

TURBIDITY AND WAVE ENERGY AFFECT COMMUNITY COMPOSITION AND
TROPHIC INTERACTIONS

A Dissertation

by

JESSICA LUNT

BS, University of West Florida, 2008

Submitted in Partial Fulfillment of the Requirements for the Degree of

DOCTOR OF PHILOSOPHY

in

MARINE BIOLOGY

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August 2014

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This dissertation meets the standards for scope and quality of
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ABSTRACT

Abiotic variables are well known community regulators and can strongly influence species distributions when they are outside of a species physiological tolerance limits. However, environmental variables within tolerance limits may also alter species distributions, morphology, predator-prey interactions, and influence the structure and function of communities. The purpose of this study was to determine how abiotic variables (notably turbidity) alter diversity, species distributions and abundances, predation rates on and species morphology.

Texas Parks and Wildlife Department Fisheries Independent Survey Data from 1991-2008 were used in addition to field surveys of St. Charles Bay to determine the effects of turbidity on fish and crab diversity and abundance. Feeding assays were conducted in the field using groups of 5 mud crabs and 10 juvenile oysters to assess feeding rates in high and low turbidity. Juvenile oysters were also allowed to grow in the field to test the effects of turbidity on oyster growth. In addition, the effects of wave energy on oyster reef species composition and size were assessed using field surveys.

I found that turbidity affects top-down control and biodiversity in estuaries and has similar effects to salinity and temperature. Elevated turbidity reduced fish diversity and abundance ($p < 0.01$), while increasing the diversity and abundance of crabs ($p < 0.01$). Predation by visual fish predators was also reduced in elevated turbidity ($p = 0.02$), which leads to an increase in the abundance of crabs and increased predation on mud crabs in high turbidities ($p = 0.03$). Juvenile oysters respond to increased crab abundance by growing heavier shells, which may lower fecundity. In laboratory assays, increased turbidity decreased the predation

efficiency of visual predators (fish) but not of chemosensory predators (crabs). Differences were found between wave exposed and wave protected areas. Areas with higher wave energy had fewer species ($p < 0.001$) and the average size of species was smaller.

This research identifies turbidity as an important variable within estuarine systems and extends the effects of wave energy from rocky intertidal systems to oyster reef communities. Both of these variables should be considered for effective management and restoration of estuarine communities.

DEDICATION

In dedication to all the people who said I should not be or could not be a Marine Biologist.

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I thank my Chair, Dr. Lee Smee for being a supportive and encouraging mentor through this long process. For never saying no when I needed to talk about data, writing, teaching or life in general. He has taught me what it means to be a mentor and a scientist. He was instrumental in the tough transition from student to professional and helping me learn to argue my own case and present my own interpretations of and ideas for research. He tested my patience and my first aid/responder training but I hope to be half as good an advisor to my own students as he was for me.

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INTRODUCTION

Predation or top-down forces have long been appreciated as important community regulators (Paine 1966, Estes and Palmisano 1974, Carpenter et al. 1985, Schmitz et al. 1997, Menge 2000, Trussell et al. 2003). Predators in marine (Paine 1966, Estes and Palmisano 1974, Estes et al. 1998, Menge 2000), freshwater (Carpenter et al. 1985), and terrestrial (Schmitz et al. 1997) environments may affect prey populations and communities by consuming lower trophic levels (lethal effect, Estes and Palmisano 1974, Carpenter et al. 1985, Sih et al. 1985) or by altering prey traits including behavior, morphology, or habitat use (nonlethal effect, Turner and Mittelbach 1990, Schmitz et al. 1997, Trussell et al. 2003). Predator-prey interactions may alter energy flow, community structure, and the importance of competitive interactions through both lethal and nonlethal effects. The effects can cascade through communities and affect multiple trophic levels by causing changes in behavior, density, and distributions of lower trophic levels (e.g., Sih et al. 1985, 1998, Menge 2000, Werner and Peacor 2003).

The ability of predators and prey to detect one another likely plays a crucial role in the outcome of predatory interactions and the resulting indirect predator effects in food webs (Powers and Kittinger 2002). The ability to perceive a potential consumer or prey organism before being detected offers an advantage which likely determines whether predators or prey prevail in a given encounter (Powers and Kittinger 2002, Smee et al. 2010). Lethal or consumptive effects (CEs) should be prevalent when predators are successful foragers, and this should occur when predators possess a sensory advantage over prey. Likewise, prey can successfully avoid predators when they have a sensory advantage causing CEs to decline. However, frequent reactions of prey to the presence of predators will increase the occurrence and importance of nonlethal or non-consumptive effects (NCEs). In situations where both predators

and prey are affected by the same environmental conditions, and conditions minimize the sensory abilities of both species, the effects of predators on prey populations may shift from a combination of direct and indirect effects to exclusively direct, lethal effects (van de Meutter et al. 2005). For example, in freshwater damselfly larvae were more active in turbid versus clear water and in the presence of a fish predator the damselfly larvae were larger in turbid treatments (van de Meutter et al. 2005). However, these results are based solely on visual cues and have neglected other sensory systems. For example, predators that hunt by chemoreception may be less affected by increases in turbidity than visual predators (Meager et al. 2005).

Turbidity is increasing in coastal systems because of erosion and nutrient input (Khan and Ali 2003, Rabalais 2005), but the effects of turbidity on food webs have not been well-studied. In freshwater systems, community structure differs dramatically between clear and turbid lakes by influencing predation rates of fish on prey populations (Moss 1990, Scheffer et al. 1993, Scheffer 1998, van de Meutter et al. 2005). In these studies, turbidity as low as 20 nephelometric turbidity units (NTU), a measure of light penetration, can diminish visual acuity and decrease prey capture success and competitive interactions between predators (Hazelton and Grossman 2009). Turbid conditions that impair the visual abilities of both predators and prey can cause the outcomes of predatory interactions to become random because of decreased anti-predator behavior in prey and a decrease in predator search efficiency (Sweka and Hartman 2003, Webster et al. 2007, Liljendahl-Nurminen et al. 2008, Hazelton and Grossman 2009). However, these results are based solely on visual cues and have neglected other sensory systems. For example, predators that hunt by chemoreception may be less affected by increases in turbidity than visual predators (Meager et al. 2005).

Perceptive ability is influenced by environmental conditions that enhance or attenuate the transmission of relevant information between organisms (Dusenbery 1992). Environmental conditions that diminish perceptive ability may act as ‘sensory stressors’, which can be thought of as a type of environmental stress that affect the perceptive abilities of organisms but are not otherwise harmful to them (Smee et al. 2010). The relative magnitude of CEs, NCEs, and overall degree of top-down forcing may be influenced by subtle changes in environmental conditions that influence perception. Classic models of community regulation note that intense environmental stress can render predation effects in communities unimportant and act as the primary agent of community regulation (Menge 1976, Menge and Sutherland 1987, Menge and Olson 1990). In these models, stress is defined as conditions that are outside tolerance limits for organisms (Rhoades 1985, Menge and Olson 1990) or impose severe physical limitations upon them and may 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 1976, Menge and Sutherland 1987). Sensory stressors differ from these traditional views of stress in that their effects modify animal behavior by influencing perception. In field studies stressors at levels that are not likely to harm organisms may have large effects on predation and the propagation of indirect predator effects. For example, outcomes of predatory interactions between hard clams and their blue crab and knobbed whelk predators are strongly influenced by small-scale turbulence that affects perception but is not otherwise detrimental (Smee et al. 2008, 2010, Ferner et al. 2009).

Environmental stress, including sensory stressors, may either strengthen or weaken predation levels depending upon whether stress has an increased negative effect on predators or the prey (Menge and Olson 1990). In stress models where predators were more

affected by stress than prey, predation declined as stress increased (Menge 1976, Leonard et al. 1998, Bertness et al. 2002). However, in stress models where prey were more affected by stress than predators, predation levels increased with stress because prey became more vulnerable to consumers (Rhoades 1985, Cronin 2001, Smee and Weissburg 2006, Smee et al. 2008). These models co-occur because predators and prey are often simultaneously affected by the same environmental conditions (Dusenbery 1992, Weissburg et al. 2002, Smee et al. 2010).

Environmental conditions influence predator-prey interactions by altering the perceptive ability of both predators and prey. This influence can alter systems as indirect effects propagate through communities. This dissertation explored the effects of abiotic conditions on community composition and top-down control. The effects of turbidity on predator-prey interactions were extended by exploring the effects on multiple sensory systems and how these differential effects caused changes in community composition.

Oyster Reefs as a Model System

Oyster reefs were used as a model system because they are a commercially important fishery, provide essential habitats for other recreational and commercially important organisms (Grabowski et al. 2005, Grabowski and Peterson 2007), and are affected by top-down forces (Grabowski 2004). The synergistic effects of biotic and abiotic conditions can influence oyster reef food webs, (Lenihan 1999, Grabowski 2004, Grabowski and Kimbro 2005, Grabowski et al. 2005, Kimbro and Grosholz 2006), but the effects of turbidity in this system had not previously been studied. Abiotic variables such as flow, salinity and disturbance affect oyster recruitment, growth, survival, and community diversity of the oyster reefs (Gunter 1955, Lenihan 1999, Kimbro and Grosholz 2006). However, most studies have focused on abiotic conditions that are considered stressful to oysters, and have not considered how abiotic conditions might influence

oyster reef communities via modifying top-down forcing. Although oyster reefs are ecologically and economically important, they are declining because of destructive fishing practices, increased disease, and human activities, which negatively affect coastal watersheds (Beck et al. 2009).

The strength of top down forces is dependent upon the predators present on the reef (O'Connor et al. 2008) Top-down control can be strengthened when predators have complementary feeding patterns because more prey is consumed (Burkepile and Hay 2008) but top-down forces can be weakened when predators interfere with one another (Schmitz 2007). In Texas, several species of predatory fish including toadfish (*Opsanus beta*), red drum (*Sciaenops ocellatus*), black drum (*Pogonias cromis*), and sheepshead (*Archosargus probatocephalus*) are associated with oyster reefs. Two predatory crabs are commonly found on oyster reefs: the blue crab (*Callinectes sapidus*) and the stone crab (*Menippe adina*). These predatory species use a wide array of foraging strategies (e.g., red drum are active hunters whereas toadfish are lie-in-wait predators), which may affect different aspects of trophic relationships (Grabowski and Kimbro 2005). Mud crabs (*Panopeus herbstii*) are also an omnipresent intermediate consumer on Texas reefs, preying on juvenile oysters and being consumed by higher order predators such as blue crabs and various fishes. I hypothesize that complementary predators may work to maintain top-down control of the habitat in shifting abiotic conditions, with visual predators (fish) maintaining control in clear conditions and chemosensory predators (crabs) maintaining control in turbid conditions. My goal was to determine how turbidity altered oyster reef communities and trophic interactions.

Wave action also shaped the size and distribution of oyster reef associated species. As a result the last chapter of this dissertation investigates the effects of wave action and flow velocity

on the size and distribution of species within natural oyster reefs. I used a combination of long-term data set analysis, field surveys, and empirical field and laboratory experiments

Chapter I. : Anthropogenic effects indirectly reduce biodiversity

ABSTRACT

Humans directly reduce natural populations and lower biodiversity through over exploitation, habitat destruction and pollution; however, understanding the indirect mechanisms by which human activities affect natural animal populations remains challenging. Coastal development and excess nutrient discharge are increasing turbidity levels in many coastal areas, but, it is unknown how changes in turbidity affect marine biodiversity via alterations in food web interactions. Estuarine biodiversity varied with turbidity in an 18 year data set of four Texas bays which included abiotic variables and species abundance. Within the data set fish diversity decreased while crab diversity increased. Within this dataset species diversity was also significantly related to temperature and salinity. In field collections I independently verified these findings and noted similar patterns between biodiversity and turbidity when other abiotic conditions (e.g., salinity, temperature) were similar. Biodiversity and distribution of ecologically and economically important fisheries are profoundly but indirectly affected by increased turbidity in estuaries.

INTRODUCTION

Overharvesting natural populations has well known, long term, adverse effects that linger after harvesting pressure is removed (Estes and Palmisano 1974, Jackson et al. 2001). Reductions of natural populations may also produce unintended, indirect effects that are often difficult to predict and mitigate (Estes et al. 1998, Myers et al. 2007). For example, overfishing is a well-known cause of widespread community changes (Pauly et al. 1998, Myers et al. 2007) with the loss of predators directly affecting ecosystem functioning by disrupting trophic cascades (Duffy

2002, Myers et al. 2007). Pronounced losses in biodiversity can occur through subtle anthropogenic changes that unintentionally alter primary productivity, remove keystone species, or create stressful abiotic conditions (Sala and Knowlton 2006).

Coastal development has led to a suite of anthropogenic effects including habitat loss, increased nutrient input and erosion that have caused changes in community composition (Duffy 2002, Khan and Ali 2003, Farber et al. 2006). For example, species diversity is known to decrease in areas of hypoxia caused by increased nutrient runoff, and eutrophic environments can decimate submerged aquatic vegetation that serves as critical habitat for many species (Rabalais 2005). However, abiotic conditions that do not exceed the tolerance ranges of a species may cause changes in animal behavior and habitat use that can produce large scale changes in communities (Minello et al. 1987, Leonard et al. 1998, Pollack et al. 2010). To better understand how increased turbidity affected communities, I examined the effects of turbidity on estuarine communities in the western Gulf of Mexico.

The effects of turbidity in estuaries remains largely unexplored even though turbidity levels in coastal waters world-wide are increasing as a result of human induced erosion and eutrophication (Khan and Ali 2003, Rabalais 2005). Erosion is one of the most damaging and widespread forms of pollution, increasing siltation which may decrease light to below levels needed for photosynthesis, decreasing food production (Khan and Ali 2003, Kuo and Lin 2010). Eutrophication is another major source of turbidity and is directly tied to human induced nutrient loading and leads to decreases in primary production as light penetration decreases and photosynthetic marine plants are lost (Kautsky et al. 1986) and an increase of harmful algal blooms and hypoxia (Rabalais 2005). Turbidity increases caused by erosion and eutrophication are generally studied in relation to the direct effects they have on communities, such as decreased

light penetration and subsequent loss of primary productivity and loss of submerged vegetation like sea grasses (Short and Wyllie-Echeverria 1996). However, turbidity may have wide-reaching indirect effects by modifying trophic interactions (Minello et al. 1987, Abrahams and Kattenfeld 1997, Ohata et al. 2011) but these indirect effects on estuarine biodiversity are unknown.

Turbidity modifies trophic interactions, although these effects are species dependent and occur primarily through alterations to predation rates (Minello et al. 1987, Liljendahl-Nurminen et al. 2008, Ohata et al. 2011). Changes in predation rates occurred in response to increased turbidity even when turbidity remained at moderate levels that were not physiologically stressful. However, predators using non-visual senses (e.g., chemoreception) to forage were less affected by increasing turbidities than were visual predators such as fish. In these laboratory studies, fish abundance decreased with increasing turbidity and a subsequent increase occurred in the fish prey, though these observations were not the focus of long-term examinations (Eiane et al. 1999, Aksnes 2007).

To address the question of how anthropogenic changes to abiotic conditions indirectly effect community composition I analyzed a long term dataset from the Texas Parks and Wildlife Department (TPWD) and conducted a field survey. The long-term dataset allowed me to examine patterns over large spatial areas and multiple years to examine how turbidity affects diversity of large crabs and fish in multiple bay systems. I analyzed the TPWD data set from 1991-2008 for San Antonio Bay, Aransas Bay, Corpus Christi Bay and the Laguna Madre, which are in Texas, USA. These bays contain a variety of habitats, including oyster reefs, seagrass meadows and mud flats. The bays differ in salinity ranges among other parameters; San Antonio Bay is relatively fresh in contrast to the Laguna Madre which is a hypersaline lagoon. I also

performed a field survey to sample areas that had different turbidities but were otherwise similar in temperature, salinity, and pH and were separated by ~50-100 m. The field study allowed me to target smaller species that are not collected by the methods used by TPWD and to measure biodiversity of small crab and shrimp species in adjacent habitats that have different turbidity levels but are otherwise similar (e.g., temperature and salinity). The field collection used a different collection method than the TPWD dataset and allowed me to assess if collection methods would account for differences in species collections across turbidity levels.

METHODS

Long-term monitoring of turbidity on species abundance

The relationship between turbidity and diversity was evaluated from an eighteen year data set provided by the Texas Parks and Wildlife Department (TPWD) Coastal Fisheries Division. TPWD conducts field surveys in all Texas bays throughout the year and records abiotic conditions including turbidity, temperature, and salinity as well as the abundance for each species collected during each sample. I analyzed the TPWD data set for San Antonio Bay, Aransas Bay, Corpus Christi Bay and the Laguna Madre to represent the Texas Coast. These bays represent a wide variety of habitats, including oyster reefs, seagrass meadows and mud flats. The bays also differ in salinity ranges among other parameters; San Antonio Bay is relatively fresh in contrast to the Laguna Madre which is a hypersaline lagoon. Principle component analysis was used to determine the abiotic variables of greatest importance and if bays were similar.

Texas Parks and Wildlife Department (TPWD) Coastal Fisheries Division conducted gill net and trawl surveys of all Texas bays throughout the year (Figure 1.1). These data include

abiotic variables and abundance data for all species collected in each sample. Data from 1991 through 2008 was analyzed; all surveys prior to 1991 were not included because of inconsistent sampling effort (J. Tolan TPWD, personal communication). Abiotic conditions were recorded at the beginning of each net deployment, including depth, salinity, temperature and turbidity.

For gill net surveys, the nets used are 182.8 m long and 1.2 m deep with separate 45.7 m sections of 7.6 and 10.1 cm (#12 monofilament), 12.7 and 15.2 cm (#18 monofilament) stretched mesh tied together in ascending mesh size. The nets were set perpendicular to shore with the smallest mesh shoreward. Gill nets were set overnight within one hour before sunset and were retrieved within four hours of sunrise. These surveys were conducted in two three-month sets: April-June and September-November with 45 samples taken over the course of each season. The spring season began in the second full week of April and extended for 10 weeks. The fall season began in the second full week of September and extended for 10 weeks. The trawl used was deployed for 10-15 minutes at a time. These surveys were conducted every month of the year for two weeks every month. Gill net surveys are selective for fish and rarely catch benthic organisms such as crabs and shrimp. Bay trawls sample the bottom and are used by TPWD to monitor populations of crabs and shrimp. Bottom conditions and water depth were not consistently recorded in the dataset and therefore were not standardized in our analysis. Simpson's diversity index was calculated for each sample and was compared when turbidities were above and below 30 NTU, because this level is sufficient to alter the visual acuity of marine organisms (Minello et al. 1987). Gear types were analyzed separately because they were not collected in a paired design.



Figure I-1 Map of TPWD sampling stations for Aransas Bay. Each dot represents a sampling station for the TPWD fisheries independent survey within the Aransas Bay system.

