FISH PREDATORS MAINTAIN ESTUARINE BIODIVERSITY AND BENEFIT ECOSYSTEM ENGINEERS

A Dissertation

by

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This dissertation meets the standards for scope and quality of
Texas A&M University-Corpus Christi and is hereby approved.

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ABSTRACT

Loss of top predators may lead to the proliferation of mesopredators (i.e., intermediate consumers), with significant consequences for entire food webs. Termed mesopredator release, this process is typically attributed to a decline in the abundance of top predators. We investigated the potential for moderate environmental changes, that disrupt sensing abilities, to trigger mesopredator release by diminishing the foraging ability of top predators without affecting their abundance. In estuaries, fishes occupy the upper trophic levels and many species rely on visual cues to forage. We hypothesized that increased turbidity would attenuate fish foraging ability, increase the abundance of crabs and other mesopredators, and significantly alter coastal food webs. In oyster reef communities, turbidity triggered mesopredator release in 2016 and 2017, even though freshwater inflow and ambient salinity varied significantly between years, suggesting that turbidity's effects on estuarine food webs are robust. Following experiments in 2017, our field site was struck by Hurricane Harvey, a category 4 storm. Oyster mortality was high following Harvey due to low salinity and trophic reliance on oysters as a basal resource. Hurricane Harvey removed human fishing pressure, causing fish populations to increase dramatically, resulting in stronger top-down control on crabs that are the primary predator of newly settled oysters. We also investigated the potential for barnacles as accessible and biologically relevant flow indicators since hydrodynamics are key regulators of species-interactions. In summary, fish predators are important components of oyster reef ecosystems, enhancing biodiversity and, at times, benefiting oysters through a trophic cascade depending on the environmental context. Turbidity and fishing reduce top down control by fishes, leading to increases in the abundance of intermediate consumers, less diverse reef communities, and often damaging juvenile oysters.

DEDICATION

To All My Relations: Aho Mitakuye Oyasin.

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INTRODUCTION

"With luck, this cycle of thesis, antithesis, synthesis leads to scientific progress in a sort of biased, random walk toward understanding." – Joel G. Kingsolver & Robert T. Paine

"The world is green because of predators" –Hairston, Slobodkin, and Smith 1960

Estuaries are dynamic systems that are incredibly productive and biologically diverse, and provide many ecosystem services (Costanza et al. 1997). Yet, estuaries are some of the most altered habitats in the world and have been overexploited and intentionally modified (e.g., concrete bulkheads, dredging of oyster reefs, destruction of marsh for parking lots). Currently there are several large movements set to restoring the functionality of estuaries and estuarine habitats (e.g., blue carbon initiatives, living shorelines, oyster reef restorations, etc.). Recognition of the dozens of ecological, economic, and cultural benefits that estuaries provide has sparked major scientific revelations on the way estuarine communities form, how they function, and how they are affected by various chronic and acute disturbances. In this dissertation, I focus on the synergistic effects by which abiotic factors affect top-down regulation in Northwestern Gulf of Mexico oyster reefs and how these processes are modified by large-scale disturbances.

In 1960, Hairston, Slobodkin, and Smith famously suggested that "*the world is green because of predators*" (Hairston et al. 1960). This statement, which is one of the first notions of a trophic cascade, highlighted the ability of predators to effect multiple trophic levels simultaneously. In other words, without predators controlling grazers, grazers would be free to forage on ("green") plants without fear of predation. Therefore, predators, by functioning to control grazers, facilitate vegetation and make the world "green." In kelp forests, otters (predators) maintain urchin (grazer) biomass, and thereby facilitate kelp forests (Estes and Palmisano 1974). This is true of other systems as well, such as temperate forests (Ripple and Beschta 2004), grassland meadows (Schmitz et al. 1997), aquatic systems (Turner and Mittelbach 1990), and saltmarshes (Silliman and Bertness 2002). Predators are important regulators of community structure through their consumptive effects (CE) (Paine 1966, 1974, Estes and Palmisano 1974) and their non-consumptive effects (NCE) (Schmitz et al. 1997, Trussell et al. 2002). Yet, the strength of top-down regulation is highly dependent on the environmental context by directly and indirectly affecting the ways species disperse, assemble, and interact. Abiotic conditions directly affect species distributions through physiological tolerance limits (Grinnell 1917, Helmuth et al. 2002, Poloczanska et al. 2013), and indirectly by influencing performance of critical life-history processes such as foraging or predator avoidance (Sanford 1999, Smee and Weissburg 2006, Smee et al. 2010).

The relative importance of these predator effects is strongly reliant on the abilities of predators and prey to perceive and interact with their environment (Smee and Weissburg 2006). For instance, the importance of predator regulation in wave-swept communities declines at high levels of hydrodynamic stress, whereas the direction and intensity of predator-prey interactions, through CEs and NCEs, shifts between low and intermediate levels of wave exposure (Menge and Sutherland 1987, Leonard et al. 1998, Lunt et al. 2017). These sensory stressors are non-linear in how they affect species and do not necessarily affect predators and prey in the same way(Smee et al. 2010), indicating that environmental stressors can affect both the strength and direction of predator-prey interactions.

Other sensory stressors, such as an alteration of light regime, have notable outcomes for predator-prey interactions particularly when predators and prey, or different classes of the two, utilize different sensory mechanisms. Changes in environmental stimuli may differentially affect the sensory ecology of these groups and can dramatically alter community structure and function. For instance, shifts in light regime differentially affects different sensory modes (i.e., visual vs. chemosensory or mechanically-oriented organisms) thereby altering predator-prey interactions and the resultant community structure. In riparian systems, light pollution alters riparian invertebrate community structure by shifting terrestrial-aquatic invertebrate fluxes, yielding additional foraging opportunities for fishes and likely releasing the benthic invertebrate community from predation.

In this dissertation, I focus on the synergistic effects by which abiotic factors affect top-down regulation in Northwestern Gulf of Mexico oyster reefs and these processes are modified by large-scale disturbances. In Chapter I, I investigate the role of turbidity in providing a differential in sensory-disruption between different sensory types (i.e., visually-oriented vs. chemosensory organisms) and the potential for this to yield a process I dubbed "*sensory-mediated mesopredator release*". When unconstrained by predators, mesopredator populations are known to over-consume basal resources and can lead to habitat conversions (i.e., cordgrass to mud-flat) (Silliman and Bertness 2002). Turbidity-driven shifts in the sensory regime could alter food-webs and community structure by differentially disrupting the abundance and success of top predators and intermediate consumers (mesopredators), cascading down to the foundation species.

While turbidity and salinity are typically thought to be tightly coupled, they can be decoupled (e.g., wind-driven resuspension of sediment) and may have ecologically notable and distinct impacts on marine communities. In Chapter II, I compared the interactive effects of wet and dry years (salinity) and turbidity level on community structure, mesopredator abundance and sizes, oyster recruitment, and oyster morphologies.

Chapter III covers the ecological effects of Hurricane Harvey (Category IV) on oyster reef communities. This chapter investigates the consequences of Hurricane Harvey on community dynamics. Most notably, the indirect effects of large disturbance events on ecological communities by disrupting the human-ecosystem linkage (i.e., effect of disruption of fishing practices on top-down control of oyster reefs). While commercial fisheries often extract far too much of target and non-target (bycatch) species, and do so using destructive techniques (e.g., bottom-trawls), recreational fisheries are typically not considered for their ecological damage despite many declining stocks only being open to recreational fishers. Here, we show that recreational fisheries remove a tremendous abundance of top-predators. With the cessation of recreational fishing due to hurricane damage, top-predator abundance spiked, intermediate consumers and mesopredators declined, and community structure changed notably on oyster reefs.

In Chapter IV, I used barnacles as a biological flow-indicator that may be affordably deployed, replicated, and paired with physical measurements of flow to illustrate differences in hydrodynamic regime. Due to the implications of hydrodynamics on predator-prey interactions and community assemblages, designing mechanisms to cheaply and effectively quantify differences in flow are important; identifying sensitive indicators that illustrate *biological* effects of flow are even more elusive and important to identify.

In summation, this dissertation details the application of biologically-relevant flow indicators and the effects of turbidity, salinity, and hurricane disturbance on top-down control of oyster reef communities.

Oyster reefs as a model system- Oyster reefs are ecologically, economically, and culturally important. Within the Gulf of Mexico and the Southern and Mid-Atlantic regions, Eastern oysters (*Crassostrea virginica*) are the third largest fishery. In 2017 alone, the commercial Eastern oyster fishery is reported to have totaled over 23 million lbs in landings and earned over $181 million USD. The oyster fishery has a deep and long-standing history with Texas. Indigenous peoples inhabiting pre-colonial coastal Texas relied on mollusks (including oysters) as a major food source and left extensive shell middens from Galveston to the Rio Grande (Gatschet 1888, Ricklis and Blum 1997), and later, many of Texas's city streets were constructed using oyster shells as a gravel substitute (Tunnell 2010). In Texas, oysters remain the third largest fishery in the state as it accounts for nearly 10% of its commercial fishery earnings (over $20 million USD of the above earnings in 2017) (NMFS 2019).

However, despite the tremendous economic value of the fishery, Eastern oysters are also a foundation species that preform *at least* eight major ecological functions (Grabowski and Peterson 2007). Oysters ameliorate wave energy, accrete sediment, provide habitat for other valuable fish and invertebrates, etc. Yet, oysters have declined globally by an estimated 85% (Beck et al. 2011), and likely much more in the decade after this estimation. Due to the tremendous value of oysters as a foundation species and basal resource, and their distributions across environmental stress gradients within Texas estuaries, they are an ideal, albeit sharp, model system to work with.

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CHAPTER I: CLOUDY WITH A CHANCE OF MESOPREDATOR RELEASE: TURBIDITY ALLEVIATES TOP-DOWN CONTROL ON INTERMEDIATE PREDATORS THROUGH SENSORY DISRUPTION

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ABSTRACT

Mesopredator release following top predator loss may reduce biodiversity and harm foundation species. We investigated the potential for moderate environmental changes to trigger mesopredator release by disrupting the foraging ability of top predators without affecting their abundance by performing an in-situ experiment designed to isolate the magnitude of mesopredator effects on oyster reefs (*Crassostrea virginica*). In estuaries, fishes occupy upper trophic levels. Most are visual foragers and become less effective predators in high turbidity. Communities were 10% more diverse, fish predation was 20% higher, and oyster recruitment four times higher in low turbidity. Crab mesopredators were 10% larger and 260% more abundant in high turbidity. Caging treatments to exclude mesopredators significantly affected communities in high but not low turbidity. Oysters had 150% stronger shells in turbid areas, a known response to crabs that was indicative of higher crab abundance. These findings indicated that increased turbidity attenuated fish foraging ability without disrupting the foraging ability of mesopredators (e.g., crabs) that forage by chemoreception. Larger and more numerous crab mesopredators significantly affected oyster reef community structure as well as the survival and growth of oysters in turbid environments. In environments where apex predators and mesopredators utilize different sensory mechanisms, sensory-mediated mesopredator release

may occur when conditions affect the foraging ability of higher order predators but not their prey.

INTRODUCTION

Extirpation of large animals in both aquatic and terrestrial realms has resulted in regime shifts in many different ecosystems, including biologically diverse systems like coral reefs (Hughes 1994) and grasslands (Ripple and Beschta 2004) once thought to be immune from these types of effects (Pace et al. 1999). Predator loss has well known, long-term, adverse effects that may irreparably alter ecosystems (Jackson et al. 2001). For example, overfishing is a well-known cause of widespread community changes (Pauly et al. 1998), and its adverse effects may linger well after harvesting pressure has been removed (Jackson et al. 2001). Changes in community properties from loss of top predators may make ecosystems more prone to invasions (DeRivera et al. 2005), alter nutrient fluxes within and between habitats (Gratton and Denno 2003), and impede recovery after disturbances (Wallach et al. 2010). Although reintroduction of top predators may benefit these and other community and ecosystem processes (e.g., Fortin et al. 2005), in many cases regime shifts following predator loss may negate benefits of reintroducing predators and/or inhibit predator reestablishment (Terborgh et al. 2001; Heithaus et al. 2008; Wallach et al. 2010).

Predator loss may directly affect ecosystem function by altering trophic relationships, particularly the abundance of intermediate consumers or mesopredators (Pace et al. 1999; Duffy 2002). Termed mesopredator release, a reduction of higher order consumers may reduce top-down control on intermediate consumers (mesopredators), leading to a reduction of basal trophic levels (Ritchie and Johnson 2009; Prugh et al. 2009) in terrestrial (Terborgh et al. 2001) and aquatic ecosystems (Heithaus et al. 2008). Loss of top-predators can affect food webs through a reduction in predation levels (Estes and Palmisano 1974), but also through changes in prey behavior (Turner and Mittelbach 1990). Nonlethal, ‘fear-induced’ predator effects can be important food web regulators as mesopredators often reduce foraging activity in the presence of top predators (Pressier 2005; Weissburg et al. 2014). Removal of top-predators thus leads to increased mesopredator populations who are free to forage in a landscape with low predation risk (Turner and Montgomery 2003; Pressier et al. 2005; Heithaus et al. 2008).

The magnitude of both lethal and nonlethal predator effects is strongly influenced by environmental conditions that enhance or attenuate predator foraging ability (Weissburg and Zimmer-Faust 1993; Large and Smee 2013) and/or affect prey ability to recognize and respond to potential consumers (Smee et al. 2010; Weissburg et al. 2014; Chivers et al. 2013). Sensory disruption of predator foraging and/or prey ability to detect and avoid consumers can alter the outcomes of predatory interactions and be driven by natural and/or artificial factors (Powers and Kittinger 2002; Myers and Sullivan 2013; Minnaar et al. 2015). Sensory disruption may affect the success of predators (Weissburg and Zimmer-Faust 1993), provide competitive advantages to certain predators or predator groups (Eiane et al. 1999), influence the susceptibility of prey to predation (Powers and Kittinger 2002), and alter community structure (Eiane et al. 1999; Myers and Sullivan 2013). The effects may be particularly profound when sensory disruption affects predators and prey unequally, thereby drastically increasing or decreasing predation rates (Smee and Weissburg 2006; Smee et al. 2010).

For instance, light pollution alters riparian invertebrate community structure by shifting terrestrial-aquatic invertebrate fluxes, yielding additional foraging opportunities for fishes and likely releasing the benthic invertebrate community from predation (Myers and Sullivan 2013). By disrupting traditional diel cycles, fishes were afforded more time to forage visually (the “*modus operandi*” of most Teleosts), while chemosensory-oriented invertebrate predators failed to obtain such a benefit (Gregory 1993). Light pollution can lead to increased growth rates of visual predators and may facilitate coexistence amongst visual predators by attracting alternative prey and reducing competition among predators (Ramirez et al. 2006). Light pollution in riparian communities enhanced fish foraging through increased foraging time, and yielded an altered, less diverse community. However, disruption of predator-prey interactions due to an altered light regime is not exclusive to aquatic systems. For instance, bat (*Neoromicia capensis*) predation on eared-moths increased 6-fold in artificial light, likely due to reduced defensive behaviors by the moths (Minnaar et al. 2015). Predator-prey interactions also shift in response to natural changes in light. Merriam’s kangaroo rats (*Dipodomys merriami*) change their foraging behavior in response to moon phases that created differences in ambient moon-light and favored different types of predators (Daly et al. 1992). Yet, the effects of sensory disruption on community structure and function remains poorly investigated, particularly for its cascading effects to foundation species.

We tested whether moderate environmental changes capable of altering foraging ability of top predators could cause mesopredator release using oyster reefs (*Crassostrea virginica*) as a model system. Specifically, we explored how turbidity affected the abundance and morphology of oysters as well as the associated benthic community including species composition, trophic interactions, mesopredator abundance, and biodiversity. Long-term fisheries independent data in this system revealed fish to be less abundant in elevated turbidity while crabs and other benthic species were more abundant (Lunt and Smee 2014). Moreover, fish predation on crabs was significantly less in high turbidity, and oyster reef community structure was significantly different in low vs. high turbidity. Yet, the mechanisms responsible for these differences have remained untested. We hypothesized that turbidity, through differential sensory disruption between visual and chemosensory foraging species, would trigger mesopredator release, causing higher predation on lower trophic levels, resulting in less diverse communities. Specifically, turbid conditions would lessen fish predation on mesopredators (crabs) and would allow for crab mesopredators to increase in size and abundance. Increased crab mesopredator abundance and size would significantly alter reef community structure, reduce oyster recruitment, and cause oysters to produce heavier, stronger shells in response to higher predation risk (Scherer et al. 2016). Fishes that inhabit oyster reefs would occupy lower trophic levels in higher turbidity due to greater predation by and competition from crabs.

METHODS

Approach – We tested the effects of turbidity in low vs. high turbid sites using a combination of predator exclusion experiments designed to isolate the effects of top and mesopredators on oyster reefs, tethering assays to measure predation, and by comparing the sizes and trophic levels of collected organisms in the study.

Study locations – Oyster reefs in the Mission-Aransas NERR near Rockport, TX, USA were selected for this study (**Supp. figure 1**). Oyster beds in this area are low relief and contain a mixture of living oyster clumps and oyster shells. This is a microtidal estuary, and the reefs used in the study were in shallow subtidal environments at ~ 0.5 m below mean low water and 100-300 m from land. Freshwater inputs into the area are primarily from run off. Higher order predators on oyster reefs in the area include red drum (*Sciaenops ocellatus*), spotted sea trout (*Cynoscion nebulosus*), sheepshead (*Archosarguys probocephalus*), and gulf toadfish (*Opanus beta*). Sheepshead also consume oysters and other shelled animals including crabs and barnacles. Reefs are inhabited by numerous small fish species (e.g., gobies and blennies), grass shrimp

(*Palaemonetes* spp.) and brown shrimp (*Farfantepenaeus aztecus*), and many crabs including stone crabs (*Menippe adina*), blue crabs (*Callinectes sapidus*), and mud crabs (*Panopeus herbstii*, *Eurypanopeus turgidus*, *E. depressus*). Crabs with carapace widths >15 mm prey heavily on newly settled oysters, and many of these predators also consume porcelain crabs (*Petrolisthes armatus*), which are common suspension feeders within oyster beds.

Salinity and water temperature were measured daily by the Mission Aransas NERR SWMP stations, and salinity was also measured near each oyster reef using a refractometer. Water temperatures were 30.7° C (+/- 0.2°) and salinities averaged 15.9 (+/- 0.5 PPT). Turbidity in the Mission Aransas NERR is caused by suspended sediment that is mixed into the water column by near continuous wind (Lunt and Smee 2014, Lunt and Smee *in press*). Although rare, all sites may have low turbidity following an extended period of low wind. In marine systems, salinity and turbidity are often coupled because freshwater inputs lower salinity while simultaneously raising turbidity. Here, selected sites varied greatly in Secchi depths (light penetration, measure of turbidity), but not with respect to salinity. Salinity was incorporated into initial analyses and was not significant. Thus, we were able to perform manipulative experiments in low and high turbidity conditions to focus on turbidity effects without confounding influence of salinity.

<u>Secchi depths and light availability</u> – Oyster reefs in this study were 0.8 – 1.1 m in depth and were divided into low and high turbid sites based upon light levels measured with a Secchi disk. Low turbidity sites were characterized by having Secchi depths above 45 cm (mean and SE 51.8 +/- 1.57 cm) and where the Secchi disk routinely touched the substrate. Sites with high turbidity had Secchi depths below 40 cm (30.9 +/- 0.94 cm). Secchi depths were measured at each field site seven times: May 3rd, 10th, 24th and June 10th, 13th, 20th, and 27th. Often in low turbidity sites,

the Secchi disk depth reached the benthos and rested on the substrate, which was noted. On 3 occasions, the Secchi depth rested on the substrate in all ten low turbid sites, but it only rested on the bottom in 4 sites (out of 20) on 1 date in the high turbid areas.

We also examined the relationship between light and Secchi depth in our field sites by placing Onset HOBO loggers in some of our field sites to record water temperature (C°) and light (lux, lumens m^{-2}) every 30 minutes. HOBO loggers were secured to PVC poles with zip ties and deployed at reef height, 20 cm above the substratum. Two data loggers were deployed as aerial loggers near our sites to measure air temperature and light levels. Submerged loggers fouled quickly, so they were scrubbed clean in the field using a soft-bristled toothbrush seven times during the study. HOBO light data were only used from the day following cleaning. Lux was calculated from light logger measurements from 11am-1pm (when the sun was directly overhead). A differential in lux between the aerial light loggers and the benthic loggers was calculated to identify relative differences in water column light-detection (known hereafter as proportional lux). Both Secchi depths and proportional lux were compared across high and low turbidity reefs using one-tailed t-tests.

Oyster reef community sampling – We used size-based exclusions to isolate the effects of different trophic levels on osyter reef communities in low and high turbidity (sensu Johnson et al. 2014). Cages were 0.5 m x 0.5 m x 0.10 m tall and were deployed in triplicates with each triplicate containing: a control cage (no mesh or covering; control to ambient levels of predation), one cage covered in mesh with large openings (5 cm^2) to exclude larger predators but permit access by mesopredators, and one cage covered with mesh with small openings (1.0 cm^2) to exclude both top and mesopredators. Cages were ~ 2.0 m apart and triplicates separated by at least 100 m. Twenty L of sun bleached oyster shells were added to each cage to form an artificial reef. We deployed 10 triplicates (30 cages) in low turbid sites and 20 in sites with high turbidity. We initially planned to have 10 sets in intermediate or fluctuating turbidity levels, but measurements revealed that light and Secchi depth in these areas were similar to high turbid sites and thus these areas were classified as high turbidity. Cages were deployed May 3rd, 2016 and remained in the field until June 30th, 2016 to coincide with peak oyster spawning. During the 8 week deployment, 16 cages were lost or compromised. 15 cages from high turbidity sites and 1 from low turbidity sites. In total, 74 cages were collected: 45 from high turbidity and 29 from low turbidity. Community assemblages were collected from cages using modified throw traps. Three, 1.0 m^3 traps were simultaneously placed over each cage within a triplicate. The cage was removed, thoroughly searched, and all organisms collected. Sweep nets (500 µm mesh-size) were then used to sweep within the throw trap to collect any organisms dislodged from the tray. Larger organisms were identified, measured, and released in situ, while smaller organisms were placed in ethanol and transported to the lab for sorting, identification, measurements and enumeration. Fish sizes were calcualted by measuring total length and crabs sizes by measuring carapace width. Mud crabs smaller than 10 mm carapace width were recorded as "unidentified mud crabs" and were not considered mesopredators (Johnson et al. 2014).

Community data were analyzed using Primer™. Numbers of individuals per cage were square root transformed, converted to a Bray-Curtis resemblance matrix, and analyzed using PERMANOVAs (Primer™ 7) with 100,000 permutations. Initial analyses included salinity, however salinity was not significant and was removed from further community analyses. A canonical analysis of principal coordinates (CAP) plot was created to illustrate community differences between low and high turbidity levels (CAP1) and across treatment types (CAP2). Communities were compared using a two-way PERMANOVA with turbidity level (high or low) and caging type (large-mesh, small-mesh, and control) as fixed factors, as well as a pairwise two-way PERMANOVA testing caging effects within high and low turbidity respectively. Similarity percentage (SIMPER) analysis was used to quantify which species contributed to differences between low and high turbidity levels. Shannon diversity (H') was calculated for all ambient community samples using Primer, and was compared across Secchi depths. Total community diversity and the total number of organsisms per sample were each compared across turbidity levels and caging treatment using two-way ANOVAs in JMP Pro 14.

Mud crabs with carapace widths greater than or equal to 15 mm were classified as mesopredators as smaller mud crabs do not routinely eat oysters (Johnson et al. 2014). For count data, particularly non-normal count data, Generalized Linear Models (GLM hereafter) are effective tools for quantifying species abundances across continuous factors (i.e., Secchi depth). Therefore, mesopredator abundance was analyzed using a two-way negative binomial GLM (generalized linear model) with Secchi depth (cm) and caging treatment as factors.

Additionally, the effects of caging treatments on mesopredator abundance and size were compared within high vs. low turbidity using one-way ANOVA. A Tukey HSD test was used to compare pairwise means. Mud crab abundance data were analyzed in RStudio (version 1.1.456) and size data were analyzed in JMP Pro 14.

Toadfish (*Opsanus beta*) are particularly important components of oyster reef systems due to their critical roles in structuring food webs (Grabowski 2004). Toadfish limit mud crab foraging on oysters through consumptive and non-consumptive effects. Therefore, we quantified toadfish abundance and size (i.e., length). We analyzed the abundance of toadfish using a two-way negative binomal GLM with Secchi depth and caging treatments as factors. Toadfish lengths were averaged for each cage and analyzed in a 2-way ANOVA with turbidity level and cage treatments as factors. Toadfish count data were analyzed in RStudio (version 1.1.456) and length data were analyzed JMP Pro 14.

Oyster recruitment – Oysters have planktonic larvae, and newly settled oysters are referred to as spat. Two PVC spat collectors (aka "spat sticks"; plastic, grooved, sticks that were 100 mm long, and 22 mm in diameter) were placed within each cage to assess oyster recruitment and mortality within each caging treatment. Upon cage retrieval, spat sticks were removed from the cages, and returned to the lab. The number of settled oysters was recorded, and the length and width measured from five oysters from each cage to be used in crushing force trials. Oyster recruitment was analyzed using a two-way negative binomal GLM with Secchi depth and caging treatment as factors. Additionally, we analyzed recruitment across the categorical variable turbidity using a 2-way ANOVA with turbidity level and cage treatments as factors. Recruitment data were analyzed in RStudio (version 1.1.456) and JMP Pro 14.

Oyster crushing force – Oysters respond to crab predators by growing heavier, stronger shells, and we measured shell strength as an indicator of crab presence (sensu Scherer et al. 2016). Shell strength was quantified by measuring the compression force, or the amount of force required to crush the shell, using a Kistler 5995 charge amplifer and a Kistler 9203 force sensor. The force sensor is a small, blunt probe (1 mm diameter) that was consistently placed centrally to be equidistant from the shells' edges and perpendicular to the shell. Gentle and consistent pressure was applied until structural failure, and the maximum force requried to break the shell recorded. Oyster crushing force was standardized by shell area (using the equation for the area of an ellipse, $a = \pi r_1 r_2$) (sensu Scherer et al. 2016). Standardized crushing force (N/mm^2) data were averaged by cage and analyzed using a two-way ANOVA with turbidity level and caging treatment as factors. Tukey's post hoc tests were used for pairwise comparisons when necessary.

Further, mean oyster size (shell area, mm^2) within each cage type was compared across turbidity levels and caging treatments. Oyster crushing force and oyster size data were analyzed in JMP Pro 14.

Mean trophic level for fishes – To ascertain if turbidty affected the trophic level of fishes that inhabit oyster reefs (due to greater predation by and competition from crabs), we calculated the trophic level of fishes within each cage by recording the trophic levels of each individual fish based upon their classification from Fishbase.org. Fishes that were unidentified due to poor preservation or quality (16 individuals) or had no diet information (Crested and stretchjaw blennies; 107 individuals) were not included in the analysis (123 total individuals). In total, 2,029 individuals were used for analyses. We then calculated an average trophic level for all fish per cage and compared mean trophic among turbidity levels and cage treatments type using a two-way ANOVA in JMP Pro 14.

Relative levels of predation – Ambient predation intensity was assessed using squidpops, which provide an estimate of fish consumption (sensu Duffy et al. 2015). Squidpops were made by attaching a 1.0 cm^2 piece of dried squid to a wooden stake, placing into the field for 24 hours, and determining if the squid was eaten or not. Squidpops were deployed in low and high turbidity sites in 2017. We deployed squidpops at sites where we had cage triplicates in 2016, and we also deployed 100 additional squidpops in high turbidity and 50 in low turbidity. Each squidpop was driven firmly into the substrate with the squid bait ~0.3m above the substrate. Squidpops were placed at least 2 m apart from one another and were left in the field for 24 hours before collections. Squidpops were recorded as eaten or unconsumed. Data were grouped all together and were analyzed as binomial data (0 = unconsumed; 1= consumed). Squidpops that were not recovered were excluded from analyses. Data were analyzed using a Wilcoxon-Rank Sum test in RStudio (version 1.1.456).

RESULTS

Secchi depths and light availability – Sites classified as low turbidity had significantly deeper Secchi depths ($t_{120} = -11.37$, $p<0.001$), even though the Secchi disk often rested on the substrate in these sites, minimizing the differences between low (51.8 +/- 1.57 cm) and high (30.9 +/- 0.94 cm) turbidity sites. Light loggers detected 3x less light (7.48% vs. 23.3%; (**Supp. figure 2**) in high turbidity sites ($t_{221} = -8.69$, $p <0.001$). Mean lux and mean Secchi depth were tightly coupled ($R^2 = 0.717$, **Supp. figure 2**). However, salinity and Secchi depth were weakly correlated ($R^2 = 0.124$). Further, salinity was not a significant factor contributing to community structure in PERMANOVA analyses.

