SENSORY LANDSCAPE IMPACTS ON ODOR-MEDIATED PREDATOR-PREY INTERACTIONS AT MULTIPLE SPATIAL SCALES IN SALT MARSH COMMUNITIES

A Thesis
Presented to
The Academic Faculty

by

Miranda L. Wilson

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy in the
School of Biology

Georgia Institute of Technology
August 2011

SENSORY LANDSCAPE IMPACTS ON ODOR-MEDIATED PREDATOR-PREY INTERACTIONS AT MULTIPLE SPATIAL SCALES IN SALT MARSH COMMUNITIES

Approved by:

Dr. Marc Weissburg, Advisor
School of Biology
Georgia Institute of Technology

Dr. Donald Webster
School of Civil and Environmental Engineering
Georgia Institute of Technology

Dr. Mark Hay
School of Biology
Georgia Institute of Technology

Dr. Julia Kubanek
School of Biology
Georgia Institute of Technology

Dr. Lin Jiang
School of Biology
Georgia Institute of Technology

Date Approved: June 29, 2011

To my parents,

whose support is unmatched

ACKNOWLEDGEMENTS

I want to thank my committee members for their guidance and support during the past six years. In particular, I would like to thank my advisor Marc Weissburg for putting up with me through endless manuscript drafts, providing insightful advice for experiments, and staying out of my way when I was actually being productive.

I would particularly like to thank my office mate, Jennifer Hill. She has put up with me, laughed at my stupid jokes, and threatened me into having fun for the last six years. I won't forget the late nights of apparent delirium which resulted in "the other other white meat" and names for the boat that we'll never ever talk about. I also thank her for all the other things that we'll never ever talk about; the good and the bad. All I can say is that we have a love-hate relationship, but it must be more love because we haven't killed each other yet.

I also would like to thank the rest of my cohorts for providing much needed emotional support. I would particularly like to thank Jennifer Page, who helped me survive the first three years of my graduate school career by cooking for me, helping me figure out fluid dynamics, and answering the phone when I called late at night freaking out. Also thanks to Rachel Lasley-Rasher for her friendship and support. I enjoyed our endless discussions about science, experimental design, and life in general.

I would like to thank Lauren Connolly, the newest member of our lab for helping me make it through the last year. I may have just gone insane without her friendship and invigorating outlook on life.

The final spot of thanks I have is for the most important people in my life; my family and loving husband. Thanks to my family, and extended family, who have

supported me throughout the entire Ph.D. process with words of kindness, strategically planned vacations, and field help. My dad has sailed with me every step of the way; which has probably resulted in more than he ever wanted to know about crab tracking, oyster reefs, ADVs, and matlab. My mom shared much of my dad's enthusiasm for my research and was there to pick me up when I got down, and of course brag about me to all of her friends.

I don't think I can say thank you enough to my loving husband for sticking with me for the last 9 years. Without him I certainly would have gone insane from overwork and unhappiness. Thanks to him for teaching me that work isn't everything and that friends and family are just as, or more important, to achieving balance in my life.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

SUMMARY

This collection of research examines how changes in the sensory landscape, mediated by both odor and hydrodynamic properties, impact odor-mediated predator-prey interactions in salt marsh communities. I examined these interactions at a variety of spatial scales relevant to mobile benthic predators and in different sensory landscapes in an effort to determine and elucidate mechanisms mediating the context-specificity of predator-prey interactions in these environments. Previous work on the topic has largely been limited to laboratory flume experimentation using single predator and prey treatments under various turbulence regimes. Although this provides excellent information as to individual predator foraging behaviors and the impact of laboratory generated turbulence on those behaviors, it fails to consider interactions between predators and multiple prey or to encompass realistic and larger scale hydrodynamic regimes. I approached this research using an interdisciplinary framework that combined field and laboratory experimentation to address issues of scale and make connections between predator behavior and patterns of predation in the field.

Oyster reefs are common structural elements in many salt marsh communities that positively impact organisms by providing settlement sites, habitat, and refuge. They also modify the sensory landscape by increasing turbulence and emitting food related odor cues. I investigated the role of oyster reefs in mediating interactions between odor-mediated predators (blue crabs [*Callinectes sapidus*] and knobbed whelks [*Busycon carica*]) and prey (hard clams [*Mercenaria mercenaria*]) associated with those oyster reefs. I found that oyster reefs indirectly impact hard clam prey in a negative manner by enhancing predator foraging success in areas next to the reef matrix despite enhanced turbulence, although patterns of predation were predator-specific. Laboratory experiments showed that oyster reef odors ameliorated the negative impact of structurally-induced turbulence on the foraging success of both predator species. Both field and laboratory experiments show predator-specific responses to oyster reef odors and structurally-induced turbulence that are a result of their species-specific perceptual capabilities. These results indicate that oyster reefs can have negative indirect effects on associated prey species because of changes in the sensory landscape that enhance predator foraging success.

