PREDATOR RISK CUE PROPERTIES AND ENVIRONMENTAL STRESS AFFECT THE IMPORTANCE OF NON-CONSUMPTIVE EFFECTS (NCES) IN SALT MARSH COMMUNITIES

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PREDATOR RISK CUE PROPERTIES AND ENVIRONMENTAL STRESS AFFECT THE IMPORTANCE OF NON-CONSUMPTIVE EFFECTS (NCES) IN SALT MARSH COMMUNITIES

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SUMMARY

In the recent decades, the presence of predators has been repeatedly demonstrated to induce behavioral, morphological, or physiological changes in prey traits (Lima and Dill 1990, Kats and Dill 1998, Ferrari et al. 2010, Bourdeau and Johansson 2012, Clinchy et al. 2013). These predator non-consumptive effects (NCEs) can initiate trophic cascades that indirectly modify community structure (Werner and Peacor 2003, Peacor et al. 2012, Suraci et al. 2016) and ecosystem function (Schmitz et al. 2008, Hawlena et al. 2012). Cascading NCE strength in many studies is similar to or stronger than indirect consumptive effects (CEs) which impact lower trophic levels through regulating intermediate prey density (Preisser et al. 2005). However, the importance of NCEs can be affected by ecological factors, such as habitat features (Trussell et al. 2011, Rasher et al. 2017), prey density (Belovsky et al. 2011, Wada et al. 2015), and resource availability (Wojdak and Luttbeg 2005, Matassa et al. 2016), thus it is still unclear how to predict NCE strength within systems.

Prey reactive range, defined as the maximum distance at which prey detect and respond to predators (Turner and Montgomery 2003), is a driving factor in determining the importance of NCEs. Prey can detect and assess predation threats by using surrounding smells, sounds and sights associated with predation risk (Dusenbery 1992, Munoz and Blumstein 2012). The strength of prey antipredator response depends on prey’s ability to detect predator risk cues and how they respond to risk cues once detected (Weissburg et al. 2014, Mitchell et al. 2017). Prey often react to predators based on the level of perceived threat, in which the intensity of response is associated with the immediacy of predation, in

order to balance the cost of forgoing other fitness-related activities while avoiding predation (Helfman 1989, Chivers et al. 2001). Predator identity and diet-associated cues influence the level of threat encoded by risk cues, which establishes cue salience (Relyea 2003, Scherer and Smee 2016). Yet, environmental conditions can alter prey reactive range by impairing prey's sensory ability to detect predators at low physical stress (Smee and Weissburg 2006, Smee et al. 2008) and physically constraining prey movement at high environmental stress (Menge and Sutherland 1987). Thus, understanding the nature of risk cues used by prey to assess predation threat and how prey reactive ranges change across environmental stress gradients is necessary to elucidate where and when NCEs should regulate top-down predator controls.

Predation events release both predator and prey-associated cues that can be used to evaluate the level of predation threat. I examined the relative importance of chemical cues released from actively foraging predators in larval recruitment processes. In a field experiment, I measured oyster larvae (*Crassostrea virginica*) recruitment to caged tiles and oyster recruit growth rates in the presence of either mud crab (*Panopeus herbstii*) predators actively foraging on juvenile oysters, crushed oyster chemical cues only, or intact juvenile oysters (positive control). I found that oyster recruitment was lower in the presence of actively foraging mud crabs (predator metabolites + crushed oyster cues) relative to recruitment near intact juvenile oysters, but there was no effect on juvenile growth rate. Oyster recruitment was not affected by the presence of crushed conspecific cues alone, but juvenile growth rates were higher when oyster recruits were exposed to these injured prey cues. Oyster larvae avoided chemical cues from either mud crabs or crushed conspecifics when presented separately in lab choice experiments. Thus, injured prey cues alone and in combination with feeding predators cause unique oyster antipredator response in turbulent flow conditions as a result of quantitative and/or qualitative differences in predator risk cues.

Prey species can discriminate among predators using predator-specific cues (Bernot and Turner 2001, Hettena et al. 2014). Tadpole prey can distinguish between more and less risky predators using predator odors and respond to combinations of more and less risky predators with the same intensity as the riskier predator alone (Relyea 2003). I investigated prey behavioral response to two potential predators from an intraguild predation system. Intraguild predator and intraguild prey that compete for a shared prey are predicted to coexist when the intraguild prey is the dominant competitor (Holt and Polis 1997). This suggests that the shared prey species should respond more strongly to intraguild prey, but intraguild predator NCEs may alter the behavior of intraguild prey and their NCEs on the shared prey. I used intraguild predator blue crabs (*Callinectes sapidus*) and intraguild prey mud crabs, which both readily consume mud snails (*Ilyanassa obsoleta*), to examine shared prey response to intraguild predation. In a laboratory experiment, I determined that mud snails only exhibit increased refuge use in response to mud crab cues and at the same intensity when mud crab and blue crab cues paired. However, mud crabs increased their own refuge use when combined with blue crabs. I also assessed if intraguild predator blue crabs could have cascading NCEs on benthic microalgae in the field and the mechanisms that trigger this potential cascade. Cascading blue crab NCEs have significant effects on benthic microalgae community composition but due to the combined effect of mud crab NCEs reducing snail grazing and blue crab NCEs reducing mud crab bioturbation activity. Thus, shared prey species may respond differently to intraguild predator and intraguild prey, but intraguild predator NCEs can have top-down controls on lower trophic levels beyond the intraguild predation trophic link.

Environmental conditions can affect prey's sensory detection of these predator risk cues I found to be important in mediating NCEs. Thus, NCE strength should be strong in sensory environments that promote predator detection, but this requires estimates of prey reactive ranges across environmental gradients. I measured mud crab reactive ranges to blue crabs across a tidal flow regime that varied spatially and temporally in order to determine the extent of blue crab NCEs. Mud crab reactive range was defined as the maximum distance at which mud crab oyster consumption was reduced by blue crab chemical cues relative to a no-blue crab control. Mud crab reactive ranges were large in low flow conditions which resulted in positive blue crab indirect NCEs on oyster survival. Blue crab NCEs were not important in high flow conditions, but physical and sensory stressors imposed by the related flow parameters had contrasting effects on oyster survival. Faster current speeds inflicted physical limitations on mud crab movement which had positive effects on oyster survival regardless of blue crab presence. High sensory stress, as a result of increased turbulent flow, altered the spread of blue crab chemical cues utilized by mud crabs for predator detection, which removed blue crab NCEs. Oyster survival was negatively affected by sensory stress because mud crabs did not respond to blue crab risk cues. Yet, blue crab CEs may increase in importance when mud crab sensory perception is hindered at high sensory stress if blue crab ability to chemically detect prey is not impaired as well.

I assessed how the relative strength of predator blue crab CEs and NCEs changed along the same flow gradient that affected mud crab physical and sensory performance.

Blue crab indirect NCEs were strong at low physical and sensory stress conditions as predicted by estimates of large mud crab reactive range and greater than CE strength. However, NCE strength declined with increasing sensory stress as a result of decreased mud crab ability to detect blue crab predators which resulted in increased importance of blue crab CEs. Thus, in high sensory stress conditions, blue crab indirect CEs had a positive effect on oyster survival that was of similar strength as cascading NCEs in low stress conditions. Neither blue crab indirect CEs or NCEs were important at high physical stress where current speeds benefitted oyster survival by physically constraining mud crab foraging. Understanding how mud crab physical and sensory performance change along a flow gradient led to accurate predictions on how the importance of blue crab CEs vs NCEs varied spatially and temporally within this oyster reef system.

In conclusion, these studies demonstrate the influence of predator risk cue properties on novel predator NCEs in salt marsh communities. These results also reveal the impact of tidal flow on prey physical and sensory abilities which modulated the relative strength of predator CEs and NCEs through distinct mechanisms. Although this work was performed in an aquatic environment, I propose that estimating prey reactive ranges across environmental gradients may provide a useful framework to predict NCEs in both aquatic and terrestrial systems. This framework also will be applicable to systems where prey use sensory modalities other than or in addition to chemosensation, since the environment can attenuate acoustic, mechanosensory, and visual cues as well. Thus, within systems, factors that structure communities can be predicted based on this understanding of how animal’s physical and sensory performance change across environmental stress gradients.

CHAPTER 1. EASTERN OYSTERS USE PREDATION RISK CUES IN LARVAL SETTLEMENT DECISIONS AND JUVENILE INDUCIBLE MORPHOLIGCAL DEFENSES

1.1 Abstract

Predation is an important factor affecting the recruitment of marine benthic populations. Larvae can reduce their risk of predation by avoiding settlement near predators, whereas juveniles can deter predation through induced morphological defenses. We examined the effect of chemical cues from actively foraging juvenile oyster predators, as well as crushed conspecifics alone, on eastern oyster (*Crassostrea virginica*) recruitment and juvenile growth rates using a 2-month field experiment to understand the nature of the predation risk cues used by settling larvae and developing juveniles. We found that oyster recruitment was highest on caged tiles near juvenile oysters, but lowest in the presence of active mud crab predators that produce a combination of predator metabolites and crushed conspecific alarm cues. Chemical cues from crushed conspecifics alone did not affect recruitment in the field, yet oyster larvae avoided either mud crab cues or crushed conspecific cues when presented separately in lab choice experiments. Alarm cues under natural environmental conditions may be either unreliable or not present at detectable enough concentrations to convey the predation threat necessary to deter oyster settlement. Oyster spat growth rates were higher only when newly settled oysters were exposed to crushed conspecifics. Oyster larvae may employ different strategies in response to unique risk cues or predation risk levels by avoiding settlement near actively feeding future predators but increasing growth rates to reach a size refuge in the presence of alarm cues.

Oyster populations could be influenced by these non-consumptive predator effects that impact settlement decisions and juvenile growth patterns.

1.2 Introduction

Predators have large impacts on community structure through consumption of prey. Prey can reduce their risk of predation through plastic antipredator responses (Lima 1998), which also have important non-consumptive effects on communities (Werner and Peacor 2003, Schmitz et al. 2008). Predation events release predator cues and injured prey cues that cause prey to modify behavioral, morphological, or life-history traits (Chivers and Smith 1998, Kats and Dill 1998, Ferrari et al. 2010). However, prey must balance the benefits of predator avoidance with the costs of antipredator defenses and forgoing other fitness-related activities (Lima and Dill 1990). Thus, prey require reliable indications of predation risk and often react to predators in a graded manner dependent on the level of perceived threat (Chivers et al. 2001, Weissburg et al. 2014).

The life cycle in many marine organisms begins with a pelagic larval stage that transitions into a benthic adult form. This recruitment phase is important for sustaining marine benthic populations (Roughgarden et al. 1988, Pineda et al. 2009), but newly settled larvae and juveniles experience heavy losses through predation (Gosselin and Qian 1997). Larvae and juveniles consequently counteract the threat of predation with behavioral and morphological antipredator responses. Larvae avoid settling near predator cues (Ellrich et al. 2015) and juveniles induce morphological defenses to become more resistant to predation (Robinson et al. 2014). Chemical cues associated with predation events mediate these responses but the relative importance of predator versus injured prey cues remains unclear.

Larvae avoid settlement near predator associated cues from both larval and benthic stage predators. Crustacean larvae avoid larval predator cues in the lab (Diaz et al. 1999, Banks and Dinnel 2000) and the field (Welch et al. 1997, Tapia-Lewin and Pardo 2014). Several species of crustacean and fish larvae avoid or decrease settlement in response to chemical cues from predators that only pose a threat to larger juvenile or adult sizes (Johnson and Strathmann 1989, Boudreau et al. 1993, Vail and McCormick 2011, Ellrich et al. 2015). Diet cues contained in predator exudates are often used by prey in combination with predator odor to assess the level of predation risk (Chivers and Mirza 2001, Scherer and Smee 2016). Settling larvae also may utilize diet cues as evidenced in fish larvae that avoid settlement near predatory and non-predatory fish fed fish diets but not herbivorous diets (Dixson et al. 2012).

Chemical cues from injured adult conspecifics also indicate future predator activity to settling larvae and may be used in settlement decisions as well. Many groups of organisms initiate antipredator responses when exposed to chemical cues from injured conspecifics, referred to as alarm cues, to reduce predation risk (Chivers & Smith 1998, Ferrari et al. 2010). There have been no direct tests of the use of alarm cues in larval settlement decisions despite the evidence that settling larvae actively avoid future predators and the natural occurrence of cues from injured prey during predation events. Fish embryos and larvae use injured conspecific alarm cues to learn predation threats (Holmes and McCormick 2010, Atherton and McCormick 2015), which suggest larvae may also have the potential to use alarm cues in habitat selection.

Alarm cues from injured prey are not always the result of a predation event and can be an unreliable cue that does not always induce antipredator responses when present without predator cues (Schoeppner and Relyea 2009, Bourdeau 2010). Conspecifics may release metabolites if injured or stressed by factors other than predation, and so this cue may be only weakly related to predation risk. The larvae of many sessile adult marine species also use adult metabolites as settlement cues because fertilization success and overall survival rates are increased when in aggregations of conspecific adults (Burke 1986, Pawlik 1992, Hadfield and Paul 2001), but it is not clear whether such cues are percieved differently from cues from injured conspecifics as a result of qualitative or quantitative differences, or both. Still, larvae confronted with chemical cues from injured adults must balance the cost of forgoing settlement in a suitable habitat with the benefit of potentially reduced predation risk. Barnacle larvae did not reduce settlement near dogwhelk predators when adult barnacles were present but did when adults were absent, which suggests the positive cue of adult conspecifics outweighs the negative cue of future predators (Ellrich et al. 2016). Yet, this study did not allow dogwhelks to forage on adult barnacles, so it unknown if injured adult alarm cues in combination with predator cues can heighten perceived predation risk enough to reduce settlement by barnacle larvae.

Settlement decisions are not the only way predation risk cues produce non-consumptive effects during recruitment. Newly attached juveniles can undergo morphological changes in response to predation events to decrease predation risk. These inducible defenses are beneficial in environments where the risk of predation is high but unpredictable and defenses are costly (Harvell 1990). In marine invertebrates, shell formation is energetically costly and detracts from other growth parameters. Thus, many gastropod and bivalve species produce thicker shells in response to reliable predation risk cues only (Brookes and Rochette 2007, Sherker et al. 2017). For example, mussels grow thicker shells and are harder to crush when exposed to cues from predators or crushed conspecifics (Leonard et al. 1999, Sherker et al. 2017). Predators fed conspecific diets also induce more types of morphological defenses in snails and oysters compared to predators fed heterospecific diets (Bourdeau 2010, Bible et al. 2017). Studies on morphological induction in juvenile bivalves have been performed either in the lab (Leonard et al. 1999, Newell et al. 2007) or using juveniles from the field that settled under unknown predator risk levels (Johnson and Smee 2012, Sherker et al. 2017), so the importance of predator presence at the time of settlement in these responses is undetermined.

In this study, we used the eastern oyster (*Crassostrea virginica*) to examine settlement decision making in larvae in response to chemical cues associated with predation events in natural and controlled settings, and to determine whether risk cues modify morphology immediately post settlement. Oysters are gregarious settlers that positively respond to chemical cues from conspecific adults in the lab (Tamburri et al. 1992, Tamburri et al. 1996) and the field (Smee et al. 2013). These aggregations of adult oysters form large reefs that provide ecosystem services and offer refugia for a wide range of species (Newell 2004, Grabowski et al. 2012). Juvenile oyster spat respond to chemical cues from predators by increasing shell mass and shell crushing force (Robinson et al. 2014, Scherer et al. 2016). Notably, the mud crab, *Panopeus herbstii,* that lives within oyster reefs and is a voracious predator of juvenile oysters, induces morphological shell responses (Johnson et al. 2014, Scherer and Smee 2017). However, oyster larvae settlement response to negative chemical cues has not been experimentally examined. The only experiments with bivalves have been in mussel species, which found that mussel larvae avoid predator cues in the lab (Morello and Yund 2016) but show either avoidance or no response in settlement near predators in the field (von der Meden et al. 2015, Ehlers et al. 2018).

We determined the effect of future predation risk on oyster recruitment using a 2-month field study and predicted that oyster larvae would avoid settling near chemical cues typical of those released from actively foraging juvenile predators (i.e. predator metabolites and cues from damaged conspecifics). We also measured shell growth rates in the newly settled oyster spat to test if the chemical risk cues induced morphological responses. Our goal was to specifically examine the role of damaged conspecific metabolites by presenting them with and without predator metabolites. We hypothesized the potential ambiguity of cues from injured conspecifics in natural environments would make this a less effective cue in the absence of cues from predators themselves. We assessed the behavioral response of oyster larvae to individual cues in still-water choice experiments to provide additional evidence regarding the role of single versus multiple cues in mediating settlement and post-settlement responses.

1.3 Methods

1.3.1 Animal collection and maintenance

All crab species and oysters used in both experiments were collected by hand from oyster reefs located within Wassaw Sound (Savannah, GA, USA) and associated tributaries. Collections were done under the approval of a scientific collection permit issued by the Georgia Department of Natural Resources. For the field recruitment experiment, animals were held in separate flow-through systems at the Skidaway Institute of Oceanography prior to their deployment. For the laboratory choice experiments, animals were transported to Georgia Institute of Technology (GT) and each species was separately housed in 28-L aquaria. Aquaria were filled with artificial seawater maintained at conditions similar to the collection site (25 ppt salinity, 22-24°C water temperature). Eyed, pediveliger oyster larvae were obtained from Auburn University Shellfish Laboratory (AUSL) oyster hatchery and shipped overnight to GT. Larvae were maintained in aerated sterile artificial seawater at conditions that matched AUSL conditions (20 ppt salinity, 22-24°C water temperature) and used in choice experiments within 2 days.

1.3.2 Field recruitment experiment

We monitored recruitment onto tiles placed in the field to determine the effect of predation risk cues on larval settlement decisions and juvenile growth rates. The field experiment was performed on intertidal mudflats at Priest Landing, Skidaway Island, GA, which is located in the Wilmington River adjacent to Wassaw Sound. This site is characterized by loose oyster clusters and patch oyster reefs bordered by *Spartina alterniflora* salt marshes. Relative to other sites in Wassaw Sound, flow velocity is moderate at this site (8-10 cm s^{-1}) but with high turbulent kinetic energy (TKE) (0.3×10^{-3}-0.65×10^{-3} m^2 s^{-2}) (Wilson et al. 2013).

Cages were used to both restrict predator access to recruitment tiles and maintain a constant source of cue treatment. Cages had an interior tile enclosure (15 cm dia) that was contained within, but separated with mesh from, an exterior treatment enclosure (30 cm dia) (Figure 1.1). Cages were constructed out of 1 cm^2 vexar mesh and had a 15 cm height.

Slate tiles (10 cm x 10 cm) were provided as a settlement substrate for oyster recruitment and placed within the interior tile enclosure. Tiles were attached to 5 cm long PVC poles so that they could be staked into the mud and raised slightly (ca. 2 cm) above the substrate to limit sedimentation. The exterior treatment enclosure contained one of four cue treatments: crushed juvenile oysters, whole juvenile oysters, mud crabs foraging on crushed juvenile oysters, and crushed dead oyster shells. This set of cues reflects that predation in natural conditions will result in the release of both injured conspecific metabolites and predator cues whereas conspecific metabolites can be released as a result of other injuries or stress. Whole oysters are a positive control and crushed shells a control for the experimental treatment involving crushed oysters.

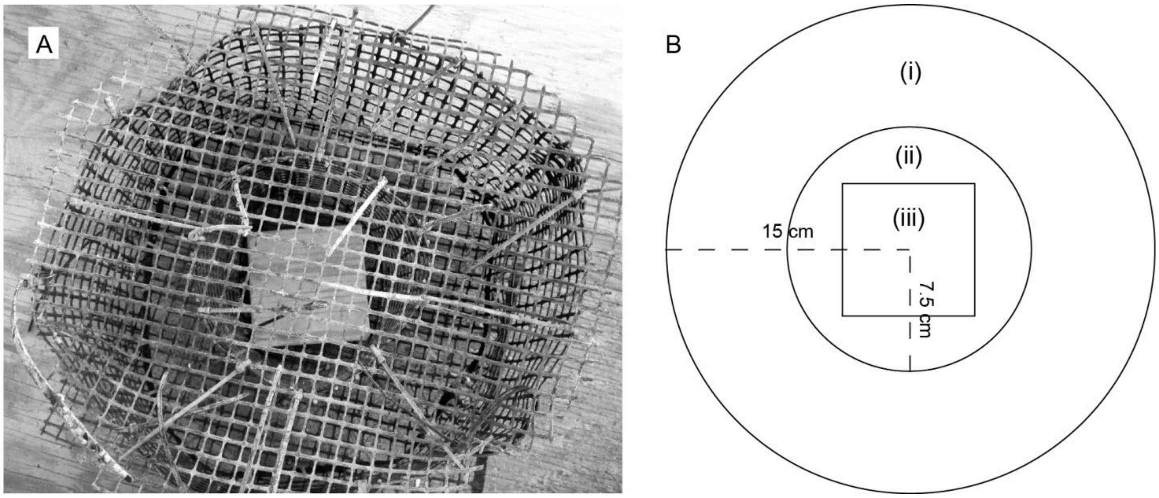

Figure 1.1 Field recruitment cage setup. (A) Top view of recruitment cage. (B) Diagram of recruitment cage showing (i) exterior treatment enclosure that contained either mud crabs foraging on crushed juvenile oysters, crushed oysters, whole oysters, or crushed oyster shell control, (ii) interior tile enclosure, and (iii) the recruitment tile (10 cm x 10 cm).

Five mud crabs (*Panopeus herbstii*, carapace width: 20-25 mm) were added to the exterior treatment enclosure for the mud crabs foraging on crushed oyster treatment. Mud crabs were fed oyster flesh *ad libitum* for 48 hours prior to the start of the experiment. Mud crabs in the cages were fed 15 crushed oysters (hinge length: 20-40 mm) every 3-4 days throughout the experiment to equal a predation rate of 1 oyster per day per crab. This rate was chosen based on preliminary laboratory feeding trials and equivalent to consumption in other field trials (Hill and Weissburg 2013b, Pruett and Weissburg 2018). Any missing or dead mud crabs were replaced during semiweekly checks. The crushed oyster treatment and whole oyster treatment also received 15 oysters each that were replaced each time the mud crabs were fed. Oysters were crushed by striking the oysters with the blunt end of an oyster knife several times and scoring the flesh to simulate crab predation. Dead oyster shells in the control treatment were obtained from Priest Landing, crushed in the same manner as previously described, and replaced at the same intervals as the other treatments.

Cages were placed on mudflats in between naturally occurring intertidal oyster patch reefs. Treatments were deployed in blocks and cages were at least 1.5 m away from oyster reefs and each other. Blocks were at least 15 m apart with 9 blocks total. Photographs were taken of each tile approximately every week in order to assess recruitment processes throughout the experiment. The experiment began in early June 2017 and ended 55 days later in late July.

The total number of oyster recruits on each tile were counted at the end of the experiment with the aid of a dissecting microscope, when we also measured mortality as the number of scars on each tile. Weekly photographs were analyzed to determine the number of new recruits in each weekly cohort. Additionally, the final shell area of oyster recruits that arrived in the cohorts between day 20 and 33 was measured using ImageJ software (version 1.51, National Institutes of Health, USA). Growth rate was then calculated as area/cohort age (day 55-cohort arrival day). We used a two-way ANOVA to assess differences in total recruitment between cue treatments, with cue treatment and block as effects. The data were square-root transformed to meet homogeneity of variances assumptions. An ANCOVA was used to analyze for an effect of cue treatment on mortality using the total number of oyster recruits as a covariate. Block did not have a significant effect on mortality so was dropped from the analysis and all data were pooled. We used a mixed-effects model fit by REML to determine differences in oyster growth rate, with cue treatment and cohort arrival day as fixed effects and block as a random effect. The growth data were square-root transformed to meet normality assumptions.

