Effects of turbidity on feeding of southern flounder on estuarine prey

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ABSTRACT: Southern flounder *Paralichthys lethostigma* are predators on young brown shrimp *Farfantepenaeus aztecus* in turbid estuarine nurseries, and this predator-related mortality can affect shrimp recruitment to the fishery. Water clarity appears important in affecting feeding rates and prey selection of this ambush predator. Earlier experiments with southern flounder showed increased feeding on brown shrimp in turbid water. We propose a simple model which predicts that increased predation rates occur at intermediate turbidity levels due to increased prey activity. The effect should vary with prey size, and predation rates should decline when the reactive zone is smaller than the strike zone. We conducted an experiment using 2 sizes of shrimp prey and 4 levels of turbidity and showed a significant interaction between prey size and turbidity. These results appeared similar to those predicted by the hypothetical model, and predation rates on small shrimp were not reduced until turbidities reached 50 Formazin Turbidity Units (FTU). In a second experiment, we found no significant effect of turbid water (up to 25 FTU) on strike distance of southern flounder. Additional experiments were conducted on prey selection. In clear water, southern flounder fed mainly (93 to 94 %) on shrimp, but at 50 FTU, these predators selected long-nose killifish (64 to 77 % of prey eaten). Our experimental results support the conclusion that environmental factors such as water clarity can have substantial effects on feeding rates, prey selection, and perhaps mortality of prey, and that such interactions should be considered when developing trophic models.

KEY WORDS: Predation · Prey selection · Turbidity · Penaeid shrimp · Flounder · Ambush

INTRODUCTION

Water is often turbid in estuaries of the northern Gulf of Mexico, particularly west of the Mississippi River. Elevated levels of suspended sediments responsible for much of this turbidity are caused by high sediment loads from rivers, shallow estuarine basins, strong wind-driven mixing, shoreline erosion, and various human activities such as trawling, dredging, shipping, and boating (US Army Corps of Engineers 2017). In shallow areas of Galveston Bay, Texas (USA), mean monthly turbidity values can range from near 0 to over 50 Formazin Turbidity Units (FTU), with elevated values occurring from late spring through the fall (Rozas et al. 2007). Ecological studies on effects of water turbidity have often centered around negative impacts on coral reefs (Fabricius 2005) and on seagrass beds (Biber et al. 2008, Adams et al. 2016, McDonald et al. 2016), but turbid water can have important and often unrecognized effects on trophic interactions in estuarine nurseries (Hecht & van der Lingen 1992, Macia et al. 2003, Lunt & Smee 2014).

Shallow nursery areas of Galveston Bay provide the setting for a predator–prey interaction between southern flounder *Paralichthys lethostigma* and young brown shrimp *Farfantepenaeus aztecus*. Juvenile southern flounder are primarily visual feed-

ers (De Groot 1971, Olla et al. 1972, Gibson et al. 2014), feeding mainly on small fishes and crustaceans (Darnell 1958, Powell & Schwartz 1979, Burke 1995), and they can be an important cause of penaeid shrimp mortality during spring months (Minello et al. 1989). Because of their role in affecting shrimp population dynamics, we have been interested in ecological factors affecting southern flounder predation. Experiments with many fish species have shown that turbidity generally reduces feeding rates on prey by reducing visual acuity of predators (Benfield & Minello 1996, Aksnes & Utne 1997, Mazur & Beauchamp 2003, Jönsson et al. 2013), but Minello et al. (1987) found that feeding rates of southern flounder on young brown shrimp were significantly increased at relatively high turbidity levels (50 FTU) compared with feeding in clear water. The ambush foraging tactics of southern flounder combined with reduced burrowing and increased shrimp activity in turbid water were considered responsible for this observed relationship. Variability in estuarine turbidity levels, therefore, has the potential to affect shrimp mortality, and we attempt here to explore these predator–prey interactions in more detail.