In order to explore other mechanisms that could mediate the sensory landscape perceived by predators, I designed a series of experiments to examine how within-patch prey density and distribution influenced predator foraging behavior and success. We exposed patches of hard clams in four combinations of density (high and low) and distribution (aggregated and random) to naturally occurring densities of blue crab and knobbed whelk predators to assess patterns of predation in the field. Blue crabs had higher predation rates on hard clams in patches containing high densities and aggregated distributions. Knobbed whelks, on the other hand, showed higher predation in patches containing randomly distributed hard clams. Laboratory choice experiments suggest that patterns of blue crab success in the field were mediated by their ability to detect and navigate efficiently toward patches with differing density and distribution. Whelks had similar patterns of foraging efficiency and success as blue crabs in the laboratory in relation to prey patches of differing density, but they showed no differences in foraging efficiency or success in relation to prey patches of differing distribution. Instead, higher encounter rates with odor plumes that are more spread out in the cross-stream direction (random patches) may account for patterns of knobbed whelk predation in the field. Predator-specific patterns of predation that are dependent on prey density and distribution within patches, suggests that the abundance and refuge characteristics of prey patch types will be dependent on the

dominant predator's identity.

Although much is known about the mechanisms that quickly moving predators like blue crabs use to efficiently navigate turbulent odor plumes (i.e. they have a high capacity for spatial integration of odors using simultaneous comparisons of odor concentration at distant chemosensors), less is known about the the high capacity to use time-averaging mechanisms that slowly moving predators like knobbed whelks utilize to efficiently navigate turbulent odor plumes. It is known that the navigational efficiency and success of time-averagers are not constrained by turbulent sensory landscapes (generated by changes in flow velocity and bed roughness) like the navigational efficiency and success of spatially-integrating foragers are.

To better understand the constraints and context-specificity of foraging efficiency and success for time-averaging predators in turbulent environments, I challenged knobbed whelks in a laboratory flume to navigate toward and locate hard clam prey in spatial configurations that varied in the magnitude of individual prey plume mixing and cross-stream odor spread. Knobbed whelk responses to differences in prey configuration at low density (3 clams) were compared to knobbed whelk responses to more realistic prey distributions at high density (10 clams, aggregated and random patches). Knobbed whelks had decreased navigational efficiency and increased spatial sampling behaviors when locomoting toward patches with individuals in perpendicular configurations (relative the the direction of bulk water flow) in low density experiments (compared to individuals in configurations parallel to the direction of bulk water flow), suggesting that information about the spatial configuration of prey individuals is maintained in downstream patch-scale odor plumes as a function of prey configuration. Whelks did not display any differences in navigational efficiency while locomoting toward patches containing more realistic distributions (aggregated and random). High density patches create mixing via individual prey plumes interacting with each other, likely resulting in low concentration, homogeneous patch-scale plumes where information about prey distribution is mitigated. Differences in navigational efficiency as a function of density and prey configuration or distribution within patches could result in differences in foraging success in the field where there are increased chances of interference and disruption the longer it takes to successfully locate prey. Despite differences in navigational efficiency as a function of prey configuration in patches, there were no differences in knobbed whelk foraging success as a function of prey configuration/distribution or density, indicating that knobbed whelks can maintain foraging success in a variety of different odor landscapes. The ability of whelks to effectively utilize temporal integration mechanisms to extract information from prey patch odor plumes allows them to maintain foraging success despite differences in the distribution of individuals within aggregations, and may enable whelks to occupy specific sensory niches that could reduce competition with other odor-mediated predators over resources.

