

## Turbidity influences trophic interactions in estuaries

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### Abstract

We investigated how changes in abiotic conditions resulting from human activities indirectly alter trophic interactions using turbidity in estuaries as a model system. Development and nutrient input are causing turbidity to increase in many coastal areas. Using an 18 yr data set from Aransas and San Antonio Bays in Texas, we found fish abundance (*Sciaenops ocellatus*, *Pogonias cromis*, *Archosargus probatocephalus*) to be highest in low turbidity (< 30 nephelometric turbidity units [NTU];  $p < 0.01$ ), while crab (*Callinectes sapidus*) abundance was highest in high turbidity (> 30 NTU;  $p < 0.05$ ). In field studies, mud crabs (*Panopeus* spp.), an important intermediate predator on oyster reefs that are not targeted in the 18 yr data set, were more abundant on oyster reefs in St. Charles Bay, Texas, when turbidity exceeded 30 NTU ( $p = 0.03$ ). Fish predation on tethered *Panopeus herbstii* was greatest when turbidity was low (< 30 NTU,  $p < 0.05$ ), but predation by crabs ( $p = 0.003$ ) and overall predation ( $p = 0.02$ ) were greatest in high turbidity (> 30 NTU). Predation on oyster spat was not different between low- and high-turbidity sites ( $p = 0.64$ ). However, oysters devoted more resources to shell growth ( $p < 0.01$ ) at a cost of less somatic growth and fecundity, a reaction known to occur in response to crab predators. Elevated turbidity can alter trophic interactions in estuaries by altering species composition and trophic interactions, leading to an increase in crab abundance, which can alter predation rates as well as growth in juvenile oysters.

Density-dependent forces such as competition and predation can have large effects on the structure and function of communities. However, intense environmental stress can render biotic effects in communities unimportant and act as the primary agent of community regulation (Menge and Sutherland 1987; Menge and Olson 1990). Classic community regulation models depict stress as conditions that are physiologically stressful because they are outside tolerance limits for organisms (Menge and Olson 1990) or are precarious for organisms because they impose severe physical limitations upon them and/or are likely to cause injury or death (Menge and Sutherland 1987). This is exemplified on wave-swept shores where hydrodynamic stress associated with waves minimizes the effects of predators by limiting predator foraging ability (Menge and Sutherland 1987), and when abiotic conditions meet or exceed tolerance limits of plants and increase vulnerability to consumer attacks (Menge and Olson 1990).

Abiotic conditions may not be overtly harmful or exceed tolerance limits for organisms but may still influence the outcomes of species interactions and have large effects on communities (Leonard et al. 1998). For example, predatory insects and fish may experience reduced foraging success in rapid flows (Malmqvist and Sackman 1996; Schaefer et al. 1999), and turbulence can reduce feeding success of planktonic organisms (Saiz et al. 2003). On wave-protected rocky shores in New England, green crabs were found to be more abundant in sites with high mean flow velocities despite suffering reduced foraging rates in fast flows. Reduced predator efficiency caused a reduction in top-down control and had large effects on community structure and successional patterns (Leonard et al. 1998). In a grassland ecosystem, increased temperatures released

grasshopper nymphs from indirect effects on growth and behavior caused by spider predators in treatments under ambient conditions (Barton 2010). Further, hypoxic areas may alter species movements and interactions, potentially increasing predation rates (Froeschke and Stunz 2012). Thus, abiotic conditions may increase the potential for indirect, context-dependent effects that propagate to multiple community members (Werner and Peacor 2006).

Identifying large-scale patterns in many systems can prove challenging when species interactions are important drivers of community structure but are context-dependent (Leonard et al. 1998; Werner and Peacor 2006). However, understanding how abiotic conditions influence species interactions can provide important insights to explain how context-dependent interactions may be scaled up to explain large-scale patterns in the distribution of organisms, changes in top-down vs. bottom-up forcing, and biodiversity. For example, habitat destruction and stressful abiotic conditions can affect species movement and habitat selection, negatively affecting refuge habitats that become overfilled with species trying to escape harmful conditions (Lenihan et al. 2001).

Recent studies have shown that abiotic conditions at levels that are not physiologically stressful can have significant effects on organismal interactions, top-down forcing, and community composition by modifying species interactions. In estuarine systems, salinity, temperature, and dissolved oxygen affect biodiversity and species distributions, primarily through organismal tolerance limits (Lenihan et al. 2001; Day et al. 2009). As species seek to escape stressful abiotic conditions, they may be driven into smaller refuge areas, increasing the magnitude of density-dependent interactions in these areas. By influencing predatory interactions, abiotic conditions can also indirectly affect community structure and biodiversity (Paine

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1966; Werner and Peacor 2006). In addition to the aforementioned abiotic conditions, turbidity may also affect predatory interactions and community structure (Van de Meutter et al. 2005). Unlike other abiotic conditions such as salinity, temperature, and dissolved oxygen, turbidity rarely exceeds the tolerance limits of aquatic animals. Rather, turbidity reduces the visual acuity of predators and alters top-down forcing (Minello et al. 1987; Liljendahl-Nurminen et al. 2008), thereby altering the distribution of species and spatial extent of top-down control as visual predators seek foraging areas that are favorable (Snickars et al. 2004). These changes have the potential to alter direct and indirect effects of predators on prey and alter aquatic food webs.

The effect of turbidity, particularly in marine food webs, has not been well studied, even though turbidity levels are increasing because of human activities in coastal areas (Sanden and Hakansson 1996). Human activity is a major cause of the two principal sources of turbidity, increased nutrient input and erosion (Candolin et al. 2008), and has increased the number of highly turbid lakes (Radke and Gaupisch 2005). Erosion is a widespread and damaging form of pollution. By increasing siltation of lakes and streams (Khan and Ali 2003), it can decrease light to below levels needed for photosynthesis, decreasing food production and dissolved oxygen solubility to levels that are harmful to fish populations (Khan and Ali 2003; Candolin et al. 2008). Marine systems primarily experience increased turbidity through eutrophication (GESAMP 1990). Eutrophication is directly tied to human-induced nutrient loading and leads to decreases in primary production (Kautsky et al. 1986) and an increase of harmful algal blooms and hypoxia (Rabalais 2005). Human-induced changes to aquatic and marine environments often have large effects even at moderate levels of increased turbidity.

