once again in this experiment. I observed an average of 6.8 (range: 0–35) approaches around all tubes in aquaria during all trials. All approaches occurred in the first few minutes following the introduction of the tubes.

Pinfish in aquaria with live prey approached tubes 72% more frequently than those with freshly killed prey (Fig. 3). Although the effect of prey activity was not significant at the 0.05 level, it was still relatively small (ANOVA,  $P = 0.1008$ )(Table IV). Tubes that contained different prey types were approached with approximately equal frequency and

tubes that contained any prey at all were approached more frequently than empty tubes (Fig. 3). Although there was a significant effect of prey type on number of approaches to tubes (ANOVA,  $P = 0.01$ ), this effect is due largely to the small number of approaches to the empty tubes in the tests (Fig. 3). Empty tubes were approached fewer times than the other prey-containing tubes (Duncan's multiple range test,  $P < 0.05$ ). There was no significant difference among tubes that contained prey (Duncan's multiple range test,

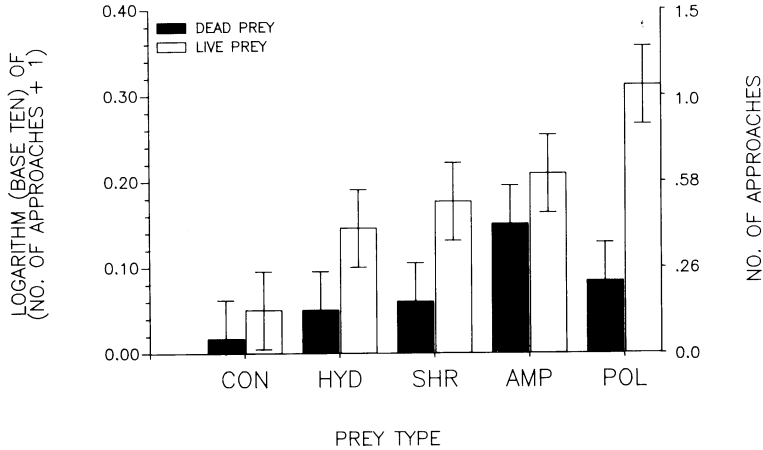


Fig. 3. The mean number of approaches ( $\pm 1$  SE) by pinfish *Lagodon rhomboides* to four types of live or freshly killed prey in Experiment 2 ( $n = 18$  for each live and dead prey type). The prey types [hydroids *Clytia* and *Sertularia* on an epibiont-covered *Thalassia testudinum* blade (HYD), shrimp *Hippolyte zostericola* (SHR), amphipods *Melita appendiculata* (AMP), and polychaetes *Nereis falsa* (POL)] were offered in clear glass tubes with screen tops in each aquarium along with an empty control tube. Live prey and dead prey were offered in separate aquaria. Prior to analysis, data were transformed by adding 1.0 and taking the logarithm (base 10) of each observation.

TABLE IV

ANOVA for Experiment 2. The response variable is the logarithm (base 10) of number of approaches to tubes + 1.0.

Source	df	SS	MS	F	P
Activity	1	0.51504	0.51504	2.87	0.10
Week	2	0.36309	0.18154	1.02	0.25
Prey type	4	0.62680	0.15670	4.25	0.01
Activity $\times$ week	2	0.11716	0.05858	0.33	0.72
Activity $\times$ prey	4	0.20361	0.05090	1.38	0.24
Week $\times$ prey	8	0.11659	0.01457	0.40	> 0.25
Activity $\times$ prey $\times$ week	8	0.14632	0.01829	0.50	0.85
Fish (activity $\times$ week)	30	5.34320	0.17811	-	-
Fish $\times$ prey (activity $\times$ week)	120	4.42379	0.03686	-	-

$P > 0.05$ ). With control tubes excluded from the analysis, the type of prey approached by the pinfish did not differ (ANOVA,  $F_{3,90} = 2.04$ ,  $P > 0.10$ ). There were no significant interactions between the factors prey activity and prey type, no significant block (week of repetition) effect, nor were any of the other interaction terms significant (Table IV). Thus, the number of approaches to tubes in this experiment depended on the absence of prey in the empty tubes and to a lesser extent on the activity level of the prey enclosed in the tubes, but pinfish did not select prey based on their identity.