Our general objective was to continue examining the effect of turbid water on feeding of southern flounder. Southern flounder are mainly visual ambush predators, and feeding rates should be affected by encounter probabilities according to the model of Gerritsen & Strickler (1977) and depend on the frequency with which prey enter the fish's strike zone (Fig. 1). Increasing turbidity should reduce the fish's reactive zone (area of prey awareness), but negative effects on feeding rates should not occur until the reactive zone becomes smaller than the strike zone, i.e. when turbidity reduces the strike zone. Until this
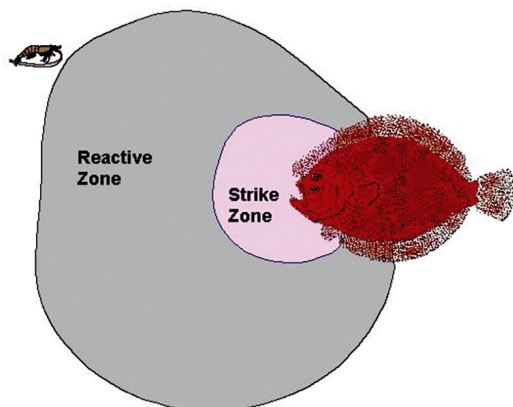
occurs, turbidity can increase feeding rates by increasing prey activity or movement and increasing the encounter probability within the strike zone. This relationship between turbidity and feeding rate should be dependent on prey size. For visual predators and zooplankton prey, there is an interaction between prey size, reactive distance, and turbidity: reactive distance increases with prey size, and the effect is greatest at low turbidities (Vinyard & O'Brien 1976, Howick & O'Brien 1983, Hansen et al. 2013). Our simple model of the predator–prey relationship between southern flounder and brown shrimp prey predicts that if prey activity does not change with turbidity, feeding rates will be constant until turbidity begins to shrink the strike zone (Fig. 2A); and that the feeding rate will begin to decline at lower turbidities for smaller prey, because the strike zone will shrink more quickly for small prey as turbidity increases. If prey activity increases with turbidity, however, maximum feeding rates should occur at moderate turbidities; but again, the peak of the curve should occur at lower turbidities for smaller prey (Fig. 2B).

The first objective of our research was to test this conceptual feeding model through laboratory experiments. To examine the feeding response of southern

Fig. 1. Schematic of relationship between reactive distance and strike distance for southern flounder *Paralichthys lethostigma*
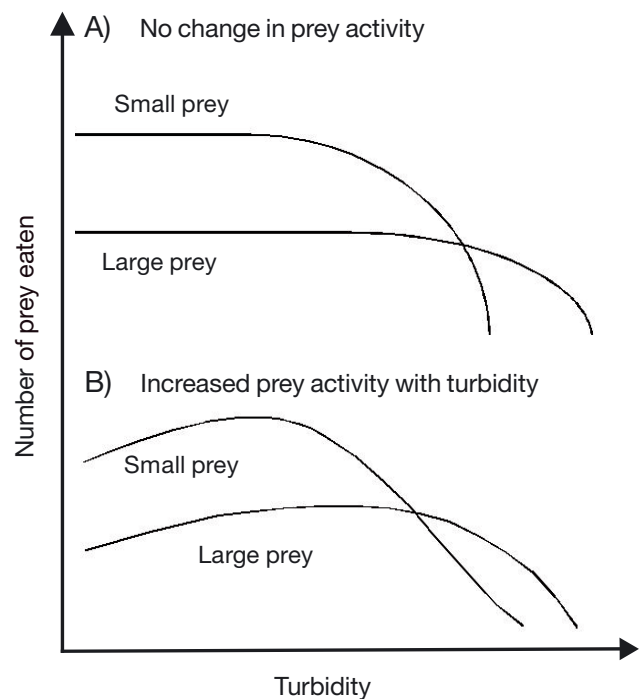

Fig. 2. Hypothetical relationship between prey size and the effect of turbidity on feeding rates of southern flounder *Paralichthys lethostigma* with (A) stable prey activity and (B) increased activity with turbidity

flounder to different sizes of prey, we conducted an experiment to measure feeding rates on 2 sizes of shrimp prey and at 4 turbidity levels. In an ancillary investigation of the model, we also conducted an experiment to examine the effect of turbidity on strike distance of southern flounder. In this experiment, video recordings were made of feeding behavior at different turbidities to determine if strike distance decreased as turbidity increased. Our hypothesis was that the strike zone would not be reduced until turbidity reached a level that reduced feeding rates in other experiments. Finally, we conducted 3 experiments to examine effects of turbid water on prey selection by southern flounder. We hypothesized that prey selection by southern flounder would be affected by turbidity, because different prey species are likely to exhibit different avoidance, escape, or activity behaviors in response to water clarity. In these separate experiments, we examined selection for 2 different prey species including (1) brown shrimp and white shrimp *Litopenaeus setiferus*, (2) brown shrimp and longnose killifish *Fundulus similis*, and (3) white shrimp and longnose killifish. In all of these experiments we used suspensions of bentonite clay particles to establish turbidity levels.

MATERIALS AND METHODS

All animals used in these experiments were collected in Galveston Bay, Texas, using trawls and seines. Sand-filtered seawater was pumped from the Gulf of Mexico, and experiments were conducted at salinities of 25 to 26 and ambient water temperatures. All experiments were conducted in compliance with animal treatment protocols put in place by the National Marine Fisheries Service.