Principle component analysis and diversity values were calculated in Primer TM. Gill net survey diversity was analyzed with a blocked two-way ANOVA with turbidity and season as fixed factors because gill net samples are conducted seasonally. Bay trawl surveys were analyzed as an ANOVA with turbidity as the fixed factor, season is not necessary as bay trawls are conducted throughout the year. To determine the relationship between turbidity and species richness regression analysis was performed.

Field Study

Study Site

Natural oyster reefs near Goose Island State Park in St. Charles Bay, TX, USA, were selected for an empirical study on the effects of turbidity (Figure 1.2). My 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 TM

Data Sondes to determine areas where turbidity is routinely low (< 30 NTU) vs. high (>30 NTU). Data Sondes were deployed every two weeks over the course of the study. Instruments were mounted approximately 15-20 cm above the sediment on wood trays anchored to the natural oyster reefs. The Data Sondes were programmed to record ambient conditions for 5 minutes every hour for 5 days. Instruments were calibrated after every deployment using standards and protocols proscribed by Hydrolab TM in the Data Sonde care manual. These instruments measured turbidity, salinity, temperature, dissolved oxygen, and chlorophyll *a*. The purpose of measuring chlorophyll *a* was to ascertain the causes of turbidity in our field sites. If chlorophyll *a* and turbidity were strongly correlated a biotic cause for turbidity could be inferred, conversely no relationship between chlorophyll *a* and turbidity is indicative of an abiotic cause such as suspended sediments that are blocking light and increasing turbidity. Ten sites were selected that typically had low turbidity levels and another 10 that had high turbidity levels (Table 1.1), 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. Chlorophyll *a* levels were similar between sites (Table 1.1), indicating that turbidity was caused by suspended sediments and not by phytoplankton, which is consistent with field observations in this area (Figure 1.3). Besides turbidity, other abiotic variables (pH, dO₂, salinity) were not significantly different among study sites (Table 1.1). All abiotic variables recorded in the study were within published tolerance limits of oysters.

Field sites were selected that had similar habitat structure, harvesting pressure, and oyster recruitment to avoid biasing our study by comparing degraded reefs to more healthy reefs (*see* Chapter 2 for detailed methods). 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 causative mechanism for differences in food webs. With this in mind, field sites were selected in St. Charles Bay that was closed to oyster harvesting. St. Charles is a shallow bay, and the 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 (Figure 1.4). Habitat structure in our study sites was qualitatively similar and was typical of other shallow reefs in the study area. To assess oyster reef associated species composition each site was sampled using a modified throw trap (Rozas and Minello 1997). Differences in communities between low vs. high turbid sites were compared with an analysis of similarity (ANOSIM) with PRIMER™.

Field Sampling

Field surveys allowed me to investigate smaller species that are not collected with the methods used by TPWD. This survey focused on oyster reefs which are the dominant habitat in our field site. Oyster reefs were created within 0.25 m² trays, constructed from lumber and vexar mesh, using sun-bleached oyster shell hash that was devoid of life. Trays were anchored within a natural reef at 10 sites that had low and 10 sites with high mean turbidity levels. The trays were deployed in the field in March 2011 and natural recruitment occurred until tray retrieval in August 2011.

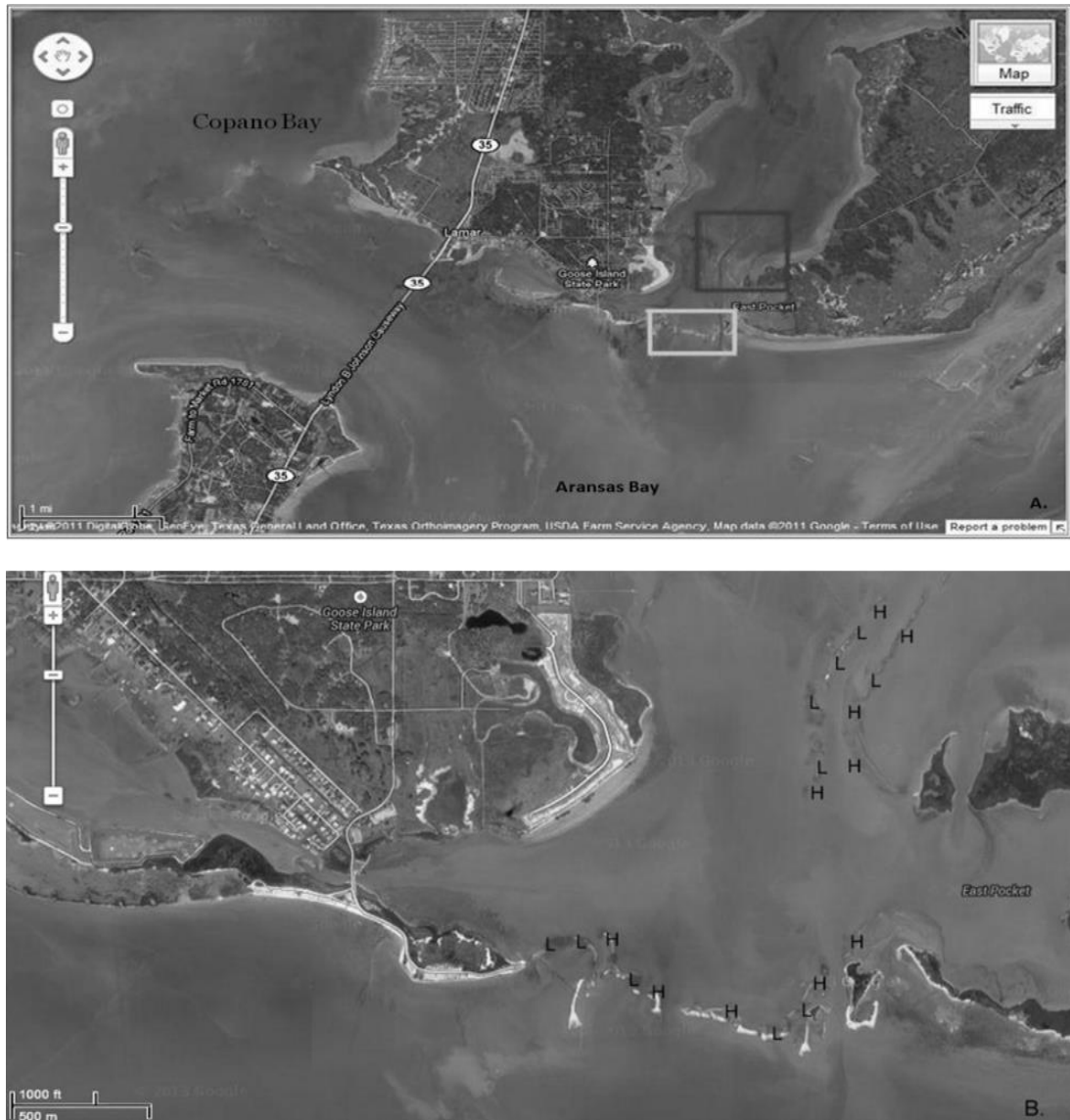


Figure I-2. Map of field sites in St. Charles Bay. (a) Relationship of existing oyster reefs used for the field study (in boxes) to larger bays within the system. (b) Enlargement of the oyster reefs within St. Charles Bay. Sites of trays are marked with symbols. H- high turbidity site, L- low turbidity site

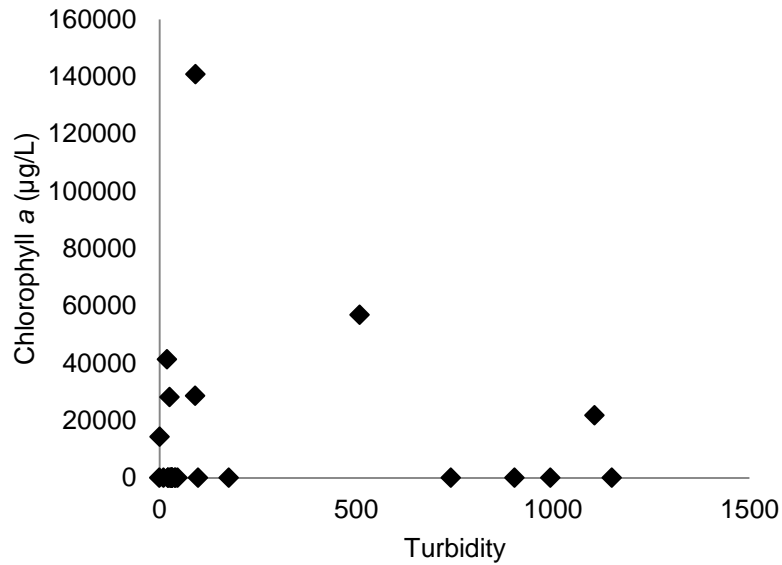


Figure I-3. Relationship between turbidity and chlorophyll *a* for St. Charles Bay, Texas.

Table I-1. Hydrographic variables in low and high turbidity sites.

	Low		High	
	Average	Range	Average	Range
Temperature (C)	27.89	25.82-31.47	29.08	25.81-32.05
Ph	8.29	8.16-8.65	8.35	7.97-11.14
Salinity (ppt)	30.30	14.52-37.82	25.42	13.79-40.58
Dissolved Oxygen (mg/L)	6.48	6.14-7.82	6.00	5.50-6.69
Turbidity (NTU)	25.48	0.00-46.00	242.50	0.28-1150.00
Chlorophyll a (µg/L)	9942.00	0.67-41395.00	6326.90	0.05-56877.00



Figure I-4. Photograph of natural oyster reefs in St. Charles Bay, Texas.

Collection and Analysis

In August, all trays were sampled using a modified throw trap (Rozas and Minello 1997) to collect the nektonic organisms. All mobile organisms were placed in ethanol, and transported to the lab for sorting, identification, measurement, and enumeration. All shells in the tray were also transported to the lab to identify and count sessile organisms, including oyster recruits. From these samples, Simpson's diversity was calculated for each tray using PrimerTM. The diversities were compared using an ANOVA with turbidity as the fixed factor; year was not a significant block and was left out of the ANOVA model.

RESULTS

Principle component analysis was conducted to determine the abiotic variables (salinity, temperature, dissolved oxygen, turbidity) that accounted for changes in biodiversity both

between different bay systems and across years. Principle component analysis reduced the abiotic variables to two primary components explaining 69.4% of the total variance of the dataset (Table 1.2). Principle component 1 accounted for 40.1% of the variance and had significantly high loadings for temperature, salinity and dissolved oxygen. Principle component 2 accounted for 29.3% of the variance and had significantly high loadings for salinity and turbidity.

Table I-2. PCA Results. Loading values for the principle component analysis of the TPWD data.

Eigenvalues				
Component	Eigenvalue	% Variation	Cumulative % Variation	
PC 1	1.61	40.1	40.1	40.1
PC2	1.17	29.3	69.4	69.4
Eigenvectors				
Variable	PC1	PC2		
Temperature	-0.603	-0.320		
Salinity	-0.419	0.541		
Dissolved Oxygen	0.669	0.181		
Turbidity	0.116	-0.756		

TPWD samples the bays with both gill nets and bay trawls to sample nektonic and benthic organisms respectively. More species were consistently collected in low turbidity (< 30 NTU) than high turbidity when samples were aggregated by bay (Table 1.3). Turbidity and species richness were significantly correlated. In gill net surveys, fish were the predominant organisms collected and species richness was negatively correlated with turbidity ($R^2 = -0.038$, $P = 0.002$). In trawl surveys that target benthic species including crabs and shrimp, species richness was positively correlated with turbidity ($R^2 = 0.01$, $P = 0.02$).

Table I-3. Aggregate species richness for TPWD samples.

Bay	Gill Net Surveys		Trawl Surveys	
	High	Low	High	Low
Aransas	30	39	53	57
Corpus	31	39	55	59
Laguna	31	39	54	59
San Antonio	32	40	50	53

Simpson's diversity within gill net and bay trawl samples was analyzed with multiple regression and ANOVA. Within gill net samples turbidity and temperature were the main variables for predicting diversity (turbidity: $F_{1, 10511} = 19.62$, $p < 0.0001$; temperature: $F_{1, 10511} = 222.70$, $p = 0.001$, respectively; $R^2 = 0.0229$). Bay trawl diversity was significantly predicted by turbidity, salinity and temperature (turbidity: $F_{1, 14189} = 103.21$, $p < 0.0001$; salinity: $F_{1, 14189} = 6.84$, $p = 0.008$; temperature: $F_{1, 14189} = 132.51$, $p < 0.0001$, respectively; $R^2 = 0.0167$). In addition to multiple regression analysis, the data were analyzed categorically and were compared when turbidities were above and below 30 NTU, because this level is sufficient to alter the visual acuity of marine organisms (Minello et al. 1987). Categorical analysis was used to support our field studies which specifically sampled low and high turbidities but also because turbidity often functions non-linearly with the largest changes in visual acuity occurring between 0 and 30 NTU. Simpson's diversity was significantly higher in gill net surveys when turbidity was below 30 NTU for both the combined dataset and all individual bays (2-way ANOVA; $F_{1, 6221} = 25.68$, $P < 0.001$; San Antonio: $F_{1, 1697} = 8.36$, $P = 0.003$; Aransas: $F_{1, 1497} = 12.42$, $P = 0.0004$; Corpus Christi: $F_{1, 11495} = 12.42$, $P = 0.0004$; Laguna Madre: $F_{1, 1495} = 12.42$, $P = 0.0004$; Figure 1.5). Season was a significant factor in gill net surveys, with higher diversities in the fall (2-way

ANOVA; $F_{1, 6221} = 62.08$, $P < 0.0001$), and I attribute this finding to fish migration for spawning (Martin and McEachron 1986). There was no interaction between season and turbidity for gill net surveys (2-way ANOVA; $F_{1, 6221} = 0.76$, $P = 0.38$). In bay trawls designed to sample crabs, significantly higher diversity occurred when turbidity exceeded 30 NTU for all bays combined (ANOVA; $F_{1, 14317} = 12.97$, $P = 0.0003$, Figure 1.6). Individual bays differed in their patterns. Corpus Christi Bay and the Laguna Madre had significantly higher diversities when turbidity was high in trawl samples (ANOVA; $F_{1, 4256} = 20.76$, $P < 0.0001$; $F_{1, 1987} = 30.74$, $P < 0.0001$; Figure 1.6). San Antonio and Aransas Bays did not have significant differences in diversity between turbidity levels (ANOVA; $F_{1, 4269} = 2.62$, $P = 0.10$; $F_{1, 3798} = 3.64$, $P = 0.05$; Figure 1.6). To determine which species were driving the patterns between turbidity levels, I performed a SIMPER analysis for both gill net and bay trawl samples in PRIMER [™] (Tables 1.4-1.7). Loss of diversity in high turbidities may be attributable to the loss of rare species (species which represented less than 1% of the total abundance). For trawl samples, only one species was present in high turbidity but not low turbidity, whereas six species were present in low but absent in high turbidity (Table 1.4). Within gill net samples, there were two species found in high turbidity but not low turbidity and four species found in low but not high turbidity (Table 1.5). Many commercially important species were also affected by changing turbidity levels, including red drum (*Sciaenops ocellatus*), which were more abundant in low turbidity, and blue crabs (*Callinectes sapidus*) and penaeid shrimps (Table 1.6-1.7) which were more abundant in high turbidity.

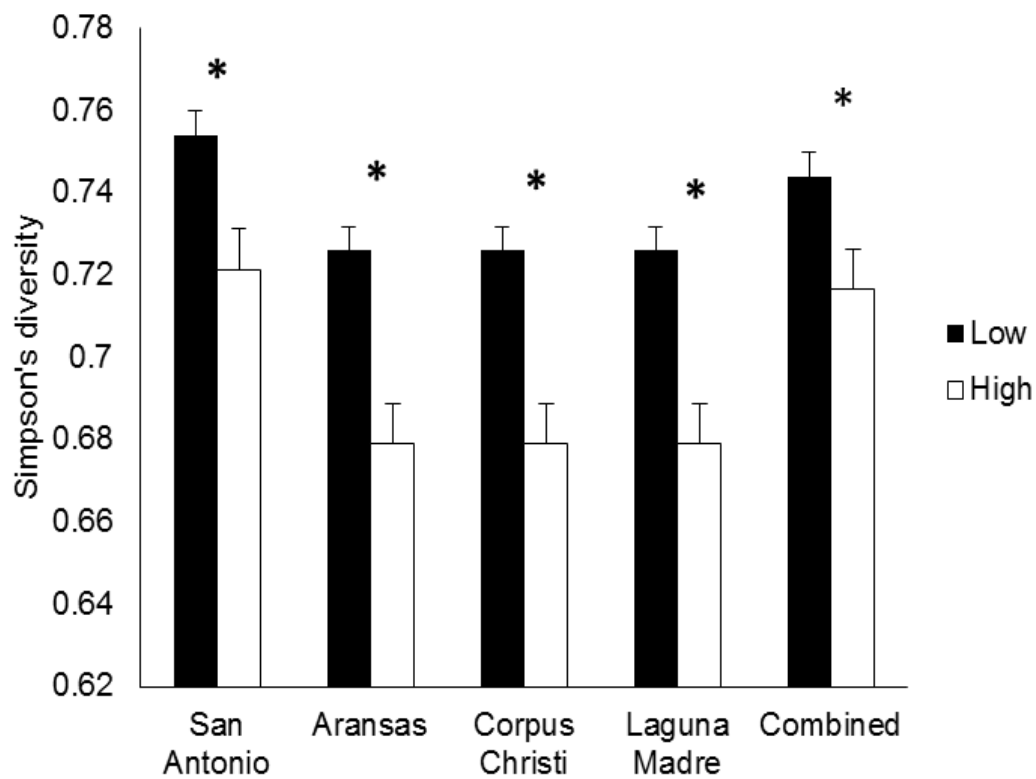


Figure I-5. Diversity of fishes caught in gill net samples in both low and high turbidity areas. Comparison of the diversity of fishes caught in Texas Parks and Wildlife Department gill net samples in low (< 30 nephelometric turbidity units) and high (> 30 nephelometric turbidity units) turbidity. Significance is indicated by (*).

