FISH PREDATION ON JUVENILE BROWN SHRIMP, *PENAEUS AZTECUS* IVES: EFFECTS OF TURBIDITY AND SUBSTRATUM ON PREDATION RATES

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ABSTRACT

Predation on juvenile brown shrimp, *Penaeus aztecus*, by three species of estuarine fishes was examined in a series of laboratory experiments to determine the effect of turbid water and the presence of a suitable substratum for burrowing. Regardless of the type of substratum, turbid water increased predation by southern flounder, *Paralichthys lethostigma*, and decreased predation by Atlantic croaker, *Micropogonias undulatus*. In both clear and turbid water, the presence of sand, which allowed shrimp to burrow, decreased predation by southern flounder but had no significant effect on feeding rates of Atlantic croaker. There was a significant interaction between the effects of turbidity and substratum on predation by pinfish, *Lagodon rhomboides*. Turbid water decreased predation in tanks with hard substrata but had no significant effect in tanks with sand. The presence of sand reduced predation only in clear-water tanks. Burrowing by brown shrimp was reduced in turbid water which may explain this interaction. Overall, the data indicate that both turbid water and a suitable substratum for burrowing may reduce predation on brown shrimp, but the value of these refugia is highly dependent upon the species of predator.

Predation by fishes appears to be a major source of mortality of juvenile brown shrimp, *Penaeus aztecus* Ives, in estuarine nurseries. Brown shrimp spend several months as juveniles in estuaries, and analyses of the stomach contents of some estuarine fishes indicate a high incidence of predation on penaeid shrimp (see Minello and Zimmerman 1983 for review). The presence of salt marsh vegetation apparently offers shrimp protection from some of these predators (Minello and Zimmerman 1983; Zimmerman and Minello 1984), but other habitat characteristics that modify or control the extent of predator-related mortality have not been examined. Estuarine systems in the northern Gulf of Mexico are generally characterized by high turbidity and fine-grained sediments owing to an abundant supply of suspended sediment from rivers and a relatively low-energy environment (Chapman 1968; Linton 1968; Folger 1972). Production of penaeid shrimp in these estuaries is high, and the presence of turbid water together with suitable substrata for burrowing may contribute to productivity by reducing predation.

The effect of turbidity on predator-prey interactions varies with the organisms examined. In laboratory experiments with the flounder, *Platichthys flesus*, Moore and Moore (1976) found that turbid water reduced the ability of the fish to see epibenthic prey and increased the ability of prey to avoid capture. The degree of this effect varied with prey species. Gardner (1981) also found that turbidity reduced predation by bluegill, *Lepomis macrochirus*, on *Daphnia* in laboratory aquaria. Boehlert and Morgan (1985), however, found that predation rates of larval Pacific herring, *Clupea harengus pallasi*, apparently increased up to a point in turbid water. Other work in the laboratory and in freshwater lakes and streams has shown that turbidity can interact with the activity, behavior, and distribution of both predators and prey (Heimstra et al. 1969; Swensen and Matson 1976; DeVore et al. 1980; Gradall and Swenson 1982; Matthews 1984; Sigler et al. 1984), and predation rates in turbid water may be reduced or enhanced (Swenson 1978).

Burrowing by prey in the substratum may also affect predation rates, and burrowing by the crayfish, *Orconectes propinquus*, has been shown to reduce predation by smallmouth bass, *Micropterus dolomieui* (Stein and Magnuson 1976). Although experimental evidence is lacking, it has frequently been suggested that burrowing by penaeid shrimp functions in a similar manner (Williams 1958; Fuss and Ogren 1966; Hughes 1966, 1968a). Diel periodicity in the burrowing behavior of brown shrimp has been

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well documented (Wickham and Minkler 1975; Lakshmi et al. 1976; Minello and Zimmerman 1983), and this species generally remains beneath the surface of the substratum throughout the daylight hours, emerging to forage at night.

The objective of this search was to determine whether turbid water and a suitable substratum for burrowing affect predation rates on juvenile brown shrimp. Experiments were conducted in the laboratory, and predatory fish were southern flounder, *Paralichthys lethostigma* Jordan and Gilbert, pinfish, *Lagodon rhomboides* (Linnaeus), and Atlantic croaker, *Micropogonias undulatus* (Linnaeus). The effect of turbidity on burrowing by brown shrimp was also examined.

METHODS AND MATERIALS

Predation Experiments

Collection and Handling of Experimental Animals

Fish were collected with trawls and seines from Galveston Bay, TX, and held in clear-water tanks without a sand substratum. They were fed live shrimp daily and starved for 24 h before an experiment. Total lengths of fish were measured after each experiment, and specimens from a subsample in holding tanks were weighed and measured. A length-weight relationship was calculated and used to estimate weights of experimental fish.

Shrimp were collected by trawling 2 to 3 d before each experiment. They were fed daily with pelleted shrimp food but not fed during experiments. Measurements of total length (tip of rostrum to tip of telson) were made on all shrimp placed into experimental tanks and all shrimp removed after an experiment. A length-weight relationship was calculated for each experiment from subsamples of shrimp and used to estimate individual weights.

