

Relative effects of turbidity and light intensity on reactive distance and feeding of an estuarine fish

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Synopsis

Gulf killifish *Fundulus grandis* were allowed to prey on daggerblade grass shrimp *Palaemonetes pugio* in clear water with bright light, turbid water containing bentonite clay, and clear water treatments where the light intensity was adjusted to match that in the bottom of the turbid tanks. Significantly fewer shrimp were consumed in the turbid tanks relative to the clear and shade treatments where predation rates did not differ significantly. The results suggested that the influence of suspended particles on predation rates was a consequence of light scattering and was not related to a decrease in light intensity. Reactive distances were subsequently determined for human observers viewing a small target in elongated tanks containing turbid water (7.3–60.5 NTU) under conditions of both low (8–10 $\mu\text{E m}^{-2} \text{s}^{-1}$) and high illumination (153–1249 $\mu\text{E m}^{-2} \text{s}^{-1}$). Reactive distance was primarily governed by turbidity while light intensity had little influence except at low turbidities. The shape of the relationship between reactive distance and turbidity for humans resembled curves reported for a variety of fish species.

Introduction

Elevated turbidity is a pervasive characteristic of shallow estuarine systems throughout the world. Studies on the effects of turbidity on predator-prey interactions have generally revolved around the influence of suspended sediments on a predator's reactive distance. Reactive distance has been defined as either the maximum distance at which visual predators can detect their prey (Vinyard & O'Brien 1976) or the maximum distance at which they will pursue their prey (Ware 1972). This distance can be a function of many factors including predator size (Hairton et al. 1982, Vandenbyllaardt et al. 1991), prey size (Vinyard & O'Brien 1976), prey movement (Howick & O'Brien 1983), and turbidity (Gardner 1981, Bar-

rett et al. 1992, Gregory & Northcote 1993). While it is generally accepted that elevated turbidity reduces the reactive distance of predators, the mechanism governing this effect remains unclear. Two hypotheses have generally been proposed to explain reduced visual acuity in turbid water: a reduction in ambient light intensity due to shading by suspended particles and scattering of light by suspended particles (Lythgoe 1979). The specific objective of this study was to evaluate the relative influence of shading and scattering in determining reactive distance. We conducted a feeding experiment with predatory fish to examine predation rates in clear, turbid and shaded treatments. In addition, we measured reaction distances of human observers at various levels of illumination and turbidity.

Methods

Predation experiment

Our predation experiment was designed to determine whether turbidity mediated predation rates of fish via scattering or shading. A series of twelve 52 l rectangular glass aquaria were painted a sand color and enclosed within individual light-tight compartments constructed of sand-colored plastic. The sand color was used to standardize background color in experimental treatments. Light was provided to each tank by an overhead 150 W incandescent floodlamp and a diffuser panel. Each tank was filled with 40 l of seawater (turbidity ≤ 2.0 NTU) which had been passed through a sand filter and a 5 μm polyester filter cartridge. A single airstone placed at one end of each tank provided vigorous aeration.

The light intensity at the bottom of each tank was measured with a LI-COR LI-193SB spherical quantum sensor attached to an LI-188B radiometer, and dimmer switches were used to initially adjust all the light intensities to $20 \mu\text{E m}^{-2} \text{s}^{-1}$. Four randomly selected tanks were designated turbid treatments and received sufficient western bentonite (UNIBAR Drilling Fluids, Houston Texas) to raise their turbidity to 100 NTU (nephelometric turbidity units). Turbidities were measured with a LaMotte Model 2008 nephelometer standardized with a 1.0 NTU polymer bead standard which recorded NTUs. Conversion to FTUs (a formazin based standard) can be performed with the equation: $\text{FTU} = 1.25 \times \text{NTU}_{\text{Polymer Standard}}$.¹ Measurement of the light intensities in the turbid tanks revealed that shading by the bentonite reduced illumination levels in the turbid treatments to approximately $14 \mu\text{E m}^{-2} \text{s}^{-1}$. In four of the remaining tanks (designated shade treatments) the light intensities were dimmed to approximately $14 \mu\text{E m}^{-2} \text{s}^{-1}$ in order to match the light present in the turbid tanks. The remaining four tanks were designated clear treatments without bentonite or shading. Two control tanks, with and without ben-

tonite, were used to evaluate non-predatory mortality and recovery efficiency.