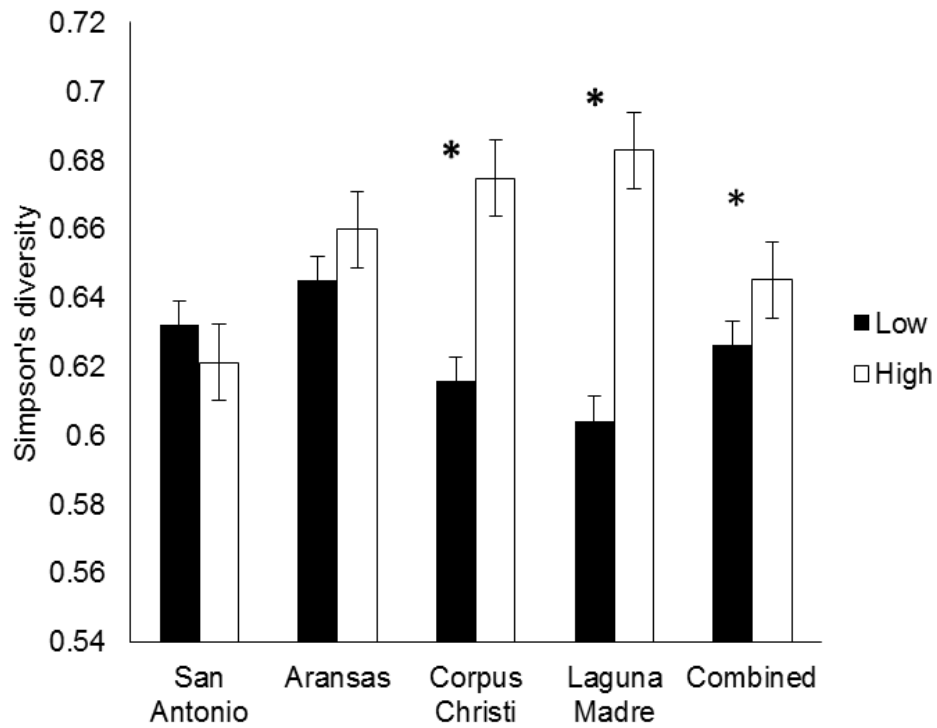


Figure I-6. Diversity of crabs caught in bay trawl samples in both low and high turbidity areas. Comparison of the diversity of crabs caught in Texas Parks and Wildlife Department bay trawl samples in low (< 30 nephelometric turbidity units) and high (> 30 nephelometric turbidity units) turbidity. Significance is indicated by (*).

The patterns noted in the analysis of the long term data set were empirically tested by investigating the effects of turbidity on species diversity associated with oyster reefs, a system of both ecological and economic importance (Grabowski and Peterson 2007). Species composition was similar between sites (ANOSIM, $R = -0.005$, $p = 0.44$). However, the relative abundance of species was different among study sites. Thus, our field sites were appropriate for testing the effects of turbidity on trophic interactions among reefs. Turbidity had a significant effect on diversity within field samples. Diversity was significantly higher in areas of high turbidity (ANOVA; $F_{1, 50} = 16.16$, $P = 0.0002$, Figure 1.7). Samples were comprised of approximately 85% small crabs (Porcellanidae, *Eurypanopeus depressus*, *Panopeus herbstii*) and shrimp (*Alpheus* sp.s, *Tozeuma carolinense*, *Palaemonetes* sp.), organisms not commonly collected by TPWD. As in TPWD samples, benthic species richness and abundance of crabs and shrimp increased with increased turbidity.

Table I-4. Species collected in TPWD trawl samples that were present at only one turbidity level.

Species	High Mean Density	Low Mean Density	High and Low % Dissimilarity
<i>Brevoortia gunteri</i>	0.01	0.00	0.005
<i>Paralichthys albiguttata</i>	0.00	0.01	0.01
<i>Menidia beryllina</i>	0.00	0.01	0.01
<i>Lysmata wurdemanni</i>	0.00	0.01	0.02
<i>Harengula jaguana</i>	0.00	0.02	0.02
<i>Menticirrhus americanus</i>	0.00	0.01	0.01
<i>Menidia peninsulae</i>	0.00	0.01	0.02

Table I-5. Species collected in TPWD gill net samples that were present at only one turbidity level.

Species	High	Low	High and Low
	Mean Density	Mean Density	% Dissimilarity
<i>Rangia flexuosa</i>	0.01	0.00	0.010
<i>Trachinotus carolinus</i>	0.00	0.04	0.050
<i>Opsanus beta</i>	0.00	0.01	0.010
<i>Dorosoma petenense</i>	0.00	0.01	0.005
<i>Mugil curema</i>	0.00	0.01	0.010
<i>Litopenaeus setiferus</i>	0.01	0.00	0.010

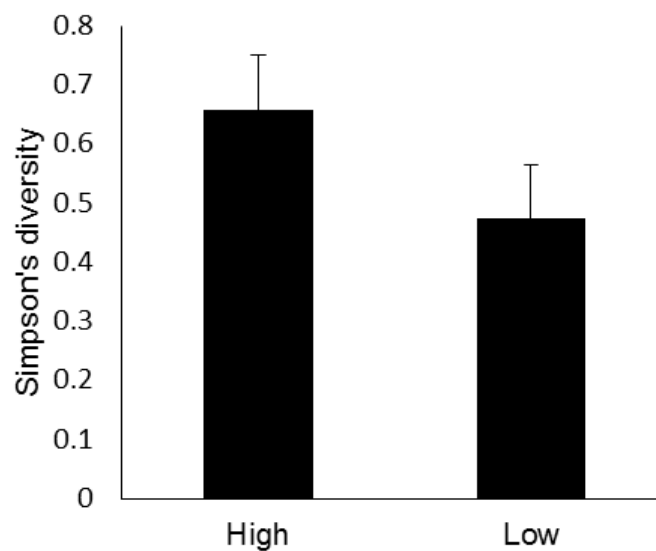


Figure I-7. Diversity of samples collected in St. Charles Bay. Comparison of the diversity of low (< 30 nephelometric turbidity units) and high (> 30 nephelometric turbidity units) turbidity samples collected in St. Charles Bay, Texas. The samples are significantly different ($p < 0.05$).

Table I-6. Bay trawl species contributing > 1% to the similarity or dissimilarity of samples.

The species listed contribute > 1 % to the similarity within a turbidity level or between turbidity levels for Texas Parks and Wildlife Department bay trawl samples for San Antonio, Aransas, Corpus Christi Bays and the Laguna Madre. Where % similarity is not given, the species did not contribute >1% to the similarity of samples within that category but did contribute to dissimilarity.

Species	High		Low		High and Low
	Mean Density	% Similarity	Mean Density	% Similarity	% Dissimilarity
<i>Micropogonias undulatus</i>	23.18	31.81	11.44	12.54	15.38
<i>Lolliguncula brevis</i>	1.09	-	3.44	6.52	2.77
<i>Anchoa mitchilli</i>	2.70	2.88	3.72	4.69	4.34
<i>Ictalurus furcatus</i>	1.44		0.21		1.49
<i>Callinectes sapidus</i>	7.02	11.60	1.93	2.93	5.51
<i>Farfantepenaeus aztecus</i>	19.46	13.02	6.90	3.12	11.51
<i>Stomolophus meleagris</i>	3.56	-	1.77	-	2.38
<i>Bagre marinus</i>	1.17	-	0.75	-	1.32
<i>Brevoortia patronus</i>	2.82	-	1.71	-	3.24
<i>Ariopsis felis</i>	2.42	2.69	2.76	3.55	2.92
<i>Lagodon rhomboides</i>	8.14	4.27	26.33	38.13	11.87
<i>Farfantepenaeus duorarum</i>	1.67	-	0.85	-	1.38
<i>Bairdiella chrysoura</i>	5.38	4.37	3.74	3.31	4.93
<i>Mugil cephalus</i>	1.14	-	0.47	-	1.18
<i>Leiostomus xanthurus</i>	14.67	9.05	18.25	17.44	12.02
<i>Litopenaeus setiferus</i>	12.85	12.26	3.43	-	8.92

Table I-7. Gill net species contributing > 1% to the similarity or dissimilarity of samples.

The species listed contribute > 1 % to the similarity within a turbidity level or between turbidity levels for bay trawl samples for Texas Parks and Wildlife Department gill net samples. Where % similarity is not given, the species did not contribute to the similarity of samples within that category but did contribute to dissimilarity.

Species	High		Low		High and Low
	Mean Density	% Similarity	Mean Density	% Similarity	% Dissimilarity
<i>Atractosteus spatula</i>	1.77	-	0.79	-	1.95
<i>Micropogonias undulatus</i>	1.57	-	2.98	-	3.05
<i>Pogonias cromis</i>	17.80	17.31	16.48	19.32	17.03
<i>Bagre marinus</i>	3.30	-	3.48	2.53	4.17
<i>Dorosoma cepedianum</i>	11.21	10.64	5.25	2.62	10.32
<i>Brevoortia patronus</i>	0.82	-	1.67	-	1.89
<i>Ariopsis felis</i>	21.96	23.43	16.61	23.55	17.7
<i>Elops saurus</i>	1.95	-	2.1	-	2.66
<i>Sciaenops ocellatus</i>	15.25	22.68	15.41	24.73	13.54
<i>Archosargus probatocephalus</i>	1.15	-	2.11	-	2.3
<i>Leiostomus xanthurus</i>	0.87	-	2.27	-	2.18
<i>Cynoscion nebulosus</i>	10.68	13.05	10.04	14.15	10.12
<i>Mugil cephalus</i>	3.13	2.96	4.26	4.57	4.41

DISCUSSION

Fish abundance and species richness decreased as turbidity increased as did predation by fish on tethered mud crabs. Crabs and shrimp that fish preyed upon were more abundant in more turbid areas that had fewer fish, suggesting that turbidity can alter top-down forcing in estuaries. Overall species richness was higher when turbidity was below 30 NTU, 10 species were only found when turbidity was below this threshold, and only 3 species were present when turbidity exceeded 30 NTU. The significant effects of turbidity were found both in the long term data set collected over a broad area and on a small scale sampling of oyster reefs within a single bay. Thus, the effects of turbidity are likely important on different spatial and temporal scales and should be further investigated.

The importance of turbidity was supported by principle component and regression analyses. Although significant relationships occurred between turbidity and diversity, R^2 values were low. Low R^2 values indicated that substantial variability within the data set, but the R^2 values for turbidity were at the same levels as those of salinity and temperature, hydrographic variables known to be important in governing estuarine systems. In addition to being related to species richness and diversity, turbidity altered the composition of estuarine communities. Fewer species were found in highly turbid areas compared to areas of low turbidity, and rare species were being lost from these systems as turbidity increases. Lower fish diversity in higher turbidities was likely a function of fish avoiding these conditions because of decreased visual acuity and foraging success (Hazelton and Grossman 2009). Fish diversity may be lower in areas of increased turbidity because fish are seeking areas of low turbidity where they are more efficient foragers. Conversely, crabs were more abundant and diverse in areas with higher turbidity, perhaps because their fish predators were less successful in consuming them when

turbidity impairs fish vision (Sørnes and Aksnes 2004, Hazelton and Grossman 2009). The ability to find prey by crabs and other predators that primarily forage using chemical cues would not be substantially reduced by turbidity (DeRobertis et al. 2003, Engström-Öst et al. 2009).

Estuaries examined in this study encompassed a wide variety of habitats and abiotic variables. The TPWD samples were collected from random locations from within bays that contained seagrass meadows, oyster reefs and mud flat bottoms. In addition to multiple habitat types, there was a range in abiotic variables: San Antonio Bay has considerable freshwater inflow, as opposed to the Laguna Madre which is a hypersaline lagoon. Turbidity is likely to influence fish predation and alter top-down forcing and food web interactions (Eiane et al. 1999, Sørnes and Aksnes 2004, Ohata et al. 2011). Turbidity, similar to salinity and temperature likely has large effects on estuarine species and should be considered in conservation and management plans.

The effects of turbidity on estuarine biodiversity are important worldwide because turbidity is increasing in coastal environments (Sanden and Hakansson 1996, Fujii and Uye 2003). The increase in turbidity is primarily a result of anthropogenic activities such as increased erosion (Khan and Ali 2003) and nutrient loading (Candolin et al. 2008). Both sources affect species composition (Khan and Ali 2003, Candolin et al. 2008), though the source of turbidity can be important in determining effects on communities (Radke and Gaupisch 2005). In freshwater systems, turbidity as low as 20 nephelometric turbidity units (NTU), can diminish visual acuity, decrease prey capture success and alter competitive interactions (Hazelton and Grossman 2009). This decrease in predator efficiency may make turbidity a refuge for lower trophic levels preyed upon by fishes (DeRobertis et al. 2003, Engström-Öst et al. 2009). This hypothesis is supported by several findings: 1) increased abundance and diversity of crabs and

shrimp in high turbidity in benthic trawl samples, 2) increased abundance of small crabs and shrimp found in high turbidity in our field study, and 3) decreased abundance and diversity of fish noted in TPWD gill net surveys when turbidity was above 30 NTU. Clearly more research is needed to understand the mechanisms by which turbidity affects diversity; the current working hypothesis is that increased turbidity reduces predation by fishes and increases the abundance of crabs, shrimp, and other prey species. Crabs are known to both consume economically and ecologically important bivalves such as oysters (*Crassostrea virginica*) and clams (*Mercenaria mercenaria*) and cause these species to adopt a different morphology that reduces their fecundity (Nakaoka 2000, Johnson and Smee 2012, Robinson et al. 2013). Increased turbidity that results from increased sediment loads may negatively affect bivalves by increasing the amount of energy they devote to sorting particles, subsequently decreasing the energy they allocate to growth. Additionally, an increased number of crabs may lead to higher predation rates in refuge habitats like oyster reefs and lower biodiversity through exclusion of less abundant species.

Predators using non-visual senses to forage are likely less affected by increasing turbidity than are visual predators such as fish. A decrease in fish abundance with increasing turbidity has been reported in other environments, such as northern fjords (Eiane et al. 1999, Aksnes 2007), and jellyfish, a tactile predator, were more abundant when turbidity was high (Ohata et al. 2011). While many marine habitats have an abundance of fauna and predator species, a majority of these predators are likely mobile fish, which become less abundant as turbidity increases. Changes in fish abundance or foraging success are likely to alter food webs and energy flow (Myers et al. 2007, O'Connor et al. 2008).

A disruption in estuarine food webs can profoundly affect terrestrial and pelagic systems that depend on estuaries for food and as nursery habitats. For example, energy from aquatic

systems often drives bottom-up processes in terrestrial systems (Polis and Hurd 1996) and instances of terrestrial predator dependence on marine and aquatic species as prey items are well known (Catenazzi and Donnelly 2007, Anthony et al. 2008). Increases in turbidity in marine and aquatic systems would therefore have indirect effects on terrestrial systems through loss of prey items. In addition, increased turbidities may also alter terrestrial predator foraging efficiency by reducing prey capture success from terrestrial predators that hunt aquatic prey visually (e.g., birds). The overall decline in biodiversity as turbidity increases may correlate with decrease in habitat value that might make these areas less suitable nursery grounds, although this supposition requires further investigation.

Changes in top-down control because of overfishing can have substantial effects on communities, and turbidity may produce similar effects by reducing top-down forcing of higher order consumers (e.g., fish) that depend on visual cues to forage successfully. Large scale changes in communities because of predator loss has already been reported in systems where fishing pressure on sharks has allowed ray populations to proliferate and decimate bivalve fisheries (Myers et al. 2007). Turbidity may act similarly to overfishing in that it reduces top-down forcing by fish, leading to an increase in crabs but an overall lowering of biodiversity, probably because of intensive predation by crabs. Turbidity is an important environmental variable that should be more widely included in management and restoration considerations for aquatic systems.

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Chapter II. : Turbidity influences trophic interactions in estuaries

ABSTRACT

I investigated how changes in turbidity indirectly alter trophic interactions in estuaries. Urban development and nutrient input are causing turbidity to increase in coastal areas. Using a 20 year data set from Aransas and San Antonio Bays in Texas I measured how abundance of crabs and fishes changed with turbidity. Fish abundance (*Sciaenops ocellatus*, *Pogonias cromis*, *Archosargus probatocephalus*) was highest in low turbidity (<30 Nephelometric Turbidity Units (NTU); $p < 0.01$), while crab (*Callinectes sapidus*) abundance was highest in high turbidity (>30 NTU; $p < 0.05$). Mud crabs (*Panopeus* spp.), an important intermediate predator on oyster reefs that are not included in the 18-yr data set, were more abundant on oyster reefs in St. Charles Bay, Texas when turbidity exceed 30 NTU ($p = 0.03$). Fish predation on tethered *Panopeus herbstii* was highest when turbidity was low (<30 NTU, $p < 0.05$). In high turbidity (> 30 NTU), predation on *P. herbstii* was highest ($p = 0.02$) as was predation by crabs ($p = 0.003$). Predation on oyster spat did not differ between low and high turbidity sites ($p = 0.64$), but, oysters devoted more resources to shell growth ($p < 0.01$), a reaction known to occur in response to crab predators. Elevated turbidity can affect trophic interactions in estuaries by altering species composition and trophic interactions, which leads to an increase in crabs that can lead to changes in juvenile oyster growth.

INTRODUCTION

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 or are likely to cause injury or death (Menge and Sutherland 1987). This is exemplified on wave-swept shores where hydrodynamic stress resulting from 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 variables 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 reduced feeding success of planktonic organisms (Saiz et al. 2003). On wave-protected rocky shores in New England, green crabs were more abundant in sites with high mean flow velocities despite suffering reduced foraging rates. This pattern in crab abundance reduced 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 variables 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 variables influence species interactions can provide insights as to 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).

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). Predation can also affect community structure and biodiversity (Paine 1966, Werner and Peacor 2006). As species seek to escape areas where abiotic variables such as salinity or dissolved oxygen levels are stressful, they may be driven into smaller refuge areas, which then increase the magnitude of density-dependent interactions in these areas (Bowling et al. 2012, Froeschke and Stunz 2012). Abiotic variables at levels not physiologically stressful can have significant effects on top-down control of communities, and community composition by modifying species interactions. For example, relatively small changes in hydrodynamics (e.g., flow velocity and turbulence) can affect top-down forcing, indirect predator effects, and the distribution and abundance of species (Leonard et al. 1998, Smee et al. 2010).

In addition to the aforementioned abiotic variables, turbidity may also affect predatory interactions and community structure (van de Meutter et al. 2005). Turbidity may reduce the visual acuity of predators and reduce top-down forcing (Minello et al. 1987, Liljendahl-

Nurminen et al. 2008) or alter the distribution of species and spatial extent of top-down control as visual predators seek foraging areas that are favorable (Snickars et al. 2004). Changes in top-down forces and predator distributions have the potential to alter direct and indirect effects of predators on prey and alter aquatic food webs.

The effect of turbidity on trophic interactions and community composition, 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 principle 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 one of the most damaging and widespread forms of pollution. Erosion increases siltation of lakes and streams (Khan and Ali 2003), which 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 with 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 in the laboratory based (Minello et al. 1987, Ohata et al. 2011). In freshwater turbidity affects predator-prey interactions but that 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 non-visual predators (e.g., crabs) than do freshwater habitats and may respond differently when turbidity increases than freshwater systems. 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 year data set from the western Gulf of Mexico, I investigated the effects of turbidity on species assemblages in estuarine habitats in two bays located in Texas. I 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. I 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: *Callinectes sapidus* and stone crabs: *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, and 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 reducing coastal erosion and water filtration (Grabowski et al. 2005, Grabowski and Peterson 2007). Abiotic variables 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, the effects of abiotic variables which are not stressful to oysters, such as turbidity, have not been considered. Turbidity may affect oyster reef communities via modifying predatory interactions within the food web rather than through physiological constraints. Turbidity may affect the distribution of mobile species, and alter predation levels by reducing visual acuity. These changes may indirectly alter food webs by indirectly effecting 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 variables including turbidity during each survey (*see* Chapter 1 for detailed methods). I examined the effects of abiotic variables including salinity, temperature, and turbidity on species abundance in San Antonio and Aransas Bays, Texas (Figure 2.1). I 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, I was able to ascertain the effects of turbidity across a range of other abiotic variables known to be important in estuarine systems. TPWD measured the abundance of species using gill nets and bay trawls, which selectively sample fish and crabs respectively. I 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 conducted in two, three-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 are selective for 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) were 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) as this level is known to reduce visual acuity in marine organisms (Minello et al. 1987, Sweka and Hartman 2003). 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 samples were 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).