The foraging efficiency and success of blue crab predators in locating patches of hard clam prey is dependent on the distribution of prey individuals within patches. Changes in prey distribution within patches can be a dynamic process mediated by predators that remove individuals from the group or mediate prey behaviors that minimize predation risk, resulting in predator-mediated changes in the sensory landscape. The relationship between prey distribution and predator foraging can be divided into three parts of a possible feedback loop including: patch detection by predators, predator impacts on prey individuals (predation or prey behavioral modifications), and changes to within patch prey distribution that affect subsequent detection by predators. I examined the ability of blue crabs to mediate hard clam distributions as a possible mechanism helping to shape prey distributions in the field. I exposed patches of hard clams to different predator exposure treatments (no predator control, predator odor cues, and access by naturally occurring predators) in the field to assess the ability of predator odors and actively foraging predators to change prey distributions. Exposure to actively foraging predators resulted in clams assuming random distributions within patches because of increased movement, but there were no changes in clam distributions mediated by predator odors. In contrast, both actively foraging predators and predator odor cues reduced growth rates in clams relative to no predator cage controls. Surveys of naturally occurring clam patches indicated that the majority of clam distributions were random, suggesting that predation and behavioral responses of clams to predator presence may help shape clam distributions in the field. There is also a possible negative feedback loop between blue crab predators and clam distributions. Blue crab predators mediate the formation of random distributions of clams, which subsequent blue crabs have a harder time detecting and foraging efficiently toward.

Changes in sensory landscapes important to odor-mediated predators are not restricted to those generated by biotic structural elements or groups of prey. Sensory landscapes can also be mediated by water flow, which transports prey odor plumes downstream to predators. The characteristics of water flow are generally site- and time-dependent in estuary and salt marsh systems, resulting in highly context-dependent odor-mediated predator-prey interactions. Little is known about water flow characteristics in natural small-scale estuary systems where blue crabs and knobbed whelks are common predators.

Thus, I sought to characterize the variation in turbulent flow parameters that odor-mediated predators may be exposed to in these estuary systems. I did this by measuring velocity time series at multiple locations within four sites across Wassaw Sound, GA at times corresponding to variation in large-scale tidal forcing (neap, normal, and spring tides), and using six acoustic Doppler velocimeters (ADVs). I found that there was significant predictive ability (based on correlation coefficients) of turbulent flow dynamics within sites between locations up to 20 m distant, but the predictive ability between sites seems to be a function of separation distance. This suggests that characterization of flow environments need to be assessed for each site but that characterizations at multiple locations within sites are not necessary (at least up to 20 m distant). Mean values of turbulent flow parameters are both site- and tidal type-dependent, indicating impacts on odor-mediated predator-prey interactions may be very context-dependent and the time and place of observations and experiments needs to be considered in data interpretation.

Characterization of local flow environments is necessary to understand the context-dependency of odor-mediated interactions, but measuring values of turbulent flow parameters can require expensive instrumentation and technological expertise that ecologists usually lack. Thus it may be beneficial to identify surrogate data that can be easily collected and interpreted to serve as a proxy for estimating flow velocity and turbulence characteristics in natural environments. I investigated wind speed and tidal range as possible candidates for surrogate data to make predictions about the hydrodynamic environment as well as their ability to mediate values of fluctuating flow parameters (wave components of turbulent kinetic energy and covariance) using data from the above study. Values of the wave components of fluctuating flow parameters were site- and tidal type-specific (based on fetch and water depth) and agreed well with values from previous studies in the same estuary system. I identified site-specific differences in the predictive capacity of wind speed on values of fluctuating flow parameters using data from 4 tidal cycles. The predictive capacity of wind speed and tidal range as a function of temporal scale suggests that wave components of fluctuating flow parameters can be accurately predicted by wind speeds at time scales greater than 9 tidal cycles and that values of all fluctuating flow parameters (except turbulence intensity) can be accurately predicted by tidal range at time scales greater than 4 tidal cycles. We suggest that these relationships only be utilized if the temporal scale of ecological experimentation matches that of significant correlations between wind speed or tidal range and fluctuating flow parameters.

This body of work suggests that the context-specificity of odor-mediated predator-prey interactions in the field cannot necessarily be predicted from single predator-prey laboratory studies. Instead, modifications of the sensory landscape through changes in structurally-induced turbulence, mixing of individual plumes from multiple prey, and bulk velocity and turbulence characteristics need to be considered when formulating predictions as to the impact of predators on naturally occurring prey populations in the field. Differences in predator perceptual abilities and foraging modes also will interact with modifications of the sensory landscape to mediate predator-specific patterns of predation. Odor-mediated predators can impact the density, distribution, and dynamics of prey populations, but predictions as to the magnitude and pattern of those impacts requires the consideration of predator identity and naturally occurring changes in the sensory landscape.