All analyses were performed in R version 3.4.2 (R Core Team 2017). The lme4 package (Bates et al. 2015) was used for mixed-effects model analysis and degrees of freedom and *P* values were based on Kenward-Roger approximations using the lmerTest package (Kuznetsova et al. 2017). Post hoc comparisons were performed using the lsmeans package (Lenth 2016).

1.3.3 Laboratory choice experiments

We observed larval behavioral responses when exposed to individual cues in choice assays to clarify the roles of these chemicals and better understand how separate cues affect recruitment in the field. Laboratory experiments were conducted at GT using assay chambers that were designed based on Morello and Yund (2016). Assay chambers consisted of two 3.75 cm long x 0.1 cm wide x 0.4 cm deep channels connected by a center well (0.5 cm dia. x 0.4 cm depth) and with two opposite end wells (Figure 1.2). These assay chambers were milled into a 1.27 cm thick acrylic plastic sheet and the total volume of the chamber was 12 mL. The center well served as the starting position for the oyster larvae. The end wells, which were 3.75 cm dia. and 0.8 cm deep with a rounded bottom, contained the chemical cues. Dye studies indicated that the channel within 0.5 cm of the center chamber remained free of cues for the duration of the experiment. Therefore, we defined the region within 0.5 cm of the center well edges on each side as the “no-choice” zone using lines marked on the underside of the acrylic sheet.

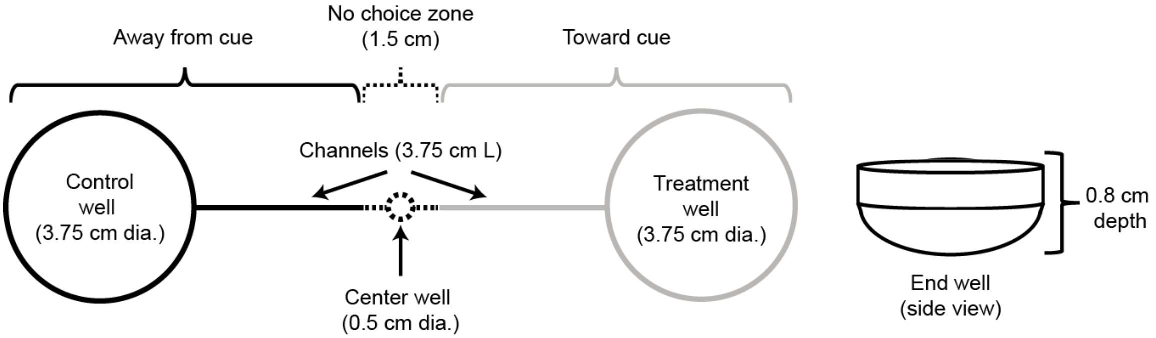

Figure 1.2 Diagram of assay chamber (based on Morello and Yund 2016). A single pediveliger oyster larvae was pipetted into the center well and cue-conditioned seawater (see text for treatments) was injected into the randomly chosen right or left end well (shown as right well above). The location of the oyster larvae after 30 minutes was recorded as either away from cue, no choice, or toward cue.

Larvae were given a choice between seawater and one of several types of cues that were used in the field experiment. These cues were: seawater conditioned with whole adult oysters, crushed adult oysters, metabolites from mud crabs or non-predatory crabs. Seawater conditioned with whole adult oysters was expected to attract oyster larvae as indicated by both the field experiment and previous work (Tamburri et al. 1992, Barnes et al. 2010). The field results were ambiguous regarding the salience of cues from crushed adult oysters because alarm cues did not deter larval settlement but did induce a growth response in recently settled juveniles (see below). Mud crab conditioned seawater was anticipated to deter oyster larvae based on juvenile induction responses (Johnson et al. 2014, Scherer and Smee 2017), but seawater conditioned with hermit crabs (*Clibanarius vittatus*) was included to discern if oyster larvae can distinguish between metabolites produced by predatory vs. non-predatory crabs fed natural diets. Mud crabs were fed oyster flesh *ad libitum* for 48 hours prior to cue-conditioning while hermit crabs were fed commercial algae wafers. The treatment water was made by bathing either 2 crushed adult oysters (hinge length: 60-70 mm), 2 whole adult oysters (hinge length: 65-75 mm), 1 mud crab (carapace width: 29-30 mm), or 1 hermit crab (carapace width: 13-15 mm) in 500 mL of sterile artificial seawater (20 ppt salinity, 22-24°C water temperature) for 8 hours. The crushed oyster treatment was prepared in the same fashion as the field experiment using the blunt end of an oyster knife. Organisms were removed after conditioning and water was passed through a 6 μm filter. Cue-conditioned seawater was then used immediately in choice experiments. Fresh batches of cue-conditioned seawater were made using different organisms for each day of trials.

Choice experiment trials were conducted under infrared (IR) illumination to eliminate the potential for phototaxis (Wheeler et al. 2017). Assay chambers were first filled with 8 mL of sterile artificial seawater. Then, a single eyed, pediveliger oyster larvae was added to the center well and confirmed to be actively swimming. One well was randomly predetermined as the treatment well and 1 mL of cue-conditioned seawater was slowly injected into the bottom of the well using a 1 mL syringe with a 26-gauge needle. The same volume (1 mL) of sterile artificial seawater was then injected in the opposite well. The position of the larvae was recorded after 30 minutes as away from treatment well, no choice (within the “no-choice zone” defined above), or toward treatment well (Figure

1.2). Trials were ended at 30 minutes because dye visualization revealed the dye had diffused to the borders of the no-choice zone by this time. One trial of each treatment cue, including a sterile seawater control, was run simultaneously as a block. Each assay chamber was rinsed thoroughly with distilled water after every trial. Blocks were repeated 17 times across 2 days with the same batch of larvae.

The choice response of larvae to move away or toward a cue treatment was tested against a random response prediction (1:1 ratio) to determine if larvae were attracted or deterred by a given cue treatment. Individual exact one-sided binomial tests were performed for choice experiments with cue treatments that were predicted to elicit a directional response in larvae (see above; crushed adult oyster cue, mud crab cue, whole oyster cue) and two-sided binomial tests were used for choice experiments for cue treatments with no predicted response (hermit crab cue, seawater control).

1.4 Results

1.4.1 Field recruitment experiment

Oyster recruitment on caged tiles depended on cue treatment (Figure 1.3; $F_{3,24}$ = 3.04, p = 0.048) with the block effect showing marginal significance ($F_{8,24}$ = 2.25, p = 0.06). Oyster recruitment was 170% higher on tiles surrounded by whole juvenile oysters (27 ± 7 recruits per tile; mean ± SE) compared to tiles surrounded by mud crabs foraging on crushed oysters (i.e. predator metabolites and alarm cue; 10 ± 3 recruits per tile). Recruitment on tiles surrounded by either crushed juvenile oysters (alarm cue only) or control crushed oyster shell was intermediate between these two treatments at 20 ± 3 recruits per tile and 18 ± 5 recruits per tile respectively.

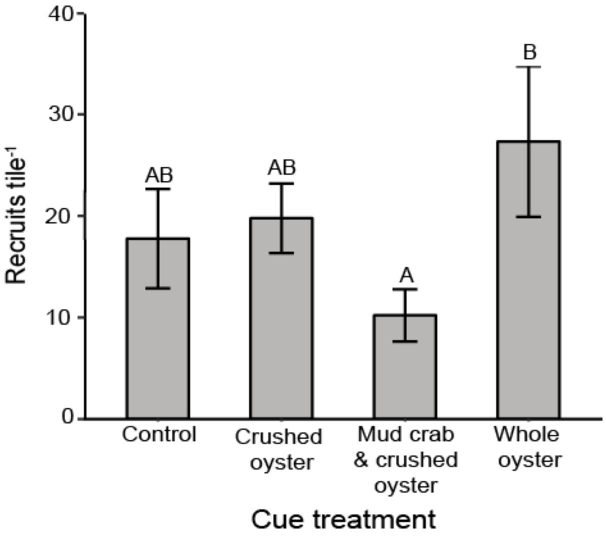

Figure 1.3 The number of oyster recruits (mean ± SE) on caged tiles surrounded by different cue treatments in the field after 8 weeks (n = 9). Different letters denote means that are significantly different based on Tukey post hoc tests ($p < 0.05$).

We monitored new oyster recruitment to caged tiles approximately weekly and observed two major recruitment events prior to day 26 and day 55 (Figure 1.4). The pattern occurring during each pulse was consistent with the overall trends obtained from the counts at the end of the experiment. Generally, oyster recruitment each week was highest on the tiles surrounded by whole oysters, and during the major recruitment events averaged 13 ± 2 new oyster recruits per tile per week. Weekly recruitment was lowest on tiles surrounded by mud crabs foraging on crushed oysters and averaged 6 ± 1 new recruits per week during the major recruitment events. Recruitment during the major recruitment events to tiles surrounded by control crushed oyster shells or crushed adult oysters was not consistently high or low relative to the other treatments and averaged about 10 ± 2 new oyster recruits during these events per week (Figure 1.4).

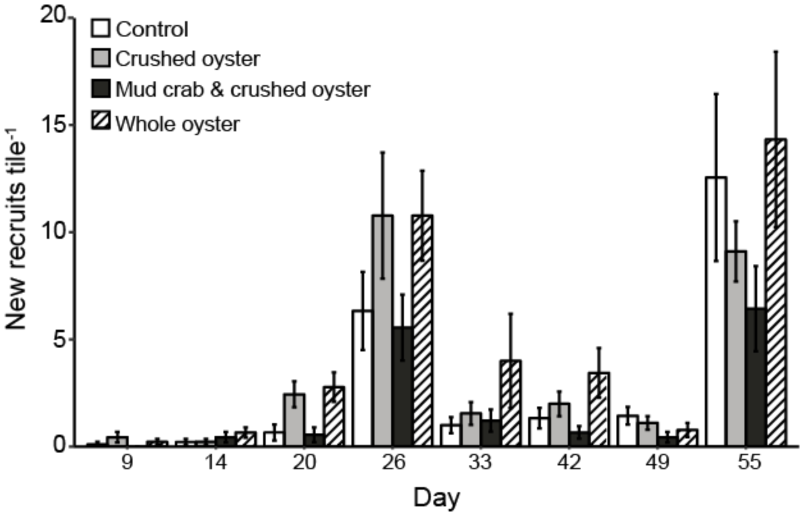

Figure 1.4 The number of new oyster recruits (mean ± SE) on caged tiles surrounded by each cue treatment at different days during the 55-day field experiment.

Oyster recruit mortality was determined as the number of scars on the tiles at the end of the experiment and was not affected by cue treatment ($F_{3,28}$ = 0.41, p = 0.75). However, the covariate significantly affected number of final recruits ($F_{1,28}$ = 23.67, $p < 0.0001$) and, thus, mortality seemed to be positively density-dependent. There was not a significant interaction between cue treatment and the covariate ($F_{3,28}$ = 0.44, p = 0.73).

Growth rate for the oyster recruits that arrived between days 20 and 33 (and survived until the end of the experiment) was significantly affected by cue treatment ($F_{3,174.1}$ = 4.88, $p < 0.01$) and cohort arrival date ($F_{2,171.8}$ = 15.18, $p < 0.0001$). There was no significant interaction between cue treatment and cohort arrival date ($F_{6,172.2}$ = 1.15, p = 0.33). Oyster recruits on tiles surrounded by crushed adult oysters on average gained shell area 47.5% faster than oyster recruits exposed to the other cue treatments (Figure 1.5). Also, oyster recruits in the older cohorts (arrival day 20 and 26) had higher growth rates than the youngest cohort (arrival day 33).

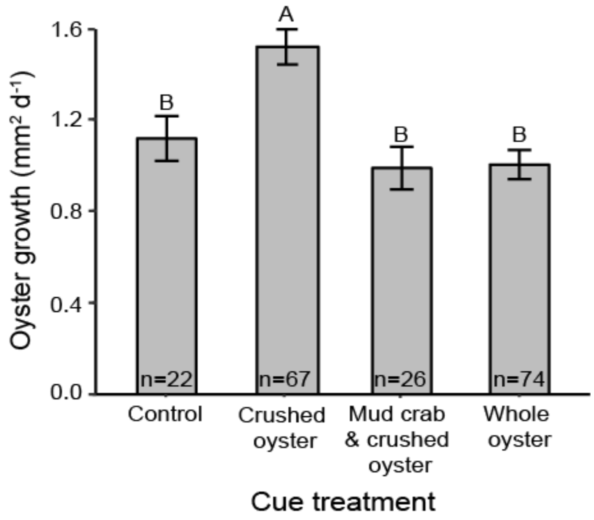

Figure 1.5 The average growth rate (± SE; mm^2 d^{-1}) of oyster recruits on caged tiles surrounded by different cue treatments in the field. Different letters denote means that are significantly different based on Tukey post hoc tests ($p < 0.05$).

1.4.2 Laboratory choice experiments

Oyster larvae moved away from wells that contained seawater conditioned with either crushed adult oysters or mud crabs with significantly higher frequencies than a null 1:1 response ratio (Exact one-sided binomial test; crushed oyster, $p < 0.01$; mud crab, $p = 0.01$) (Figure 1.6). In contrast, oyster larvae moved toward wells with seawater conditioned with whole adult oysters (Exact one-sided binomial test; $p = 0.01$) (Figure 1.6). Oyster larvae showed no aversion or attraction to wells that contained hermit crab conditioned seawater or no cue seawater control (Exact two-sided binomial test; hermit crab, $p = 1.0$; no cue, $p = 0.69$) (Figure 1.6).

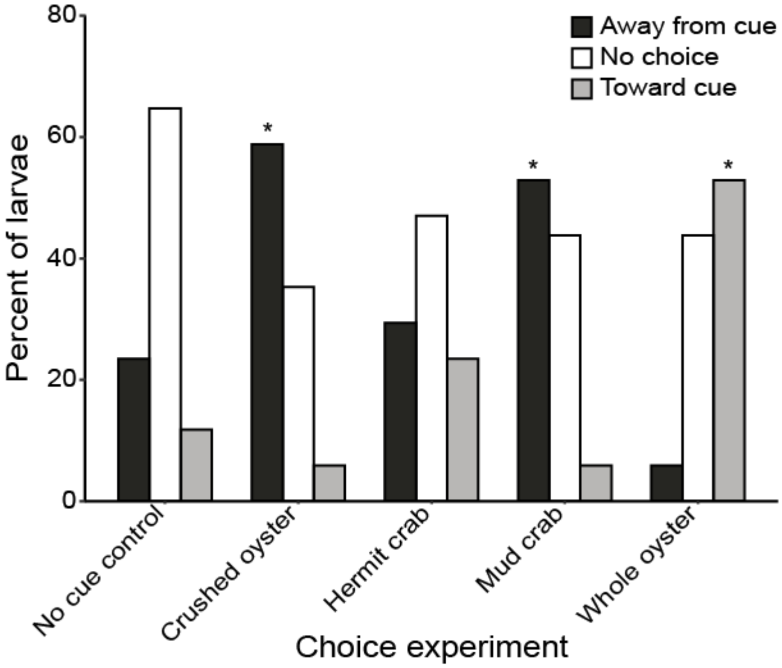

Figure 1.6 The percent of larvae that moved away from cue (black), remained in center of assay chamber (no choice; blank), or toward cue treatment (gray) for each choice experiment which presented larvae with cue-conditioned seawater versus seawater control (n = 17). Asterisks denote that oyster larvae moved away from or toward cue treatment with significantly higher than expected frequency relative to a 1:1 ratio ($p < 0.05$).

1.5 Discussion

Mortality due to predation is high during marine invertebrate recruitment (Gosselin & Qian 1997) but larvae can reduce their risk of predation by avoiding settlement near predation risk cues (Ellrich et al. 2015, Ehlers et al. 2018). We found that oyster recruitment in our field experiment was reduced only when chemical cues from both foraging predators and crushed conspecifics were present and there was no effect of conspecific alarm cues alone. Oyster recruitment was highest in the presence of juvenile oysters, but this positive effect was mitigated by the combined negative effects of mud crabs foraging on crushed oysters (Figure 1.3). Weekly recruitment patterns also showed that the number of oyster recruits always was lowest near the combination of predator and injured prey cues (Figure 1.4). Oyster larvae were deterred by crushed oyster chemicals in the absence of flow and background odors in the lab choice experiment (Figure 1.6), but these alarm cues by themselves were insufficient to affect recruitment under natural conditions.

Several taxa of larvae avoid future predator-associated cues during settlement (Ellrich et al. 2015, Benkwitt 2017, Ehlers et al. 2018) but we believe this is the first demonstration that oyster larvae also are deterred by predation risk cues. Further, reduced settlement in the field required a combination of injured conspecific and predator cues even though both seem aversive in the laboratory assays. Due to the high cost of delayed metamorphosis (Pechenik et al. 1998, Bishop et al. 2006), oyster larvae may require a more reliable indication of high predation risk to avoid settlement than alarm cues encode, which only signal prey are being damaged but not necessarily by a foraging predator. Generally, more costly defenses, such as morphological changes, are not induced by alarm cues alone, but require cues from predators fed conspecific prey (Schoeppner and Relyea 2009, Bourdeau 2010). It is not clear if this is because predator diet cues provide qualitatively different information that conveys greater risk than alarm cues or the quantitative concentration of both cues work additively (Scherer & Smee 2016). Thus, settlement in our field experiment was reduced either because the combination of mud crab and crushed conspecific cues produced a greater concentration of predation risk cues or the addition of predator cues with the alarm cue encodes a higher level of predation threat. The effect of crushed conspecific cue in the lab may reflect high and persistent alarm cue concentrations due to the lack of flow and background chemical noise. Waterborne cues are mixed by turbulent flow in the field which creates filaments of cues with variable concentrations that larvae transiently encounter (Koehl and Hadfield 2010) and may not be present in high enough concentrations to be a reliable signal for predation in the field in the absence of predator metabolites.

As in other systems, predator identity and diet affect the salience of predator-derived cues (Weissburg et al. 2014, Scherer and Smee 2016) for oysters. Oyster larvae were seemingly able to distinguish between predatory and non-predatory crabs in the lab choice experiments. Larvae were about equally as likely to move away or towards seawater conditioned with hermit crabs (Figure 1.6), which do not represent a future threat to oysters because they are primarily grazers and have weak claws that are unable to crush oyster shells (Williams 1984). It is unclear if oyster larvae encoded this difference in risk by using predator-specific chemical cues or diet-associated cues since hermit crabs were fed an algae diet. As previously mentioned, fish larvae interpret risk during settlement decisions using dietary cues and avoid chemical cues released by either predatory or non-predatory fish fed fish diets (Dixson et al. 2012). Juvenile oysters also only induce production of stronger shells when exposed to blue crabs fed fresh oyster flesh and do not respond to starved blue crabs or blue crabs fed aged oyster flesh (Scherer et al. 2016, Scherer et al. 2017), which suggests that oyster larvae may use dietary cues as well. Further research is needed to determine if oyster larvae can identify and respond to other predators during settlement decisions and if risk is encoded through predator diet. Regardless, these results show that consumption of oyster flesh is at the very least necessary for larvae to interpret metabolites released from predators as indicative of predation risk.

Oyster larvae that settled near crushed conspecifics grew faster (i.e. shell area grew more quickly) than any of the other treatments despite a lack of reduced recruitment (Figure

1.5). This may reflect a less costly strategy to respond to predation risk when it is perceived as less certain. Frog tadpoles only increase hiding behavior in response to crushed conspecifics but decrease activity and alter morphology in response to the riskier cue of an actively foraging predator (Schoeppner & Relyea 2009). Oyster larvae may avoid settling near actively feeding future predators that convey immediate risk but disregard ambiguous conspecific alarm cues when making settlement decisions, while still defending themselves at least partially once settled. The faster shell growth in response to conspecifics may be a generalized response to reach a size refuge more quickly. Oysters may utilize inorganic calcium carbonate that is energetically inexpensive in order to rapidly reach larger sizes more resistant to predation (Scherer et al. 2018).

The growth rate increase in the presence of crushed oysters may not reflect an antipredator response but may be the result of increased dissolved nutrients in the water column that could benefit growth in several ways. First, crushed oysters leak dissolved organic matter, such as amino acids (Carr et al. 1996, Zimmer et al. 1999), that oysters can uptake directly and potentially use to supplement metabolism and enhance growth (Ferguson 1982, Langdon and Newell 1996, Wendt and Johnson 2006). Secondly, the dissolved organic matter leaked from crushed oysters may be rapidly mineralized by bacteria which provides a secondary source of nutrition for oyster spat leading to increased growth (Crosby et al. 1990). Although either dissolved nutrients or bacteria may be utilized by bivalves as a dietary supplement it is still unclear if this benefits shell growth, especially under field conditions (Knauer and Southgate 1999). Lastly, the increase in food availability may stimulate feeding activity (Higgins 1980), but little is known about chemical feeding stimulants in suspension-feeders and no isolated waterborne compounds have been shown to increase feeding rates (Ward and Targett 1989, Tamburri and ZimmerFaust 1996).

The combination of mud crab and injured oyster metabolites had no effect on shell growth despite previous lab studies that show both mud (Scherer & Smee 2017) and blue crab predator cues (Robinson et al. 2014, Scherer et al. 2016) increase shell size. However, other studies have shown that oyster spat can increase shell strength without noticeable changes in shell size or weight. Predator cues from mud crabs may increase the proportion of energetically costly organic shell material to add strength independent of shell mass (Newell et al. 2007, Robinson et al. 2014). Thus, at high levels of predation risk encoded by actively feeding mud crab predators, juvenile oysters may invest in stronger organic shell material that is more resistant to crushing compared to cheaper inorganic shell content that is more beneficial for overall shell growth at moderate risk levels conveyed by alarm cues alone (Scherer et al. 2018). Direct measurements of shell strength are required to evaluate fully the responses of oysters, and perhaps other bivalves, to aversive cues.

Inducible morphological defenses are costly and thus may not be produced when resources are scarce (Harvell 1990). Recently settled oysters may have been resource limited in our field experiment resulting in a lack of growth response in the combination mud crab and crushed oyster cue treatment. Yet, 3-week old oysters induced the same intensity of morphological responses to mud crab predators under both low and high resource availability in an 8-week laboratory experiment (Scherer & Smee 2017), which suggests oysters may respond morphologically to predation risk even when resources are limited. The duration of our field experiment may not have been long enough to detect morphological changes in the mud crab with crushed oyster treatment (i.e. only 3 to 5-

week exposure) or perhaps juvenile oysters must reach a certain point in development before changes in shell structure due to predation risk occur.

Predation has a strong influence on oyster recruitment and population structure (Knights et al. 2012, Johnson et al. 2014, Carroll et al. 2015). Our study demonstrates that an important juvenile oyster predator may also affect population densities through non-consumptively deterring oyster larvae settlement. Additionally, for the oysters that still settle in the presence of predators they may alter their shell morphology to resist predation attempts (Newell et al. 2007, Robinson et al. 2014, Scherer et al. 2016). These induced morphological changes may come at the cost of reduced fecundity (Harvell 1990, Johnson & Smee 2012, Scherer et al. 2018), which will further modify oyster populations. Thus, consumptive and non-consumptive predator effects at each life stage of the oyster need to be considered to understand the persistence of this foundation species.