Gulf killifish *Fundulus grandis* Baird and Girard (mean live mass 11.9 g, range 3.4–23.9 g) were used as predators and daggerblade grass shrimp *Palaeomonetes pugio* Holthuis were used as prey. Animals were collected from brackish ponds and salt marsh areas on Galveston Island, Texas (29°15' N, 94°52' W) and gradually acclimated to the experimental salinity (22–24‰) in holding tanks. Shrimp were fed Tetra-Marin commercial flake food once daily. Fish were fed shrimp twice daily, and starved for 24 h before each experiment.

Four hours prior to each experiment, three randomly selected fish were added to each experimental tank. Turbidities and light intensities were adjusted to experimental conditions two hours before each experiment. Twenty five shrimp prey were randomly assigned to tanks and placed within a cylindrical PVC enclosure 30 min before the start of the experiment. When the enclosures were removed, the predators and prey were permitted to interact for 2 h; tanks were checked at 30 min intervals to ensure that any shrimp which had jumped up and were stuck to the sides of the tanks were returned to the water. At the same time a small quantity of water was withdrawn from each tank through a fixed siphon in order to monitor turbidity. After 2 h the tanks were drained and both predators and prey were removed and counted. The experiment was repeated on three separate days using new predators and prey.

For each treatment, light intensity and turbidity did not vary significantly among replicate days. The overall treatment means \pm S.E. for these variables were: clear ($20.2 \pm 0.1 \mu\text{E m}^{-2} \text{s}^{-1}$; 0.6 ± 0.2 NTU), shade ($14.2 \pm 0.2 \mu\text{E m}^{-2} \text{s}^{-1}$; 0.6 ± 0.1 NTU), and turbid ($14.3 \pm 0.4 \mu\text{E m}^{-2} \text{s}^{-1}$; 100.8 ± 1.6 NTU). Mean fish mass was significantly different (ANOVA $p < 0.0001$) among replicate days, but not among experimental treatments within days. Predation results were analyzed in a randomized block ANOVA using the experimental day as the blocking variable. A posteriori multiple comparisons of treatment means were made using Ryan's Q (Day & Quinn 1989).

¹ LaMotte Chemical 1990. Operator's manual for model 2008 turbidimeter. LaMotte Chemical Products Co., Chestertown, Maryland 21620.

Human observers

Preliminary observations designed to measure the distances at which human observers could detect a small target in turbid water suggested that reactive distance was primarily determined by suspended solid concentration and not by light intensity. The experiment described here was designed to further test this hypothesis. Observers indicated when they could first detect a small target in a 10 cm wide \times 10 cm tall \times 91 cm long acrylic tank (Fig. 1) with a transparent base, top and view port on one end. The end opposite the view port and sides were painted the same sand color on their external surfaces as was used on the predation experiment aquaria. An opaque shroud, which fitted over the observers head, was attached to the edges of the observation port in order to eliminate glare at higher light intensities. The tank was filled with suspensions of bentonite clay in distilled water; turbidities ranged from 7.3–60.5 NTU. Replicate observations by at least three different observers were taken inside under fluorescent lighting ($8\text{--}10 \mu\text{E m}^{-2} \text{s}^{-1}$) over a range of turbidities. In addition, single observations by different observers were collected outside over a range of natural light intensity (153 and $1249 \mu\text{E m}^{-2} \text{s}^{-1}$)-turbidity ($25\text{--}53$ NTU) combinations. The light intensity was measured with a LI-COR LI-188B radiometer using a 10s integration and a LI-192SB quantum sensor. Turbidities were measured with a LaMotte Model 2008 nephelometer.