CHAPTER I

BIOTIC STRUCTURE INDIRECTLY AFFECTS ASSOCIATED PREY IN A PREDATOR-SPECIFIC MANNER VIA CHANGES IN THE SENSORY ENVIRONMENT

1.1 Abstract

Indirect effects are important in predator-prey interactions because of their ability to mediate both predator and prey population densities, distributions, and dynamics. Indirect effects, which can manifest either positively or negatively, may be important in areas containing structural elements because of their ability to modify the sensory landscape in which predator-prey interactions occur. Biotic structural elements may have conflicting impacts on associated prey populations because they provide refuge and habitat (positive impact) as well as sensory cues from alternative prey that may attract predators (negative impact). To determine the indirect effects of biotic structural elements on prey populations, I performed field experiments examining predation on patches of hard clams (*Mercenaria mercenaria*) by two large predators that forage using olfactory cues (blue crabs [*Callinectes sapidus*] and knobbed whelks [*Busycon carica*]) at 0 m, 5 m, and 10 m from oyster reefs in intertidal salt marsh communities. Oyster reefs had an indirect negative effect on hard clams, with higher predation rates closer to the reef than farther away. Predator-specific patterns of predation showed that blue crabs consumed more clams right next to the reef, while whelks consumed more clams at the intermediate distance. These patterns are the result of predator-specific responses to the changed sensory

environment produced by oyster reefs. Oyster reef structure creates turbulence that diminishes foraging efficiency, particularly in rapidly mobile predators such as blue crabs. The addition of oyster reef chemicals ameliorated the negative impact of structurally-induced turbulence on foraging success for both predator species, but measures of navigational efficiency (path linearity and walking speed) show that blue crab predators are more adversely affected by turbulence than whelks. I have found that biotic structural elements have both potentially positive and negative impacts on associated prey, but that the sign of the interaction, as well as where it is expressed is a function of changes to both the sensory landscape and predator perceptual ability.

1.2 Introduction

Indirect effects, or the impacts of one species on another which are mediated or propagated by a third species, have been shown to be as important, or more important, than direct effects in many systems (Menge 1995). Indirect effects are especially significant in predator-prey interactions and manifest as either positive or negative impacts on prey species that do not directly participate in the interaction. Indirect effects can be seen in trophic cascades (Estes & Palmisano 1974), keystone predator mediation of superior competitors (Paine 1966), generation of prey refuges by structural elements (Huffaker 1958), and apparent competition (Holt 1977; Schmitt 1987; Holt & Lawton 1994). These indirect interactions affect prey population maintenance, regulation of trophic levels, prey coexistence, and sometimes extinction. The abundance of interactions and diversity of predator behavior in communities make it hard to predict and detect the magnitude and type of indirect effects occurring between organisms.

Structural elements that also function as alternative prey (biotic structure) potentially can result in either positive or negative indirect impacts on associated prey species. Biotic structure could provide refuge for associated prey (positive effect), but could also function to attract predators that consume associated prey (negative effect). It is unknown whether structural elements will have positive or negative impacts on associated prey if they represent alternative sources of food. Structural elements are important components of many ecosystems because of their traditional roles in providing habitat (Woodin 1978; Soniat *et al.* 2004), refuge (Huffaker 1958; Langellotto & Denno 2004), and settlement sites (Abelson & Denny 1997) for organisms. Structural elements have been shown to impact prey positively by reducing the foraging efficiency of predators (Irlandi 1994; Grabowski 2004) and reducing prey apparency (Grear & Schmitz 2005). Negative indirect effects between biotic structure and associated prey could arise due to predator aggregation to multiple prey species which have been observed in many systems including; terrestrial insect-host plant communities (reviewed in Price *et al.* 1980; Karban 1997; Rand 1999; VanVeen *et al.* 2006), insect-parasitoid communities (Bonsall & Hassell 1997), marine rocky subtidal invertebrates (Schmitt 1987), and parasite-bird interactions (Tompkins *et al.* 2000). The indirect effects of structural elements when they also function as alternate prey have not been explored despite numerous examples of biotic structural elements including; coral reefs, oyster reefs, and many host plant species.