Turbidity studies have been conducted predominantly on freshwater organisms in the laboratory with visual predators (Radke and Gaupisch 2005; Liljendahl-Nurminen et al. 2008), and the few marine studies performed have been short term and laboratory based (Minello et al. 1987; Ohata et al. 2011). These studies have found that turbidity affects predator-prey interactions, but these effects are species dependent (Minello et al. 1987; Liljendahl-Nurminen et al. 2008) and reflect the degree to which predators depend on visual cues vs. cues that are not compromised by increases in turbidity (e.g., chemosensory, mechanosensory; Dusenbery 1992). Marine systems have a more diverse assemblage of nonvisual predators (e.g., crabs) than do freshwater habitats and may respond differently when turbidity increases. To date, the community-level effects caused by changes in turbidity are not well understood in either system, and field experiments assessing turbidity effects are rare.

Using an 18 yr data set from the western Gulf of Mexico, we investigated the effects of turbidity on species assemblages in estuarine habitats in two bays located in Texas. We then used oyster (*Crassostrea virginica*) reef communities in a third bay as a model system to investigate the effects of turbidity on predatory interactions. Oyster reefs provided an excellent model system because they are home

to a diverse predator assemblage, including predators that forage primarily using visual cues and others that locate prey using chemoreception. We focused on a three-tier food web with fish (red drum: *Sciaenops ocellatus*, black drum: *Pogonias cromis*, sheepshead: *Archosargus probatocephalus*, and toadfish: *Opsanus beta*) and crab (blue crab: *Callinectes sapidus* and stone crab: *Menippe adina*) top predators, an intermediate predator (mud crabs: *Panopeus* spp.), and a basal prey resource (oysters: *Crassostrea virginica*). Both top and intermediate predators exert top-down forces on oyster reef communities and may consume oysters; intraguild predation between the top predators is also common (Grabowski et al. 2005; O'Connor et al. 2008).

Oysters are a commercially important fishery, provide essential habitats for other recreational and commercially important organisms, and provide numerous benefits such as water filtration and reducing coastal erosion (Grabowski et al. 2005; Grabowski and Peterson 2007). Abiotic conditions such as flow, salinity, and hypoxia affect oyster recruitment, growth, and survival, as well as community diversity on oyster reefs (Lenihan 1999; Kimbro and Grosholz 2006). However, most studies have focused on abiotic conditions that are considered stressful to oysters (e.g., salinity, temperature) and have not considered how turbidity influences oyster reef communities via modifying predatory interactions within the food web. Our data indicate that turbidity affects the distribution of mobile species, alters predation levels and the abundance of intermediate predators, which indirectly alters food webs, and causes an indirect effect on juvenile eastern oysters, an important ecosystem engineer in estuarine systems.

## Methods

*Long-term monitoring of turbidity on species abundance*—The relationship between turbidity and abundance of recreationally important fish and crab species was evaluated from a long-term data set (1991–2008) provided by the Texas Parks and Wildlife Department (TPWD) Coastal Fisheries Division. TPWD conducts monthly field surveys to measure the abundance of recreational and commercially fished species in Texas bays and records abiotic conditions including turbidity during each survey. We examined the effects of abiotic conditions including salinity, temperature, and turbidity on species abundance in San Antonio and Aransas Bays, Texas (Fig. 1). We elected to use the data from San Antonio and Aransas Bays because these bays have extensive natural oyster reefs that are commercially harvested. San Antonio Bay receives more freshwater input than does Aransas Bay and routinely has lower salinity, and thus, we were able to ascertain the effects of turbidity across a range of other abiotic conditions known to be important in estuarine systems. TPWD samples species abundances with both gill nets and trawls, which target fish and crabs, respectively. We used data from gill net surveys to analyze the abundance of the most common fish predators in the system (red drum: *Sciaenops ocellatus*, black drum: *Pogonias cromis*, sheepshead: *Archosargus probatocephalus*, and Gulf toadfish: *Opsanus beta*). Gill net collections were

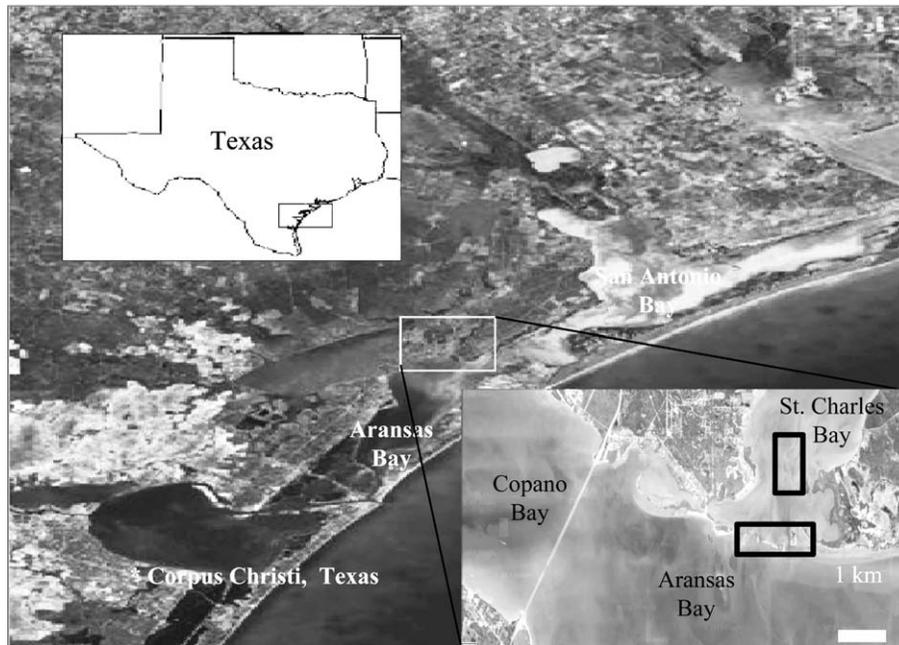


Fig. 1. Map showing location of study sites for both the long-term data set and field study. The small inset map of Texas has a box around the area of coastline where San Antonio and Aransas Bays are located. The larger map shows the relationship between our field site, boxed in white, and the long-term data set sites. The inset map shows our field sites with the oyster reefs sampled boxed.

conducted in two 3 month sets: April–June and September–November during each year. Crab abundance, primarily composed of blue crabs (*Callinectes sapidus*), stone crabs (*Menippe adina*), and mud crabs (*Panopeus* spp.), was analyzed from benthic trawls that were conducted monthly.

