

FISH PREDATION ON JUVENILE BROWN SHRIMP, *PENAEUS AZTECUS* Ives: THE EFFECT OF SIMULATED *SPARTINA* STRUCTURE ON PREDATION RATES

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Abstract: The effect of artificial *Spartina* structure on the predation rates of four estuarine fish on juvenile brown shrimp (*Penaeus aztecus* Ives) was examined under laboratory conditions. Vegetative structure reduced predation rates of pinfish and Atlantic croaker but did not affect predation rates of red drum and speckled trout. Pinfish and Atlantic croaker were inefficient predators, needing several strikes before successfully capturing prey. This inefficiency, necessitating repeated detection of prey organisms, probably contributed to the reduced predation rates by these fish in vegetated treatments. Although pinfish and speckled trout appeared to be strictly visual feeders, Atlantic croaker and red drum could apparently detect and feed upon shrimp through other sensory mechanisms. Differences in the mode of feeding among the fish, however, did not appear to be related to the effect of vegetative structure on predation rates. Over all of the experiments, predation rates on shrimp (50–69 mm) ranged between ≈ 2 and 13 shrimp \cdot fish⁻¹ \cdot day⁻¹, and there was a positive relationship between the number of shrimp eaten and the size of the predator.

INTRODUCTION

Predation by fishes is an important source of mortality of juvenile penaeid shrimp in estuarine systems (Pearson, 1928; Knapp, 1949; Miles, 1949; Kemp, 1950; Overstreet & Heard, 1978a). Postlarval penaeids move into the estuaries along the northern coast of the Gulf of Mexico from early spring until fall (Baxter & Renfro, 1967) and remain in these areas over a period of several months before moving back offshore as subadults (Trent, 1966). This period in their life cycle is one of rapid growth and maximum availability to a large number of juvenile and subadult fish predators present in estuaries.

Estuaries in the northern Gulf of Mexico usually have large stands of the smooth cordgrass *Spartina alterniflora* Loisel. Field work in the Galveston Bay system has demonstrated a preference by young brown shrimp, *Penaeus aztecus* Ives, for areas vegetated by *Spartina* (Trent *et al.*, 1969; Zimmerman *et al.*, in prep.). It has been suggested that this emergent vegetation functions, at least partially, as a refuge for juvenile

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shrimp from predators (Giles & Zamora, 1973). In laboratory experiments, Vince *et al.*, (1976), and Van Dolah (1978) have shown that *Spartina* can function as protective cover for amphipods. Other estuarine vegetation, mostly seagrasses, has been reported to reduce predation on small fish (Lascara, 1981), bivalves (Peterson, 1982), and crustaceans (Nelson, 1979; Stoner, 1979; Coen *et al.*, 1981; Heck & Thoman, 1981).

Studies of fish predation on shrimp in estuaries have focused on stomach content analyses. The sciaenids appear to be the most important predators, and within this family, speckled trout, *Cynoscion nebulosus* (Cuvier), red drum, *Sciaenops ocellatus* (Linnaeus), and to a lesser extent Atlantic croaker, *Micropogonias undulatus* (Linnaeus), have often been reported to feed on penaeid shrimp.

Penaeids have been reported as a major dietary component of speckled trout in Texas estuaries by Pearson (1928), Knapp (1949), Miles (1949), Kemp (1950), and Seagle (1969) and in other estuaries in the Gulf of Mexico by Moody (1950) and Stewart (1961). Penaeid shrimp have been recorded as present but not abundant in the stomachs of these fish by Gunter (1945), Darnell (1958), Springer & Woodburn (1960), Lorio & Schafer (1966), Fontenot & Rogillio (1970), Carr & Adams (1973), and Diener *et al.* (1974).

Large numbers of penaeid shrimp in the stomachs of red drum have been reported by Pearson (1928), Gunter (1945), Knapp (1949), and Kemp (1950) in Texas estuaries and by Yokel (1966), Boothby & Avault (1971), Bass & Avault (1975), and Overstreet & Heard (1978a) in other Gulf of Mexico estuaries. Miles (1949) and Fontenot & Rogillio (1970), however, found relatively few penaeid shrimp in similar studies on red drum.

In general, stomach analyses on the Atlantic croaker from estuaries of the Gulf of Mexico have indicated that penaeid shrimp are a relatively minor dietary constituent (Darnell, 1958; Fontenot & Rogillio, 1970; Diener *et al.*, 1974; Sheridan, 1978). In Mississippi Sound, however, Overstreet & Heard (1978b) reported that >40% of the Atlantic croaker examined during the summer and winter contained penaeid shrimp.

Among other relatively abundant fishes found in estuaries of the Gulf of Mexico and southeastern United States, only a few species have been reported to feed extensively on penaeid shrimp. These include the sea catfish, *Arius felis* (Knapp, 1949; Harris & Rose, 1968), the southern flounder, *Paralichthys lethostigma* (Miles, 1949; Stokes, 1977), and the weakfish, *Cynoscion regalis* (Welsh & Breder, 1923; Merriner, 1973). Although the pinfish, *Lagodon rhomboides*, one of the most ubiquitous estuarine fishes in vegetated areas, has been reported to feed on shrimp (Hanson, 1969; Carr & Adams, 1973; Brook, 1977; Stoner, 1980), penaeids have not been specifically identified in their stomach contents. However, the feeding behavior of pinfish, discussed in detail in this paper, makes it difficult to identify penaeid shrimp remains through stomach analyses.

The large variability reported in the presence and relative abundance of penaeid shrimp in fish stomach analyses is undoubtedly due to differences among these studies in sampling methods, preservation techniques, sizes and numbers of fish examined,

seasonal availability of penaeids, and presence of alternative prey. The availability of protective habitats may also be a factor. The presence of vegetative cover, optimal substrata for burrowing, and highly turbid water may affect the susceptibility of penaeids to fish predation. In addition, the protective nature of habitats may vary depending upon specific predators and prey.

Although surveys of stomach contents suggest potentially important predators, these data offer little information on predation rates or on factors, such as vegetative cover, which may influence predator related mortality in estuarine systems. This study examines the effect of vegetative structure on predation rates of pinfish, Atlantic croaker, red drum, and speckled trout on juvenile brown shrimp, *Penaeus aztecus*.