CHAPTER 2. CASCADING PREDATOR NON-CONSUMPTIVE EFFECTS IN A FOUR-LEVEL FOOD CHAIN ALTER BENTHIC MICROALGAE COMMUNITY COMPOSITION BUT NOT BIOMASS

2.1 Abstract

Predators alter prey behavior and phenotype, which can influence community structure and function through cascading non-consumptive effects (NCEs). Most empirical examples of cascading NCEs come from simple, linear three-level food chains that lack the inherent complexity of many ecological communities. Top predators in four-level food chains are well-known to have cascading consumptive effects on basal resources, but their NCEs have been less considered, especially in conjunction with the NCEs of intermediate predators. We examined predator NCEs in a four-level food chain that is further complicated by the presence of intraguild predation. In a lab experiment, we examined the NCEs of an intraguild predator (blue crabs) and intraguild prey (mud crabs) on a shared prey species (mud snails) when presented separately and together. We found that NCEs from mud crabs, but not blue crabs, increased refuge use by mud snails. Mud snail refuge use was the same intensity when both blue crab cues and mud crabs were present as to mud crabs alone, but the presence of blue crabs caused mud crabs to utilize refuges. We also examined cascading effects in the field by assessing the influence of these interactions on benthic microalgae in intertidal mudflats. Total benthic microalgae biomass, as approximated by chlorophyll *a* concentration, was not affected by any combination of snails, nonlethal mud crabs, or blue crab cues. Yet, chlorophyll *b* concentration was higher

when both nonlethal mud crabs and blue crab chemical cues were present with snails. Thus, the interaction of suppressed snail foraging due to mud crab NCEs and decreased mud crab activity as a result of blue crab NCEs may impact competitive outcomes within microalgae communities. Cascading NCEs can persist in complex, four-level food chains and regulate primary producer dynamics.

2.2 Introduction

Predators regulate community structure via top-down controls that propagate throughout food webs (Ripple et al. 2016). Trophic cascades, which are indirect effects of top predators on lower trophic levels, can be initiated by either consumption of intermediate prey (consumptive effects; CEs) or changes in prey traits in response to predation risk (non-consumptive effects; NCEs) (Schmitz et al. 2004, Peckarsky et al. 2008). For example, predatory spiders in old field communities can either decrease grasshopper density through consumption, which increases grass biomass, or induce a grasshopper behavioral shift in foraging preference, which benefits grasses but reduces herb biomass (Schmitz 1998, Schmitz and Suttle 2001). Spider NCEs, compared to their CEs, produce contrasting effects on community structure and ecosystem function (Schmitz and Suttle 2001, Schmitz 2008). Cascading NCEs, or trait-meditated indirect interactions (TMIIs), are documented in a diverse range of systems and often measured to be equal to or greater than predator CEs (Werner and Peacor 2003, Preisser et al. 2005). Thus, considering the mechanism through which predators generate trophic cascades is necessary to understand community dynamics.

Most empirical examples of cascading NCEs arise from simple, linear food chains with few species. Limited evidence from community-level investigations in tritrophic systems demonstrates that top predator NCEs can change primary producer composition and abundance (Peacor et al. 2012), but with context-dependency (Schmitz 2008, Forbes and Hammill 2013). Top-down CEs are well-known to transfer through four-level food chains by reducing intermediate prey populations and releasing herbivores from predation pressure (Carpenter et al. 1985, Estes et al. 1998, Dyer and Letourneau 1999, Ritchie and Johnson 2009). Despite often consuming relatively few prey, top predators generally have disproportionately large effects on community structure, suggesting NCEs are important in four-level trophic cascades (Ritchie and Johnson 2009). Top predator NCEs from vocalization playbacks in a coastal island community caused racoons to alter foraging activities in intertidal habitats which enhanced intertidal crab prey abundance but negatively affected the crab’s competitor and prey (Suraci et al. 2016). It is unclear if this top predator cascading NCE was due to weakened racoon CEs and/or NCEs on intertidal crab prey. Top predator NCEs can decrease intermediate predator foraging, which decreases intermediate predator CEs, but also decrease intermediate predator activity, which decreases intermediate predator NCEs. Thus, how top predator NCEs mitigate intermediate predator NCEs and CEs depends on the intermediate predator behavioral response to top predator cues, which is not always apparent.

Food webs are further complicated by the prevalence of omnivory, such as intraguild predation, which may modify cascading interactions (Polis and Holt 1992, Arim and Marquet 2004). Intraguild predation involves a predator and prey that also compete for a shared resource (Polis et al. 1989). Intraguild prey respond to NCEs from their intraguild predator (Hill and Weissburg 2013a), but also the shared prey may respond to NCEs from both the intraguild predator and intraguild prey resulting in complicated indirect effects on basal resources. Prey have been shown to assess predator identity using predator-specific risk cues and tailor behavioral (Bernot and Turner 2001) or morphological antipredator response (Hoverman and Relyea 2012) so best protected against a specific predator hunting style. Yet, predator richness also increases antipredator behavioral responses relative to a single predator species at a similar density (Byrnes et al. 2006, Steffan and Snyder 2010, Reynolds and Bruno 2013). Thus, in intraguild predation systems, shared prey may have non-additive responses to multiple predator NCEs due to facilitation or interference of antipredator response to the presence of unique predators (Sih et al. 1998).

We investigated the effect of top predator cascading NCEs on primary producer communities using a 4-level food chain found on intertidal mudflats. Benthic microalgae (BMA) are the significant contributors to primary production in mudflats (MacIntyre et al. 1996). Large, motile diatoms often form golden-brown mats on the surface of mudflats limiting growth of other less motile microalgae shaded beneath (Underwood and Kromkamp 1999, Sullivan and Currin 2000). Mud snails (*Ilyanassa obsoleta*) are highly abundant mudflat deposit feeders that selectively graze on motile diatoms (Pace et al. 1979, Connor and Edgar 1982, McLenaghan et al. 2011). Mud crabs (*Panopeus herbstii*) are small xanthid crabs that commonly live within oyster reefs, but also inhabit shallow dug out burrows in mudflats (Williams 1984, Silliman et al. 2004). BMA communities can be negatively affected by mud crab burrowing activities through direct physical disturbance (Armitage and Fong 2006). Blue crabs (*Callinectes sapidus*) are highly mobile, opportunistic omnivores that regulate the abundance and distribution of many benthic organisms, including mud crabs, across salt marsh habitats (Virnstein 1977, Micheli 1997, Silliman and Bertness 2002, Hill and Weissburg 2013a). Blue crabs and mud crabs have many common overlaps in prey species, including mud snails (Laughlin 1982, Silliman et al. 2004), and thus engage in intraguild predator-prey interactions (Hill and Weissburg 2013a, Byers et al. 2017). Chemical cues from blue crabs suppress mud crab foraging activity and increase refuge use (Hill and Weissburg 2013b, Weissburg and Beauvais 2015, Belgrad and Griffen 2016). Mud crab chemical cues decrease snail grazing in microcosm experiments, which enhances BMA biomass (Premo and Tyler 2013).

The goals of this study were to examine the potential for interactive effects of blue crab and mud crab NCEs on mud snail behavior and how these interactions may indirectly mediate BMA communities. First, we investigated the effect of separate or combined blue crab and mud crab presence on mud snail refuge use in a laboratory experiment. Next, we assessed the NCEs of blue crab chemical cues on BMA communities via modifications of mud crab-snail interactions in the field (Figure 2.1). We predicted that in the presence of mud crabs only, snails would reduce grazing on BMA, but mud crab bioturbation may offset any positive indirect NCEs on BMA (Figure 2.1.b). Based on the lack of response to blue crabs in the lab, snails grazing was not expected to change in the presence of blue crab chemical cues in the field (Figure 2.1.c). We anticipated blue crab chemical cues would reduce mud crab activity, which would limit the negative effect of bioturbation on BMA but could also diminish mud crab NCEs on snail grazing resulting in a classic 4-level trophic cascade predication (Figure 2.1.d).

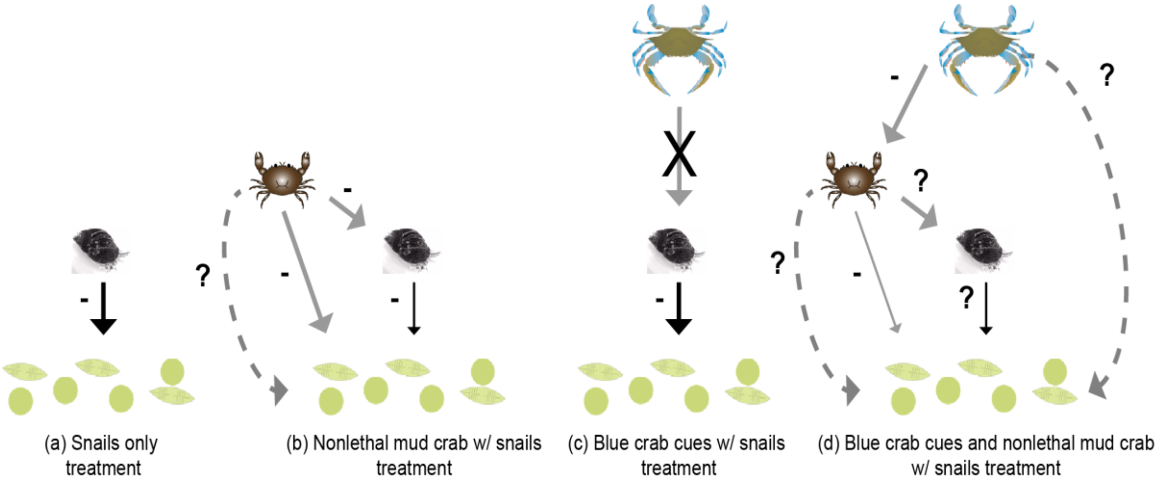

Figure 2.1 Predicted direction and magnitude of direct (solid line) and indirect (dotted line) interactions in each treatment (a-d) for the field experiment examining blue crab NCEs on BMA through modifications of mud crab-snail interactions. Black arrows represent snail CEs on BMA and gray arrows illustrate blue crab or mud crab various NCEs. Arrow thickness corresponds to the predicted magnitude of effect. Blue crab and BMA images from the Integration & Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). Mud crab and snail images by the author.

2.3 Methods

2.3.1 Animal collection and maintenance

All animals were collected from Wassaw Sound (Savannah, GA, USA) under a collection permit from the Georgia Department of Natural Resources. Blue crabs were collected with baited crab traps. Mud crabs were caught by hand in natural oyster reefs during low tide. Snails were collected by hand on mudflats adjacent to oyster reefs. All animals were kept in separate flow-through seawater systems at the Skidaway Institute of Oceanography (SkIO). In order to establish distinct trophic interactions and maximize NCEs between these trophic interactions, blue crabs were fed an *ad libitum* diet of crushed mud crabs 48 h prior to the lab or field experiment and mud crabs were fed one crushed snail a day for 3 days prior. Both crabs were housed individually in their respective flow-through systems while being fed experimental diets to ensure all crabs were receiving uniform amount of prey. All experiments were performed at SkIO during the summer months of 2018.

2.3.2 Laboratory experiment

We assessed the behavioral response of snails to different predatory crab NCEs in a laboratory experiment. Experiments were performed in 28-L aquaria (51 cm x 26 cm x 30 cm) that were divided in half using styrene egg crate covered with mesh netting (5 mm^2 mesh size). Each aquarium was filled with 8 L of filtered seawater from the SkIO flow-through seawater system. A small natural sun-bleached oyster cluster (~ 5 cm dia.) was placed on one side of the tank as refuge for mud crabs. Twenty-five snails (shell length $\geq$ 15 mm) were added to the side with the oyster cluster and given 15 minutes to acclimate. Tanks were then assigned one of four crab treatments: mud crab only, blue crab only, mud crab and blue crab, and no crab control. Mud crab (30-35 mm carapace width (CW)) chelipeds were superglued shut so they were unable to crush snails but could still move freely. One mud crab was added to the side with snails and oyster cluster for the mud crab only and mud crab and blue crab treatment. For treatments with blue crabs, one blue crab (12-16 cm CW) was placed on the side of the tank without snails so that snails and mud crab received blue crab risk cues, but blue crabs could not physically interfere with snail or mud crab behavior. Snail and mud crab refuge use were monitored through the duration of the 4-h experiment. For snail refuge use, the number of snails within 2.5 cm of the water surface were counted hourly. Mud snails flee in response to chemical cues from predators (Rahman et al. 2000) and freshwater snails are shown to move to the surface in response to predator risk in the absence of covered habitat (Turner 1996). The location of mud crabs within or outside the refuge was monitored hourly as well. Five replicates of each treatment were performed simultaneously, and two trials were performed to total 10 replicates for each treatment. The average percentage of snails within 2.5 cm of the surface during the 4-h trial was calculated and then analyzed using a two-way ANOVA for the effects of trial and crab treatment. The average percentage of time the mud crab spent in the oyster refuge during the 4-h trial was calculated and analyzed using a Mann-Whitney U test.

2.3.3 Field experiment

We analyzed the cascading NCEs of crab predators on BMA communities in a field experiment. The field experiment was conducted on an intertidal mudflat near the SkIO main campus located in the Skidaway River which is a tributary of the Wilmington River that directly feeds into Wassaw Sound. Tidal range is between 2-3 m in this area. This site is primarily a bare mudflat with a few patchy oyster clusters bordered by *Spartina alterniflora* salt marshes. The average water temperature during the duration of the experiment ranged between 25°C and 28°C and salinity was between 25 to 28 ppt.

Snail cages were staked into the mudflat 2.5 m away from the edge of the *Spartina* salt marsh. Snail cages (30 cm dia. x 25 cm tall) were constructed out of mesh netting (5 mm^2 mesh size) with no bottoms but a mesh top to prevent snail emigration. Vexar mesh was attached to the bottom half of the cage siding to provide structure and aid in submerging cages 10 cm into the mud substrate to prevent snails from escaping out of the open bottom. Blue crab cages (25 cm dia. x 25 cm tall) were fully enclosed and constructed out of 1 cm^2 vexar mesh. One blue crab cage was staked directly adjacent to the snail cage in the direction of tidal flow, so that the blue crab cage was upstream of the snail cage during flood tide. The same crab treatments used in the lab experiment were applied to the snail cages (mud crab only, blue crab only, mud crab and blue crab, no crab control) along with a no snail control to assess BMA communities in the absence of any grazing or bioturbation. Twenty-five snails (≥ 15 mm shell length) were placed inside the snail cage for all treatment except the no snail control. Treatments that required mud crabs (mud crab only, mud crab and blue crab) contained one mud crab (30-35 mm CW) with superglued shut chelipeds. The mud crab was also tethered to prevent escape and to assist with replacing mud crabs every 3-4 days with minimal substrate disturbance. Mud crabs were replaced in order to maintain a source of conspecific diet risk cues (Scherer and Smee 2016). Tethers were 45-cm long monofilament line (~11.3 kg test) that were tied around the carapace of the mud crab between the chelipeds and the legs. Blue crab treatments (blue crab only, blue crab and mud crab) contained one blue crab (12-16 CW) in the blue crab predator cage that was fed crushed mud crabs every 3-4 days when nonlethal mud crabs were replaced. Any dead blue crabs found during the semiweekly checks were replaced. Blue crab predator cages were left empty for the other treatments that did not require blue crabs.

Treatments were deployed in blocks and each treatment cage within a block was about 2 m away from each other. There were 10 blocks total which were placed about 20 m apart. The experiment began in the end of May 2018 and ended 3 weeks later. We collected the snails in each cage at the conclusion of the experiment by sifting the top 10 cm of sediment through a 5-mm sieve. We analyzed the number of snails recovered in each snail cage using a one-way ANOVA with block to ensure there was no effect of treatment or block on snail final density. No snails were found in any of the no snail controls, so this treatment was dropped from the final snail density analysis.

We collected sediment cores from each snail cage at the beginning and end of the experiment to assess changes in the BMA community. Three randomly located cores were collected from each snail cage using a modified 5-mL syringe (1.5 cm dia. x 1 cm deep) and were pooled together for chlorophyll analysis. Cores were stored on ice in a black bag until taken back to the laboratory to be frozen at -18°C until processing. Pigments were extracted from sediment cores using 90% acetone and chlorophyll *a*, *b*, and *c* concentrations were estimated with spectrophotometric methods (Parsons et al. 1984). Chlorophyll *a* concentration was corrected to prevent the inclusion of phaeopigments by obtaining absorption values before and after acidification with 2 drops of 1N HCl (Lorenzen 1967). Corrected chlorophyll *a* concentration was measured to assess total BMA biomass. Chlorophyll *b* approximates chlorophyte, euglenophyte and protochlorophyte contribution to total biomass and chlorophyll *c* approximates diatom biomass (Jeffrey and Vesk 1997, Richie 2008). Sediment from pooled cores was dried at 60°C for 24 hours after chlorophyll analysis, then weighed, and concentration per g dry sediment was obtained. We calculated the difference in corrected chlorophyll *a* and chlorophyll *b* and *c* between the final and initial concentrations. One-way ANOVAs with block were used to determine the effect of treatment and block on changes in each chlorophyll pigment.

At the end of the experiment, two randomly located sediment cores (1.5 cm dia. x 5 cm depth) were taken from each snail cage and pooled together to measure sediment organic content. Samples were dried at 60°C for 48 hours and combusted at 550°C for 5 hours to assess ash free dry weight. Percent organic matter was calculated as the percentage of the total sediment mass lost on combustion (i.e. organic matter). The effects of treatment and block on percent organic matter were analyzed using a one-way ANOVA with block.

2.4 Results

2.4.1 Laboratory experiment

Snail use of near surface refuge was affected by crab predator treatment (Figure 2.2; $F_{3,32}$ = 14.1, $P < 0.001$). Cues from nonlethal mud crabs doubled the percentage of snails in the near surface refuge compared to the no crab control or treatment with blue crab cues only. Snail refuge use was similarly high when either only mud crabs were present or in the presence of both blue crab and mud crab. Trial also affected snail refuge use ($F_{1,32}$ = 20.8, $P < 0.001$), but there was no significant interaction between trial and crab treatment ($F_{3,32}$ = 2.73, $P = 0.060$). The percentage of time spent in the oyster refuge by mud crabs was significantly increased by the presence of blue crabs (Figure 2.3; Mann-Whitney U test, $W = 19$, $P < 0.05$). Mud crabs barely utilized the oyster refuge in the absence of blue crabs but spent more than half their time in the refuge when blue crab cues were present.

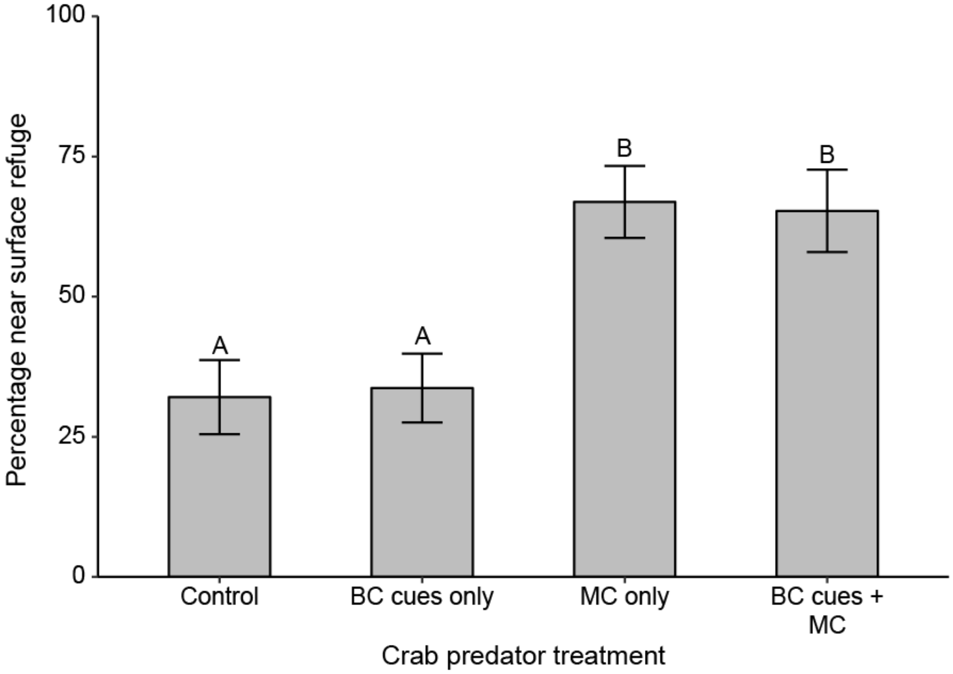

Figure 2.2 The average percentage of snails during the 4-h lab trial (mean + SE) located within 2.5 cm of the water's surface (n=10). Different letters denote means that are significantly different from each other at *P* < 0.05 (Tukey post hoc test).

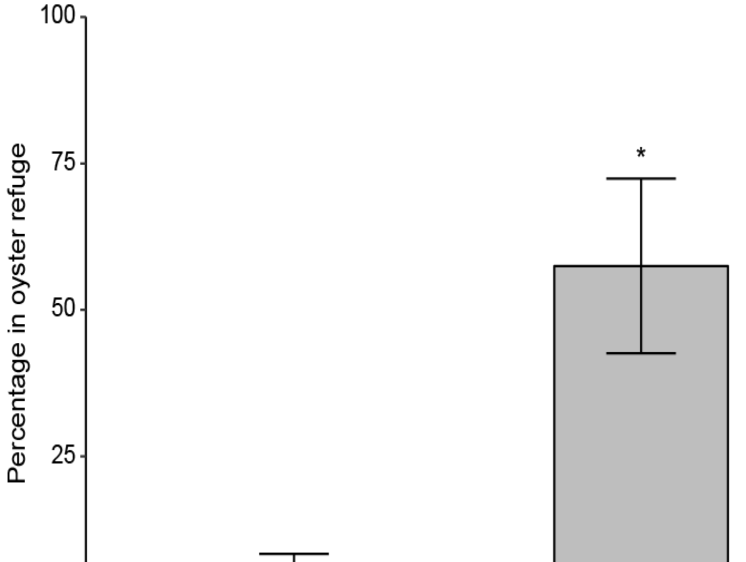

Figure 2.3 The average proportion of mud crabs during the 4-h lab trial (mean + SE) found in the oyster refuge (n=10). Asterisk denotes means are significantly different from each other at *P* < 0.05 (Mann-Whitney U test).

2.4.2 Field experiment

Overall, chlorophyll concentrations decreased in snail cages during the experiment regardless of treatment (Figure 2.4). Crab predator treatment had no effect on the change in corrected chlorophyll *a* concentration (Figure 2.4.a; $F_{4,36} = 0.92$, $P = 0.46$) or chlorophyll *c* concentration (Figure 2.4.c; $F_{4,36} = 1.01$, $P < 0.41$). Yet, there was a significant block effect for both change in corrected chlorophyll *a* ($F_{9,36} = 3.31$, $P < 0.01$) and chlorophyll *c* ($F_{9,36} = 3.63$, $P < 0.01$). Change in chlorophyll *b* concentration was significantly affected by crab predator treatment (Figure 2.4.b; $F_{4,36} = 5.52$, $P < 0.01$), but there was no block effect ($F_{9,36} = 1.96$, $P = 0.07$). The decrease in chlorophyll *b* concentration was half the amount when both blue crab cues and mud crabs were present compared to when either only snails present or the no snail control. The final snail density was not affected by crab predator treatment ($F_{3,27} = 0.06$, $P = 0.98$) or block ($F_{9,27} = 0.84$, $P = 0.59$) and over 70% of snails were recovered. There was no effect of crab predator treatment ($F_{4,36} = 1.20$, $P = 0.33$) or block ($F_{9,36} = 2.10$, $P = 0.06$) on percent organic matter. The average percent organic matter in snail cages at the end of the experiment was 11.8%.