Prey size and turbidity

In this experiment, we examined the effect of 2 brown shrimp prey sizes and 4 turbidity levels on feeding rates of southern flounder. The experiment was conducted in 20 circular tanks (1.5 m diameter, 0.9 m height) with no substrate. Tanks were located in a greenhouse under a translucent plastic roof that provided natural photoperiods but reduced ambient light intensity by about 80%. At the surface of the water and at 14:30 h (local time) during experiments, mean light levels were 316 $\mu E\ s^{-1}\ m^{-2}$ (SE = 4.2 among tanks) measured with a LI-COR integrating quantum meter. On the first day of the experiment,

each treatment combination of turbidity and shrimp size was replicated in 2 experimental tanks (total of 16 tanks), and the 4 remaining tanks were used to examine shrimp mortality without predators. The entire experiment was then repeated on a second day, providing a total of 4 replicate observations of feeding rates per treatment combination.

Southern flounder ranged in size from 130 to 150 mm total length (TL); the mean size of small brown shrimp was 34 mm TL (range = 31 to 36 mm) and that of large shrimp was 45 mm TL (range = 42 to 47 mm). Experimental tanks were randomly assigned to treatment combinations. One randomly selected predator and 20 shrimp were placed into clear water in each experimental tank on the evening before an experiment was initiated; the fish predator was held inside a 60 cm diameter circular bottomless cage. Water depth during the experiment was 25 cm and temperatures ranged between 24 and 27.5°C. Turbidity treatment levels included clear water (0 FTU) and 3 target levels of turbid water (10, 25, and 50 FTU). A slurry of bentonite (UNIBAR Drilling Fluids) and seawater was used to raise turbidity levels at 06:00 h on the day of the experiment. Air stones within the tanks provided vertical mixing to help keep the clay in suspension. Turbidity levels were checked approximately every 2 h using an HR Instruments Model DRT 100B nephelometer calibrated to a formazin standard, and additional bentonite was added as needed to maintain target levels. Actual mean (±SE) turbidity levels were 0.5 (±0.04), 10.1 (±0.26), 24.8 (±0.50), and 48.1 (±0.60) FTU. The inside of all tanks was colored sandy brown to reduce effects of differences in background contrast between clear and turbid treatments.

At 07:00 h, the circular cages were lifted, allowing the predators and prey to interact. At 19:00 h, the tanks were drained, and remaining shrimp were counted to determine the number eaten. Shrimp survival in the absence of predators was high, and 99.4% of the 160 control shrimp were recovered alive.

Strike distance

Observations of predatory behavior and strike distance in turbid water are hindered by the observer's inability to see the predators and prey. In addition, experiments using suspended clay particles to create turbid water are plagued by particle settling, and vertical mixing of the water is generally needed to maintain elevated turbidity levels. Vigorous agitation

or aeration of the water, however, can also interfere with animal behavior and behavioral observations. The experimental tank system we used to measure strike distance was designed to solve these problems.

The observation tank (0.88 m diameter, 0.61 m²) was hydraulically connected to a large mixing reservoir (Fig. 3). Bentonite particles were kept suspended in seawater (salinity of 25) through vigorous agitation in the mixing reservoir with several electric pumps. Turbid water flowed from the mixing reservoir into the observation tank at a rate of 4.2 l min⁻¹ through 8 evenly spaced tubes mounted on the wall of the tank; these supply lines extended to within 1 cm of the observation tank bottom. Water returned to the mixing reservoir by gravity flow through a screened drain in the center of the tank. The water depth in the observation tank was maintained

Fig. 3. Schematic diagram of experimental tank system used to measure effects of turbidity on strike distance

at 10 cm, allowing an observer to readily see predators and prey from above in moderately turbid water up to 25 FTU. Predatory fish, however, had to detect shrimp laterally through the water. The system was similar in this regard to that of Abrahams & Kattenfeld (1997). Turbidity in the observation tank was the same as in the mixing reservoir where it could be monitored and adjusted without disturbing experimental animals. The bottom of the observation tank was painted white to improve contrast for the observer, and the tank walls were painted sand brown to standardize background contrast for the southern flounder.