Results

Predation experiment

Turbidity reduced predation rates in gulf killifish, and this effect was apparently due to the presence of suspended sediments and unrelated to shading (Fig. 2). There was no evidence of heterogeneity among treatment variances (Hartley's $F_{\max} = 3.48$, $p > 0.05$), thus no transformation was applied to the data. Turbid water reduced predation by fish, and there was a significant treatment effect in the ANOVA ($p = 0.0001$). The predation rate in the treatment containing bentonite (6.8 shrimp consumed

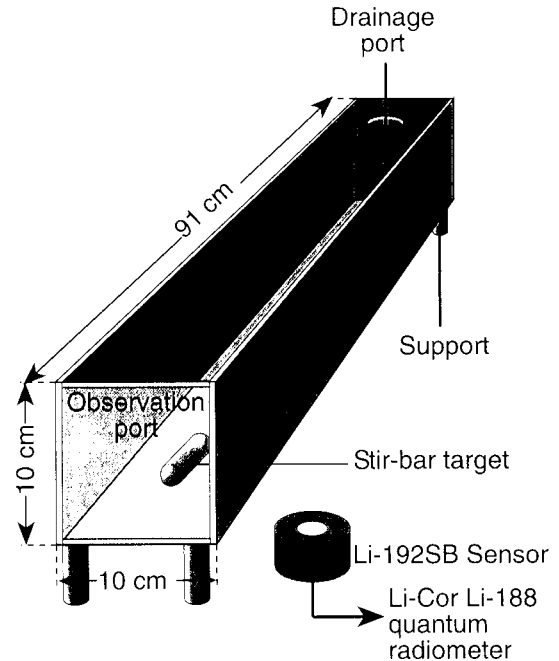


Fig. 1. Schematic diagram of the plexiglas observation chamber. The clear observation port is surrounded by a black cloth shroud (not shown) to eliminate glare. Observers positioned their eyes level with the base of the chamber and approximately 10 cm from the observation port. The distance between the leading edge of the target and the observation port was used as the detection distance. Movement of the magnetic stir-bar target is accomplished by a second stir-bar attached to a meter-stick which can be pushed below the chamber. Light intensity was measured approximately 10 cm to the right of the observation point.

2 h^{-1}) was significantly lower than in either the shaded (17.6 shrimp consumed 2 h^{-1}) or clear (17.2 shrimp consumed 2 h^{-1}) treatments (Ryan's Q , $\alpha = 0.05$). There was no significant block (day) effect in the analysis ($p = 0.08$). Recovery rates for shrimp in the two control tanks were 100% with no evidence of non-predatory mortality.

Human observers

The relationship between reactive distance and turbidity was best described by a power function (Fig. 3). Reactive distance declined most rapidly as turbidity was increased from low to moderate levels (up to 20 NTU), and the slope of the curve appeared to drop towards an asymptotic value at

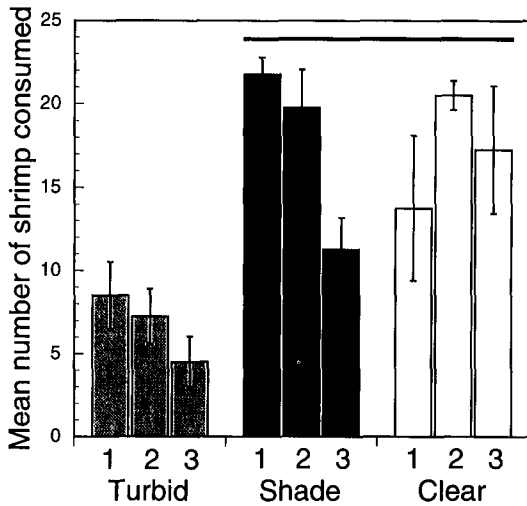


Fig. 2. Mean number of daggerblade grass shrimp consumed by gulf killifish in turbid (100 NTU, $14 \mu\text{E m}^{-2} \text{s}^{-1}$), shade (< 2 NTU, $14 \mu\text{E m}^{-2} \text{s}^{-1}$) and clear treatments (< 2 NTU, $20 \mu\text{E m}^{-2} \text{s}^{-1}$) in three replicate experiments. Vertical bars indicate ± 1 standard error of the mean. Treatments sharing the horizontal bar do not differ significantly ($p < 0.05$) according to Ryan's Q multiple comparison test.