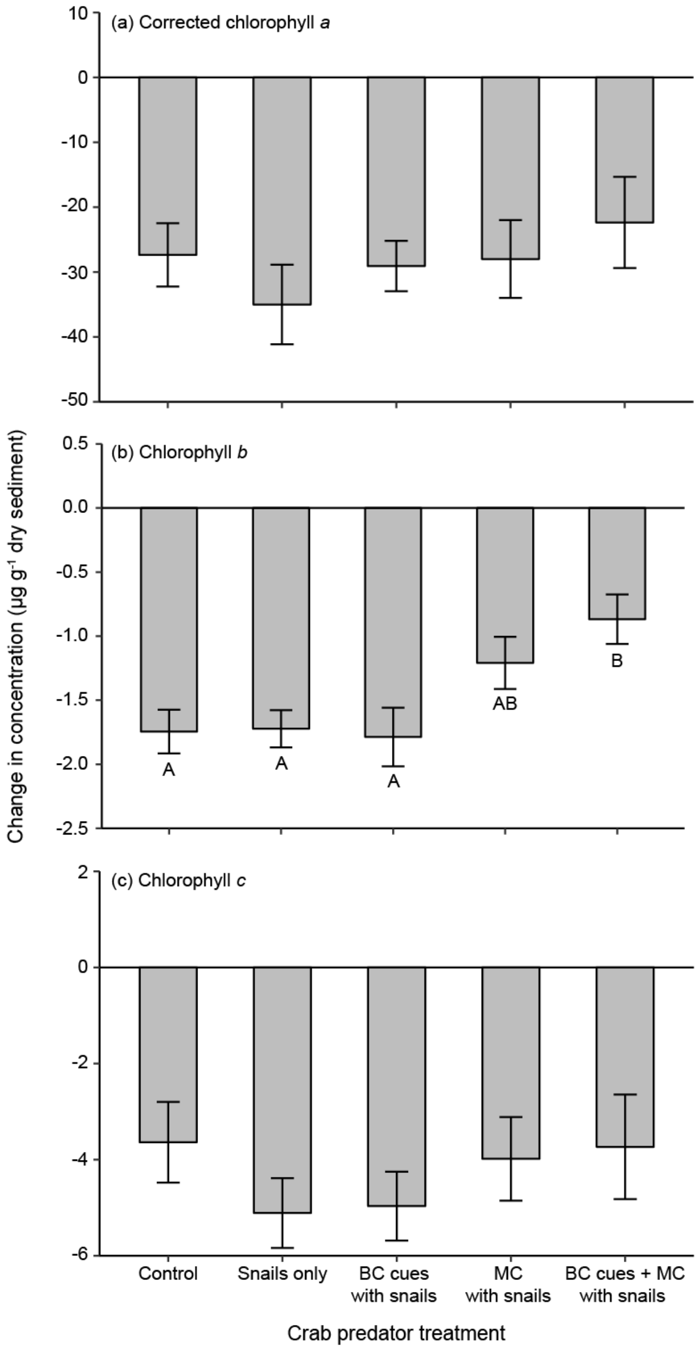

Figure 2.4 The average change in a) corrected chlorophyll *a*, b) chlorophyll *b*, and c) chlorophyll *c* concentration (µg g^{-1} dry sediment; mean ± SE) after 21-d field experiment in each treatment (n=10). Different letters denote means that are significantly different from each other at *P* < 0.05 (Tukey post hoc test).

2.5 Discussion

The presence of predators ubiquitously alters prey phenotypes across diverse communities (Lima and Dill 1990, Kats and Dill 1998, Stankowich and Blumstein 2005, Ferrari et al. 2010). The prevalence of NCEs suggests they should be important in community structure (Schmitz et al. 2004), but we still lack a rigorous body of literature examining cascading NCEs in complex food webs (but see Peacor et al. 2012, Forbes and Hammill 2013). Our results demonstrate that predator NCEs influence primary producers in a non-linear 4-level food web by behaviorally modifying species interactions.

Predator properties, either identity or diet, modulated snail avoidance behavior in the lab. Both blue crabs and mud crabs readily consumed snails in flow-through holding tanks (*personal observation*), but only treatments with mud crabs caused snails to increase near surface refuge use (Figure 2.2). Differences in predator hunting styles between blue crabs and mud crabs may explain the lack of snail refuge use in response to blue crabs despite posing a risk of predation. Active predators, such as blue crabs, are thought to produce less reliable risk cues due to movement across a wide area diluting cue availability (Schmitz and Suttle 2001, Preisser et al. 2007). Blue crabs were relatively confined in our lab experiment and in close proximity to snails, which makes it unlikely that blue crab cues were unavailable to snails. Alternatively, snails may have been responding to conspecific diet cues that were only associated with mud crabs fed snails and not blue crabs fed mud crabs. Two species of freshwater snails only increase refuge use in response to crayfish predators fed conspecifics or congeners and not to other more distantly related prey diets (Turner 2008). Yet, mud snails demonstrate antipredator responses to predatory crabs fed bivalves (Premo and Tyler 2013) or starved (Rahman et al. 2000) in other lab experiments, so further investigations of mud snail response to predator risk cues are warranted. Also, we chose our experimental diets to maximize NCEs between trophic levels, but to understand the relevance of NCEs under natural conditions, generalist predators should be fed a mixed diet of multiple potential prey species (Weissburg et al. 2014, Scherer and Smee 2016).

Prey behavioral responses to predators in the lab may explain cascading NCEs on BMA in the field. Predatory crab NCEs did not affect overall BMA biomass, but enhanced chlorophyll *b* concentrations (Figure 2.4), which represents chlorophytes, euglenophytes and protochlorophytes (Underwood and Kromkamp 1999, Sullivan and Currin 2000). Mud snails selectively forage on motile diatoms (Connor and Edgar 1982), which at low snail densities or grazing intensities can benefit less motile microalgae that are normally trapped beneath diatom mats (Novak et al. 2001, Alvarez et al. 2013). The presence of nonlethal mud crabs in snail treatments potentially reduced snail activity along with grazing intensity to a level that benefitted other BMA populations by removal of larger diatom competitors. However, in the absence of blue crab chemical cues, mud crab burrowing limited the positive indirect effects on diatom competitor's biomass. Mud crab bioturbation can bury surface BMA, which removes access to light and has negative affect on photosynthetic microalgae (Armitage and Fong 2006, Kristensen et al. 2012). Blue crab risk cues increased mud crab refuge in our lab experiment (Figure 2.3), as well as in other lab (Hill and Weissburg 2014, Belgrad and Griffen 2016) and field experiments (Hill and Weissburg 2013a, Weissburg and Beauvais 2015). Thus, in the presence of blue crab NCEs, mud crabs most likely decreased activity and increased time spent in burrow, which when combined with mud crab NCEs on snail foraging, benefitted microalgae that compete with diatoms.

The use of caged predators in NCE studies has been cautioned because it restricts the natural distribution of risk cues across a landscape (Weissburg et al. 2014), but our results demonstrate that caged predators may also inhibit predator NCEs that affect basal resources through disturbance behavior.

While we demonstrated that blue crabs have cascading NCEs on BMA community composition, the seasonal dynamics of microphytobenthos in intertidal mudflats may temporally regulate the importance of these NCEs. BMA populations naturally fluctuate with the seasons and show a peak in biomass in the spring, which declines as summer temperatures increase, followed by another bloom in the fall (MacIntyre et al. 1996, Gerwing et al. 2016). We believe the strong decreases in chlorophyll concentrations across treatments throughout our experiment were a result of starting the field experiment at the tail end of the spring bloom which naturally declined by the end of our experiment. Preliminary experiments in late July/early August the previous summer did not show any effect of cage mesh on chlorophyll *a* concentration due to shading (*unpublished data*). Temporal fluctuations in resource availability can either increase or decrease the strength of indirect NCEs. NCEs are stronger when high resources increase prey state, which decreases the cost of predation risk (Luttbeg et al. 2003, Matassa et al. 2016). Yet, opportunity cost of reduced foraging efforts can increase when resources are high, so prey response to predators decrease (Wojdak and Luttbeg 2005). Long-term field investigations are needed within systems that vary seasonally to understand the importance of NCEs on community dynamics over temporal productivity scales (Wada et al. 2017).

Top predator cascading NCEs have broader ecosystem impacts by influencing primary production (Schmitz 2008, Burkholder et al. 2013, Painter et al. 2015). Classic trophic cascade theory, which only considers predator CEs, predicts that primary production will be grazer limited in food chains with even numbers and free from grazer control in odd number systems (Fretwell 1977, Carpenter et al. 1985). Our results showed more complicated effects on primary producer communities in a 4-level cascade due to top predator NCEs altering behavioral interactions. NCEs can have counterintuitive cascading effects that qualitatively differ from CEs and are not homogenous across spatiotemporal landscapes (Peckarsky et al. 2008, Schmitz et al. 2008) For example, the presence of tiger shark in seagrass beds shifts herbivore grazing from perceived high-risk interior habitats to low-risk edge habitats, which results in high biomass of slow-growing seagrasses in the risky habitat and low biomass of fast-growing seagrass species in the safer habitat (Burkholder et al. 2013). Yet, top predators worldwide are in decline and experiencing range contraction due to anthropogenic impacts (Heithaus et al. 2008, Ritchie and Johnson 2009, Estes et al. 2011, Ripple et al. 2014). Thus, the mechanisms that trigger cascading NCEs, which are not always straightforward as evidenced by this study, should be considered to help predict ecosystem consequences of top predator extirpation.

CHAPTER 3. HYDRODYANMICS AFFECT PREDATOR CONTROLS THROUGH PHYSICAL AND SENSORY STRESSORS

3.1 Abstract

Predators influence communities through either consuming prey (consumptive effects, CEs) or altering prey traits (non-consumptive effects, NCEs), which has cascading effects on lower trophic levels. CEs are well-known to decrease in physically stressful environments, but NCEs may be reduced at physically benign levels that affect the ability of prey to detect and respond to predators (i.e. sensory stress). We investigated the influence of physical and sensory stressors created by spatial and temporal differences in tidal flow on predator controls in a tritrophic system. We estimated mud crab reactive ranges to blue crab NCEs by evaluating mud crab CEs on juvenile oysters at different distances away from caged blue crabs across flow conditions. Mud crab reactive ranges were large at lower physical and sensory stress levels and blue crabs had a positive cascading effect on oyster survival. Blue crab NCEs were not important at higher flow conditions. Oyster survival was a complicated function of both types of stressors. Physical stress (i.e. current speed) had a positive effect on oyster survival by physically limiting mud crab CEs at high current speeds. Sensory stress (i.e. turbulence) interfered with the propagation of blue crab chemical cues used by mud crabs for predator detection, which removed blue crab NCEs. Mud crab CEs increased as a result and had a negative effect on oyster survival in turbulent conditions. Thus, environmental properties, such as fluid flow,

can inflict physical and sensory stressors that have distinct effects on basal prey performance through impacts on different predator effects.

3.2 Introduction

Predators promote species coexistence and influence community structure (Paine 1966, Lubchenco 1978, Ripple et al. 2014). Traditionally, predators were thought to control lower trophic levels by reducing prey density through direct consumption (consumptive effects, CEs), but the alteration of prey behavior and phenotype in response to predation risk (non-consumptive effects, NCEs) can impact communities as well (Werner and Peacor 2003, Peckarsky et al. 2008, Suraci et al. 2016). Many studies suggest the effect of cascading NCEs can be as strong as or stronger than CEs (Preisser et al. 2005). Full understanding of the role of predators requires understanding how CEs and NCEs are modulated by environmental context. Although it is well known that physical stress imposed by harsh environmental conditions can reduce the strength of CEs (Menge 1978, Menge and Sutherland 1987, Leonard et al. 1998, Bertness et al. 2002, Shears et al. 2008), how environmental conditions affect NCEs in communities is less well studied (Weissburg et al. 2014; but see Van de Meutter et al. 2005, Smee and Weissburg 2006, Large et al. 2011).

Direct and indirect predator CEs can be modulated by environmental gradients, particularly those that have the capacity to cause injury or damage. Consumer stress models postulate that physically harsh conditions may interfere with predator motility, and the release of prey from predation may cascade to affect other organisms (Menge and Sutherland 1987). For example, the intensity of crab predation on dog whelks in tidal estuaries decreased at sites with higher water flow, resulting in increased dog whelk abundances and higher growth rates due to potentially increased consumption of their preferred prey, barnacles (Leonard et al. 1998).

Current environmental stress models generally only consider physical stress constraining CEs, but some environmental conditions can diminish the ability of animals to collect information about prevailing conditions. Such “sensory stress” can occur at physically benign levels, but still may interfere with sensing the smells, sounds, and sights associated with predation (Munoz and Blumstein 2012, Weissburg et al. 2014). In turn, reduced predator sensing can modify interactions between these prey and other organisms (i.e. NCEs such as behaviorally mediated trophic cascades; Schmitz et al. 2004). The maximum distance at which prey detect and respond to predators, which we refer to as prey reactive range, sets the spatial limits of NCEs (Turner and Montgomery 2003).

The physical environment alters prey reactive range (Robinson et al. 2007, Smee et al. 2008) and thus can modulate when and where NCEs may be important. For instance, acoustic cues from predatory bats are attenuated in forested areas compared to in open fields. This diminishes the ability of moths to detect predators and increases predation rates on moths by bats (Jacobs et al. 2008). Similarly, visual perception can be hindered in aquatic environments by water clarity. Antipredator responses of fish to visual predator cues are reduced in turbid compared to clear waters (Hartman and Abrahams 2000). These and other examples (Weissburg et al. 2014) indicate the environment can interfere with sensory perception in conditions that are not noticeably stressful physically, and these sensory stressors may modify cascades produced by prey responses to risk.

Certain environmental gradients within a system can impose both physical and sensory stress, which complicates predicting the importance of predator effects on community regulation. For example, fluid flow can simultaneously impose physical stress on locomotion due to hydrodynamic forcing and sensory stress on chemosensory abilities through turbulent mixing (Weissburg et al. 2003). Physical stress has been shown to limit crustacean foraging abilities at high flow conditions in tidally-driven estuaries, which decreases the importance of predator CEs (Leonard et al. 1998). Yet, flow is also important in modulating chemical perception in aquatic systems (Weissburg and Zimmerfaust 1993, Finelli et al. 2000, Jackson et al. 2007, Webster and Weissburg 2009). Turbulence creates greater cue mixing within odor plumes, which reduces information available for crustacean predators and reduces foraging success (Weissburg and Zimmerfaust 1993, Powers and Kittinger 2002, Jackson et al. 2007). But, in contrast to physical stressors, the impact of sensory stress is contingent on the proximity of predators to prey. Greater fluid mixing may reduce the effectiveness of signals over larger, but not smaller distances, whereas a predator affected by physical stress is simply unable to forage.

CEs and NCEs are important in a variety of species interactions within oyster reefs that are exposed to tidally-driven flows (Grabowski et al. 2008, Byers et al. 2014, Hughes et al. 2014). Blue crabs (*Callinectes sapidus*) are important predators of salt marsh crustaceans and bivalves (Micheli 1997, Smee and Weissburg 2006, Hill and Weissburg 2013a). Mud crabs (*Panopeus herbstii*) are small, cryptic xanthid crabs that reside inside oyster beds (Lee and Kneib 1994, Hollebone and Hay 2007) and prey on juvenile oysters and other bivalve species (Bisker and Castagna 1987, Silliman et al. 2004, Toscano and Griffen 2012). Chemical cues from top predator blue crabs suppress the foraging of intermediate mud crab consumers on juvenile oysters (*Crassostrea virginica*) (Hill and Weissburg 2013b, Weissburg et al. 2016). Yet, hydrodynamic conditions vary spatially and temporally in tidally-driven salt marshes (Wilson et al. 2013), which suggests that the importance of environmental (i.e. physical and sensory) stressors on modulating blue crab-mud crab-oyster interactions may be context-dependent.

We investigated the effect of physical (i.e. current speed) and sensory stress (i.e. turbulence) on oyster survival through potential alterations of blue crab cascading NCEs and mud crab direct CEs. Specifically, we estimated the reactive range of mud crabs to blue crabs by quantifying mud crab consumption of juvenile oysters in the presence of blue crab risk cues. We examined how oyster survival changes as a function of distance between blue crab sources of aversive chemical cues and mud crabs in different flow regimes. This allowed us to estimate the spatial extent of blue crab NCEs. We predicted that predator effects shift from blue crab NCEs to mud crab CEs as flow increases. NCEs should be greatest when low flow environments permit large reactive ranges in mud crabs. Greater turbulence initially compromises sensing and reduces mud crab reactive range to blue crab cues, but mud crab foraging ultimately declines at high flow speeds despite limited ability to sense predators from a distance. Understanding the environmental conditions where each stressor exerts effects lends insights into the spatial and temporal variance of predator effects, given their different mode of operation.

3.3 Methods

3.3.1 Animal collection and maintenance

Both blue crabs and mud crabs were collected from Wassaw Sound (Savannah, GA, USA) and associated tributaries. Blue crabs were caught using baited crab pots. Mud crabs were collected by hand from natural oyster reefs during low tide. Collections were permitted under a scientific collecting permit obtained from the Georgia Department of Natural Resources. Blue crabs and mud crabs were maintained in separate flow-through seawater systems at the Skidaway Institute of Oceanography (SkIO). Mud crabs were sorted and housed separately according to carapace width (CW) size classes: 15-20 mm, 20-25 mm, and 25-30 mm. Mud crabs were fed every two days a diet of *ab libitum* oyster spat to prevent starvation. Blue crabs (12-16 cm CW) were housed individually and 48 hours prior to experiment fed an *ad libitum* diet of crushed mud crabs daily. Blue crabs fed strictly mud crab diets induce greater reductions in mud crab foraging (Weissburg et al. 2016) and this diet was chosen to maximize blue crab NCEs. Oyster spat (10-16 mm hinge length) were obtained from local commercial hatcheries. Oysters were maintained in a separate flow-through seawater system prior to field experiments.

3.3.2 Site description

The field experiments described below were performed at sites located in Skidaway and Wilmington Rivers, which are estuarine rivers that flow into Wassaw Sound. Skidaway Narrows site was located along the Skidaway River, which flows into the Wilmington River where Priest Landing site was located (Figure 3.1). Both sites are characterized by mudflats bordered by *Spartina alterniflora* salt marshes. Priest Landing contained a higher density of loose oyster clusters and isolated patches of oyster reefs, but ambient blue crab predation threat level was equivalent at each site based on consumption rates of tethered mud crabs in the field (Figure A.1).

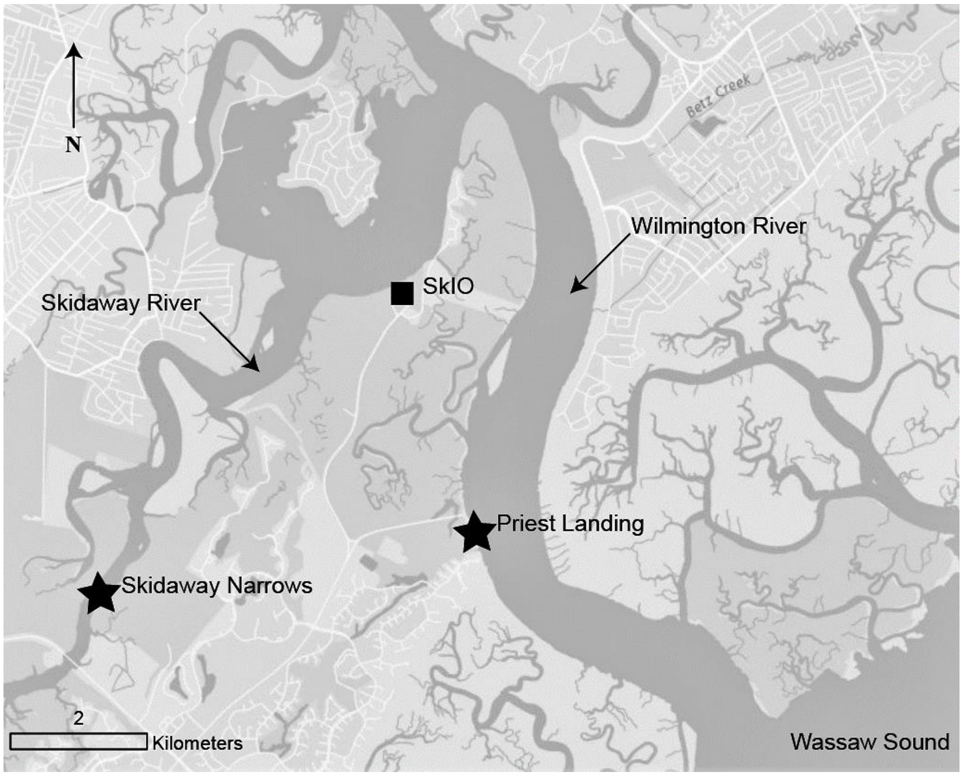

Figure 3.1 Map of study area.

3.3.3 Flow measurement analysis

Previous extensive flow measurements by Wilson et al. (2013) demonstrated that flow parameters vary significantly between these sites. These flow characteristics have been highly conserved across multiple years of monitoring and are strongly predicted by tidal height and range (Wilson 2011, Wilson et al. 2013). We used, and further analyzed, this extensive data set to categorize the flow properties during different tidal types at our sites based on tidal height. Briefly, current speed and turbulent kinetic energy (TKE) were measured using acoustic Doppler velocimeters (ADVs; Nortek) for multiple consecutive tidal cycles. The ADV measurements were taken 10 cm above the substrate, which is within the vertical boundary layer experienced by benthic estuarine organisms. See

Appendix A for a more descriptive summary of the methods by Wilson et al. (2013). We characterized the probability density functions of current speed, $(|\bar{u}|)$, and turbulent kinetic energy (TKE) using this data. We also used the relationships between tidal range and flow properties provided by this data to estimate the flow properties during our experiments, as described fully below.

3.3.4 Field experiment

We evaluated oyster survivorship in the presence of mud crab predation at different distances away from caged blue crabs and across spatial and temporal flow environments. Mud crab enclosures were 2.2 m by 0.75 m by 0.3 m (LxWxH) and constructed out of 1 cm^2 vexar mesh and PVC frame. An oyster reef was created at one end of the enclosure to serve as a refuge for mud crabs. The oyster reef consisted of 4 natural sun-bleached oyster clusters (~30 cm dia.) and 4 artificial oyster clusters. The artificial oyster clusters were constructed by gluing together 4 to 6 sun bleached oyster shells to create small clusters of approximately 6 cm diameter. The artificial oyster clusters were interspersed within the oyster reef and 4 additional artificial oyster clusters were placed 25-30 cm away from the oyster reef (Figure 3.2). Top predator cages (0.3 m dia. by 0.3 m tall, 1 cm^2 vexar mesh) contained an individual blue crab to produce predation risk cues and were placed at varying distances away from the center of the oyster reef (see below).