We measured strike distance of southern flounder feeding on juvenile white shrimp *Litopenaeus setiferus*. Brown shrimp were unavailable in the bay at the time of the experiments, and our prey selection experiment (see 'Results: Prey selection') indicated no significant selection for either of these species by southern flounder. We conducted 13 feeding trials in clear water, 10 trials at 10 FTU, and 10 trials at 25 FTU. For each feeding trial, 2 southern flounder (190 to 240 mm TL) were placed in the observation tank with 10 white shrimp (31 to 41 mm TL), and the animals were allowed to interact for 6 h. Using 2 predators increased our ability to record predatory strikes, and the fish did not appear to interact with each other. The prey density (15.6 m⁻²) in these trials was increased slightly compared with our prey size and turbidity experiment to increase the frequency of
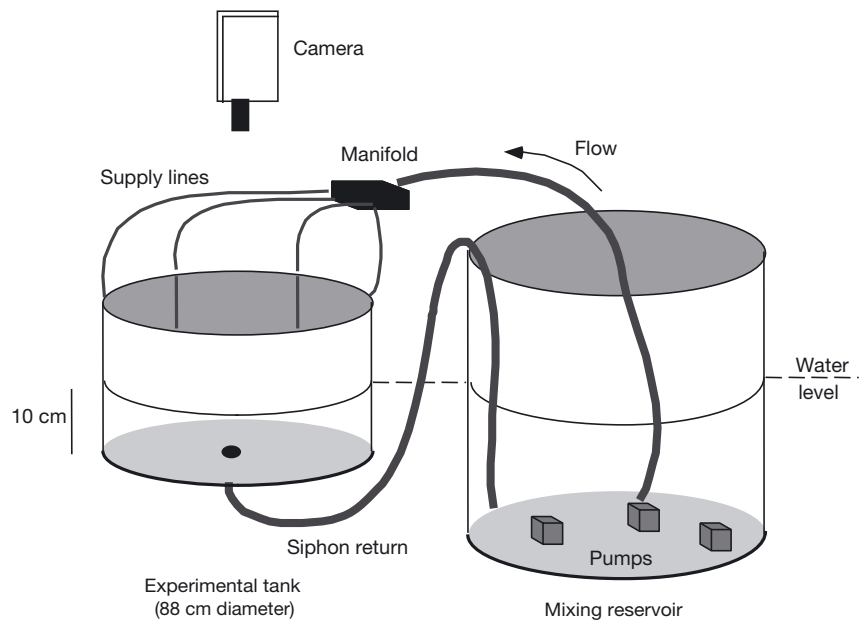
strikes. The experimental tank system was located in a windowless laboratory maintained at a temperature near 28°C. Light was supplied by daylight fluorescent tubes on a 12 h light:12 h dark cycle. Intensity was between 37 and 42 µE at the surface of the water during the observation period.

Predation events were recorded with a video camera mounted above the experimental tank. A predatory strike was defined as an abrupt movement directed towards a shrimp. We used a scale marked on the tank floor and measured strike distance as the distance from the fish's snout to the prey, immediately before the strike was initiated. We also recorded the number of successful strikes and the number of ambush strikes during each feeding trial. An ambush strike was defined as a strike in which the fish was stationary immediately before the strike.

Prey selection

We examined prey selection by southern flounder in clear water and at 50 FTU. These experiments were conducted with the same tank system and under similar conditions as the brown shrimp prey size and turbidity experiments. Separate selection experiments were conducted using brown shrimp and white shrimp prey (12 replicate tanks for each turbidity level), brown shrimp and longnose killifish (6 replicate tanks per turbidity level), and white

shrimp and longnose killifish (8 replicate tanks per turbidity level). Ten individuals of each prey species were placed in each experimental tank along with 1 southern flounder, and the predator was allowed to feed for 12 h (07:00 to 19:00 h). Southern flounder ranged in size between 129 and 208 mm TL, and all prey were between 37 and 50 mm TL. Water depth in tanks was 25 cm, and temperatures ranged between 27 and 30.5°C. Before each experiment, southern flounder were held in the laboratory for a minimum of 1 wk and fed a mixture of the experimental prey to be used in the selection experiment. In the experiment with brown shrimp and longnose killifish, we included 4 tanks with prey (40 of each species) and without predators to check for interactions among prey. Overall, 95% of the shrimp and 98% of the longnose killifish were recovered alive, and there did not appear to be any effect of turbidity on prey survival.

Data analysis

Analysis of variance (ANOVA) was used to analyze the effects of brown shrimp prey size and turbidity on predation rates. The number of prey eaten in each experimental tank was used as the observation in a 2 × 4 factorial model with interaction. Day was included as a blocking variable in the model. An F_{max} test for homogeneity of variances was not significant (p > 0.05).

A 1-way ANOVA was used to analyze the effect of turbidity on strike distance. Strike distance had to be ln-transformed to meet the assumption of homogeneity in variances; an F_{max} test on transformed data was not significant at p > 0.05.