Experimental Tanks

Experiments were conducted in fiberglass tanks (1.75 m × 5.8 m × 0.5 m) located in a building with a white translucent roof which allowed the use of natural photoperiods. Each tank was divided in half by a wall of 1.5 mm mesh fiberglass forming two compartments (1.75 m × 2.9 m) of 5.07 m^2 bottom area. A 5 cm layer of washed beach sand (well sorted with a graphic mean grain size of 2.95 ϕ; analyzed according to Folk 1980) was placed in four tanks. In four other tanks, approximately 1 mm of sand was used to reduce the contrast between prey and the bottom of the tank. Tanks were filled to a depth of 26 cm with seawater (24-26‰) pumped from the beachfront off Galveston Island. During experiments, water temperatures varied among tanks by only 0.5°C, and diurnal ranges are listed in Table 1.

Pulverized kaolinite was used to make the water turbid in four tanks (two with sand bottoms and two without sand). Particle size analysis (Folk 1980) indicated that the kaolinite was poorly sorted with a graphic mean grain size of 8.82 ϕ. A clay slurry was introduced into tanks through a 19 L settling bucket with an outlet hose (5 mm ID) located 5 cm from the bottom. This settling bucket served to remove some of the heavier particles and flocculated aggregates from the clay suspension. Each tank contained a small submersible pump (252 L/minute capacity) connected to a discharge pipe which extended along the length of the tank and sprayed water over the surface. This pump together with 12 airstones/tank provided some vertical mixing which helped keep clay particles suspended.

Turbidity, light, and temperature were measured at 2-h intervals during each experiment. Turbidity

TABLE 1.—Design and conditions for predator-prey experiments.

Experiment	Date (1984)	Predator density[1]	No. of replicates[2]	Predator size (mm TL)	Prey size (mm)	Turbidity[3] (FTU)	Light[4] ($\mu E\ s^{-1} m^{-2}$)	Temperature (°C)
Southern flounder I	May 11	1	2	84-126	30-40	46-30	152	21.0-23.0
Southern flounder II	May 15	1	2	82-111	30-40	54-37	73	22.0-24.5
Pinfish I	May 18	3	4	62-80	30-40	53-36	48	23.0-24.0
Pinfish II	May 31	3	4	64-75	30-42	64-42	162	17.0-19.0
Atlantic croaker	June 6	3	4	98-117	30-40	58-37	132	26.0-27.5

[1]Number of predators per compartment.
[2]Number of replicate compartments used per treatment combination.
[3]Average initial and final turbidity in turbid tanks over experimental period.
[4]Average light levels measured in clear tanks over the first 5 h of the experimental period (n = 16).

was measured with an HF Instruments DRT-15 turbidimeter[2] (calibrated with a Formazin standard) and recorded as Formazin Turbidity Units (FTUs). A typical turbidity curve for acclimation and experimental periods is shown in Figure 1, and mean values from turbid tanks for each experiment are listed in Table 1. These turbidities were within the range of values measured over a 2-yr period in the Galveston Bay system (pers. obs.). Clear treatments ranged between 0.1 and 2.4 FTUs. Light levels in each tank were measured 13 cm below the surface of the water with a LI-COR integrating quantum meter (Model LI-188B) equipped with an underwater sensor. This sensor measures radiation in the 400 to 700 nm waveband, and light energy is expressed in microeinsteins ($\mu E\ s^{-1}\ m^{-2}$). Due to variability in the thickness of the roof over the experimental tanks, there were differences among the tanks in incident light reaching the surface of the water. During one experiment, light levels were measured at the water's surface, and these values were considered to be indicative of the differences among tanks during all experiments.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Experimental Design

In all experiments, there were two replicate tanks (each divided into two compartments) for each of the four treatment combinations: clear water/no sand, clear water/sand, turbid/no sand, and turbid/sand. Feeding by fish was restricted to daylight hours. Twenty-four hours before the initiation of an experiment, fish were placed in circular release cages (0.75 m diameter) within experimental compartments, and clay was then added (200 mg/L) through the settling system to four of the tanks over a 3-h period. Twenty-five brown shrimp were placed in each compartment (4.9 shrimp/m^2) approximately 15 h before the start of an experiment. At 0600 h on the day of the experiment, turbidities were measured and additional clay was added to elevate the turbidity levels and reduce variability among the four tanks. The release cages were lifted at 0700 h, and fish were allowed to feed for 12 h. The tanks were drained at the end of the experimental period, and missing shrimp were assumed to be eaten. For each experiment, two control compartments (one turbid and one clear) were stocked only with shrimp to check survival and recovery of prey.