METHODS AND MATERIALS

COLLECTION AND HANDLING OF EXPERIMENTAL ANIMALS

Fish were collected in trawls and seines and by hook and line from Galveston Bay, Texas. They were held in 1.8-m diameter circular tanks for a minimum of 5 days prior to an experiment. Fish readily ate live shrimp in the holding tanks and were fed shrimp daily. All fish, except speckled trout, were starved for 24 h before an experiment. Trout were starved for 48 h because preliminary results indicated that they frequently would not feed during an experiment after a 24-h starvation period.

Total lengths were recorded for all fish. Wet weights of pinfish and speckled trout were measured after predation experiments. Since Atlantic croaker and red drum were to be used in other experiments, weights of these fish were estimated using the length-weight relationships of White & Chittenden (1977) and Harrington *et al.* (1979) in an effort to reduce handling. Deviations of predicted weights from actual weights were checked and found to be $\approx 3-4\%$.

Shrimp were collected with trawls and seines. They were held in circular tanks with a crushed oyster shell substratum and fed daily with pelleted shrimp food. They were not fed during experiments. The total length (measured from the tip of the rostrum to the tip of the telson) was recorded for all individuals used in each experiment. The length-weight relationship of Mercer (1981) was used to estimate shrimp weights.

EXPERIMENTAL APPARATUS

Experiments were conducted in circular cages (1.5-m diameter, 1 m high) constructed of 12.7-mm mesh plastic coated wire lined with 6.4-mm plastic mesh. Five cages were placed in each of two large cement tanks (2.9 m \times 7.6 m \times 0.6 m), located in a building with a white translucent roof which allowed the use of natural photoperiods. Individual subgravel filters of crushed oyster shell were constructed for each cage. Sea water was pumped from the surf zone off Galveston Island, and salinities were maintained within a range of 23-28‰. Water temperatures during the pinfish experiment ranged from 22.0

to 23.9 °C, and during all other experiments from 26.5 to 29.6 °C. The water depth within the cages was ≈ 40 cm.

Spartina structure was simulated using 50-cm long straws (6.4-mm diameter) mounted in plastic mesh. Straws were painted green using lead-free spray paint after checking for toxicity to shrimp. The entire bottom area was filled with straws in vegetated treatments. To simulate natural *Spartina* growth patterns, straws were arranged in a clumped distribution. The spatial distribution of clumps and straws within clumps for the three densities of artificial vegetation is shown in Fig. 1. Cages with the lowest density

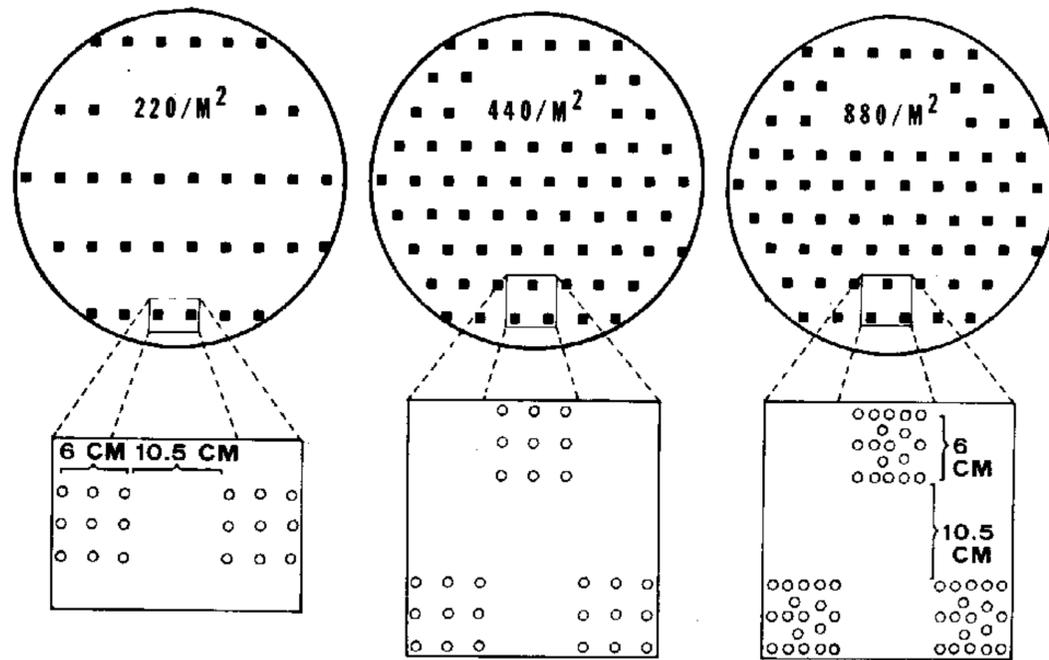


Fig. 1. Distribution of artificial vegetation within cages for the three stem densities used in experiments: ■, clumps of straws; ○, individual straws.

of vegetation (220 stems \cdot m $^{-2}$, used only in the pinfish experiment) contained 43 clumps of straws. Cages with 440 stems \cdot m $^{-2}$ and 880 stems \cdot m $^{-2}$ both had 86 clumps of straws, and the stem densities were increased by doubling the number of straws in a clump. This method of increasing stem densities to 880 stems \cdot m $^{-2}$ was necessary to allow large fish free movement within the vegetation, although it confounded the effect of stem density with clump density. In all experiments where no effect of vegetation was detected, however, the highest stem densities and clump densities were used. All stem densities were approximately within the range of *Spartina alterniflora* stem densities found naturally in a West Galveston Bay salt marsh. The distribution, density, and size of clumps of *Spartina* in the field is highly variable, and all of the combinations used in the laboratory are represented in the marsh. The even distribution of stems and clumps, however, was unnatural.

The plastic mesh with straws was placed over the shell substratum and covered with

40 mm of blasting sand. Straws extended ≈ 42 cm above the sand. Plastic mesh without straws was placed in nonvegetated cages. The upper 20 mm of sand was well sorted with a graphic mean of 2.91 ϕ (analyzed according to Folk, 1980). Following the initial pinfish experiment, a thin layer of washed marsh or beach sand was placed over the light colored blasting sand, to reduce the contrast between prey and substratum.