Gill net and bay trawl data sets were analyzed separately because these gear types target different kinds of species, and preliminary analysis indicated that gear type significantly affected collections. To determine the importance of each abiotic factor measured by TPWD, the data sets were analyzed using multiple regression. In this analysis, each abiotic factor measured by TPWD (salinity, temperature, dissolved oxygen, and turbidity) was compared to the abundances of fishes and crabs in each collection. In addition to multiple regression analysis, ANOVA was also used because turbidity effects do not function linearly. Abundances were compared above and below 30 nephelometric turbidity units (NTU) because this level is known to alter visual acuity in marine organisms (Minello et al. 1987; Sweka and Hartman 2003), and because most of the turbidity values in the data set were less than 25 NTU and above 40 NTU. Gill net surveys were analyzed with a two-way ANOVA with turbidity (low vs. high) and season (spring vs. fall) as fixed factors because gill net sampling was conducted seasonally. Trawl surveys were analyzed using a one-way ANOVA with turbidity as a fixed factor. Season was not included as a factor because trawls were conducted monthly throughout the year (Sokal and Rohlf 1995).

*Study site*—Natural oyster reefs (*Crassostrea virginica*) near Goose Island State Park in St. Charles Bay, Texas, were selected for an empirical study on the effects of

turbidity (Figs. 1, 2). Our goal was to select oyster reefs that differed in turbidity but otherwise experienced similar abiotic conditions. Turbidity was monitored intermittently from April 2010 to September 2012 using Hydrolab™ Data Sondes to determine areas where turbidity is routinely low (< 30 NTU) vs. high (> 30 NTU). These instruments measured turbidity, salinity, temperature, dissolved oxygen, and chlorophyll *a* (Chl *a*). The purpose of measuring Chl *a* was to ascertain the causes of turbidity in our field sites. Turbid water combined with increased levels of Chl *a*

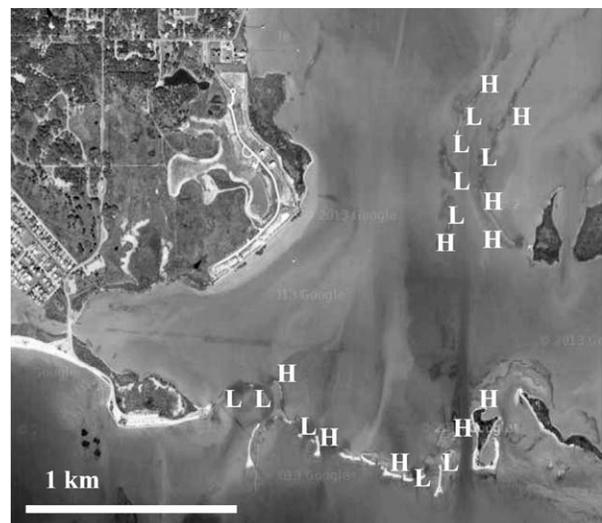


Fig. 2. Map of our field sites with high- (H) and low-turbidity (L) sites labeled.

Table 1. Abiotic conditions measured in field sites with low and high levels of turbidity.

	Low		High		<i>p</i> -value
	Average	Range	Average	Range	
Temperature	27.89	25.82–31.47	29.08	25.81–32.05	0.08
pH	8.29	8.16–8.65	8.35	7.97–11.14	0.61
Salinity	30.3	14.52–37.82	25.42	13.79–40.58	0.06
Dissolved oxygen	6.48	6.14–7.82	6.00	5.5–6.69	0.07
Chlorophyll <i>a</i>	9320.3	0.9–41,395.4	14,600.3	0.01–14,0851.9	0.68

suggests turbidity is biotic in nature, while low Chl *a* levels in high-turbidity conditions suggest abiotic factors such as suspended sediments are blocking light and increasing turbidity. Ten sites were selected that typically had low turbidity levels, and another 10 were selected that had high turbidity levels, although turbidity in all sites could vary from 0 to over 100 NTU depending upon wind speed and direction. Field observations suggested that turbidity levels varied based on local features such as flow patterns along the reef or proximity to bare, muddy substrate. Chl *a* levels were similar between sites, indicating that turbidity was caused by suspended sediments and not by plankton, which is consistent with field observations in this area (Table 1). Besides turbidity, other abiotic features had similar ranges and were not different among study sites (Table 1). All abiotic conditions recorded in our field sites were within known tolerance limits of oysters.

We also selected field sites that had similar habitat structure, harvesting pressure, and oyster recruitment to avoid biasing our study by comparing degraded reefs to more healthy reefs. That is, on degraded oyster reefs, turbidity might increase because of a low number of oysters filtering the water or a transition from reef to mud bottom, and thus turbidity would be a consequence of reef degradation and not a cause for differences in food webs. With this in mind, we selected field sites in St. Charles Bay that are closed to oyster harvesting. St. Charles is a shallow bay, and our study reefs were ~ 0.5 m in depth. The oyster reefs within this bay are low relief and are a mix of oyster clumps and loose shell. Habitat structure in our study sites was qualitatively similar and was typical of other shallow reefs in the study area.

Within each study site, we measured oyster recruitment and adult oyster growth, and we compared these factors between low- and high-turbidity sites using a *t*-test. Adult oysters collected from neighboring Copano Bay were planted within field sites and allowed to grow for 5 months. Once adult oysters were collected, the number of spat that had settled onto the adults was quantified, and several metrics were measured. Adult oysters were used because

they do not alter their growth in response to predators (Johnson and Smeets 2012), and our goal was to assess if growth differences between low- and high-turbidity sites were related to abiotic factors or food availability. Adult oysters did not differ in length, wet weight, and adductor size (*t*-test:  $t = 0.86$ , degrees of freedom [df] = 48,  $p > 0.05$ ;  $t = 1.62$ , df = 48,  $p > 0.05$ ;  $t = 0.90$ , df = 48,  $p > 0.05$ ) for low- vs. high-turbidity sites. In addition, there were no differences in oyster recruitment between low- and high-turbidity sites (*t*-test:  $t = -0.35$ , df = 48,  $p > 0.05$ ; Table 2). To assess oyster reef-associated species composition, each site was sampled using a modified throw trap (Rozas and Minello 1997; see detailed methods below). Differences in communities between low- vs. high-turbidity sites were compared with an analysis of similarity (ANOSIM) using PRIMER™. ANOSIM indicated that sites were similar in species composition ( $R = -0.005$ ,  $p = 0.44$ ). However, the relative abundance of species was different among study sites, a pattern described in detail below. Thus, our field sites were appropriate for testing the effects of turbidity on trophic interactions among reefs.