The data were analyzed using the mean number

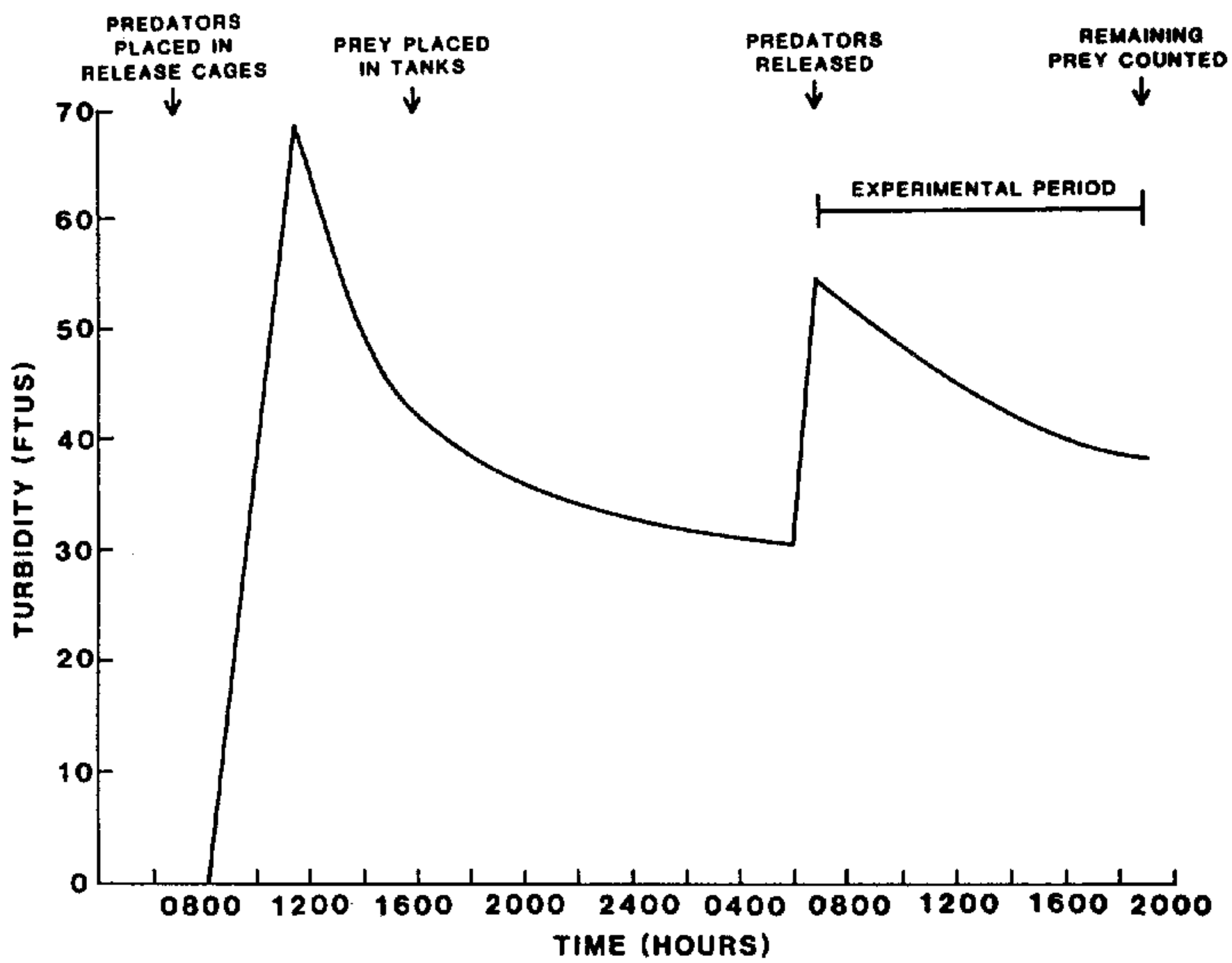

FIGURE 1.—Typical experimental sequence and turbidity (Formazin Turbidity Units) curve for predation experiments.

of shrimp eaten by a predator in a tank over the experimental period as the observation in a two-way analysis of variance (ANOVA). A second ANOVA was also performed on the weight of shrimp eaten per fish. In experiments with pinfish and Atlantic croaker, where both compartments within a tank contained predators, observations from the two compartments were considered to be within tank replicates or subsamples. With southern flounder, only one compartment was used in each tank. This experiment was repeated on a second day, and day was considered a blocking variable in the analysis. Because differences in incident light among tanks could potentially affect predation rates and increase within treatment variability, an analysis of covariance (ANCOVA) was also performed on the data from all experiments using incident light as the covariate.

The size range of shrimp available to predators was kept as narrow as possible (Table 1) to avoid problems associated with size-selective predation. In addition, we attempted to keep the distribution of shrimp within this size range similar for all replicates. The size-frequency distributions of shrimp placed in the tanks and shrimp removed from the tanks after each experiment were compared to check for evidence of size-selective predation.

Turbidity and Burrowing of Brown Shrimp

The effect of turbidity on burrowing by juvenile brown shrimp was examined in eight rectangular tanks each with a bottom area of 0.92 m^2. Water depth was maintained at 25 cm, and temperature and salinity were adjusted to 25°C and 25‰, respectively. Light was provided through white translucent skylights. Lengths of PVC pipe were installed along the walls on the bottom of each tank. The tanks were filled with washed beach sand to a depth of 5 cm, and the sand surface was approximately 5 mm below the top of the PVC pipe. The number of shrimp burrowed was determined using a net composed of fiberglass screen mounted on a wooden frame. The frame was the same width as the tanks and was pushed over the PVC runners along the bottom, passing just above the sand surface. Shrimp caught in the net were assumed to be in the water column or on the surface of the substratum.