higher turbidities. The general positioning of the single observations on or below the $8\text{--}10 \mu\text{E m}^{-2} \text{s}^{-1}$ curve further supports the primacy of turbidity in determining detection distance. These data points were collected at much higher light intensities ($> 150 \mu\text{E m}^{-2} \text{s}^{-1}$) and should be shifted above the $8\text{--}10 \mu\text{E m}^{-2} \text{s}^{-1}$ curve if light exerted strong influence over reactive distance.

Discussion

Our two complimentary studies suggest that turbidity mediates visual acuity and therefore, predatory success, via scattering of light by suspended particles. The presence of suspended bentonite (100 NTU) reduced the light intensity by 30% and was associated with significantly reduced predation rates; an equivalent shift in illumination in clear water failed to alter the predation rate relative to the clear $20 \mu\text{E m}^{-2} \text{s}^{-1}$ treatment. Substantial increases in light intensity did not increase the reactive distance of human observers while moderate shifts in turbidity dramatically reduced reactive distance.

Other data suggest that for visual predators, reductions in light intensity may influence reactive distance and reduce predation rates only at very low levels of illumination. Greccay (1990) monitored daily rations of mysids *Neomysis americana* consumed by juvenile weakfish *Cynoscion regalis* at four turbidities (0.95, 3.1, 6.1, 11.0 NTU) and four light intensities (0, 1.7, 3.4, $16.6 \mu\text{E m}^{-2} \text{s}^{-1}$). Light intensity only exerted a significant negative effect on daily ration at the lowest illumination levels. The turbidity levels examined did not significantly alter daily ration at the higher illuminations but did reduce predation at the lowest light intensity (below detectable levels). These results suggest that light intensity only affected reactive distance and feeding of his experimental fish as illumination increased from near darkness to very low levels. Vinyard & O'Brien (1976) noted a similar trend for bluegills feeding on *Daphnia pulex*. Increasing illumination above 10.8 lux ($0.2 \mu\text{E m}^{-2} \text{s}^{-1}$) had little effect on the reactive distance which was largely a function of turbidity above this threshold. James & Heck (1994) evaluated the influence of light intensity and seagrass density on predation rates by lined seahorse *Hippocampus erectus* on caridean shrimp *Hippolyte zostericola*. Predation rates were not statistically different among low and high light intensities, but were significantly reduced in complete darkness, with the

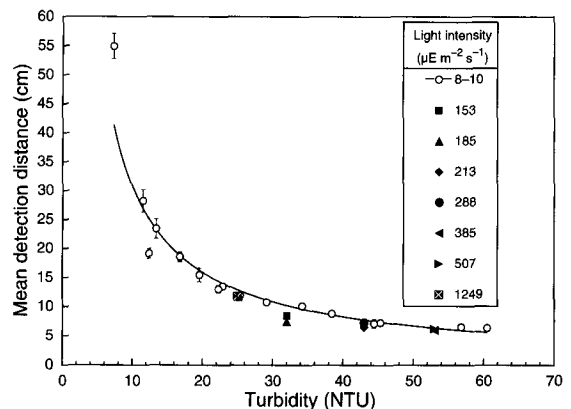


Fig. 3. Mean distances required for replicate human observers to detect a 1 cm wide white target in bentonite suspensions of 7.3–60.5 NTU at $8\text{--}10 \mu\text{E m}^{-2} \text{s}^{-1}$ (—○—). Additional solid data points are detection distances for individual observers at different light intensity-turbidity combinations.

threshold for visual location of prey by *H. erectus* falling between 0–0.4125 $\mu\text{E m}^{-2} \text{s}^{-1}$. Given the low light intensities required to reduce predation rates in these cited studies, the absence of a predation effect in our shade treatments (14 $\mu\text{E m}^{-2} \text{s}^{-1}$) suggests that the threshold for effective visual feeding by *F. grandis*, must lie well below this level.