## DISCUSSION

Based on results of this paper, pinfish use chemoreception in addition to vision in detecting live, uninjured prey and pinfish attack live prey more frequently than dead prey. Further, my results and those of other workers suggest that prey selection by pinfish is not a function of prey identity, but rather prey size and activity.

Chemoreception has been previously demonstrated in pinfish using prey extracts that are ecologically unrealistic. Carr *et al.* (1976) were able to elicit feeding responses in pinfish with relatively low concentrations of shrimp extract (0.1–6.25  $\mu\text{l}$  pink shrimp *Penaeus duorarum* extract  $\cdot \text{ml}^{-1}$  filtered seawater); they demonstrated the pinfish's ability to locate the source of a prey extract using chemoreception (primarily olfaction) alone. However, these extracts were prepared by homogenizing 1 part shrimp muscle with 5 parts seawater in a blender. This process destroyed the integrity of the prey species' body and facilitated detection by the pinfish. Such extracts are much stronger than any olfactory cue the prey may emit naturally.

I have demonstrated that pinfish are able to utilize chemoreception while searching for intact, living prey. Pinfish approached prey in tubes with equal frequency when allowed to use either visual cues alone or chemical cues alone. Thus, it seems unlikely that pinfish are primarily visual feeders. In the field, the concentrations of odors from uninjured prey should be much greater than in my experiments, since field prey densities are much greater than tested here. It is possible that the tube with "open" 500- $\mu\text{m}$  screen tops may have allowed other types of sensory stimuli besides chemical cues (e.g., the open tube tops may have allowed cues relating to water movement by the prey); I cannot rule out this possibility. However, in light of the already demonstrated ability of pinfish to detect low levels of prey extracts, it is likely that pinfish used olfaction to detect prey in these experiments.

It appears that pinfish prey preferences depend on the activity and size of prey and not the prey's identity. In laboratory choice experiments, pinfish (55–76 mm SL) show attack preferences for large individuals of the caridean shrimp *Tozeuma carolinense* over the smaller *Hippolyte zostericola* offered enclosed in glass tubes; however, similar-sized individuals of these species are attacked at equal rates (Main, 1985). In choice tests that measured consumption of prey, pinfish (35–45 mm SL) did not show significantly different preferences for three amphipod species at two densities, although small pinfish

(20–30 mm SL) significantly preferred the amphipod *Elasmopus levis* (Nelson, 1979). Although prey sizes are not given by Nelson (1979), it is stated that the preferred amphipod was the smallest species tested, suggesting that this apparent preference could be due to morphological limitations imposed by the mouth size of these small pinfish. All of these results are consistent with the hypothesis that pinfish respond to prey mainly with regard to their size and not their identity *per se*.

Prey activity influences the frequency of approaches and attacks by pinfish. In the present work, tubes that contained live, and presumably active prey, were more frequently approached than tubes that contained inactive, dead prey. The live prey tested varied somewhat in their patterns of activity during the experiments: amphipods, *Melita appendiculata*, and shrimp, *Hippolyte zostericola*, tended to cling to the seagrass blade enclosed in each tube, but the amphipods were more active than the shrimp, occasionally swimming away from the blade. The polychaetes, *Nereis falsa*, also clung to the blade surface, but frequently left the blade to crawl along the sand or the side of the glass tube (a possible artifact); thus, they were the most active prey. Hydroids, *Sertularia* and *Clytia*, were the least active of all live prey, since they are sessile. Although pinfish did not exhibit significant differences in the frequency of approaches to each of these prey types, these patterns of activity correspond well with the observed trend in Experiment 2: pinfish most frequently approached the most active prey species. Overall, the live prey were rather inactive in the presence of the fish predators. It is likely that these prey have evolved behavioral patterns that tend to minimize their conspicuousness to predators like the pinfish that detect moving prey more frequently than inactive prey. Prey motion has been suggested as a factor that may elicit attacks by pinfish (Main, 1985, 1987) and other fishes (Kislalioglu & Gibson, 1976; Zaret, 1980; Magnhagen & Wiederholm, 1982). Future work should be directed towards quantifying prey activity patterns in the presence and absence of predatory fishes. Higher predation rates and lower survival rates should be experienced by prey showing greater activity and hence greater detectability by predatory fishes.