*Field sampling*—Because crab abundance was affected by turbidity in TPWD samples, we performed field sampling to ascertain the effects of turbidity on mud crab abundance. Mud crabs are an important intermediate predator on oyster reefs (O'Connor et al. 2008) but are not often caught within TPWD bay trawls. Within each study site, a 0.25 m<sup>2</sup> area was cleared of oyster clumps and shells. With the clearing, a 0.25 m<sup>2</sup> tray containing 25 liters of sun-bleached oyster shells was placed. Trays were anchored within natural reefs at each of our low- and high-turbidity sites. The trays were deployed in the field in March, and natural recruitment occurred until tray retrieval in August; sampling was performed in 2010 and 2011.

*Collection and analysis*—In August, all mobile organisms were collected from the trays using a modified throw trap (Rozas and Minello 1997), placed in ethanol, and

Table 2. Oyster growth and settlement data.

	High		Low		<i>p</i> -value
	Average	Range	Average	Range	
Length (mm)	55.1	39.5–73.2	57.4	40.9–82.6	0.39
Wet weight (g)	3.5	2.1–5.5	4.0	2.3–6.8	0.11
Adductor diameter (mm)	10.4	7.3–14.1	10.9	6.9–14.0	0.37
Juvenile oyster recruitment	0.4	0–5	0.3	0–1	0.72

transported to the laboratory for sorting, identification, measurement, and enumeration. This method of sampling is not an effective way to sample highly mobile organisms such as large fish and blue crabs, but it does allow the small cryptic species not commonly caught by TPWD to be sampled. From these samples, we calculated the number of mud crabs (*Panopeus herbstii*, *Eurypanopeus depressus*, and *Panopeus turgidus*) found on each tray. Large (> 10 mm) and small (< 8 mm) mud crabs were also analyzed separately because of differences in foraging preferences at different sizes (Johnson and Smee 2012). Smaller mud crabs tend to be scavengers and primarily consume dead bivalves and conspecifics, whereas larger mud crabs are able to crush bivalve prey including oysters. The numbers of mud crabs were compared using a blocked ANOVA, with year as the block and turbidity as the main factor (Sokal and Rohlf 1995).

*Mud crab predation trials*—Predation on mud crabs was measured by haphazardly placing groups of five tethered mud crabs (10–20 mm) in 10 low-turbidity sites and in 10 high-turbidity sites and recording the number of mud crabs consumed within 24 h. Hydrolab Data Sondes were deployed with each group of crabs to record turbidity for the duration of the trial. Turbidity for these trials was found to be either very low (0–20 NTU) or very high (50–200 NTU), maintaining earlier documented differences in turbidity between sites. Crabs were placed on 15-cm-long monofilament line glued to their carapaces and tied to a small metal stake inserted into the sediment. In preliminary experiments, crabs were not injured or killed by tethering, although tethers likely increased predation on crabs in the field. Within groups, crabs were arranged ~ 1 m apart to avoid interference. Groups of crabs were spaced ~ 50 m apart on naturally occurring oyster reefs within the sites. After 24 h, the number of crabs eaten and the condition of any crab parts left on the tether for each group were recorded. We found that tethered crab carapaces remained on the tethers when the tethered crabs were consumed by other crabs but not by fish (J. Lunt pers. obs.; Fernandez et al. 1993). Thus, by counting the number of crab carapaces remaining, we were able to estimate mortality caused by crab vs. fish predators in each site. Mud crabs survived in the field after tethering when protected by cages in preliminary experiments, indicating that natural mortality did not bias our results. We were unable to perform all replicates simultaneously, and so we instead deployed tethered crabs simultaneously in both low- and high-turbidity sites on several dates in June–August of 2011. The number of crabs consumed was compared using a blocked ANOVA with turbidity as a fixed factor (low vs. high) and sampling date as the blocking factor (Sokal and Rohlf 1995). The number of carapaces recovered was compared with a chi-square test (Sokal and Rohlf 1995).

*Juvenile oysters*—To determine the effects of turbidity on juvenile oysters, oyster growth and oyster mortality resulting from predation were measured. Juvenile oysters were purchased as larvae from a local supplier and settled onto oyster shells (for methods, see Johnson and Smee

2012). The juvenile oysters used in this experiment were raised in the laboratory until reaching a size of 10–20 mm across, as at this size the oysters are most vulnerable to consumers and are still large enough to see and count (Lenihan 1999; Johnson and Smee 2012). The number of newly settled oysters was thinned so that 15 juvenile oysters were present per shell. The oyster shell containing the juvenile oysters was covered with Vexar mesh to exclude predators and attached to a rebar pole that was 1.0 m long and inserted ~ 0.90 m into the sediment to ensure it was well anchored and of similar height to other adjacent oyster shells. To assess growth parameters, 10 shells, each containing 15 newly settled oysters, were placed within each site for 2 months. Predation rates were assessed by deploying 10 shells, each containing 15 newly settled oysters, in low- and in high-turbidity sites for 1 week in July and again in August. Juvenile oysters protected by a Vexar mesh cage (1.0 cm<sup>2</sup> openings) survived in preliminary trials (J. Lunt unpubl. data), and thus we attributed oyster mortality to predators.

*Collection and analysis*—Juvenile oysters devote more resources to shell growth in response to predators, which decreases growth of soft tissue and may lower their fecundity (Newell et al. 2007; Johnson and Smee 2012). To determine overall growth and the percentage of growth juvenile oysters were devoting to shell vs. soft tissue, the juvenile oysters were collected from the field and then removed from the larger shell onto which they were initially settled. Then, we placed them into a conventional drying oven at 90°C for 2 d, and the dry mass of each individual was recorded. This provided a measure of the shell and soft tissue weight combined. The oysters then were transferred to a muffle furnace and baked for 2 h at 500°C to remove all soft tissue and were reweighed to obtain weights of the shell only (ash-free dry mass). The percent of new growth allocated to shell was found by dividing the ash-free weight by the total dry weight. Percent new shell growth was analyzed with a one-way ANOVA with turbidity as a fixed factor. For predation trials, a blocked one-way ANOVA with oyster deployment date as the blocking factor and turbidity as a fixed factor was used to compare the number of surviving juvenile oysters (Sokal and Rohlf 1995). This technique provides a conservative estimate of shell weight because it removes some organic material from the shell, which also increases in response to some predators (Newell et al. 2007).