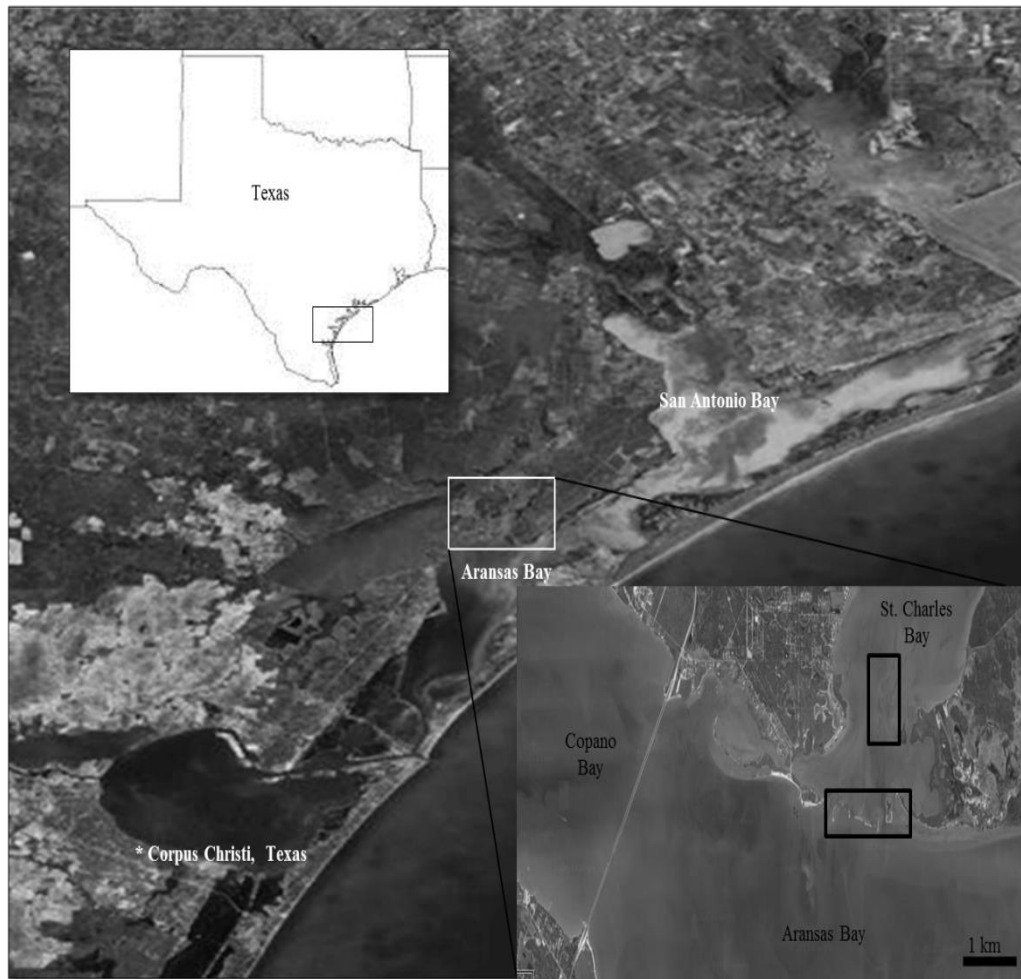


Figure II-1. Map of study sites. Location of study sites for both the long-term data set and field study. The small inset map of Texas has a box around the area of coastline where San Antonio and Aransas Bays are located. The larger map shows the relationship between the field site, boxed in white, and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

Field study

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 (Figure 2.1 & 1.1B). Oyster reefs were selected that differed in turbidity but otherwise experienced similar abiotic conditions. Turbidity was monitored intermittently from April 2010 to September 2012 using Hydrolab TM Data Sondes to determine areas where turbidity was routinely low (< 30 NTU) vs. high (>30 NTU). Data Sondes were deployed every two weeks over the course of the study. Instruments were mounted approximately 15-20 cm above the sediment on wood trays anchored to the natural oyster reefs. The Data Sondes were programmed to record ambient conditions for 5 minutes every hour for 5 days. Instruments were calibrated after every deployment using standards and protocols proscribed by Hydrolab TM in the Data Sonde care manual. These instruments measured turbidity (NTU), salinity (ppt), temperature (C), dissolved oxygen (mg/L), and chlorophyll *a* (µg/L). The purpose of measuring chlorophyll *a* was to ascertain the causes of turbidity in my field sites. Turbid water combined with increased levels of chlorophyll *a* suggests turbidity is biotic in nature while low chlorophyll *a* levels in highly turbid conditions suggest abiotic variables such as suspended sediments are blocking light and increasing turbidity. Ten sites were selected that typically had low turbidity levels and another 10 that had high turbidity levels, although turbidity in all sites could vary from 0-100 NTU depending upon wind speed and direction. Turbidity levels varied based on local features such as flow patterns along the reef or proximity to bare, muddy substrate. Chlorophyll *a* levels were similar between sites, indicating that turbidity was caused by suspended sediments and not by phytoplankton, which is consistent with field observations in this area (Table 1.1). Besides turbidity, other abiotic

variables had similar ranges and were not different among study sites (Table 1.1). All abiotic variables recorded in the field sites were within known tolerance limits of oysters and had similar ranges.

Field sites were selected that had similar habitat structure, harvesting pressure, and oyster recruitment to avoid biasing my study by comparing degraded reefs to healthier 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, field sites were selected in areas of St. Charles Bay, a bay that is not commercially harvested for oysters. St. Charles is a shallow bay, and the 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, oyster recruitment and adult oyster growth were measured, and compared between low and high turbid 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 which had settled onto the adults was quantified and a number of metrics were measured. Calipers were used to measure length along the longest axis, and adductor size. Wet weight was the weight of all soft tissue. Adult oysters were used as they do not alter their growth in response to predators (Johnson and Smee 2012), and our goal was to assess if growth differences between low and high turbidity sites were related to abiotic variables 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, $p > 0.05$; $t = 1.62$, degrees of freedom (df) = 48, $p > 0.05$; $t = 0.90$, degrees of freedom (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: $t = -0.35$, degrees of freedom (df) = 48, $p > 0.05$; Table 2.1). To assess the composition of species associated with oyster reefs each site was sampled using a modified throw trap (Rozas and Minello 1997, see detailed methods below). Differences in communities between low vs. high turbid sites were compared with an analysis of similarity (ANOSIM) with PRIMER™. Sites were similar in species composition (ANOSIM, $R = -0.005$, $p = 0.44$). However, the relative abundance of species was different among study sites, a pattern described in detail below. Thus, my field sites were appropriate for testing the effects of turbidity on trophic interactions among reefs.

Table II-1. Oyster growth and settlement data. Metrics measured for adult oysters planted in St. Charles Bay. Length is total length along the longest axis, wet weight is weight of soft tissue, and juvenile oyster recruitment is the number of spat counted on the adult oysters after collection.

	High		Low		p -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 spat	0.4	0.0-5.0	0.3	0.0-1.0	0.72

Field sampling

Because crab abundance varied with turbidity in TPWD samples, I 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 in TPWD bay trawls because TPWD does not sample oyster reefs with the bay trawl where mud crabs are most abundant. Within each study site, a 0.25 m² area was cleared of oyster clumps and shells. With the clearing, a 0.25m² tray containing 25 L 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, and sampled 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), and placed in ethanol, and transported to the lab 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 does allow the small cryptic species not commonly caught by TPWD to be sampled. From these samples, I calculated the number of mud crabs (*Panopeus herbstii*, *Eurypanopeus depressus*, and *Panopeus turgidus*), found on each tray. I focused on mud crab abundances because they are an omnipresent species which are important juvenile oyster predators and are commonly consumed by other reef species. 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). 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 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. Turbidities for these trials were found to be either very low (0-20 NTU) or very high (50-200 NTU), maintaining earlier documented differences in turbidities 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. Prior to field experiments 10 mud crabs were tethered in the lab for 48 hours. After 48 hours tethers were removed and mud crabs were monitored for a week. Mud crabs that had been previously tethered were also placed within a cage and left in the field for 48 hours to determine if the tethering procedure affected survival in the field. All mud crabs survived these preliminary experiments. Within groups, crabs were arranged ~ 1 meter 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 was recorded. 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, I was 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. I was unable to perform all replicates simultaneously, and so instead deployed tethered crabs simultaneously in both low and high turbid 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 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 (*see* Johnson and Smee 2012 for methods). The juvenile oysters used in this experiment were raised in the lab until reaching a size of 10-20 mm across, as at this size the oysters are most vulnerable to consumers but 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. Ten shells, each containing 15 newly settled oysters, were placed within each site for 2 months to determine juvenile oyster growth rates. Predation rates were assessed by deploying 10 shells, each containing 15 newly settled oysters, in low and in high turbidity sites for one week in July and again in August. Juvenile oysters protected by a vexar mesh cage (1.0 cm² openings) survived in preliminary trials (J. Lunt unpubl. data), and thus oyster mortality could be attributed 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. Pre-deployment weight could not be recorded because weighing the juvenile oysters requires oyster mortality. They were placed them into a conventional drying oven at 90°C for 2 days, 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 combust 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 provided 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

Abundance varied significantly with 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 0.57 % ($R^2 = 0.0057$) of the variation in fish 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, abundance varied significantly with turbidity and temperature (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 an important variable in either gill net or bay trawls, and dissolved oxygen levels were not hypoxic in our study period.

Turbidity had an effect on crab and fish abundance in both Aransas and San Antonio Bays (Figure 2.2). 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). Abundances of fish were higher in gill net surveys when turbidity was below 30 NTU (Aransas: $F_{1,1631} = 8.72$, $p = 0.01$, Figure 2.2A; San Antonio: $F_{1,1701} = 10.55$, $p = 0.0012$, Figure 2.2B), 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: $F_{1,3800} = 154.23$, $p < 0.001$, Figure 2.2C; San Antonio: $F_{1,4281} = 83.54$, $p < 0.001$, Figure 2.2D).

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 ($F_{2,49} = 0.93$, $p = 0.35$; Figure 2.3A). However, the abundance of large mud crabs (> 10 mm) was higher in sites with high turbidity ($F_{2,49} = 2.2$, $p = 0.03$; Figure 2.3B). 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.

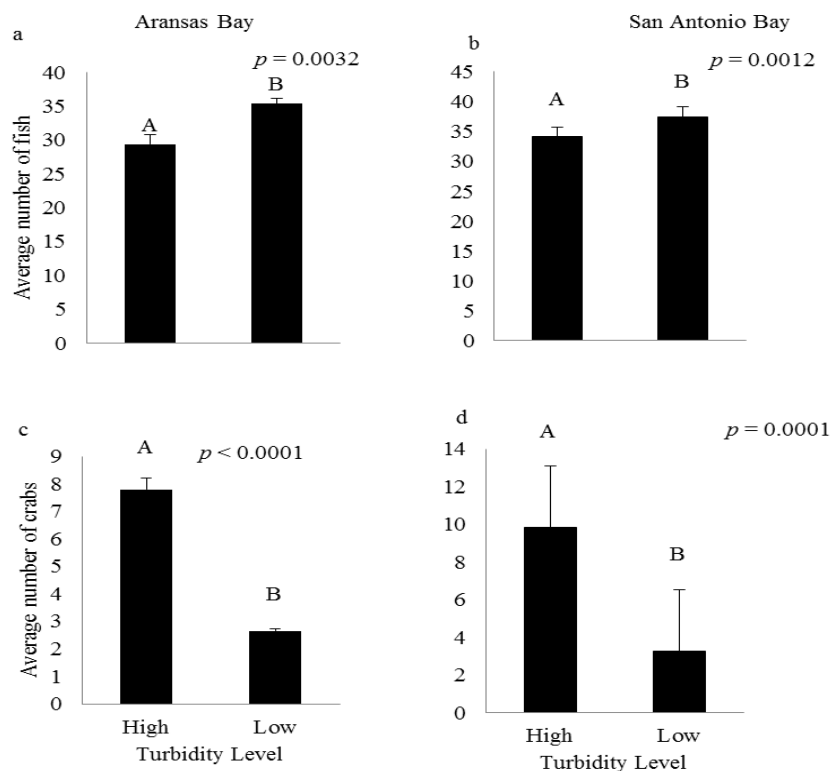


Figure II-2. Average abundance of species caught by TPWD by turbidity. Mean + Standard Error number of organisms collected in low vs. high turbidity areas by TPWD from 1991-2008. Mean low turbidity was 10 NTU. Mean high turbidity was 60 NTU. Letters denote significant differences based upon ANOVA. Fish were collected by gill nets and crabs 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; and (d) crab abundance San Antonio, 97.5% of crabs were blue crabs, 0.5% were stone crabs, and 2% were mud crabs. Letters denote significant differences. Note that mud crabs are not targeted or effectively collected by TPWD sampling protocols.

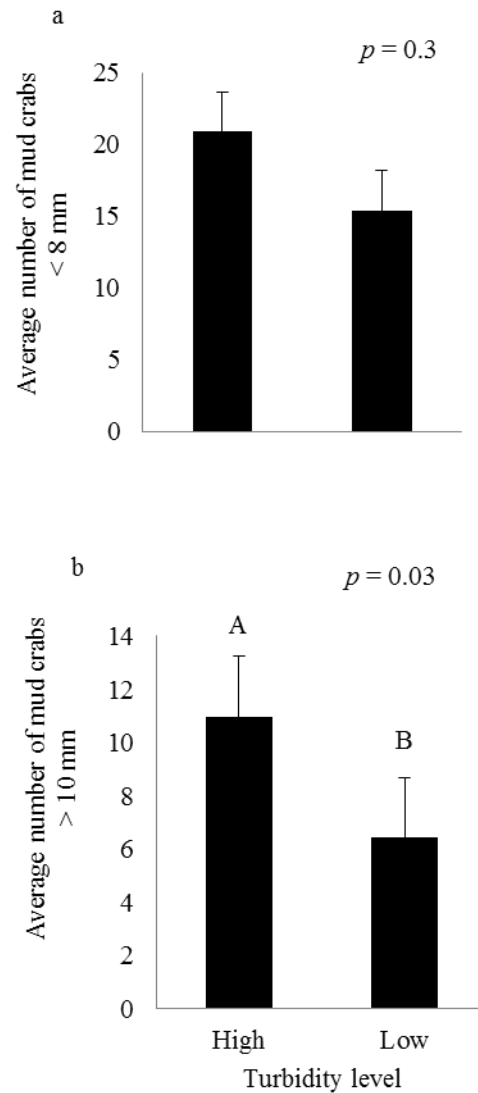


Figure II-3. Average number of mud crabs caught in St. Charles Bay by turbidity. Mean + SE number of mud crabs collected in low vs. high turbidity areas of St. Charles Bay. Letters denote significant differences based upon ANOVA. (a) all mud crabs, and (b) large mud crabs (> 10 mm carapace width) Letters denote significant differences.

Mud crab predation trials

Tethered mud crabs were more likely to be eaten in sites with high turbidity ($F_{1,30} = 5.43$, $p = 0.02$; Figure 2.4A). 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 ($\chi^2_{1,30} = 12.78$, $p = 0.003$; Figure 2.4B), 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 ($F_{1,50} = 0.21$, $p = 0.64$; Figure 2.5A). 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 ($F_{1,85} = 29.45$, $p < 0.001$; Figure 2.5B), a response known to occur in response to crab predators (Newell et al. 2007, Johnson and Smee 2012).

DISCUSSION

The abundance and distribution of species and the interactions between them were strongly influenced by turbidity. Fish were the dominant predator type in lower turbidity and crabs were dominant in higher turbidity. This switch influenced interactions within the food web causing an increase in the abundance of mud crabs, an intermediate predator, an increase in predation on the intermediate predator by crabs, a decline in fish

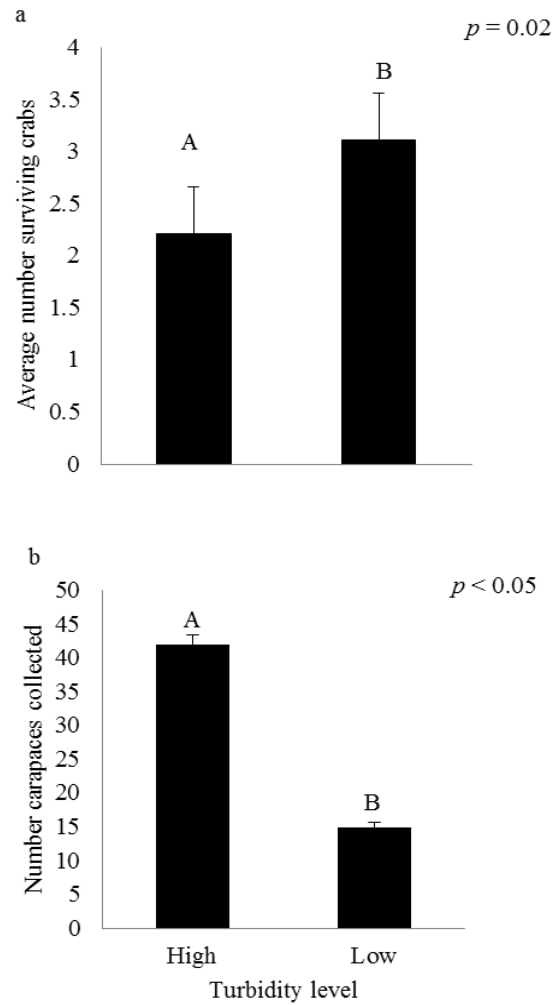


Figure II-4. Predation rates on mud crabs in St. Charles Bay by turbidity. (a) Mud crab survivorship between high and low turbidities in tethering experiments in St. Charles Bay; (b) Number of carapaces retrieved between high and low turbidities in tethering experiments in St. Charles Bay. Carapace presence is indicative of predation by crabs. Letters denote significant differences.