EXPERIMENTAL DESIGN

The experimental designs used for each species of fish predator in our experiments varied. A summary of the vegetation densities and predator and prey densities and sizes used is shown in Table I. Size ranges of predators and prey were chosen on the basis of availability at the time of the experiment. Since direct observations on the number of shrimp present in a cage were unreliable due to the burrowing behavior of *Penaeus aztecus*, two methods were used to measure predation rates. The method used was selected on the basis of differences in feeding behavior among the predators.

For pinfish, which did not consume an entire shrimp when feeding, the presence of the carapace and tailfan of a shrimp on the substratum was used as evidence of a successful predatory attack. Three fish and 10 shrimp were placed in each experimental cage. Every 3 h over a 3-day period, the number of shrimp eaten was recorded, and the carapace and tailfan of eaten shrimp were removed. The total weight of shrimp remnants from each cage was also recorded. Eaten shrimp were replaced during each observational period, maintaining the density at 10 shrimp \cdot cage $^{-1}$. This density (5.6 shrimp \cdot m $^{-2}$) was similar to the maximum densities recorded for *P. aztecus* > 30 mm in length from a Galveston Bay salt marsh (Zimmerman *et al.*, in prep.). To examine the relationship between the burrowing behavior of the shrimp and the feeding periodicity of the fish, the percent of shrimp burrowed during each observational period was estimated by recording the number not burrowed and comparing this number to the number of shrimp present in each cage. This was necessary since burrowed shrimp were usually completely beneath the substratum. All observations at night were made using a red light.

Atlantic croaker, red drum, and speckled trout ate shrimp whole and did not leave remnants. With these fish, predation experiments were run over 24-h periods. Initial densities of shrimp were usually increased to 20 \cdot cage $^{-1}$, and predator densities ranged between 1 and 3 fish per cage. Predator densities were adjusted depending upon the size and species of fish to insure that some shrimp were eaten in all cages, and that the number of shrimp was not greatly depleted over the 24-h period. Fish were measured and placed in the experimental cages at least 6 h before introducing the shrimp. Shrimp were measured and added after dark (usually around 2400 hours) when they normally would not be burrowed in the substratum. After 24 h, the tanks were drained, and the remaining shrimp were counted and measured. All shrimp missing from a cage at the end of an experiment were considered eaten. Final prey densities were generally 10–13 shrimp \cdot cage $^{-1}$.

TABLE I

Summary data on predator and prey (*Penaeus aztecus*) densities and sizes used in predation experiments, and the densities of vegetation examined.

Predator	Predator density (no. · cage ⁻¹)	Pred. size (mm TL)	Prey density (no. · cage ⁻¹)	Prey size (mm)	Exp. duration (h)	Density of vegetation**		
						No veg.	220 stems · m ⁻²	440 stems · m ⁻²
Pinfish	3	61-74	10*	50-58	72	xxx	xxx	xxx
Atlantic croaker	3	115-133	20	50-60	24	xxx	xxx	xxx
Red drum I	1	154-182	20	50-60	24	xxx	xxx	xxx
Red drum II	1	190-245	20	50-60	24	xxx	xxx	xxx
Red drum III	1	160-195	15	55-65	24	xxx	xx	xx
Speckled trout	2	119-170	20	50-69	24	xxx	xxx	xxx

* With replacement every 3 h.

** x's indicate the number of replicate cages.

Since the effect of vegetation on feeding rates might be related to the mode of feeding of the fish, separate experiments were conducted to examine feeding periodicity in Atlantic croaker and red drum. Fish that fed only during daylight hours were considered to be strictly visual feeders. In these experiments, fish and 10 shrimp were placed in nonvegetated cages with a substratum of crushed oyster shell and a thin layer of sand. Shrimp did not burrow out of sight in this substratum. Shrimp were counted every 3 h, and those eaten were replaced.

A control cage, with the same density of shrimp but no fish, was included during all predation experiments to check for mortality not due to predation. Deaths unrelated to predation were exceptionally low, and overall, only 1.9% of 267 control shrimp died.

STATISTICAL ANALYSES

Analysis of variance (ANOVA) was utilized to examine the effect of vegetation density on predation rates, using the number of shrimp eaten · fish⁻¹ · day⁻¹ as the observation. In the pinfish experiment, data on the number of shrimp eaten were summed over each of the 3 days. Main effects of vegetation density and days, plus the vegetation density-day interaction were examined. Although there may have been some dependency in feeding rates among days, it was considered to be small, and days were assumed to be independent in the analysis. The related potential problem of fish in some cages consistently not eating over the 3-day period was addressed by an additional factor in the model for a cage effect. This variability due to cages within vegetative treatments was used to test for the main effect of vegetation density. In the experiments with other fish predators, a one-way ANOVA or a *t*-test was used to test for an effect of vegetation density.

In order to determine whether there was selection by the fish for a particular size of shrimp, a Kolmogorov-Smirnov two-sample nonparametric test was used to compare the size-frequency distributions of shrimp eaten versus those not eaten (Conover, 1971). A significant difference (0.05 level) between size-frequencies indicated that selection by the fish occurred.

RESULTS

PINFISH

Predation on *P. aztecus* by pinfish occurred mostly during daylight hours (Fig. 2). When the data were analyzed using the number of shrimp eaten · fish⁻¹ · day⁻¹ in the ANOVA, the vegetation density-day interaction and the main effect of vegetation density were the only factors with significant *F* values at the 0.05 level (Table II). The mean predation rate was greatest in the nonvegetated cages (Table III). Fish consistently ate more shrimp in the nonvegetated cages over the 3-day period compared to the high density (440 stems · m⁻²) cages, and the significant interaction term was due to a high predation rate in the low density (220 stems · m⁻²) treatment on the third day

of the experiment (Fig. 3). A Duncan's multiple range test on the main effect of vegetation density showed that the nonvegetated treatment was significantly different (0.05 level) from both vegetated treatments, and the means in the two vegetated treatments were not significantly different. A one-way ANOVA examining only vegetation density was also calculated from these data, and the *F* value was significant (*P* = 0.026). Overall the results indicate that the presence of vegetative structure significantly reduced the predation rates.