Oyster reef community data – Turbidity significantly influenced community structure (**Figure I.1**, Pseudo-$F_{1, 73} = 43.9$, $p < 0.001$), while caging was not significant (Pseudo-$F_{2, 73} = 1.32$, $p = 0.169$). However, the interaction between turbidity and cage type was significant (Pseudo-$F_{2, 73} = 2.00$, $p = 0.048$). Pairwise comparisons of caging effects within each turbidity level demonstrated that large-mesh communities that were accessible only to mesopredators were significantly different from both small-mesh (Pseudo-$F_{2, 73} = 2.11$, $p < 0.001$) and control cage communities (Pseudo-$F_{2, 73} = 1.55$, $p = 0.019$) within high turbidity sites. These differences were not found within low turbidity reefs (**Supp. table 1**).

The largest sources of dissimilarity between high and low turbidity reef communities, as identified by SIMPER analysis, were green porcelain crabs (*Petrolisthes* armatus), grass shrimp (*Palaemonetes spp.*), unidentified mud crabs (mud crabs <10 mm), ridgeback mud crabs (*Eurypanopeus turgidus*), and flatback mud crabs (*Eurypanopeus depressus*) (**Supp. table 2**).

The average similarity within and between community samples was lowest in low turbidity, indicating that clearer sites tend to have more variation in community structure than turbid sites (**Supp. table 3**). Further, large-mesh community samples maintained the highest degree of similarity amongst each other within turbid sites.

Oyster reef community diversity was significantly higher in low turbidity sites ($F_{1, 68}$ = 4.87, p = 0.031; **Supp. figure 3**), while caging type ($F_{2, 68}$ = 0.23, p = 0.796) had no effect on sampled community diversity. The interaction between turbidity and caging was not significant ($F_{2, 68}$ = 0.401, p = 0.67). Organisms were significantly more abundant in low turbidity (339.9 +/- 23.8) than in high turbidity (279.7 +/- 19.3) ($F_{1, 68}$ = 3.98, p = 0.0498), though both cage type ($F_{2, 68}$ = 0.469, p = 0.629) and the interaction term ($F_{2, 68}$ = 0.533, p = 0.589) were not significant.

Mesopredator (mud crabs $\geq$15 mm carapace width) abundance significantly increased as Secchi depth decreased (estimate =-0.0592, z = -5.42, p <0.001; **Figure I.2**; **Supp. table 4**). Caging treatment and the interaction between Secchi depth and cage treatment were not significant (**Supp. table 4**). Mud crab mesopredators were significantly smaller in low turbidity ($F_{2, 72}$ = 35.6, p <0.001; **Figure I.3**). However, in high turbidity, crab sizes were significantly different among cage treatments ($F_{2, 40}$ = 4.63, p = 0.016). Large-mesh cages had significantly larger mud crab mesopredators than ambient (control) cages within high turbidity (p = 0.02; **Figure I.3**). Small-mesh cages were intermediate and not significantly different from either large-mesh or control cages. There were no pairwise differences in mesopredator sizes within low turbidity sites ($F_{2, 19}$ = 0.471, p = 0.632; **Figure I.3**).

Toadfish were significantly more abundant on turbid reefs. As Secchi depths increased, toadfish abundances declined (estimate = -0.02, z = -2.14, p = 0.0327; **Supp. table 5**; **Figure I.4**). However, there were no significant caging effects, nor was the interaction significant

(**Supp. table 5**). Toadfish were also significantly larger within high turbidity sites ($F_{1,43} = 4.55$, p=0.039; **Figure I.4**), though caging effects ($F_{2,43} = 0.833$, p=0.84) and the interaction were not significant ($F_{2,43} = 0.66$, p=0.52).

Oyster recruitment – Juvenile oyster abundance significantly increased as Secchi depth increased (estimate = 0.0447, z = 3.92, p< 0.001; **Supp. table 6**; **Figure I.2**), though cage type and the interaction between Secchi depth and cage type were not significant (**Supp. table 6**; **Figure I.5**). Oyster recruits were significantly more abundant in low turbidity ($F_{1,68} = 49.9$, p<0.001; **Figures I.2&5**). Cage type significantly influenced oyster abundance ($F_{2,68} = 4.51$, p=0.015). Small-mesh cages had significantly higher oyster abundances than control cages, while large-mesh cages were not statistically different from either small-mesh or control cages. The interaction between caging type and turbidity regime was not significant ($F_{2,68} = 1.47$, p = 0.236). The sites with highest oyster recruitment had fewer numbers and smaller sized oyster predators (**Figure I.2**). On average, each spat stick had nearly five more juvenile oysters in low turbidity than high turbidity, regardless of cage exposure level. This accounts for approximately a 380% difference in oyster recruitment between high and low turbidity.

Oyster crushing force – In turbid sites, juvenile oysters had stronger shells per unit area (0.186 +/- 0.021 N/mm^2 in turbid sites, 0.137 +/- 0.0064 N/mm^2 in clear sites; $F_{1,44} = 11.2$, p = 0.002; **Figure I.6**). Oysters from control cages had significantly stronger shells per unit area than oysters from large-mesh or small-mesh communities across both turbidity levels ($F_{2,44} = 8.35$, p < 0.001). The interaction between turbidity and caging treatment was also significant ($F_{2,44} = 4.8$, p = 0.01). Oysters from control cages in high turbidity had significantly stronger shells per unit area than oysters from every cage and turbidity combination other than the small-mesh cages in high turbidity (**Figure I.6).** Juvenile oysters that recruited to control cages in turbid sites required nearly double the crushing force than oysters in any other group.

Oysters were significantly larger (~1.8 x larger on average; 293.8 mm^2 in low turbidity and 166.5 mm^2 in high turbidity) in low-turbidity sites ($F_{1, 46} = 20.7$, $p < 0.001$). Neither caging treatment ($F_{2, 46} = 1.48$, $p = 0.237$) nor the interaction between turbidity level and caging treatment ($F_{2, 46} = 1.67$, $p = 0.199$) affected the mean size of oysters.

Mean trophic level of fishes and relative levels of predation – The mean trophic levels of fishes were significantly higher at low Secchi depths ($F_{1, 69} = 12.2$, $p < 0.001$; **Supp. figure 4**), though there were no significant cage effects ($F_{2, 69} = 2.16$, $p = 0.123$) and the interaction was not significant ($F_{2, 69} = 1.34$, $p = 0.268$). Additionally, consumption of squidpops was higher in low turbidity sites (mean= 90% consumed) than high turbidity sites (mean= 68.9% consumed) ($W = 1212$, $p = 0.008$).

DISCUSSION

Disruption of sensory mechanisms may alter the outcomes of predatory interactions by enhancing or attenuating predator foraging ability or prey ability to detect and avoid consumers (Smee et al. 2010; Weissburg et al. 2014). In food webs where predators and prey detect one another using different sensory modalities, changes in environmental conditions may unequally influence the sensory performance of one member of the interaction. Sensory mediated mesopredator release may occur when conditions interfere with the foraging ability of higher order consumers, releasing mesopredators from top-down control, while mesopredator foraging is unimpeded. Previous work indicated fish were less common and were less successful foragers in high turbidity and that crabs were more abundant in these conditions (Lunt and Smee 2014). We empirically tested if turbidity caused mesopredator release in this system. In high turbidity, crab mesopredators were larger and more abundant, newly settled oysters were smaller, less abundant and grew stronger shells (which is a known response to crab predators), and fish predation was significantly less. Notably, excluding mesopredators in high turbidity had significant effects on oyster reef community composition while there were no effects in low turbidity.

Figure I.7 provides a conceptual model of sensory mediated mesopredator release constructed from these findings and previous published work (Minello et al. 1987; Benfield and Minello 1996; Ramirez et al. 2006; Myers and Sullivan 2013; Lunt and Smee 2014; Lunt and Smee 2015). In this model, as light scatter increases and image formation decreases, fish foraging ability decreases. Some turbidity levels may enhance fish foraging by increasing contrast with prey (Wenger et al. 2013), and thus the model shows an increase in fish foraging ability from low to an intermediate turbidity level followed by a decline in foraging when light levels interfere with vision. While crabs have visual receptors, they rely more heavily on chemoreception to forage and avoid predators, and thus in our model their sensory performance does not diminish substantially in high turbidity. In contrast, fishes rely heavily on vision to forage, and their sensory performance degraded rapidly in high turbidity, releasing crabs from fish predation, leading to increased crab mesopredator abundance and size.

Our data supports this model in several ways. First, consumption of squidpops, which are considered gauges of fish predation (Duffy et al. 2015), was higher in low turbidity. This is consistent with earlier crab tethering experiments in these sites that also found higher fish predation in low turbidity (Lunt and Smee 2014) as well as lab-based studies revealing reduced foraging by fish in high turbidity (Minello et al. 1987; Benfield and Minello 1996; Zamor and Grossman 2007; Lunt and Smee 2015). Second, crab mesopredators were larger and more numerous in turbid sites, and both newly settled oysters and biodiversity were lower in turbid conditions. Third, mesopredator exclusion had significant effects on oyster reef communities in high turbidity, but not low turbidity, likely because there were few mesopredators in low turbidity. Low turbidity reefs contained nearly double the number of small (<10mm) mud crabs, which operate trophically as primary consumers. Our working hypothesis is that fish predation in low turbidity limits crab survival and few crabs reach the large sizes observed on turbid reefs where they become secondary consumers (Aarnio et al. 2015). Finally, Lunt and Smee (2014, in press) found fish abundance and diversity to decline in elevated turbidity in an 18 year fisheries independent data set spanning much of the Texas, USA, coast, and Lunt and Smee (2014) also noted significantly less fish predation on crabs in elevated turbidity, which is predicted by our conceptual model of sensory mediated mesopredator release model.

Community structure was different between low and highly turbid sites, and communities were more diverse in low turbid areas. Habitats dominated by mesopredators are often less diverse than areas where mesopredators are controlled by higher order consumers (Ritchie and Johnson 2009). The main species accounting for ambient community differences, based on mean abundances, were green porcelain crabs (*P. armatus*), grass shrimp (*Palaemonetes spp.*), ridgeback mud crabs (*E. turgidus*), unidentified mud crabs (mud crabs <10mm), and flatback mud crabs (*E. depressus*) (**Supp. table 2**). Those five species/groups accounted for 60.3% of the cumulative differences in community structure between high and low turbidity reefs, illustrating the relative structural weight of mud crabs on oyster reef communities. Yet, turbidity affected these species differently. Porcelain crabs and flat back mud crabs were more abundant in high turbidity, while the other species were less abundant. More work is needed to investigate the responses of different organisms to elevated turbidity to understand the mechanisms generating these patterns.

On turbid reefs, crab mesopredators were 260% more abundant, and oyster abundance was lower, likely due to predation by crabs. Moreover, oysters were smaller and grew stronger shells in high turbidity, a response known to occur in response to crab exudates (Scherer et al. 2016; Scherer et al. 2018). Juvenile oysters likely had to reallocate energy away from somatic growth and reproduction and towards fortifying shell defenses (Johnson and Smee 2012; Scherer et al. 2018). Fish predation was significantly higher in low turbidity, consistent with previous studies (Minello et al. 1987; Benfield and Minello 1996; Lunt and Smee 2014; Lunt and Smee 2015). Most telling, communities in the large-mesh cages that were accessible to mesopredators, but not larger predators, were significantly different from control cages on highly turbid reefs but were similar to total predator exclusion via small mesh cages in low turbidity. This result indicates that mesopredators, even when protected from higher order consumers, had little effects on communities in low turbidity, likely because of their low abundance and/or smaller size in these areas.

Predator exclusions significantly increased survival of newly settled oysters in low turbidity. Although there were more oysters in both large and small mesh cages in high turbidity, these differences were not significantly different from each other or from controls. Note that while caging treatments limited oyster exposure to mud crabs, we were unable to completely exclude them, thus there was predation on oysters by mesopredators in all treatments in high turbidity. The number of newly settled oysters was lower in high turbidity overall, which is where the largest numbers of oyster predators occurred. Sedimentation in turbid sites might have also reduced survival of newly settled oysters in all treatments. Still, oysters were nearly twice as abundant in small mesh cage treatments that restricted predator access (2.9) vs. controls (1.5) suggesting that sedimentation or other abiotic factors are unlikely to account for the differences observed.

Mud crab mesopredators have strong impacts on juvenile oyster populations (Bisker and Castagna 1987; Carroll et al. 2015). Oyster recruitment was significantly lower in high turbidity where crab mesopredators were larger and more numerous. This is notable as mesopredator size is a key determinant of mesopredator impacts, especially for mud crabs (Kulp and Peterson 2016). Mesopredators were over 10% larger (~ 2 mm) in high turbidity; specifically, mesopredators were largest in large-mesh cages within high turbidity (1.65 mm larger than mesopredators in control cages) (**Figure I.3**). This is likely an ecologically relevant difference as mechanical advantages in crab chelae are strongly correlated with body-size (i.e., carapace width), especially with Xanthid crabs (Schenk and Wainwright 2001). Crab carapace width (and chelae size) affects their diet preferences (Aarnio et al. 2015) and the critical lengths of the prey they consume (Milke and Kennedy 2001). The difference in the number, and size, of prey consumed may be notable, even at a ~2 mm difference in mesopredator size. Consequently, decreased mesopredator abundance correlated with significantly higher oyster recruitment, larger oysters, and lower relative crushing forces, a phenotypic characteristic oysters employ to defend against crab predation but that also lowers fecundity (Scherer et al. 2018). However, oysters were most well- defended (had stronger shells) within control cages on turbid reefs, where recruits likely suffered predation from both crabs and fish predators (e.g., sheepshead*, A. probatocephalus*). Thus, when unprotected in high turbidity in control cages, predation on oysters from multiple trophic levels yielded fewer oysters and those that survived were well-defended. In other systems, fish predation on oyster spat may account for ~40% of oyster predation (e.g., Anderson and Connell 1999). Despite being less abundant in high turbidity, the fishes present, particularly durophagous fishes such as sheepshead, may yield an additive consumptive effect on oysters leading to further declines in oyster recruitment and increased defensive morphologies. Likewise, the total consumptive effects on oysters was not as substantial on low turbidity reefs since predation by mesopredators was relatively low.

Although turbidity, at low levels, can benefit visual-predators by providing contrast between the background and prey (Wenger et al. 2013), increased turbidity reduces fish foraging behavior (Zamor and Grossman 2007), foraging success (Lunt and Smee 2015), and fish abundance (Lunt and Smee 2014). However, turbidity differentially effects different feeding modes, even for visually-oriented fishes. For instance, piscivores pursued less prey and were less successful at prey capture in increased turbidity, while planktivores suffered no such decline (De Robertis et al. 2003). Turbidity may act as a refuge from piscivorous fish. Known as the "turbidity as cover" hypothesis, predators (birds and other fishes) are thought to be less successful hunters of juvenile and larval fishes in turbid water (Gregory 1993), allowing juvenile fishes to increase feeding activity and use less shelter (Gregory 1994). While turbidity may provide a refuge for some fish species, in this study fish were more abundant and diverse in low turbidity reefs.

Previous analysis of long-term fisheries independent monitoring in the area revealed that fish diversity and abundance was significantly lower in high turbidity (Lunt and Smee 2014). Correspondingly, fish diversity remained significantly lower in high turbidity in this study. However, Gulf Toadfish (*Opsanus beta*) were significantly larger and more abundant in turbid communities (**Figure I.4)** and are known to exhibit strong top-down control on oyster reefs (Grabowski 2004). Toadfish may benefit from elevated turbidity due to reduction in predation from other piscivorous fishes and/or from competitive release if they can better forage in turbid conditions than other fishes. Toadfish, which are successful hunters at night, have eyes that appear to share more structural similarities to some deep-sea fishes than neritic fishes. They have yellow eyeshine, which is common for nocturnal organisms, while lacking the classic *tapetum lucida* that is common in most nocturnal vertebrates (Nicol 1980). Instead, toadfish have a yellow argenteum posited to function in mesopic conditions (Nicol 1980). Thus, toadfish may be adapted to foraging in turbid/low-light conditions, potentially dampening the effects of sensory-mediated mesopredator release. Toadfish are voracious predators of mud crabs (i.e., **Supp. table 2**, rows 3-5), at times ~2/3 of their diets are composed of secondary consumers or mesopredators such as mud crabs including Atlantic mud crabs (*P. herbstii*) and flatback mud crabs (*E. depressus*) (Wilson et al. 1982). Toadfish presence causes behavioral modifications in mud crabs, reducing their feeding on juvenile oysters (Grabowski 2004). While large mud crabs were significantly more abundant in high turbidity, their numbers and foraging rates on juvenile oysters may have been limited by toadfish.

The greater abundance (and increased size) of toadfish in residence on turbid reefs may have dampened, while not completely ameliorating, the effects of sensory-mediated mesopredator release. Indeed, mud crab mesopredators were significantly larger, and community structure significantly different, within large-mesh cages in high turbidity (when protected from larger predators), though mesopredator abundances remained similar across cage types within high turbidity. Further, it is possible that the foraging-mode of toadfish is distinct on turbid reefs, or that they forage more opportunistically on turbid reefs, and therefore consume relatively more visually-oriented organisms despite the abundance of mud crabs in turbid conditions. Phillips and Swears (1979) suggested that toadfish may switch their foraging modes at night, switching from ambush predators during the day to actively stalking prey at night. We cannot say conclusively, within the scope of this study, which causal mechanism(s) were at play here; further investigations (e.g., mesocosm studies) would be enlightening.

Coastal turbidity continues to increase in many areas around the world (Cloern 2001; Dupont and Aksnes 2013), perhaps facilitating mesopredator release and reducing community diversity. Anthropogenic impacts on coastal systems are broad and significant. Elevated coastal turbidity mimics the effects of harmful overfishing practices: both can lead to mesopredator release and can result in modified/damaged marine habitat. In freshwater-systems, turbidity reduces vegetation growth (Ryan 1991), alters species behaviors (Becker and Gabor 2012) and predator-prey interactions (Van de Meutter et al. 2005), leading to shifts in community structure. Here, increased turbidity appears to have led to an unfavorable sensory regime for visual top predators and caused sensory-mediated mesopredator release and the significant changes to oyster abundance and the oyster reef community. However, depending on the source, elevated turbidity can be reversible (Borkman and Smayda 1998). While turbidity receives scant attention in marine management efforts, our findings indicate that turbidity should be considered in the conservation and management of marine environments.

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FIGURES

Figure I.1

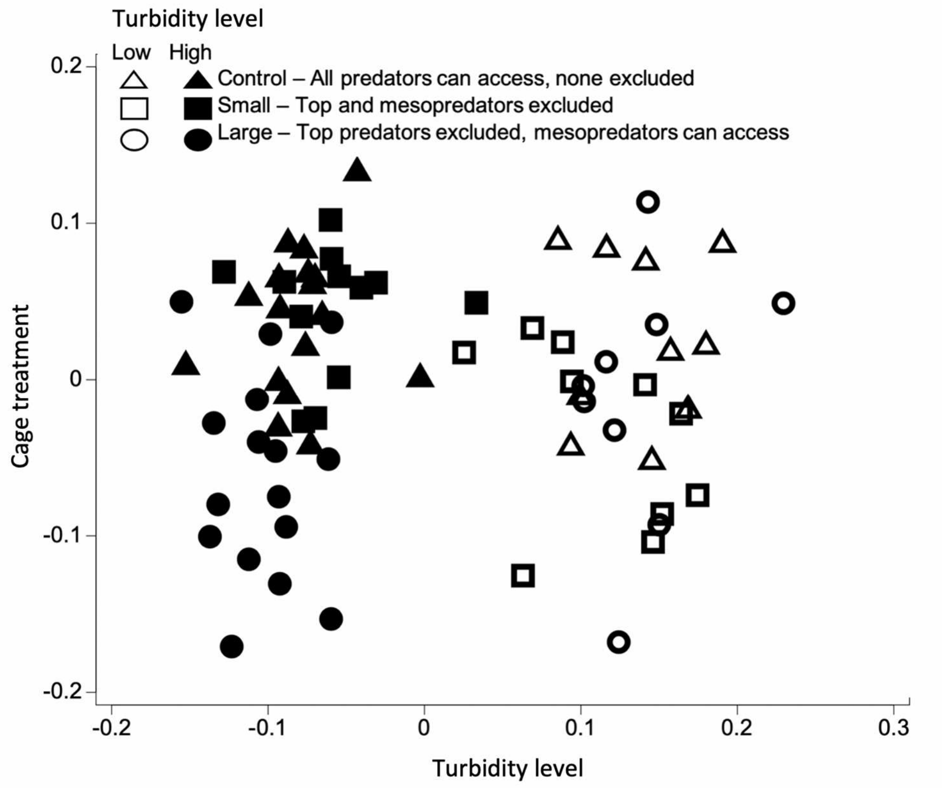


Figure I.1: Canonical analysis of principle coordinates (CAP) plot comparing communities between high and low turbidity and caging types. High turbidity communities are black and low turbidity communities are white. Cage types are represented by different shapes; open/control cages accessible to all predators are denoted by circles, small-mesh cages excluding all predators are denoted by squares, and large-mesh cages excluding top predators but that are accessible by mesopredators are denoted by circles.

Figure I.2

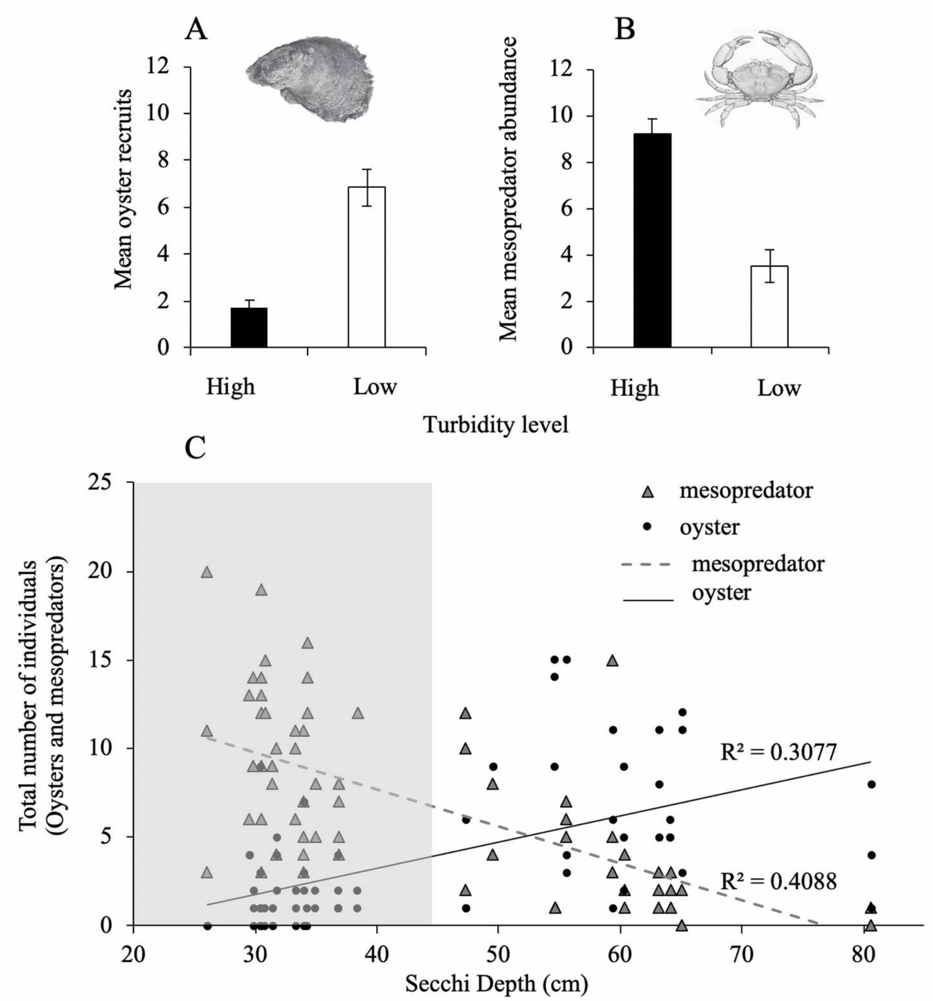


Figure I.2: Mean number ± SE oyster recruits (A) and mesopredator abundances (B) in low and high turbidity. (C) The relationships between abundances of oyster recruits and mesopredators across Secchi depths. The shaded rectangles indicate highly turbid sites where mean Secchi depths were less than 45 cm. Low turbidity sites, which are unshaded, had mean Secchi depths of greater than 45cm. Crab image sourced from the Freshwater and Marine Image Bank at the University of Washington.

Figure I.3

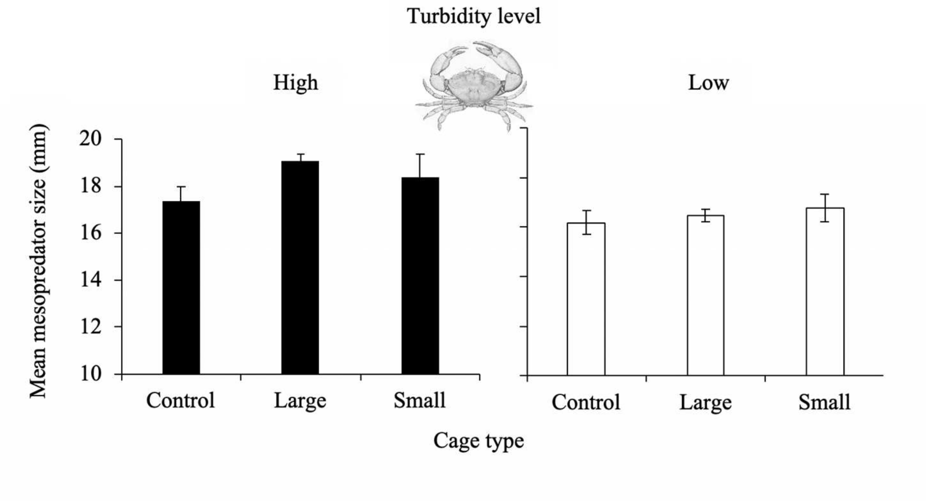


Figure I.3: Mean mesopredator size + SE per cage across caging types within high (left) and low (right) turbidity levels. Different letters indicate significantly different means as found by a Tukey post-hoc test. Crab image sourced from the Freshwater and Marine Image Bank at the University of Washington.

Figure I.4

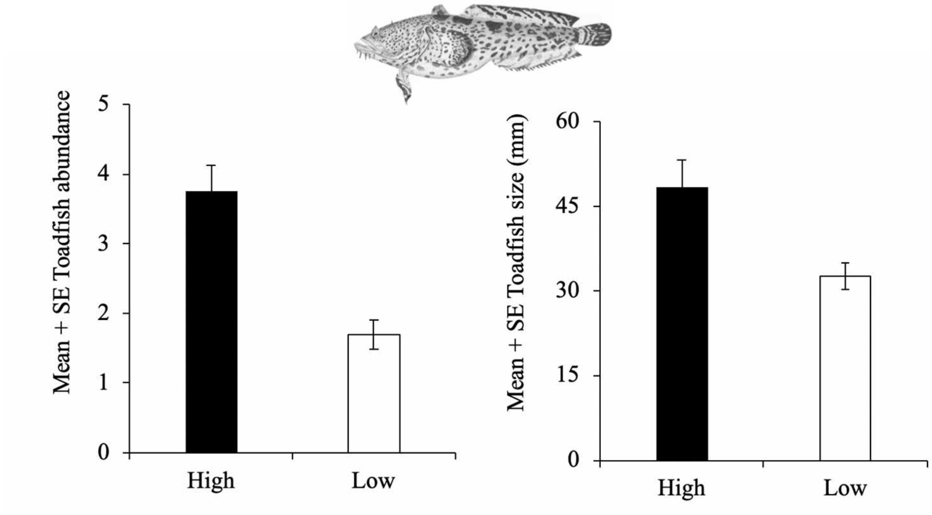


Figure I.4: Gulf Toadfish (*Opsanus beta*) abundance + SE (left) and length + SE (right) per cage across cage types and high (left) and low (right) turbidity levels. Toadfish image sourced from the Freshwater and Marine Image Bank at the University of Washington.

Figure I.5

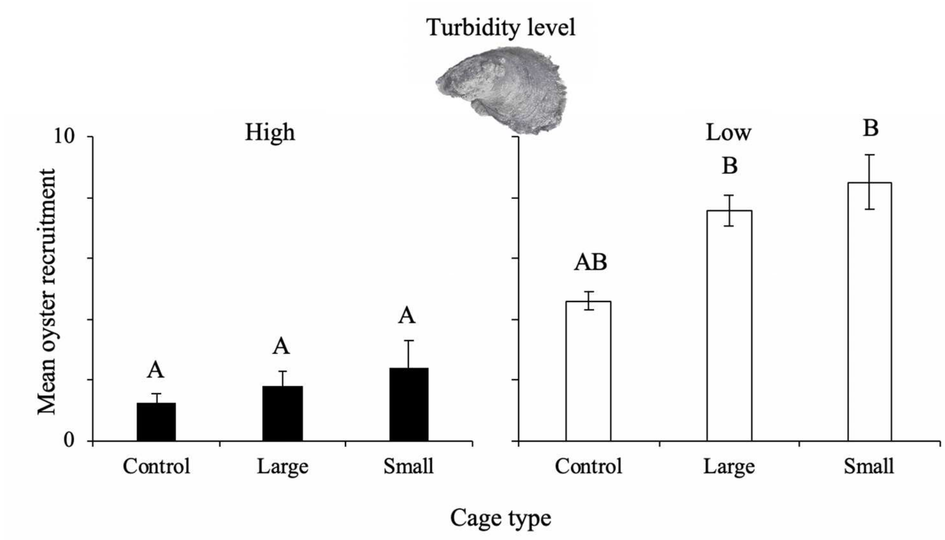


Figure I.5: Mean number ± SE oyster recruits per cage across caging types and high (left) and low (right) turbidity levels. Eastern oyster image sourced from the Freshwater and Marine Image Bank at the University of Washington.