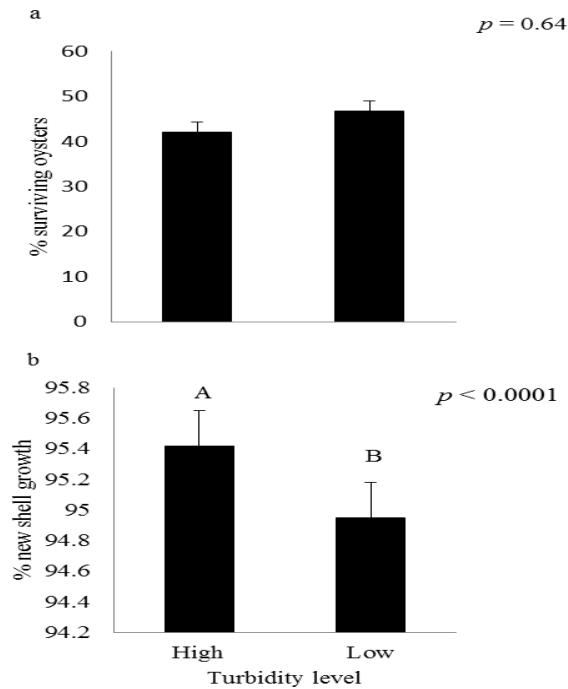


Figure II-5. Oyster survivorship and growth by turbidity. (a) Percent of surviving oysters from oyster predation experiments in St. Charles Bay; (b) Percent of growth dedicated to new shell in juvenile oysters protected from predation in St. Charles Bay. Letters denote significant differences.

predation and an increase in crab predation on tethered crabs, and a change in juvenile oyster morphology. While the decline in fish abundance in higher turbidity was seemingly small, the change is abundance altered predation rates as well as indirect effects propagating to lower trophic levels. In this regard, a change in fish abundance may mimic effects caused by overfishing. Removal of large predators is known to have drastic effects on terrestrial and aquatic food webs (Jackson et al. 2001, Myers et al. 2007, Anthony et al. 2008), and variables like turbidity that alter top-down forcing may produce similar effects.

In addition to turbidity, temperature and salinity were also important variables in this system, and these variables are well known to affect estuarine organisms (Day et al. 2009). I found significant relationships between turbidity and diversity, but our R^2 values were low. Low R^2 values are indicative of substantial variability within the data set, but the R^2 values for turbidity were similar to those of salinity and temperature, variables known to be important in governing estuarine systems (Day et al. 2009).

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 of 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 are taken monthly throughout the year while gill net surveys are conducted in the spring and fall when temperatures are more similar. The effect of salinity on

the abundance of species 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. Turbidity was the only variable to affect species abundance across gear types and is indicative of its importance in shaping estuarine communities. Turbidity, like temperature and salinity, should be considered an important factor affecting the abundances of estuarine species and interactions between them.

Over an 18 year period, fish (primarily red drum) were more abundant in low turbidity areas compared to highly turbid areas and crabs (primarily blue crabs) had the opposite pattern. Initially I was 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, I predicted that fish might avoid the sampling gear in clear water, but I saw the opposite pattern with fish abundance highest when turbidity was less than 30 NTU. A significant, negative relationship occurred between fish abundance and turbidity within the long term data set. Second, blue crab and mud crab abundances were higher in more turbid water in the 18 year data set and in field collections using modified throw traps on oyster reefs. Thus, sampling crabs across different turbidity levels using different gear types yielded similar results.

On oyster reefs, fish predation on mud crabs declined and large mud crabs were more abundant in higher turbidity. Although turbidity affected the abundances of fishes and crabs and predation on crabs, it did not alter predation on juvenile oysters. The omnivorous nature of predators in the system, (i.e, black drum, sheepshead and blue crabs) may explain this finding, as oysters are likely to be eaten in both low and high turbidity levels. 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 to produce heavier shells in response to the presences of 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.

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 larger size, they are more apparent to predators. 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 research is needed to test these hypotheses.

Predation on mud crabs was higher in higher turbidity and was attributed more often to crab than fish predators, which corresponds to the higher abundance of crabs in turbid conditions. I 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). It is also possible that the presence of fish predators cause mud crabs to seek refuge and decrease their feeding

rates (Grabowski and Kimbro 2005). These predation trends are in agreement with my findings that significantly more large mud crabs were present in more turbid areas and suggest that foraging of chemosensory predators like crabs is not influenced by turbidity at the levels measured in this study.

Turbidity also affected the basal trophic level, though the effects of turbidity on juvenile oysters were indirect as opposed to the direct effects seen in the top and intermediate trophic levels. In turbid areas with more mud crabs, juvenile oysters allocated more resources toward shell growth, which occurs in the presence of predators such as oyster drills and mud crabs (Lord and Whitlatch 2012, Johnson and Smee 2012), but which results in the production of less soft tissue (Johnson and Smee 2012). Heavier shells may have resulted from 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 phytoplankton, which suggests that food differences for oysters among study sites was not affecting growth rates (Table 1.1). Finally, adult oysters of similar initial size that were planted in these sites for several months did not differ in growth (Table 2.1). 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 variables or food availability. Because I did not find growth differences in the adult oysters, I attributed the changes in shell growth found in juvenile oysters to differences in crab abundance that were caused by increased turbidity.

Direct predation on juvenile oysters was not different between low vs. high turbidity sites, which may be attributed to the omnivorous nature of many oyster reef species (Bruno and

O'Connor 2005). Within this system, both fish and crabs consume juvenile oysters, and thus turbidity may not provide oysters with protection from predators but instead may change the type of predator preying on them. However, 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 research is necessary to determine to what degree fecundity is affected and how the tradeoff between shell and somatic growth in response to predators influences oysters on a long term time scale.

Turbidity decreases perceptive 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). Non-visual 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 variables 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 and 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 as 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 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 and other sensory mechanisms species may utilize to compensate for a reduction in visual capability (Dusenbery 1992). These effects of turbidity on predator-prey interactions were supported by my study and extended to include long-term, wide spread effects on community composition. This expands our knowledge of how abiotic variables within an organism’s tolerance range can act as a constraint on sensory information, acting as a sensory stressor (Smee et al. 2010) and alter community dynamics.

Oyster reef communities are indirectly affected by turbidity through modifications of trophic interactions. These effects are important as turbidity is increasing in coastal environments worldwide because of anthropogenic activities (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, seagrasses, and salt marshes reduce coastal stability and increase erosion (Grabowski and Peterson 2007), which may increase turbidity. Oysters act as filters removing suspended sediments, nutrients, phytoplankton and heavy metals from the water column (Jackson et al. 2001). Obviously, the interaction between turbidity effects and oyster reefs are complex, as by their very nature oysters can reduce turbidity levels caused by plankton blooms and are likely to be adversely affected by higher levels of turbidity. Thus, declining oyster populations may result in higher turbidities that ultimately lower oyster fecundity and

population size via indirect mechanisms. Clearly the effects of turbidity on oyster populations require further investigation.

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Chapter III. : Effects of turbidity on predation efficiency

ABSTRACT

Predation or top-down forcing can significantly affect communities, but predator effects can be attenuated when variables interfere with foraging activities. In estuarine communities, turbidity can affect species richness and abundance; I tested the effects of turbidity on modulating predatory interactions. Turbidity is increasing in many areas because of coastal development, but its effects on estuarine food webs are largely unexplored. I measured the predation rates of two predators: a visual predator (pinfish, *Lagodon rhomboides*) and a chemosensory predator (blue crabs, *Callinectes sapidus*) in clear and turbid water (0 and ~100 nephelometric turbidity units). Feeding assays were conducted with two prey items, mud crabs (*Panopeus herbstii*) that rely heavily on chemoreception to detect predators, and brown shrimp (*Farfantepenaeus aztecus*) that use visual cues to detect predators. Turbidity reduced pinfish foraging on shrimp (shrimp: $p = 0.01$). In contrast, blue crab foraging was unaffected by turbidity, and blue crabs were able to successfully consume nearly all mud crab and shrimp prey in all treatments. Adding oyster shells as a predation refuge reduced predation by both predators. Turbidity is important in regulating predator-prey interactions by reducing the feeding efficiency of visual predators but not those of chemosensory predators. These effects may alter trophic interactions by interfering with vertebrate predators that rely on vision to forage, releasing mesopredators like crabs from top-down control, resulting in over consumption of lower trophic levels.

INTRODUCTION

Predators may affect prey populations and communities through lethal effects (e.g., consumption) and nonlethal effects (e.g., changes in prey behavior, Sih et al. 1985, Trussell et al.

2003). These effects can cascade through communities by causing changes in behavior, density, and distributions of multiple trophic levels (Sih et al. 1985, 1998, Menge 2000, Werner and Peacor 2003). The outcomes of predatory interactions are largely influenced by the ability of predators and prey to detect and respond to one another (Powers and Kittinger 2002). Perceiving a potential consumer or prey item before being detected offers a perceptive advantage that influences which organism will prevail in a given encounter (Powers and Kittinger 2002, Smee et al. 2010). When predators possess a sensory advantage over prey, lethal effects should be prevalent as predators should more often prevail in a given encounter. Likewise, prey can successfully avoid predators when they have a sensory advantage over predators and can detect and avoid them before being consumed. In these situations, nonlethal effects are likely to be prevalent. Perception is not static but can be strongly affected by environmental variables that alter the sensory abilities of both predators and prey (Dusenbery 1992, Weissburg et al. 2002, Smee et al. 2010). Understanding how environmental variables influence sensory abilities of predators and prey will yield insights into mechanisms that influence the nature and strength of indirect effects.

Hydrodynamic stress on wave-swept shores acts as the primary community regulator by reducing predator foraging ability rendering predation unimportant (Menge 1976).

Environmental stress may also alter predator-prey interactions less severely by influencing perceptive ability but not eliminating predation as a structuring force. For example, outcomes of predatory interactions between hard clams and their blue crab and knobbed whelk predators are strongly influenced by small-scale turbulence that affects perception but is not otherwise detrimental (Smee et al. 2008, 2010, Ferner et al. 2009). In situations where both predators and prey are affected by the same environmental variables, and variables minimize the sensory

abilities of both species, top-down forcing is likely to decline and the effects of predators on prey populations may shift from a combination of lethal and nonlethal effects to exclusively lethal effects as encounters become random (van de Meutter et al. 2005).

In freshwater systems, turbidity as low as 20 nephelometric turbidity units (NTU), a measure of light penetration, can diminish visual acuity and decrease prey capture success and competitive interactions (Hazelton and Grossman 2009). This decrease in predator efficiency may make turbidity a predation refuge from visual predators (DeRobertis et al. 2003, Engström-Öst et al. 2009). In contrast, turbidity would not likely interfere with chemosensory foragers and might actually increase predation if it compromised a prey's ability to avoid predators (Chapters 1&2).

Variable predation rates often noted within turbidity studies may result from use of chemical, mechanical, or auditory cues by predators and prey that would not be affected by turbidity (Minello et al. 1987, Abrahams and Kattenfeld 1997, DeRobertis et al. 2003, Radke and Gaupisch 2005). Use of sensory cues other than vision decreases the effect of turbidity on predation rates. For example, in a previous experiment the effect of turbidity was not consistent in three different fish species based on the number of sensory cues used. Pinfish are primarily visual and were most affected by turbidity. Croaker predation success was also decreased by turbidity but less so as they use olfaction and touch in addition to vision (Minello et al. 1987). However, southern flounder predation on juvenile brown shrimp increased in elevated turbidity likely as a result of flounder using additional sensory cues and using lie-in-wait predation tactics (Minello et al. 1987).

Turbidity alters predator-prey interactions in both freshwater and marine systems by altering perceptive ability of predators and prey (Minello et al. 1987, DeRobertis et al. 2003,

Sweka and Hartman 2003, Webster et al. 2007, Ohata et al. 2011). Previously, the abundance of fish and crabs was found to be significantly affected by turbidity with fish predators being more abundant in low turbidity areas and crabs in high turbidity (Chapters 1&2). These changes in predator type altered predation efficiency: fish predation decreased with increasing turbidity whereas crab predation increased with increasing turbidity (Chapter 2). I hypothesized that turbidity influences predator-prey interactions by offering a perceptive advantage to non-visual species and alleviating predation pressure by fishes on them.

To test this hypothesis I measured the predation efficiency of a visual predator (pinfish, *Lagodon rhomboides*) and a chemosensory predator (blue crabs, *Callinectes sapidus*) in both low (0 NTU) and high (100 NTU) turbidity on a visual (brown shrimp, *Farfantepenaeus aztecus*) and chemosensory (mud crabs, *Panopeus* spp.) prey resource. While turbidities as low as 20 NTU in freshwater systems (Hazelton and Grossman 2009) and 30 NTU in marine systems (Minello et al. 1987), 100 NTU was used in this study for logistical reasons. These species were chosen because their abundances were affected by turbidity in an analysis of a 20 year data set from Texas Parks and Wildlife Department (Table 1.5) and are locally abundant and easily collected for experimental trials. Pinfish were used as a model fish predator because they are at a similar trophic level to blue crabs preying on smaller predators (e.g., mud crabs) but also being preyed on by larger fish and birds. Mud crabs are an omnipresent meso-predator on oyster reefs that are chemosensory and have low mobility. Conversely, brown shrimp are prey items which are more visually oriented and more mobile. To determine if the effects of turbidity on predation efficiency extended to lower trophic levels, juvenile oysters (*Crassostrea virginica*) were used as a basal resource for mud crabs in a separate experiment. This model system allowed me to test the effect of turbidity on predator-prey interactions that include multiple sensory modalities.

METHODS

Mesocosms

The study was conducted in outdoor mesocosms at Texas A&M University – Corpus Christi. The mesocosms consisted of 16 opaque, polyethylene tanks with lids. Tank lids had small windows covered with Vexar mesh that allowed a small amount of light in over the course of the experiment; in addition there was a safety light which was on at night near where the tanks were kept which prevented natural lighting conditions. Each tank contained 68 L of artificially created saltwater at a salinity of 20, and an Aqueon aquarium filter and Oceanic 250 gallon per hour aquarium pump. The filter and pump were used to aid in water circulation and to keep sediments suspended in the turbidity treatments. For turbid treatments, 235 mL of finely ground kaolinite clay was added to the tanks. Kaolinite clay is inert clay commonly used in previous turbidity research to mimic turbidity caused by sediments. Pumps were used in both clear and turbid treatments to avoid bias.

The model food web consisted of two predators and two prey. Pinfish (*Lagodon rhomboides*; 125-188 mm total length) were used as the visual predator and blue crabs (*Callinectes sapidus*; 100-130 mm carapace width) as the chemosensory predator. Both predator species varied with turbidity (Table 1.5) and both are abundant and easily collected locally. Both a chemosensory (mud crabs, *Panopeus sp.*; 10-15 mm) and visual (brown shrimp, *Farfantepenaeus aztecus*; 70-100 mm) prey source were used to investigate the effect of turbidity on both predators and prey.

To determine if the effects of turbidity on predation rates altered trophic cascades, additional mud crab feeding assays were performed using created oyster reefs and juvenile oysters. Oyster reefs were created in the tanks with 2.5 L of sun-bleached oyster shell to mimic a

natural reef. A three-tier food web was used with pinfish, and blue crabs as top predators, mud crabs as an intermediate predator and juvenile oysters (*Crassostrea virginica*, 2-5 mm) as a basal resource .

Feeding Assays

Feeding assays were conducted with 8 mud crabs or 4 brown shrimp as a prey resource. The tanks were randomly assigned, one of four predator treatments and one of two turbidity treatments: no predator control, blue crab (2 crabs), pinfish (2 fish) and mix (1 fish and 1 crab) in either turbid (>100 NTU) or clear (~ 0 NTU) water (Table 3.1). The turbidity in the turbid treatment was determined because of logistical reasons. Maintaining the turbidity at lower levels was inconsistent within the mesocosm tanks and therefore a very high turbidity value was used. Treatments were fully crossed (all predator treatments were conducted in both clear and turbid treatments) and trials lasted for 72 hr (n=6). Trials were conducted weekly until all replicates were completed. At the end of each trial the number of live and non-consumed dead prey items were recorded. No blue crabs or pin fish perished during the study.

Trophic Cascade

Turbidity effects on trophic cascades were measured using the three-tier food web described above. To the created reefs, 2 oyster shells containing 10 marked spat (2-5 mm) per shell were added as the basal resource. Oyster spat from a local supplier were settled onto sun-bleached oyster shell in a large outdoor tank. Four mud crabs were added to each tank. Treatments were fully crossed and performed weekly (n=9). Each experimental trial lasted 72 hr. At the end of each trial the number of live mud crabs, non-consumed dead mud crabs and live oyster spat were recorded. No blue crabs or pin fish died during the study.

Table III-1. Experimental design for feeding assays. Predator treatments included Crab (2 blue crabs), Fish (2 pinfish), Mix (1 blue crab and 1 pinfish), and Control (no predator). Prey treatments included MC (4 mud crabs) and S (2 brown shrimp)

	High (100 NTU)								Low (0 NTU)							
Predator	Crab		Fish		Mix		Control		Crab		Fish		Mix		Control	
Prey	MC	S	MC	S	MC	S	MC	S	MC	S	MC	S	MC	S	MC	S

Analysis

Differences in the number of eaten prey between predator and turbidity treatments were analyzed using a blocked 2-way ANOVA with predator and turbidity treatments as fixed factors and week as the blocking factor (Sokal and Rohlf 1995). For the trophic cascade analysis the number of consumed mud crabs and juvenile oysters were analyzed separately using a blocked 2-way ANOVA with predator and turbidity treatments as fixed factors and week as the blocking factor (Sokal and Rohlf 1995). Juvenile oyster consumption was analyzed for a single shell. Approximately half of the shells were not recovered at the conclusion of the trials because of the impermanence of markings.

RESULTS

Feeding Assays

Predation on mud crabs was affected by the predator treatment ($F_{3,44} = 118.41, p < 0.0001$; Figure 3.1b) but was not significantly affected by turbidity ($F_{1,44} = 1.95, p = 0.17$; Figure 3.1 a & c). There was no interaction between turbidity and predator type ($F_{3,76} = 0.28, p = 0.84$) and week was not significant ($F_{2,44} = 0.85, p = 0.44$). Blue crabs consumed all available prey items in both crab and mix treatments. Trials lasted 3 days to detect predation rates in pinfish,

however, this duration may have been too long to detect any effects of turbidity on blue crab predation rates.

The number of shrimp consumed was affected by both turbidity ($F_{1, 65} = 6.74, p = 0.01$) and predator type ($F_{3, 65} = 90.83, p < 0.0001$). Fewer shrimp were eaten in the turbid treatments. This pattern was driven by a reduction in pinfish predation in turbid treatments (Figure 3.2). When blue crabs were present, all shrimp were consumed regardless of turbidity. There was no interaction between predator type and turbidity ($F_{3, 65} = 1.93, p = 0.14$) and week was not a significant factor ($F_{3, 65} = 0.92, p = 0.44$).