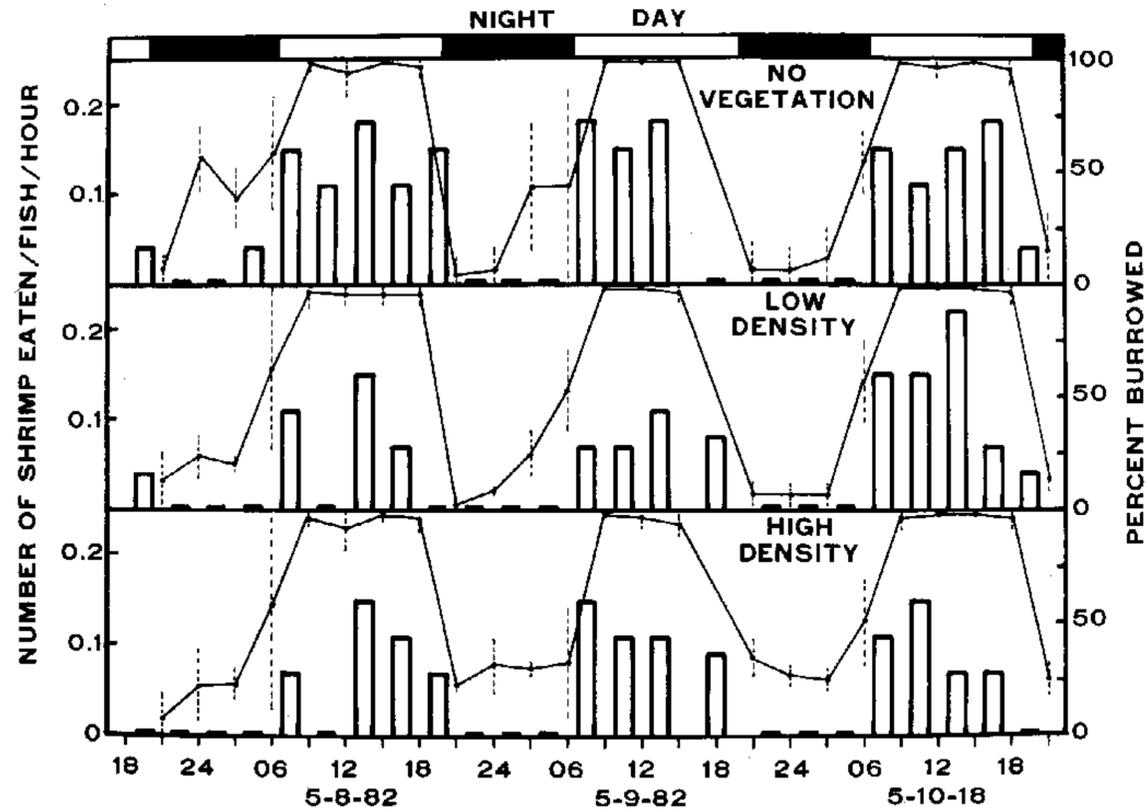


Fig. 2. Diel changes in the feeding rates of pinfish and the burrowing behavior of brown shrimp in the three vegetation density treatments over the 3-day experiment: the mean number of shrimp eaten \cdot fish $^{-1} \cdot$ h $^{-1}$ from three replicate cages for 3-h periods is represented by the histograms; the solid line represents the mean percent of shrimp burrowed, and the vertical dashed line indicates \pm 1 SD around these means (untransformed data).

TABLE II
ANOVA results from the 3-day pinfish experiment.

Source of variance	d.f.	SS	<i>F</i>	<i>P</i>
Total	26	8.667		
Vegetation density	2	3.472	7.04	0.027
Cage (veg. density)	6	1.480	2.00	0.145
Day	2	0.405	1.64	0.235
Day-veg. density	4	1.828	3.70	0.035
Error	12	1.482		

TABLE III

Mean number of *Penaeus aztecus* eaten \cdot fish $^{-1} \cdot$ day $^{-1}$ at different vegetation densities for predators examined: ANOVA probability values are also listed; additional information on experiments is given in Table I.

Predator	Pred. size (mm TL)	No. of obs/mean	Mean number of shrimp eaten \cdot fish $^{-1} \cdot$ day $^{-1}$			ANOVA <i>P</i>
			No. veg.	220 stems \cdot m $^{-2}$	440 stems \cdot m $^{-2}$	
Pinfish	61-77	9	2.2	1.4	1.4	0.03**
Atlantic croaker	115-133	3	3.4	2.6	2.0	0.04
Red drum I	154-182	3	6.7		6.3	0.86
Red drum II	190-245	3	10.3		9.3	0.67
Red drum III	160-195	3*	9.7		8.5	0.52
Speckled trout	119-170	3	3.8		3.8	1.0

* *n* = 2 for vegetated treatment.
** Taken from Table II.

Pinfish (61–77 mm TL) ranged from 3.7 to 6.9 g in weight with a mean value of 5.2 g (SD = 0.9, $n = 27$). Shrimp (50–58 mm) weights ranged from 1.1 to 1.6 g. The weight of shrimp eaten in each cage was estimated from the number eaten, using a median

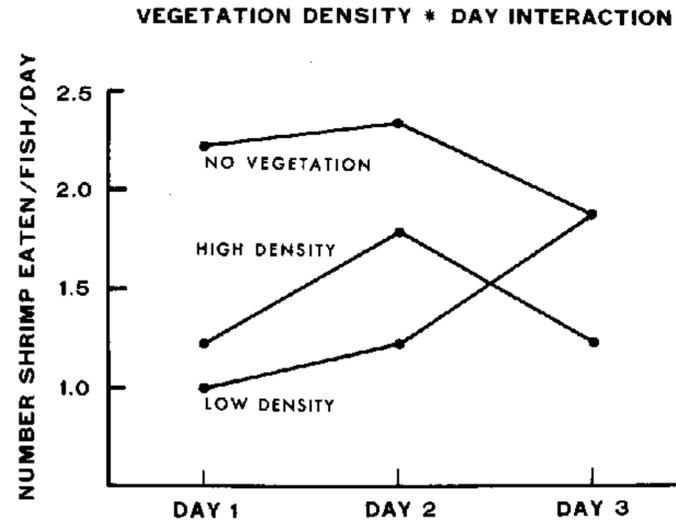


Fig. 3. Daily predation rates on brown shrimp by pinfish during the 3-day experiment: the mean number of shrimp eaten \cdot fish $^{-1}$ \cdot day $^{-1}$ from three replicate cages is shown for each vegetation density.

value of $1.3 \text{ g} \cdot \text{shrimp}^{-1}$. The weight of shrimp remnants was subtracted from this estimate. The grams of shrimp eaten \cdot g fish $^{-1}$ \cdot day $^{-1}$ at each vegetation density are shown in Table IV. These data correct for differences in weights of fish, and the results compare well with the ANOVA results on the number of shrimp eaten \cdot fish $^{-1}$ \cdot day $^{-1}$. The largest biomass of shrimp, in $\text{g} \cdot \text{g fish}^{-1}$ \cdot day $^{-1}$, was eaten in the nonvegetated cages. In all nine cages, pinfish ate between 17 and 44% of their body weight in shrimp per day.