## Results

*TPWD analysis*—Significant relationships were found between species abundance and turbidity, salinity, and temperature in the regression models, but only the effects of turbidity were significant for both gill net and bay trawl surveys. Within gill net samples, salinity and turbidity predicted abundance (turbidity:  $F_{1,3314} = 5.92$ ,  $p = 0.0150$ ; salinity:  $F_{1,3314} = 15.03$ ,  $p = 0.0001$ ;  $R^2 = 0.0057$ ). In bay trawl samples, turbidity and temperature were the factors accounting for abundance (turbidity:  $F_{1,7939} = 72.46$ ,  $p < 0.0001$ ; temperature:  $F_{1,7939} = 13.10$ ,  $p = 0.003$ , respectively;  $R^2 = 0.0109$ ). Dissolved oxygen was not found to be

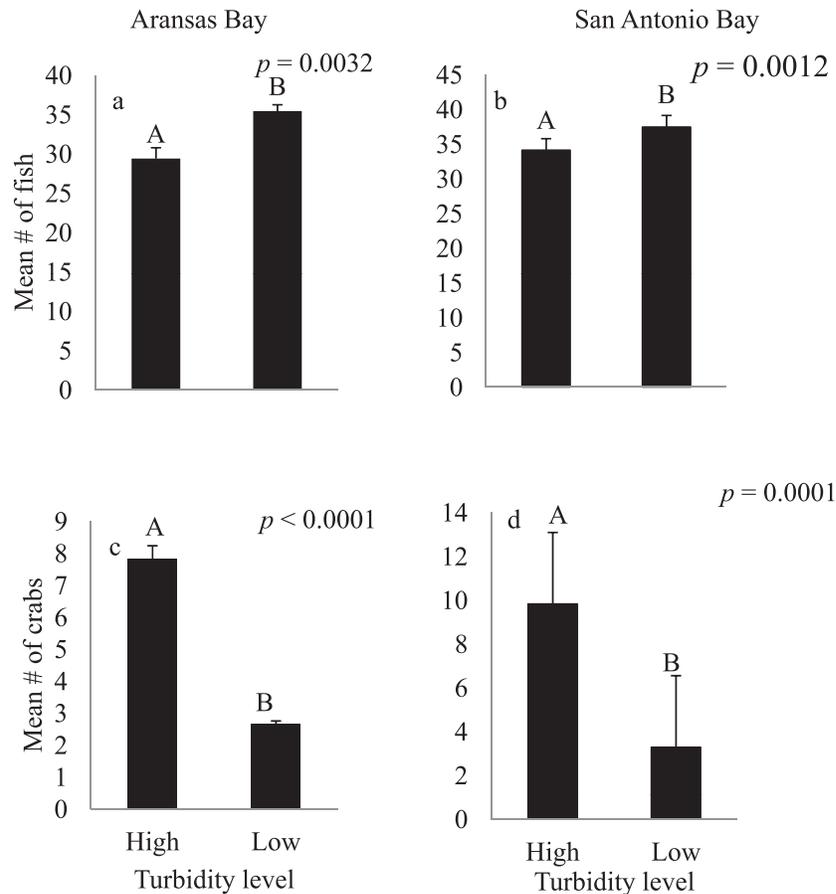


Fig. 3. Mean + standard error number of organisms collected in low- vs. high-turbidity areas by TPWD from 1991 to 2008. Mean low turbidity was 10 NTU. Mean high turbidity was 60 NTU. Letters denote significant differences based upon ANOVA. Fish were collected by gill nets, and crabs were collected by trawls. (a) Fish abundance in Aransas Bay: 48% of fish were black drum, 0.02% of fish were Gulf toadfish, 47.18% were red drum, and 4.8% of fish were sheepshead. (b) Fish abundance in San Antonio Bay: 47% of fish were black drum, 45% of fish were red drum, and 8% of fish were sheepshead. (c) Crab abundance in Aransas Bay: 98.5% of crabs were blue crabs, 1% were stone crabs, and 0.5% were mud crabs. (d) Crab abundance in San Antonio Bay: 97.5% of crabs were blue crabs, 0.5% were stone crabs, and 2% were mud crabs. Note that mud crabs are not targeted or effectively collected by TPWD sampling protocols.

a significant factor in either gill net or bay trawls, and dissolved oxygen levels were not found to be hypoxic in the data set.

When considered as a fixed factor in our ANOVA model at a level known to disrupt visual acuity in fishes, turbidity had a significant effect on both crab and fish abundance in Aransas and San Antonio Bays (Fig. 3). Although 30 NTU was selected as the boundary for low vs. high turbidity, the majority of turbidity measurements within the data set were less than 25 NTU (low) or higher than 40 NTU (high). Gill net surveys revealed higher abundances of fish when turbidity was below 30 NTU (Aransas:  $F_{1,1631} = 8.72$ ,  $p = 0.01$  [Fig. 3a]; San Antonio:  $F_{1,1701} = 10.55$ ,  $p = 0.0012$  [Fig. 3b]), and gill nets collected few crabs. Season was not a factor in fish abundance (Aransas:  $F_{1,1631} = 3.12$ ,  $p = 0.07$ ; San Antonio:  $F_{1,1701} = 0.12$ ,  $p = 0.73$ ). There was no interaction between season and turbidity for fish

abundance levels measured with gill nets (Aransas:  $F_{1,1631} = 0.56$ ,  $p = 0.45$ ; San Antonio:  $F_{1,1701} = 2.33$ ,  $p = 0.12$ ). In trawls designed to target crabs and other benthic species, more crabs were collected when turbidity exceeded 30 NTU (Aransas:  $F_{1,3800} = 154.23$ ,  $p < 0.001$  [Fig. 3c]; San Antonio:  $F_{1,4281} = 83.54$ ,  $p < 0.001$  [Fig. 3d]).