Ten brown shrimp (50-100 mm) were placed in each tank on the day before an experiment. Before sunrise on the day of the experiment, kaolinite was added to four of the tanks through the settling bucket system. Airstones in all tanks provided enough turbulence to keep the clay in suspension. At 1100 h, turbidity and light levels were measured in the center of the water column in each tank, and nonburrowed shrimp were collected. The tanks were then drained, and the burrowed shrimp were recovered. The experiment was repeated with different shrimp on a second day, and an ANOVA, with day used as a blocking variable, was performed to test for an effect of turbidity. The percentage of shrimp burrowed in a tank was used as the observation after an arcsin transformation. The accuracy of our collecting technique was examined by comparing visual observations of the number of shrimp burrowed in the clear tanks with the catch in the net. All nonburrowed shrimp were captured in six out of seven trials, but one nonburrowed shrimp avoided capture. In one trial, a burrowed shrimp was collected.

RESULTS

Predation Experiments

Data from the two control compartments (one turbid and one clear) used in each experiment indicated that mortality of prey was low. Only 1.6% of the 250 control shrimp were not recovered alive. This mortality was considered negligible, and all shrimp not recovered in predation experiments were assumed eaten by predators. The use of a relatively narrow size range of prey also appeared to eliminate problems associated with size-selective predation. Comparisons of size-frequency distributions of shrimp introduced into experimental compartments to those removed following the experimental period showed no apparent size-selective predation in any of the experiments.

Southern Flounder

Predation by southern flounder was highest in tanks with turbid water and without sand substrata (Table 2A). The interaction term in the ANOVA was not significant, and both main effects of turbidity and substratum were significant at the 0.05 level (Table 2B). Predation rates of these fish increased from a mean of 2.2 shrimp/fish in clear water to 4.4 shrimp/fish in turbid water. Predation rates were reduced in the presence of sand from a mean of 4.8 shrimp/fish in tanks without sand to a mean of 1.9 shrimp/fish in tanks with sand. An ANCOVA with incident light and an ANOVA using the weight of shrimp eaten as the observation gave similar results. The mean weight of shrimp eaten, expressed as a

percentage of body weight eaten by the fish over the experimental period, ranged from 6.1% in clear/sand tanks to 24.8% in turbid/no sand tanks.

The feeding behavior of southern flounder (84-94 mm TL) on brown shrimp was also observed in aquaria. These fish exhibited a variety of feeding behaviors including active searching for prey on the bottom and in the water column as described by Olla et al. (1972) for summer flounder, *Paralichthys dentatus*. Generally, however, the fish remained motionless on the bottom and waited for potential prey to come within striking distance before attacking. Fish in the family Bothidae have been classified as primarily visual feeders by de Groot (1971). In our observations, all stalking activity by southern flounder was accompanied by active eye movements, tracking potential prey, which suggested the primary use of vision in prey detection. A study of diel feeding periodicity, similar to that conducted on red drum and Atlantic croaker by Minello and Zimmerman (1983), however, indicated that southern flounder could also feed at night even when tanks were enclosed in black plastic to completely eliminate light (unpubl. data). This finding suggests that sensory mechanisms, in addition to vision, can be used by these fish to detect prey.

TABLE 2.—Predation on brown shrimp by southern flounder. A) Number of shrimp eaten per fish over the 12-h experimental period for treatment combinations of turbidity and substratum. B) ANOVA results using the number of shrimp eaten per fish as the observation.

A		Turbid		Clear	
	Date (1984)	Sand	No sand	Sand	No sand
	May 11	2	4	0	4
		4	10	1	4
	May 15	1	5	2	1
		2	7	3	3
	$\bar{x}$	2.2	6.5	1.5	3.0

B	Source of error	df	SS	*F*	*P*
	Turbidity	1	18.06	5.65	0.037
	Substratum	1	33.06	10.34	0.008
	Turbidity/ substratum	1	7.56	2.36	0.152
	Day	1	1.56	0.49	0.499
	Error	11	35.19		

Pinfish

In both experiments with pinfish, the largest number of shrimp were eaten in tanks with clear water and without sand (Fig. 2). The ANOVA on the number of shrimp eaten in the first experiment (pinfish I) indicated a significant interaction between turbidity and substratum (Table 3). The substratum apparently did not affect predation in tanks with turbid water, but in clear water the presence of sand significantly reduced predation rates (Fig. 2A). In a similar manner, turbidity did not significantly affect predation in tanks with sand substrata, but it did reduce predation rates in tanks without sand. An ANCOVA with incident light and an ANOVA using the weight of shrimp eaten (Table 3) did not alter