We assumed unequal variances and used t-tests to analyze the prey selection data for each experiment. The total number of prey eaten and the percentage of 1 prey eaten out of the total number of prey were used as the observations in the analyses. In the experiment using 2 shrimp species, we used a z-test to test the null hypothesis that the proportion of brown shrimp consumed was not different from 0.5. Analyses were conducted using JMP (Version 11.1.1, SAS Institute).

RESULTS

Prey size and turbidity

Feeding rates of southern flounder were significantly higher on small shrimp than on large shrimp,

Table 1. Analysis of variance for southern flounder *Paralichthys lethostigma* feeding experiment on 2 sizes of brown shrimp *Farfantepenaeus aztecus* prey and at 4 turbidity levels. The observation in the analysis was the number of shrimp eaten per tank

Source	df	SS	MS	*F*-value	p-value
Turbidity (Turb)	3	7.375	2.458	2.356	0.0983
Prey size (Preysz)	1	72.000	72.000	69.000	0.0001
Turb × Preysz	3	10.500	3.500	3.354	0.0364
Day (block)	1	2.000	2.000	1.917	0.1795
Residual error	23	24.000	1.043		

and this effect of shrimp size varied with turbidity. The significant interaction between prey size and turbidity (Table 1) indicated that turbidity affected feeding rates, and this effect was different for different prey sizes. The highest mean predation rate for small shrimp occurred at 10 FTU while the highest mean value for large shrimp occurred at 25 FTU (Fig. 4). There was little difference in mean feeding rates at different turbidities for large shrimp. *A priori* contrasts of feeding rates at 0 and 50 FTU were not significant for large shrimp (df = 1, 23; p = 0.30), but feeding on small shrimp was significantly reduced at 50 FTU (df = 1, 23; p = 0.024).
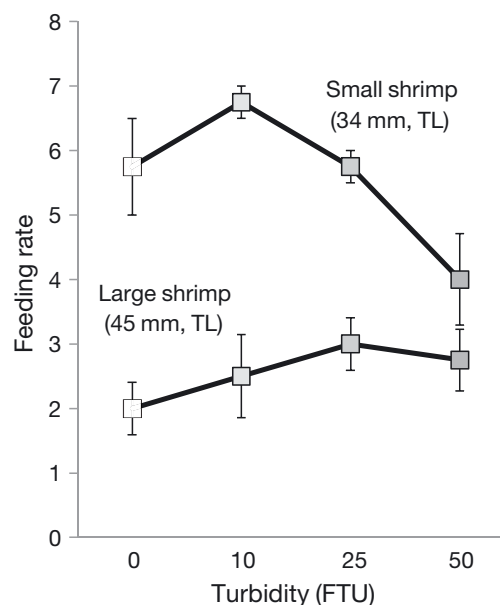

Fig. 4. Effect of prey size and turbidity on feeding rates of southern flounder *Paralichthys lethostigma*. The feeding rate is the mean number of brown shrimp *Farfantepenaeus aztecus* eaten over the 12 h experimental period; error bars are ±1 SE. Shading (white to 50% grey) indicates increasing turbidity

Strike distance

In 198 h of observation, 127 predatory strikes by southern flounder were observed. The overall strike distance (mean ± SE) was 4.6 ± 0.29 cm, and although mean values for different turbidity levels ranged between 4.0 and 5.1 cm (Table 2), these differences were not statistically significant (ANOVA; df = 2,124; p = 0.49). Mean strike distance was lowest and the percent of successful strikes was greatest at a turbidity of 10 FTU (Table 2). The mean strike distance for successful strikes was 4.2 ± 0.31 cm, but we still found no significant difference in strike distance related to turbidity when we only considered successful strikes (ANOVA; df = 2,87; p = 0.74). Overall, southern flounder used ambush strike tactics 79% of the time, with the highest mean percentage of ambush strikes also occurring at 10 FTU.

We standardized the data to determine the number of strikes per fish per hour. If we considered each feeding trial as an independent observation, mean strikes per hour were highest at 10 FTU (Table 3), but differences among the 3 turbidity levels were not statistically significant (ANOVA; df = 2,30; p = 0.29). There was a significant effect of turbidity on the predation rate (ANOVA; df = 2,30; p = 0.025), and the mean number of shrimp eaten per fish per hour was highest at 10 FTU.