*Field sampling*—Small mud crabs (*Panopeus herbstii*, *Panopeus turgidus*, and *Eurypanopeus depressus*; < 8 mm carapace width) were ubiquitous in the study site, and their abundance was not affected by turbidity ( $F_{2,49} = 0.93$ ,  $p = 0.35$ ; Fig. 4a). However, the abundance of large mud crabs (> 10 mm) was higher in sites with high turbidity ( $F_{2,49} = 2.2$ ,  $p = 0.03$ ; Fig. 4b). Year was a significant blocking factor for both small and large mud crabs ( $F_{2,49} = 2.18$ ,  $p = 0.03$ ;  $F_{2,49} = 2.05$ ,  $p = 0.04$ ; respectively), indicating variation in mud crab abundance between years.

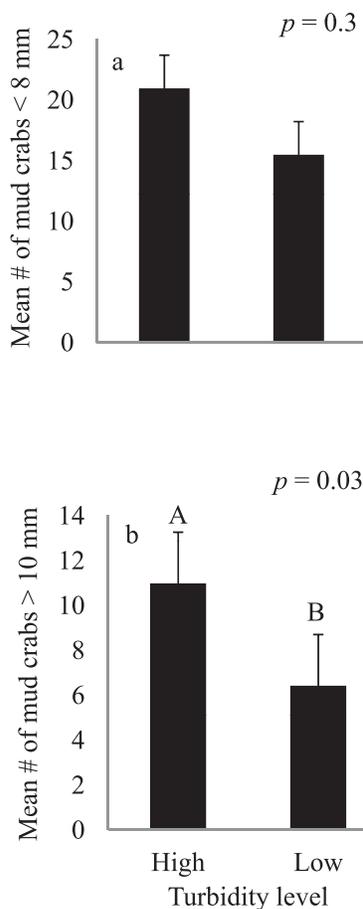


Fig. 4. Mean + SE number of mud crabs collected in low- vs. high-turbidity areas of St. Charles Bay. Letters denote significant differences based upon ANOVA. (a) All mud crabs. (b) Large mud crabs (> 10 mm carapace width). Letters denote significant differences.

*Mud crab predation trials*—Tethered mud crabs were more likely to be eaten in sites with high turbidity ( $F_{1,30} = 5.43$ ,  $p = 0.02$ ; Fig. 5a). Data were log transformed to meet normality assumptions. Date was a significant blocking factor in the ANOVA model ( $F_{1,30} = 6.09$ ,  $p < 0.001$ ), indicating variation in predation pressure over time. More mud crab carapaces were found on tethers in high-turbidity sites ( $\chi^2_{1,30} = 12.78$ ,  $p = 0.003$ ; Fig. 5b), suggesting that crab predation was more prevalent in areas where crabs were abundant.

*Juvenile oysters*—Predation on oysters was not different in low- vs. high-turbidity sites ( $F_{1,50} = 0.21$ ,  $p = 0.64$ ; Fig. 6a). Date was a significant blocking factor in the ANOVA model, indicating temporal variation in oyster predation ( $F_{2,50} = 19.78$ ,  $p < 0.001$ ). In contrast to oyster mortality, oyster growth was different in low- vs. high-turbidity sites. In sites that were more turbid, oysters devoted a higher proportion of the new growth toward shell ( $F_{1,85} = 29.45$ ,  $p < 0.001$ ; Fig. 6b), a response known to occur in response to crab predators.

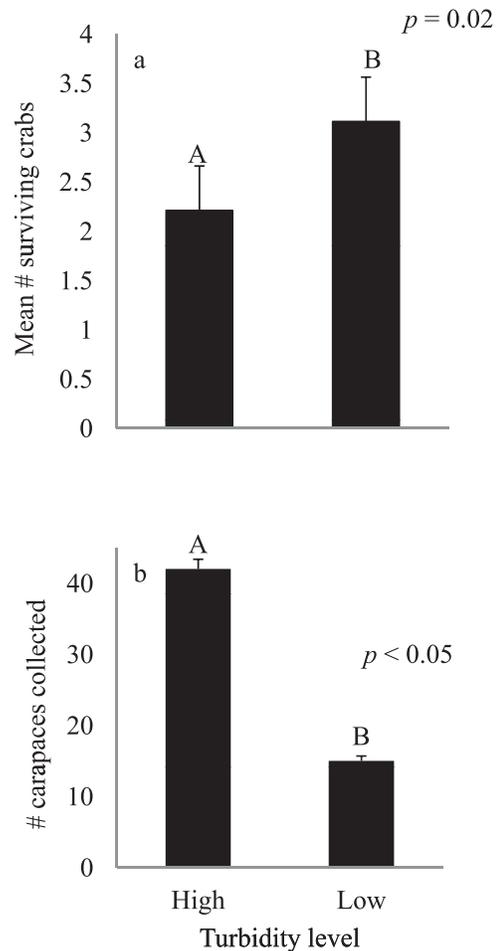


Fig. 5. (a) Mud crab survivorship between high and low turbidities in tethering experiments in St. Charles Bay. (b) Number of carapaces retrieved between high and low turbidities in tethering experiments in St. Charles Bay. Carapace presence is indicative of predation by crabs. Letters denote significant differences.

## Discussion

Scaling up context-dependent interactions to explain broad spatial and temporal patterns in natural communities requires a thorough understanding of how biotic and abiotic factors influence interacting organisms. This can be particularly challenging when biotic factors are important community-structuring agents but are strongly affected by abiotic conditions that enhance or attenuate biotic effects such as predation (Smee et al. 2010). Turbidity is known to affect estuarine communities through limiting primary productivity (Kuo and Lin 2010), but our findings indicate that turbidity can also modify food webs by altering predatory interactions. Turbidity affects vision and alters the ability of visual predators such as fish to effectively forage (Minello et al. 1987). This effect is analogous to how hydrodynamics affect chemoreception of marine organisms (Menge and Sutherland 1987; Weissburg et al. 2003), changing predatory interactions by modifying the sensory environment (Dusenbery 1992).