Figure I.6

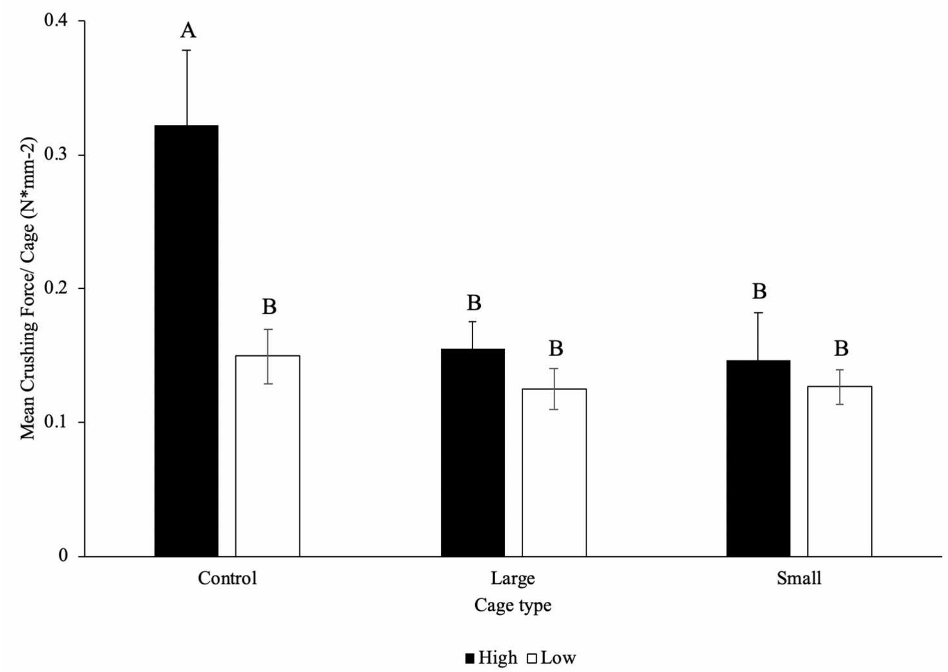


Figure I.6: Mean ± SE force needed to crush oyster shells from individuals settling within experimental cages. Crushing forces among caging types and turbidity levels is presented, and letters indicate significantly different means as found by a Tukey post-hoc test.

Figure I.7

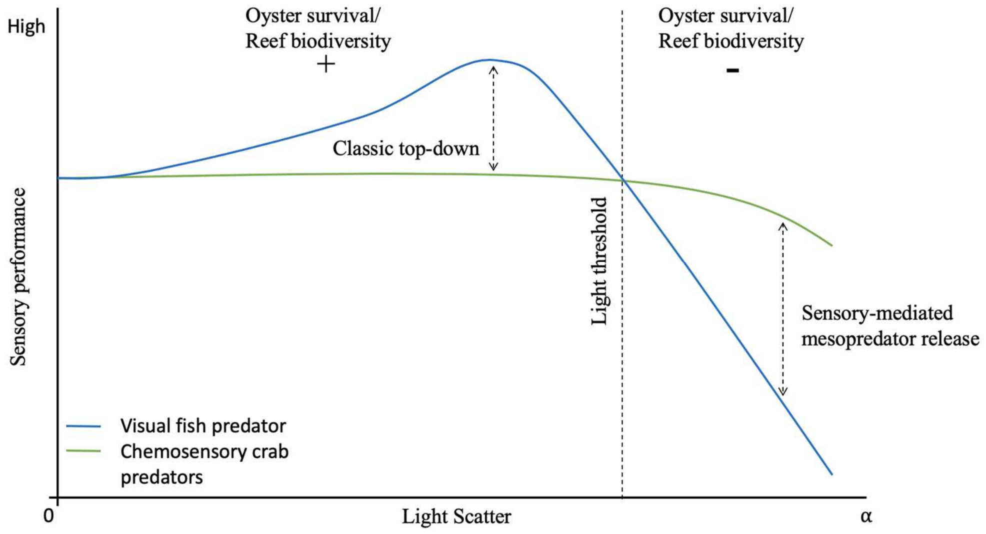


Figure I.7: Conceptual model of sensory mediated mesopredator release hypothesis showing how an environmental factor, in this case turbidity causing light scatter, interacts with sensory performance of different predator types. Our model is based upon the consequences of light scatter for oysters and reef communities but is applicable to other systems. The blue line represents visually oriented predators and the green line represents other (non-visual) sensory modes, such as chemosensory and mechanosensory oriented predators. In low turbidity with little light scatter, neither fish nor crab sensory performance is inhibited; however, as light scatter increases to high levels it increases the relative performance of non-visual organisms (green line) over visual organisms (blue line) resulting in sensory-mediated mesopredator release. The dashed line represents a light scatter threshold where the differential in performance of visual and chemosensory predators switches from top-down control to sensory-mediated mesopredator release. Intermediate turbidity levels may enhance foraging by visual predators by providing contrast with prey, and thus performance of visual organisms may peak in these conditions.

Supplemental Tables

Supplemental table I.1

Turbidity level	Cage types		T	P(perm)	Unique permutations
High	Control	Large	1.5527	0.0194	93763
	Control	Small	1.3684	0.0852	94261
	Large	Small	2.1922	0.0002	94522
Low	Control	Large	0.72529	0.8803	58715
	Control	Small	1.1211	0.2299	58441
	Large	Small	0.97417	0.5025	58553

Supplemental table I.2: Two-way PERMANOVA pairwise test results. Significant effects of predator exclusion were found in high but not low turbidity among all cage treatments. In high turbidity controls were different than small-mesh cages that excluded all predators, large-mesh cages that excluded top predators per were accessible to mesopredators, and large and small-mesh cages were also significantly different.

Supplemental table I.2

Species	Com. name	High Turbidity Av.Abnd	Low Turbidity Av.Abnd	Av.Diss	Diss/SD	Contrib %	Cum.%
Petrolisthes armatus	Green porcelain crab	12.37	4.85	9.09	1.71	17.26	17.26
Palaemonetes spp.	Grass shrimp	2.82	7.68	6.22	1.59	11.82	29.08
unidentified mud crabs	Mud crabs < 10 mm	5.42	10.04	6.09	1.31	11.56	40.65
Eurypanopeus turgidus	Ridgeback mud crab	1.30	5.78	5.24	2.61	9.95	50.60
Eurypanopeus depressus	Flatback mud crab	4.56	0.14	5.12	2.16	9.72	60.32
Ctenogobius boleosoma	Darter goby	0.06	1.62	1.80	1.02	3.41	63.73
Gobiosoma bosc	Naked goby	3.48	2.67	1.79	1.24	3.40	67.13
Chasmodes longimaxilla	Stretch jaw blenny	0.32	1.54	1.47	1.63	2.79	69.92
Gobiesox strumosus	Skillet fish	1.16	0.00	1.37	1.59	2.60	72.52
	Average dissimilarity		**52.65**				

Supplemental table I.2: SIMPER analysis of communities between high and low turbidity (square root transformed) collected in control cages accessible to all predators. Column abbreviations: “Av. Abnd” is the average abundance per sample; “Av. Diss” is the average dissimilarity between samples; “Diss/SD” is the dissimilarity divided by the standard deviation; “Contrib%” is the percent contribution of that species to differences amongst communities; “Cum.%” is the cumulative percent differences amongst communities. A 70% cumulative cutoff was applied to the analysis.

Supplemental table I.3

	Control	Large	Small
	Low turbidity		
Control	57.67		
Large	57.406	54.08	
Small	59.286	58.275	59.946
	High turbidity		
Control	65.44		
Large	67.986	73.706	
Small	64.725	65.853	65.486

Supplemental table I.3: Average similarity between and within communities in low turbidity (top) and high turbidity (bottom). Values, which were obtained from a pairwise two-way PERMANOVA test in Primer (turbidity x cage type), represent the relative similarity between and within samples from caging treatments in high and low turbidity. Larger values are indicative of samples with a heightened degree of similarity.

Supplemental table I.4

	Estimate	**Std. error**	**Z value**	**Pr(>|z|)**
(Intercept)	3.99977	0.40502	9.875	< 2e-16 *
Secchi depth	-0.05919	0.01092	-5.419	5.98e-08 *
Cage treatment: large-control	-0.41315	0.54168	-0.763	0.4456
Cage treatment: large-small	-0.79748	0.54185	-1.472	0.1411
Secchi depth * cage treatment: large-control	0.01334	0.01430	0.933	0.3508
Secchi depth * cage treatment: large-small	0.02551	0.01384	1.844	0.0652

Supplemental table I.4: Negative binomial GLM output of mudcrab mesopredator counts across Secchi depths and cage treatments.

Supplemental table I.5

	Estimate	**Std. error**	**Z value**	**Pr(>|z|)**
(Intercept)	2.0789225	0.4310543	4.823	1.42e-06 *
Secchi depth	-0.0220928	0.0103445	-2.136	0.0327 *
Cage treatment: large-control	-0.0913314	0.6143990	-0.149	0.8818
Cage treatment: large-small	-0.2085622	0.6689157	-0.312	0.7552
Secchi depth * cage treatment: large-control	0.0005240	0.0147151	0.036	0.9716
Secchi depth * cage treatment: large-small	-0.0008245	0.0156628	-0.053	0.9580

Supplemental table I.5: Negative binomial GLM output of toadfish counts across Secchi depths and cage treatments.

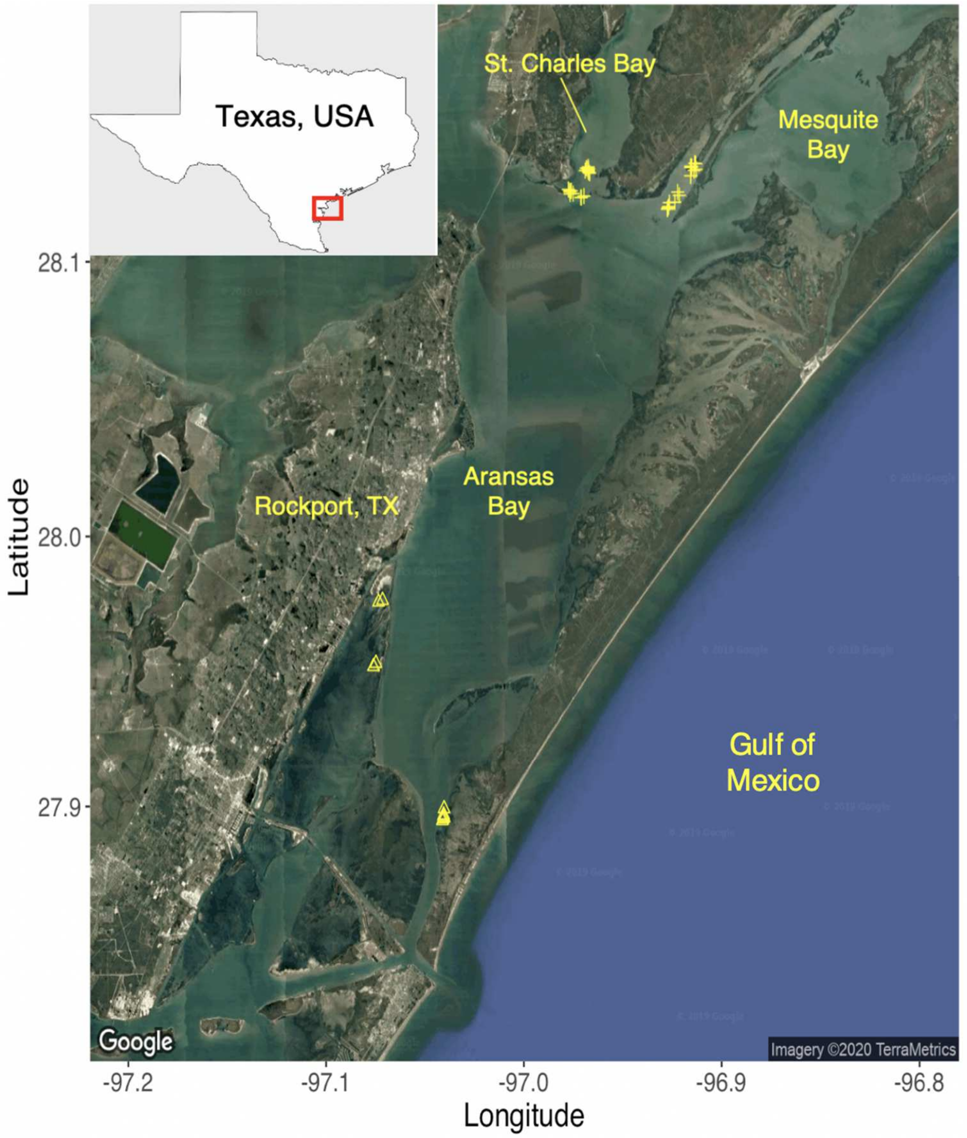
Supplemental table I.6

	Estimate	**Std. error**	**Z value**	**Pr(>|z|)**
(Intercept)	-0.755737	0.557146	-1.356	0.175
Secchi depth	0.044670	0.011408	3.916	9.01e-05 *
Cage treatment: large-control	-0.117178	0.813844	-0.144	0.886
Cage treatment: large-small	0.447422	0.809307	0.553	0.580
Secchi depth * cage treatment: large-control	-0.006162	0.016646	-0.370	0.711
Secchi depth * cage treatment: large-small	-0.004793	0.016356	-0.293	0.769

Supplemental table I.6: Negative binomial GLM output of oyster recruits across Secchi depths and cage treatments.

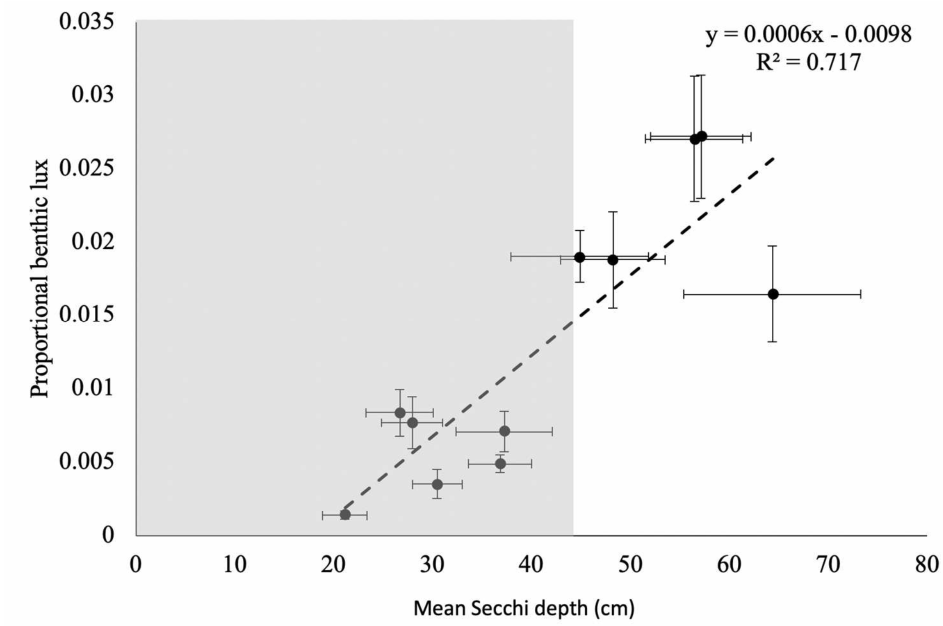
Supplemental Figures

Supplemental figure I.1



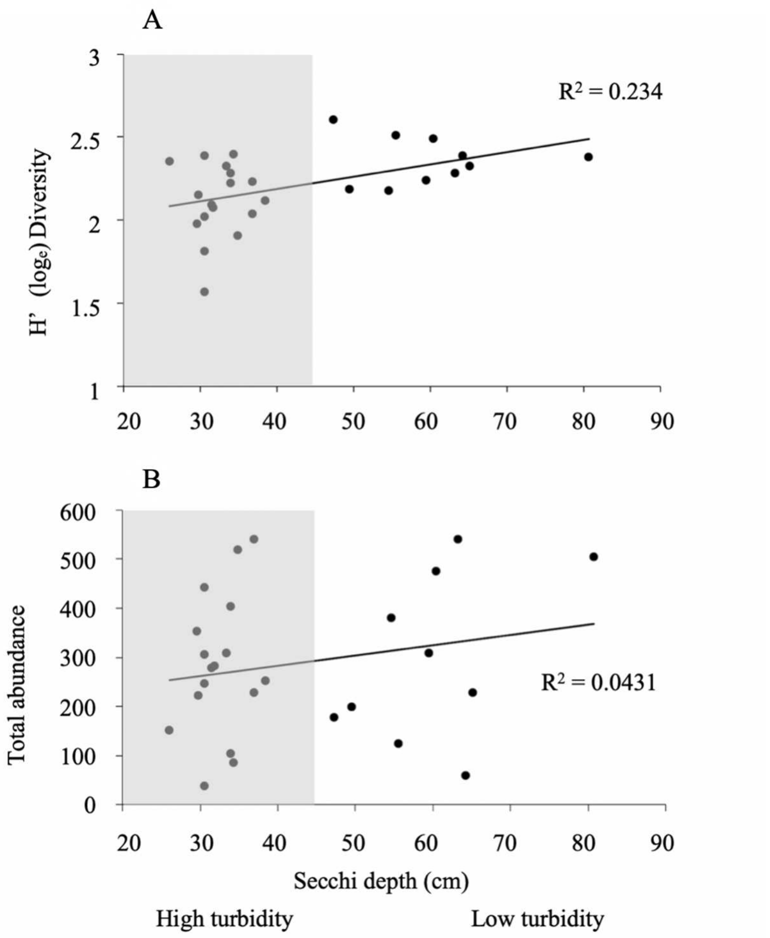
Supplemental figure I.1: Map of field sites (illustrated by "+" symbols in yellow for high turbidity sites, yellow "Δ" for low turbidity sites) in South Texas, USA. Mapped GPS coordinates are displayed in decimal degrees (DD) format and were obtained at each site in the field using a handheld Garmin GPSmap 76CSx. Maps were built in RStudio version 1.1.456 using the ggmap (Kahle and Wickham 2013), mapdata (Becker et al. 2018), and ggplot2 (Wickham 2016) packages.

Supplemental figure I.2



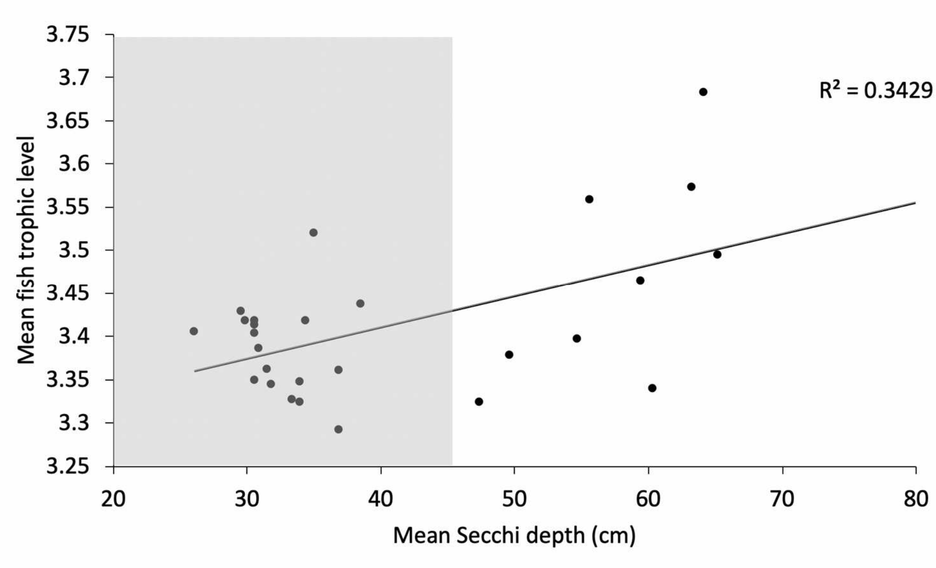
Supplemental figure I.2: Mean ± SE proportional light intensity (lux) and Secchi depths (cm) across sites. Low turbid sites had greater light levels as measured by data loggers as well as deeper Secchi depths. The shaded rectangles indicate highly turbid sites where mean Secchi depths were less than 45 cm. Low turbidity sites, which are unshaded, had mean Secchi depths of greater than 45cm.

Supplemental figure I.3



Supplemental figure I.3: Shannon diversity (H'(log$_e$)) (A) and total abundance (B) of communities plotted across Secchi depths (cm) in control (open) cages accessible to predators. The shaded rectangles indicate highly turbid sites where mean Secchi depths were less than 45 cm. Low turbidity sites, which are unshaded, had mean Secchi depths of greater than 45cm.

Supplemental figure I.4



Supplemental figure I.4: Mean trophic levels of fishes (calculated using Fishbase.org) across Secchi depths (cm) from control cages. The shaded rectangles indicate highly turbid sites where mean Secchi depths were less than 45 cm. Low turbidity sites, which are unshaded, had mean Secchi depths of greater than 45cm.

CHAPTER II: TURBIDITY AND SALINITY INFLUENCE TROPHIC CASCADES ON OYSTER REEFS THROUGH MODIFICATION OF SENSORY PERFORMANCE AND FACILITATION OF DIFFERENT PREDATOR TYPES

Chapter published as Reustle JW, Smee DL (2020) Turbidity and salinity influence trophic cascades on oyster reefs through modification of sensory performance and facilitation of different predator types. Mar Ecol Prog Ser 639:127-136. https://doi.org/10.3354/meps13283. Reprinted with permission from Inter-Research Science Publisher.

ABSTRACT

Abiotic factors can influence the distribution of organisms through physiological tolerance limits and by influencing their performance in critical life history functions such as foraging or predator avoidance. In estuaries, salinity and turbidity directly influence the distribution of organisms but the indirect, synergistic effects of these factors on trophic interactions and community structure remain obscure. We investigated the effects of salinity and turbidity on oyster reef communities by comparing oyster reef community structure in low vs. high turbidity in consecutive years that varied considerably in rainfall and ambient salinity levels. Turbidity had significant effects in both 2016 and 2017 by interfering with fish foraging ability and consumption. In turbid sites, fish predation decreased by ~21%, crab mesopredators were 11% larger and nearly 5 times more abundant due to reduced top-down control by fish, and oyster reef biodiversity was 12% lower. In 2016, oysters were 350% less abundant in sites with abundant crab predators. However, in 2017, salinity increased, facilitating a new predator (oyster drills, *Stramonita haemastoma*) to emerge onto reefs, and oysters were 7 times less abundant in sites with oyster drills despite having fewer crab predators. Thus, salinity and turbidity can indirectly affect food webs by facilitating different predators and influencing their foraging ability. Turbidity had significant effects on estuarine food webs regardless of salinity levels, and like salinity, turbidity should also be considered in future management of estuarine ecosystems.

INTRODUCTION

The interplay between abiotic and biotic factors often leads to complex and context-dependent changes in species interactions and distributions across space and time (*e.g.,* Connell 1961, Menge and Sutherland 1987). Abiotic conditions directly affect species distributions and interactions through physiological tolerance limits (Grinnell 1917, Helmuth et al. 2002, Somero 2005, Poloczanska et al. 2013), and indirectly by influencing performance of critical life-history processes such as foraging or predator avoidance (Sanford 1999, Smee et al. 2010, Large and Smee 2013). Changes in environmental conditions that affect sensory performance can significantly affect ecological processes as well as the structure and function of communities (Leonard 1998, Robinson et al. 2011, Large & Smee 2013). For instance, the intensity of hydrodynamic conditions results in distinct ecological communities by favoring prey, predators, or completely reducing predation and switching to a community modulated by stress (Menge & Sutherland 1987, Smee et al. 2010). Species must balance stress-tolerance with foraging and predator avoidance capability, which can be challenging in dynamic environments such as estuaries where factors such as salinity and turbidity can vary substantially in space and time.

Salinity is widely regarded as the most important factor influencing the composition and distribution of estuarine organisms (Copeland 1966, Day et al. 2009). Managing estuarine salinity and its variance, through regulation of freshwater inflow, is necessary to ensure estuarine resources remain viable (Alber 2002). Drought and freshwater diversion raise salinity (Montagna et al. 2013) and can cause considerable damage to estuarine communities, particularly when salinity is variable and bounces between extremes (*i.e.*, flood and drought conditions) (Van Diggelen & Montagna 2016). Yet, some municipalities release freshwater only during flood conditions, when it is least helpful and most harmful, and withhold freshwater during droughts when it is most needed. Poor management techniques, coupled with exceedingly variable climatic conditions, exacerbate these salinity swings that damage estuarine communities. Drought and altered salinity regimes can negatively affect primary productivity (Wetz et al. 2011) as well as economically and ecologically valuable species such as halibut (*Hippoglossus hippoglossus*), lobster (*Homarus americanus*) (Sutcliffe Jr 1972, 1973), and oysters (*Crassostrea virginica*) (Copeland 1966, Pollack et al. 2011). For example, in Apalachicola Bay, Florida droughts increased coastal salinity levels to within the tolerance limits of predatory oyster drills, *Stramonita haemastoma* (Kimbro et al. 2017), leading to high oyster mortality (Booth et al. 2018). In turn, commercial oyster fishing crashed (Camp et al. 2015), reducing critical habitat for numerous other ecologically and economically important species (Scyphers et al. 2011, Pine III et al. 2015). Conversely, extensive rainfall and coastal flooding can rapidly lower salinity and damage Eastern oysters; yet, floods also reduce oyster diseases, remove drill predators, and can enhance oyster spawning facilitating recovery (Copeland 1966, Pollack et al. 2011, Pusack et al. 2018).

Like salinity, turbidity can affect the structure and function of marine communities by altering light regimes, primary production, and trophic dynamics (Cloern 1987, Gregory 1993, Gregory & Levings 1998). Turbidity directly governs the distribution and morphology of submerged aquatic vegetation (Duarte 1995, Longstaff & Dennison 1999, Scheffer et al. 2001), especially seagrasses, and can cause vegetation die-off leading to sediment resuspension and further increases in turbidity (Duarte 1995). Turbidity increases light absorption and scatter, which hampers image formation and reduces the effectiveness and efficiency of visual organisms (Benfield & Minello 1996, Aksnes & Utne 1997). By interfering with the visual acuity of piscivorous fishes, turbidity can alter trophic interactions and significantly affect community structure and function (Eiane et al. 1999, Aksnes 2004, Lunt & Smee 2014). Turbidity and salinity may be coupled in estuaries where freshwater inputs both lower salinity and increase turbidity. However, in shallow estuarine systems where wind-driven mixing increases the amount of suspended sediments in the system regardless of salinity, turbidity can have substantial community structuring power through modification of sensory regimes (Reustle and Smee *in press*, Lunt & Smee 2014).

Turbidity interferes with organisms that rely on visual cues for foraging (Gregory & Levings 1998, Zamor & Grossman 2011, Lunt & Smee 2015), finding suitable habitat (Wenger et al. 2011), and risk perception (Gregory 1993), while organisms that use other sensory modalities are largely uninhibited (Eiane et al. 1999, Lunt & Smee 2015). In aquatic systems that are primarily structured through top-down forcing by visually-oriented predators, turbidity can alter top-down control and have significant ecological consequences (Reustle and Smee *in press*, Eiane et al. 1999, Lunt & Smee 2014), particularly when turbidity differentially affects sensory performance of marine species (Eiane et al. 1999, Lunt & Smee 2014). These effects may be particularly poignant in the face of global environmental change.

The purpose of this study was to ascertain the separate and synergistic effects of turbidity and salinity in estuarine communities. While salinity's effects in estuaries are well known and actively considered in management and conservation, the role of turbidity has largely been overlooked or has been considered to be directly coupled with salinity effects. Although salinity and turbidity may be coupled (*e.g.*, freshwater inflow may lower salinity and increase turbidity), in wind-dominated systems, turbidity can vary independently of salinity. Thus, we selected oyster reefs in the western Gulf of Mexico as a model system to study the combined effects of turbidity and salinity. This area is microtidal, arid, and turbidity is primarily driven by prevailing winds that resuspend sediment. Oyster reefs from areas with low (Secchi depths ≥45 cm) and high turbidity (Secchi depths <45 cm) were studied during consecutive years that varied substantially in rainfall and ambient salinity. Higher order predators on oyster reefs in the area include red drum (*Sciaenops ocellatus*), spotted sea trout (*Cynoscion nebulosus*), sheepshead (*Archosarguys probocephalus*), and gulf toadfish (*Opsanus beta*). Reefs are inhabited by numerous small fish species (*e.g.*, gobies and blennies), grass shrimp (*Palaemonetes* spp.) and brown shrimp (*Farfantepenaeus aztecus*), and many crab species including stone crabs (*Medippe adina*), blue crabs (*Callinectes sapidus*), and mud crabs (*Panopeus herbstii*, *Eurypanopeus turgidus*, *Eurypanopeus depressus*). Crabs with carapace widths >15mm prey heavily on newly settled oysters, causing many oysters to develop heavier and stronger shells to combat crushing and drilling predators (Lord and Whitlatch 2012, Robinson et al. 2014). Additionally, many of these predators also consume porcelain crabs (*Petrolisthes armatus*), which are common suspension feeders and algae scrapers within oyster beds (Kropp 1981, Hollebone and Hay 2007, Zimba et al. 2016).