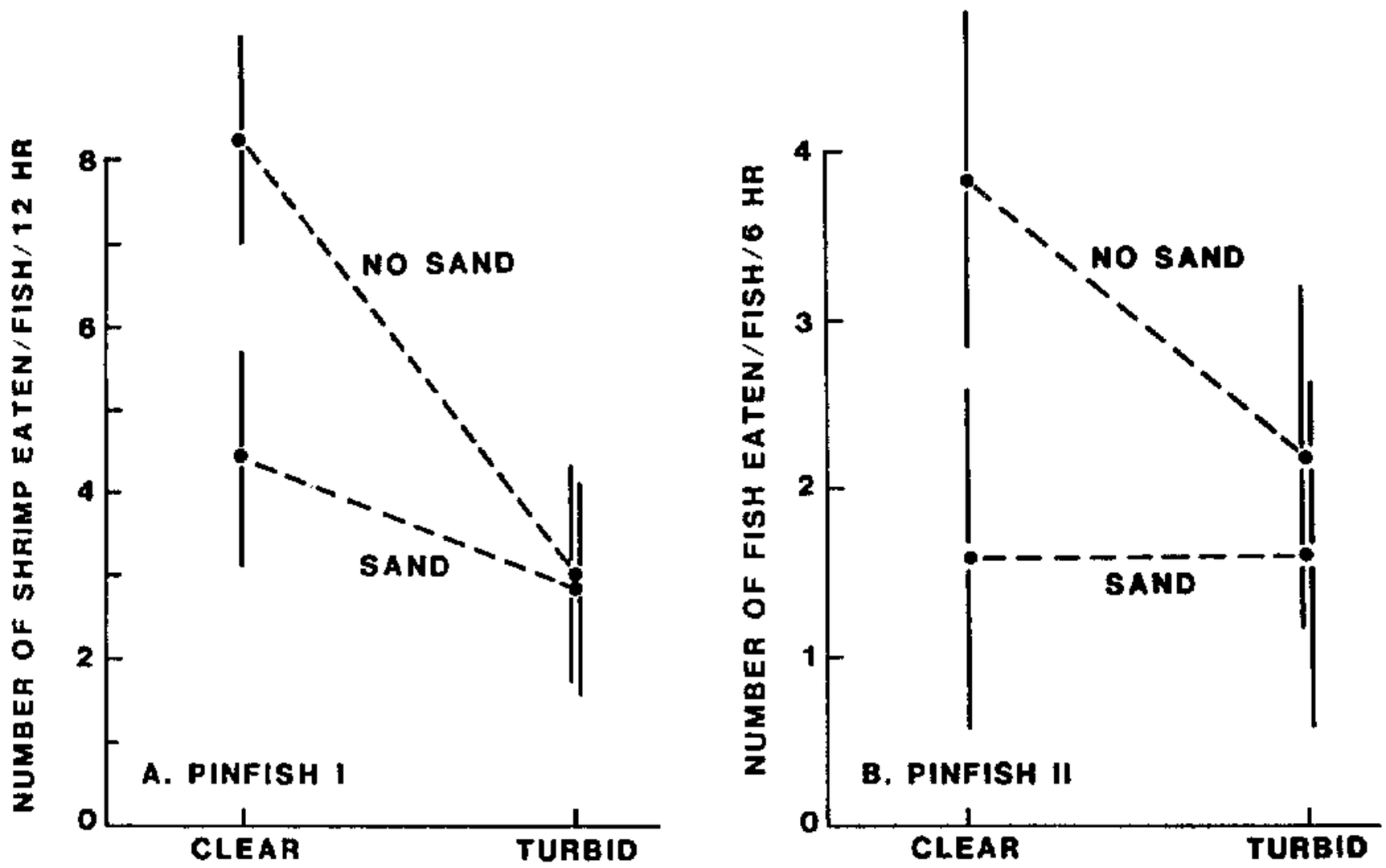

FIGURE 2.—Mean predation rates on brown shrimp by pinfish in treatment combinations of turbidity and substratum. Vertical lines, representing one half of Tukey's ω (Steel and Torrie 1960) on either side of the mean, can be used to compare means at the 0.05 significance level.

TABLE 3.—ANOVA results from predation experiments with pinfish using the number of brown shrimp eaten per fish as the observation. Probability values are also listed from an ANOVA using the weight of shrimp eaten as the observation. Turb/subs = Turbidity/substratum.

Source of error	df	SS	*F*	*P*	P (weight)
Pinfish I					
Turbidity	1	23.39	55.2	0.002	0.003
Substratum	1	8.00	18.9	0.012	0.019
Turb/subs	1	6.70	15.8	0.016	0.033
Error	4	1.70			
Pinfish II					
Turbidity	1	1.39	5.4	0.081	0.040
Substratum	1	4.00	15.5	0.017	0.040
Turb/subs	1	1.38	5.3	0.082	0.110
Error	4	1.03			
Combined					
Turbidity	1	18.10	53.1	<0.001	
Substratum	1	11.66	34.2	<0.001	
Day	1	21.81	63.9	<0.001	
Turb/subs	1	7.08	20.7	0.002	
Turb/day	1	6.68	19.6	0.002	
Subs/day	1	0.34	1.0	0.34	
Turb/subs/day	1	1.00	2.9	0.12	
Error	8	2.73			

the results. Pinfish were voracious feeders eating between 19.8% (turbid/sand) and 57.1% (clear/no sand) of their body weight in shrimp over the 12-h experimental period. Predation rates were probably underestimated in clear-water treatments without sand, since in three out of four of these compartments the three pinfish ate all of the available shrimp.