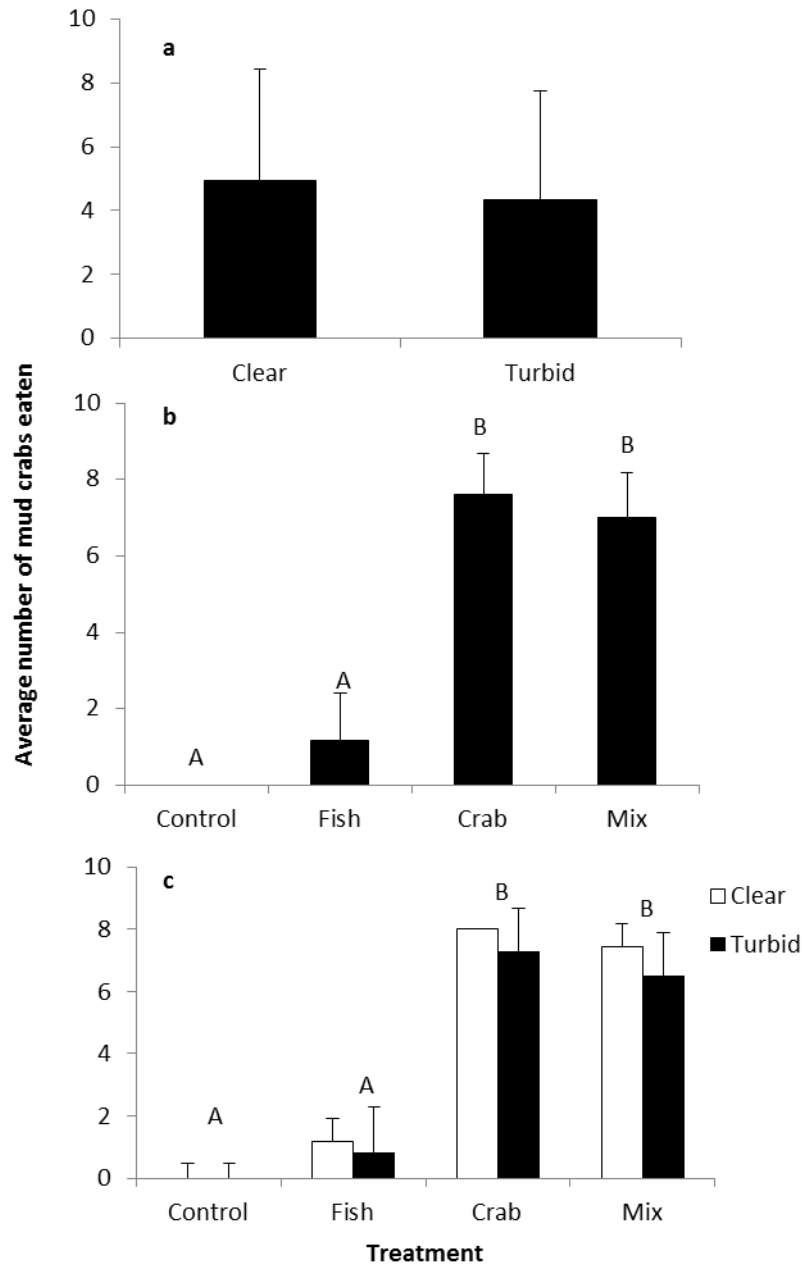
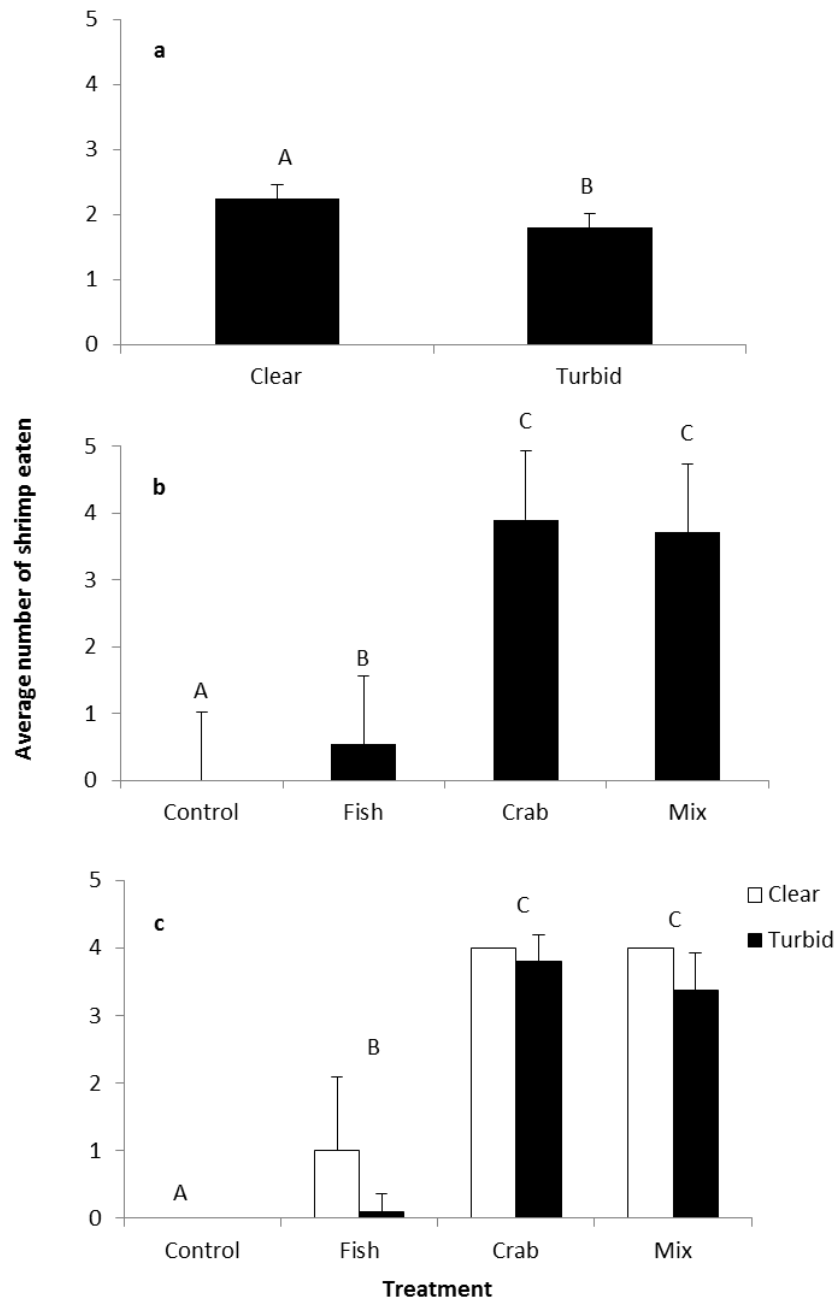


Figure III-1 Results of mud crab feeding assay. a. Average number of mud crabs eaten by turbidity level. b. Average number of mud crabs eaten by predator treatment. c. Comparison of mud crabs eaten between clear and turbid treatments for each predator treatment. Letters denote significant differences.



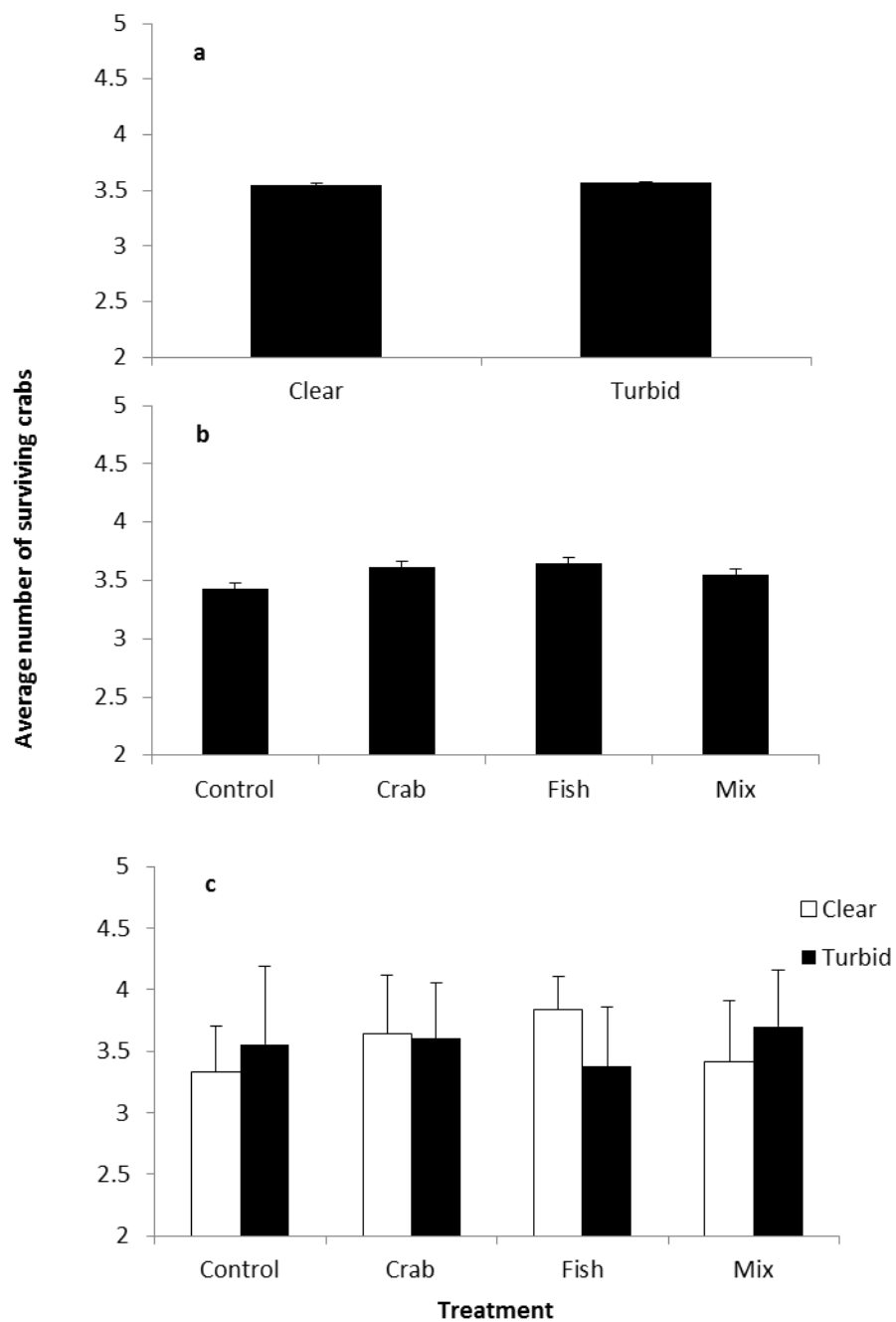


Figure III-3. Trophic cascade mud crab results. a. Average number of mud crabs eaten between clear and turbid treatments. b. Average number of mud crabs eaten by predator treatment. c. Comparison of mud crabs eaten between clear and turbid treatments for each predator treatment. Letters denote significant differences.

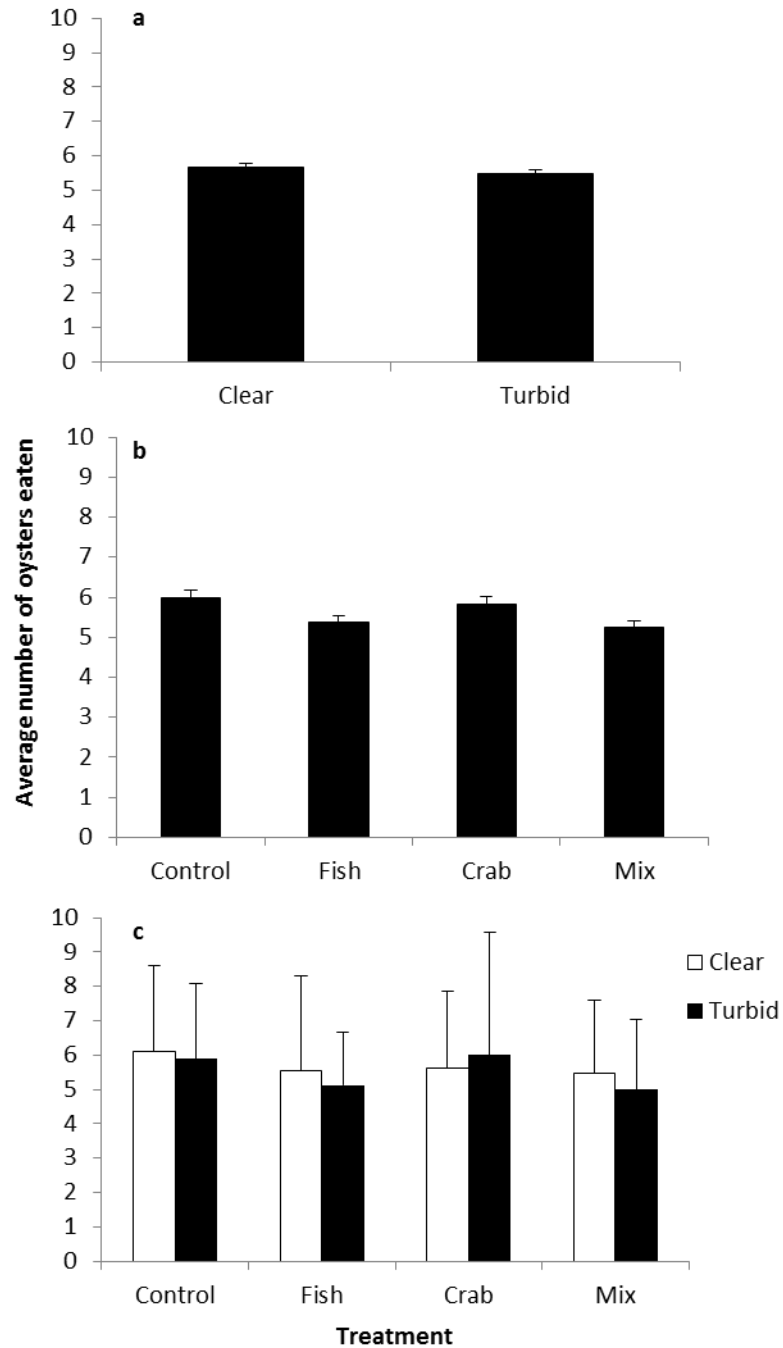


Figure III-4. Trophic cascade oyster results. a. Average number of oysters eaten between clear and turbid treatments. b. Average number of oysters eaten by predator treatment. c. Comparison of oysters eaten between clear and turbid treatments for each predator treatment.

Food Web Design

There was no effect of turbidity or predator type on mud crab survival. Mud crabs were successful in avoiding all predators ($F_{3,84} = 0.79, p = 0.50$; Figure 3.4b-c) in both low and high turbidity ($F_{1,84} = 0.44, p = 0.51$; Figure 3.4a). There was no interaction between predator type and turbidity level ($F_{3,84} = 0.60, p = 0.62$) and week was not a significant factor ($F_{5,84} = 1.37, p = 0.24$). Despite the lack of direct predation on mud crabs, juvenile oysters were also not affected by top predators ($F_{3,76} = 0.42, p = 0.74$; Figure 3.5b-c) or turbidity level ($F_{1,76} = 1.45, p = 0.23$; Figure 3.5a). There was no interaction between predator type and turbidity ($F_{3,76} = 0.46, p = 0.71$), though week was a factor ($F_{5,76} = 5.23, p = 0.0004$).

DISCUSSION

Turbidity can alter food webs in coastal marine environments and switch predator fields from fish to crab dominated, which alters predation pressure and biodiversity (Chapters 1&2). This switch is explained by the negative effects of turbidity on pinfish and on other visual predators (van de Meutter et al. 2005, Hazelton and Grossman 2009). As turbidity increases, visual predators like pinfish are less successful in foraging and may avoid areas of high turbidity where they are less efficient foragers and are perhaps vulnerable to their own consumers (Snickars et al. 2004, Liljendahl-Nurminen et al. 2008). Crabs forage primarily through chemoreception, which would not be affected by increased turbidity at the levels used in this study; crabs become the predominant predator in highly turbid areas. Blue crabs are also a prey species to many fish and bird species and may seek out turbidity as a refuge from these consumers (DeRobertis et al. 2003, Engström-Öst et al. 2009), thereby increasing their abundance in high turbidity sites (Table 1.5, Chapters 1 & 2). This could lead to a collapse of the food web in areas of high turbidity where crabs may decimate prey items. Yet, blue crab

predation was mediated by providing a predation refuge. When oyster shell was present, blue crabs were unsuccessful in consuming mud crabs. However, in the absence of oyster shell substrate, blue crabs were not affected by turbidity and consumed all of the prey available in both the crab and mix predator treatments.

Pinfish were less successful consumers in high turbidity treatments and consumed significantly fewer shrimp in these conditions. Predation by pinfish on mud crabs was not statistically significant. The lack of significance could be attributable to an outlier in the data. In a high turbidity replicate four mud crabs were consumed as opposed to zero mud crabs consumed in all other high turbidity replicates. Reduced consumption in turbid treatments by pinfish is more likely a result of pinfish being unable to find shrimp because of their reliance on vision to forage. Brown shrimp are more active in turbid treatments though this does not affect foraging success with active predators (Minello et al. 1987). However, brown shrimp are also not purely visual and may have been better able to avoid encounters in turbid treatments by reacting before a fish could see the shrimp. These results mirror previous studies in which predation by visual predators declined in elevated turbidity (DeRobertis et al. 2003, Sørnes and Aksnes 2004, Engström-Öst et al. 2009, Ohata et al. 2011). However, turbidity would not be expected to affect predators using other sensory modalities at the levels used in this study (Eiane et al. 1999, Ohata et al. 2011). The effects of turbidity on foraging efficiency of visual predators but not chemosensory predators helps explain the reduction in fish abundance but increase in crab abundance areas of increased turbidity (Chapters 1&2).

The effects of turbidity on visual predators did not extend to lower trophic levels when simulated oyster reefs were used. These results are similar to results from the field where predation on juvenile oysters was not affected by increased turbidity (Chapter 2). Lack of an

effect of predators on mud crab survival in tanks with simulated oyster reefs may be a result of increased refuges which were inaccessible to predators as the tanks prevented much movement of oyster shell. Oyster reefs provide structured habitat which may act as a refuge for mud crabs from predation attenuating the negative effects of turbidity. Small mud crabs utilize the interstitial spaces on oyster reefs as a refuge from predators (Meyer 1994). In this way structure may interact with increased turbidity to reduce predation rates by chemosensory predators attenuating the negative effects of turbidity. The attenuation of negative predator effects by habitat structure is unlikely to increase juvenile oyster consumption by mud crabs as the presence of a predator suppresses mud crab feeding regardless of habitat complexity (Grabowski and Kimbro 2005). However, in the field, increased turbidity indirectly affected juvenile oysters which allocated a higher percentage of their energy toward shell growth (Chapter 2). This indirect effect may decrease fecundity and limit the growth of oyster reefs in continually turbid areas. Smaller oysters would increase loss of habitat complexity removing the mitigating effects and allowing chemosensory predators to decimate lower trophic levels.

The effects of turbidity on foraging efficiency may have large-scale implications for coastal systems as turbidity increases. Many chemosensory predators are crabs which are also consumed by higher order visual predators such as fish and birds. Increased turbidity decreases visual predators foraging efficiency likely causing visual predators to avoid these areas and releasing crabs from top-down control (Domenici et al. 2007). Meso-predator release can result in the collapse of food webs (Jackson et al. 2001, Myers et al. 2007). For example, overfishing has removed many shark species allowing ray species to proliferate and decimate their bivalve prey (Myers et al. 2007). This study indicates that environmental variables can mimic the effects of overfishing and potentially cause widespread changes to coastal communities.