Pinfish appeared to be visual predators, feeding primarily during daylight hours (Fig. 2). Diel stomach content analyses by Kjelson *et al.* (1975), Peters & Kjelson (1975), Adams (1976), and Brook (1977) also indicated that these fish feed mostly during the day. They were not efficient predators on the size of shrimp used in these experiments and generally needed to make several predatory attacks on a shrimp before a successful kill. Frequently the fish attacked in groups, and some of our preliminary experiments suggested that feeding rates were higher when more than one fish was present in a cage. After being attacked, shrimp generally swam near the surface of the water. Each attack elicited an escape response which included a rapid unflexing of the abdomen causing a jump through and frequently out of the water. A successful attack occurred when one fish removed an eye or several pleopods, causing the shrimp to become disabled and swim in an erratic manner. Generally, all three fish participated in the kill, tearing pleopods and muscle tissue from the ventral abdomen. A dominance hierarchy was frequently established after a kill. The dominant, generally the largest, fish prevented the others from feeding until it abandoned the remains.

TABLE IV

Mean feeding rates of fish in $\text{g shrimp} \cdot \text{g fish}^{-1}$ \cdot day $^{-1}$ from the three replicate cages of each vegetation density: additional information on experiments is given in Table I.

Predator	Pred. weight (g)	Prey* weight (g)	Mean g shrimp eaten \cdot g fish $^{-1}$ \cdot day $^{-1}$ (SD)	
			No. veg.	stems \cdot m $^{-2}$
Pinfish	3.7–6.9	1.0–1.6	220	880
Atlantic croaker	17.0–26.9*	1.0–1.8	440	880
Red drum I	36.9–61.4*	1.0–1.8	0.26 (0.08)	0.16 (0.05)
Red drum II	69.9–151.5*	1.0–1.8	0.28 (0.05)	0.21 (0.09)
Red drum III	41.5–75.7*	1.4–2.4	0.19 (0.06)	0.13 (0.04)
Speckled trout	16.5–44.9	1.0–2.9	0.28 (0.03)	**0.26 (0.03)
				0.23 (0.06)

* Estimated from length data.

** $n = 2$.

Under our experimental conditions, pinfish fed throughout the day despite a high percentage of burrowed shrimp during daylight hours (Fig. 2). The shrimp replaced during the day were especially vulnerable to predation until they could burrow. To determine whether this unnatural situation was responsible for the predation observed throughout the day, the experiment was repeated replacing shrimp only at night. Feeding still occurred throughout the day, suggesting that the fish could detect and feed upon burrowed shrimp. On two occasions during daylight hours, fish were observed searching the bottom, pulling burrowed shrimp out of the substratum by their eyestalks, and completing a successful predatory attack.

ATLANTIC CROAKER

Feeding rates of Atlantic croaker (115–133 mm TL), in number of shrimp eaten \cdot fish $^{-1} \cdot$ day $^{-1}$, were significantly reduced by the presence of vegetation (Table III). Results from a Duncan's multiple range test (0.05 significance level) indicated that the mean number of shrimp eaten in the nonvegetated treatment (3.4 shrimp \cdot fish $^{-1} \cdot$ day $^{-1}$) was significantly higher than the mean from the high density vegetative treatment (2.0 shrimp \cdot fish $^{-1} \cdot$ day $^{-1}$). Neither of these means, however, was significantly different from the mean in the medium density vegetation. Comparisons of the size-frequency distributions of shrimp eaten versus those not eaten indicated that no apparent size selection occurred by the fish in vegetated or nonvegetated treatments.

When lengths of both the fish and the shrimp were converted to weights, the largest weight of shrimp, in g \cdot g fish $^{-1} \cdot$ day $^{-1}$, was eaten in the nonvegetated cages (Table IV). In all nine cages, the fish ate between 11 and 27% of their weight per day in shrimp.

Atlantic croaker appeared to be inefficient predators on the brown shrimp used in our experiments. Fish were frequently observed pursuing shrimp and several strikes were needed before a successful kill occurred. Although fish generally ate entire shrimp, the presence of shrimp remains was monitored every 3 h throughout the experiment. These data along with data from a 1-day experiment on diel feeding periodicity indicated that croaker could feed on shrimp at any time of the day or night. This would suggest that they are not strictly visual feeders but also use other sensory mechanisms (Chao & Musick, 1977).

RED DRUM

Three experiments were analyzed for an effect of vegetative structure on predation by red drum, and the results from all three were similar. Although the mean number of shrimp eaten in the nonvegetated cages was higher than in the vegetated cages for all three experiments, there were no significant differences between the treatments (Table III).

When the data were converted to g shrimp eaten \cdot g fish $^{-1} \cdot$ day $^{-1}$, a similar pattern was evident (Table IV). The red drum ate between 10 and 31% of their weight in

shrimp \cdot day $^{-1}$, and in each experiment the greatest weight of shrimp \cdot weight of fish $^{-1}$ was eaten in the nonvegetated cages. The within treatment variances, however, were too great to allow detection of statistically significant differences between treatments (vegetation densities).