The duration of the pinfish II experiment was reduced to 6 h (0700-1300 h) to lower the overall number of shrimp eaten by the predators. Similar trends were apparent in the number of shrimp eaten for each treatment combination (Fig. 2B), but the interaction term (P = 0.082) in the ANOVA was not significant at the 0.05 level (Table 3). The size range of the prey in the second experiment was slightly larger than in pinfish I (Table 1), and variability in the size of shrimp available or small differences in size-selection may have affected our results. Using the weight of shrimp eaten as the observation should reduce this problem, and in this ANOVA (Table 3) both turbidity and substratum were significant effects, but the F-test for interaction had a probability value of 0.110.

To increase the error degrees of freedom and hence the power of the statistical test, the data from both pinfish experiments were combined and analyzed. In one such ANOVA, day was considered to be a blocking variable (no interaction with other factors), and the results on the number of shrimp eaten were similar to those from the pinfish I experiment, showing a significant interaction between turbidity and substratum (P = 0.021). We also analyzed the data in a completely randomized crossed design with day as a main effect (Table 3). In this ANOVA the turbidity/substratum interaction was highly significant, but the turbidity/day interaction was also significant indicating that the effect of turbidity on predation was less during the second experiment. In addition to the shorter duration of pinfish II, overall light levels were higher during this second pinfish experiment (clear sunny day) compared with the first experiment (overcast day) (Table 1).

Atlantic Croaker

Mean predation rates for Atlantic croaker were highest in clear-water tanks without sand, and rates in all turbid tanks were low (Table 4A). The ANOVAs with both the number (Table 4B) and weight of

TABLE 4.—Predation on brown shrimp by Atlantic croaker. A) Number of shrimp eaten per fish over the 12-h experimental period for treatment combinations of turbidity and substratum. B) ANOVA results using the number of shrimp eaten per fish as the observation. Probability values from an ANCOVA using incident light as the covariate are also included.

A		Turbid		Clear	
Experimental tank		Sand	No sand	Sand	No sand
Tank 1	compartment 1	0	0.7	1.0	4.7
	compartment 2	0	0	0.3	0
Tank 2	compartment 1	0.3	0.3	1.0	3.3
	compartment 2	0.7	0	0.3	1.0
$\bar{x}$		0.2	0.2	0.7	2.2

B Source of error	df	SS	*F*	*P*	*P* (ANCOVA)
Turbidity	1	2.92	1.8	0.251	0.027
Substratum	1	1.26	0.8	0.428	0.108
Turb/subs	1	1.26	0.8	0.428	0.943
Error	4	6.49			

shrimp eaten, however, showed no significant treatment effects. Overall, Atlantic croaker ate 2.7% of their weight in shrimp over the experimental period. Differences among tanks in incident light apparently increased the within treatment variability in the experiment. There was a significant negative linear correlation between incident light and the number of shrimp eaten in the 16 experimental compartments ($r = -0.51$, $n = 16$, $P = 0.046$). An ANCOVA using incident light as a covariate lowered the error sum of squares, and the main effect of turbidity became significant (Table 4B). This was the only experiment in which variability in incident light among tanks had a major effect on our results. Atlantic croaker appeared to feed more actively at low light levels, but predation rates were higher in clear water than in turbid water. Turbidity therefore did not appear to affect predation by simply reducing the light in the water column.

Turbidity and Burrowing of Brown Shrimp

Burrowing by juvenile brown shrimp was measured in both clear and turbid water to aid in the interpretation of significant interactions in the predation experiments. The percentage of shrimp burrowed was reduced from a mean of 85.7% in clear-water tanks to 46.9% in turbid tanks (Table 5). In the ANOVA the effect of turbidity was highly significant ($P < 0.001$). The effect of day was also significant ($P = 0.041$), and fewer shrimp burrowed on the second day of the experiment. Overall, light levels were lower on the second day, and a similar ANOVA on light measured 13 cm below the surface of the water also showed significant differences related to turbidity ($P < 0.001$) and day ($P = 0.011$). The turbidities used (30-47 FTUs) reduced the average light level in the water by 29% compared with values in clear tanks. Burrowing did not appear to be related to shrimp size, and there was no significant difference between the mean length of burrowed shrimp compared with nonburrowed shrimp (paired t-test, $P > 0.40$, 14 df).

DISCUSSION

Effect of Turbidity on Predation

Turbidity reduces predation on prey possessing limited escape capabilities by reducing the visual reactive distance of the predator (Moore and Moore 1976; Vinyard and O'Brien 1976; Gardner 1981). Turbid water should have less of an effect on predation if the predator-prey size ratio is large (Moore and Moore 1976; Vinyard and O'Brien 1976) or if the predator has the ability to use sensory mechanisms other than vision to detect prey. The significant decrease in predation rates by pinfish in our experiments may be explained in part by the strict reliance of this predator on vision for prey detection (Minello and Zimmerman 1983) and upon the relatively small predator:prey size ratio (Table 6). Turbidity appeared to have less of an effect on predation by Atlantic croaker. This predator does not depend solely upon vision for prey detection, but also uses olfaction and touch (Chao and Musick 1977). The increased predation rates for southern flounder in turbid water may be related to the ambush feeding tactics of this predator and the effect of turbidity on prey behavior. The activity level of brown shrimp increased in turbid water as evidenced by a decrease in burrowing and the frequent observation of actively swimming shrimp in turbid tanks. According to the model of Gerritsen and Strickler (1977), increased prey movement dramatically increases encounter rates with slow moving or stationary predators. This effect of prey movement is

TABLE 5.—The effect of turbidity on burrowing by juvenile brown shrimp. All measurements were taken at approximately 1100 h. Percentages of shrimp burrowed in each tank (generally 10 shrimp/tank) are listed with turbidity levels and light levels in the water column.