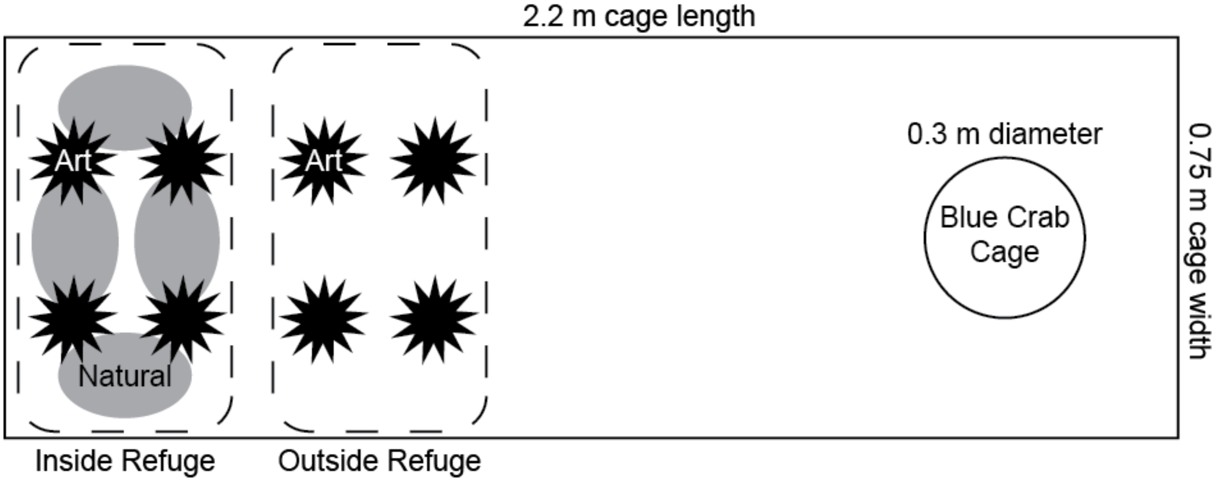

Figure 3.2 Diagram of the mud crab (*Panopeus herbstii*) enclosure design. The refuge contained four artificial clusters (black; "ART") interspersed within four natural clusters (gray; "Natural"). Four additional artificial clusters were placed outside the refuge as well. Juvenile oyster spat (*Crassostrea virginica*) were epoxied to the surface of the artificial clusters. Blue crab (*Callinectes sapidus)* cages were placed on both sides of the refuge, with one cage inside the enclosure (shown) and another outside the enclosure (not shown) (Hill and Weissburg 2013b, Weissburg and Beauvais 2015).

Enclosures were staked down on intertidal mudflats parallel to tidal flow and approximately one tidal foot below mean low water. Four juvenile oyster spat (10-16 mm hinge length) were attached to the surface of each artificial cluster with marine epoxy, so that there was a total of 16 oyster spat inside and outside the refuge (32 spat total). Mud crabs were placed within the oyster reef that was inside the enclosure. Fifteen mud crabs (8 mud crabs 15-20 mm CW, 4 mud crabs 20-25 mm CW, and 3 mud crabs 25-30 mm CW), which reflects the natural field density and size distribution of mud crabs (Hill and Weissburg 2013b), were placed in the oyster reef within the enclosure. Mud crabs were marked with fluorescent paint prior to field deployment in order to distinguish them from potential immigrating mud crabs. However, most cages (>90%) lacked any immigration and only 7 out of 215 cages had more than 1 immigrant. Top predator cages contained a blue crab (12-16 cm CW) and were placed at either 0.25 m, 0.5 m, 1.0 m, 1.5 m, or 2.0 m away from the center of the oyster reef at each end of the cage along the direction of tidal flow. One top predator cage was placed inside the enclosure and the other outside (Figure 3.2) to take into account the opposing effects of the cage mesh on flow; Hill and Weissburg (2013b) demonstrated that current speed was slightly weakened by the cage mesh, but the mesh also enhanced turbulence. The overall effect is that TKE remained the same or slightly increased inside the enclosure relative to the ambient flow, but conditions within the cages are well within the range of ambient conditions measured outside the cage. Control treatments consisted of empty top predator cage placed 0.25 m from the reef.

The number of oysters consumed inside and outside the refuge was measured after 24 hours. Each 24-hour block had 2 replicates of each distance treatment and no-blue crab cage control, placed at least 5 m apart in random order. Only one site at a certain tidal type could be tested at a time due to distance between sites and the limited time mudflats were exposed during low tide when experiments could be set up and taken down. Tidal type (mean or spring) was defined according to the average low tide height during each deployment. Mean tide low tide heights were between -0.067 m to 0.033 m and spring tide low tide heights were between -0.33 m to -0.17 m for both sites (Table A.1).

We deployed 7 experiments in 2014, 10 in 2015, and 6 in 2016 between the months of June to August. Two blocks, one for Priest Landing at mean tide in 2016 and another for Skidaway Narrows at mean tide in 2015, were removed from the analysis due to extreme heat during the experiment, in which the water temperatures were above 30^{o}C and air temperatures were above 37^{o}C. Replicates were also removed if one or more blue crabs were found dead or missing after 24 hours. However, blue crab survival generally was high (~92%) and only 11 out 200 distance replicates were omitted due to blue crab death.

3.3.5 Statistical analysis

To provide an estimate of the ability of mud crabs to sense blue crab chemical cues, we analyzed the effect of site, tidal type, and distance of blue crabs from mud crabs on normalized oyster consumption and refuge use. As noted, distance is defined relative to the artificial reef where mud crabs take refuge. Detecting the effects of blue crab chemical cues on mud crabs is facilitated by normalizing consumption to the controls in each block, because the no-blue crab control represents the response of mud crabs in the absence of blue crab chemical cues. Thus, data for total oyster consumption was normalized by dividing the total oyster consumption in a given distance treatment over the average total oyster consumption in the controls in that block. Refuge use was defined as the proportion of oysters consumed within the oyster reef. Data was analyzed using a mixed model analysis. Fixed effects were site, tidal type, and distance treatment. Distance treatment was designated as a categorical factor so that the no-blue crab control could be included as a distance treatment. Block date was designated as a random effect. The model was fit using a restricted maximum likelihood (REML) approach, which is appropriate for unbalanced data (Kenward and Roger 1997).

Individual mixed-effects models fit by REML were conducted for each site and tidal type combination to approximate the mud crab reactive range for each site and tidal type, using the number of oysters consumed. The fixed effect was distance from blue crab, including the no-blue crab control, and the random effect was block date. Planned contrast *t*-tests were used to compare the control treatment to each distance treatment, if there was a significant distance treatment main effect. Mud crab reactive range was interpreted as the farthest distance treatment at which oyster consumption differed from the no-blue crab control.

We also analyzed the relationship between oyster survival over 24 hours and flow properties in the presence of blue crab risk cues to understand how predator effects change along physical and sensory stress gradients. We regressed oyster survival in the presence of blue crab chemical cues against current speed and TKE, separately. The flow properties during our experiments were estimated for each site and tidal type block based on the predictive relationship between tidal range and flow properties from Wilson (2011). Regression equations on the relationship between tidal range and either mean current speed or average TKE were derived from the flow data for each site respectively, as obtained by Wilson (2011) and Wilson et al. (2013) (Table A.2).

All data analysis was performed in R version 3.3.1 (R Core Team 2017), using the lme4 package for mixed-effects model analysis (Bates et al. 2015). Degrees of freedom and *P*-values for the mixed-effects models were based on Kenward-Roger approximations using the lmerTest package (Kuznetsova et al. 2017).

3.4 Results

3.4.1 Flow measurement analysis

Site and tidal type had strong effects on flow conditions. Site and tide specific regressions showed robust relationships between tidal range and both mean current speed and turbulent kinetic energy (TKE) at these sites (Table A.2). In general, data collected by Wilson et al. (2013) showed that mean current speed and TKE were higher during spring tide relative to mean tide, regardless of site (Table A.3). However, between sites, Priest Landing (PL) had greater mean TKE and slower mean current speed compared to Skidaway Narrows (SN), which had faster speeds and lower TKEs (Table A.3). The distribution of these parameters was consistent with these trends; the distribution of TKE at PL skewed to higher values but current speed to lower values compared to SN (Figure A.2). A more exhaustive description of the flow characteristics is found in Appendix A.

3.4.2 Field experiment

Chemical cues from blue crab top predators reduced normalized oyster consumption (consumption relative to no-blue crab control), but only during mean tide and with site-specific patterns (Table 3.1; Figure 3.3). Tidal type had a significant effect on mud crab normalized oyster consumption, with less normalized consumption at mean versus spring tide (Table 3.1). Normalized consumption during spring tide appeared similar to the no-blue crab controls across distance treatments, whereas the average normalized consumption in the blue crab distance treatments at mean tide was 0.637 ± 0.035 (mean ± SE). There also was an effect of blue crab distance treatment on normalized oyster consumption that was site dependent (Table 3.1), which seems to result from site-specific consumption patterns during mean tides. During mean tides, normalized oyster consumption was lower than the no-blue crab control in each blue crab predator distance treatment at PL, but consumption was only reduced in the distance treatments up to 1.5 m at SN.

Table 3.1 Mixed-effects model analysis of the effects of site, tidal type, and distance treatment on normalized oyster consumption (* denotes significant *P* < 0.05). Significance did not change with removal of three-way interaction from the model.

Source	*df* (num, den)	*F*-value	*P*-value
Site	1, 17.1	0.583	0.455
Tidal type	1, 17.1	12.969	0.002*
Distance	5, 175.4	2.525	0.031*
Site*Tidal type	1, 17.1	0.053	0.820
Site*Distance	5, 175.4	2.619	0.026*
Tidal type*Distance	5, 175.4	1.766	0.122
Site*Tidal type*Distance	5, 175.4	0.674	0.644

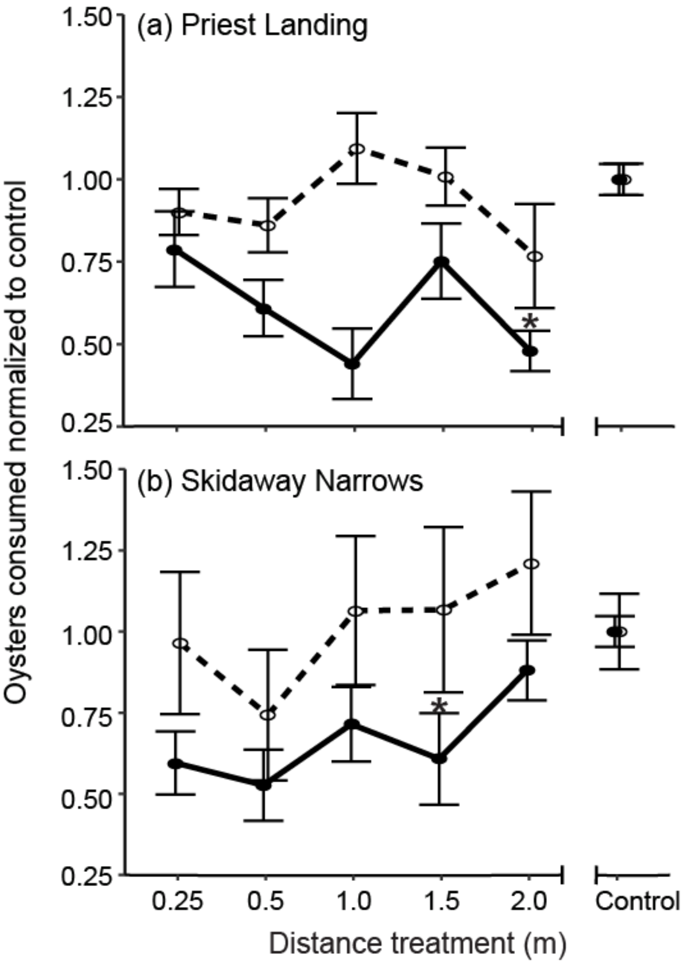

Figure 3.3 Normalized oyster consumption by mud crabs (mean + SE) at different distances away from caged blue crabs during mean tide (closed symbols, solid lines) and spring tide (open symbols, dashed lines) at (a) Priest Landing (PL; *n* for mean tide=64, *n* for spring tide=49) and (b) Skidaway Narrows (SN; *n* for mean tide=61, *n* for spring tide=48) Asterisks denote the mud crab reactive range for PL and SN at mean tide based on the farthest distance in which oyster consumption was significantly lower than the control (Table 3.2). There was no difference in oyster consumption in the distance treatments and the controls at PL and SN during spring tide.

Tidal type also had a significant effect on refuge use by mud crabs, with mud crabs consuming a larger proportion of oysters inside the refuge during mean tide (Table A.4, Figure A.3). Approximately 80% of the total oysters consumed by mud crabs during mean tide were inside the refuge, compared to only 67% at spring tide. Distance treatment also affected refuge use, but unlike normalized oyster consumption was not site specific (Table A.4). Tukey post hoc test revealed that only the 0.25 m distance treatment differed in refuge use from the control. Refuge use was uniformly higher in each distance treatment compared to the no-blue crab control at mean tide for both sites. Yet, during spring tide, the proportion of oysters consumed inside the refuge was highest at 0.25 m and declined linearly, but weakly, as distance away from blue crab increased (Figure A.3).

Individual mixed-effects models within each site and tidal type revealed spatial and temporal differences in the mud crab reactive ranges inferred from oyster survival. During spring tide at both sites, the mud crab reactive range was 0 m and oyster consumption was similar across all treatments (Figure 3.3; PL: $F_{5,39}$=1.63, P=0.176; SN: $F_{5,32}$=0.926, P=0.477). There was an effect of blue crab distance treatment at SN during mean tide ($F_{5,50}$=3.978, P=0.004) and oyster consumption was suppressed ~39% compared to the no-blue crab control in all distance treatments except at 2 m (Table 3.2; Figure 3.3.b). The mud crab reactive range was 1.5 m (Table 3.2). There also was an effect of distance treatment at PL during mean tide ($F_{5,53}$=3.781, P=0.005), despite some variation in the reduction of consumption. There was no significant difference in oyster consumption at the 1.5 m distance compared to the no-blue crab control. However, consumption was significantly lower in the other distance treatments, including the 2 m distance where oyster consumption was decreased by 52% relative to the no blue crab control (Table 3.2; Figure 3.3.a).

Table 3.2 Planned contrast *t*-tests for PL and SN during mean tide on the number of oysters consumed by mud crabs after 24 h, which had significant effects of distance treatment in the individual mixed-effects model analysis (* denotes significant *P* < 0.05).

Contrast	Priest Landing (PL)			Skidaway Narrows (SN)		
	Df	*t*-value	*P*-value	*Df*	*t*-value	*P*-value
Control-0.25 m	53	-2.099	0.041*	50	-2.897	0.006*
Control-0.5 m	53	-2.930	0.005*	50	-3.683	<0.001*
Control-1.0 m	53	-3.696	<0.001*	50	-2.052	0.045*
Control-1.5 m	53	-1.913	0.061	50	-2.539	0.014*
Control-2.0 m	53	-3.583	<0.001*	50	-0.472	0.639

The relationships between oyster survival, mud crab reactive range, and flow parameters varied between the physical (current speed) and sensory stress (turbulence) gradients (Figure 3.4). Oyster survival and mud crab reactive ranges were highest at both sites during mean tides where estimated current speeds and TKE were lowest. Oyster survival also was high at the highest estimated current speed (SN-spring), which corresponded to low mud crab reactive ranges. In contrast, oyster survival was lowest during PL-spring tide conditions where mud crab reactive range was also 0. Here, current speed was intermediate between mean tide conditions at both sites and SN-spring tide conditions. Thus, at speeds < 11 cm s^{-1}, low TKE is associated with large mud crab reactive ranges, suggesting foraging suppression from perception of blue crab chemical cues enhances oyster survival. At speeds above 11 cm s^{-1}, higher TKEs are coincident with low mud crab reactive range and oyster survival is low (PL-spring) until speeds exceed 13 cm s^{-1}, suggesting physical stress limits mud crab foraging (SN-spring). These complex relationships result in no association between average estimated current speed and oyster survival ($F_{1,182}$=0.006; P=0.940; r^2<0.001), and a significant but weak relationship between estimated TKE and oyster survival ($F_{1,182}$=6.757, P=0.010, r^2=0.036).

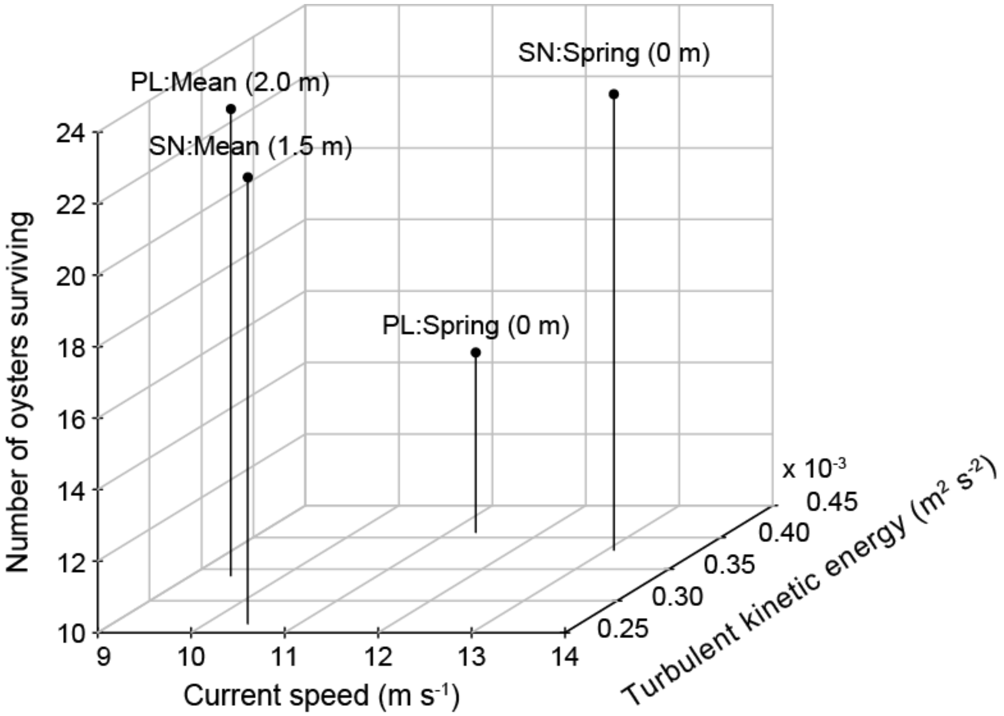

Figure 3.4 Average oyster survival in the presence of blue crab risk cues (z-axis) at different mean current speeds (cm s^{-1}; x-axis) and turbulent kinetic energies (TKE; m^2 s^{-2}; y-axis). Current speeds and TKEs correspond to estimated flow conditions during each trial block derived from each site and tidal type based on regression equations (Table A.2). Labels above points denote site (PL=Priest Landing, SN=Skidaway Narrows) and tidal type (mean tide, spring tide), and mud crab reactive range determined for that site and tidal type combination (Table 3.2; *n*=55 for PL:Mean, *n*=42 for PL:Spring, *n*=51 for SN:Mean, *n*=36 for SN:Spring).

3.5 Discussion

Environmental forces can inflict either physical or sensory stressors that alter predator direct and indirect effects, which in turn influence the abundance and spatial distribution of basal resources. Our results suggest that within a tritrophic system both these stressors can interact to produce distinct patterns of predator control. We found that mud crab reactive ranges were large under conditions when ambient flows were likely relatively slow and less turbulent. Here, oyster survival was high suggesting mud crabs foraged less, resulting in a classic behaviorally mediated cascade. Mud crab response to blue crab cues declined under tidal conditions that were predicted to increase current speed and turbulence, and blue crab NCEs were not important at higher physical and sensory stress levels. There was a positive effect of flow on oyster survival at the highest mean speed because foraging was likely physically constrained in mud crabs, but a negative effect at the highest turbulence because mud crabs apparently no longer responded to blue crab chemical cues but could still consume oysters. The difference in the sign of these effects suggests hydrodynamics affected oyster survival through different stressors.

Blue crab NCEs had a positive indirect effect on oyster survival when estimated current speeds and TKEs were lowest, which occurred during mean tide at both sites (Figure 3.4). The estimated mud crab reactive range at SN during mean tide was 1.5 m and at least 2 m (the farthest distance tested) at PL during mean tide (Table 3.2). Reactive ranges of prey are important since they define the landscape of fear perceived by prey, but relatively few studies have measured prey reactive ranges (but see Turner and Montgomery 2003, Morgan et al. 2016). Habitat heterogeneity creates areas of risky versus refuge space (i.e. “landscape of fear”, Laundré et al. 2001), which alters NCE strength and the distribution of basal resources across landscapes (Creel et al. 2005, Matassa and Trussell 2011, Burkholder et al. 2013). These sensory landscapes that govern the strength of NCEs are strongly affected by the physical environment, and, as shown here, are constant neither in time nor space. More estimates of prey reactive ranges are needed to understand the spatial extent of NCEs under natural conditions.

Chemical cues from blue crabs did not influence mud crab oyster consumption at PL during spring tide, which had the highest estimated TKEs (Figure 3.4). Oyster survival was greatly reduced during spring tide compared to mean tide at this site and mud crab refuge use was also lower (Figure A.3). Thus, turbulence appears to act as a sensory stressor by interfering with mud crabs' ability to detect blue crab chemical cues, which decreased reactive range to zero in conditions where turbulence was expected to be greater and removed blue crab NCEs. Increased turbulent mixing creates odor plumes that contain short, highly intermittent burst of chemical signals at lower peak concentrations (Koehl 2006, Jackson et al. 2007). Alteration of plume structure due to turbulence has been shown to reduce odor-mediated foraging success in blue crabs (Weissburg and Zimmerfaust 1994, Powers and Kittinger 2002, Jackson et al. 2007). Clam reactive ranges to predators also decreased when turbulence was increased while holding velocity constant (Smee et al. 2008). Mud crabs are known to decrease the strength of antipredator responses when presented with lower concentrations of blue crab chemical cues, either due to decreased predator biomass or diet amount (Hill and Weissburg 2013a, Weissburg and Beauvais 2015, Weissburg et al. 2016). Thus, mud crabs may not have detected blue crab cues in flows estimated to have higher turbulences, or the reduction in cue concentration at higher turbulences was perceived as a less risky environment where foraging suppression was not warranted (Chivers et al. 2001).

Mud crab consumption of oysters was not affected by blue crab NCEs at SN during spring tide, where estimated current speeds were greatest, but oyster survival was higher than that seen at PL during spring tide (Figure 3.4). Analysis of data obtained by Wilson et al. (2013) shows that, although mean current speed was only 2 cm s^{-1} faster at SN during spring tide than at PL, the mode was 11 cm s^{-1} higher (Table A.3, Figure A.2.a). Additionally, these differences in flow between the two sites at spring tide may have been even greater during the field experiments than when flow was measured because the tidal range for ADV deployment at PL during spring tide was larger than the tidal ranges for SN and the field experiments during spring tide, potentially overrepresenting flow values for PL at spring tide (Table A.1; Appendix A). Thus, the most likely explanation is that physical forcing reduced mud crab foraging abilities in conditions indicative of higher current speeds, which decreased mud crab CEs. Hydrodynamic forces, such as lift and drag, inflict physical limitations on animal locomotion and foraging abilities (Denny 1988, Weissburg et al. 2003). Drag force increases at higher flow velocities creating more environmentally stressful environments (Weissburg et al. 2003). Physical stress from increased current speeds of 15 cm s^{-1} compared to 3 cm s^{-1} has been shown to increase handling time in green crabs (*Carcinus maenas*; Robinson et al. 2011).

The physical environment modulated when and where certain predator effects were important, which had distinct effects on oyster survival. Oyster survival was negatively affected by sensory stress due to reduced importance of blue crab NCEs. This suggests turbulence impaired mud crab's ability to detect blue crabs, which enhanced negative mud crab CEs and removed the positive cascading blue crab NCE seen at lower sensory stress conditions. Physical stress had a positive effect on oyster survival by possibly physically constraining mud crab foraging, which decreased mud crab CEs. However, oyster survivorship was dependent on the interaction between physical and sensory stressors (as discussed below) and should be included in existing environmental stress models.

We created a simple conceptual model based on our results that incorporates the distinct effects of physical and sensory stressors on predator controls that simultaneously interact to create different impacts on basal resources across environmental gradients (Figure 3.5). Top predator NCEs are important at low physical and sensory stress conditions because intermediate prey can detect and respond to top predators. Cascading NCEs will have positive effects on basal prey survival because top predators decrease intermediate prey foraging rates.