The weight of the red drum used in these experiments ranged between \approx 37–152 g. The larger fish generally ate a smaller percent of their weight in shrimp \cdot day $^{-1}$, and a linear regression of g shrimp eaten \cdot g fish $^{-1} \cdot$ day $^{-1}$ over the weight of the fish had a significant negative slope ($P = 0.005$). This explained 43% of the variability in the weight of shrimp eaten (Fig. 4). Because some of the within treatment variability could

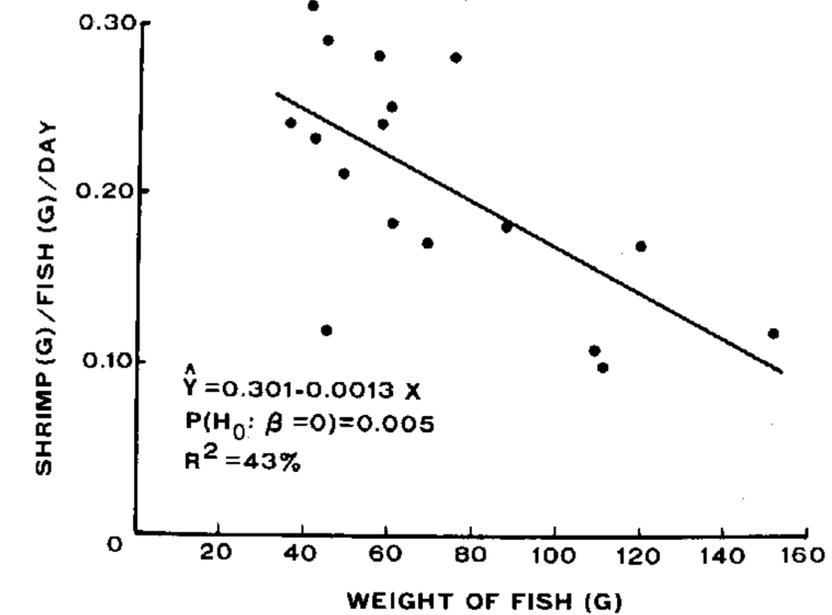


Fig. 4. The relationship between the weight of red drum and the g shrimp eaten \cdot g fish $^{-1} \cdot$ day $^{-1}$.

have been caused by differences in weights of fish, an analysis of covariance (ANCOVA) was calculated using grams of shrimp \cdot g fish $^{-1} \cdot$ day $^{-1}$ as the observation and the weight of the fish as the covariate. All of the data were pooled in this analysis, and we considered the cages from the three experiments to be replicates (nine nonvegetated and eight vegetated). The effect of vegetation density was still not significant in this analysis ($P = 0.42$).

Overall, there was no selection by red drum for a particular size of shrimp within the sizes available, and the presence of vegetative structure did not affect size selection. Kolmogorov–Smirnov tests comparing size-frequency distributions of shrimp eaten versus those not eaten were not significant at the 0.05 level.

The red drum used in our experiments appeared to be extremely efficient predators on juvenile penaeid shrimp. Shrimp seldom escaped a predatory attack, and the fish spent very little time pursuing prey. Experiments on feeding periodicity by these fish were conducted with both brown and white shrimp. There were no obvious differences in feeding on the two species of shrimp, and the combined data are shown in Fig. 5.

Although variances were large, and few statistically significant differences were apparent over time, mean feeding rates were highest near sunrise and sunset. Feeding occurred throughout the day and night indicating that red drum are not strictly visual feeders.

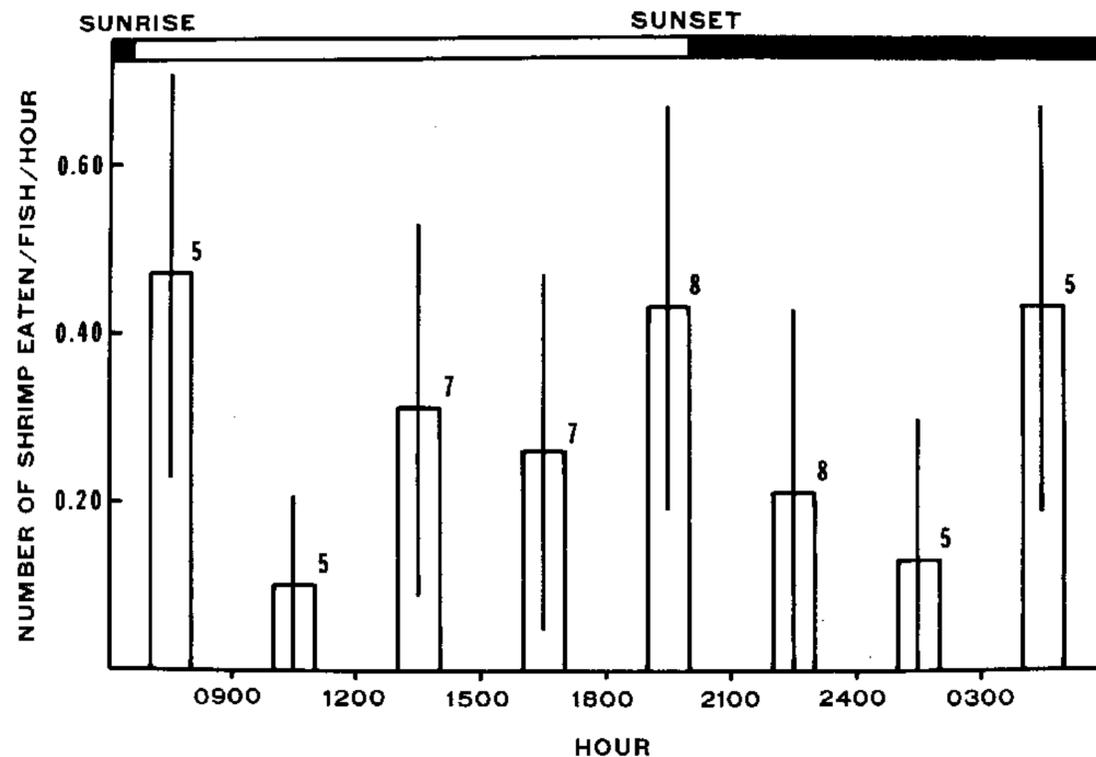


Fig. 5. Feeding periodicity of red drum (202–257 mm TL) on *Penaeus aztecus* and *P. setiferus* (65–80 mm): bars represent the mean number of shrimp eaten \cdot fish $^{-1}$ \cdot h $^{-1}$ over each 3-h period; data were combined from several experiments and the number of observations per mean is indicated over each bar; vertical lines represent 95% confidence intervals.