	Turbid tanks			Clear tanks		
Date (1984)	Burrowed (%)	Turbidity (FTU)	Light ($\mu E\ s^{-1}m^{-2}$)	Burrowed (%)	Turbidity (FTU)	Light ($\mu E\ s^{-1}m^{-2}$)
Aug. 15	56	49	51	90	5.6	89
	50	30	66	100	3.2	93
	80	42	54	80	5.9	87
	50	47	59			
Aug. 17	20	39	49	80	3.2	73
	20	32	52	90	3.2	76
	60	33	51	80	4.1	73
	40	36	51	80	2.9	46
$\bar{x}$	47.0	38.4	54.1	85.7	4.0	76.7

TABLE 6.—Summary data on possible factors affecting predation rates for the species of predators examined.

Predator	Mode of feeding	Predator searching speed (activity)	Size ratio of predator:prey[1]	Effect on predation rates	
				Turbidity	Substratum (burrowing)
Southern flounder	visual and nonvisual	low	3:1	increased	decreased
Atlantic croaker	visual and nonvisual	high	3:1	decreased	no change
Pinfish	strictly visual	high	2:1	decreased	decreased

[1]measured as total length.

reduced as predator speed increases, and changes in prey activity should only have a negligible effect on encounter rates with more active predators such as pinfish and Atlantic croaker. Increased predation rates by fish in turbid water may also be related to the effect of turbidity on the reactive distance and escape behavior of prey. The ability of the predator to detect the prey before the prey detects the predator is dependent upon differences in visual acuity, apparent size, and motion (Cerri 1983; Howick and O'Brien 1983). Although brown shrimp have the ability to visually detect predators and avoid attack, the acuity of the crustacean compound eye is much lower than that of the vertebrate eye (Waterman 1961; Goldsmith 1973), and shrimp do not respond to stationary predators. This last prey characteristic may explain why the southern flounder is a very effective predator on brown shrimp.

Effect of Substratum on Predation Rates

Juvenile brown shrimp readily burrowed in experimental tanks with fine sand substrata, but they could not burrow in tanks without sand. Burrowing should reduce the apparent density and availability of brown shrimp to visually feeding predators (Minello and Zimmerman 1984). Predators using olfactory or tactile mechanisms of prey detection, however, may have less difficulty detecting and feeding upon burrowed shrimp. Predation rates for pinfish and southern flounder, both visual feeders, were significantly reduced in tanks with sand substrata. Predation rates of Atlantic croaker were not affected by the presence of sand which suggests that burrowing does not protect brown shrimp from this predator. In other clear-water experiments conducted in our laboratory with Atlantic croaker (Albrecht et al. 1983[3]), we have been unable to detect any reduction in predation on brown shrimp related to the presence of sand substrata. This predator does not depend solely on vision to detect prey (Minello and Zimmerman 1983), and Chao and Musick (1977) hypothesized that Atlantic croaker fed mostly by olfaction and touch. These fish also search through the upper layers of the substratum while foraging for food (Roelofs 1954; Chao and Musick 1977), and this behavior may reduce the number of burrowed shrimp.

The presence of sand may also affect predation by altering the activity levels of both prey and predator. Increased activity of brown shrimp in tanks without sand may have increased encounter rates with southern flounder in accordance with the model of Gerritsen and Strickler (1977). In addition, southern flounder periodically burrow in sand, and Olla et al. (1972) found that burrowed summer flounder did not respond to the presence of prey.

Interactions Between Turbidity and Substratum

Burrowing by juvenile brown shrimp is reduced in turbid water (Table 5), and in situations where burrowing protects shrimp from predators, an interaction might be expected between the effects of turbidity and substratum on predation rates. This type of interaction was present in the pinfish experiments. Predation rates of pinfish were reduced in the presence of a sand substratum only in clear water; in turbid water predation was not significantly affected by substratum. Turbidity reduced predation in tanks without sand, but in tanks with sand substrata the effect of turbid water on feeding by pinfish was apparently attenuated by a reduction in shrimp burrowing and an increase in the number of available prey. In experiments with southern

[3]Albrecht, C., T. J. Minello, and R. J. Zimmerman. 1983. The role of substrates in predation on brown shrimp (*Penaeus aztecus*) by Atlantic croaker (*Micropogonias undulatus*). NOAA/NMFS Unpublished Report to Laboratory Director, SEFC, Galveston Laboratory, 18 p.

flounder, burrowing also appeared to reduce the number of shrimp eaten, but this reduction occurred in both turbid and clear water as evidenced by the nonsignificant turbidity/substratum interaction term ($P = 0.152$). In fact, the reduction in mean predation rates associated with the presence of a sand substratum was greatest in turbid water, and the positive effect of turbidity on predation appeared greatest in tanks without sand (Table 2A). Further analysis of the effects of turbidity and substratum on the activity of brown shrimp and the feeding behavior of southern flounder would be needed to explain interactions between these variables. Burrowing does not appear to protect brown shrimp from predation by Atlantic croaker, and there was no experimental evidence for an interaction between turbidity and substratum.