Our experimental light intensities were representative of those found in shallow estuarine environments. According to a model developed by Martinez (1991), daytime light intensities near the substrate in Galveston Bay at a depth of 1 m and a turbidity of 19 FTU (= 15.2 NTU) will be approximately 6.6 $\mu\text{E m}^{-2} \text{s}^{-1}$. Gut content data from *Fundulus heteroclitus* (Weisberg et al. 1981), *F. notatus* (Atmar & Stewart 1972), and *F. similis* (Bennett 1973) suggest that this genus feeds primarily during daylight hours with limited crepuscular foraging. At dawn and dusk, light in Martinez's model was below 10 $\mu\text{E m}^{-2} \text{s}^{-1}$ regardless of turbidity or water depth. Thus, 14 $\mu\text{E m}^{-2} \text{s}^{-1}$ in our shade treatments represented a light intensity which normally prevails within the shallow regions of Galveston Bay during the period of the day when *F. grandis* may be expected to forage.

Mean monthly turbidities in a shallow salt marsh area in West Bay of the Galveston Bay system, ranged from 0.9–53.4 NTU over the period 1988–1992 (Minello unpublished). The majority of means (90%) fell within 5–50 NTU which is similar to the range of turbidities used in our observation tank. If the relationship between turbidity and reactive distance for fish is similar to that observed for humans in our study, then the prevailing turbidity range in an area such as Galveston Bay might alter reactive distances for fish predators by an order of magnitude. In addition, the asymptotic nature of the curve in Fig. 3 suggests that there is an upper bound to the influence of turbidity beyond which reactive distance is independent of turbidity. This threshold appeared to lie in the vicinity of 60 NTU, and it is possible that at extremely high turbidities shading by suspended particles could reduce light intensities to the point where further declines in reactive distance are a function of illumination.

We recognize that caution must be exercised in relating the visual acuity of humans viewing an un-

derwater target through a Plexiglass port to fish vision underwater. Comparable information on reactive distances for fishes is much harder to obtain. Although visual acuity differs among fish species (Douglas & Hawryshyn 1990), the shape of the relationship between reactive distance and turbidity is similar for all fish species examined. Wright & O'Brien (1984) suggest that the relationship for fishes is hyperbolic. The shape of the relationship between reactive distance and turbidity for our human observers is very similar to published data for juvenile chinook salmon (Gregory & Northcote 1993), bluegills (Vinyard & O'Brien 1976) and models of fish vision (Wright & O'Brien 1984, Aksnes & Giske 1993).

Prey capture is frequently dependent on visual detection by the predator (Hairston et al. 1982) which is a function of the reactive distance. Unfortunately, the influence of turbidity on reactive distance does not appear to have been examined experimentally for *Fundulus grandis* or other species in this genus.

We hypothesize that the reduction in predation observed in the turbid treatment was a consequence of a diminished reactive distance in *F. grandis* caused by suspended clay particles. Other factors, however, may have been responsible for the altered predation rates noted in our turbid treatment. Reduction in prey contrast in turbid water has been suggested (Duntley 1963, Eggers 1977; Aksnes & Giske 1993) as a cause for reduced prey visibility or predation rates. We standardized the background in all our experiments by painting the exteriors of the tanks and the observation chamber a sand color. Altered prey behavior such as schooling, aggregation or increased activity in response to elevated turbidity or diminished light may modify predation rates (Shaw 1961, Cerri 1983, Minello et al. 1987). We could not make behavioral observations of *Palaemonetes pugio* in our turbid tanks, however, the absence of any experimental effect in the reduced light treatments suggests that shrimp behavior was unaffected by shade.

We conclude that daylight predator-prey interactions of visual predators in shallow turbid water appear to be regulated by the scattering of light by suspended particles rather than attenuation of light.

Reactive distance can change by an order of magnitude with typical changes in water clarity found in a turbid estuary. The influence of suspended particles on light intensity may increase in importance in deeper waters where ambient light intensities are low, and during periods of low light such as dusk through dawn.

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