Biotic structural elements also may mediate indirect interactions by modifying the sensory environment in which predators detect prey species. Their ability to provide refuge and represent alternative prey sources suggest possibly conflicting effects of these structures. Changes in apparency of prey residing in or near structure may reduce predator foraging efficiency. On the other hand, chemical (or other) cues from biotic structural elements can represent sources of attraction relative to associated prey species, and may aggregate organisms to produce negative effects. Attractiveness to biotic structural elements is seen in the use of host plant odors by insects to locate conspecifics in the vicinity (Landolt & Phillips 1997) and in settling benthic larvae that use conspecific odors and habitat cues to initiate settlement behavior (Pawlik 1992; Tamburri *et al.* 1992; Abelson & Denny 1997). These biotic structural elements also modify the hydrodynamic landscape by increasing turbulence in areas downstream of those structures (Murlis *et al.* 1992; Leonard & Luther 1995; Finelli *et al.* 2000; Green 2005), which can affect the perception of predators or prey. Studies examining the role of biotic structural elements also have not considered the possible impacts that the sensory landscape will have on interactions between organisms, especially those between odor-mediated predators and their prey.

Predator-specific sensory abilities may result in different intensity and types of indirect interactions in the presence of biotic structural elements. Changes in the sensory landscape in the vicinity of structural elements may reduce or enhance the success of predators in locating prey in a species-specific manner. For example, blue crabs and moths are both more successful tracking plumes containing intermittent filaments of high concentration (Weissburg & Zimmer-Faust 1993; Mafra-Neto & Carde 1994; Vickers 2000), indicating they may not be as successful in environments containing structurally-induced turbulence as those where induced turbulence is absent. Whelks and crayfish, on the other hand, are just as, or more successful at locating prey when plumes are homogeneous and have low chemical concentrations (Moore & Grills 1999; Ferner & Weissburg 2005). Depending on their perceptual abilities, predators may be more or less successful in environments containing different turbulence levels, resulting in predator-specific patterns of predation. Understanding the context-sensitivity of indirect effects is a major challenge, but insights gained from considering both the sensory environment and predator perceptual abilities may help to generate a more predictive framework.

In this study I examined the predator-specific indirect impacts of biotic structural elements on associated prey. My goal was to further understand the mechanisms determining the intensity of predator-prey interactions and the context-sensitivity of indirect effects. Specifically, I examined the impact of oyster reefs (eastern oyster [*Crassostrea virginica*]) on the ability of two large and mobile odor-mediated predators (blue crabs [*Callinectes sapidus*] and knobbed whelks [*Busycon carica*]) to locate and consume hard clams (*Mercenaria mercenaria*) in the vicinity of those reefs. Both blue crabs and whelks have strong impacts on prey species in intertidal salt marsh systems along the East coast of the United States. Blue crabs have been show to control the abundance and distribution of bivalves in these systems (Virnstein 1977). Bivalves (clams, mussels, oysters) make up at least 50 % of blue crab diets (Hines *et al.* 1990) and a majority of knobbed whelk diets (Carriker 1951). Hard clams are commonly found in aggregations near oyster reefs, but have very patchy distributions at multiple spatial scales (Wells 1957; Walker & Tenore 1984). Eastern oysters form complex reef matrices that constitute one of the main biotic structural components found in intertidal salt marsh systems. They function as habitat and settlement sites (Soniat *et al.* 2004), enhance the population densities of fish and resident crustaceans (Peterson *et al.* 2003), and improve water quality (Newell 2004; Coen *et al.* 2007; Fulford *et al.* 2007). Some studies have examined the indirect effect of oyster reefs on trophic cascades and predator-prey interactions (Grabowski 2004; Hughes & Grabowski 2006), but these have been restricted to interactions occurring directly on or within the oyster reef matrix or use mesocosms that prevent inquiry on how changes in the sensory landscape may impact predator success.

I addressed these specific questions in my efforts to explore the indirect impacts of biotic structural elements on predator-prey interactions: 1) Do biotic structural elements indirectly mediate distance-specific patterns of predation in areas nearby? 2) Do biotic structural elements function as refuges or do they negatively impact prey populations? How might this change the traditional view of the roles structure has in community interactions? 3) What is the role of the sensory landscape surrounding biotic structural elements in mediating patterns of predation? Are these patterns predator-specific? I used a multi-pronged approach of laboratory and field experiments to establish whether indirect interactions among these species occur in the field, and the mechanisms that might explain observed patterns from the field. I tested the success of odor-mediated predators in locating patches of hard clams at three distances from live oyster reefs in the field. To determine how changes in the sensory landscape impacted the foraging behavior of both predators, I then challenged both blue crabs and whelks to locate injured hard clams directly downstream of oyster reefs in a controlled laboratory setting with treatments consisting of different combinations of oyster reef odors and structurally-induced turbulence. The flow environments in both the field and laboratory were characterized in order to determine the impact of oyster reefs on the hydrodynamic landscape as well as allow for basic comparisons between field and laboratory physical conditions.