Experiments With Red Drum, *Sciaenops ocellatus* (Linnaeus)

During the course of this study two experiments were also conducted on the effects of turbidity and substratum on predation rates of another fish predator, the red drum (420-592 mm TL). An in depth analysis of these data was not included due to poor survival of shrimp in control compartments (18% of control shrimp died from unknown causes). Control mortalities, however, did not appear to be related to experimental variables, and data obtained in these experiments suggested that predation rates of red drum are not affected by turbid water or the presence of sand substrata. That substratum has no significant effect on predation rates is supported by additional unpublished but well-controlled experiments in our laboratory, indicating that burrowing does not protect juvenile brown shrimp from predation by red drum. Yokel (1966) described the feeding behavior of these fish which consists of searching along the bottom with the head down and lower jaw rubbing along the surface of the substratum. He concluded that this method of feeding would enable the fish to locate animals in shallow burrows.

CONCLUSIONS

The artificial nature of these laboratory experiments certainly must be considered when attempting to interpret the data in relation to natural phenomena. One major advantage of the apparatus used in our experiments was the relatively large size of the experimental enclosures (5.07 m^2 bottom area) which allowed the use of prey densities commonly found in natural populations. The use of these large enclosures, however, made replicating treatment combinations more difficult, hence reducing the power of statistical tests. Despite this limitation, general conclusions about relationships between turbidity, substratum, and predation on brown shrimp can be made on the basis of our experimental results. Under certain conditions, turbid estuarine water should provide juvenile brown shrimp protection from fish predators such as pinfish and Atlantic croaker. Turbidity does not appear, however, to reduce predation by southern flounder on juvenile brown shrimp. The effect of turbidity on predator-prey relationships apparently depends upon the feeding behavior and morphology of predators and on the behavior of the prey. Burrowing into the substratum also appears to protect brown shrimp from some fish predators, and the ability of brown shrimp to burrow is affected by substratum characteristics (Williams 1958; Aldrich et al. 1968; Rulifson 1981). A change from hard shell botton to soft silty mud should enhance burrowing and reduce predation by estuarine fish such as pinfish, southern flounder, and perhaps spotted seatrout. Fishes such as Atlantic croaker and red drum, however, are apparently well adapted for feeding upon burrowed organisms, and differences in estuarine sediments may not affect predation by these species. Because turbidity and substratum do not appear to alter predation of all fishes in a similar manner, the effects of these habitat characteristics on the mortality of juvenile brown shrimp should strongly depend upon the dominant fish predators present in an estuarine system.

Comparisons of estuaries with regard to their protective capacity for juvenile brown shrimp are complicated by interactions among habitat characteristics and their effects. In addition to the type of substratum, light levels (Wickham and Minkler 1975), temperature (Aldrich et al. 1968), and salinity (Lakshmi et al. 1976) have been shown to affect burrowing of brown shrimp. Starvation (Hughes 1968a), tidal movements (Hughes 1968b), shrimp size (Eldred et al. 1961; Hughes 1968a; Moctezuma and Blake 1981), and dissolved oxygen (Egusa and Yamamoto 1961) affect burrowing of other penaeids and may have a similar effect on brown shrimp. The presence of rhizomes and roots of estuarine vegetation may also reduce burrowing by these animals. All of these factors, therefore, can potentially interact with predator-related mortality. In our experiments, burrowing by brown shrimp was reduced in turbid water, and this had a significant effect on predation rates of pinfish. Interactions that control the presence of protective habitat characteristics are

also common. In low-energy areas, estuarine systems with large amounts of suspended sediments and high turbidities frequently have fine sediments (Guilcher 1967; Folger 1972). Submerged vegetation, shown to offer many crustaceans protection from predators (Nelson 1979; Stoner 1979; Coen et al. 1981; Heck and Thoman 1981), is associated with estuarine areas of low turbidity (Zieman 1982; Thayer et al. 1984), and these beds of submerged vegetation also reduce turbidity (Short and Short 1984) and alter sediment characteristics (Thayer et al. 1984). Determining the protective value of any suite of environmental characteristics, therefore, may be quite complex.

Turbidity and sediment characteristics, however, appear to be important factors governing predation rates on juvenile brown shrimp, and anthropogenic modifications of estuarine systems that influence these characteristics may affect shrimp survival. Turbidity levels and patterns of sediment deposition in estuaries are mainly influenced by riverine inputs, tidal properties, and wave action (Postma 1967; Davis 1983), although biological processes are also important (Haven and Morales-Alamo 1972; Biggs and Howell 1984). Modifications of estuarine systems through dredging, channelization, and alteration of freshwater inflows, therefore, can impact predator-prey relationships, and such effects should be addressed in evaluating these activities.

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