In low turbidity, fish predation was higher and crabs that fish prey upon were less abundant. However, in low salinity, by preying on crabs and reducing their abundance, fish facilitated the recruitment and growth of newly settled oysters. When salinity increased, the positive effects of fish on oysters disappeared as a new predator, oyster drills, moved onto reefs and consumed many newly settled oysters. Salinity and turbidity significantly affected oysters and reef communities through different mechanisms that altered trophic interactions.

METHODS

Study locations- Oyster reefs in the Mission-Aransas National Estuarine Research Reserve near Rockport, TX, USA were selected for this study (**Supplemental Figure II.1**). Oyster reefs in this area are low relief (short vertical heights) and contain a mixture of living oyster clumps and oyster shells. This is a microtidal estuary, and the reefs were in shallow subtidal environments at ~ 0.5 m below mean low water and 100-300 m from land.

Salinity and water temperature were measured daily by the Mission-Aransas NERR SWMP stations which were roughly 4-9 km away from experimental trays. Salinity was also measured within 5 m of each oyster reef sampling location using a refractometer. Turbidity in the Mission-Aransas NERR is caused by suspended sediment that is mixed into the water column by near continuous wind. Although rare, all sites may have low turbidity following an extended period of low wind. Turbidity was quantified using a Secchi disk. Secchi measurements were taken 11 times over the study period, seven times in 2016 and four times in 2017. In 2016, high turbidity sites had mean Secchi depths of 30.9 (SE +/- 0.94) cm, while low turbidity reefs had mean Secchi depths of 51.8 (SE +/- 1.57) cm. Mean Secchi depths in 2017 were similar to the year previous between high (Mean and SE 31.1 +/- 0.509 cm) and low (Mean and SE 52.4 +/- 1.67 cm) turbidity sites. We also measured light levels (lux) using HOBO Pendent data loggers. High turbidity sites had ~3x less available light than low turbidity sites (Reustle and Smee *in press*).

In 2015, central Texas received abnormally high rainfall and salinity in the Mission-Aransas NERR salinity reached 0 ppt in some areas and remained below 10 ppt for several weeks (Diskin & Smee 2017). By spring 2016, salinity had risen to 15-20 ppt. However, 2017 was a drought year and in some estuaries salinity reached 35 ppt (**Figure 1**). These broad shifts in salinity can have substantial effects on estuarine communities such as soft-bottom systems (Ritter et al. 2005) and oyster reefs (Pollack et al. 2011). In our study area, oyster reefs can be found in both low and high turbidity areas, which varied considerably in salinity between 2016 and 2017.

<u>*Community sampling-*</u> We sampled oyster reef communities by using 0.25m^2 (0.5m x 0.5m) wooden sampling trays with 1.0 cm^2 vexar mesh along the bottom. Twenty L of sun bleached oyster shells were added to each tray to form an artificial reef imbedded within the natural reef. We deployed 20 trays in high turbidity and 10 in low turbidity sites with each tray separated by at least 100 m to increase spatial resolution We initially had planned to have 10 trays in intermediate turbidity sites, but Secchi and light measurements revealed these sites to be turbid. In 2017, we deployed trays in the same general areas to examine effects of low and high turbidity, placing 18 trays in sites with high turbidity and 9 trays in low turbid sites. Trays were always separated by at least 100 m. Trays were deployed May 3 – June 30 2016 and April 26 – June 6 2017 to capture peak oyster spawning and recruitment. Organisms will recruit into trays within 1-2 weeks (Smee unpublished data), and in both years, were in the field long enough for reef communities to develop and for oysters to recruit and grow. Organisms inhabitng each tray were collected using modified throw traps. A 1.0 m^3 throw trap was placed over the tray, the tray was removed, thoroughly searched, and all organisms collected. Sweep nets (500 µm mesh-size) were then used to sweep within the area enclosed by the throw trap to collect any organisms dislodged from the tray. Larger organisms were identified, measured, and released *in situ*, while smaller organisms were placed in ethanol and transported to the lab for sorting, identification, measurements, and enumeration. Community data were analyzed using PRIMER^{TM} (Clarke 1993), which houses some methodologies (*e.g.*, PERMANOVA) that are more robust and effective in testing unbalanced designs (Anderson et al. 2008). Community data were square-root transformed and assembled in a Bray-Curtis resemblance matrix and analyzed using a 2-way

PERMANOVA (turbidity * year) with 10,000 permutations allowing permutations of residuals under a reduced model. Distance-based tests for homogeneity of multivariate dispersions (PERMDISP) were used to determine how turbidity level and year, respectively, affected group dispersions. For each PERMDISP test, dispersion was compared using permutations (100,000) across centroid distances.

A Canonical Analysis of Principle coordinates (CAP) plot was constructed to illustrate shifts in community structure due to year and turbidity level. Simpson's diversity was calculated using the "Vegan" package in R (Oksanen et al. 2019) and total community diversity and the total number of organsisms per sample were compared between turbidity level and year using a Two-Way ANOVA in Rstudio version 1.1.456.

Mud crabs with carapace widths greater than or equal to 15 mm were classified as mesopredators. Smaller mud crabs do not routinely eat oysters (Johnson et al. 2014). The abundance of crab mesopredators per site (n = 52) was analyzed using a generalized linear model (GLM) with a negative binomial distribution with the MASS package (Venables and Ripley 2002) in Rstudio version 1.1.456. Secchi depth and year served as explanatory variables in the model. Though the design is unbalanced, negative binomial GLMs are capable of handling these data and are often more powerful than other methodologies (Warton et al. 2016), especially with our robust sample size (n = 52). All models were tested to ensure that they satisfied assumptions of GLMs.

Other mesopredators found in this study demonstrated unique distributions, which required different analytical approaches. Oyster drills tend to form dense, patchy, aggregates (*i.e.,* <30 m^{-2}), but may be completely absent just meters away. Thus, we used a zero-inflated negative binomial regression model (ZINB) following (Zuur et al. 2009) to quantify differences in oyster drill abundances across turbidity levels in 2017. No oyster drills were collected in 2016 at any sites, so only 2017 data were used in this analysis. Oyster drill data were analyzed using the pscl package (Zeileis et al 2008) in Rstudio version 1.1.456.

Oyster recruitment- Two PVC spat collectors (aka spat sticks, grooved PVC, 100 mm long, and 22 mm in diameter that oysters settle and grow on) were placed within each tray to assess oyster recruitment. Upon retrieval, spat sticks were returned to the lab. The number of settled oysters was recorded as well as the length and width of five oysters from each tray. Oysters respond to predators by growing heavier, stronger shells (Scherer et al. 2016). Therefore, we quantified the relative crushing force of oysters using a force sensor as an indicator of predator presence and predation risk. Oyster recruitment was analyzed using a GLM with a negative binomial distribution and Secchi depth and year as fixed factors (MASS package) (Venables and Ripley 2002). Recruitment and crushing force data were analyzed in RStudio version 1.1.442 and JMP Pro 14. Oyster crushing force was standardized by area (crushing force/mm^2) and compared between turbidity regimes and year using a two-way ANOVA. Tukey's post hoc tests were used for pairwise comparisons when necessary.

Relative levels of predation- Ambient predation intensity was assessed using squid pops, which provide an estimate of fish consumption (Duffy et al. 2015). Squid pops were made by attaching a 1.0 cm^2 piece of dried squid to a fiberglass stake, placing into the field for 24 hours, and determining if the squid was eaten or not. Squid pops were deployed in low and high turbidity sites in 2017 where trays had been deployed. Each squid pop was driven firmly into the substrate with the squid bait ~0.3m above the substrate. Squid pops were placed at least 2 m apart from one another and were left in the field for 24 hours before collections. Squid pops were recorded as eaten or unconsumed. Data were grouped all together and were analyzed as binomial data (0 =

unconsumed; 1= consumed). Squid pops that were not recovered were excluded from analyses. Data were analyzed using a Wilcoxon-Rank Sum test in R (MASS package) (Venables and Ripley 2002).

RESULTS

Turbidity and lux- Mean Secchi depths were similar within each turbidity level each year ($F_{1,16}$ = 0.055, p = 0.8173), but differed between turbidity levels in both years ($F_{1,16}$ = 65.4, $p < 0.001$). The interaction between turbidity level and year was non-significant ($F_{1,16}$ = 0.18, p = 0.678). Similarly, lux did not differ between years ($F_{1,15}$ = 0.858, p = 0.369), but was distinctly different between turbidity levels (**Supplemental Figure II.2**; $F_{1,15}$ = 72.6, $p < 0.001$). The interaction between turbidity level and year was not significant ($F_{1, 15}$ = 0.438, p = 0.518).

Community results- Community diversity (Simpson's diversity index) was significantly different between turbidity levels ($F_{1,48}$ = 4.08, p = 0.0491), though year ($F_{1, 48}$ = 0.54, p = 0.467) and the interaction of turbidity and year were non-significant ($F_{1,48}$ = 0.56, p = 0.458). Total abundance of organisms was not significantly different between turbidity levels ($F_{1,48}$ = 0.394, p = 0.53), years ($F_{1,48}$ = 0.854, p = 0.36), and the interaction-term was not significant ($F_{1,48}$ = 0.04, p = 0.843). PERMANOVA indicated turbidity (Pseudo-$F_{1,48}$ = 13.6, $p < 0.001$) and year (Pseudo-$F_{1,48}$ = 4.88, $p < 0.001$) were both significant in explaining community structure (**Figure II.2**). The interaction between turbidity level and year was also significant (Pseudo-$F_{1,48}$ = 2.17, p = 0.03). PERMDISP tests found that groups did not differ significantly in dispersion between turbidity levels ($F_{1,50}$ = 0.706, p = 0.474; means: high = 30.9, low = 28.2); however, there were significant differences in dispersion across years ($F_{1,50}$ = 5.89, p = 0.028; means: 2016= 30.3, 2017= 36.0). The sampling design between years was only slightly unbalanced (samples: 2016= 27, 2017=25), indicating that the PERMDISP test was reliable.

The abundance of mud crab mesopredators on oyster reefs was affected by Secchi depth (estimate = -0.0492, z = -4.10, $p < 0.001$), but not by year (estimate = -0.0853, z = -0.124, p = 0.9). The interaction between Secchi depth and year did not affect mud crab mesopredator abundance (estimate = 0.00035, z = 0.020, p = 0.984). On average, there were 8.88 +/- 3.2 (sd) and 4.9 +/-3.61 (sd) mesopredators/tray ($0.25m^2$) in high and low turbidity sites, respectively, in 2016. In 2017, turbid sites had 9.13 +/- 7.14 (sd) mud crab mesopredators/tray and low turbidity sites had 1.33 +/- 1.32 (sd).

Oyster drills were significantly more abundant in low turbidity (estimate = 1.58, z = 2.13, p = 0.033). Year was not tested since there were no oyster drills found in any samples in 2016.

Size Measurements- Crab mesopredators were significantly larger in high turbidity than low turbidity sites ($F_{1,42} = 5.79$, p = 0.021), and they were also significantly larger in 2017 than in 2016 ($F_{1,42} = 7.56$, p = 0.009). The interaction between turbidity level and year was not significant ($F_{1,42} = 0.69$, p = 0.408). On average, mud crab mesopredators had mean carapace widths of 18.5 ± 0.42 (mean ±SE) mm in high turbidity and 16.7 ± 0.64 mm in low turbidity.

Oyster Recruitment- Oyster recruitment differed significantly between years (**Figure II.3**; estimate= 5.62, z = 7.27, $p < 0.001$) and Secchi depths (estimate = 0.036, z = 3.10, p = 0.002). However, the interaction between year and Secchi depth was also significant (estimate= -0.10, z = -5.80, $p < 0.001$). In 2016, oyster recruitment and Secchi depths were positively correlated; however, in 2017 oyster recruitment and Secchi depths were strongly and negatively correlated (**Figure II.4**). Across years, Secchi depth (estimate = 0.13, z = 2.25, $p < 0.024$) and salinity (estimate = 4.22, z = 3.64, $p < 0.001$) were both significant in explaining oyster recruitment, as were the interactive effects between salinity and Secchi depth (estimate= -0.008, z = -3.05, p = 0.002). 2017 was overall a higher recruitment year for oysters, with four times more settlement observed. In 2016, oyster recruitment was significantly greater on low turbidity reefs, but the opposite pattern was found in 2017.

Oyster crushing force- Neither turbidity ($F_{1,34} = 1.27$, $p = 0.267$) nor year ($F_{1,34} = 0.002$, $p = 0.964$) significantly affected oyster crushing forces in the full model; however, the interaction term was significant ($F_{1,34} = 9.40$, $p = 0.004$). In 2016, oysters from turbid reefs were significantly stronger than oysters from low turbidity reefs (**Figure II.5**). In 2017, there was no difference in oyster crushing forces between high or low turbidity (**Figure II.5**).

Relative levels of predation- Squid pop consumption was higher in low turbidity sites (mean= 90% consumed) than high turbidity sites (mean= 68.9% consumed) ($W = 1212$, $p = 0.008$).

DISCUSSION

Because salinity and turbidity covary in some well-studied estuaries, the relative importance of turbidity has often been difficult to ascertain and been poorly quantified. Yet, salinity and turbidity often operate independently of one another and affect food webs through different mechanisms. Tolerance to salinity stress dictates community composition and distributions, while turbidity alters how communities assemble and interact (although turbidity can influence the presence of submerged vegetation). Salinity and turbidity are not always tightly linked, particularly in the Western Gulf of Mexico where prevailing winds influence turbidity via re-suspension of sediment regardless of salinity. We found that turbidity and salinity each had significant effects on communities. Communities in low and high turbidity were distinctly different from each other and these differences persisted across wet and dry years that varied considerably in salinity (**Figures II.1-2; Supplemental Table II.1**). Consumption of squid pops, which measure fish consumption (Duffy et al. 2015), was significantly higher in low turbidity. This finding was consistent with earlier work in this system using tethered crabs, which also revealed fish predation to decline in turbid conditions (Lunt and Smee 2014, 2015). High turbidity was associated with an increase in the abundance and size of crab mesopredators. In 2016, oysters benefited from fewer crab predators and lower shell-defense costs in low turbidity (**Figures II.3-5**). However, in 2017, the benefits yielded by intact top-down control was foiled by higher salinity that facilitated oyster drills (**Figures II.3-5**).

Community structure was significantly different across years and turbidity levels as was the interaction between these factors. Communities were more diverse (Simpson's index) in low turbidity, though year and the interaction term were non-significant. Turbidity primarily drove community differences through location-effects. However, communities differed in both location and dispersion across years as drought increased the variability in community assemblages. Further, drought conditions and corresponding higher salinity promoted the abundance of several oyster predators, and increased inducible defenses in oysters. Still, turbidity had significant and consistent effects on oyster reef inhabitants in both years. Oyster recruitment is notoriously variable in Texas (Pollack et al. 2011) and it is common for high recruitment events/ higher oyster CPUE to follow after low salinity/high flow years (Wilber 1992). Consistent with past observations, 2017 had significantly higher oyster recruitment after low salinity values associated with floods and storms had persisted the previous two years (2015 and 2016). However, the pattern for recruitment was quite different between turbidity levels and years. This change, where recruitment was higher in low turbidity sites in a wet year but lower in drought conditions, is likely attributed to the change in salinity facilitating the emergence of oyster drill predators that cannot tolerate low salinity (Menzel et al. 1966). Specifically, drills were ~23x more abundant on community samples from low turbidity reefs, juxtaposing the relative importance of mud crab mesopredators and oyster drills on oyster recruitment and inducible defenses. Despite the emergence of oyster drills and the contrasting effects on oysters, the effects of turbidity were significant in both years, even though salinity varied, indicating that turbidity effects are not directly tied to salinity in the study area.

Mud crabs have large effects on oyster populations despite being generalists (Meyer 1994). Mud crabs pose little threat to oysters when the crabs are small (*i.e.,* <10mm in carapace width), but become mesopredators and readily consume oysters when they grow larger (*i.e.*, $\geq$15mm). Ontogenetic shifts have been identified isotopically, illustrating that mud crabs become less enriched with $\delta^{13}C$ and group more closely with fishes and other secondary consumers levels after they reach ~12mm in carapace width (Aarnio et al. 2015). However, oyster drills have a much narrower diet and prefer oyster epibionts (*e.g.*, mussels and barnacles) and juvenile oysters over larger adult oysters (Butler 1985). Additionally, few predators are known to prey on oyster drills. Stone crabs are known predators of drills; however, they were significantly less abundant in low turbidity sites in 2016 and 2017, presumably due to higher predation by fishes. When food is scarce, oyster drills will cannibalize and consume other smaller drills, but this scenario is unlikely on the large oyster reefs studied here. Thus, light may be a double-edged sword for some oyster reefs. When light promotes fish predation on crabs, crabs are less abundant, and oyster growth and survival increases. Yet, the absence of crabs may make oysters more vulnerable to oyster drills, which flourish in the absence of crustacean predators (Fodrie & Heck 2011).

Turbidity and salinity are each affected by numerous anthropogenic activities which can modify community organization, diversity, and function. These shifts may yield profoundly different and novel ecosystems. Nutrient loading and increased sedimentation in estuaries increase turbidity and light scatter, altering predator-prey interactions and estuarine food webs.

Drought and freshwater diversions change species assemblages and ensuing species interactions. However, drought and turbidity can act synergistically to create distinct ecological interactions and communities, and changes in salinity and turbidity may stress estuarine fauna already in decline, such as oysters.

Oysters, which have already declined by over 85% (Beck et al. 2011), face a challenging future due to risks associated with climate change and ocean acidification (Beniash et al. 2010, Kroeker et al. 2013, Scanes et al. 2017). Land use changes and nutrient inputs, coupled with shifts in precipitation and sea level that alter salinity, will intensify declines in oyster populations. Reduced availability of potable freshwater, symptomatic of and hastened by climate change, will increase freshwater diversions and cause further damage to oysters and estuarine systems. Considering the enormous economic, ecological, and cultural value of oysters, climate change related damage will need to be combatted through concerted conservation and mitigation efforts (*e.g.*, pre-treating hatchery oysters with predator exudates to increase survivorship). However, restoration and conservation attempts need to address the biota as well as the environmental factors. Attempts to restore reefs by only addressing biota without addressing underlying environmental conditions, such as turbidity and salinity, will likely yield diminished results due to the structuring power of both factors. In particular, restoring the top-down maintenance of reef communities through trophic cascades must incorporate the sensory ecology of the community, and the physiological tolerances of the organisms. Here, salinity and turbidity both indirectly affected oyster reef food webs by facilitating different predators and influencing their foraging ability.

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FIGURES

Figure II.1

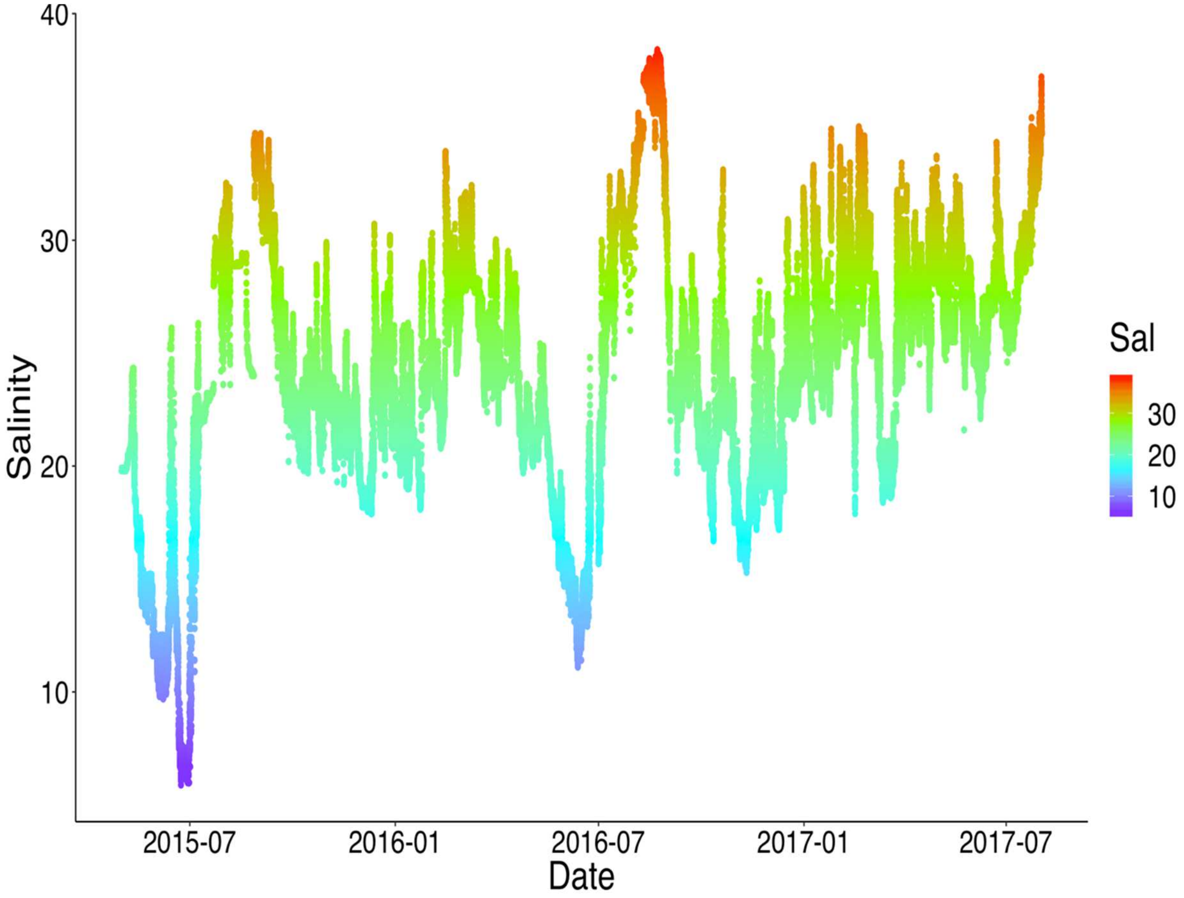


Figure II.1: Salinity from 2015 - 2017 in the study system. Salinity data were obtained from the Mission-Aransas NERR System Wide Monitoring Program (SWMP). Warmer colors are indicative of higher salinity. Figure was constructed in RStudio version 1.1.456 using the ggplot2 package (Wickham 2016).

Figure II.2

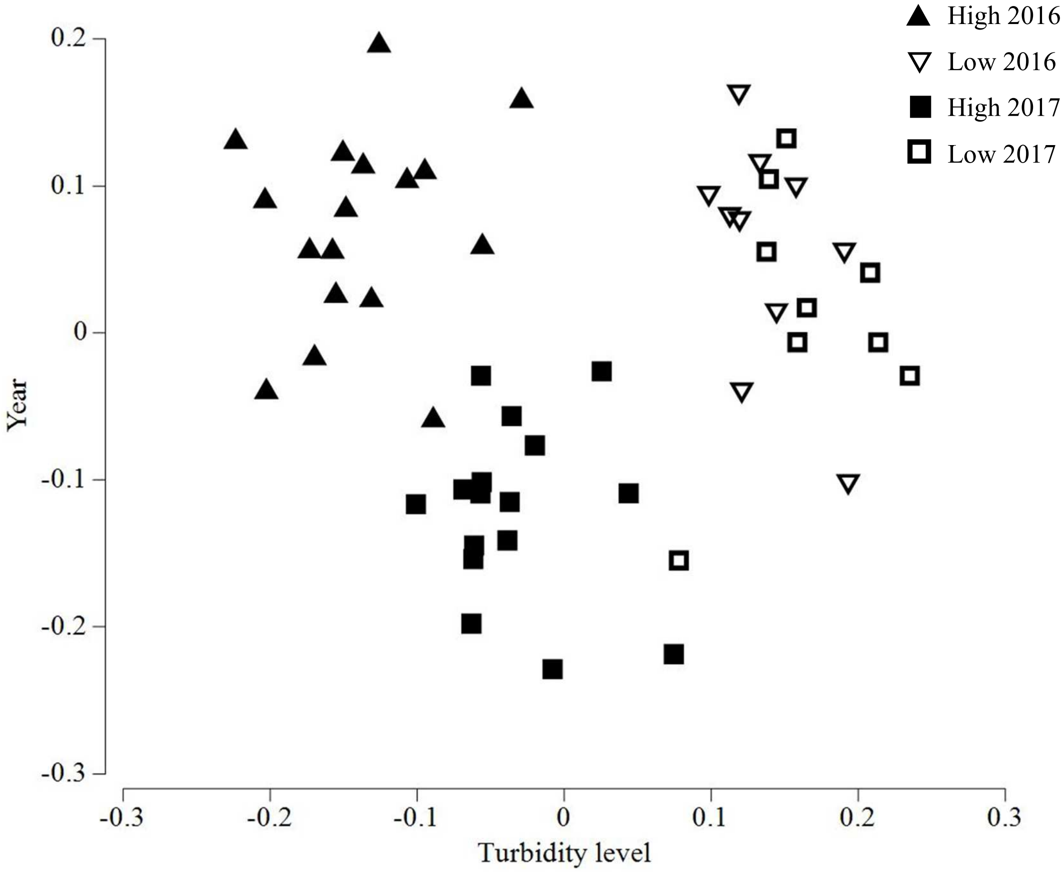


Figure II.2: Canonical Analysis of Principal coordinates (CAP) of community structure across turbidity level and year. Solid shapes represent high turbidity samples and open shapes represent low turbidity samples. Triangles indicate wet -year communities (2016) and squares indicate drought-year communities (2017). The differences in communities between turbidity levels was primarily driven by location-effects, while year (e.g., wet vs. drought years) had notable differences in both the dispersion and location of communities in multivariate space.

Figure II.3

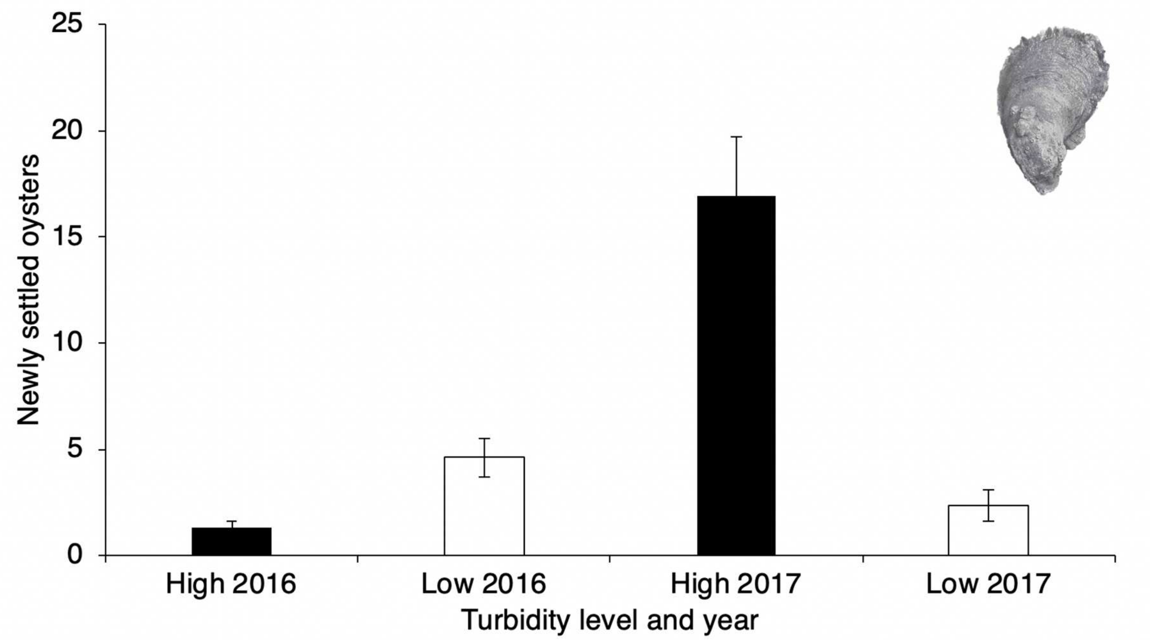


Figure II.3: Mean ± SE oyster recruitment across turbidity levels and years. Eastern oyster image courtesy of the Freshwater and Marine Image Bank at the University of Washington.