It should be noted that the live and dead prey may have differed in ways other than their activity patterns in these experiments. The dead prey may have begun to lose body fluids after death and these prey may have been more detectable or repulsive to the fish. Although live prey were approached more frequently than dead prey, increased attractive odors from the dead prey may have lessened the difference between the fish's responses to the two groups of prey. Thus, my test was at least conservative for determining if live prey were more easily detected than dead prey, since dead prey may have been more readily detected chemically, and some live prey tended to be inactive in the presence of fish predators. The choices made by the fish should not be based on energetic differences, but only on prey detectability, because all tubes contained equal weights of prey (Table II).

Based on the experiment in which I offered a choice of prey types (Experiment 2), pinfish did not exhibit strong preferences for epifaunal, seagrass-meadow prey that differ greatly in appearance and behavior. I was able to measure true predator preference

because the effects of prey avoidance (Stein & Magnuson, 1976; Sih, 1982; Main, 1987), differential escape abilities of the prey (Vinyard, 1980), prey palatability (Russell, 1966; Prezant, 1980; Young & Bingham, 1987) and predator mouth morphology (Schmitt & Holbrook, 1984) did not confound the results. These factors would confound the measurement of predator preference if the response variable measured was the actual ingestion of prey. Although the ingestion of prey is the final and most significant step in the predatory sequence, it does not measure predator preference, but rather selectivity due to the combined effects of predator preference, prey avoidance, prey availability, prey size, and prey palatability.

The possible causes of selective feeding have been the subject of an intense controversy in the literature relating to planktivorous fishes. Fishes that selectively consume prey are often observed to consume the largest prey available (Brooks & Dodson, 1965), the most detectable prey or most novel prey (Zaret & Kerfoot, 1975) and prey that show the greatest return of energy per unit time (Werner & Hall, 1974). In the future, investigators of the causes of selective feeding in fishes should include other mechanisms of prey detection besides vision in developing their null models. A bias towards visual detection by planktivorous fishes is apparent from the names given to the hypotheses – “visibility selection” (Zaret & Kerfoot, 1975) or “apparent size selection” (O’Brien *et al.*, 1976) – and the names used in the null models – “reactive visual spheres” (O’Brien *et al.*, 1976; Eggers, 1982). Foraging fishes use other sensory modalities to detect prey, such as chemoreception and mechanoreception, and these modalities must be considered in future tests. Size-selectivity for large zooplankton may not be based solely on visual cues, as has been assumed for the interpretation of the results of experiments designed to test the “apparent size” hypothesis (Gardner, 1981). If chemoreceptors and lateral line receptors play a large role in the detection of prey in low light and high turbidity conditions, then tests which assume a strictly visual mechanism for prey detection may be invalid.

The selective feeding of predators can greatly influence the structure of prey communities. Pinfish are the most common predator on epifaunal communities in seagrass meadows and affect the structure of these communities because of their selective feeding. My results suggest that prey that are conspicuous (i.e., highly active) members of epibenthic prey communities will be more readily attacked by pinfish and that the fish themselves do not make an active choice for one prey type over another based on prey identity. In addition, since turbid conditions often persist in these habitats, chemoreception is likely to be an important method of finding prey by pinfish. The results reported here extend our knowledge of the causes of selective feeding by pinfish and fishes in general. Knowledge of the process by which pinfish selectively remove prey will increase our understanding of the mechanisms that structure epifaunal communities in seagrass meadows.

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