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Chapter IV. : Wave energy reduces the abundance and size of benthic species on oyster reefs

ABSTRACT

Hydrodynamic forces associated with waves are a well-known to affect the structure and function of rocky intertidal communities, but the effects of waves on species composition and size within soft sediment communities are less understood. Using oyster reefs as a model system, the effects of hydrodynamics (i.e. wave height, wave period, flow velocity) on diversity and species size were examined among Copano, Aransas and St. Charles Bays which are within the Mission-Aransas National Estuarine Research Reserve near Rockport, TX, USA. Oyster reef communities were sampled at sites adjacent to the wave measurement locations in each bay. Wave height and flow velocity were lowest and species richness and abundance were highest in St. Charles Bay. Crabs were the most abundant organisms collected, and they were significantly larger in St. Charles Bay. Copano Bay was intermediate between St. Charles and Aransas Bays for wave height and species richness but had the highest abundances of organisms. Aransas Bay had the highest waves and flow velocities and the lowest species richness, and abundances. Increased wave height decreased organism size for all bays. As along rocky shores, waves also appear to regulate species diversity, abundance and size on oyster reefs.

INTRODUCTION

Hydrodynamic forces are important community regulators in rocky intertidal systems (Sousa 1979, Denny et al. 1985, Denny and Gaylord 1996, Leonard et al. 1998, García-March et al. 2007), morphologies (Denny and Gaylord 1996, Boulding et al. 1999, Denny 1999), influencing species distributions (Leonard et al. 1998, García-March et al. 2007), and interactions (Powers and Kittinger 2002, Smee et al. 2010, Robinson et al. 2011). Species are

often smaller in areas of intense hydrodynamic conditions than conspecifics in wave-protected areas (Denny et al. 1985, Denny 1999). For example, *Pinna nobilis*, a large bivalve mollusk, are smaller in areas of increased hydrodynamic energy and alters its orientation to reduce drag (García-March et al. 2007). Similarly, plate urchins have lost their identifying spines, streamlining their morphology to adapt to intense hydrodynamic forces within the surf zone (Denny and Gaylord 1996).

Interactions between hydrodynamic forces and predation also affect species morphology when species choose habitats with intense hydrodynamic forcing to avoid predation. For example, intense wave pressure in rocky intertidal systems causes a littorinid gastropod to be smaller, have thinner shells and larger apertures; and these morphological changes compensate for increased hydrodynamic stress and reduced predation risk (Boulding et al. 1999). This type of phenotypic plasticity is widespread in intertidal gastropods and is dependent on the habitat in which the snail developed and predator presence. Although marine snails exhibit phenotypic plasticity, the degree of expression is strongly dependent upon the habitat from which they are collected. For example, *Nucella* collected from wave-protected sites grew heavier shells than did those from wave-exposed sites in response to predator exudates from both native and invasive crabs (Large and Smee 2013).

However, intense wave pressure and flow velocity can also render predation effects unimportant and act as the primary agent of community regulation by limiting predator foraging ability and increasing competition (Menge 1976, Menge and Sutherland 1987, Leonard et al. 1998). Hydrodynamic forces also influence predatory interactions by altering perceptive abilities. For example, blue crabs are less able to perceive hard clam prey as flow velocity and turbulence increase (Smee et al. 2010). In fast flow areas, crabs are actually more abundant than in adjacent

low flow sites, but, overall predation pressure is reduced by hydrodynamic forces that compromise crab predator's ability to find and handle prey (Leonard et al. 1998, Robinson et al. 2011). However, the effects of flow on predation success are dependent on predator identity. For example, blue crabs are less effective predators in fast flows with high turbulence, but knobbed whelks are more efficient in these same conditions (Powers and Kittinger 2002).

Hydrodynamic forces in rocky intertidal systems have been studied primarily for their effects predator movement and distribution (Menge 1976, Sousa 1979, Menge and Lubchenco 1981, Leonard et al. 1998), but in soft-sediment communities, effects of hydrodynamics have been largely studied for their effects of chemical signaling between organisms (Weissburg and Zimmer-faust 1993, Ferner and Weissburg 2005, Smee et al. 2010). Here, we elected to study the relationship between waves and the size and distribution of organisms on oyster reefs, a community in which wave effects have not been well studied. Oyster reefs are one of the most degraded marine habitats, but there is considerable interest and efforts in restoring them because they provide numerous ecosystems services (Coen and Luckenbach 2000, Coen et al. 2007, Beck et al. 2009). Oyster reefs provide essential habitats for other recreational and commercially important organisms, protect shorelines, and remove harmful organisms and excess nutrients from the water through filtration (Grabowski et al. 2005, Grabowski and Peterson 2007) and they are the subject of extensive restoration efforts (Coen and Luckenbach 2000, Coen et al. 2007, Beck et al. 2009). However, the success of oyster reef restoration efforts are variable (Coen and Luckenbach 2000). Understanding how abiotic variables shape oyster reef communities is essential to increasing restoration success. Abiotic variables such as flow, salinity and disturbance are known to affect oyster recruitment, growth, and survival as well as community diversity on the oyster reefs (Gunter 1955, Lenihan 1999, Kimbro and Grosholz 2006, Pollack et

al. 2010). However, the effects of hydrodynamic forces on oyster reef fauna have not been well investigated.

The Aransas Bay complex is an ideal system in which to test the effects of hydrodynamic forces on soft sediment communities. The bays have a network of natural, intertidal, oyster reefs that are subject to a variety of wave regimes but otherwise have similar abiotic conditions. These reefs also have similar species inhabiting them allowing size comparisons to be made between different hydrodynamic conditions. To test the hypothesis that organism size and abundance on oyster reefs are influenced by wave energy, a field survey was conducted to compare wave size and frequency with species richness, abundance, and size of individuals.

METHODS

Study site

Natural oyster reefs (*Crassostrea virginica*) near Goose Island State Park in St. Charles, Aransas and Copano Bays, Texas were selected for an empirical study on the effects of waves on community composition and organism size. To ensure selection of oyster reefs that differed in wave action but otherwise experienced similar abiotic variables and had similar habitat structure, we selected field sites along an oyster reef at the mouth of St. Charles Bay at the interface of St. Charles and Aransas Bays in addition to sites within Copano Bay (Figure 4.1). The St. Charles and Aransas Bay sites were separated by ~100 m but were connected by small channels . All study reefs were ~ 0.5 m in depth. The oyster reefs within this bay system were 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.

Wave Energy Monitoring

Acoustic Doppler Velocimeters were deployed within our sites to measure wave action within Copano, St. Charles and Aransas Bays. Two ADVs were placed along an oyster reef in Copano Bay. Within St. Charles and Aransas Bays two pair of instruments were splaced across the oyster reefs from one another, with one instrument in St. Charles Bay and one in Aransas Bay.

Instruments were deployed for one week in May 2013. Instruments were programmed to record for 20 seconds every 15 minutes at 8 Hz. Wave data were processed with the QuickWave 2.10 and Explore V Pro © software packages. These software packages summarized wave height, period, and direction, as well as velocity and turbulence (Table 4.1).



Figure IV-1. Map of field sites. Stars represent the general areas sampled. There were 2 advs and 6 community sampling replicates per star.

Community sampling

To assess oyster reef associated species composition each site was sampled using a modified throw trap (Rozas and Minello 1997). Within each study site, a 0.25 m² area was cleared of oyster clumps and shells. Within the clearing, a 0.25m² tray containing 25 L of sun-bleached oyster shells was placed. Trays were anchored within natural reefs in six pairs with a caged and uncaged tray at each site. Caged trays were covered in vexar mesh with 10 x 10 cm openings cut out. Caging was done to prevent loss of oyster shell to wave action and also to determine if larger organisms would be attracted to more stable substrate. Trays in St. Charles and Aransas Bays were paired across the oyster reef that separates the bays. The trays were deployed in the field in March and natural recruitment occurred until tray retrieval in August.

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 transported to the lab 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 does allow the small cryptic species to be sampled. Total length was measured for all fish and shrimp species, and carapace width was used for crab species. Organisms were measured using digital calipers. The following species were found in all 3 bays: snapping shrimp (*Alpheus* sp.), pinfish (*Lagodon rhomboides*), skillet fish (*Gobiesox strumosus*), gulf toadfish (*Opsanus beta*), porcelain crabs (Porcellanidae), mud crabs (*Panopeus* spp.) and gulf stone crabs (*Menippe adina*). For length analysis, all brachyuran crabs (*Panopeus herbstii*, *Panopeus turgidus*, *Eurypanopeus depressus*, and *Menippe adina*) were combined into a single category because the low abundance of several species did not allow separate comparisons. Simpson's diversity, species richness, and total

abundance were calculated for each sample in PRIMER™. Differences in communities among sites were compared with SIMPER analysis in PRIMER™. Porcelain crabs were so abundant that they masked other species, so the data were analyzed again without porcelain crabs as a group. Simpson's diversity, species richness, total abundance, and average size of regularly occurring species were compared individually using a 2-way ANOVA, with bay and cage as fixed factors (Sokal and Rohlf 1995).

RESULTS

Wave Energy Monitoring

Wave height and flow velocity differed between bays but wave period and direction did not. Wave height was smallest in St. Charles Bay and largest in Aransas Bay (Table 4.1). Similarly, flow velocity was highest in Aransas Bay and lowest in St. Charles Bay (Table 4.2). Wave height and flow velocity in Copano Bay were intermediate between St. Charles and Aransas Bays. Logistics precluded the use of instruments to record other abiotic features over the course of this study.

Community Sampling

Community dissimilarity values were 76.5% between St. Charles Bay and Aransas Bay, 59.7% between Aransas Bay and Copano Bay, and 66.6% between Copano Bay and St. Charles Bay. Porcelain crabs (Porcellanidae) were the most abundant species within the samples and were most important in determining dissimilarity between the bays (Table 4.3). When porcelain crabs were removed from analysis, shrimp and gastropods were most influential in the

dissimilarity patterns between bays with Aransas Bay and St. Charles being 74.4% dissimilar, Aransas Bay and Copano Bay 71.7% dissimilar, and Copano Bay and St. Charles Bay are 81.82% dissimilar (Table 4.4).

When porcelain crabs were included in the analysis; St. Charles Bay which had the lowest wave heights was more diverse than Aransas Bay but not Copano Bay ($F_{2,35} = 38.71, p < 0.0001$; Figure 4.2a). Aransas Bay had the highest waves and the highest abundance of organisms when porcelain crabs were included followed by Copano Bay (intermediate wave heights) and finally St. Charles (lowest wave heights) had the least abundance ($F_{2,35} = 11.53, p = 0.0002$; Figure 4.2e). However, when porcelain crabs were removed, Simpson's diversity was higher in St. Charles Bay than Copano Bay but not Aransas Bay ($F_{2,35} = 16.86, p < 0.0001$; Figure 4.2b). Total abundance was highest in Copano Bay which had intermediate wave heights and not different between Aransas Bay and St. Charles Bays ($F_{2,35} = 23.14, p < 0.0001$; Figure 4.2f). Species richness was not different between St. Charles and Copano Bays but was lower in Aransas Bays regardless of whether porcelain crabs were considered in the analysis ($F_{2,35} = 8.36, p = 0.001$; $F_{2,35} = 23.14, p = 0.0001$; respectively; Figure 4.2c-d). There was no effect of the cage or an interaction between the cage and bay with or without porcelain crabs ($p > 0.2$; For all ANOVAS, Table 4.5 & 4.6).

Table IV-1. Summary of wave data. Significant Height is the mean height in meters of the highest third of all waves recorded, Zero Crossing Period is the average period in seconds for all the waves in a burst, Unidirectivity Index is how much of the wave energy is going in one direction on a 0-1 scale with 1 meaning the energy is coming from a single direction. SC stands for St. Charles Bay, AB stands for Aransas Bay and CB stands for Copano Bay.

	Significant Height (m)		Zero Crossing Period (s)		Unidirectivity Index	
	Average	Range	Average	Range	Average	Range
SC	0.03	0.01-0.13	1.31	1.22-1.39	0.95	0.24-1
SC	0.07	0.01-0.15	1.29	1.24-1.37	0.96	0.4-1
AB	0.18	0.01-0.35	1.31	1.23-1.35	0.98	0.24-1
AB	0.26	0.02-0.59	1.38	1.24-1.43	0.99	0.27-1
CB	0.08	0.01-0.6	1.31	1.23-1.35	0.93	0.33-1
CB	0.14	0.01-0.57	1.32	1.24-1.35	0.99	0.66-1

Table IV-2. Summary of flow data. Flow and turbulence columns are for the instrument. Velocity (cm/s) and turbulence (cm/s) measurements are also reported for each probe. X, Y, and Z represent directional velocity components.

			X		Y		Z	
	Flow	Turbulence	Velocity	Turbulence	Velocity	Turbulence	Velocity	Turbulence
SC	2.44	4.88	1.31	1.79	0.55	2.89	1.75	3.53
SC	5.06	1.83	1.82	0.99	2.61	1.19	3.78	0.92
AB	5.17	18.53	4.86	8.18	1.37	11.19	0.49	7.36
AB	8.19	18.76	6.53	10.34	4.71	13.47	0.74	7.49
CB	5.60	8.25	1.30	4.29	0.99	4.42	5.23	5.52
CB	5.89	5.10	2.20	3.38	0.70	2.82	5.07	2.96

Brachyuran crabs were larger in the site with the lowest waves and velocities than in the sites with higher waves and flow velocities ($F_{2,36} = 3.86$, $p = 0.03$; Figure 4.3a). Snapping shrimp were larger in the high flow sites than in sites with lower waves and flows ($F_{2,17} = 4.2535$, $p = 0.04$; Figure 4.3b). Porcelain crabs were smaller in the high wave and flow sites in Aransas Bay than in Copano or St. Charles Bays ($F_{2,34} = 13.07$, $p < 0.0001$; Figure 4.3c). Pinfish, skillettfish and toadfish lengths were not different between bays ($F_{2,10} = 0.09$, $p = 0.91$; $F_{2,12} = 1.79$, $p = 0.25$; $F_{2,28} = 0.83$, $p = 0.45$; respectively; Figure 4.3d-f). Too few pinfish were collected to test for an effect of the caging treatment. There was no effect of cage and no interaction between cage and bay for any species ($p > 0.2$; for all ANOVAS, Table 4-7).

DISCUSSION

Hydrodynamic forces are important community regulators within rocky intertidal systems (Sousa 1979, Denny et al. 1985, Denny and Gaylord 1996, Leonard et al. 1998, García-March et al. 2007). In my research wave energy also plays a role in oyster reef communities by altering species distributions and sizes. On oyster reefs, species richness and crab size decreased with an increase in wave height and flow velocity. The effects of wave energy on oyster reef communities are more pronounced between St. Charles and Aransas Bays likely because these sites are closer and more likely to differ only in wave energy. Copano Bay sites were intermediate to Aransas and St. Charles Bay sites in wave height and flow velocities but not always intermediate in community metrics. This discrepancy could be a result of other differences among the sites. The Copano Bay site typically has lower salinities than do the St. Charles and Aransas Bay sites and is more exposed as it is situated in the middle of a large bay rather than near the shore. These differences likely account for the variability in the patterns seen in Copano Bay.

Aransas bay had the highest waves and the fastest flow velocities of the three bays sampled. St. Charles bay had the smallest waves and lowest flow velocities and Copano Bay was intermediate in both parameters of the bays sampled. Of the species collected, six were found in all three bays: brachyuran crabs, snapping shrimp, porcelain crabs, pinfish, skillettfish and toadfish. Crabs and shrimp sizes were significantly different between bays but fish sizes were not. Porcelain crabs were smaller in Aransas Bay than in Copano or St. Charles Bays, though they were more abundant in Aransas Bay. Porcelain crabs are suspension feeders and increased flows decrease their foraging efficiency (Achituv and Pedrotti 1999) perhaps contributing to their smaller sizes in the faster flow sites. Brachyuran crabs (mud and stone crabs) were smaller in Aransas and Copano Bays than in St. Charles Bay. The crabs found in Aransas and Copano Bays were ~10 mm carapace width, a size that still allows them to utilize interstitial spaces within oyster reefs as a potential refuge from waves and predators (Mcdonald 1982). The larger crabs found in St. Charles Bay are less able to exploit these interstitial spaces and are perhaps eroded from Aransas and Copano Bay reefs as a result of hydrodynamic forces. Snapping shrimp were larger in Aransas Bay than in Copano Bay and St. Charles. These shrimp project a smaller frontal area than the crabs and are likely not as detrimentally affected by hydrodynamics (Denny 1999). Fewer fish in Aransas Bay may decrease predation risk for the shrimp allowing them to achieve larger sizes.

Table IV-3. SIMPER with porcelain crabs. SIMPER analysis of community composition with Porcelain crabs. AB is Aransas Bay, SC is St. Charles Bay, and CB is Copano Bay

Species	Aransas Bay		Copano Bay		St. Charles Bay		AB vs SC	AB vs CB	CB vs SC
	Mean Density	% Similarity	Mean Density	% Similarity	Mean Density	% Similarity	% Dissimilarity	% Dissimilarity	% Dissimilarity
Alpheids	0.5	-	0.92	-	5.42	7.31	2.28	-	2.62
<i>Crassostrea virginica</i>	3.00	-	6.50	-	2.83	4.17	-	-	2.38
Gastropoda	8.92	-	72.00	34.11	2.25	-	2.63	19.55	31.16
<i>Palaemonetes</i> sp.	0.00	-	0.00	-	8.83	15.43	3.55	-	4.48
<i>Eurypanopues depressus</i>	0.83	-	2.50	-	3.67	4.49	-	-	-
Penaeids	0.00	-	0.00	-	9.58	5.89	3.35	-	5.12
Porcellanids	338.17	96.04	120.42	46.36	57.75	46.36	80.09	69.96	39.62
Brachyura	4.58	-	17.25	6.55	4.92	9.91	-	4.50	6.41

Table IV-4. SIMPER without porcelain crabs. SIMPER analysis of community composition without Porcelain crabs. AB is Aransas Bay, SC is St. Charles Bay, and CB is Copano Bay

Species	Aransas Bay		Copano Bay		St. Charles Bay		AB vs SC	AB vs CB	CB vs SC
	Mean	%	Mean	%	Mean	%	%	%	%
	Density	Similarity	Density	Similarity	Density	Similarity	Dissimilarity	Dissimilarity	Dissimilarity
Alpheids	0.5	-	0.92	-	5.42	12.18	10.03	-	4.16
<i>Crassostrea virginica</i>	3.00	15.26	6.50	6.68	2.83	9.22	6.61	5.47	4.06
Gastropoda	8.92	32.87	72.00	72.99	2.25	-	16.47	63.67	52.89
<i>Gobiesox strumosus</i>	0.67	-	1.17	-	0.42	-	2.19	-	-
<i>Ischadium recurvum</i>	1.58	5.86	1.58	-	0.33	-	3.33	2.07	-
<i>Menidia beryllina</i>	0.00	-	0.00	-	1.17	-	2.44	-	-
<i>Opsanus beta</i>	1.08	7.40	2.42	-	2.25	5.69	4.18	1.62	1.57
<i>Palaemonetes</i> sp.	0.00	-	0.00	-	8.83	29.74	17.71	-	7.26
<i>Eurypanopeus depressus</i>	0.83	5.31	2.50	-	3.67	7.5	5.83	3.25	3.12
Penaeids	0.00	-	0.00	-	9.58	8.66	14.31	-	7.07
Brachyura	4.58	28.41	17.25	13.99	4.92	18.24	8.37	15.25	11.06

Table IV-5. ANOVA for community assemblage metrics. ANOVA results reported for all community assemblage metrics. The left-hand column has results for analyses with porcelain crabs and the right-hand column has results for analyses without porcelain crabs.