Figure II.4

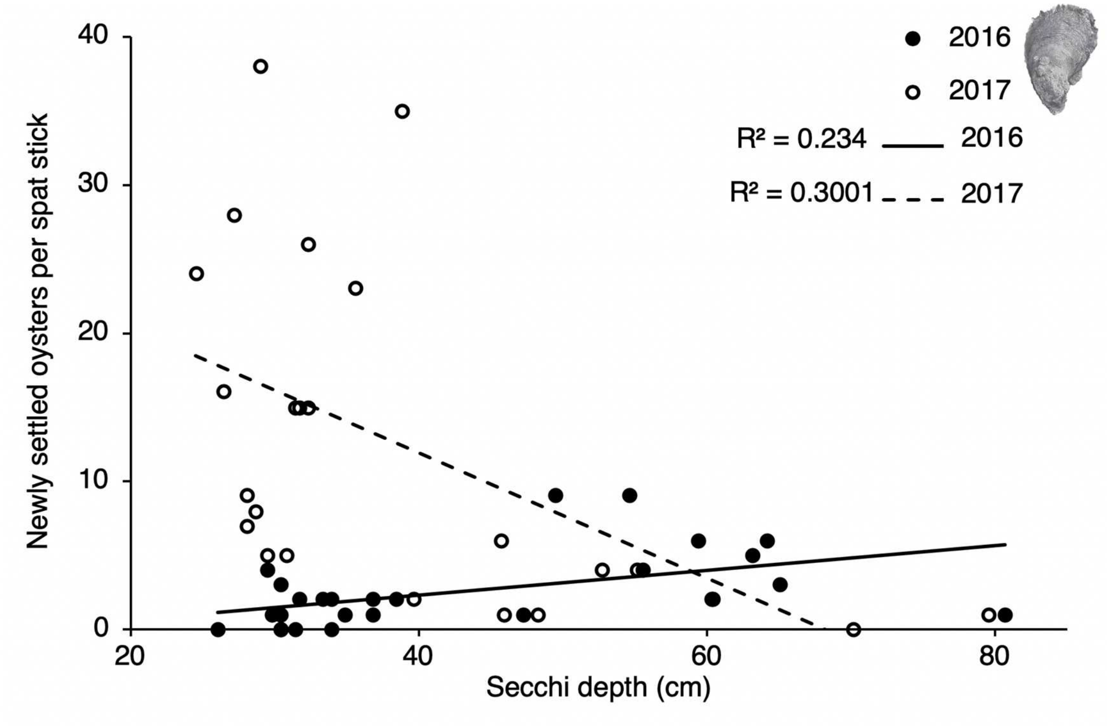


Figure II.4: Total oyster recruitment per spat stick plotted across Secchi depths for 2016 (wet year; solid circles) and 2017 (dry year; open circles). Eastern oyster image courtesy of the Freshwater and Marine Image Bank at the University of Washington.

Figure II.5

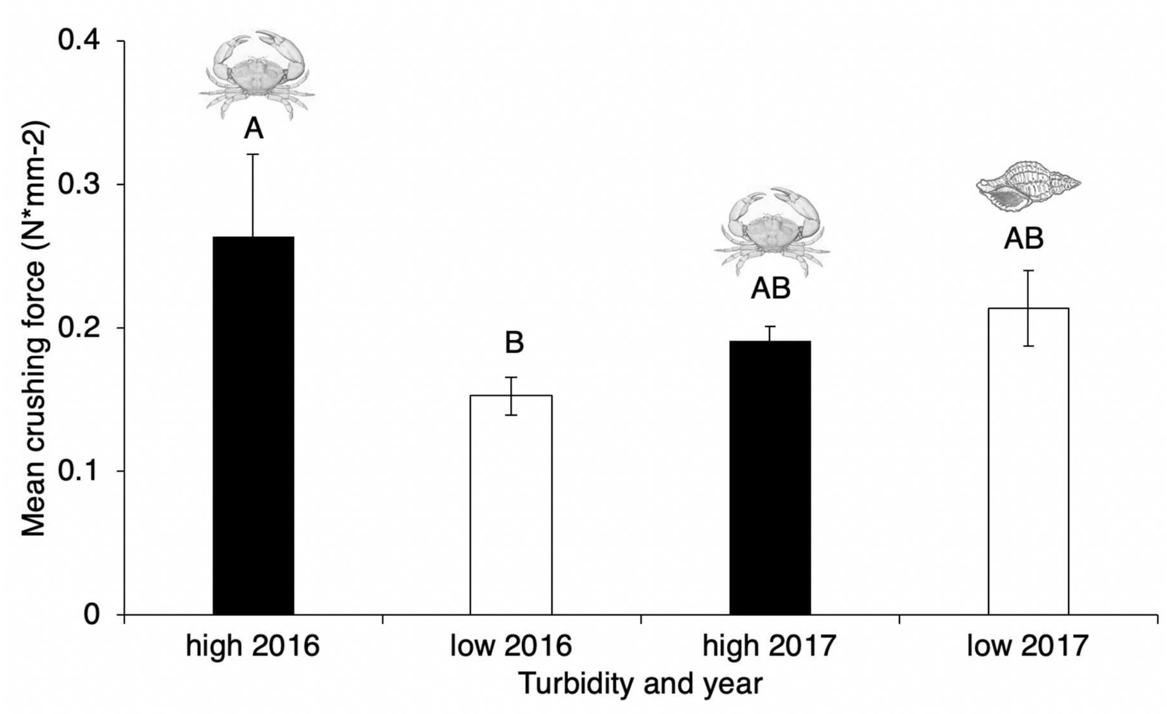


Figure II.5: Mean ± SE oyster crushing force (N/mm^2) across turbidity levels and years. Different letters indicate significantly different means as found by a Tukey post-hoc test. The abundant mesopredator (if present) is characterized above each combination of turbidity level and year. Stone crab image courtesy of the Freshwater and Marine Image Bank at the University of Washington. Oyster drill artwork courtesy of Texas Parks and Wildlife Department © 2004.

Supplemental Tables

Supplemental Table II.1

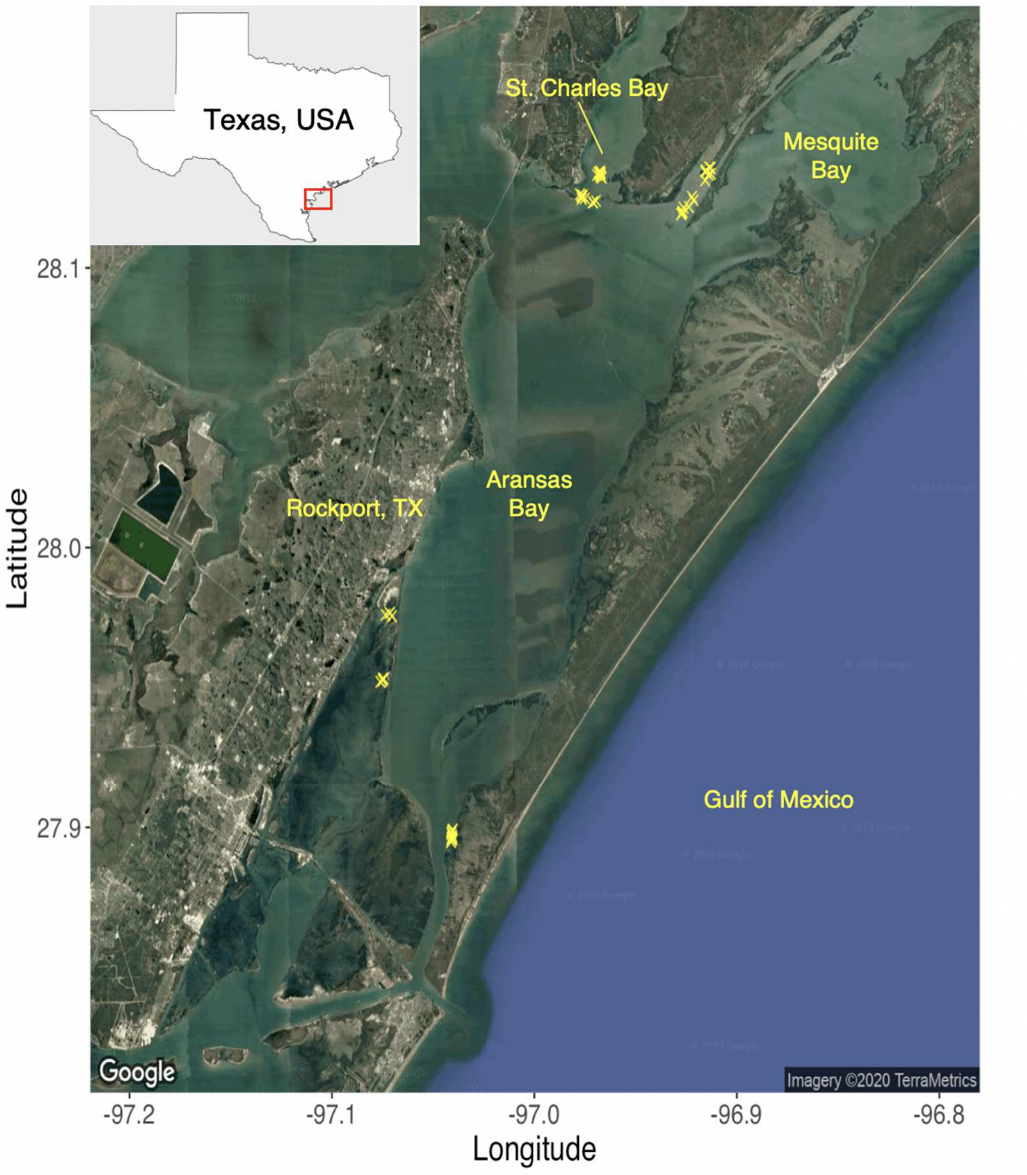
Species	Common name	High 2016	Low 2016	High 2017	Low 2017
Opsanus beta	Toadfish	3.76	1.8	0.938	2.89
Gobiesox strumosus	Skillet fish	1.89	0	1.5	0.111
Bairdiella chrysoura	Silver perch	2.18	0	20.3	7.11
Lagodon rhomboides	Pinfish	0.760	2.2	0.375	2.56
Orthopristis chrysoptera	Pigfish	0.0588	0.8	0.0625	0.222
Archosargus probatocephalus	Sheepshead	1.53	2.9	2.44	0.444
Chasmodes longimaxilla	Stretchjaw blenny	0.353	3	1.31	1.11
	Unidentified blenny 2	0	0.2	0	0
Hypsoblennius hentz	Feather blenny	0	0.2	0	0
Hypleurochilus geminatus	Crested blenny	0.0588	0.1	0	0
Cyprinodon variegatus	Sheepshead minnow	0	0.9	0.0625	0
Ophichthus gomesii	Shrimp eel	0	0.2	0	0.222
Fundulus similis	Longnose killifish	0	0	0	0
Lucania parva	Rainwater killifish	0	0	0	0
Fundulus grandis	Gulf killifish	0	0.3	0	0
Adinia xenica	Diamond killifish	0	0.2	0	0
Lutjanus griseus	Mangrove snapper	0.0588	0	0.188	0.111
Lutjanus synagris	Lane snapper	0	0	0	0
Symphurus plagiusa	Blackcheek tonguefish	0	0	0	0
Eucinostomus argenteus	Spotfin mojarra	0	0	0	0
Lobotes surinamensis	Triple tail	0	0.1	0	0
Bathygobius soporator	Frillfin goby	0.0588	0	0	0
Gobiosoma bosc	Naked goby	14.2	8	1.69	3.78
Ctenogobius boleosoma	Darter goby	0.0588	5.9	0.688	3.78

Gobiosoma robustum	Code goby	0	0.6	0	3.11
Microgobius gulosus	Clown goby	0	1	0	0
Mugil curema	White mullet	0	0.8	0	0
Mugil cephalus	Striped mullet	0	0.4	0	0
Etrumeus teres	Round herring	0	0	0	0
Menidia beryllina	Inland silverside	0	0.4	0	0
Membras martinica	Rough silverside	0	0	0.0625	2.44
Anchoa mitchilli	Bay anchovy	0.0588	0	0	0
Sygnathus spp.	Pipefish	0	0.3	0.125	0
Cynoscion nebulosus	Spotted seatrout	0	0.1	0.0625	0
Brevoortia patronus	Gulf menhaden	0	0	0	0.111
	Unidentified goby	0.0588	0.2	0.1875	0
	Unidentified blenny 1	0.118	0	0	0
Callinectes sapidus	Blue crab	0.765	2.7	1.69	0.444
Menippe medina	Stone crab	0.412	0.5	1.69	0.111
Panopeus herbstii	Atlantic mud crab	1	0	1.19	0.111
Eurypanopeus turgidis	Ridgeback mud crab	3.53	34.8	5.69	22.8
Eurypanopeus depressus	Flatback mud crab	25.1	0.2	16.2	0
Rhithropanopeus harrisii	Harris mud crab	0	0.1	0	0
Panopeus simpsonii	Grassflat mud crab	0	0.1	0	0
	Unidentified mud crab	32.6	124.7	45.5	78.3
	Dark shore crab	0	0	0	0
Petrolisthes armatus	Porcelain crab	175.6	26.7	77.9	34
Farfantapenaeus aztecus	Brown shrimp	0.235	2.2	1.94	2.22
	Grass shrimp	12.2	74.1	50.8	113.6
Alpheus heterochaelis	Snapping shrimp	3.88	3.7	0.813	7.78
	Wither's shrimp	0	0	0	0.111
Stramonita haemostoma	Oyster drill	0	0	0.188	4.44

Supplemental Table II.1: Mean species abundances across turbidity level (high or low) and year (2016 or 2017). 2016 was a wet year and 2017 featured drought conditions. The table depicts 52 different species found during the study.

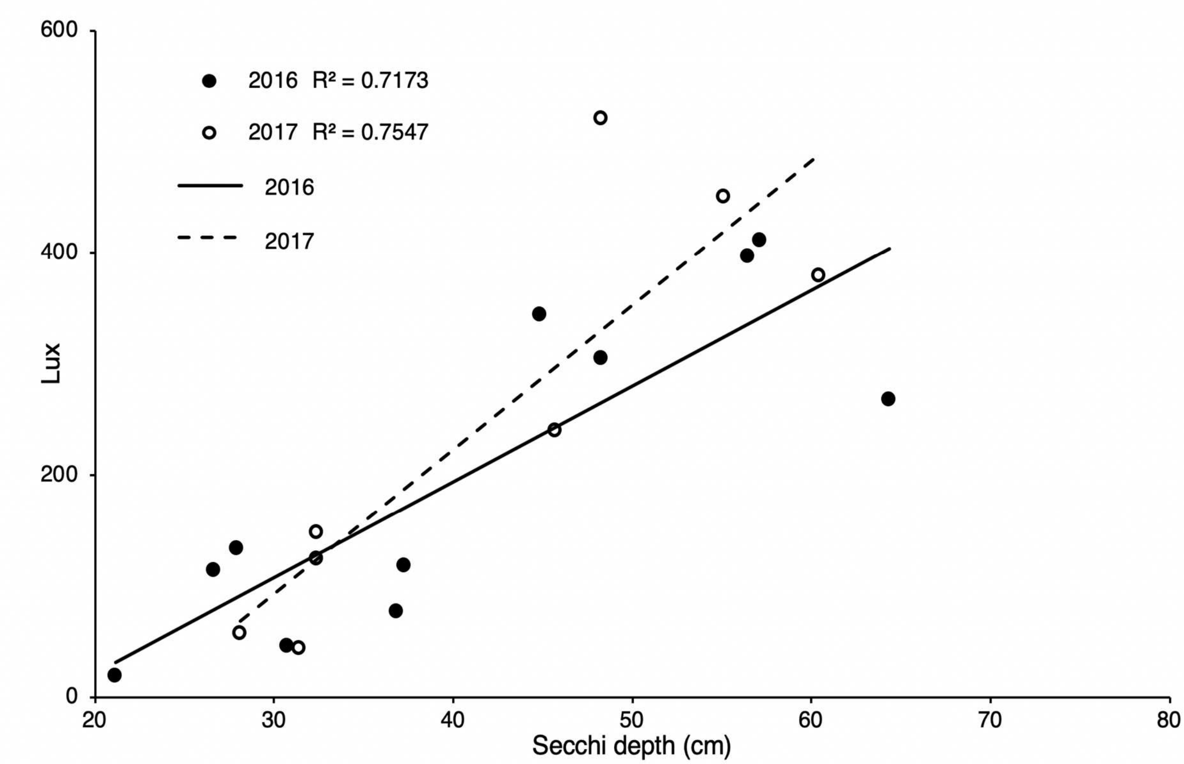
Supplemental Figures

Supplemental Figure II.1:



Supplemental Figure II.1: Map of field sites (illustrated by "x" symbols in yellow) in South Texas, USA. Mapped GPS coordinates are displayed in decimal degrees (DD) format and were obtained at each site in the field using a handheld Garmin GPSmap 76CSx. Maps were built in RStudio version 1.1.456 using the ggmap (Kahle and Wickham 2013), mapdata (Becker et al. 2018), and ggplot2 (Wickham 2016) packages.

Supplemental Figure II.2:



Supplemental Figure II.2: Correlation between mean lux and mean Secchi depth in years 2016 and 2017. Lux (lumens/m^2) data were obtained from Onset Hobo pendant light loggers and Secchi depth data from a custom-built Secchi disk. 2016 sites are depicted as solid circles and 2017 are open circles. R^2 values are listed within the legend in the top left corner.

CHAPTER III: HURRICANES DISRUPT HUMAN-INDUCED TROPHIC CASCADES AND PROMOTES ECOSYSTEM RECOVERY

ABSTRACT

Intense disturbances such as hurricanes may drastically affect ecosystems, and their effects may persist long after the storm. However, while hurricanes are best known for their destruction, these storms may provide indirect ecological benefits by disrupting harmful human activities. Most notably, by disrupting human fishing pressure, hurricanes may indirectly facilitate population increases in top-predators that are most commonly fished. We performed predator exclusion experiments on oyster reefs one-year before category 4 Hurricane Harvey and one-year post-hurricane, and we examined a decade of fisheries independent data to gauge how fishing pressure and fish populations were affected by the storm. Fishing effort was significantly lower following the storm, and fish predators commonly targeted by anglers were significantly more abundant. Oyster reef communities were significantly different after the hurricane with ~30% increase in diversity. Decreased fishing pressure resulted in increased fish abundances (i.e., ~1.7-6.9x higher CPUE immediately after the hurricane), 45% decrease in the abundance and 10% decrease in size of intermediate consumers such as crabs that are eaten by fish and prey on oysters. Our results indicate that hurricanes disrupted human-ecosystem linkages (i.e., fishing), and reconstituted top-down control of estuarine systems, at least in the short term. Our results suggest recreational fishing can have substantial effects on estuarine food webs, and provide further evidence that humans exert major pressure on natural systems and disturbance events that interrupt or weaken those interactions may yield significant ecological effects.

INTRODUCTION

The effects of hurricanes on ecosystems are often characterized by iconic physical damage. Both direct and indirect effects of hurricane disturbance can yield significant ecological change. For example, hurricane damage in Jamaica interacted with overfishing and a disease outbreak which resulted in a phase shift from high species diversity coral reefs to macro-algal-dominated systems of low species diversity (Hughes 1994). Similarly, cyclones in Nova Scotia are associated with disease spread among the urchin fishery and are expected to shift the landscape to a kelp dominated system (Scheibling and Lauzon-Guay 2010). Despite their damage, hurricanes may reduce human activities that are detrimental to ecosystems, helping ecosystem recovery (Scheibling and Lauzon-Guay 2010).

In the Anthropocene, humans exert strong top-down and bottom-up influences on ecosystems (Muhly et al. 2013, Worm 2015, Worm and Paine 2016, Smith et al. 2017). This is particularly resonant for marine systems, which are heavily impacted by anthropogenic activities such as nutrient loading, pollution, and overfishing (Darimont et al. 2015, Worm 2015). Therefore, perturbations in the connectivity between human activities and coastal ecosystems may have particularly notable outcomes (Fodrie and Heck Jr 2011). Specifically, fishing pressure and predator removal has substantial consequences for community structure and function (Hughes 1994, Pauly et al. 1998, Jackson et al. 2001, Myers and Worm 2003). Humans, known as hyperkeystone predators and super predators, exert the strongest ecological forces of any species (Darimont et al. 2015, Worm 2015, Paine and Worm 2016, Altieri et al. 2012). For instance, the competition for space between corals and algae is heavily influenced by fish grazers (Miller and Hay 1996, 1998), which bite the reef ~10,000x/m^2/day (Carpenter 1986). Fish declines (e.g., through intensive fishing pressure) promote algal growth (Eriksson et al. 2009) and can facilitate phase shifts to macroalgal-dominated states (e.g., Hughes 1994). In Marine Protected Areas/no-take areas, the abundance and biomass of herbivorous fishes (e.g. parrotfish) reduced macroalgae and turf algae (Mumby et al. 2006), which facilitated coral recruitment and survival (Kuffner et al. 2006, Webster et al. 2015). Thus, reduction of fishing pressure in protected zones affected communities by reconstituting top-down control by fishes.

Commercial and industrialized fishing fleets are not the only source of fishing pressure; recreational landings make significant contributions to global fish declines (Cooke and Cowx 2004) and have gone relatively unrestrained and underreported (Coleman et al. 2004). Recreational fisheries can account for higher values than reported catch data and primarily target the top trophic levels of fishes (Coleman et al. 2004, Zeller et al. 2008). In some cases, the recreational fishery targets vulnerable fish populations such as red drum (*Scianops ocellatus*), bocaccio (*Sebastes paucispinus*), and red snapper (*Lutjanus campechanus*) (Coleman et al. 2004) that are inaccessible to commercial fishers. Additionally, recreational anglers may be able to fish in times or regions protected from commercial harvest. Recreational fisherman account for high landings of already stocks (McPhee et al. 2002), yielding further difficulties for species and ecosystem management. Systematic exploitation and reduction of predatory fishes in estuarine and nearshore ecosystems have wide-reaching ecological consequences. The loss of ecologically important species through recreational fishing disrupts trophic cascades, releases mesopredators, and causes habitat conversion (Altieri et al. 2012).

However, disturbances that disrupt fishing pressure may benefit marine species and allow their abundance to increase (Fodrie and Heck 2011, Yamada et al. 2014). After the Fukushima disaster and BP oil spill, fish populations increased when fishing was restricted (Foedrie and Heck 2011, Yamada et al. 2014). Disturbances such as hurricanes may reduce fishing pressure by damaging fishing infrastructure and boats as well as reduce coastal access, tourism, and amenities. Coupled with the physical disturbance, these disruptions in human-ecosystem links are likely to have significant community-level effects, yet the cascading effects of these disturbances to other trophic levels have rarely been quantified.

Here, we investigated the effects of a Category 4 hurricane (Hurricane Harvey) on fishing pressure and cascading effects to oyster reef communities through field experiments and analysis of fisheries independent data. We found that disrupting human-induced trophic cascades benefitted fish and oyster reef communities, even months after high fishing pressure returned, by reinserting fish predators as the primary enforcers of top-down control. Yet, the boom in top-down control coalesced with low oyster recruitment and high trophic omnivory.

METHODS

Storm background- Hurricane Harvey struck the study site near Rockport, TX on August 26th, 2017 with wind speeds in excess of 130 mph that decimated local fishing fleets and infrastructure (**Supplemental Figure III.1**). The hurricane was a ~1:9,000-year storm event and produced more than 1.0 m of rain within the Houston area in just three days (van Oldenborgh et al. 2017). The intense flooding overcorrected salinity-stressed estuaries as salinity dropped from hypersaline in some estuaries (>35 ppt) to essentially fresh (~2-5ppt) before recovering to previous levels (**Supplemental Figure III.2**).

Study locations- We examined oyster reefs within the Mission-Aransas National Estuarine Research Reserve (MANERR) TX, USA. Selected reefs reside within St. Charles (~ 28°08' N 96°58' W) and Aransas bays (~28°07'N 96°58' W) at Goose Island State Park, TX (**Supplemental Figure III.3**). In 2016, one year prior to Hurricane Harvey, these reefs were selected for a study to determine how mesopredator abundance influenced oyster reef community structure. In 2018, one year after Hurricane Harvey, we returned to these reefs to determine how resilient the affected reef communities were to the hurricane and its concomitant effects.

Angler data- In order to estimate the extent that Hurricane Harvey reduced fishing pressure and caused changes in the abundance of fish populations, we analyzed fishery independent data collected betweeen 2007 and 2018 by the Texas Parks & Wildlife Department (TPWD). As an estimate of fishing activity, TPWD randomly surveyed sites that provided access to the Aransas Bay system in proportion to the percentage of bay-wide fishing pressure that occurred at each site (i.e. sites more frequently utilized by anglers were surveyed more often). During the high-use season, May 15th – November 20th, 31 weekend surveys and 66 weekday surveys were performed (~16 surveys per month) while 12 weekend and 24 weekday surveys were conducted during each low-use season (November 21st – May 14th; ~6 surveys per month).

The number of anglers intercepted each month was compared to the 10-year average of intercepeted anglers using a paired t-test. To assess the effect of the hurricane and year on the number of boaters, survey data were aggregated across September – December, corresponding to the four months immediately after the hurricane. These data were analyzed using a two-way ANOVA with Type II sum of squares due to an uneven sample size of surveys carried out during the year of the hurricane (5 surveys) and non-hurricane years (13 surveys).

Fisheries data- Fisheries independent data were collected by TPWD to estimate relative species abundance. TPWD set out gill nets during spring (April – June) and fall (September – November) each year. Each season, 45 gill nets were set out along the shoreline of Aransas Bay (2 – 3 nets per trial; 45 nets per season). Net locations were randomly selected from a sample grid consisting of 212 1-minute longitude x 1-minute latitude quadrants. Gill nets were 1.2 m from top-to-bottom and consist of four continuous 45.7 m sections of monofilament webbing of different mesh sizes (7.62, 10.16, 12.70, and 15.24 cm). Gill nets were set perpendicular to shore within an hour of sunset, with mesh size incrementally decreasing towards the shore and retrieved immediately after sunrise the following day. Catch number of the three most commonly fished species were recorded during each deployment (spotted seatrout, *Cynoscion nebulosus*; black drum, *Pogonias cromis*; and red drum, *Sciaenops ocellatus*; >75% surveyed anglers targeted just these species). Catch per unit effort (CPUE) for each species was calculated by dividing the total number of specimens landed by the total hours of net soak time.

Gill net data were aggregated across three different time periods to assess the effect of the hurricane: the month corresponding to just after the hurricane (September, n = 15 per year), the three months corresponding to after the hurricane (September – November, n = 45 per year), and the summer months when oyster trays were deployed (April – June, n = 45 per year). Separate zero-inflated generalized linear models with a Tweedie distribution were run for each time period to assess the effect of year and fish species on CPUE (three models; R package: glmmTMB). The Tweedie family is a two-parameter family of distributions consisting of a linear exponential family and a dispersion parameter. This family encompasses the normal, Poisson, gamma, and inverse gaussian distributions, and allows for the modeling of continuous data with zeros (Jørgensen 1987, Dunn and Smyth 2005). Pairwise comparisons of CPUE across years were done using Tukey post-hoc tests (R Package: multcomp). Statistical analyses of fishery data were conducted in R v3.5.1 (R Development Core Team, 2018).

<u>Community sampling</u>- We performed a predator exclusion experiment on oyster reefs in 2016 and in 2018 at Goose Island State Park near Rockport, TX, USA to ascertain how higher order predators affect oyster reef community structure (**Supplemental Figure III.3**). Higher order predators on oyster reefs in the area include red drum (*Sciaenops ocellatus*), spotted sea

trout (*Cynoscion nebulosus*), sheepshead (*Archosarguys probocephalus*), and gulf toadfish (*Opsanus beta*). Reefs are inhabited by numerous small fish species (*e.g.*, gobies and blennies), grass shrimp (*Palaemonetes* spp.) and brown shrimp (*Farfantepenaeus aztecus*), and many crab species including stone crabs (*Medippe adina*), blue crabs (*Callinectes sapidus*), and mud crabs (*Panopeus herbstii*, *Eurypanopeus turgidus*, *Eurypanopeus depressus*). Crabs with carapace widths >15mm prey heavily on newly settled oysters, causing many oysters to develop heavier and stronger shells to combat crushing and drilling predators (Lord and Whitlatch 2012, Robinson et al. 2014). Additionally, many of these predators also consume porcelain crabs (*Petrolisthes armatus*), which are common suspension feeders and algae scrapers within oyster beds (Kropp 1981, Hollebone and Hay 2007, Zimba et al. 2016). We used size-based exclusions to isolate the effects of different trophic levels on oyster reef communities (*sensu* Johnson et al. 2014) in one year pre-hurricane (2016) and one year post-hurricane (2018). Cages were deployed in pairs with each pair containing: a control cage (no mesh or covering; ambient levels of predation) and a cage covered in mesh with large openings (5 cm^2) to exclude larger predators but permit access by mesopredators, mainly mud crabs. Twenty L of sun bleached oyster shells were added to each cage which was embedded into a natural reef. We deployed 10 pairs in 2016 and 8 pairs in 2018 at the same GPS locations within St. Charles Bay and Aransas Bay. Cages were deployed each year at the beginning of spring oyster spawning (May 3 – June 30 2016, April 25 – June 4 2018). Cages become saturated with natural recruitment within 14 days after deployment (Smee unpublished data).

Community assemblages were collected from cages using modified throw traps. Two 1.0 m^3 traps were simultaneously placed over each cage within a pair. The cage was removed, thoroughly searched, and all organisms collected. Sweep nets (500 µm mesh-size) were then used to sweep within the throw trap to collect any organisms dislodged from the tray. Larger organisms were identified, measured, and released in situ, while smaller organisms were placed in ethanol and transported to the lab for sorting, identification, measurements, and enumeration. Fish sizes were calculated by measuring total length and crabs sizes by measuring carapace width to the nearest tenth of a millimeter. Mud crabs smaller than 10mm carapace width were identified to family and were not considered mesopredators (Johnson et al. 2014) while all other organisms were identified to species. Prior to all statistical analyses, tests for normality and homogeneity of variance were conducted using the Shapiro–Wilk test.