1.3 Methods

1.3.1 Measuring Indirect Effects in the Field

In order to assess predation in proximity to oyster reefs, I exposed hard clams (*Mercenaria mercenaria*) to naturally occurring blue crab (*Callinectes sapidus*) and knobbed whelk (*Busycon carica*) predators at 0 m, 5 m, and 10 m from natural oyster reefs ($N = 8$, 10-20 m^2) in Romerly Marsh Creek, Wassaw Sound, GA. Fifteen juvenile clams (obtained from Bay Shellfish, Sarasota, FL; 15-25 mm in length) were attached to "clam plots" using monofilament, super glue, and tape to yield a density of 60 clams/m^2, which is within the range of natural densities (Walker & Tenore 1984). Clam plots were constructed by attaching three pieces of 0.5 m long rope between two 0.5 m pieces of 1.27 cm PVC (creating a 0.25 m^2 grid; see Smee & Weissburg 2006a). Five clams were tied equidistant on each rope. Plots for each replicate reef were placed parallel to the main channel at the mean low tide level.

Clam plots were left in the field for three days to ensure that predation was high enough to maintain statistical integrity (e.g. predation was observed in all replicates and no plots had all organisms consumed), at which time the number of missing and eaten clams was counted and predation was attributed to either crab or whelk predators based on shell chipping characteristics (Micheli 1997). Each replicate reef was tested with a single distance during each three day period in order to prevent predator aggregation, and all distances at each replicate reef were tested over the same 9 day period in July 2007. The order of testing was randomly chosen for each reef. The proportion of clams eaten per day was calculated but I was unable to transform the data to achieve normality for whelk predation data. I decided to analyze the data using a two-way analysis of variance (ANOVA) blocked by reef, with predator identity and distance as factors based on the assumption that ANOVA analyses are fairly robust to issues of non-normality (Zar 1999). I did this to determine if there was a significant interaction between predator identity and distance. A block effect was not detected so I normalized the data to the reef-specific highest predation rate and re-ran the analysis without blocking by reef. Normalizing the data allowed me to focus on distance-specific patterns of predation as opposed to the magnitude of predation. Qualitative analysis of the raw data showed similar trends for distance-specific patterns of predation as the normalized data, with the proportion of clams consumed ranging from 0.33 (at 0 m) to near 0 (at 10 m). Because I could not transform all the data appropriately, I also employed nonparametric Kruskal-Wallis tests in lieu of ANOVA where normality could not be achieved to confirm statistical significance of one-way comparisons between distances. A Nemenyi test was used to determine differences between distances for non-parametric analyses (Zar 1999). Post hoc comparisons of parametric analyses consisted of Tukey tests.

1.3.2 Turbulent Flows near Biotic Structural Elements

I measured turbulent flow characteristics near oyster reefs using acoustic Doppler velocimeters (ADVs). Four instruments were deployed simultaneously at 0 m, 3.3 m, 6.6 m, and 10 m from two different reefs. Flows were sampled over 12 hour periods, during which time the instruments collected data continuously in 5 minute bursts separated by 10 minutes. Three-dimensional velocity fluctuations (u, v, w) were measured at 16 Hz approximately 10 cm above the substrate. The instrument was rotated during data collection such that the u-velocity was predominately the along-stream component. v-velocity represented the cross-stream component and the w-velocity represented the vertical component. The data was filtered according to the established methodology of Berry *et al.* (2011) and Goring & Nikora (2002). Turbulent flow characteristics (net velocity and net root mean squared [RMS] velocity [a proxy for turbulent mixing]) were calculated for each burst according to the following equations:

$$Net\ Velocity = \sqrt{\overline{u} + \overline{v} + \overline{w}} \tag{1.1}$$

$$Net\ RMS\ Velocity = \sqrt{\overline{u^2} + \overline{v^2} + \overline{w^2}} \tag{1.2}$$

Burst average values ($N = 48$) were calculated for each burst over the 12 hour period. Since I was primarily interested in across-distance patterns, I then compared average burst values between the four distances using one-way ANOVAs for each reef. A post hoc Tukey Test was used to determine significant differences between distances.