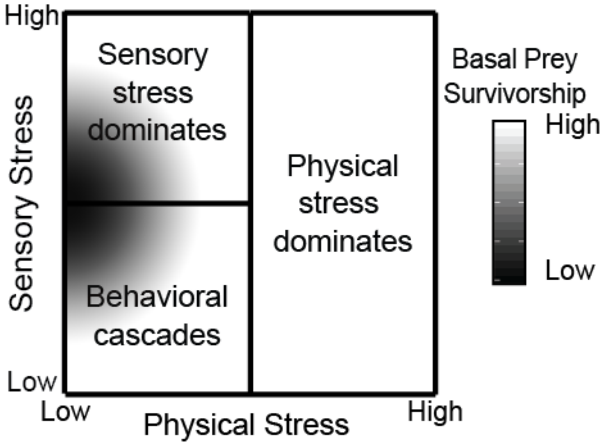

Figure 3.5 A conceptual model of basal prey survivorship in a tritrophic system across an environmental gradient that imposes both physical and sensory stress. Top predator NCEs initiate behavioral trophic cascades at low physical and sensory stress levels because intermediate prey detect and respond to top predators. As sensory stress increases, intermediate prey no longer detect top predators as easily, which reduces positive cascading NCEs on basal prey (lower left panel). Here, the decline of intermediate prey reactive range also creates spatial variation in NCEs. Sensory stress interferes with intermediate prey ability to detect basal prey at high sensory stress levels, which decreases intermediate prey CEs (upper left panel). This also produces a spatially non-uniform pattern of basal prey survival. However, regardless of sensory stress levels, physical forcing reduces intermediate prey foraging at high physical stress levels, which removes intermediate prey CEs and results in uniformly high basal prey survival across space (right panel).

As sensory stress increases but physical stress remains low, sensory abilities of intermediate prey diminish and NCEs decline until intermediate prey no longer detect and respond to top predators (Figure 3.5; lower left panel). Note this implies that indirect effects on basal resources will be spatially variable because intermediate prey can perceive their predators if they are very close; basal prey survival will depend on the distance away from the source of aversive cues. We found that the reactive range was 0.5 m shorter at SN during mean tide, which had lower estimated TKEs, compared to PL, but reactive ranges were zero during spring tide in both sites which had higher estimated turbulence. Large et al. (2011) documented a similar pattern where predator avoidance by *Nucella* snails increased at intermediate turbulences along a flow gradient before declining, possibly because moderate turbulence increases the spatial coverage of the predator cue plume without diluting concentrations sufficiently to affect perception. Despite some variation in responses at low estimated TKEs, sensory stress clearly reduced the ability of mud crabs to detect blue crabs at the highest estimated turbulence level. Thus, at higher sensory stress, intermediate prey CEs increase because they are released from top predator NCEs and basal prey survivorship decreases as a result. Larger reactive ranges at low levels of sensory stress will produce a more coarse-grained spatial pattern of basal prey survival compared to that produced when higher levels of sensory stress reduce reactive ranges.

Although not seen in our study, as sensory stress continues to increase, intermediate prey sensory detection of basal resources may erode, and sensory stress can have an indirect positive effect on basal prey abundances by reducing intermediate prey CEs (Figure 3.5; upper left panel). For example, along a turbidity gradient, zooplanktivorous fish foraging rates increased as turbidity increased, due to suspected decreases in the importance of piscivorous fish NCEs (Pangle et al. 2012). Yet, zooplanktivore foraging rates decreased at higher turbidity levels due to a decline in visually-mediated foraging abilities (Pangle et al. 2012).

Regardless of sensory stress, physical stress hinders intermediate prey motility and so foraging declines as physical stress increases. Like predictions in traditional models (consumer stress model: Menge and Sutherland 1987; Menge and Olson 1990), CEs are not important in high physical stress environments and basal prey are released from intermediate consumer control (Figure 3.5; right panel). In this study, at the tide-site combination where we estimated current speed to be the highest, blue crab NCEs were not important and consumer stress models predicted mud crab and oyster interactions (i.e. SN during spring tide). We saw a positive effect of abiotic conditions on oyster survival due to reduced mud crab CEs. However, unlike sensory stress, a given level of physical stress produces a spatially homogenous effect on basal prey survival.

Our model was influenced by results from this study in which prey chemosensory detection was modified by hydrodynamics. However, the interaction between sensory and physical stressors likely is general and this conceptual model can be used to predict predator controls and indirect effects in other environmental contexts. Odor cues are also transported as filamentous plumes by turbulent air flow in terrestrial habitats, which affects the spatial and temporal distribution of chemical signals (Koehl 2006). Thus, wind may affect chemoperception of predators by prey while also imposing physical limitations on walking and flying, which could inhibit prey ability to respond to predators (Cherry and Barton 2017). Mechanosensory detection, which is important in predator detection for arthropod prey in both aquatic and terrestrial habitats (Casas and Dangles 2010), can be hindered in high flow environments due to decreased signal to noise ratio (Robinson et al. 2007). Related environmental properties that impose different stressors should both be considered when determining how predator effects vary across environmental gradients.

CHAPTER 4. HYDRODYNAMIC PHYSICAL AND SENSORY STRESSORS AFFECT THE RELATIVE IMPORTANCE OF CASCADING PREDATOR CONSUMPTIVE AND NON-CONSUMPTIVE EFFECTS

4.1 Abstract

Predators affect community structure by influencing prey density and traits via consumptive (CEs) and non-consumptive effects (NCEs). Physical stress from the environment can reduce the strength of CEs by limiting predator foraging abilities. However, the environment can also affect sensory detection of predators by prey and so change the relative strength of CEs versus NCEs. We measured the strength of blue crab predator effects on mud crab consumption of juvenile oysters across physical (i.e. current speed) and sensory (i.e. turbulence) stress gradients indicated by related flow parameters. The strength of blue crab indirect CEs and NCEs were dependent on flow conditions and regulated uniquely by the different environmental stressors. At low sensory stress, the mere presence of blue crabs indirectly increased oyster survivorship by reducing overall mud crab oyster consumption. This indirect NCE decreased as sensory stress increased with turbulence. At the highest turbulences, mud crabs no longer detected and responded to nonlethal blue crabs. Indirect blue crab CEs on oyster survival increased as sensory stress intensified and enhanced oyster survivorship at high turbulences. Yet, at the highest current speeds, mud crab foraging was severely limited by physical stress and oyster survival benefited from the physical environment irrespective of blue crab presence. Overall, NCEs dominated in relatively benign flow conditions, where total indirect blue crab effects were

strongest. Blue crab indirect CEs became more important in high sensory stress environments, but at strong physical stress levels predator effects diminished.

4.2 Introduction

Predation is fundamentally important in the structure and function of ecosystems (Ripple et al. 2014). Top predators in a tritrophic food chain can increase the abundance of the basal trophic level by eating primary consumers and decreasing their grazing pressure. The ability of predators to indirectly impact lower trophic levels through regulating intermediate prey abundance is known as a density-mediated indirect interaction (DMII). DMIIs have been well-documented as influential in the structuring of a diverse array of ecological communities (Estes and Palmisano 1974, Power et al. 1985, Carpenter et al. 1987, Terborgh et al. 2006, Shurin et al. 2010). In addition to the consumptive effects (CEs) of predators, the presence of predators can induce behavioral, morphological, or life-history changes in prey traits, which has indirect effects on lower trophic levels (Lima 1998, Schmitz 1998, Werner and Peacor 2003, Suraci et al. 2016). Meta-analysis suggests that these indirect non-consumptive effects (NCEs), also known as trait-mediated indirect interactions (TMIIs), can be as strong or at times stronger than CEs (Preisser et al. 2005). However, recent long-term field studies investigating the relative importance of CEs versus NCEs reveal contrasting conclusions about the strength of TMIIs in natural systems (Kimbro et al. 2017, Rinehart et al. 2017, Wada et al. 2017).

Environmental conditions are known to modulate the relative importance of CEs (Menge 1978, Leonard et al. 1998, Bertness et al. 2002, Shears et al. 2008). The consumer stress model predicts that prey are released from predation pressure at high physical stress levels due to reduced predator motility and foraging abilities in harsh environments that impose strong mechanical forces (Menge and Sutherland 1987). For example, the importance of predation in rocky intertidal community structure is reduced at wave exposed sites compared to protected sites because snail predation on mussels and barnacles is physically constrained by hydrodynamic stress inflicted by intense wave action (Menge 1978). In terrestrial systems, wind is a physical stressor that hinders predatory ladybeetle foraging on aphids, which results in increased aphid abundances on soybean plants (Barton 2014). Yet, the consumer stress model does not consider that within physically benign settings some environmental forces can reduce the ability of prey to detect predators (i.e. sensory stress), which may influence the magnitude of CEs and NCEs.

Prey can detect and assess predation threats by using surrounding smells, sounds, and sights associated with predation risk (Munoz and Blumstein 2012, Weissburg et al. 2014). Yet, the physical environment alters prey sensory capabilities (Robinson et al. 2007, Jacobs et al. 2008, Large et al. 2011), and may modify NCEs that mediate trophic cascades. Fish prey species respond to visual predator cues in clear water, but not turbid due to impaired visual perception in turbid conditions (Hartman and Abrahams 2000, Becker and Gabor 2012). Anthropogenic sensory stressors, such as noise and light pollution, affect prey ability to detect predators as well (Barber et al. 2010, Halfwerk and Slabbekoorn 2015). Several species of ground foraging birds reduce the distance at which they respond to an approaching predator stimulus in more noise polluted areas (Petrelli et al. 2017). Many other environmental gradients affect various sensory modalities at levels that are not necessarily stressful physically (Weissburg et al. 2014), but we lack investigations that explore the effect of sensory stress on top-down NCE controls.

Parallel to the consumer stress model, a "sensory stress model" suggests the relative importance of CEs versus NCEs is dependent on whether predator or prey sensory perception declines more rapidly with increasing sensory stress (Smee et al. 2010, Weissburg et al. 2014). In situations where the prey is more affected by sensory stress than the predator, NCEs will decrease as sensory stress increases, but CEs will increase until a sensory stress threshold at which predator sensory detection begins to decline. For example, clams reduce activity in response to blue crab cues in low flow conditions, which decreases blue crab predation rates, yet at intermediate sensory stress levels clams are unable to detect and respond to predation threats causing blue crab predation rates to increase (Smee et al. 2010). However, blue crab CEs decrease in high sensory stress environments because their sensory ability to locate clams is diminished (Smee et al. 2010). Yet, if predators are more affected by sensory stress compared to prey, CEs will decrease in strength as sensory stress increases, yet NCEs will remain important until a point at which prey detection of predators begins to decline. Piscivorous fish foraging rates decline more rapidly than their planktivorous fish prey with increasing turbidity due to differences in distance at which they must visually detect their prey (De Robertis et al. 2003). However, planktivorous fish foraging rates only increase gradually with turbidity due to piscivorous fish NCEs decreasing activity at turbidity levels at which their CEs are limited (Pangle et al. 2012). Yet, knowledge of how environmental variables affect both sensory perception in prey and predators is needed to make predictions using this framework, which is not always well-known.

Neither stress model considers that some environmental features, such as fluid flow, can both physically constrain animal locomotion and diminish sensory perception

(Weissburg et al. 2003, Cherry and Barton 2017), which further complicates the relationship of predator controls across environmental gradients. The importance of predator CEs lessens at high flow conditions in tidal estuaries as a result of physical stress from hydrodynamic forces limiting crustacean foraging success (Leonard et al. 1998, Robinson et al. 2011). Yet, fluid flow can also impair chemosensory detection of potential predators or prey through turbulent mixing, which reduces the concentration and availability of chemical cues (Webster and Weissburg 2001, Jackson et al. 2007). For example, increasing turbulence, while holding flow velocity constant, decreases the distance at which clams detect and respond to blue crab chemical cues which decreases the strength of blue crab NCEs (Smee et al. 2008). Thus, the importance of CEs and NCEs can change along flow gradients based on the results of physical and sensory stress on predators and prey.

We used a tritrophic food chain (blue crab-mud crab-oyster) found in oyster reefs to assess the importance of environmental gradients that impose both physical and sensory stress on top-down predator effects. Tidally driven flows vary spatially and temporally in estuarine systems (Wilson et al. 2013), which has the capacity to regulate predator controls. Blue crabs (*Callinectes sapidus*) are mobile predators found commonly in salt marsh communities that feed primarily on smaller crustaceans and bivalves (Laughlin 1982, Micheli 1997, Byers et al. 2017). Fluid forces restrict blue crab locomotion (Weissburg et al. 2003) and turbulence interferes with blue crab sensory ability to locate prey (Weissburg and Zimmerfaust 1993), which limits blue crab top-down effects in high flow conditions (Smee et al. 2010). Mud crabs (*Panopeus herbstii*) are small xanthid crabs that live within the interstitial spaces of oyster reefs (Meyer 1994) and prey heavily on recently settled oysters (Bisker and Castagna 1987, Rindone and Eggleston 2011, Toscano and Griffen 2012). Mud crabs are readily consumed by blue crab predators (Grabowski et al. 2008, Hill and Weissburg 2013a) and respond to chemical cues from blue crabs by reducing foraging on juvenile oysters (Hill and Weissburg 2013b, Weissburg et al. 2016). While both blue crabs and mud crabs are consumers of juvenile oysters, the small body size and crushing claw morphology of mud crabs make them a more efficient oyster predator within oyster reefs (Hill and Weissburg 2013a, Carroll et al. 2015). Flow conditions affect mud crab foraging performance at high flow velocities and the distance at which mud crabs detect and respond to blue crab chemical cues decreases as turbulence increases (Pruett and Weissburg 2018). Thus, oyster survivorship may vary along flow gradients based on the interaction of physical and sensory stressors modulating blue crab-mud crab dynamics.

In this study, we investigated how physical (i.e. current speed) and sensory (i.e. turbulence) stress gradients affect the strength of blue crab direct predator effects (CEs and NCEs) on mud crab foraging and indirect effects (DMIIs and TMIIs) on juvenile oyster survivorship. Specifically, we examined mud crab consumption of oysters in the presence of simulated blue crab predation, nonlethal blue crab predators, and lethal blue crabs at different flow regimes. These site and tidal type combinations previously demonstrated hydrodynamic effects on mud crab oyster consumption and chemosensory blue crab detection (Pruett and Weissburg 2018). We predicted at low environmental stress conditions, blue crab NCEs would dominate because mud crabs are able to detect and respond to blue crab risk cues, which will reduce foraging on oysters. The outcomes in high sensory stress environments with intermediate physical stress depend on if blue crab sensory detection of mud crabs is impaired at the same turbulence levels that limit mud crab perception of blue crabs. Thus, either blue crab CE strength will increase in high turbulent flow or mud crabs will be released from blue crab predator controls. Lastly, at high physical stress, indirect blue crab effects on oyster survival will not be important because hydrodynamic forcing limits mud crab foraging and the environment enhances oyster survival.

4.3 Methods

4.3.1 Animal collection and maintenance

Blue crabs and mud crabs were obtained from Wassaw Sound (Savannah, GA, USA) and associated tributaries. Blue crabs were collected using baited crab traps. Mud crabs were caught by hand during low tide from oyster reefs. A scientific collecting permit issued by the Georgia Department of Natural Resources approved the collections. Oyster spat (10-16 mm hinge length) were purchased from local commercial hatcheries. All animals were housed in separate flow-through seawater systems at the Skidaway Institute of Oceanography (SkIO). Blue crabs (12-16 cm carapace width (CW)) were maintained individually and fed an *ad libitum* diet of mud crabs beginning 48 hours prior to a field trial. A mud crab diet was chosen to maximize blue crab NCEs because blue crabs fed conspecifics reduce mud crab foraging at higher intensities than when fed oysters (Weissburg et al. 2016). Mud crabs were housed based on CW size classes (15-20, 20-25, 25-30 mm) to prevent cannibalism. Mud crabs were fed an *ad libitum* diet of oysters every 2 days to avoid starvation.

4.3.2 Site description

Field experiments were performed at two sites located in associated tributaries of Wassaw Sound. Priest Landing (PL) site was in Wilmington River, which was downstream of Skidaway Narrow (SN) site located in Skidaway River. Both sites contain mudflats bordered by *Spartina alterniflora* salt marshes, but PL has a higher amount of both loose oyster clusters and patch oyster reefs. PL also had a higher density of blue crabs (~7 blue crabs per trap at PL versus ~2 blue crabs per trap at SN) based on the number of blue crabs captured in baited traps at each site after 24 hours.

4.3.3 Flow estimation

Flow conditions significantly vary between these sites based on previous extensive flow measurements by Wilson et al. (2013). PL is characterized by higher mean turbulent kinetic energy (TKE) and slower current speed relative to SN, which has faster mean current speed and lower TKE (Wilson et al. 2013, Pruett and Weissburg 2018, Appendix A). However, both mean current speed and TKE increase during spring tide compared to mean tide, irrespective of site. Flow parameters are strongly related to tidal range and can be predicted using the relationship between tidal range and either current speed or TKE (Wilson 2011, Pruett and Weissburg 2018). Regression equations calculated by Pruett and Weissburg (2018), which were obtained from flow measurements acquired by Wilson et al. (2013), were used to estimate flow properties during our experiment (Table A.2).

4.3.4 Field experiment

We measured the strength of blue crab predator effects on mud crab consumption of juvenile oysters across physical (i.e. current speed) and sensory (i.e. turbulence) stress gradients indicated by related flow parameters. Experiments were conducted on intertidal mudflats about one tidal foot below mean low water. Mud crab enclosure cages (1.25 m x 1.25 m x 0.3 m) consisted of PVC frames covered by 1 cm^2 vexar mesh. Cage mesh affects flow inside the enclosures by slightly slowing current speed, but mildly increasing turbulence (Hill and Weissburg 2013b). Yet, flow conditions inside the cages are within the range and reflective of the natural conditions documented outside the cages (Hill and Weissburg 2013b, Wilson et al. 2013). An oyster reef was constructed in the center of the enclosure to provide a habitat for mud crabs. The oyster reef was created using a combination of four natural sun-bleached oyster clusters and four artificial oyster clusters. Natural oyster clusters (~0.2 m dia.) were sun bleached to remove live organisms that could provide additional cue sources or food resources but maintain the natural structure of oyster reefs. Smaller artificial oyster clusters (~6 cm dia.) were created by attaching several sun-bleached oyster shells together. Artificial oyster clusters were used to manipulate the placement of oyster spat within the cages. Four oyster spat (10-16 mm) were attached to the surface of artificial clusters using marine epoxy. Four artificial oyster clusters were interspersed within the oyster reef and an additional four artificial oyster clusters were placed 0.3 m away from the reef equidistant from each other. In total, each cage contained 32 oyster spat with 16 inside the reef and 16 outside the reef.

Each enclosure also contained mud crabs and a blue crab predator treatment. Fifteen mud crabs (8 crabs 15-20 mm CW, 4 crabs 20-25 mm CW, and 3 crabs 25-30 mm CW), which mimicked local size distribution and density (Hill and Weissburg 2013b), were added to the oyster reef. Mud crabs were painted with bright paint markers to distinguish from possible mud crab immigrants, but no immigrating mud crabs were found in any cages. Enclosures were assigned to one of four blue crab predator treatments: no blue crab control, mud crab cull (CE only), nonlethal blue crab (NCE only), or lethal blue crab (CE & NCE). The mud crab cull treatment simulated blue crab predation without the presence of blue crab cues and consisted of removing 5 mud crabs (3 crabs of 15-20 mm CW, 1 crab of 20-25 mm CW, 1 crab of 25-30 mm CW). The culling rate and distribution were based on preliminary experiments that measured blue crab 24 h predation rate on mud crabs in enclosures with the same experimental set-up as the field experiment. Nonlethal blue crabs were mobile and able to release chemical cues but chelipeds were clamped shut with heat-shrink tubing covered by duct tape and cinched down by a cable tie to prevent blue crabs from attacking mud crabs. Lethal blue crabs were unrestrained and able to consume mud crabs as well as release chemical cues. Nonlethal blue crabs were replaced after 24 hours to match the NCE strength of an actively foraging blue crab (i.e. lethal blue crab) because blue crab NCEs decrease after 24 hours if not fed (Weissburg and Beauvais 2015).

The number of surviving oysters and remaining mud crabs were counted after 48 h in each enclosure. Per capita mud crab foraging rate for a given enclosure was calculated as the total number of oysters eaten divided by the average mud crab density for the 48-h period. Each 48-h block had 3 replicates per treatment that were randomly placed 5 m apart. The number of replicates was constrained by the limited amount of time enclosures could be set up and taken down during low tide mudflat exposure. Also, only one site at either mean or spring tide could be tested on a given date because of the distance between sites as well as limited mudflat exposure time. Mean or spring tidal type was assigned according to the average low tide height during the 48-h block (Wilson et al. 2013). Mean tide low tide heights ranged between -0.07 m and 0.29 m, while spring tide low tide heights were between -0.37 m and -0.09 m. The average tidal range for each site and tidal type combination blocks was 2.24 m and 2.25 m during mean tide for PL and SN respectively, and 2.65 m for PL and 2.60 m for SN during spring tide.

We performed 24 trial blocks from 2015 to 2018 in the months of late May through early August. One block for PL at mean tide experienced much higher water temperatures (> 30 °C) and air temperatures (> 37 °C) than the other blocks so was omitted from data analysis. One block for SN during spring tide occurred during a tropical storm and was removed from analysis as well. Occasionally (7 out of 22 blocks), there were not enough animals to perform three replicates of each blue crab treatment, so a third replicate of some treatments were omitted. One block at PL during mean tide only had two replicates of each blue crab treatment due to cage shifting as a result of improper staking into mudflat.

4.3.5 Statistical analysis

Mud crab recovery after 48 hours was analyzed using a mixed-effects model fit by REML to assess the effect of blue crab predator treatment on mud crab densities and if this differed between sites and tidal types. Fixed effects were site, tidal type, and blue crab predator treatment with block date as a random effect. Per capita mud crab foraging rates and oyster survival were also analyzed using this mixed-effects model. Oyster survival data were square-root transformed to meet normality assumptions. Mixed-effects model analysis was performed using the lme4 package (Bates et al. 2015) for R version 3.3.1 (R Core Team 2017) and the degrees of freedom and *P* values were calculated using Kenward-approximations in the lmerTest package (Kuznetsova et al. 2017). Any post hoc comparisons were done using the lsmeans package (Lenth 2016).

We calculated the effect size of blue crab predator direct effects on per capita mud crab foraging using ratio-based indices (Trussell et al. 2006, Okuyama and Bolker 2007). We defined CE, NCE, and total direct effect (TE) as:

$$\mathrm{CE} = 1 - \frac{\text{per capita foraging with lethal blue crab}}{\text{per capita foraging with nonlethal blue crab}}$$

$$\mathrm{NCE} = 1 - \frac{\text{per capita foraging with nonlethal blue crab}}{\text{per capita foraging with no blue crab}}$$

$$\mathrm{TE} = 1 - \frac{\text{per capita foraging with lethal blue crab}}{\text{per capita foraging with no blue crab}}$$

The numerator was per capita mud crab foraging rate in a single replicate for the given treatment and the denominator was the average per capita mud crab foraging rate of the stated treatment for a given trial block. We calculated CEs by comparing per capita foraging in the lethal blue crab treatment to the nonlethal blue crab treatment because the cull treatment did not mimic the same predation rate as the lethal treatment and may have underestimated CEs (see *Mud crab recovery* results). Negative direct effect sizes indicate that the blue crab direct effect enhances mud crab foraging.