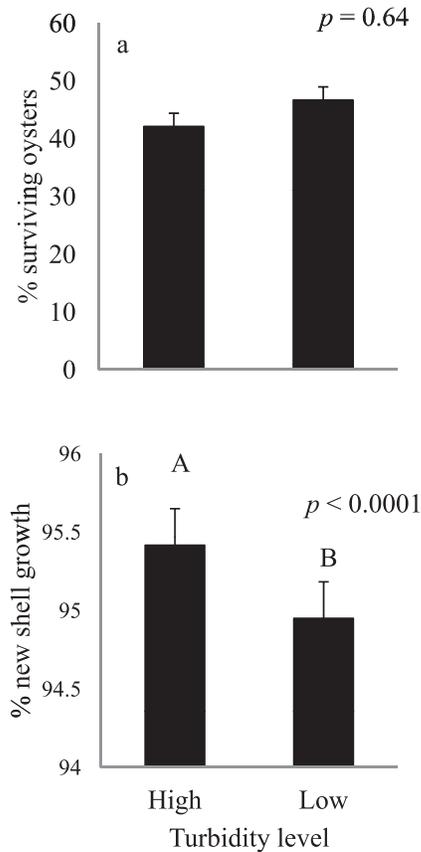


Fig. 6. (a) Percent of surviving oysters from oyster predation experiments in St. Charles Bay. (b) Percent of growth dedicated to new shell in juvenile oysters protected from predation in St. Charles Bay. Letters denote significant differences.

In the TPWD data set spanning 18 yr, we found fish were more abundant when turbidity was below 30 NTU, and in our field study, fish preyed more heavily on tethered mud crabs when turbidity was low. Fish rely on visual cues when foraging, and may avoid turbid areas that would decrease their perceptive abilities. Turbidity likely interferes with their ability to forage and to detect and avoid their own predators. In contrast to fish, crabs were more abundant when turbidity exceeded 30 NTU both in the TPWD data set and on oyster reefs in St. Charles Bay. Predation on tethered mud crabs and predation on mud crabs by other crabs were also higher in highly turbid areas. Turbidity may not alter crab foraging since crabs rely on chemoreception (Weissburg et al. 2003), and their ability to find food would not be expected to be compromised by turbidity.

While the decline in fish abundance in higher turbidity was seemingly small in the long-term data set, our findings indicate that turbidity altered predation rates as well as having indirect effects that propagated to lower trophic levels. Specifically, higher turbidity was associated with less fish predation on tethered mud crabs and higher crab abundances, which subsequently caused a change in the growth of newly settled oysters. These widespread effects of turbidity indicate that it can be an important community

regulator in estuarine systems. In this regard, a change in fish abundance may mimic effects caused by overfishing. A decline of apex predators is known to have drastic effects on terrestrial and aquatic food webs, and factors like turbidity that alter top-down forcing by limiting the foraging ability of top predators may produce similar effects.

In addition to turbidity, multiple regression analysis indicated that temperature and salinity were also important factors in this system, and these factors are well known to affect estuarine organisms (Day et al. 2009). We found significant relationships between turbidity and diversity, but our  $R^2$  values were low. Low  $R^2$  values are caused by substantial variability within the data set and possible interactions among turbidity, salinity, and temperature. It is noteworthy that the  $R^2$  values for turbidity were similar to those of salinity and temperature, factors known to be important in governing estuarine systems (Day et al. 2009). The data set spanned 18 yr and included measurements across two large bays in multiple subtidal habitats (e.g., sea grass, oyster reef, mud flat). Conditions such as wind speed and direction, bottom composition, and water depth were not consistently recorded, and sampling in different habitats in different conditions likely contributes to large variation in the TPWD data. In large data sets such as this, significant  $p$  values may be more easily detected because of large sample sizes. Yet, we did not find significant effects of dissolved oxygen in either gill net or trawl data sets nor of temperature on gill net samples or salinity on trawl samples. Turbidity was the only significant factor in regression analysis on both gill net and trawl data, and its  $R^2$  value is similar to that of other abiotic conditions (e.g., salinity, temperature) in this data set known to affect abundance and distribution of estuarine species.

Besides variability within the TPWD data, low  $R^2$  values for turbidity found in regression analysis may also be caused by nonlinear effects of turbidity on species abundance. That is, an increase in turbidity may not have a linear effect on vision. In high-turbidity ranges, the effects of turbidity are likely to be asymptotic once vision is obscured. Thus, turbidity between 75 and 1000 NTU could have similar effects on visual predators because any turbidity values within this range would reduce visual ranges to near 0. In this scenario, a significant relationship between species abundance and turbidity could be observed, but  $R^2$  values would be low because of similar effects of turbidity on fish abundance across a large range of high-turbidity levels. Fish may elect to leave an area when turbidity reaches a given threshold that sufficiently reduces their visual ability. This threshold likely varies between species, further contributing to variation in relationships between turbidity and fish abundance. It is important to note that using turbidity as a fixed factor in an ANOVA indicated a significant effect of turbidity on fish and crab abundance and that the results from our field experiments indicate that turbidity can significantly affect the abundance of organisms, predation rates, and oyster growth.

Temperature affected species abundance within bay trawl samples but not gill net samples, possibly because

trawls were taken monthly throughout the year, while gill net surveys were conducted in the spring and fall when temperatures are more similar. The effect of salinity in gill net samples but not in bay trawl samples may be attributed to highly mobile organisms (fish) being able to seek out preferred salinities, while benthic species are either less mobile or more tolerant to salinity changes. Regardless, turbidity was the only factor to affect species abundance across gear types, which is indicative of its importance in shaping estuarine communities. Our experiments in St. Charles Bay further demonstrate the significant effects on turbidity on species interactions and abundances and, combined with the long-term data set, suggest that turbidity, like temperature and salinity, should be considered an important factor affecting estuarine species.

Over an 18 yr period, fish (primarily red drum) were more abundant in low-turbidity areas compared to highly turbid areas, and crabs (primarily blue crabs) were found to have the opposite pattern. Initially, we were concerned that sampling artifacts could bias our results if gear efficiency varied between turbidity levels. Two observations suggest this is not the case. First, fish abundance was higher in less turbid conditions. Since fish are visual, we predicted that fish might avoid the sampling gear in clear water, but we saw the opposite pattern, with fish abundance greatest when turbidity was less than 30 NTU. We also found a significant, negative relationship between fish abundance and turbidity over the long term. Second, blue crab and mud crab abundance was higher in more turbid water in the 18 yr data set and in our field collections using modified throw traps on oyster reefs. Thus, sampling crabs across different turbidity levels using different gear types yielded similar results.