Community data were analyzed using PRIMER^{TM}. Community data were square-root transformed and assembled in a Bray-Curtis resemblance matrix and analyzed using a 2-way PERMANOVA (year * cage type) with 100,000 permutations allowing permutations of residuals under a reduced model. To determine pairwise differences in community structure, year and cage type factors were combined and run in a 1-way pairwise PERMANOVA with 100,000 permutations and unrestricted permutations of raw data. Distance-based tests for homogeneity of multivariate dispersions (PERMDISP) were used to determine how year and cage type, respectively, affected community structure. For each PERMDISP test, dispersion was compared using permutations (100,000) across centroid distances.

A Cannonical Anaylsis of Principal Coordinates (CAP) plot was created to illustrate community differences between years and cage type. Shannon diversity (H') was calculated using the “vegan” package in R (Oksanen et al. 2019) and total community diversity and the total abundance per sample were compared between years and cage treatments using Two-Way ANOVAs.

Many reef-dependent species rely on reefs not only for physical structure, but also consume oysters at various stages of their life-cycle (i.e., gobies and blennies as a source of oyster-veliger larvae mortality; mud crabs consume newly settled oysters; porcelain crabs may incidentally be a source of newly-settled oyster morality through algal scraping). Therefore, reef-dependent fishes and invertebrates, such as Gulf Toadfish (*Opsanus beta*), naked (*Gobiosoma* bosc) and darter gobies (*Ctenogobius boleosoma*), stretchjaw blennies (*Chasmodes longimaxilla*), and skillet fish (*Gobiesox strumosus*), Atlantic (*Panopeus herbstii*), Ridgeback (*Eurypanopeus turgidus*), and Flatback mud crabs (*E. depressus*), stone crabs (*Menippe adina*), porcelain crabs (*Petrolisthes armoratus*), and snapping shrimp (*Alpheus heterochaelis*), were compared individually across years and cage type to determine the relative impact of the hurricane disturbance on the most common reef species.

Mud crabs (*P. herbstii*, *E. turgidus*, *E. depressus*) with carapace widths greater than or equal to 15 mm were classified as mesopredators (*sensu* Reustle and Smee *in press*). Smaller mud crabs do not routinely eat oysters (Johnson et al. 2014), and are trophically more similar to grazers at small sizes. The abundance of crab mesopredators was analyzed using a two-way ANOVA with year and cage type as fixed factors.

Measurements- To determine how the hurricane and exposure-level affected the sizes of fishes and crabs, mean total lengths and carapace widths were calculated for each cage type at each site and were compared across cage type and year using two-way ANOVAs with year and cage type as fixed factors. Specifically, we hypothesized that if the hurricane altered the top-down dynamics on reefs, this would be evident in significant cage-effects. Data were analyzed in JMP Pro 14.

Oyster recruitment- Two PVC spat collectors (aka spat sticks, 100 mm long, and 22 mm in diameter) were placed within each cage to assess oyster recruitment and mortality within each caging treatment. Upon cage retrieval, spat sticks were removed from the cages, and returned to the lab. Oyster recruitment was analyzed using a two-way ANOVA with year and cage treatment as fixed factors. Recruitment data were analyzed in JMP Pro 14.

RESULTS

Fishing pressure - Hurricane Harvey caused a substantial decrease in the number of anglers intercepted by TPWD (t = 5.39, df = 13, $p = 0.0001$). In the first month after the hurricane (September, 2017), the number of intercepted anglers was 7.3x lower than the 10-year average while the subsequent four months (October – January) had 1.9x fewer intercepted anglers than the 10-year average. Additionally, the number of boats on the water during the four months after the hurricane was a third of the average number observed for the same time period in non-hurricane years (F = 9.20, df = 1, p = 0.0084). However, by March 2018, angler numbers matched historic levels.

Gill net CPUE after the hurricane was significantly different for each of the three fishery species across all time periods (Table 2). However, not all species responded to the hurricane in the same way, producing a significant interaction between the two parameters (**Figure III.1**; **Table III.1**). While all three species of fish increased in abundance in the month after the hurricane, spotted sea trout were caught 6.9x more frequently than the year prior for the same time period (**Figure III.1 a**; Tukey test, p < 0.01) whereas black drum were caught only 1.7x more frequently (**Figure III.1 d**, Tukey test, p = 0.99), and red drum were caught 2.6x more frequently (**Figure III.1 g**, Tukey test, p = 0.02). Indeed, spotted seatrout showed the greatest response for all three time periods after the hurricane, where CPUE was, on average, 47% higher than the 10-year mean (**Figure III.1 a,b,c**). Although species CPUE changed the most in the month just after the hurricane, during the next three months, all three species were caught more frequently than the prior year (**Figure III.1 b,e,h)**. Additionally, both spotted seatrout and red drum showed increased catch rates seven months after the hurricane with 52% and 17% increases over the 10-year mean, respectively (**Figure III.1 c,i**).

<u>*Community structure*</u>- Oyster reef community structure changed significantly between 2016 and 2018 (Pseudo-$F_{1,27} = 13.7$, $p < 0.001$), and between cage treatments (Pseudo-$F_{1,27} = 2.88$, $p=0.004$) with no significant interaction between year and treatment (Pseudo-$F_{1,27} = 1.47$, $p=0.16$; **Figure III.2**). The pairwise PERMANOVA for combined factors found that each iteration of year and cage treatment yielded a significantly different community (**Supplemental Table III.1**). PERMDISP tests on community dispersions indicated that community structure for both year ($F_{1,29} = 0.273$, $p=0.625$; means: 2016= 17.7, 2018 = 18.5) and cage treatments ($F_{1,29} = 0.132$, $p=0.722$; means: large = 20.8; open = 21.4) were driven by location effects. Community diversity (Shannon diversity " H' ") was significantly higher one year after hurricane Harvey with a 30% increase in diversity across both cage types ($F_{1,27} = 11.0$, $p=0.003$). Neither cage type ($F_{1,27} = 2.48$, $p=0.127$), nor the interaction ($F_{1,27} = 0.362$, $p=0.553$) significantly affected community diversity. Total species abundance did not differ by year ($F_{1,27} = 2.91$, $p = 0.1$), cage treatment ($F_{1,27} = 0.620$, $p = 0.438$), or the interaction ($F_{1,27} = 3.12$, $p = 0.089$).

<u>*Reef-dependent species*</u>- Gulf toadfish (*Opsanus beta*) were ~6x more abundant in 2016 than in 2018 ($F_{1,27} = 38.9$, $p < 0.001$). Both cage effects ($F_{1,27} = 0.196$, $p = 0.662$) and the interaction between year and caging-treatment ($F_{1,27} = 1.33$, $p = 0.258$) were not significant in explaining toadfish count data. There were significant reductions in the abundance of naked gobies ($F_{1, 27} = 4.96$, $p = 0.0344$), though none of the other abundant reef-dependent fishes had any detectable

changes in abundance in response to the hurricane. Interestingly, cage type had no effects on the abundance of any of these small, reef-associated fishes (**Table III.2**).

Atlantic mud crabs ($F_{1,27} = 0.254$, $p = 0.618$), ridgeback mud crabs ($F_{1,27} = 3.10$, $p = 0.09$) flatback mud crabs ($F_{1,27} = 0.110$, $p = 0.743$) had no detectable changes in abundance in response to the hurricane. Porcelain crabs ($F_{1,27} = 9.77$, $p = 0.004$), and snapping shrimp ($F_{1,27} = 15.8$, $p < 0.001$) all declined significantly after the hurricane; however, stone crabs increased nearly four-fold after the hurricane (**Table III.2**; $F_{1,27} = 9.39$, $p < 0.0049$).

The abundance of mud crab mesopredators (mud crabs > 15mm carapace width) declined by roughly 45% after the hurricane ($F_{1,27} = 4.67$, $p = 0.04$). Mesopredator abundance was not significantly affected by cage treatment ($F_{1,27} = 0.123$, $p = 0.729$) and the interaction between year and cage type was not significant ($F_{1,27} = 2.78$, $p = 0.107$).

Measurements- Fishes were significantly smaller in 2018 ($F_{1,26}=14.0$, $p < 0.001$). Cage effects were also significant across years, ($F_{1,26} = 8.77$, $p = 0.007$). The interaction between year and cage type was not significant ($F_{1,26} = 3.03$, $p = 0.09$). A Tukey HSD test indicated that after the hurricane, fishes from open cages were significantly smaller than fish protected from top-predators (large-mesh cages) (**Figure III.3**).

Crabs (excluding porcelain crabs) were nearly 10% smaller one-year post-Harvey ($F_{1,28} = 12.19$, $p=0.002$). Neither Cage type ($F_{1,28} = 0.936$, $p = 0.343$), nor the interaction term ($F_{1,28} = 4.48$, $p = 0.044$) significantly affected crab size. Mud crab mesopredator sizes were not affected by year ($F_{1, 27} = 0.022$, $p = 0.884$), cage type ($F_{1,27} = 3.42$, $p = 0.077$), or the interaction term ($F_{1,27} = 1.33$, $p = 0.26$). Stone crabs, despite being nearly 5 times more abundant, were far smaller after the hurricane ($F_{1,14} = 27.7$, $p < 0.001$).

Oyster recruitment- Oyster recruitment was significantly lower in 2018 ($F_{1,27} = 5.61$, $p = 0.0253$). Cage treatments significantly affected recruitment dynamics ($F_{1,27} = 9.06$, $p = 0.006$); although the interaction between year and cage type was not significant ($F_{1,27} = 0.706$, $p = 0.408$). A Tukey HSD found that the primary distinction in recruitment dynamics was the difference in oyster recruitment in ambient conditions (open cages) (**Figure III.4**).

DISCUSSION

Storms can drastically lower salinity and cause large shifts in community structure (Montagna and Kalke 1992, Montagna et al. 2002, Ritter et al. 2005, Van Diggelen and Montagna 2016); however, salinity returned to pre-hurricane levels fairly quickly (~4 months) after the hurricane (**Supplemental Figure III.2**). While the physical disturbance of the hurricane (destruction and extensive flooding) certainly had major, immediate effects, the observed differences in fish and oyster reef community structure are likely attributed to the disruption of human fishing pressure from the hurricane. The fishery data indicated that predatory fish became substantially more abundant following reduction in fishing after the hurricane (**Figure III.1**). The increased abundance of predatory fish was unlikely to be an artefact of high recruitment as several different gear types and methodologies all found higher abundances of top predators and stronger top-down control. For example, gill nets sampled four distinct size ranges (four different mesh sizes) to provide more coverage across multiple species and age/sizes. The sizes selected by gill nets primarily targeted fishes that were too large to have been the result of increased recruitment. In other words, these were fishes that were alive prior to the hurricane and benefitted from the release of human-induced fishing pressure. The gill net data clearly demonstrated higher CPUE of top predators following the fishing disruption associated with Hurricane Harvey. Restoration of top-down control on reefs is further supported by the 45%

reduction in mud crab mesopredators on oyster reefs, ~30% decrease in the size of reef fishes under ambient predator exposure levels (open cages), and a 30% increase in community diversity.

The reduction in intermediate consumers and crab mesopredators after the hurricane was in stark contrast to the pre-hurricane communities despite similar abiotic conditions. In 2015, there was tremendous flooding (**Supplemental Figure III.2**) that drove down salinity to near 0 in many coastal estuaries. By 2016, salinity values had rebounded to intermediate levels prior to the 2016 caging study. Similarly, in late 2017, the hurricane flooded Texas with a ~1:9,000-year storm and by 2018, salinity values had rebounded to levels seen in 2016. Therefore, changes in top-down structure are attributed to the hurricane's disruption of human-induced trophic cascades and not to changes in salinity.

Strong top-down control from higher order predators is often associated with increased biodiversity (Schmitz 2003, Ripple and Beschta 2004), while removal of higher order predators often causes mesopredator release and subsequent overconsumption of basal trophic levels and declines in biodiversity (Ripple and Beschta 2004, Ritchie and Johnson 2009, Reustle and Smee *in press*). Increased top-down control in aquatic systems can foster greater diversity by suppressing secondary consumers and promoting basal species (Shears and Babcock 2002, Frank et al. 2005). In this study, reduced fishing and increased abundance of fish predators was associated with both mesopredator decline and increased biodiversity, suggesting disturbances can also promote recovery when they remove harmful anthropogenic activities such as fishing.

Changes to oyster reef communities after the hurricane were observed across multiple trophic levels as the abundance and size of mesopredators (e.g. gobies, blennies, crab species) on uncaged reefs substantially decreased as did the recruitment of oysters (**Table III.2**). This concomitant loss in oyster recruitment despite the reduction in mesopredators likely occurred due to several additive processes. First, the larval supply was likely reduced because of the loss of reproducing adults. Low salinity events following storms are known to be a source of high mortality for adult oysters (e.g. Munroe et al. 2013), and many reefs within the Rockport region were damaged following Hurricane Harvey (personal observations).

Secondly, the nearly 6x decrease in toadfish abundance may have stimulated an increase in mesopredator predation rates of oysters. Toadfish are known to considerably reduce the foraging behavior of their prey and this modification of prey behavior is suggested to be even greater than the direct consumptive effects of the toadfish (Grabowski and Kimbro 2005). Despite mud crab abundances declining significantly, the coupled (albeit disproportionate) losses in both toadfish and mud crabs may have actually caused oyster consumption to exceed previous years. Increased abundance of fishes like sheepshead and black drum may have also increased consumption on juvenile oysters, leading to the apparent differential in surviving oyster recruits across cage types (**Figure III.4**). Diverse communities typically feature higher trophic flexibility/variability amongst consumers (Casula et al. 2006). On oyster reefs, this likely translates to an increase in the consumption of newly settled oysters by durophagous consumers across several trophic levels.

Reduction of recreational fishing pressure produced massive shifts in the size and abundance of predatory fishes, which rippled throughout the rest of the estuarine food web. These results emphasize the magnitude and apparency of human-interactions in estuarine and nearshore ecosystems and further supported the notion that recreational fishing is a potent ecological force. Further, many recreational anglers utilize productive nursery habitats, such as seagrass meadows and oyster reefs, as their fishing grounds. In these cases, this additional source of mortality and stress for spawning adults and juveniles weakens the strength of top-down community regulation in one of the most ecologically and economically valuable regions of the world (Barbier et al. 2011). Thoughtful regulation of recreational fishing is clearly an important task for bay managers and regional governing institutions.

Ecological Implications- Hurricanes have the potential to completely alter and restructure near shore ecosystems. Yet, due to the strong linkages of humans to coastal systems, hurricanes may also facilitate community resilience and recovery by curtailing human activities. The source of top-down forcing was transferred from humans back to fish predators, yielding a more diverse community. In other systems, reductions of human-impacts on top-predators have elicited strong ecosystem-level responses, such as the reintroduction of Gray Wolves (*Canus lupis*) into Yellowstone National Park and the associated returns in ecosystem characteristics (i.e., restored flow to the river, etc.) (Ripple and Beschta 2004), or the reintroduction of largemouth bass (*Micropterus salmoides*) into freshwater lakes yielding fewer planktivores and greater water visibility (Mittlebach *et al.* 1986, 1995). However, the failure to maintain the protection of these top-predators leads to major ecological shifts in the biological composition and habitat characteristics of the system (Russ and Alcala 1989) and communities are not guaranteed to return to its previous state following restoration of top-down forcing (Schmitz 2004; Barkai and McQuaid 1988). Despite being absent from classic food-web models, humans exert the strongest ecological forces of any predators (Darimont et al. 2015), even in distantly linked systems, and have been deemed superpredators (Worm 2015) and hyperkeystone species (Worm and Paine 2016).

In marine systems, fishing pressure is a strong and nearly universal pressure with significant ecological outcomes (Dayton et al. 1995, Jackson et al. 2001). This is particularly notable given the primacy of top-down structuring dynamics in nearshore and coastal systems (see Heck and Valentine 2007). Removing human-induced top-down control (i.e., fishery closures, imposing MPAs, etc.) has important consequences that extend beyond the target species, especially for communities fished using broad and/or destructive fishing practices, such as trawls, dredges, long-lines, and other non-selective methods (i.e., fishing with explosives). However, when the strong top-down forcing of fishing-pressure is removed, depressed populations & communities can rebound in unique ways. After the Deepwater-Horizon oil spill, fish populations increased dramatically in abundance due to total fishery closures (Fodrie and Heck Jr 2011); although, these population spikes were temporary and the long-term & sub-lethal effects of oil hydrocarbons are numerous (Montagna et al. 2013, Tarnecki and Patterson III 2015). Here, we show that human-driven trophic cascades are important structural features in estuarine and near-shore ecosystems; perturbations in the connectivity between 'hyperkeystone' humans predators and coastal ecosystems has major ecological consequences, particularly when coupled with major disturbance events.

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TABLES:

Table III.1

Common name	**Species name**	**Δ abundance** ± SD	**Δ size**± SD
Toadfish	*Opsanus beta*	-3.91 ± 2.61*	-12.5 ± 26.3 mm
Skillet fish	*Gobiesox strumosus*	-1.05 ± 1.57	-5.32 ± 9.43 mm
Stretchjaw blenny	*Chasmodes longimaxilla*	-0.371 ± 0.682	-8.12 ± 17.7 mm
Naked goby	*Gobiosoma bosc*	-6.84 ± 8.78*	-8.53 ± 10.7 mm
Darter goby	*Ctenogobius boleosoma*	-0.338 ± 0.920	
Stone Crab	*Menippe adina*	+2.44 ± 2.46*	-10.9 ± 4.41 mm*
Atlantic mud crab	*Panopeus herbstii*	+0.304 ± 1.59	0.821 ± 5.24 mm
Flatback mud crab	*Panopeus depressus*	-1.78 ± 11.6	-0.031 ± 2.11 mm
Ridgeback mud crab	*Panopeus turgidus*	-1.02 ± 1.75	+0.667 ± 2.32 mm
Porcelain crab	*Petrolisthes armatus*	-114.6 ± 115.4*	-0.417 ± 2.10 mm
Snapping shrimp	*Alpheus heterochaelis*	-2.41 ± 2.40*	

Eastern oyster	*Crassostrea virginica*	-1.18 ± 1.93*	-139.2 ± 106.2 mm^2

Table III.1: Changes in abundance (Δ abundance) and size (Δ size) of structure-dependent reef fauna before and after Hurricane Harvey. Both abundance and length/size values were calculated as the differential in means between 2018 and 2016: $\bar{x}_{2018} - \bar{x}_{2016}$. Standard deviation was calculated for the species across both years. Both open and large-mesh cage data were incorporated here. Statistically significant differences between groups are denoted by an asterisk. Darter gobies and snapping shrimp 'Δ size' were left blank due to insufficient measurements to compare between years.

Table III.2:

Time period	**Model parameter**	**Estimate**	**z-value**	***p-value***
Sep	Hurricane year	0.87	3.28	**0.0011**
	Species	0.84	7.05	**<0.0001**
	Interaction	-1.43	-3.79	**0.0001**
Sep – Nov	Hurricane year	0.35	1.98	**0.0474**
	Species	1.08	15.59	**<0.0001**
	Interaction	-0.80	-3.49	**0.0004**
Apr – Jun	Hurricane year	0.38	2.47	**0.0135**
	Species	0.26	4.03	**<0.0001**
	Interaction	-0.55	-2.57	**0.0101**

Table III.2: Estimates from three generalized linear models comparing the effects of hurricane years and fishery species on catch per unit effort across three different time periods.

FIGURES

Figure III.1:

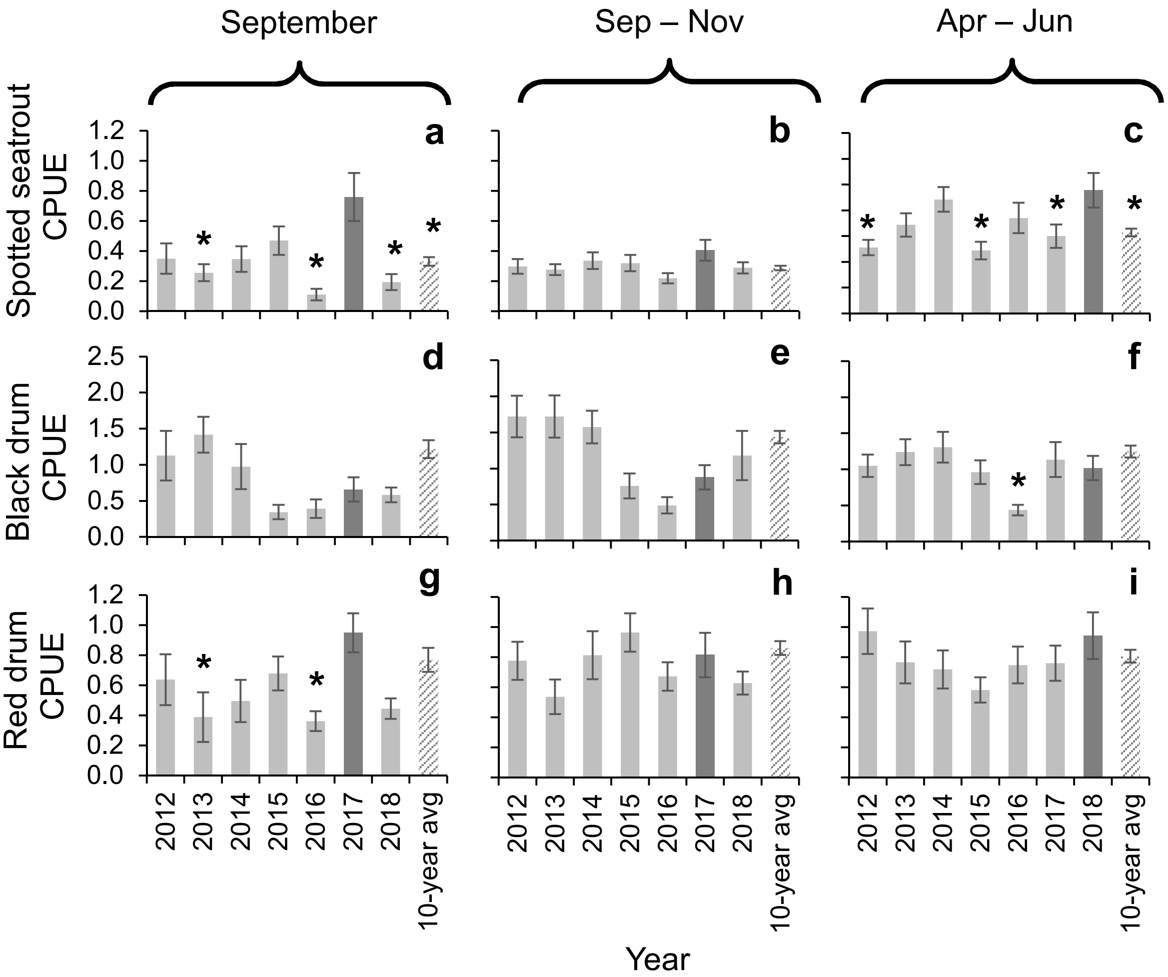


Figure III.1: Mean ± SE catch per unit effort (CPUE) for a,b,c) spotted seatrout, d,e,f) black drum, and g,h,i) red drum collected each year during the time periods of a,d,g) September (n = 15), b,e,h) September – November (n = 45), and c,f,i) April – June (n = 45). Dark gray bars represent the first time period after Hurricane Harvey while dashed bars represent the 10-year average prior to the hurricane (n for September = 150, n = 450 for fall and early summer time periods). Asterisks represent values significantly lower than time periods immediately post-hurricane.

Figure III.2:

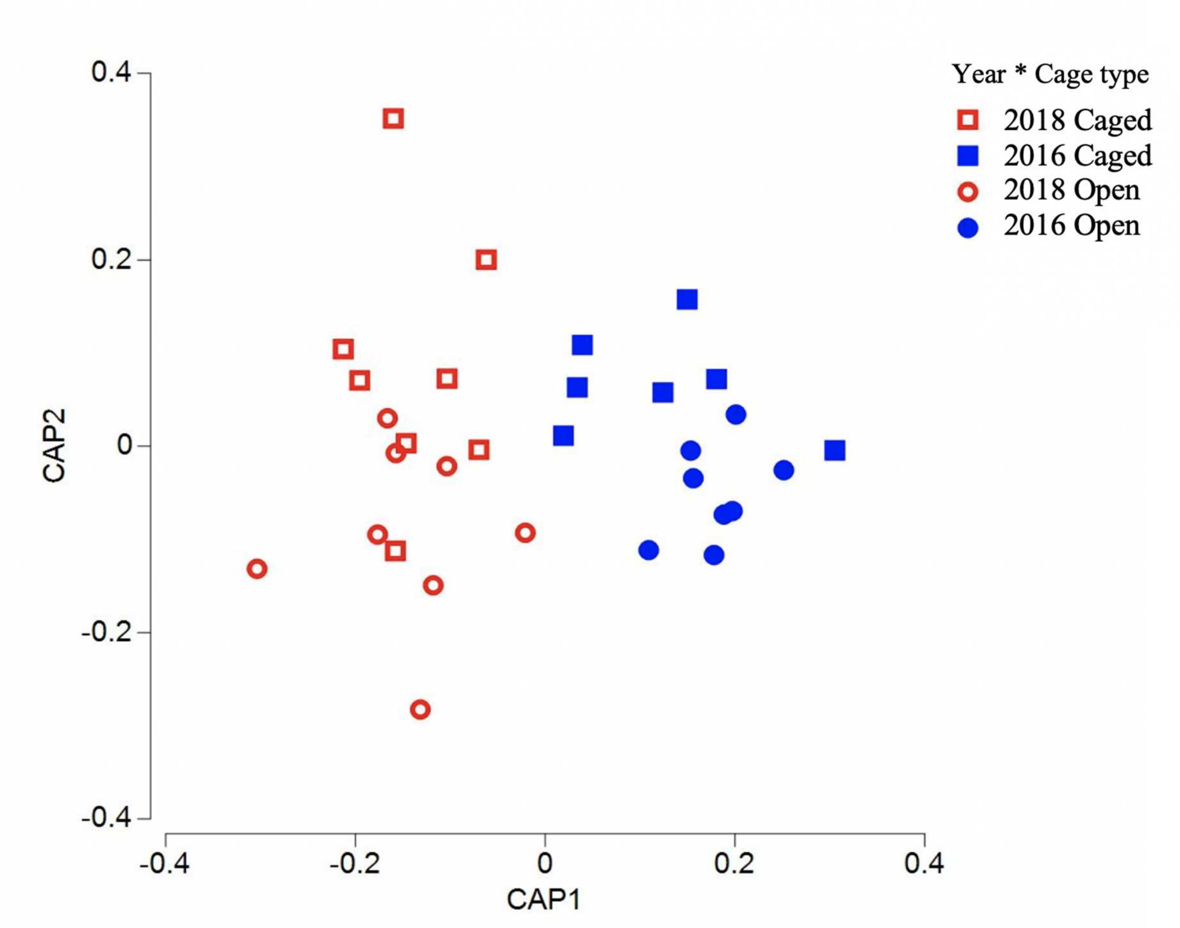


Figure III.2: CAP plot of community structure across years and cage types. Years are illustrated with different colors (solid blue = 2016, open red =2018) and cage types with different shapes (circles = open/control cages, squares = large-mesh cages).

Figure III.3:

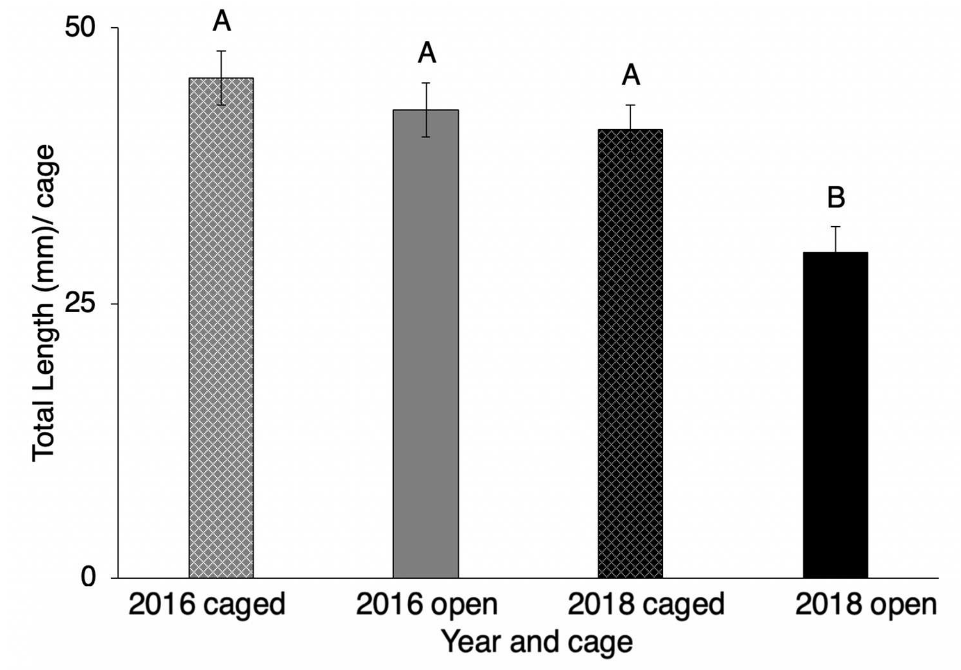


Figure III.3: Mean ± SE total length of fishes (mm) across years and cage types. Different letters indicate significantly different means as found by a Tukey post-hoc test (n = 30). Years are illustrated by different colors (gray = 2016, black = 2018). Solid bars represent open cages and diamond-grid filled bars represent large-mesh cages.