Prey selection

When brown shrimp and white shrimp were offered to southern flounder as prey, the fish ate a mean of 4.7 shrimp (both species combined) over the 12 h experimental period; there was no significant effect of turbidity on this feeding rate (t = 0.90; df = 18.1; p = 0.90). Brown shrimp made up 63% of the prey eaten in clear water and 60% in turbid water (50 FTU), and there was no significant effect of tur-

Table 2. Mean strike distance for southern flounder *Paralichthys lethostigma* at 3 turbidity levels. Each observed strike was considered as an independent observation. The percentage of successful strikes was determined by whether the white shrimp *Litopenaeus setiferus* prey was consumed. Ambush strikes were those where the predator was stationary immediately before striking

FTU	No. observations	Mean strike distance, cm (SE)	% Successful	% Ambush
0	50	5.1 (0.65)	66	78
10	49	4.0 (0.26)	84	82
25	28	4.7 (0.46)	57	75

Table 3. Strike and feeding rates (number per fish per hour) for southern flounder *Paralichthys lethostigma* in feeding trials with white shrimp *Litopenaeus setiferus* prey at 3 turbidity levels. Feeding trials were considered independent observations in determining means and standard errors

FTU	Trials	Strikes (SE)	Shrimp eaten (SE)
0	13	0.32 (0.062)	0.23 (0.057)
10	10	0.42 (0.102)	0.39 (0.070)
25	10	0.23 (0.069)	0.14 (0.048)

bidity on prey selection between the 2 shrimp species (t = −0.32; df = 21.8; p = 0.75). A *z*-test confirmed that the proportion of brown shrimp consumed did not differ from 0.5 (z = 1.1022; p = 0.2704).

Prey selection by southern flounder between shrimp and longnose killifish, however, was dramatically affected by turbidity (Fig. 5). When brown shrimp and longnose killifish were prey, the southern flounder ate significantly more (t = 2.66; df = 5.9; p = 0.038) total prey in the turbid tanks (mean ± SE = 4.5 ± 0.72) compared with the clear tanks (2.5 ± 0.22). This difference, however, was due to an increase in killifish eaten from a mean of 0.2 ± 0.40 fish in clear water to a mean of 3.2 ± 0.98 fish in turbid water. The mean percentage of brown shrimp eaten shifted from 95% in clear water to only 23% in turbid water, and this difference was highly significant (t = −6.0; df = 7.5; p = 0.0004). When white shrimp and longnose killifish were prey, southern flounder ate an overall mean of 3.4 prey over the experimental period, and there was no significant difference in the number of total prey eaten in the clear and turbid treatment (t = −0.99; df = 14.0; p = 0.34). As in the experiment with brown shrimp, the number of killifish increased and the number of white shrimp decreased in turbid water, and the mean percentage of white shrimp eaten was significantly reduced from 94% in clear water to 36% in turbid water (t = −4.83; df = 11.6; p = 0.0004).

DISCUSSION

Southern flounder can be an important predator on penaeid shrimp in estuaries of the Gulf of Mexico (Minello et al. 1989). Reduced water clarity caused by suspended sediments is common in these estuaries, and the impact of this turbidity on the reactive distance and predation success of fish predators can be complex. Turbid water generally reduces visual acuity and reactive dis-
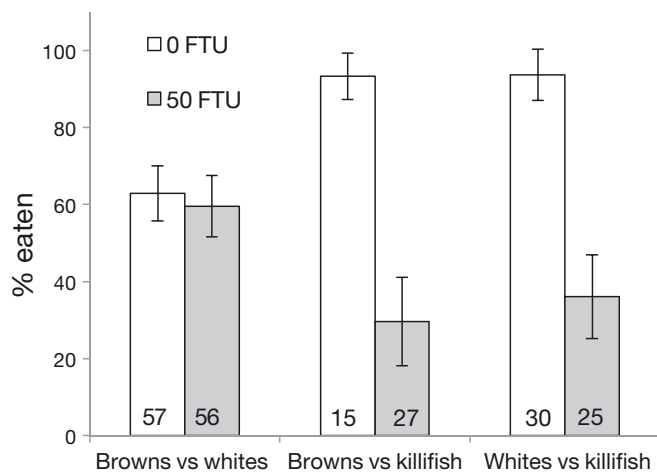
Fig. 5. Effect of turbidity on prey selection by southern flounder *Paralichthys lethostigma*. Two prey types (brown shrimp *Farfantepenaeus aztecus*, white shrimp *Litopenaeus setiferus*, killifish *Fundulus similis*) were offered to southern flounder in equal numbers during each experiment. The percentage eaten is shown for the first prey type in the pair. The total number of prey eaten is shown at the bottom of each bar

tance of fish predators, causing reduced predation rates (Hecht & van der Lingen 1992, Aksnes & Utne 1997). For visual ambush predators such as southern flounder feeding on penaeid shrimp, however, increasing turbidity appears to produce an interaction between decreasing visual acuity of the predator, which can reduce predation rates, and increasing prey activity which can increase predation rates. Our experimental results support this conclusion, and this interaction likely results in peak feeding rates of southern flounder on shrimp occurring at intermediate turbidity levels.