SPECKLED TROUT

Speckled trout consumed prey whole and appeared to be very efficient predators. They spent only a small amount of time pursuing prey, and shrimp seldom escaped a predatory attack. Although large trout (> 300 mm TL) caught by hook and line would frequently not feed under our experimental conditions, smaller trout (119–170 mm) caught in seines fed readily in the experimental cages. The mean feeding rate in number of shrimp eaten \cdot fish $^{-1}$ \cdot day $^{-1}$ for the three vegetated cages was the same as the mean rate from the three nonvegetated cages (Table III).

When the data were examined in the form of g shrimp eaten \cdot g fish $^{-1}$ \cdot day $^{-1}$, the results were similar. Although a slightly higher weight of shrimp/weight of fish was eaten in the nonvegetated cages (Table IV), a *t*-test comparing the two means was not significant ($0.20 > P > 0.10$). Over the six experimental cages, the trout ate between 18 and 31% of their body weight in shrimp per day.

The size range of the shrimp available to the trout (50–69 mm) was larger than the ranges used in the experiments with other fish. Although there was no significant

difference between the size-frequency distributions of shrimp available in vegetated versus nonvegetated cages ($P > 0.20$), the trout in nonvegetated cages fed selectively on smaller shrimp (Fig. 6). A comparison of the size-frequency distributions of shrimp

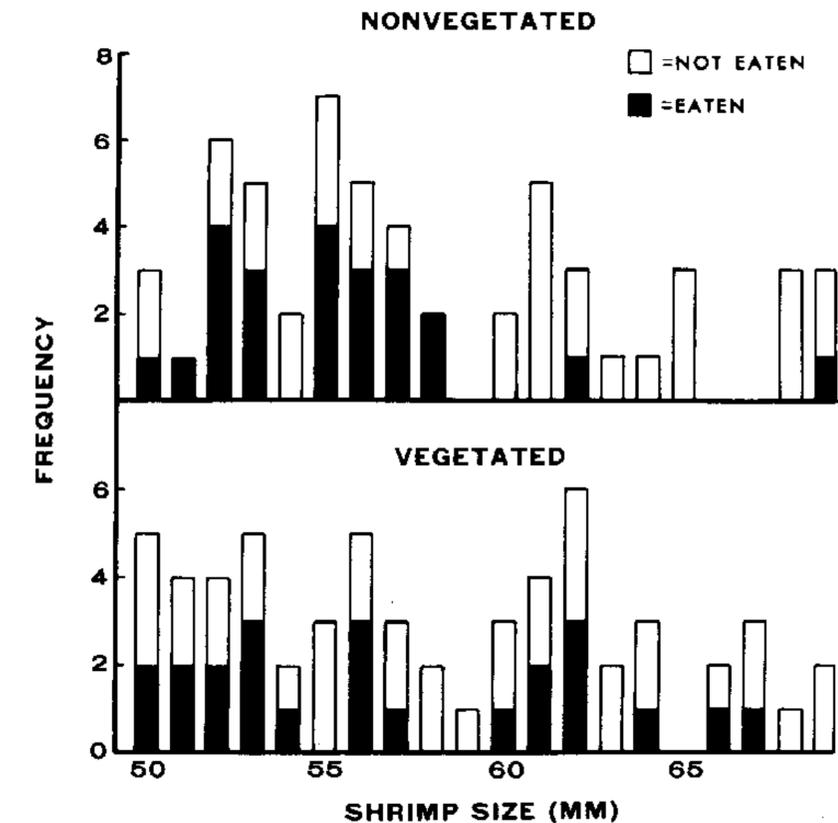


Fig. 6. Size-frequency distributions of shrimp eaten and not eaten by speckled trout in vegetated and nonvegetated cages: data from three cages ($n = 60$) were pooled for each frequency distribution; the total height of the bar represents the frequency of each size present at the start of the experiment.

eaten versus those not eaten in these cages was highly significant ($P < 0.01$). A similar test in the vegetated treatment indicated no selection occurring ($P > 0.20$). A difference in predator size could have been responsible for the difference in size selection for shrimp between the two treatments. Although the mean length of the trout in the nonvegetated cages ($\bar{X} = 132$ mm, $SD = 13$, $n = 6$) was smaller than in the vegetated cages ($\bar{X} = 139$ mm, $SD = 18$, $n = 6$), the difference was not statistically significant (*t*-test, $P > 0.20$). In the replicate of the vegetated treatment with the smallest fish (130 and 140 mm), however, there appeared to be some selection for smaller shrimp.

DISCUSSION

The presence of large stands of *Spartina alterniflora* in many of the estuaries of the Gulf of Mexico possibly provides a refuge for juvenile penaeid shrimp from fish predators. *Spartina* structure increases habitat complexity in these systems, and this has

often been demonstrated to reduce predator related mortality in aquatic environments (Cooper & Crowder, 1979). In the few studies examining this aspect of predation in salt marshes, Vince *et al.* (1976) and Van Dolah (1978) have shown that *Spartina* probably does offer amphipods and small gastropods protection from fish predators. The results of our laboratory experiments have indicated that, at least for some estuarine fishes, the presence of artificial *Spartina* structure also reduces predation on juvenile *Penaeus aztecus*.

Field work in a West Galveston Bay salt marsh has established the presence of the organisms used in our experiments. *P. aztecus* (50–70 mm) is present in the marsh and exhibits a preference for areas vegetated by *Spartina alterniflora* compared to adjacent nonvegetated areas (Zimmerman *et al.*, in prep.). Rotenone sampling has shown that the sizes and species of fish utilized in our experiments are also commonly found in these salt marshes (W. Baker, Texas Parks and Wildlife Dept., pers. comm.).

The presence of vegetative structure reduced predation rates of pinfish and Atlantic croaker on *Penaeus aztecus*, while predation rates of red drum and speckled trout apparently remained unaffected. Both pinfish and Atlantic croaker were relatively small as predators (Table V) on the size of brown shrimp used in these experiments

TABLE V
Summary of differences among predators.

Species	Size (mm TL)	Method of prey detection	Efficiency in capturing prey	Affected by structure
Pinfish	61–77	Visual	Poor	Yes
Atlantic croaker	115–133	Visual and nonvisual	Poor	Yes
Speckled trout	119–170	Visual	Good	No
Red drum	154–245	Visual and nonvisual	Good	No

(50–69 mm), and they appeared to be inefficient predators, needing several strikes to capture prey. Although the speckled trout used were similar in size to the Atlantic croaker, both the trout and red drum were extremely efficient predators. This difference in the ability to feed efficiently on brown shrimp may have contributed to our results.