Figure III.4:

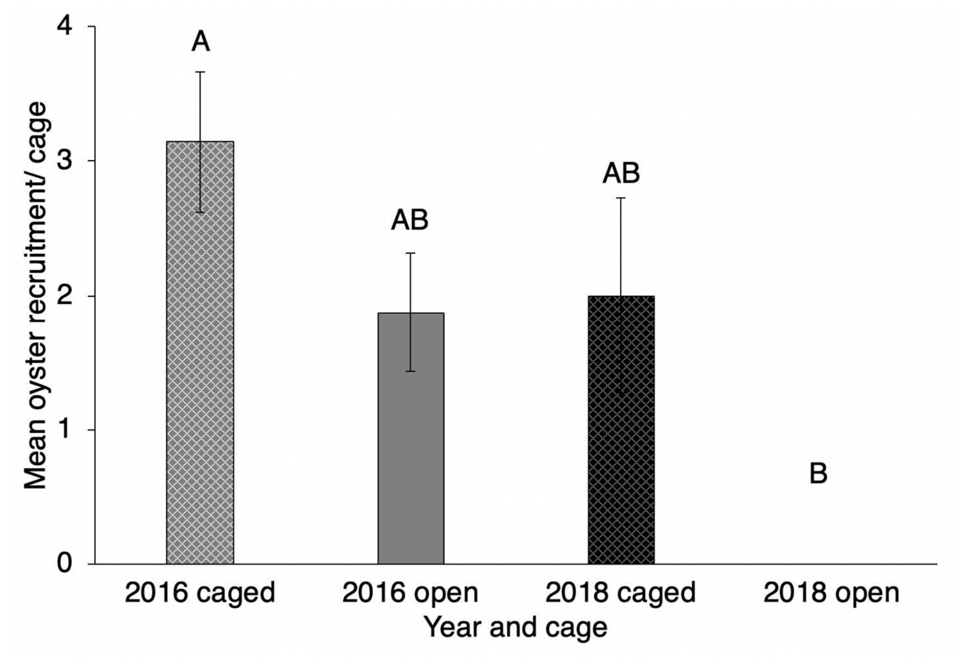


Figure III.4: Mean ± SE oyster recruitment across years and cage types. Different letters indicate significantly different means as found by a Tukey post-hoc test (n = 29). Years are illustrated by different colors (gray = 2016, black = 2018). Solid bars represent open cages and diamond-grid filled bars represent large-mesh cages.

Supplemental Tables

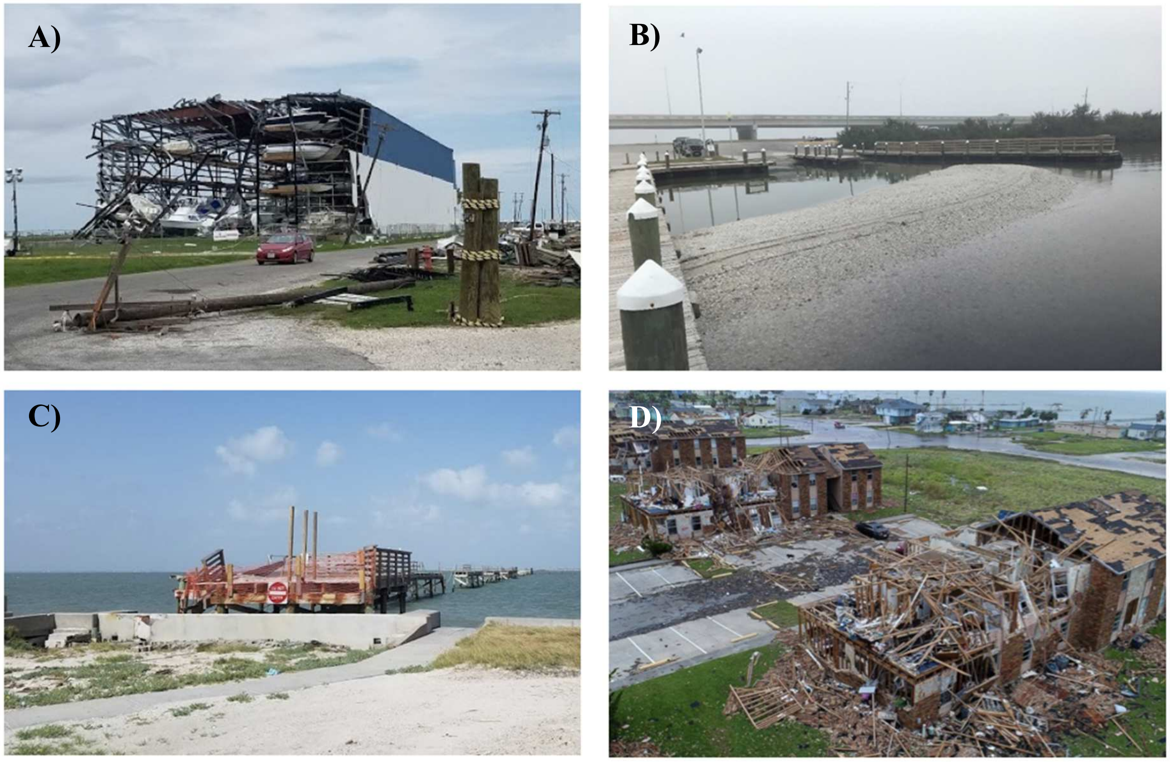
Supplemental Table III.1

Groups	t	P(perm)	Unique perms
2018large, 2016large	2.3412	0.0001	6403
2018large, 2018open	1.5106	0.0269	6414
2018large, 2016open	3.3315	0.0002	6410
2016large, 2018open	2.4405	0.0001	6407
2016large, 2016open	1.4441	0.0332	6404
2018open, 2016open	3.1912	0.0002	6406

Supplemental Table III.1: Pairwise 1-way PERMANOVA with combined year and cage type as factors results. PERMANOVA was run with 100,000 permutations and allowed unrestricted permutations of raw data.

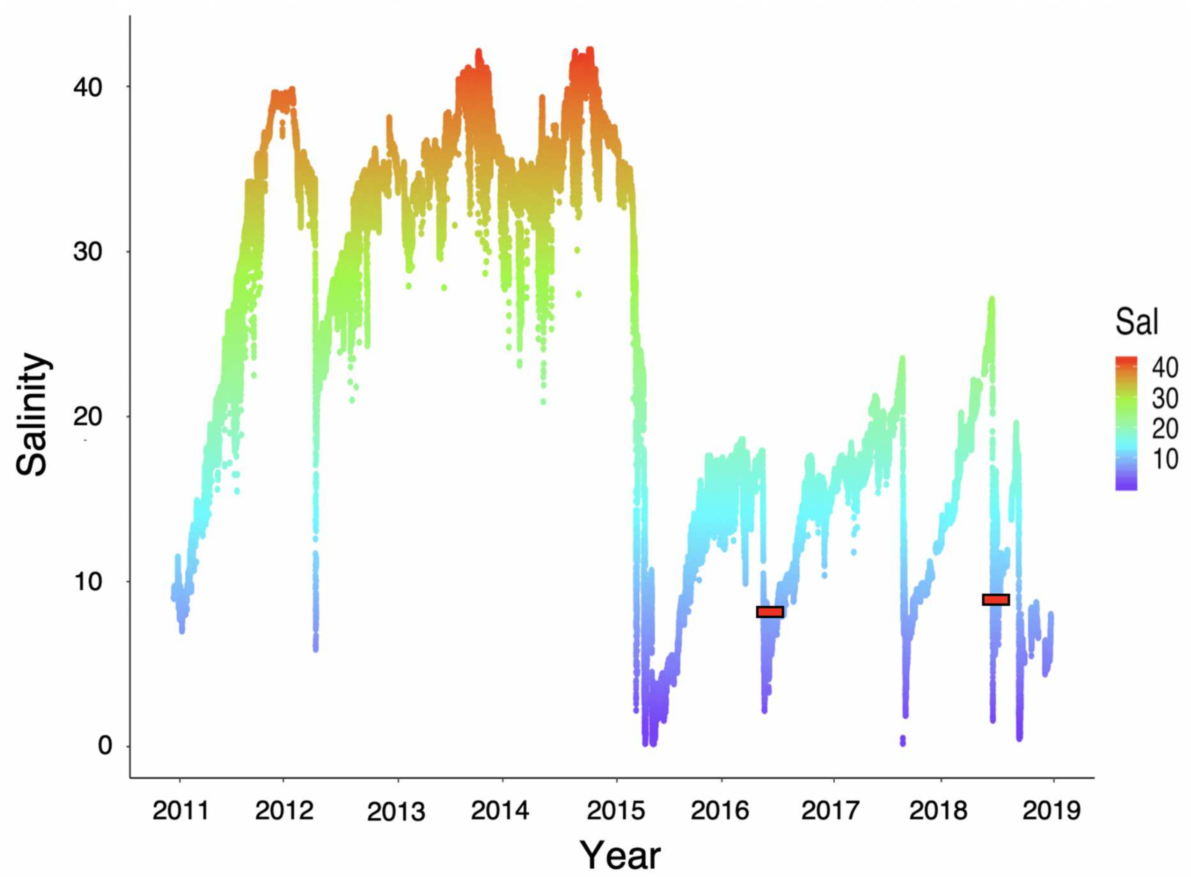
Supplemental Figures

Supplemental Figure III.1:



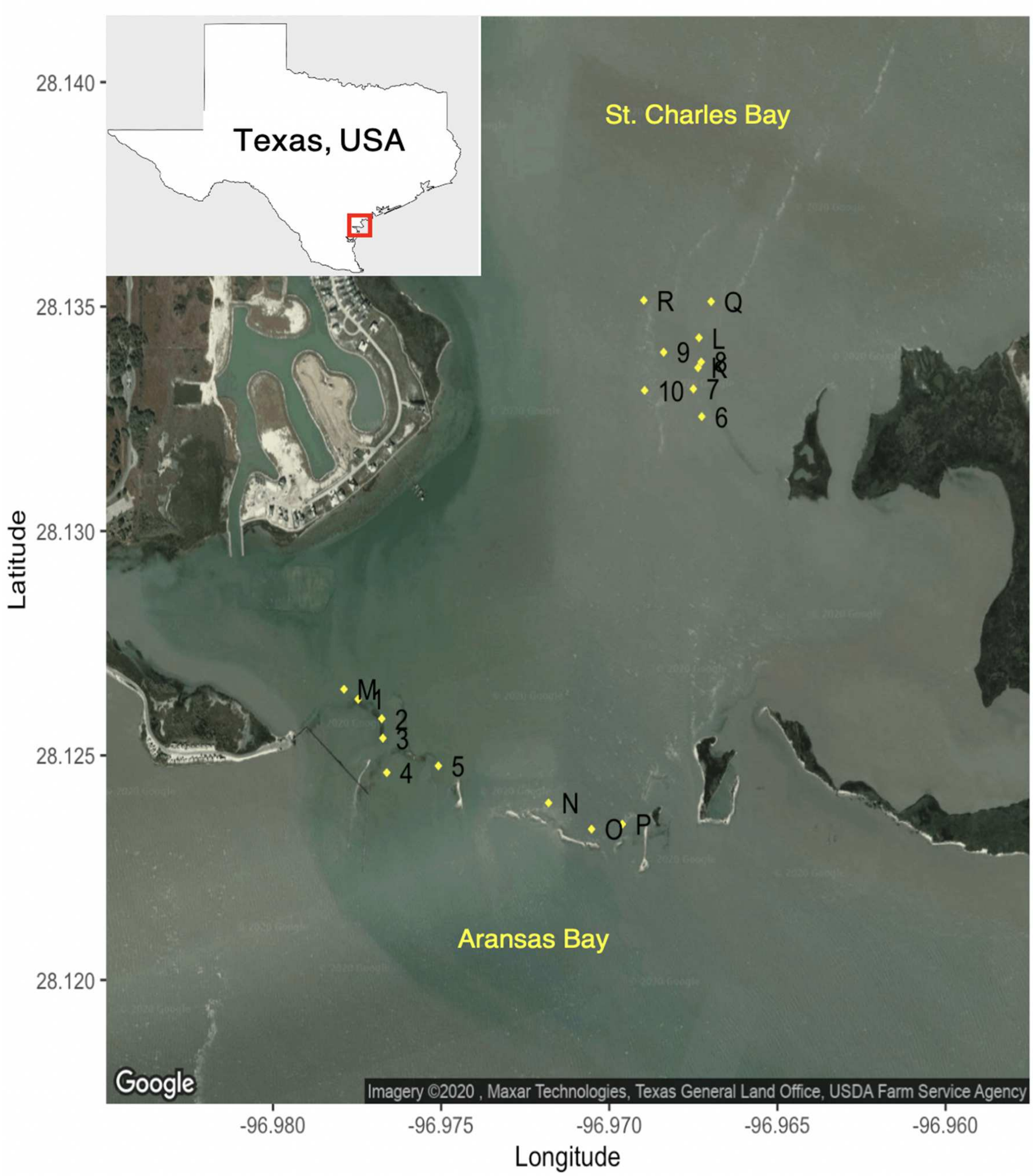
Supplemental figure III.1: Photographs following the aftermath of Hurricane Harvey. Photo credits to Ethan Pettis (A-C) and ABC News (D).

Supplemental Figure III.2:



Supplemental figure III.2: Salinity from 2011 - 2019. Red marks represent cage-study sampling periods in 2016 and 2018. Salinity data were obtained from the Mission-Aransas NERR System Wide Monitoring Program (SWMP). Warmer colors are indicative of higher salinity. Figure was constructed in RStudio version 1.1.456 using the ggplot2 package (Wickham 2016).

Supplemental Figure III.3:



Supplemental figure III.3: Map of field sites (illustrated by yellow diamonds) in South Texas, USA. Mapped GPS coordinates are displayed in decimal degrees (DD) format and were obtained at each site in the field using a handheld Garmin GPSmap 76CSx. Maps were built in RStudio version 1.1.456 using the ggmap (Kahle and Wickham 2013), mapdata (Becker et al. 2018), and ggplot2 (Wickham 2016) packages.

CHAPTER IV: BIOLOGICAL FLOW INDICATORS? BARNACLES EXHIBIT LOCAL-SCALE PHENOTYPIC PLASTICITY TO HYDRODYNAMIC STRESS

ABSTRACT

Hydrodynamic stress shapes the flora and fauna that exist in wave-swept environments and may become the primary community structuring agent. Although important, hydrodynamics can prove difficult to quantify. Instrumentation is expensive, labor intensive, and logistical challenging to accurately measure spatial and temporal differences. Here, we explored the utility of two circumglobal species of barnacles as potential biological flow-indicators. Barnacles, nearly ubiquitous within the estuarine and intertidal environment, have demonstrated notable phenotypic plasticity in the dimensions of their feeding appendages (cirri) and genitalia in response to flow. Transplanting barnacles between high energy and low energy flow environments causes barnacles to adjust their phenotype to the new flow conditions. In high flow, barnacles have shorter, stockier cirri with shorter setae; in low flow, barnacles have longer, thinner cirri with longer setae. By measuring the relative differences in cirral dimensions across flow regimes, we can determine bulk differences in flow between and within sites. We performed reciprocal transplants to determine if barnacles (*Amphibalanus eburneus*) would demonstrate phenotypic plasticity over a local spatial scale and short (4-week) timeframe. Then, we transplanted barnacles into low (<5 m/s) and high flow (>25 m/s) environments and then shielded half of the transplanted barnacles to lessen flow speed. In both experiments, barnacles had significant differences in cirral morphologies across high and low flow sites. Ameliorating flow within sites did not affect barnacle morphologies in low-flow, but had pronounced effects in high flow environments. These results highlight the utility of barnacles as cheap, accessible, and

biologically-relevant indicators of flow, across both broad and local scales. Given the importance of hydrodynamic conditions in nearshore and intertidal environments, we recommend the application of this methodology to effectively and affordably monitor hydrodynamic conditions.

INTRODUCTION

Hydrodynamic forces, such as flow velocity and turbulence influence the morphology and behavior of organisms, and its influence is clearly seen in morphology of intertidal flora and fauna (Denny and Gaylord 1996, Blanchette 1997) and in the foraging and predator avoidance behaviors of benthic organisms (Menge and Sutherland 1987, Smee et al. 2010). In wave-swept environments, organisms experience significant lift, drag, and acceleration and use both behavioral and morphological adaptations to reduce the chances of being swept off of the substrate. Behaviorally, organisms may change body orientation to minimize frontal area or adopt streamlined shapes, limit movement during intense flows, and seek refuge within microhabitats such as crevices. Morphologically, organisms may possess streamlined body shapes, higher area/basal strength ratios, or have different sizes and shapes of appendages than conspecifics or heterospecifics in low flow environments.

Many marine organisms disperse broadly and interact with variable conditions. This is especially true within estuaries where conditions are incredibly dynamic and may shift dramatically over short periods of time or space. This poses a great strain on sessile and slow-moving organisms who cannot escape and must therefore tolerate harsh conditions. For example, wave-swept algae typically feature flexible body plans that conform to streamlined shapes and limit applied forces and strong holdfasts that anchor them to the substrate (Denny and Gaylord 2002). Sessile invertebrates must utilize plastic phenotypes in both behavior and morphology to adequately respond to differences in hydrodynamic stress on short and long-term time scales.

Behavioral plasticity is often the cheapest and most immediate tactic to limit exposure to deleterious conditions (e.g., predators, hydrodynamics, temperature, etc.); however, when unfavorable conditions persist, other costlier forms of plasticity may be necessary. For mobile invertebrates, such as the limpet *Lottia gigantea,* they may respond behaviorally to limit movement and exposure to high flows (Judge 1988). Morphologically, marine gastropods grow a larger muscular foot while not changing their projected surface area (surface area/basal strength ratio) in regions of high flow velocity to reduce the risk of dislodgement (Trussell 1997). For instance, Eastern oysters (*Crassostrea virginica*) exhibit a two-tiered defense strategy in shell strength against crab predators. Oysters can rapidly, and relatively cheaply, thicken and strengthen their shells using calcium carbonate. However, when threats of predation persist, or appear more dangerous, oysters can allocate more significant resources towards a much stronger shell using a proteinaceous matrix (Scherer et al. 2018). Without being able to flee, sessile invertebrates much be able to tolerate stronger, more intense, and/or more frequently stressful conditions.

Phenotypic plasticity of marine organisms may serve as bio indicators and provide a relatively inexpensive means to quantify hydrodynamic conditions. Methodological approaches to quantify hydrodynamics range from bulk flow investigations (i.e., chalk-blocks, sensu (Sanford et al. 1994) to expensive instruments that make high precise measurements (e.g., Acoustic Doppler Velocimeter (ADV), sensu (Williams 3rd et al. 1987). While the bulk-flow approaches are much cheaper and can easily be replicated, they only provide erosion rate data (mass lost/time deployed) non-specific to which hydrodynamic force was involved and are questioned for their biological relevance (Gaylord 1999, Porter et al. 2000). Further, chalk blocks are subjected to scouring, which can accelerate erosion rates in areas with strong waves or high sediment loads, limiting their usefulness in comparing spatial differences among areas. Instruments that measure flow are often expensive (ADVs ~ $10,000 – $20,000), making replication and measuring spatial differences in flow difficult (turbulence, wave periodicity, flow velocity, direction, etc.). Thus, using common marine organisms as biological flow meters can provide a useful mechanism to compare spatial differences in hydrodynamics (Lunt et al. 2017).

Balanidae barnacles are quite common in coastal environments and are heavily influenced by hydrodynamics (Trager et al. 1990, Leonard et al. 1998, Marchinko 2003, Neufeld and Palmer 2008, Pineda et al. 2010). Hydrodynamics effect nearly every aspect of a barnacle's life-cycle; from larval recruitment, predation-risk, feeding behavior, morphology, and reproduction (Arsenault et al. 2001, Marchinko and Palmer 2003, Marchinko 2003, Neufeld and Palmer 2008). As sessile suspension feeders, balanid barnacles must be capable of coping with notable shifts in flow regime throughout their lifetime (i.e., tidal shifts, seasonal shifts, storm-events, etc.). Barnacles are phenotypically plastic and can alter the size and dimensions of their appendages (cirri and genitalia) (Marchinko and Palmer 2003, Marchinko 2003), as well as their feeding behavior in response to changes in flow (Trager et al. 1990). In areas of high flow, barnacles have predictably shorter, stockier cirri with shorter setae; in low flow, barnacles have longer, thinner cirri with longer setae. This is a fairly sensitive process and some data suggest that barnacles respond to local-scale differences in flow even at the mm to cm scale (Reustle, unpublished data). Further, barnacles adjust to changes in flow rather quickly. Behaviorally, barnacles respond to changes in flow direction instantaneously, even appearing to anticipate oscillating flow (Trager et al. 1990). Persistent shifts in flow illicit morphological responses that take place in only two-three weeks (or one to two 2 molts) for some species (*e.g.*, *Balanus glandula*, (Lunt et al. 2017).

Here, we completed a reciprocal transplant experiment to determine if barnacles (*Amphibalanus eburneus*) would demonstrate phenotypic plasticity over a local spatial scale and short (4-week) timeframe. Then, we transplanted barnacles to low and high flow areas and shielded half the barnacles to reduce flow speed. The reciprocal transplant study found that barnacles adjusted quickly to the flow environment, though different measured cirral dimensions responded in unique ways. For the flow manipulations, two species of barnacles (*A. eburneus* and *A. amphitrite*) demonstrated strong responses to both site-related differences and in-situ manipulations of flow. The interaction between flow regime and exposure level was a significant predictor of cirral traits, suggesting that barnacles potentially may serve as useful predictors of spatial differences in flow.

METHODS

Rationale- We hypothesized that barnacles would have longer, thinner cirri with longer setae when protected from fast, turbulent flows. Likewise, we hypothesized the converse: barnacles exposed to fast, turbulent flows would have shorter, stockier cirri with shorter setae. Finally, we hypothesized that the difference between exposed or protected barnacles would deteriorate in low flow. That is, in low-flow conditions, there would be very little morphological differentiation in barnacle feeding appendages as flow conditions were likely not much different biologically. Unfortunately, there was high mortality in the barnacles transplanted to the high flow sites. This was particularly the case for *A. amphitrite*, where only 8 individuals survived and only one within the protected treatment. Interestingly, this fate was not apparently shared by *A. eburneus*.

Reciprocal transplant study- Four ADVs were deployed across oyster reefs (2/side) that separate Aransas bay (windward side) from St. Charles bay (leeward) at Goose Island State park in

Rockport, Texas. ADVs found leeward sides to have smaller wave heights (lw: 0.05 m, ww: 0.22 m) and lower current speeds (lw: 3.75 cm s^{-1}, ww: 6.68 cm s^{-1}). PVC poles (20 total) were deployed along the same oyster reefs on April 26th, 2017. The windward reef side experiences significantly more waves, higher waves, and faster flows (Lunt et al. 2017). Poles were marked with different colored zip ties to indicate their initial deployment location. After suitable barnacle recruitment, half of the poles from the leeward side were moved to the windward side and vice versa. One month later, all PVC poles were collected and taken to Texas A&M University-Corpus Christi for processing. Barnacles were removed and measured by recording the basal diameter of each barnacle (Rasband 1997). Barnacles were then dissected, and the 6th cirri was removed and photographed using an Amscope stereo-microscope with a mounted 14 megapixel camera. Photographs were uploaded into ImageJ and ramus length, width, and setae length were each measured using the segmented line function (**Figure IV.1**). Barnacle sizes were compared between treatments using a one-way ANOVA in JMP. Cirral data were analyzed using a One-Way ANCOVA in JMP and then compared across treatments using a Tukey HSD test.

Characterizing flow at field sites- Flow characteristics were measured at each location using (NortekUSA™) Vector model Acoustic Doppler Velocimeters (ADVs) and analyzed using ExploreV software. On three separate occasions during the study period (July 13th, August 3rd, and August 10th), ADVs were deployed for 24-hours, ADVs were secured to piers using cable-ties and the transmitter and receivers were suspended 0.5m below surface. Flow velocity was measured at a frequency of 8 Hz in X-minute bursts every 15 minutes for 24 hours.

ADVs measure three dimensional flow. The net flow velocity (U) was calculated by taking the velocity from each dimension (x, y, z) and combining into a single value using the equation: $U = \sqrt{(x^2 + y^2 + z^2)}$. Flow velocity was calculated in this manner for each 4-minute burst and averaged across all bursts for each site. Turbulence was calculated using the root mean square (RMS) of the flow velocity data. Turbulence was calculated, similarly to U described above, for each 4-minute burst using the equation: $RMS= \sqrt{(RMS_x^2 + RMS_y^2 + RMS_z^2)}$. Flow characteristics were not compared statistically, but were quantified using ADVs at each location (**Table IV.1**).

<u>Barnacle flow indicators-</u> PVC poles were placed in the Laguna Madre near the field sites used for the experiment. After suitable barnacle recruitment, 10-15 cm segments of each PVC pole containing the greatest number of barnacles were selected for the experiment. Barnacles were spaced far enough apart to prevent hummocking. Pairs of PVC segments containing barnacles were attached with zip ties to a PVC frame (Fig) and frames were deployed into a low and high flow area. On each frame, one of the PVC segments was protected from flow using a plastic shield (**Figure IV.2**) and remained in the field from 7/01/2018 to 8/11/2018. Barnacles were recovered and taken to the lab and placed in a freezer to await dissections. Barnacles were identified, basal diameters were measured to the nearest 0.01 mm, and their sixth cirri excised using dissection probes. Dissected cirri were photographed using an Amscope SM-2TZ-LED-14M3 dissection scope. Cirral dimensions (ramus length, ramus width, and setae length) were then measured using the segmented-line tool in imageJ version 1.51 (Carlton et al. 2011) (sensu Lunt et al. 2017). One setae length measurement was not made due to poor image resolution; however, the other cirral traits were unaffected and were still measured for this individual.

Barnacle basal diameters were compared across locations and treatments using a two-way ANOVA. Each cirral dimension was analyzed using a two-way ANCOVA with flow level, treatment, and the interaction term as factors and basal diameter as the covariate. ANCOVAs were used to analyze response variables (ramus length and setae length) for both *Amphibalanus* species grouped together. Statistics were run in JMP Pro 14.2.0.

Reynolds number- Reynolds number is a proportional value describing the relative importance of inertial and viscous forces for movement relative to fluid (Vogel 1994). Relatively large Reynolds numbers are indicative of stronger inertial forces, while small values are indicative of stronger viscous forces. For suspension feeding organisms like barnacles, Reynolds numbers may suggest whether the feeding apparatus is being dominated by inertial or viscous forces and functioning biomechanically like leaky sieves or like paddles, respectively.

Reynolds number was calculated for barnacles using the equation:

$$\mathrm{Re} = \frac{\rho \iota u}{\mu}$$

Where ρ is the density of seawater (1025 $\mathrm{kg/m^3}$), ι is ramus width, u is the mean flow velocity of the water recorded by the ADV, and μ is the dynamic fluid viscosity of seawater (0.0011 $\mathrm{kg/m \cdot s}$). Only the exposed barnacles were used for calculations of Reynolds numbers since we have no ADV data quantifying the degree of flow amelioration within protected treatments. After Reynolds numbers were calculated, a Bartlett test on variance was calculated to determine homogeneity of variance. The Bartlett test indicated unequal variance between flow sites; therefore, Reynolds numbers were compared across flow regimes using a Welch's t-test in RStudio (version 1.1.456).

RESULTS

Reciprocal transplant experiment- Barnacles had significantly larger basal diameters on the leeward side of the reef than on the windward side ($F_{3,43} = 5.41$, $p > 0.003$), while transplanted barnacles were intermediate to the leeward and windward sides and did not differ significantly (**Figure IV.3A**).

Barnacle ramus lengths differed between treatments ($F_{4,42} = 9.27$, $p < 0.001$). Ramus lengths were the longest for leeward and leeward transplants (barnacles transplanted from the windward side to the leeward side), while windward and windward transplant (barnacles transplanted from the leeward side to the windward side) had smaller ramus lengths (**Figure IV.3B**). Leeward barnacles were not significantly different from leeward transplants, though they were significantly longer than both windward and windward transplants (**Table 1**). Transplanted barnacles had significantly different ramus lengths (**Figure IV.3B**), while windward barnacles had intermediate ramus lengths that were not significantly different from either transplanted treatment.

Setae lengths were significantly different between treatments ($F_{4,42} = 14.1$, $p < 0.001$). Leeward and leeward transplant barnacles had significantly longer setae than windward or windward transplant barnacles (**Figure IV.3D; Table 2**). Here, however, there were no intermediate lengths between treatments. Leeward and leeward transplants were not-significantly different from each other (**Figure IV.3D**). Similarly, windward and windward transplants did not differ significantly (**Figure IV.3D**). Essentially, wherever barnacles were *collected* from determined how they grouped by setae lengths.