With Porcelain Crabs				Without Porcelain Crabs			
Simpson's Diversity				Simpson's Diversity			
Factor	d.f.	F-statistic	p-value	Factor	d.f.	F-statistic	p-value
Bay	2	18.8800	0.0001	Bay	2	10.3056	0.0004
Cage	1	0.2201	0.6424	Cage	1	0.2837	0.5982
Interaction	2	0.8185	0.4507	Interaction	2	0.6462	0.5312
Species Richness				Species Richness			
Factor	d.f.	F-statistic	p-value	Factor	d.f.	F-statistic	p-value
Bay	2	10.6324	0.0003	Bay	2	10.9467	0.0003
Cage	1	0.6830	0.4151	Cage	1	0.9191	0.3454
Interaction	2	0.9865	0.3846	Interaction	2	0.8915	0.4206
Total Abundance				Total Abundance			
Factor	d.f.	F-statistic	p-value	Factor	d.f.	F-statistic	p-value
Bay	2	10.9496	0.0003	Bay	2	24.7076	0.0001
Cage	1	0.1649	0.6875	Cage	1	0.0077	0.9306
Interaction	2	0.9423	0.4010	Interaction	2	0.3259	0.7244

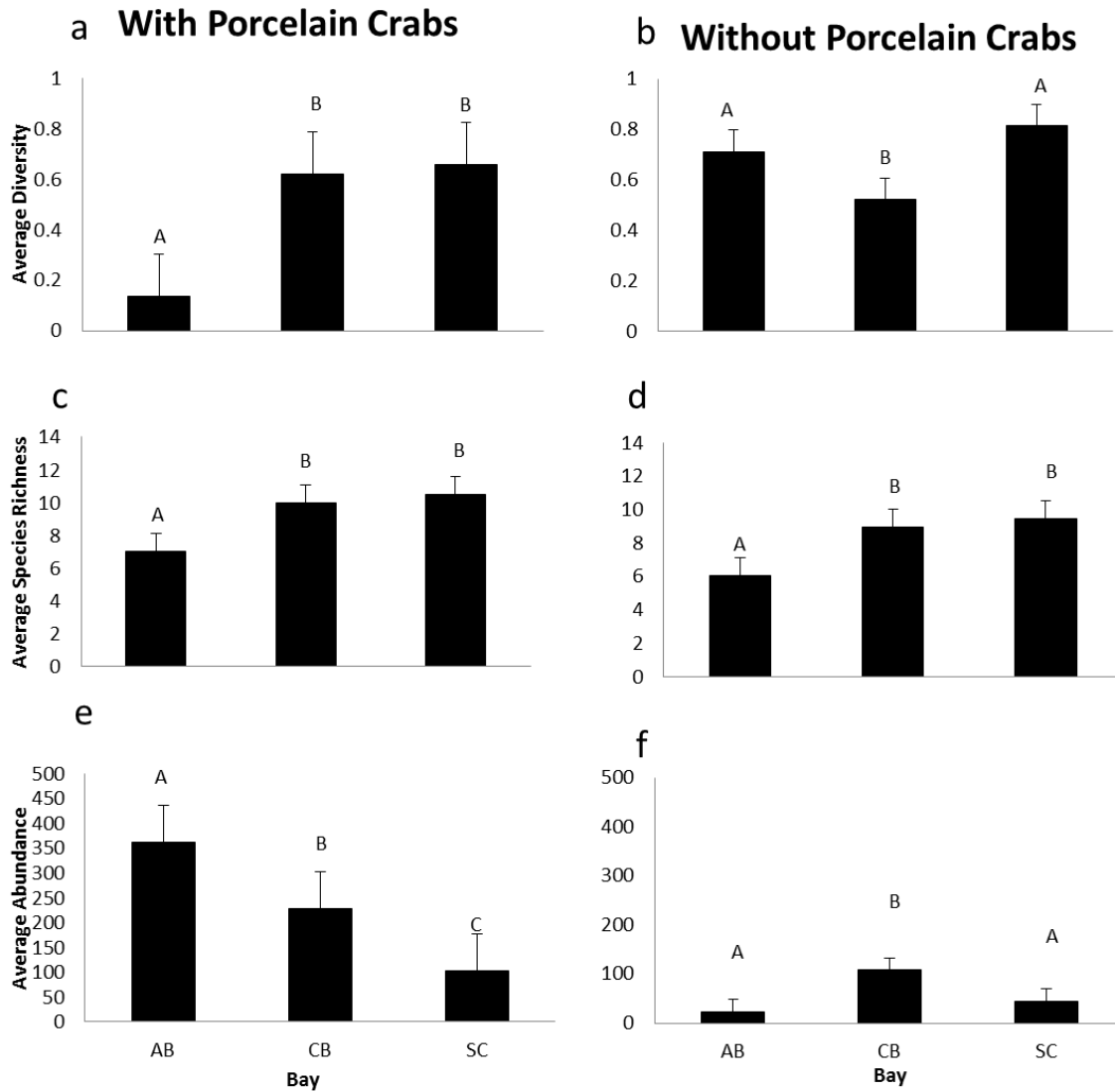


Figure IV-2. Community measurements. Comparisons of diversity, species richness and species abundance for Aransas Bay (AB), Copano Bay (CB), and St. Charles Bay (SC) with and without porcelain crabs. Letters denote significant differences.

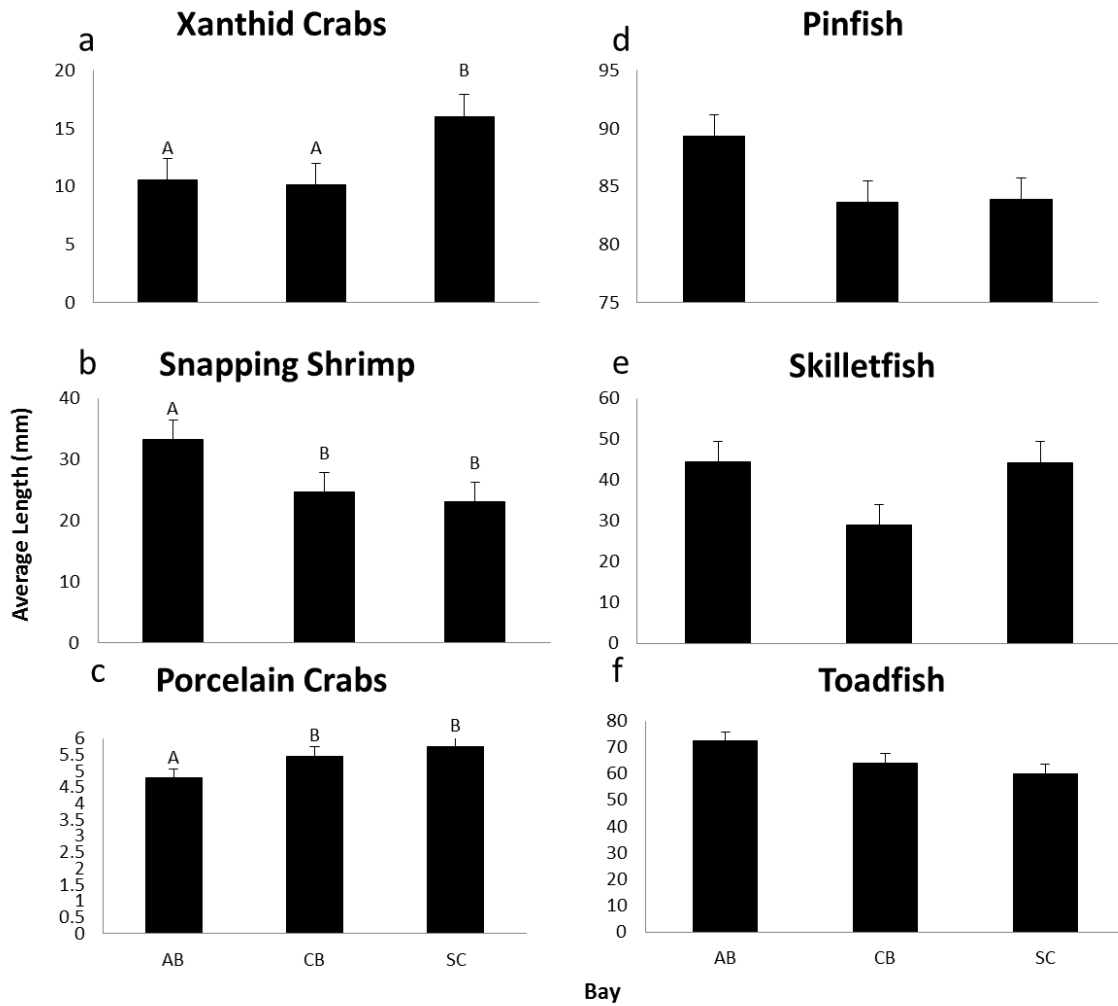


Figure IV-3. Organisms sizes. Average sizes for organisms occurring in all three bays. AB is Aransas Bay, CB is for Copano Bay and SC is for St. Charles Bay. Letters denote significant differences.

Table IV-6. ANOVA tables for organism lengths. ANOVA results for analyses of organism lengths. Too few pinfish were collected to compare between cage treatments.

Brachyuran Crabs				Skilletfish			
Factor	d.f.	F-statistic	p-value	Factor	d.f.	F-statistic	p-value
Bay	2	3.86	0.032	Bay	2	1.7938	0.2451
Cage	1	0.74	0.395	Cage	1	0.0427	0.8431
Interaction	2	0.56	0.578	Interaction	2	0.0106	0.9894
Snapping Shrimp				Toadfish			
Factor	d.f.	F-statistic	p-value	Factor	d.f.	F-statistic	p-value
Bay	2	4.2535	0.0428	Bay	2	0.8348	0.4472
Cage	1	0.0277	0.8707	Cage	1	0.2245	0.6403
Interaction	2	1.4591	0.2741	Interaction	2	1.2677	0.3012
Porcelain Crabs				Pinfish			
Factor	d.f.	F-statistic	p-value	Factor	d.f.	F-statistic	p-value
Bay	2	13.07	0.0001	Bay	2	0.0901	0.9149
Cage	1	0.4906	0.4894				
Interaction	2	0.5384	0.5896				

A number of factors play a role in how hydrodynamics shape communities including lift, drag and wave acceleration (Denny 1999). These forces often act in concert and it is rarely a single force that alters a species habitat use or morphology (Denny et al. 1985, Denny 1999). For example, plate urchins have lost their identifying spines which reduced drag but was offset by an increase in lift. However this morphological change makes the organism more resistant to the forces of water acceleration allowing it to utilize the surf zone (Denny and Gaylord 1996). These same forces could influence the sizes of oyster reef species. Larger mud crabs, not present in higher wave sites, may be washed off reefs with faster flows and larger waves through a combination of lift and drag forces that change with area. This effect of hydrodynamics on species influences a species ability to inhabit an area of reef and ultimately the associated community within the reef.

Sites were approximately 60% dissimilar in species composition. Aransas and Copano samples did not contain grass or penaeid shrimp species and fewer of the fish species found in St. Charles samples. Copano Bay had higher abundances of species found in both Copano and Aransas Bays than did Aransas Bay. Copano samples also included a large number of gastropods not found in other sites. Porcelain crabs were a very influential species in determining site dissimilarity. Aransas Bay was dominated by porcelain crabs with an average of 340 crabs per sample. St. Charles Bay had a much lower abundance of porcelain crabs averaging approximately 50 crabs per samples. However, brachyuran crabs were much more abundant and larger in St. Charles Bay than Aransas Bay. This difference in crab abundances is likely a result of porcelain crabs being readily consumed by xanthid crabs (Hollebone and Hay 2007).

The extremely high level of abundance of porcelain crabs obscured the effects of wave energy on other community members. Therefore, the communities were analyzed both with and

without porcelain crabs. When porcelain crabs were present in the analysis diversity and species richness were lowest in Aransas Bay but did not differ between St. Charles and Copano Bays. Aransas Bay had the highest abundance, followed by Copano Bay and then St. Charles Bay with the lowest abundance. The differences in abundance among bays was driven by porcelain crabs with an average of 340 crabs in Aransas samples, 120 crabs in Copano samples, and 50 crabs in St. Charles samples. When porcelain crabs were removed from the data analysis Aransas and St. Charles Bays did not differ in diversity or abundance but were different from Copano Bay. These similarities are likely a result of species and predators being able to move easily between sites through channels in the reef. Copano Bay samples had the lowest Simpson's diversity but the highest abundance. Species richness did not differ between St. Charles and Copano Bays but was lower in Aransas Bay. The similarity in species richness between Copano and St. Charles Bays may be because they have similar wave heights and flow regimes. These similarities may allow species to inhabit both sites that are unable to inhabit the more intense Aransas Bay sites.

Increased hydrodynamic stress can shape communities by alleviating predation pressure by actively interfering with predator movement and by making prey finding more challenging (Menge 1976, Menge and Sutherland 1987, Leonard et al. 1998, Smee et al. 2008). In this study, fewer nektonic fish, such as inland silversides and pinfish were found in the sites with higher flow and wave heights. The reduction in fish species richness and abundance among sites may be a result of fish being more limited by increased hydrodynamic stress than benthic species which can utilize the reef as a refuge. Mud crabs were most abundant in Copano Bay and least abundant in Aransas Bay. This pattern in mud crab abundance may be a result of the interaction between hydrodynamics and predation pressure. Copano Bay had an intermediate flow regime allowing mud crabs to inhabit the reef without being washed away but very few nektonic fish alleviating

predation pressure on the crabs. Aransas Bay and St. Charles Bay had very similar abundances of mud crabs perhaps because abundance is limited in Aransas Bay by hydrodynamics but by predation in St. Charles Bay. This pattern is similar to the nonlinear effect of flow on chemosensory prey and predators (Smee et al. 2010). The sampling method used in this study does not effectively sample large, mobile organisms (i.e., blue crabs and red drum) which are major predators on oyster reefs.

Oyster reefs are a critically endangered habitat of both ecological and economic importance (Grabowski and Peterson 2007, Beck et al. 2009) that are currently the subject of widespread restoration efforts (Coen and Luckenbach 2000). In order to successfully restore the ecosystem services offered by oyster reefs, the effects of abiotic variables on their ecosystem functioning must be well understood. Loss of fish species and larger crabs in areas of high wave energy may reduce prey availability for larger commercial and recreational species disrupting the food web. However, oyster reefs also attenuate wave energy as an ecosystem service (Grabowski and Peterson 2007) and the interaction between wave attenuation, and commercial and recreational benefits should be considered carefully. Reefs being restored to provide all three services should likely be created in a way mimicking the oyster reef sampled between Aransas and St. Charles Bays. This reef is far enough away from the coast for a sheltered community with many fish and shrimp species to develop on the St. Charles side while still providing wave attenuation. Oyster reef management plans should take wave energy into account when determining sampling locations for monitoring efforts. Areas along the reef subject to high waves and faster flows are not likely to be representative of all the species present on the reef.

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SUMMARIES AND CONCLUSIONS

This study demonstrates the importance of environmental variables in modulating the behavior of individual organisms as well as interactions between them that ultimately alter community structure and function. Turbidity was an important abiotic condition within estuarine systems and the effects of wave energy, well documented in rocky intertidal systems, was extended to oyster reef communities. The effects of these variables on estuarine communities should be considered in management and restoration efforts both on land and in the sea.

The effects of turbidity on trophic interactions and communities in estuaries is largely unexplored even though turbidity levels in coastal waters world-wide are increasing as a result of human induced erosion and eutrophication. Previous freshwater research documented the effects of turbidity on the predation efficiency of visual predators (Radke and Gaupisch 2005, van de Meutter et al. 2005, Liljendahl-Nurminen et al. 2008) but not the effects of turbidity on whole communities. Increases in turbidity decreased the abundance and diversity of large fish, while increasing the abundance and diversity of benthic organisms including crab predators in a long-term data set. Cryptic benthic species not sampled in the data set also increased in abundance with increased turbidity.

I attributed the change in community composition to decreased predation efficiency by fish predators, which leads to an increase in crab abundance and then alters communities through flattening of the trophic pyramid. Field tethering experiments and mesocosms were used to demonstrate that turbidity interfered with fish foraging but did not impede crabs. High turbidity reduced pinfish consumption of shrimp but did not affect blue crab predation rates. In the field fish predation on mud crabs decreased in high turbidity sites, but crab predation on mud crabs

increased. The increase in abundance of benthic species may be a result of turbidity providing a refuge from fish predators. Mud crabs are known to reduce their foraging when fish predators are present (Grabowski 2004). Turbidity did not affect juvenile oyster survivorship but did affect juvenile oyster morphology. Juvenile oysters devoted more growth to shell in high turbidity sites at a cost of somatic tissue. Loss of large predator diversity because of increased turbidity may exacerbate loss of predators to fishing pressure, likely disrupting the trophic cascades. Changes in top-down control because of overfishing can have substantial effects on communities, and turbidity may produce similar effects by reducing top-down forcing of higher order consumers that depend on visual cues to forage successfully. As a result of the community wide changes seen in this study, we have determined that turbidity is an important estuarine factor that should be more widely considered for management and restoration efforts.

Hydrodynamic forces are important community regulators in rocky intertidal systems (Denny et al. 1985, Denny and Gaylord 1996, Boulding et al. 1999). However, these effects are not well studied in other systems. On oyster reefs diversity and species richness decreased with an increase of wave height and flow when all species were analyzed. However, when porcelain crabs were removed from the samples, increased wave height and flow reduced species richness and crab size on oyster reefs but was not linked with diversity or abundance. These effects on oyster reef communities should be considered in future restoration efforts. Changes to diversity, abundance and organism size may result in alterations to the food web, and ecosystem services offered by the reef and therefore the success of restoration attempts.

Coastal systems are subject to a wide array of degradations because of anthropogenic influences. These effects should be considered carefully for both mitigation and restoration as

they may have widespread indirect effects on coastal systems. These effects may not be readily apparent but could cause large effects to the food web by interrupting trophic cascades.

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BIOGRAPHICAL SKETCH

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