Savino & Stein (1982) stressed the role of structure in reducing visual contact with prey organisms. Predatory fishes relying strictly on vision, therefore, might be expected to be most affected by the presence of vegetative structure. The effect of structure in our experiments, however, did not appear to be directly related to the mode of feeding of the predators. Data on the feeding periodicity of pinfish indicate that they are strictly visual feeders and do not feed in the absence of light. The general morphology of

speckled trout, however, suggests that these fish are also visual feeders (Chao & Musick, 1977). Laboratory observations on feeding behavior by Lascara (1981) indicate that the closely related weakfish (*Cynoscion regalis*) does not feed in the absence of light. Red drum and Atlantic croaker do not appear to be restricted to feeding during the day and apparently are able to detect and capture prey through other sensory mechanisms. The manner in which vegetative structure affected predation in our experiments, therefore, is unclear. Factors including the restriction of predator movement caused by the structure, the mode of feeding of the predator, and the diel periodicity in the burrowing behavior of the prey, may all be involved. Inefficiency in capturing prey, however, necessitating repeated detection of prey organisms before a successful kill, probably magnified the effect of structure on predation rates.

Although there was no detectable effect of vegetative structure on the predation rates of red drum and speckled trout in our experiments, natural *Spartina* may provide protective cover for shrimp from these predators. Stem densities used in our highest density treatments ($880 \cdot \text{m}^{-2}$) were comparable to the highest stem densities observed for *Spartina alterniflora* in a Galveston Bay salt marsh (Zimmerman *et al.*, in prep.). The presence of leaves, however, undoubtedly makes natural vegetation more structurally complex than our artificial vegetation. In addition, in our vegetated treatments, both predators and prey were restricted to an entirely vegetated environment. Differences in distributions associated with selectivity for vegetation by predators and prey could modify this predator-prey relationship. Lascara (1981) observed reduced predation rates by *Cynoscion regalis* on small fish in partially vegetated wading pools, compared to nonvegetated pools. There also may have been some differences in energy expenditures by fish in the vegetated and nonvegetated treatments. The relatively long duration of our experiments (24 h) prevented us from detecting differences of this type. Vegetation could provide protection from predators, if additional energy is necessary to capture prey in vegetated habitats.

Predation rates for the four species of fish (using only nonvegetated data for pinfish and Atlantic croaker) ranged between 2 and 13 shrimp $\cdot \text{fish}^{-1} \cdot \text{day}^{-1}$. A positive relationship existed between the size of the fish and the number of shrimp eaten. This relationship was best demonstrated by the data from the 17 cages with red drum ranging in size from 154 to 245 mm (TL). These fish ate between 3 and 13 shrimp per day, and there was a positive linear correlation between the total length of the fish and the number of shrimp eaten ($r = +0.62$, $P < 0.01$). A similar relationship was present for red drum when length data were converted to biomass estimates, and the pattern was also apparent when the data from all four species of fish were examined (Table VI). A negative relationship existed, however, between the weight of the fish and the g shrimp eaten $\cdot \text{g fish}^{-1} \cdot \text{day}^{-1}$ (Table VI). Pinfish were the smallest fish examined (≈ 4 –6 g), and they ingested a relatively high percentage of their weight in shrimp per day (37–44%). For comparative purposes, these feeding values for pinfish are probably conservative since water temperatures were $\approx 5^\circ \text{C}$ lower during the pinfish experiment in relation to the experiments with other fish predators. At comparable temperatures,

TABLE VI

A summary of the data on the length and weight of the fish and the number and weight of shrimp eaten per day for the four species of estuarine fish examined: data from only nonvegetated cages are included for Atlantic croaker and pinfish.

Species	Length of fish (mm TL)	Weight of fish (g)	No. of cages	No. of fish · cage ⁻¹	No. shrimp eaten · fish ⁻¹ · day ⁻¹	g shrimp eaten · fish ⁻¹ · day ⁻¹	g shrimp eaten · g fish ⁻¹ · day ⁻¹	T (°C)
Red drum	154-245	37-152	17	1	3-13	5.5-21.2	0.10-0.31	28.0-29.2
Speckled trout	119-170	17-45	6	2	3.0-4.5	4.6- 7.8	0.18-0.29	26.5-26.9
Atlantic croaker	119-126	19-23	3	3	3.3-3.7	4.9- 5.6	0.23-0.27	28.0-28.9
Pinfish	63-77	4-6	3	3	1.7-2.4	1.6- 2.5	0.37-0.44	22.0-23.9

ingestion rates could have been higher. Peters *et al.* (1976) reported a positive relationship between ingestion rates and temperature for pinfish. The apparent relationship between the weight of the fish and the g shrimp eaten · g fish⁻¹ · day⁻¹ may reflect lower metabolic requirements for larger fish associated with slower growth. Hoss (1967) showed a similar relationship for several species of estuarine fish, including pinfish and Atlantic croaker, through a comparison of oxygen consumption rates with fish weights. Although oxygen consumption in mg · h⁻¹ · fish⁻¹ increased with the weight of the fish, oxygen consumption in mg · h⁻¹ · g of fish⁻¹ decreased with the weight of the fish. This relationship, however, may vary with temperature (Wohlschlag & Cech, 1970), and as Hoss (1967) noted, not only the weight but the developmental stage of the fish must be considered. In addition, in our experiments, the smallest fish appeared to be most active which would also contribute to higher metabolic requirements.

These experimental predator-prey data represent a starting point for eventually assessing the magnitude of natural mortality on shrimp due to fish predation in estuaries. Although extrapolating data from restricted enclosures in the laboratory to the field is dangerous, experiments of this type are necessary in order to isolate the large number of factors which could affect predation rates under field conditions. The effect of variations in density and size of both predators and prey and the role of alternate prey must be analyzed. A greater understanding is also needed of the effects of possible protective habitats other than vegetation, such as turbid water and the presence of suitable substrata for burrowing. Data on distributional patterns associated with selectivity by shrimp and fish predators for these habitats is necessary. In addition, all of the above factors may interact with abiotic parameters such as temperature and salinity. Although the problems appear formidable, a combination of laboratory and field experiments addressing these questions appears to be the best method of eventually estimating predator related mortality of penaeid shrimp in these complex estuarine systems.

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