1.3.3 Mechanisms Producing Indirect Interactions

All behavioral experiments were conducted in a paddle-driven racetrack flume at the Skidaway Institute of Oceanography, Savannah, GA (working section 4.8 m long, 1 m wide, 0.25 m water depth; see Ferner & Weissburg 2005 for a more detailed description of the flume apparatus). All experiments were conducted using a naturally representative flow speed of 0.05 m/s (Berry *et al.* 2011, Chapter 5). All animals were obtained from Wassaw Sound, GA and its tributaries. Adult clams were obtained via clam rake, blue crabs were caught using commercially available crab pots, and knobbed whelks were collected by hand. All animals were housed in flow through sea tables using water pumped from the Skidaway River and filtered through both sand and gravel filters. Salinity and temperature ranged from 15 to 30 ppt and 25 to 30 °C, respectively. Animals were held in these tanks for at least 48 hours before being used in experiments; if held longer, predators were fed clams every three days and were starved for 48 hours before being used in experiments.

I challenged blue crab and knobbed whelk predators to find potential prey upstream in one of four combinations of oyster reef chemical cues and/or structurally-induced turbulence. This series of studies was designed in order to determine the influence of both the hydrodynamic and odor properties of biotic structural elements on predator foraging success. Treatments included: control (empty flume); oyster reef chemical cues only (C); dead oyster reef (turbulence only [T]); live oyster reef (both chemicals and turbulence [CT1]); and dead oyster reef plus oyster reef chemical cues (both chemicals and turbulence [CT2]). Treatments containing oyster reef were constructed by placing 5 oyster clusters (approximately 0.15 m × 0.2 m × 0.2 m) in the upstream end of the test arena. All clusters of live oysters were soaked in freshwater and rinsed to remove small organisms (mainly small crustaceans and gastropods). Additional small organisms were removed by hand. I left clusters used for treatments containing dead oyster reef (T and CT2) outside to be cleaned of flesh by ants and sun-bleached. The same dead clusters were used to generate structurally-induced turbulence for the T and CT2 treatments. Odors from live oyster reefs were introduced into the flume for treatments containing added chemicals (C and CT2) by pumping water over a live oyster reef (the same live reef as used in the CT1 treatment) at the same rate as in the flume and re-introducing that water into the flume isokinetically near the substrate via plastic tubing. Oyster reefs and/or the chemical delivery apparatus were placed in the cross-stream direction 1.8 m upstream of the predator starting position.

I challenged predators to locate a recently injured prey item 1.6 m upstream of the predator starting position (0.2 m downstream of the oyster reef or chemical delivery apparatus). Hard clam prey (0.064 ± 0.0049 m in length) were injured by dropping individuals from a height of 2 m, causing the shell to crack. This mimics damage that other predators have caused (such as other blue crabs, bonnethead sharks, eagle rays, or birds). The treatment order was randomly assigned for all behavioral assays.

Blue crabs were placed into a flow-through box at the starting position at the same time as one injured prey clam was introduced upstream. The crab was confined to the starting box for 10 min to allow for acclimation, after which, the starting box door was lifted upwards slowly to minimize disturbance. Individuals were allowed 10 min to exit the starting box and move in an upstream or downstream direction. Individuals moving in an upstream direction had an additional 10 min to locate the injured prey clam, contact the oyster reef, or contact the chemical delivery apparatus.

Whelks also were introduced into the flume concurrently with an injured prey clam, but were not constrained by a starting box. Individuals were then given 30 min to initiate movement in an upstream or downstream direction. Individuals were given an additional 60 min to reach the injured prey clam, oyster reef, or chemical delivery apparatus once movement was initiated. The total amount of time given each predator to forage reflects differences in predator mobility; blue crabs move quickly whereas whelks move slowly.

Both blue crabs and whelks that moved downstream were not included in future analyses. The presence of a cage during blue crab trials prevents comparison of numbers of individuals in this category based on species, as this behavior could be due to lack of food motivation or because the cage may create unknown stimulus dynamics for blue crabs. Nonetheless, the number of animals excluded by this criterion was small (14.3 % of blue crabs and 8 % of whelks). Assays were terminated when the predator moved in a downstream direction from the start, contacted the injured prey clam and started to feed, contacted the oyster reef, or contacted the chemical delivery apparatus. Individuals contacting the oyster reef or chemical delivery apparatus were given a piece of clam to determine food motivation immediately following trial termination. Predators were considered not properly food motivated if they did not consume the clam within 3 min for blue crabs and 10 min for whelks. Individuals in this category were not included in future analyses (12.4 % of blue crabs and 0 % of whelks tested). Predators were tested individually and no individual was tested more than once.