Our experimental results showed such an increase in mean feeding rates at intermediate turbidity levels, and the effect changed with prey size as predicted in the model shown in Fig. 2B. For small shrimp, the highest mean predation rates were at 10 FTU, in contrast with the results for similar sized shrimp obtained by Minello et al. (1987), where feeding rates were highest at 50 FTU. These 2 experiments differed in the density of prey, the intensity of light, and the clay used to make the

water turbid (Table 4). All of these factors have the potential to affect prey activity, encounter probabilities, and reactive distance of predators (Aksnes & Utne 1997). In particular, our use of bentonite rather than kaolinite may have been important. Kaolinite has a lighter color that reflects light readily, and this right-angle reflection off clay particles is measured as nephelometric turbidity. In preliminary comparisons, it took almost 3× as much of the suspended bentonite (mg ml^{-1}) used here to obtain the same nephelometric turbidity as with the kaolinite used by Minello et al. (1987). Our unpublished trials with human observers also showed that reactive distance at a similar FTU was less using bentonite compared with kaolinite: reactive distance was similar at 50 FTU of kaolinite and only around 25 FTU of bentonite (see Benfield & Minello 1996 for experimental methods). Based on these observations, we would expect any increase in predation rate with turbidity using bentonite to occur at lower FTU levels than with kaolinite, as suggested by our results here. Because the relationship between nephelometric turbidity and reactive distance appears to change with the type of suspended particles, these results also support the contention of Kirk (1985), Davies-Colley & Smith (2001), and others that nephelometric turbidity can be misleading as a measure of water clarity and reactive distance.

Table 4. Comparison of methods for our prey size and turbidity experiment and our predator strike distance experiment for southern flounder *Paralichthys lethostigma* preying on brown shrimp *Farfantepenaeus aztecus* and white shrimp *Litopenaeus setiferus* with those of Minello et al. (1987). Potentially important differences are highlighted in grey

Variable	Prey size × Turbidity expmt	Predator strike distance	Minello et al. (1987)
Predator species	*P. lethostigma*	*P. lethostigma*	*P. lethostigma*
Prey species	*F. aztecus*	*L. setiferus*	*F. aztecus*
Predator size (mm, TL)	130–150	190–240	82–126
Prey size (mm, TL)	31–36, 42–47	31–41	30–40
Clay used	Bentonite	Bentonite	Kaolinite
Turbidity (FTU)	0, 10, 25, 50	0, 10, 25	0, 50
Experimental duration (h)	12	6	12
Prey number/tank	20	10	25
Tank shape	Round	Round	Rectangular
Tank size (m^2)	1.8	0.64	5.07
Prey density (m^{-2})	11.1	15.6	4.9
Water depth (cm)	25	10	26
Light source	Skylight	Fluorescent	Skylight
Light intensity (µE)	314, 263[a]	37–42	73–152
Salinity	25	25	24–26
Temp (°C)	24–27.5	28	21–23

[a]Mean light levels above the tanks at 14:30 to 15:00 h on the 2 d of the experiment

The lack of any significant effect of turbidity at the levels tested for feeding on larger shrimp is complicated by the above factors, but we suspect that our highest turbidity levels did not reduce the strike zone for these prey. We found no significant effect of turbidity on strike distance in our experiment, but we could not make visual observations at turbidities greater than 25 FTU. Future experiments may be able to extend this range of turbidities using a variety of low light level detection approaches, transparent tank floors with infrared LEDs mounted below the observation tanks (Meager & Batty 2007), or tagging experimental fish with light sources. Strike distance in our experiment also might not have been affected if southern flounder switched to an alternative mode of prey detection such as olfaction (Gibson et al. 2014) at high turbidity levels (Higham et al. 2015).