The indirect effect of blue crab predators on oyster survival was also calculated. We calculated the effect size for density-mediated indirect interactions (DMII), trait-mediated indirect interactions (TMII), and total indirect interactions (TII) as:

$$\mathrm{DMII} = \frac{\text{oyster survival with lethal blue crab}}{\text{oyster survival with nonlethal blue crab}} - 1$$

$$\text{TMII} = \frac{\text{oyster survival with nonlethal blue crab}}{\text{oyster survival with no blue crab}} - 1$$

$$\text{TII} = \frac{\text{oyster survival with lethal blue crab}}{\text{oyster survival with no blue crab}} - 1$$

Like direct effect size, the numerator was the number of remaining oysters in a single replicate for the given treatment and the denominator was the average number of remaining oysters of the stated treatment for a given trial block. Positive indirect effect sizes indicate blue crab indirect effect benefits oyster survival.

We used multiple regression models to analyze the relationship between blue crab predator effect size and flow properties. Flow measurements during each trial block were estimated using the predictive relationship between tidal range and flow conditions (regression equations derived by Pruett and Weissburg 2018, Table A.2). Four multiple regression analyses were performed in R, in which each direct and indirect predator effect size was regressed against current speed and TKE. Current speed was not a significant predictor in any of the multiple regressions ($P > 0.05$), so was dropped from the model and individual regressions with only TKE were ran. Indirect effect sizes (DMII and TMII) were log-transformed to meet normality assumptions.

4.4 Results

4.4.1 Mud crab recovery

Only blue crab treatment had a significant effect on the number of mud crabs recovered after 48 hours (Table 4.1). All treatments significantly differed from one another but the most mud crabs were recovered in the control and nonlethal blue crab treatment (Figure 1.1). Mud crab recovery was lowest in the cull and lethal blue crab treatments, with 28% and 50% less recovery compared to the control in the cull and lethal treatments respectively (Figure 4.1). The difference in mud crab final densities between the cull and lethal treatment suggests the cull treatment did not sufficiently mimic true blue crab consumption rates on mud crabs.

Table 4.1 Mixed-effects model analysis of the effects of site, tidal type, and blue crab treatment on the number of mud crabs recovered after 48 h (* denotes significant *P* < 0.05). Significance did not change with removal of three-way interaction from the model.

Source	*df* (num, den)	*F*-value	*P*-value
Site	1, 18.0	0.366	0.553
Tidal type	1, 18.0	0.036	0.852
Treatment	3, 215.3	40.2	<0.001*
Site*Tidal type	1, 18.0	0.800	0.383
Site*Treatment	3, 215.3	0.539	0.656
Tidal type*Treatment	3, 215.3	0.587	0.624
Site*Tidal type*Treatment	3, 215.3	0.771	0.511

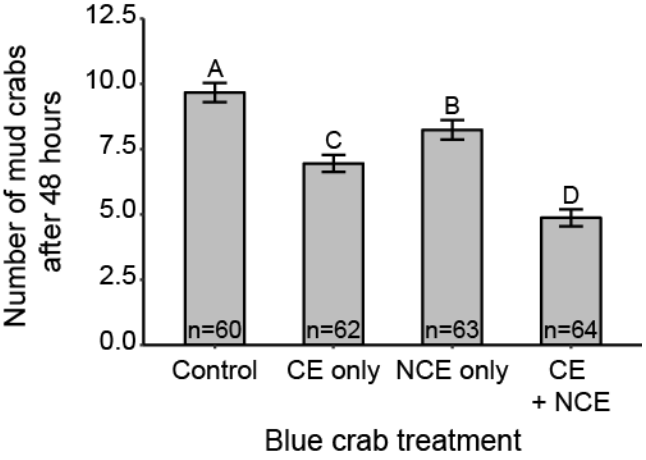

Figure 4.1 Number of mud crabs (mean ± SE) recovered from cages after 48 hours for each blue crab predator treatments (control=no blue crab, CE only=cull, NCE only=nonlethal blue crab, CE + NCE= lethal blue crab). Different letters denote means that are significantly different based on Tukey post hoc tests (*P* < 0.05).

4.4.2 Mud crab foraging

Mud crab per capita foraging rate was only influenced by site (Table 4.2), in which mud crab foraging was 26% greater at Priest Landing (PL) relative to Skidaway Narrows (SN). Blue crabs did not have a significant effect on mud crab foraging, which resulted in weak direct blue crab effects (Figure 4.2). The largest magnitude of direct effect strength was negative CEs at PL during mean tide, which has moderate turbulence, but low flow speed compared to the other site and tidal type combinations (Figure 4.2.a). The negative effect indicates reduced mud crab density may have weakly enhanced mud crab per capita foraging at this site and tidal type. The strength of CEs on mud crab foraging had no relationship with estimated turbulent kinetic energy (TKE; Figure 4.2.b; $F_{1,61} = 2.48$, $P = 0.077$, $r^2 = 0.034$), but non-consumptive effects (NCEs) decreased with increasing TKE (Figure 4.2.c; $F_{1,61} = 6.60$, $P = 0.013$, $r^2 = 0.083$).

Table 4.2 Mixed-effects model analysis of the effects of site, tidal type, and blue crab treatment on mud crab per capita foraging rate (* denotes significant *P* < 0.05). Significance did not change with removal of three-way interaction from the model.

Source	*df* (num, den)	*F*-value	*P*-value
Site	1, 18.0	7.08	0.016*
Tidal type	1, 18.0	2.21	0.154
Treatment	3, 215.2	2.09	0.102
Site*Tidal type	1, 18.0	0.883	0.360
Site*Treatment	3, 215.2	0.507	0.678
Tidal type*Treatment	3, 215.2	0.572	0.634
Site*Tidal type*Treatment	3, 215.2	1.12	0.341

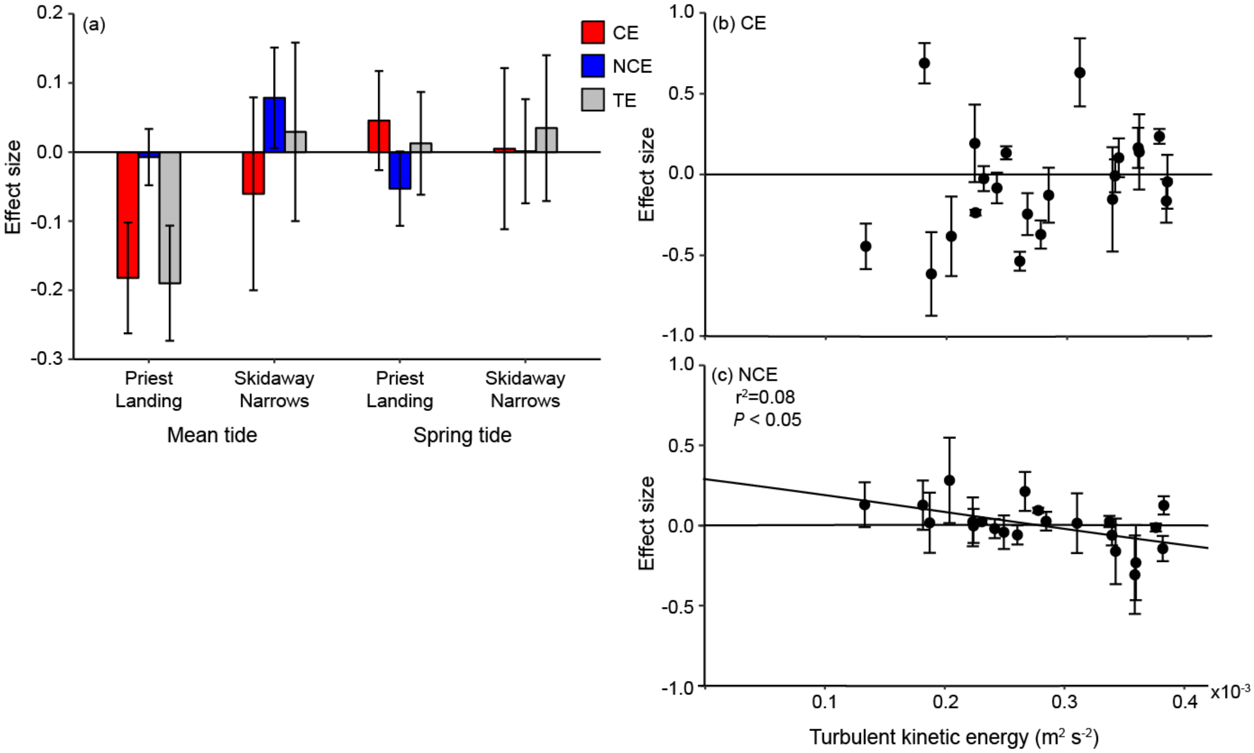

Figure 4.2 a) Consumptive (CE, red bars), non-consumptive (NCE, blue bars), and total predator (TE, gray bars) effect size (mean + SE) on per capita mud crab foraging at each site and tidal type. The strength of b) CEs and c) NCEs (mean + SE) on per capita mud crab foraging during each trial as a function of turbulent kinetic energy (TKE, m^2 s^{-2}).

4.4.3 Oyster survival

Blue crabs had significant indirect effects on oyster survival, as well as significant differences in oyster survivorship between sites (Table 4.3). The number of oysters remaining after 48 hours was 57% higher at SN compared to PL, irrespective of blue crab treatment. Oyster survival was only significantly higher than the no blue crab control when lethal blue crabs were present, which produce both CEs and NCEs, based on Tukey post-hoc test (*P* < 0.05). Survivorship with nonlethal blue crabs was intermediate between the control and lethal blue crab treatment.

Table 4.3 Mixed-effects model analysis of the effects of site, tidal type, and blue crab treatment on the number of oysters surviving after 48 h (* denotes significant *P* < 0.05). Significance did not change with removal of three-way interaction from the model.

Source	*df* (num, den)	*F*-value	*P*-value
Site	1, 18.0	6.69	0.019*
Tidal type	1, 18.0	2.62	0.123
Treatment	3, 215.2	7.29	<0.001*
Site*Tidal type	1, 18.0	1.90	0.184
Site*Treatment	3, 215.2	1.26	0.288
Tidal type*Treatment	3, 215.2	0.757	0.519
Site*Tidal type*Treatment	3, 215.2	2.12	0.098

Individual two-way ANOVAs revealed the importance of indirect blue crab CEs and NCEs on oyster survival differed between site and tidal type combinations (Figure 4.3). There was no effect of blue crab treatment ($F_{3,43} = 1.01$, $P = 0.40$) at PL during mean tide, which had the lowest oyster survival among the site and tidal type combinations regardless of treatment (Figure 4.3.a). Date of trial ($F_{5,43} = 1.20$, $P = 0.32$) and the interaction with blue crab treatment ($F_{15,43} = 1.40$, $P = 0.19$) had no effect either. Blue crabs had a significant effect on oyster survival during mean tide at SN ($F_{3,37} = 6.51$, $P = 0.0012$) by increasing survivorship when nonlethal (NCE only) or lethal (CE + NCE) blue crabs were present relative to no-blue crab control (Figure 4.3.b). There was also an effect of trial date ($F_{4,37} = 10.3$, $P < 0.001$), but no significant interaction with treatment ($F_{12,37} = 1.33$, $P = 0.24$). Blue crab treatment also significantly affected oyster survival at PL during spring tide ($F_{3,46} = 6.11$, $P = 0.0014$), but only in the presence of lethal blue crabs (CE + NCE) was survival higher than the no-blue crab control (Figure 4.3.c). Trial date also influenced oyster survival ($F_{5,46} = 10.9$, $P < 0.001$), but not in combination with blue crab treatment ($F_{15,46} = 1.48$, $P = 0.15$). At SN during spring tide, blue crabs had no effect on oyster survival ($F_{3,35} = 0.41$, $P = 0.74$), but survivorship in the no-blue crab control was about 42% higher than SN during mean tide and PL during spring tide, as well as 66% higher than PL during mean tide (Figure 4.3.d). The date of trial had a significant effect on oyster survival ($F_{4,35} = 15.3$, $P < 0.001$), but this was dependent on complicated interaction with blue crab treatment that had no discernible pattern ($F_{12,35} = 2.76$, $P = 0.0094$).

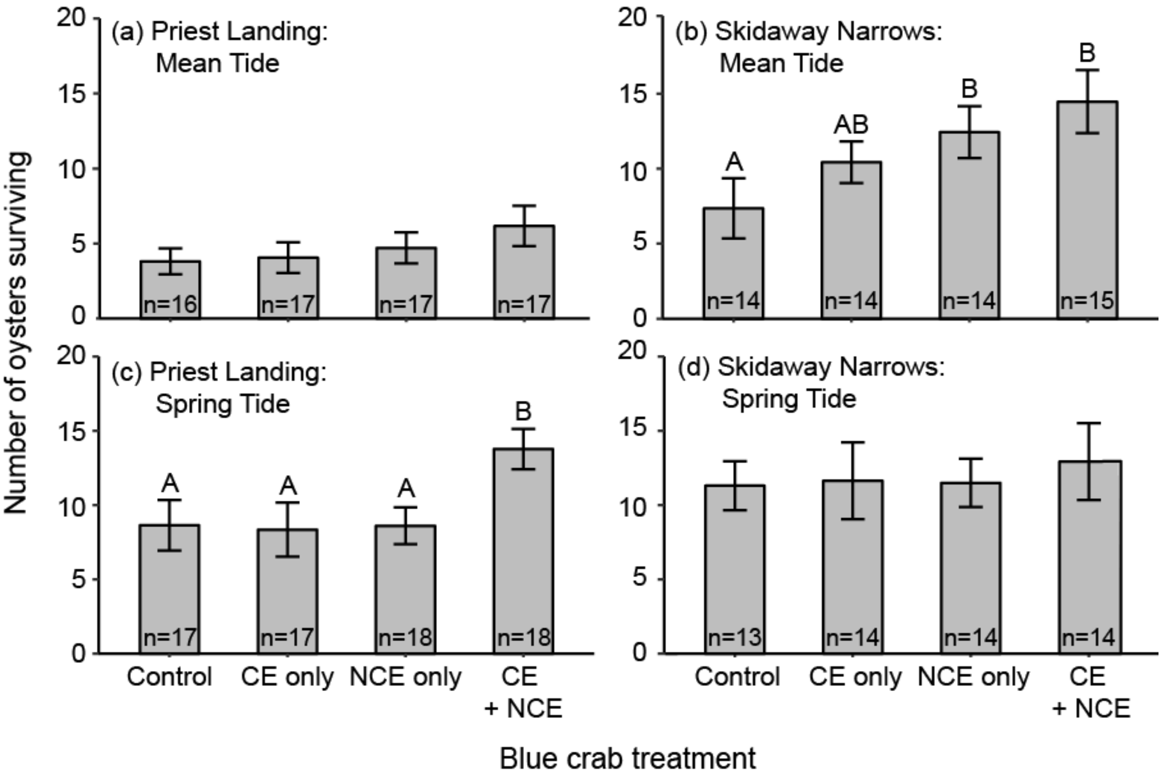

Figure 4.3 Number of oysters surviving (mean ± SE) after 48 hours in each blue crab treatment (control=no blue crab, CE only=cull, NCE only=nonlethal blue crab, CE + NCE= lethal blue crab) during mean tide at a) Priest Landing (PL) and b) Skidaway Narrows (SN) and during spring tide at c) PL and d) SN. There was a significant effect of blue crab treatment at SN during mean tide and at PL during spring tide. Different letters denote means that are significantly different based on Tukey post hoc tests (*P* < 0.05) within these site and tidal type combinations.

Blue crabs had strong indirect effects on oyster survival at certain site and tidal type combinations, but the relative contribution of indirect CEs versus NCEs depended on flow environment. Indirect CEs, also known as density-mediated indirect effects (DMII), were stronger at PL than SN (Figure 4.4.a), in which PL has higher turbulence levels, but lower current speeds than SN. The strength of DMIIs on oyster survival had a positive relationship with estimated TKE (Figure 4.4.b; $F_{1,62} = 11.5$, $P = 0.0012$, $r^2 = 0.14$). Indirect NCEs, which are also called trait-mediated indirect effects (TMII), were strongest at SN during mean tide (Figure 4.4.a), which has low turbulence and moderate flow speeds compared to the other site and tidal type combinations. The strength of TMIIs on oyster survival decreased with increasing estimated TKE (Figure 4.4.c; $F_{1,61} = 6.23$, $P = 0.015$, $r^2 = 0.078$). Neither DMIIs nor TMIIs had appreciable effects on oyster survival at SN during spring tide, which has the highest current speeds (Figure 4.4.a).

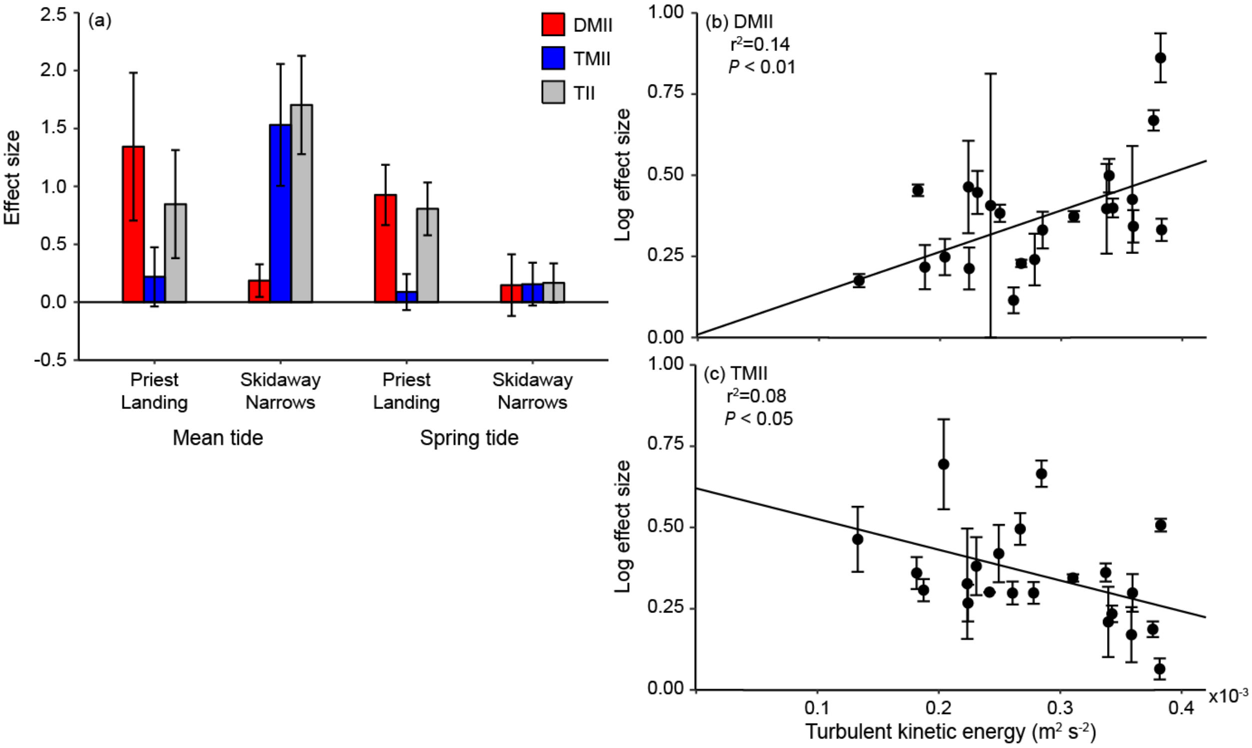

Figure 4.4 a) Density-mediated (DMII, red bars), trait-mediated (TMII, blue bars), and total predator indirect (TII, gray bars) effect size (mean ± SE) on oyster survival at each site and tidal type. The log strength of b) DMIIs and c) TMIIS on oyster survival during each date block (mean ± SE) as a function of estimated turbulent kinetic energy (TKE, m^2 s^{-2}).

4.5 Discussion

Our results suggest that the importance of blue crab cascading CEs and NCEs change across environmental flow conditions that impact mud crab physical and sensory performances through different stressors (Figure 4.5). Blue crab positive TMIIs on oyster survival were strong at low estimated TKEs but decreased in magnitude as sensory stress increased and the ability of mud crabs to detect and respond to blue crab predators diminished. In return, blue crab DMIIs grew in importance as sensory stress increased and were highest in the maximum estimated TKEs. Oyster survival was relatively high regardless of blue crab predator treatments at the fastest estimated current speeds, which physically restricted mud crab foraging on oysters.

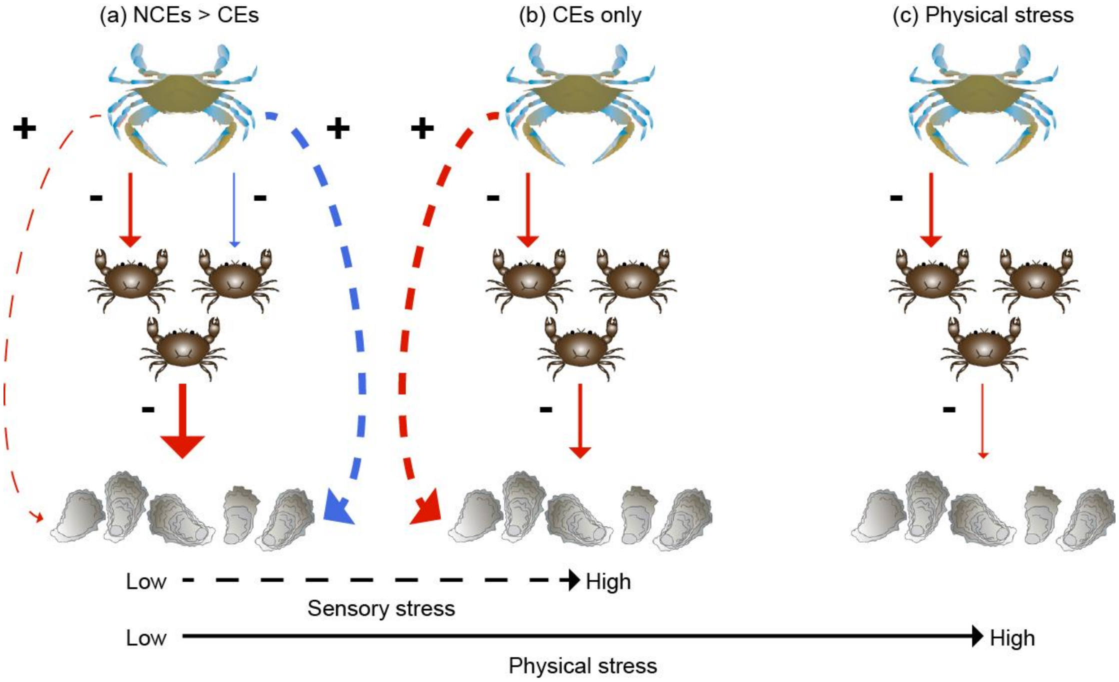

Figure 4.5 Conceptual model of how blue crab direct (solid lines) and indirect (dotted lines) CE (red) and NCE (blue) strengths change across a flow gradient that imposes sensory stress at high turbulence and physical stress at high current speeds on intermediate mud crab prey. Arrow thickness corresponds to magnitude of effect strength. a) At low sensory and physical stress, mud crab foraging is enhanced by blue crab CEs due to reduced interference competition at lower conspecific densities producing weak indirect blue crab CEs on oyster survival. Mud crab reactive range is large due to low sensory stress so blue crab NCEs decrease mud crab foraging which has strong positive indirect effects on oyster survival. b) Mud crab sensory perception is impaired at high sensory stress and blue crab direct and indirect NCEs are not important. Intermediate physical stress begins to limit mud crab foraging abilities so per capita foraging no longer benefits from decreased competition and blue crabs have strong positive indirect effects on oyster survival. c) High physical stress constrains mud crab foraging and physical stress increases oyster survival. Blue crabs only have direct CEs on mud crab survival. Blue crab and oyster images from the Integration & Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). Mud crab image by the author.