<u>*Barnacle flow indicators-*</u> Both barnacle species, *A. eburneus* and *A. amphitrite* exhibited significant morphological differences between locations and treatments. Barnacles did not have measurably different basal diameters across flow regimes ($F_{1,95} = 1.79$, $p = 0.185$), treatment type ($F_{1,95} = 1.27$, $p = 0.262$), or the interaction ($F_{1,95} = 0.76$, $p = 0.385$). Ramus lengths appeared to be the most sensitive to differing flow velocities ($F_{1,94} = 8.37$, $p = 0.005$). Ramus widths were

also significantly different between flow sites ($F_{1,94} = 5.02$, $p = 0.0274$), while setae lengths were not statistically different ($F_{1,93} = 2.73$, $p = 0.102$). Treatment effects were not significant for any cirral dimensions (ramus length: $F_{1,94} = 3.09$, $p = 0.082$; ramus width: $F_{1,954} = 2.49$, $p = 0.118$, setae length: $F_{1,93} = 3.88$, $p = 0.052$); however, cirral dimensions were strongly affected by the interaction between location and treatment (ramus length: $F_{1,94} = 6.94$, $p = 0.009$, **Figure IV.4A**; ramus width: $F_{1,94} = 20.1$, $p < 0.001$, **Figure IV.4B**; setae length: $F_{1,93} = 13.67$, $p = 0.004$, **Figure IV.4C**).

Reynolds number- Barnacles exhibited vastly different Reynolds numbers between high and low flow sites ($t = 10.2$, $p < 0.001$; **Figure IV.5**). On average, exposed barnacles in high flow sites had nearly 5x higher Reynolds numbers ($high_{Re} = 43.4$, $Low_{Re} = 8.92$).

DISCUSSION

Reciprocally transplanted barnacles developed morphologies appropriate for the hydrodynamic conditions they were transplanted to within four weeks of placement. Morphological convergence appeared to occur quickest for setae as evidenced by the transplanted groups having setae lengths that were indistinguishable from the side from which they had initially be placed (**Figure IV.3D**). Ramus lengths, however, had not completely converged after four weeks (**Figure IV.3B**). While windward barnacles were hypothesized to have the shortest ramus lengths, the windward transplant barnacles were even shorter still– perhaps indicating that the dramatic increase in flow may have caused an overcorrection in response to flow conditions (**Figure IV.3B**). Alternatively, the sudden change in flow conditions may have rendered the longer feed appendages less effective, changing energy acquisition and growth parameters.

Localized differences in flow regimes created by the plastic shield treatments produced distinct differences in barnacle morphologies in high flow sites, showcasing local-scale phenotypic plasticity on small spatial scales with flow differences. Further, these differences highlight that plasticity was driven by flow and not by other environmental differences. Barnacles did not differentially alter their cirral morphologies in response to treatments in low flow sites, presumably because the differences between treatments were minimal in low flow conditions.

Barnacles exhibited significant differences in ramus length, ramus width, and setae length between high and low flow sites (**Figure IV.4**). Further, barnacles exhibited differences in all three cirral dimensions across the interaction between flow velocities and treatment levels. Ameliorating hydrodynamic forces did not affect barnacle cirral appendages in low flow environments; however, local-scale plasticity was evident in the high-flow sites. Additionally, barnacles experienced vastly different Reynolds numbers between high and low flow sites (**Figure IV.5**), which can affect the functional-performance of suspension feeding appendages (Cheer and Koehl 1987). Barnacles exposed to ambient flow conditions experienced approximately 5 times greater Reynolds numbers in high flow conditions than in low flow conditions; even the smallest barnacles in high flow experienced far greater Reynolds numbers than the largest barnacles in low flow conditions (**Figure IV.5**). At higher Reynolds numbers, cirral nets often become “leakier” and function more as rakes (or sieves) than paddles (at $Re < 1$) (see Cheer and Koehl 1987, Geierman and Emlet 2009). Together, these data show that barnacles were both functionally and morphologically distinct across the flow gradient. While we did not have quantitative measures of the degree of flow amelioration provided by the plastic shields, the morphological evidence points to dramatically different morphologies between treatment levels in high flow conditions (**Figure IV.4**).

Both barnacle species have broad geographic distributions. *A. amphitrite* is more widely distributed throughout temperate and sub-tropic systems; however, *A. eburneus* is invading expanding into new regions (Carlton et al. 2011). Many of the *Amphibalanaus* species share near circumglobal distributions and often co-associate (Henry and McLaughlin 1975), making them ideal candidates as biological flow indicators, while also justifying the analysis of their data combined as a genus. Therefore, researchers with limited experience working with and identifying barnacles may still be able to use barnacles as flow indicators.

We included *A. amphitrite* in this study, despite the mortality events in the high flow sites, primarily due to its broad geographic distribution. *A. amphitrite* is an incredibly common species around temperate and sub-tropic systems, making it an ideal candidate species as a biological flow indicator. Further, it is part of the *"amphitrite* complex"; a complex of several species that can be difficult to discern between one another (Carlton et al. 2011).

While we are uncertain of the ultimate cause of the striped barnacle mortality events, it primarily occurred within one treatment level (protected treatments in high flow sites). Future studies are needed to ascertain if this was an example of demonic intrusion of related but yet unknown mechanism within this species. We note that barnacles were indeed deployed in poly-culture groupings, and so it is possible that the mortality events were driven by interspecific competition within the protected treatment. This may be the most parsimonious explanation of all; ivory barnacles tended to be larger in basal diameter than striped barnacles and would have a competitive advantage in suspension feeding within flow-protected treatments. Other explanations, such as predation, are possible albeit unlikely. It is possible that this was due to increased predation within the flow-protected treatments, as reduced hydrodynamic stress can strengthen top-down dynamics (e.g., Leonard et al. 1998; Menge and Sutherland 1987); yet, *A. eburneus* in these same conditions did not share this fate. Further, nearly all of the dead *A. amphitrite* tests were completely intact, indicating that mortality was unlikely due to crushing predators as seen by most crabs or durophagous fishes; however, other drilling predators are notorious for leaving behind intact barnacle tests after consuming the soma (the soft-body) of the barnacle. These smaller *A. amphitrite* barnacles may have been more vulnerable to predation by shore crabs (*Pachygrapsus gracilis*), whose delicate algae-scraping chelae would likely prevent them from consuming barnacles, especially larger barnacles, in the iconic crab-crushing way. If *P. gracilis* crabs are capable of feeding on barnacles without crushing barnacle tests, then they may have been the source of mortality. *P. gracilis* crabs were noted for being highly abundant along the piers in the high flow sites. If so, this could help to explain the mortality patterns that seemingly targeted only one species within one treatment level. There could have been a preference for striped barnacles over ivory barnacles (i.e., mechanical preference; size-dependent predation, etc.), or alternatively, localized conditions within the protected treatments were unsuitable/intolerable for the striped barnacles (e.g., food-availability) particularly when paired with the larger ivory barnacles. Again, additional studies are necessary to understand why so many striped barnacles perished in the shield treatment in high flow sites.

Here, we document the utility of barnacles as biological flow indicators and we encourage their use as a low-cost alternative to expensive sensors or to represent biologically relevant differences in flow for use in selecting sites for field studies or assessing spatial differences in flow. We note differences in barnacle morphology in areas with and without waves, indicating barnacles can be useful flow indicators in a variety of hydrodynamic conditions. Careful consideration must be paid to morphological limitations in high flow (e.g., >4 m/s as seen in (Li and Denny 2004), but also the size class of the barnacle influences the functionality of the cirral net and the Reynold's number generated by the beating of the cirri (Geierman and Emlet 2009). In one occasion at our high flow site, flow velocities exceeded those found by Li and Denny (2004) to cause cessation of feeding in barnacles. If flow velocities commonly exceeded 4 m/s in our high flow site, this may explain why barnacles had higher growth rates in low flow sites. We demonstrated great potential for the application of this technique across both localized and broad-scale differences in flow. Given the incredible structural power of hydrodynamics in nearshore and shallow-water ecosystems, using barnacles as flow indicators represents a biologically relevant and accessible technique for investigations of recent hydrodynamic conditions.

FIGURES

Figure IV.1

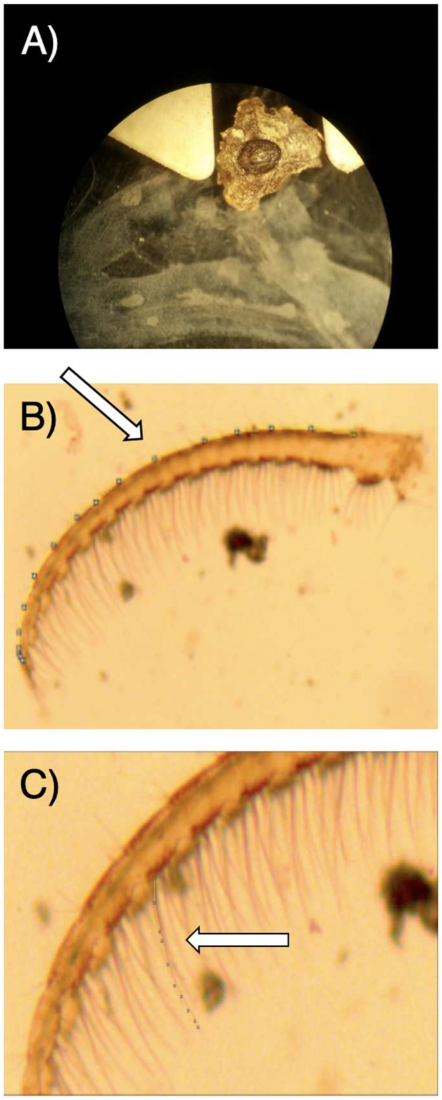


Figure IV.1: Progression of barnacle dissections. Basal diameters are measured from rostrum to carina (A). After barnacles are removed from their tests, their sixth cirri was excised and the ramus length measured along the outer edge of the cirri (B) and setae lengths measured along the middle endopodite (C).

Figure IV.2

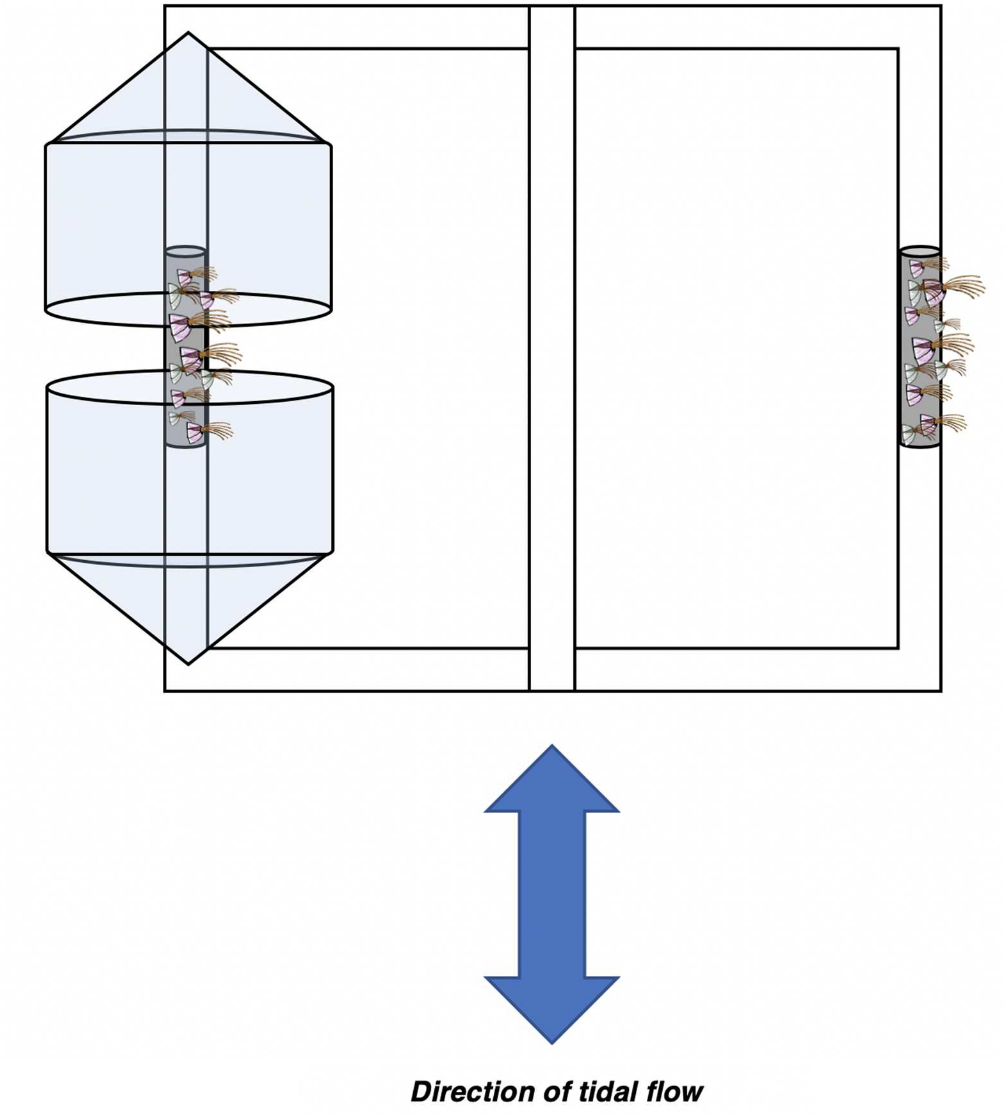


Figure IV.2: Schematic of barnacle “house” designs. A) Large steel L-brackets and large cable ties were used to attach PVC frames to the pier. Additional cable ties were used to fasten the frames tight to limit the pitch and roll of the frame. Frames were deployed approximately 0.3m below the surface at high tide. B) Conical plastic “protectors” were used to modify flow regime within treatments. C) “Exposed” barnacles were not shielded from flow in any regard.

Figure IV.3

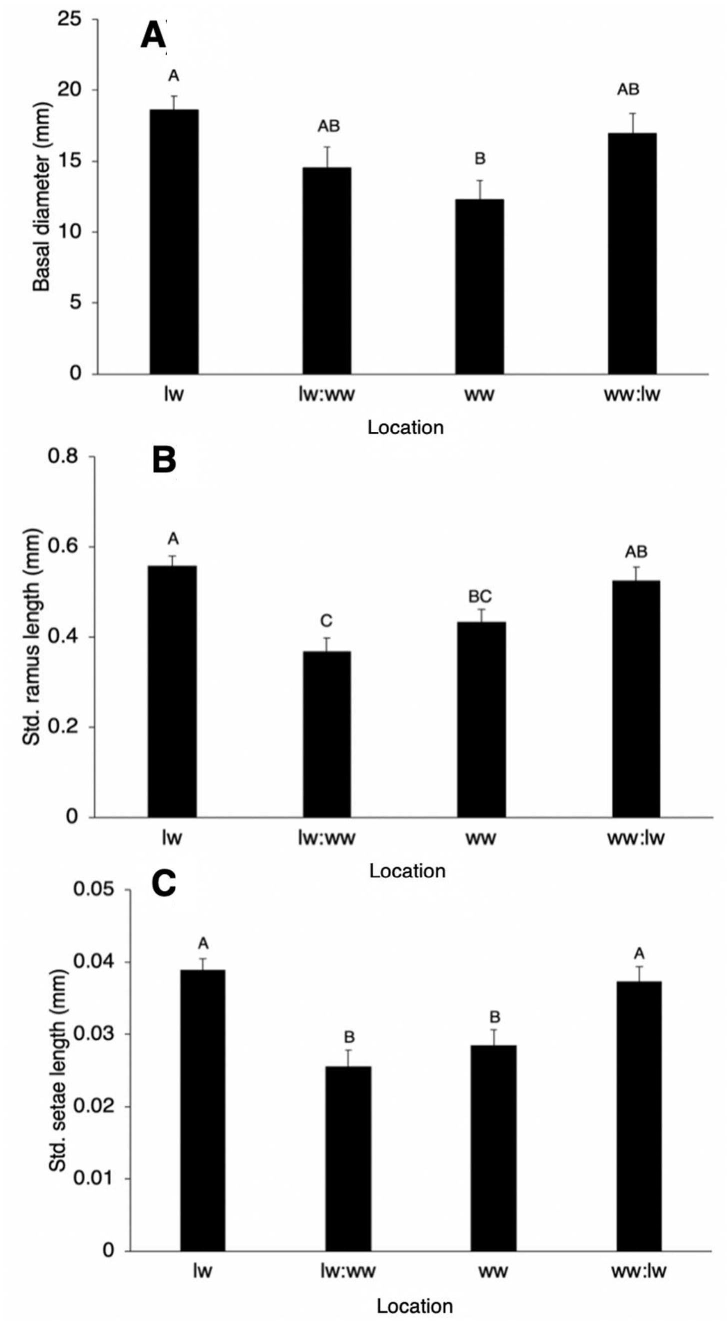


Figure IV.3: Reciprocal transplant experiment. Mean basal diameters + SE for each location (A). Mean + SE for ramus lengths (B), and setae lengths (C) across each location.

Figure IV.4

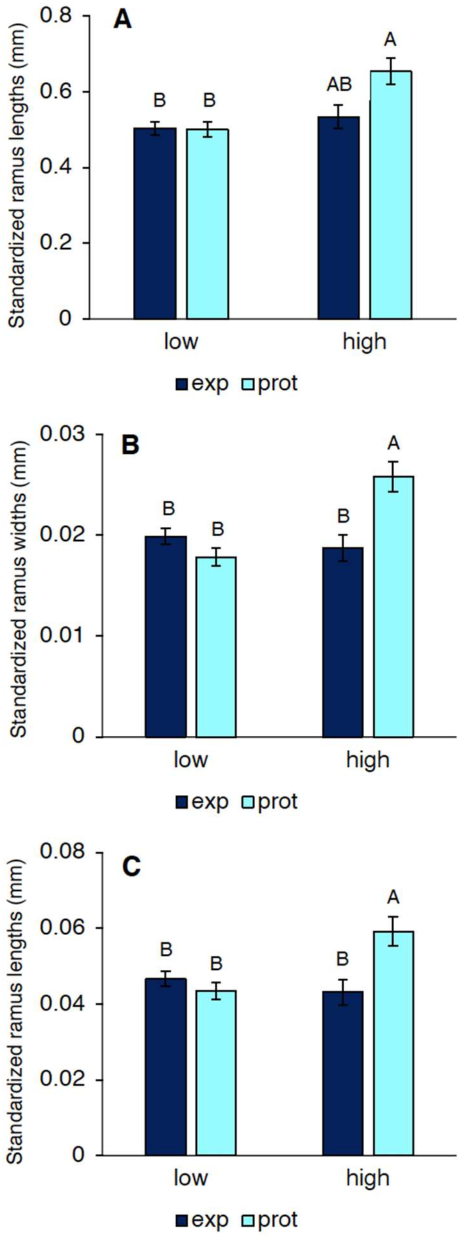


Figure IV.4: Barnacle contraption experiment. Mean + SE for ramus lengths (A), ramus widths (B), and setae lengths (C) across each location. Barnacle houses deployed along the John F. Kennedy Memorial Causeway are labeled as "low" flow. Barnacle houses deployed along the LeClerc family pier are labeled as "high" flow. Navy blue bars represent the exposed treatments, cyan bars represent the protected treatments.

Figure IV.5

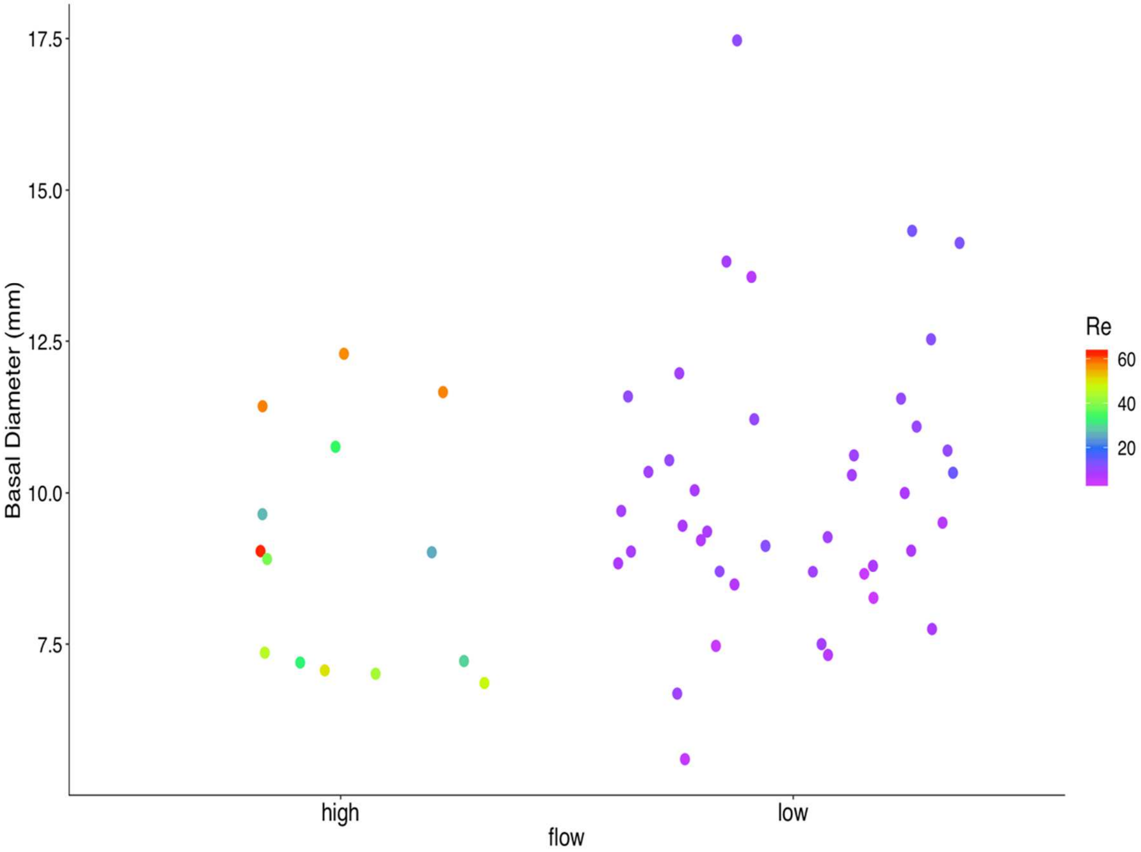


Figure IV.5: Reynolds numbers for exposed treatment barnacles at high and low flow sites. Warmer colors are indicative of higher salinity. Figure was constructed in RStudio version 1.1.456 using the ggplot2 package (Wickham 2016).

TABLES

Table IV.1:

Velocity ($cm{\cdot}s^{-1}$)		
Date	Low	High
13-Jul	3.55	16.92
3-Aug	7.67	8.45
10-Aug	3.36	59.96
Mean	**4.86**	**28.44333333**

RMS Turbulence ($cm{\cdot}s^{-1}$)		
Date	Low	High
13-Jul	3.74	15.73
3-Aug	8.01	7.71
10-Aug	4.25	20.99
Mean	**5.333333**	**14.81**

Table IV.1: ADV data from the John F. Kennedy Memorial Causeway ("Low") and the LeClerc family pier ("High").

Table IV.2:

trt	**-trt**	**diff**	**std error**	**t Ratio**	**Prob> |t|**
lw	lw_ww	3.107	0.633	4.91	<0.0001*
lw	ww	2.285	0.64	3.57	0.0048*
lw	ww_lw	0.656	0.579	1.13	0.6713
lw_ww	ww	-0.822	0.687	-1.2	0.6321
lw_ww	ww_lw	-2.451	0.705	-3.48	0.0063*
ww	ww_lw	-1.623	0.7	-2.33	0.1065

Table IV.2: Reciprocal transplant experiment. Table denotes Tukey HSD test of ramus lengths across treatments.

Table IV.3:

trt	**-trt**	**diff**	**std error**	**t Ratio**	**Prob> |t|**
lw	lw_ww	0.0129	0.0178	0.72	0.8867
lw	ww	-0.0272	0.018	-1.51	0.4403
lw	ww_lw	0.000815	0.0163	0.05	1
lw_ww	ww	-0.0401	0.0193	-2.08	0.1779
lw_ww	ww_lw	-0.0121	0.0198	-0.61	0.9286
ww	ww_lw	0.028	0.0197	1.43	0.4904

Table IV.3: Reciprocal transplant experiment. Table denotes Tukey HSD test of setae lengths across treatments.

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CONCLUSION

Heightened turbidity led to distinct reef communities by altering the sensory regime and facilitating mesopredator release. The effects of turbidity were pervasive across wet and dry years, and demonstrated that salinity and turbidity may act independently. Investigations into the relative effects of Hurricane Harvey on estuarine systems found that, surprisingly, the largest ecological effects of hurricanes may not be the iconic damage from 135mph winds but from the damaged human-ecosystem links that occur as a result. Damaged fishing infrastructure released apex predators from fishing pressure, strengthened top down control, and lead to an increase in the consumption of intermediate consumers and mud crab mesopredators. It should be noted that the antecedent conditions to both 2016 and 2018 were historic floods such that environmental conditions in 2018 resembled that of 2016 (wet year). These results demonstrate the unique ways in which environmental conditions and disturbance modify the strength of top-down control in coastal ecosystems.

Turbidity also affected other components of reef communities that I did not describe within the body of this dissertation. Of note, turbidity appeared to affect parasite prevalence (*Loxothylacus panopaei*) as majority of infected mud crabs were found on turbid reefs. This has also been documented with other Rhizocephalan parasites that infect crabs, such as *Briarosaccas callosus* and their King crab hosts in Southeastern Alaska (Hawkes et al. 1986). In 2016, low turbidity sites had significantly higher numbers of small mud crabs (<10mm in carapace width) while larger mud crabs ($\geq$15mm) exhibited opposite trends in abundance. These dynamics are important for the host-parasite dynamics because smaller crabs, and those with thin cuticles, are the most vulnerable to infections by the parasite due to the limited size of the parasite's stylet. Larger mud crabs, which are typically safe from *L. panopaei* infection, may also be a source of mortality for small mud crabs. However, it is also possible that the removal of larger, potentially more territorial, mud crabs allowed larger gatherings of smaller mud crabs. I hypothesize that the mechanisms behind the changes in parasite prevalence between 2016 and 2018 were due to a combination of abiotic conditions and augmented top-down dynamics. Specifically, I hypothesize that parasite prevalence was affected by salinity, turbidity, and strong top-down control by apex predators. While these may seem contradictory, under "normal" (high) fishing pressure intermediate fish predators are largely released from predation and they themselves become the most abundant (visual) predators. Because fish predators are gape limited (Webb 1986, Persson and Andersson 1996), crabs may reach size refuges at smaller sizes due to the smaller gape of intermediate fish predators. Smaller-gaped fishes are most likely to feed on smaller crabs, such as those most vulnerable to (or infected with) the parasite. Therefore, restoration of apex predators might increase parasite prevalence by consuming both the intermediate fish predators as well as larger mud crabs that the parasites are unable to infect. Furthermore, the non-consumptive effects of fish predators may have reduced crab movements, confining them to small spaces within the reef matrix as refuge from predators and facilitating parasite transmission and the completion of parasite life-cycles.

In addition to differences observed between high and low turbidity, there were noticeable differences in infection rates between years. *Loxothylacus spp.* are sensitive to low salinity and had extremely low infection rates in 2016 (2 infected crabs with visible externae out of 6,207 individuals). After drought conditions persisted throughout the rest of 2016 and into 2017, infection rates increased by over 17x (2016 infection rate: 3.22×10^{-4}; 2017: 5.58×10^{-3}). However, Hurricane Harvey, which caused massive flooding, did not cause a decline in infection rates. In fact, despite salinity values near 0 for several months, infection rates increased even further

(2018: 2.43×10^{-2}). This outcome is puzzling for two reasons: 1) flooding from Harvey took nearly 4-months to rebound and 2) fishing pressure had decreased almost completely, leading to significant increases in the abundance of apex predators and a 45% reduction in mud crab mesopredators. *L. panopaei* infected crabs and their larvae are known to be very sensitive to low salinity (Tindle et al. 2004, Tolley et al. 2006), even dropping the parasite during periods of low salinity. Therefore, a 4-month period would likely see reductions in parasite prevalence. Yet, the change in the density of crab mesopredators remains puzzling. However, the demographics of larger mud crabs (deemed mesopredators $\geq$ 15mm carapace width) and smaller mud crabs (those vulnerable to the parasite) were decoupled, infection rates could increase despite larger crabs becoming less abundant. Thus, despite similarly low salinity values in 2016 and 2018, the disruption in fishing pressure, and ensuing increase in top-down control, may have facilitated the ~75x increase in infection rates.

There is already an established connection between fishing pressure and host-parasite dynamics. Wood and colleagues (2010) found that fishing had strong, negative impacts on parasite abundance. Beyond simply removing fish hosts and their parasites, the consequences of fishing cascades well past the targeted species and their parasites. Fishing also indirectly affects community level-processes by altering food-web complexity, species-interactions, and top-down control. Here, the indirect reinforcement of top-down control from hurricane Harvey is very likely to have affected many host-parasite systems, including *L. panopaei*.

This dissertation has assessed several different mechanisms of community change and turnover across shifts in environmental conditions and after a major large-scale disturbance event. Each chapter focused on a different environmental mechanism, or a combination of two mechanisms, capable of altering the strength and direction of top-down control. The contributions of this work should be incorporated into conservation of estuarine systems and habitats, but should also be explored in terrestrial and aquatic contexts.

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