Our experimental results only partially validate the theoretical model proposed here, but they do provide supporting evidence for the conclusion that turbidity is important in affecting feeding behavior of southern flounder. Ambush predators obviously cannot remain stationary, and they periodically move to improve their search environment; O'Brien et al. (1989) characterized this behavior as saltatory searching. We observed that 79% of southern flounder strikes, however, were initiated from a stationary position, and by documenting this ambush predatory behavior, we have presented some evidence that encounter probabilities should be important in determining feeding success for southern flounder. Reactive distance of southern flounder likely changes with turbidity as it does for other fish (Vinyard & O'Brien 1976, Hansen et al. 2013, Chapman et al. 2014). Strike distance should change with turbidity as well, although we could not support such a conclusion with experimental data, perhaps because it was difficult to make observations in water greater than 25 FTU. The strike distances we measured for southern flounder appeared similar to those measured for summer flounder by Olla et al. (1972). Predators may change their strike distance with turbidity, light availability, or the frequency with which prey enter their strike zone. At low prey densities, when few prey are available, predators may also expand their strike zone or change tactics to more actively hunt prey. Seahorses and largemouth bass have been shown to change from ambush tactics to actively pursuing prey in relation to the presence of vegetative structure (Savino & Stein 1989, James & Heck 1994), and saltatory predator behavior has been related to prey size and reactive distance (O'Brien et al. 1989).

Our prey selection experiments showed no significant selection by southern flounder for brown shrimp or white shrimp and no effect of turbidity on selection. In similar prey selection experiments in clear water with Atlantic croaker *Micropogonias undulatus* as predators, Minello & Zimmerman (1985) also found no evidence for selection between brown shrimp and white shrimp in cages without vegetative structure. In contrast, there was a highly significant selection apparent when shrimp and killifish were presented as prey. In clear water, flounder strongly selected shrimp as prey; and in turbid water, they selected killifish over shrimp. For actively foraging fish predators, turbidity has been shown to alter selection for both prey size (Reid et al. 1999, Sohel et al. 2017) and species (Shoup & Wahl 2009, Carter et al. 2010, Shoup & Lane 2015), mainly through an effect on reactive distance (Vogel & Beauchamp 1999). The effect of turbidity on an ambush predator, however, may be more complex, and perhaps the best strategy for prey to avoid these predators is to move slowly (Gerritsen & Strickler 1977). Turbidity may have increased movement of killifish in our experiments more than shrimp. Schooling of killifish was also observed in our clear water tanks, but we could not observe whether this behavior occurred in the turbid treatment. Schooling can protect killifish from predation (Godin & Morgan 1985, Morgan & Godin 1985), and since vision appears to be important in maintaining schooling behavior (Partridge 1982, Hall et al. 1986, Kimbell & Morrell 2015), schooling may have been reduced in our turbid water treatment (Cerri 1983, Ohata et al. 2014), increasing predation on killifish. Laboratory observations in clear water indicate that penaeid shrimp do not respond visually to the presence of stationary predators such as southern flounder, and they do not initiate escape behaviors until attacked (Minello & Zimmerman 1983, Minello et al. 1987). Fish prey, however, can change their behavior when they visually detect the presence of predators (McLean & Godin 1989, Abrahams 1994, Ferrari et al. 2010), and perhaps turbid water reduced the ability of killifish to detect southern flounder. Regardless of the mechanisms involved, highly turbid water apparently protected shrimp by increasing relative predation on these alternate fish prey. Even if predation rates on shrimp increase in moderately turbid water when only shrimp are available as prey, turbidity may still protect shrimp by shifting selection when alternative fish prey are available.

Many variables can affect the biomechanics of predator–prey interactions (Higham et al. 2015). Alternative refuges were unavailable in our experi-

ments for either prey species, and interactions between turbidity and other refuges may change prey selection patterns (Macia et al. 2003, Wishingrad et al. 2014, Ajemian et al. 2015). Brown shrimp can get protection from fish predators by burrowing in the substrate (Minello & Zimmerman 1984, Minello et al. 1987), and both shrimp and killifish may reduce predator-related mortality by moving to structurally complex habitats (Minello & Zimmerman 1983, 1985, McLean & Godin 1989).

The results of these experiments confirm the conclusion that turbidity can be an important factor affecting foraging of southern flounder. This estuarine predator appears to be well adapted to feeding on prey in turbid environments. Evidence from prey selection experiments that document the potential for dramatic shifts in selection suggests that caution should be used in the development of diet matrices for southern flounder and perhaps many predators. While gut contents certainly reflect fish diets at the time of capture, and large datasets may encompass variability in these diets, the potential effect of environmental factors on prey selection should be considered. Trophic models often depend on assumptions that fish diets are fixed or that they do not change in relation to environmental variables such as turbidity (Vallino 2000, Kemp et al. 2001, Christensen & Walters 2004), and variability in prey selection may be important when such models are used to assess impacts of changing environmental conditions. As an example, developers of large-scale engineering projects such as river diversions, which have the potential to alter estuarine turbidity, should consider how such changes may alter predator–prey interactions among estuarine fauna.

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