Despite strong indirect blue crab effects on oyster survival, blue crab predators only weakly influenced mud crab foraging behavior. Only at the lowest current speeds estimated at the PL site during mean tide did blue crabs appear to affect mud crab foraging, in which blue crab CEs increased per capita foraging through mud crab density reductions (Figure 4.2.a). Predatory fish cues in a mesocosm experiment also showed no effect on individual mud crab foraging rates but decreases in mud crab density enhanced individual crab foraging on oysters (Hughes et al. 2012). Reduced prey densities by predators in systems where competition for resources is intense generally benefit prey foraging and growth rates by decreasing interference competition both within and between species (Grabowski and Powers 2004, Trussell et al. 2006, Belovsky et al. 2011). Thus, when physical stress is low, prey foraging abilities are at peak performance and can fully take advantage of reduced interference competition which potentially offsets predator DMIIs.

Blue crab TMIIs were strongest in low estimated TKE conditions at SN during mean tide, where the sensory environment allowed for mud crabs to sufficiently detect and respond to blue crab predators, which increased oyster survival. SN during mean tide is the only site and tidal type combination where oyster survival was significantly higher in the non-lethal blue crab treatment compared to the no-blue crab control (Figure 4.3). TMII strength decreased as turbulence increased (Figure 4.4.c). Higher turbulent mixing changes chemical plume structures by creating more infrequent and shorter bursts of cue signals at lower peak concentrations (Koehl 2006, Jackson et al. 2007), which reduces predator and prey chemosensory abilities (Weissburg and Zimmerfaust 1993, Powers and Kittinger 2002, Smee et al. 2008). The lack of indirect blue crab NCEs at PL is probably a result of reduced mud crab ability to detect and respond to blue crabs at this higher estimated TKE site. We previously found large mud crab reactive ranges, defined as the maximum distance away from caged blue crabs at which mud crab oyster consumption differed from the no-blue crab control, at both PL and SN during mean tide (Pruett and Weissburg 2018). However, we found no effect of indirect blue crab NCEs on oyster survival in this study at PL during mean tide, despite similar estimated flow conditions (Figure 4.3.a). Caged blue crabs were placed on both sides of the oyster reef in Pruett and Weissburg (2018), which allowed mud crabs to receive blue crab chemical cues during both ebb and flow tide. There was only one blue crab during this study, rendered nonlethal but still able to hunt naturally within the mud crab enclosure, which may have produced a different distribution or concentration of chemical risk cues (Schmitz et al. 2004, Weissburg et al. 2014). Mud crabs and other prey species often reduce the intensity of their antipredator responses in the presence of lower concentration of chemical cues as a result of lower predator density or biomass (Ferrari et al. 2006, Hill and Weissburg 2013b, Gosnell et al. 2017). Thus, moderate turbulence levels and variable risk cue distribution or concentration due to a mobile predator may have caused the strength of blue crab indirect NCEs to decline.

Concomitantly, blue crab DMIIs increased with sensory stress as a result of mud crab sensory performance declining more rapidly than blue crab predators (Figure 4.4.b). Lethal blue crabs increased oyster survival at PL during spring, which has the highest estimated TKE levels, despite no effect of the simulated predation (cull) or non-lethal blue crab predator treatment (Figure 4.3.c). The cull treatment attempted to mimic natural blue crab predation rates on mud crabs, but average final mud crab density was about 30 percent higher in the cull treatment compared to lethal blue crab cages (Figure 4.1). Oyster survivorship has been shown to increase with decreasing mud crab densities in both laboratory (Hughes et al. 2012) and field studies (Kimbro et al. 2017). Thus, the positive indirect blue crab effect on oyster survival only in the lethal blue crab treatment at PL during spring tide was likely a result of mud crab density reduction by blue crab predators. Yet, blue crab predation rates on mud crabs were similar at both the lowest sensory stress site and tidal type combination (SN mean tide) and the highest (PL spring tide), suggesting that blue crabs were unable to fully exploit mud crab decreased ability to detect blue crabs. Blue crabs also may experience some sensory deficiency, which is known to be affected by turbulence (Weissburg and Zimmer-Faust 1993, Powers and Kittinger 2002, Jackson et al. 2007), at sensory stress levels that greatly hinder mud crab predator detection which limits blue crab CEs. Overall, the mismatch in the extent that the same sensory stressor affects both mud crab and blue crab chemosensory performance has a positive effect on basal resource abundance.

Consumer stress models (Menge and Sutherland 1987, Menge and Olson 1990) predicted the outcome of interactions at the highest current speeds, in which blue crab predator effects were negligible because mud crab foraging was constrained by hydrodynamic physical forcing. Mud crab foraging was lower at SN which has higher estimated current speeds than PL. Oyster survival was relatively high at SN during spring tide regardless of predator treatment (Figure 4.3.d). Previous results from SN during spring tide (Pruett and Weissburg 2018) and other field studies measuring reef-dwelling crab species foraging rates on bivalves (Leonard et al. 1998, Robinson et al. 2011) demonstrate depressed crab foraging in higher flow velocities. Although blue crabs had no effect on mud crab foraging behavior or oyster survival, they still decreased mud crab abundance, which has important consequences for prey demography.

This study demonstrates that environmental gradients which inflict physical and sensory stress can be a driving force in regulating the relative importance of top predator controls within a system. We believe our results may provide a general framework to predict the relative strength of cascading CEs and NCEs in tritrophic systems in which prey sensory detection of predators declines more rapidly than their physical ability to forage along an environmental stress gradient (Figure 4.5). Odor-mediated predator-prey interactions across a diverse array of taxa are prevalent in both aquatic and terrestrial systems that contain environmental features that impose substantial sensory stress at levels that are not physically limiting (Kats and Dill 1998, Dicke and Grostal 2001, Ferrari et al. 2010, Parsons et al. 2018). Like in aquatic environments, wind can physically constrain animal locomotion and alter odor plume structure to reduce chemosensory perception (Wilson et al. 2015, Cherry and Barton 2017). Other sensory modalities used by prey to detect predators are also impaired in environments that are not physically harmful, such as visual detection in turbid waters (Chivers et al. 2013) and mechanosensory abilities in moderate turbulences (Buskey et al. 2012). Anthropogenic stressors often affect sensory processes through increased background noise, altered quality or quantity of risk cues, or disturbed sensory mechanisms before harming physical or physiological performance (Lurling and Scheffer 2007, Leduc et al. 2013, Halfwerk and Slabbekoorn 2015). Thus, we anticipate understanding how predator and prey sensory performances change across environmental conditions will aid in forecasting when and where NCEs should dominate.

In this conceptual framework, top predator NCEs regulate total predator effects in low physical and sensory stress conditions due to high prey reactive ranges that alleviate predator CEs (Figure 4.5.a). NCE strength will begin to decline as sensory stress increases and prey reactive ranges decrease. The presence of predator chemical cues reduces whelk consumption of barnacles, but this whelk antipredator response decreases in intensity along a sublethal copper concentration gradient that inhibits whelk chemosensory abilities at higher concentrations (Kwan et al. 2015). At high sensory stress conditions but moderate physical stress levels, CEs should dominate (Figure 4.5.b). Copepod reactive distances to mechanical stimuli simulating predation threat decrease in more turbulent flow conditions (Robinson et al. 2007). Consequently, predatory fish foraging in flume experiments was more successful at turbulence levels in which copepod reactive distance was hindered (Clarke et al. 2009), supporting that predator CEs prevail in environments in which prey sensory detection is compromised but predators themselves are still able to locate prey. However, sensory perception can decline more rapidly in predators than prey in some cases, which would lessen CEs and potentially releases prey from predator controls. Release from CEs will have negative effects on basal resources until sensory or physical stress limits intermediate prey foraging. High physical stress hinders intermediate prey foraging and eliminates top predator indirect effects (Figure 4.5.c), but predators may still affect intermediate prey populations through direct consumption if predator foraging is not physically restrained.

The landscape of fear has been a useful framework for assessing the potential importance of NCEs across heterogeneous environments that create spatial variation in prey perception of predation risk (Laundré et al. 2001, Gaynor et al. 2019). Habitat heterogeneity produces areas of risk and refuge as a result of actual differences in predation risk, which can be perceived by prey and result in modifications of prey foraging behavior (Matassa and Trussell 2011, Gorini et al. 2012, Burkholder et al. 2013). However, prey perception of predation threat is dependent on the availability and reliability of predator risk cues (Luttbeg and Trussell 2013). The distribution of these risk cues is affected by the physical environment and habitat structure which shapes the sensory landscape (Jacobs et al. 2008, Riffell et al. 2008, Wilson and Weissburg 2013). We found that sensory landscapes not only differ between sites, but also within sites due to temporal fluctuations in flow environments as a result of the regulation of tidal amplitude by lunar cycles. Although the short time scale of our study (48 hours) allowed us to identify environmental mechanisms important in regulating the relative strength of CEs and NCEs on prey behavior, we need long-term investigations to determine if NCEs have significant effects on population dynamics that persist across temporal landscapes of fear.

APPENDIX A. SUPPLEMENTAL MATERIALS FOR CHAPTER 3

A.1 Flow measurement methods

Briefly, flow characteristics in the x (along-stream), y (cross-stream), and z (vertical) directions were collected by acoustic Doppler velocimeters (ADVs; Nortek) at 16 Hz in 5-minute burst with 15-minute gaps between bursts. Water flow measurements were taken 10 cm above the substrate with the ADV positioned so that the u-velocity (x-direction) component was aligned with the direction of the primary tidal-flow. Four or six ADVs were deployed simultaneously at one site for four consecutive tidal cycles (roughly 48 hours). Mean burst velocity and turbulent kinetic energy (TKE) were calculated after the flow data was phase filtered and wave motion contribution was removed. Additionally, bursts with any mean component correlation coefficients less than 70% or that contained more than 500 consecutive data points with an average correlation coefficient less than 70% were removed. See Wilson et al. (2013) for detailed methods. The exact tidal heights at spring and mean tidal types differed somewhat during measurement of flow versus the field experiments (Table A.1). Despite the slight differences, the flow measurement data set involved multiple instruments collecting data simultaneously over four consecutive tidal cycles for each tidal type and site combination, and thus gives a good general characterization of the impact of tidal type and site on flow properties during the field experiments. Mean velocity was analyzed as vector averaged current speed which is the absolute value of flow velocity independent of tidal direction.

Table A.1 Average low tide height and tidal range during 12-h ADV deployments (one tidal cycle) for flow measurements and 24-h field caging experiments (2 tidal cycles) at each site and tidal type.

Site	Tidal type	ADV deployment		Field experiments	
		Average low tide height (m)	Average tidal range (m)	Average low tide height (m)	Average tidal range (m)
Priest Landing	Mean	-0.098	2.032	-0.031	2.163
	Spring	-0.350	2.798	-0.193	2.537
Skidaway Narrows	Mean	-0.124	1.904	0.006	2.211
	Spring	-0.292	2.548	-0.222	2.673

A.2 Flow measurement results

Tidal type and site both had a strong impact on flow properties. Average current speed was higher during spring tide compared to mean tide at both sites, but mean speed was faster at Skidaway Narrows (SN) relative to Priest Landing (PL) (Table A.3). Mean current speed was about 2 cm s^{-1} higher at SN compared to PL during each tidal type and about 5 cm s^{-1} higher during spring versus mean tide for both sites. Overall, mean speed had a two-fold increase during ebb compared to flood tides within a tidal cycle, but the difference between ebb and flood tidal speed was site and tidal type specific (Table A.3). Mean speed was uniformly high during flood and ebb tide (roughly 12 cm s^{-1}) at SN during spring tide but increased from about 4 cm s^{-1} to 9 cm s^{-1} during mean tide. Mean speed at PL was always higher during ebb tides, increasing by roughly 6 cm s^{-1} and 8.5 cm s^{-1} during mean and spring tide, respectively.

Average TKE was also affected by tidal type and site, leading to stronger TKEs during spring tide at both sites. Unlike mean speed however, average TKE was higher at

PL (Table A.3). Average TKE was almost twice as large at spring tide and nearly 50 % greater at PL compared to SN. Similar to mean speed trends, TKE was twice as strong during ebb tide relative to flood. Yet, average TKE at mean tide increased about 7 times at PL between flood and ebb tide, but only twice at SN. At the SN site, the pattern of difference in TKE during flood versus ebb tides was like the pattern in mean speed; TKE showed little change during the two tidal stages at spring tide. Average TKE at SN during spring tide only increased from 0.274 x 10^{-3} m^2 s^{-2}, which was the highest average TKE for flood tide, to 0.282 x 10^{-3} m^2 s^{-2} during ebb tide.

The distributions of flow parameter values were also noticeably different between site and tidal type (Figure A.2). Tidal type influenced the distribution of current speed, with a higher frequency of larger current speed values during spring as opposed to mean tide. During spring tide, the mode at SN (the high mean speed site) was greatly right shifted (Figure A.2.a). There was a peak in distribution at about 2 cm s^{-1} for PL and around 4 cm s^{-1} for SN during mean tide, with the peak height being about 20% lower at SN, which also had a longer right tail. The frequency of high-speed values was higher during spring tide, with both sites having peaks of equivalent heights and shifted further right than the mean tide peaks. The difference between mode at PL and SN during spring tide was much more pronounced than the difference in mean speed. There was almost a three time increase in mode between sites at spring tide, with a peak at about 6 cm s^{-1} at PL and 17 cm s^{-1} at SN, although PL had a slightly longer right tail.

TKE distributions also showed effects of tidal type and site, with a higher frequency of larger TKE values during spring tide compared to mean tide, and with the distributions at PL (the high TKE site) more skewed toward higher values (Figure A.2.b). Distributions peaked at about 0.05 x 10^{-3} m^2 s^{-2} at both sites during mean tide. The height of the peak was over twice as large at SN, and with a shorter right tail. There was a higher frequency of higher TKE values at spring tide; modes were only shifted right slightly compared to mean tide, the peaks were generally smaller, and the right tails longer. The modal peak at SN was larger and slightly shifted right relative to PL, but the right tail was much longer at PL, skewing it towards higher TKE values.

In summary, broadly speaking, the SN site had generally higher current speed and lower TKE when compared to the PL site and these differences were much greater during spring versus mean tides. Observed differences in averages and distributions of flow parameters are conservative due to the slight variation in tidal heights during flow measurements versus field experiments (Table A.1). Average low tide heights for both sites during mean tide were lower for the ADV deployments than field experiments, which suggest that current speed and TKE during the field experiments were lower than represented here and the disparity between mean and spring tide may be even larger. Also, the difference in current speed between PL and SN during spring tide may have been even more pronounced than depicted. The tidal range at PL for ADV deployment was higher than at SN and for field experiments, thus actual flow measurements at PL for spring tide during the field experiments may have been lower than reported.

Table A.2 Regression analysis results for comparison of tidal range and 12-h average (one tidal cycle) of flow parameters (current speed (|ū|) and turbulent kinetic energy (TKE)) for Priest Landing and Skidaway Narrows.

Site	Flow parameter	*df* (num,den)	*F*-value	*P*-value	R^2	Regression Equation
Priest	|ū|	1,6	106.084	<0.001*	0.946	-10.082 + 7.548 (range)
Landing	TKE	1,6	14.790	0.008	0.711	-0.379 + 0.278 (range)
Skidaway	|ū|	1,6	6.168	0.048	0.507	-1.484 + 4.825 (range)
Narrows	TKE	1,6	12.959	0.011	0.684	-0.215 + 0.194 (range)

Table A.3 Mean current speed (|ū|) and average turbulent kinetic energy (TKE) for flood and ebb tide at each site and tidal type during the ADV deployments in Table A.1.

Site	Tidal Type	Current speed |ū| (cm s^{-1})		Turbulent kinetic energy (TKE) (m^2 s^{-2} x 10^{-3})	
		Flood	Ebb	Flood	Ebb
Priest	Mean	2.187	8.136	0.047	0.395
Landing	Spring	5.649	14.232	0.263	0.515
Skidaway	Mean	3.781	9.201	0.094	0.194
Narrows	Spring	12.121	12.152	0.274	0.282

Table A.4 Mixed-effects model analysis of the effects of site, tidal type, and distance treatment on mud crab refuge use (* denotes significant *P* < 0.05). Significance did not change with removal of three-way interaction from the model.

Source	*df* (num, den)	*F*-value	*P*-value
Site	1, 17.1	0.027	0.872
Tidal type	1, 17.1	9.409	0.007*
Distance	5, 175.4	2.268	0.049*
Site*Tidal type	1, 17.1	0.123	0.730
Site*Distance	5, 175.4	0.032	0.999
Tidal type*Distance	5, 175.4	0.822	0.536
Site*Tidal type*Distance	5, 175.4	0.165	0.975

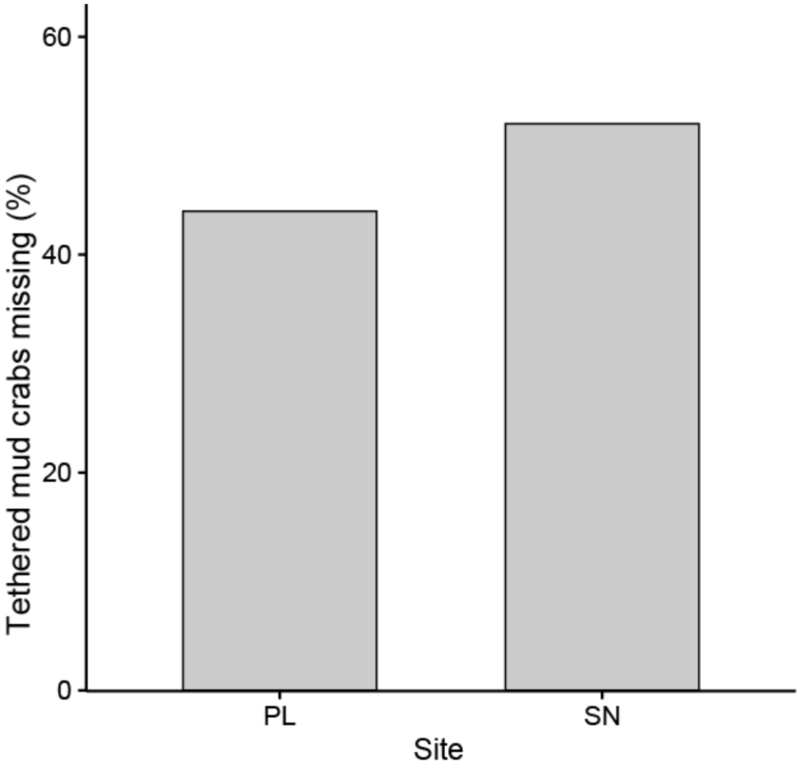

Figure A.1 The percent of tethered mud crabs not recovered (i.e. consumed) from Priest Landing (PL, *n*=173) and Skidaway Narrows (SN, *n*=120).

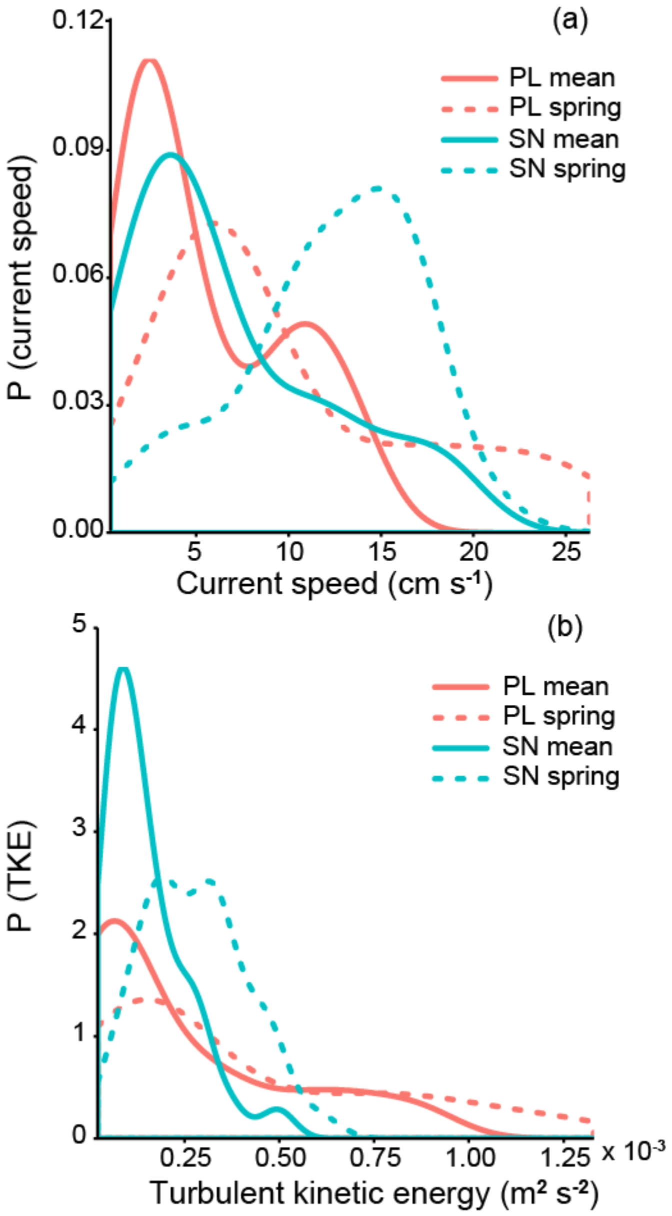

Figure A.2 The probability density function (PDF) of (a) current speed and (b) turbulent kinetic energy (TKE) at Priest Landing (PL, blue lines) and Skidaway Narrows (SN, red lines) at mean tide (solid lines) and spring tide (dashed lines).

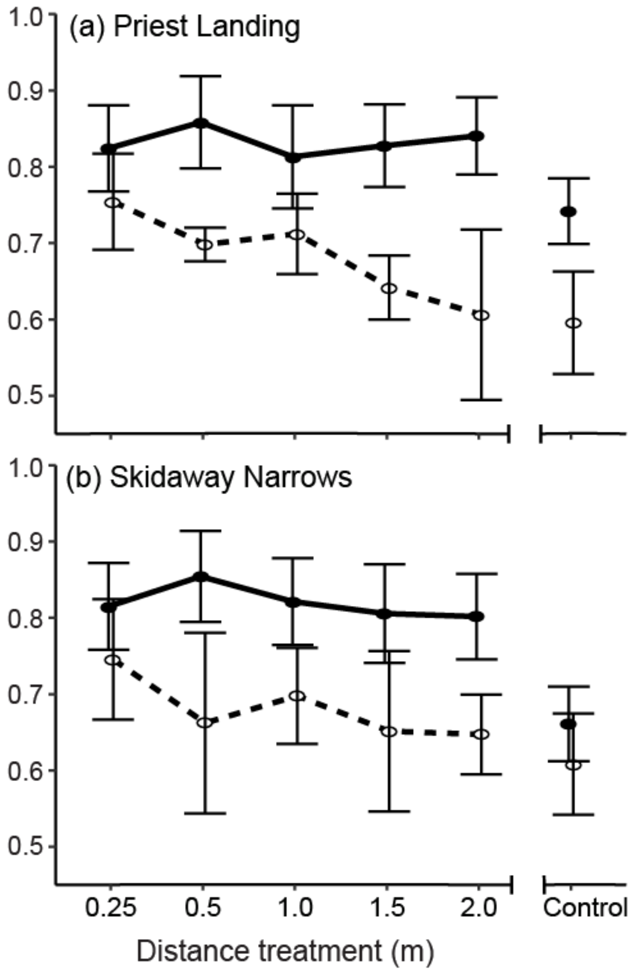

Figure A.3 Proportion of oysters consumed by mud crabs inside the refuge (mean ± SE) at different distances away from caged blue crabs during mean tide (closed symbols, solid lines) and spring tide (open symbols, dashed lines) at (a) Priest Landing (PL; *n* for mean tide=64, *n* for spring tide=49) and (b) Skidaway Narrows (SN; *n* for mean tide=61, *n* for spring tide=48).

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