Turbidity affected the distribution of mud crabs (*Panopeus* spp.) that were larger than 10 mm. Large mud crabs were more abundant in highly turbid conditions, perhaps because turbidity affords them some protection against fish predators that hunt them primarily using visual cues (Snickars et al. 2004). Small mud crabs (< 8 mm carapace width) were abundant and ubiquitous in the field, and turbidity had no effect on their distribution. Smaller mud crabs can take advantage of refuge spaces within the shell matrix of an oyster reef, thereby avoiding predation by limiting interactions between themselves and larger predators. This predator avoidance strategy would allow them to avoid both crab and fish predators regardless of turbidity regime. In contrast, larger mud crabs require larger refuges, which are more limited. Because of their higher size, they are more apparent to consumers. They also consume more food and forage over larger areas to meet energetic requirements. Turbidity may provide refuges for these larger mud crabs that have limited refuge space within the shell matrix of oyster reefs and are likely more apparent to visual predators (Meyer 1994). More work is needed to test these hypotheses.

Predation on mud crabs in high turbidity was attributed more often to crab than fish predators, which corresponds to the higher abundance of crabs in turbid conditions. We cannot definitively determine which crabs are the cause of the increased predation, though it is likely a combination of

species, including other mud crabs, which are cannibalistic and readily consume each other (Lunt pers. obs.; Reames and Williams 1984). Since mud crabs were more abundant in turbid conditions, we anticipated that predation on tethered mud crabs would be lower in these conditions. We offer three possible mechanisms for this counterintuitive result. First, large mud crabs may find a refuge from visual predators in highly turbid conditions but increase their vulnerability to chemosensory predators by congregating in turbid areas. Crabs are antagonistic, and an increase in crab numbers would predictably lead to a more frequent encounter rate and higher predation rates by crabs. Alternatively, the presence of fish in sites with low turbidity may have suppressed crab foraging and caused tethered crabs to remain in refuges and forgo foraging opportunities, thereby reducing predation on the tethered crabs (Grabowski and Kimbro 2005). The effects of turbidity would also be influenced by predator type. Actively hunting predators such as red drum would not increase their chances of encountering prey items in turbid conditions as the encounters would become random (Van de Meutter et al. 2005). Conversely, lie-in-wait predators may benefit from reduced antipredator behavior in turbid conditions and consume more prey items. For example, southern flounder consumed more brown shrimp in elevated turbidity because brown shrimp were more active in high-turbidity treatments (Minello et al. 1987).

Although turbidity affected the abundances of fishes and crabs and predation on crabs, it did not alter predation on juvenile oysters. We attribute this finding to the omnivorous nature of predators in the system. Black drum, sheepshead, and blue crabs are common in the study area and readily consume oysters, and thus oysters are likely to be eaten at both low- and high-turbidity levels by different types of predators. Turbidity did affect juvenile oysters indirectly by altering their growth. Juvenile oysters allocated a higher percentage of their energy toward shell growth in sites with high turbidity, which had higher numbers of large mud crabs. Juvenile oysters are known to produce heavier shells in response to large mud crabs at a cost of producing less soft tissue (Newell et al. 2007; Johnson and Smee 2012), and a higher abundance of mud crabs in turbid sites likely accounts for the differences in resource allocation between juvenile oysters.

We attributed heavier shells to increased predation risk rather than a direct effect of turbidity for several reasons. First, juvenile oysters are known to produce heavier shells in response to large mud crabs (Newell et al. 2007; Johnson and Smee 2012), which were more abundant in more turbid sites. Second, turbidity in this system is caused by sediments and not by plankton, which suggests food differences for oysters among study sites is not affecting growth rates (Table 1). Finally, adult oysters of similar initial size that were planted in these sites for several months did not differ in growth (Table 2). Adult oysters do not alter shell growth in response to mud crabs (Johnson and Smee 2012), and any growth differences would have been caused by either abiotic conditions or food availability. Since we did not find growth differences in the adult oysters, we attribute the changes in shell growth found in

juvenile oysters to differences in crab abundance caused by increased turbidity.

The indirect effect of increased shell growth in turbid water may have long-term negative effects on oyster populations because of decreases in fecundity caused by growing thicker shells. This decrease in fecundity would limit the growth of oyster reefs in continually turbid areas, compounding problems associated with harvesting and potentially hindering restoration efforts. Plastic responses to predators, such as an increase in shell growth seen in juvenile oysters, are universally associated with a cost; otherwise organisms would always make the most predator-resistant morphology. More work is necessary to determine the degree to which fecundity is affected and the way in which the tradeoff between shell and somatic growth in response to predators influences oysters long term.

Turbidity decreases perceptible ability and reduces predator efficiency (Minello et al. 1987; Liljendahl-Nurminen et al. 2008), although the effect is species dependent (Minello et al. 1987). Visual predators are often less effective in higher turbidity because of reduced reactive distances (Minello et al. 1987; Liljendahl-Nurminen et al. 2008). Nonvisual predators may not experience this decrease in efficiency because they rely on other cues (e.g., chemical) to find prey (Ohata et al. 2011). In this respect, turbidity acts similarly to other abiotic conditions in mediating predatory interactions. For example, chemosensory foragers such as crabs are less effective predators in fast and turbulent flows, while other predators such as knobbed whelks are more efficient in faster flow conditions (Powers and Kittinger 2002). Turbulent flows can also affect the responses of prey to consumers, increase their vulnerability, and alter the prevalence of nonlethal predator effects (Smee et al. 2010; Large et al. 2011). Turbidity may mediate the predatory efficiency of visual predators analogous to the way in which flow mediates that of chemosensory predators. Moderate turbidity may enhance feeding efficiency of visual predators by providing increased contrast (Liljendahl-Nurminen et al. 2008), though past a certain level, visual acuity and feeding efficiency will decrease. Turbidity effects have been shown to be species dependent (Minello et al. 1987; Liljendahl-Nurminen et al. 2008), and the lack of consensus on a threshold value for “high” turbidity may support this continuum of predatory effects. Species may utilize multiple sensory mechanisms to compensate for a reduction in visual capability in elevated turbidity (Dusenbery 1992).

Turbidity is increasing in coastal environments worldwide because of anthropogenic factors (Sanden and Hakansson 1996). Nutrient loading in coastal areas leads to eutrophication of coastal waters, which may result in phytoplankton blooms that increase turbidity. In addition to nutrient loading, human removal of coastal habitats such as oyster reefs, sea grasses, and salt marshes reduces coastal stability and increases erosion (Grabowski and Peterson 2007), which may also increase turbidity. As turbidity increases, oyster fecundity and oyster populations may decline via indirect mechanisms. The interactions between turbidity and oyster reefs are complex and require further investigation.

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