Predators that contacted the injured prey item and initiated feeding were considered successful, whereas predators that contacted the oyster reef or chemical delivery apparatus and were properly food motivated were considered unsuccessful. There were no significant differences between patterns of predation as a function of predator identity using a G-test of independence with 3 nominal variables (treatment, successfulness, and predator identity; $G = 7.98$, $4 d.f.$, $P = 0.09$), so the data from both predators was pooled. A G-test of independence with two nominal variables (treatment, successfulness) was then used to determine differences between patterns of predation as a function of oyster reef chemical cues and turbulence (control not included).

Each trial was recorded using a video camera mounted approximately 2.5 m above the test arena (Fieldcam M370 mono camera. Furhman Diversified). Video of each predator's path was then analyzed using motion analysis software (Motion Analysis Corp. Model VP110) according to Jackson *et al.* (2007) to determine differences in tracking efficiency. Blue crab paths were analyzed at 15 frames/second and whelks were analyzed at 1 frame/second. For each species, path kinematics of successful predators (walking speed normalized to carapace width or shell length and path linearity) were compared between treatments using one-way ANOVAs (arcsine transformed as needed to achieve normality). Additionally, I divided the test arena into three smaller sections to determine differences in tracking behavior relative to distance from the injured prey clam. Divisions were determined using photos of plume dye visualizations where the number of pixels containing dye were calculated using ImageJ. Three sections were identified that represented equal mass fluxes (i.e. contained equal proportions of the total pixel number), and were determined independently for each treatment. Walking speed and path linearity were calculated for each section and then compared (for each predator) between treatments and sections using a repeated measures ANOVA, with section as the repeated factor.

Preliminary analysis indicated that the proportion of successful predators and their path kinematics were not significantly different for both treatments containing chemical cues and turbulence (CT1 and CT2). These treatments were combined (henceforth CT) and the data re-analyzed.

1.3.4 Turbulent Flows During Behavioral Assays

Turbulent flow characteristics were measured downstream of the oyster reef treatments to confirm and compare differences in their hydrodynamic landscapes. This also allowed for a basic comparison of flow velocity and turbulence between the field and the laboratory setting and helped ensure the use of realistic physical parameters in the behavioral assays (Zimmer & Zimmer 2008). Three dimensional velocity fluctuations were measured in the flume using an ADV mounted above the test arena. In addition to measuring flow in all oyster reef treatments, we also measured velocity fluctuations in an empty flume (control) as a comparison to ensure that the chemical delivery apparatus in the chemical only (C) and both turbulence and chemical (CT2) treatments was not artificially modifying the flow environment.

Preliminary measurements were used to determine the treatment-specific sampling time needed to get convergence in values of net velocity and net RMS velocity using a continuous sampling rate of 16 Hz (T, CT1, CT2 = 40 min; C and control = 30 min). I measured flow at three locations in the cross-stream direction (arena center = 0 m, - 0.245 m, and 0.245 m) and at four locations in the upstream-downstream direction (at the injured prey clam = 0 m, 0.533 m downstream of clam, 1.066 m downstream of clam, and 1.6 m downstream of clam [location of starting box]) for a total of 12 locations. The flow at each location was measured at 6 cm above the substrate, representative of chemosensor height in blue crabs and whelks (Page *et al.* 2011). I was unable to reliably measure flow at heights this close to the substrate in the field because of sediment transport and instrument instability. I obtained a basic characterization of net velocity and net RMS velocity by pooling all cross-stream measurement points at a given downstream location and then examining these flow parameters using a two-way ANOVA with downstream distance and treatment as factors. I also measured flow at 1.5 cm above the substrate, but patterns of turbulent flow characteristics as a function of distance and treatment were qualitatively similar to those at 6 cm above the substrate. Therefore, I only report data from the 6 cm height.

1.4 Results

1.4.1 Negative Indirect Interactions in the Field

Field experiments designed to determine the indirect effects of oyster reefs on associated bivalves at various distances from reefs showed a significant effect of distance on predation rates ($F_{2,42} = 3.99$, $P = 0.026$), with higher predation rates on hard clams closer to than farther away from biotic structural elements. There was a significant effect of predator identity on predation rates ($F_{1,42} = 12.71$, $P = 0.001$), with blue crabs showing higher predation rates than whelks. I also saw a significant interaction between predator identity and distance from the reef ($F_{2,42} = 4.10$, $P = 0.024$); that is, the relationship of predation intensity to distance from the reef differed between the two predators. One-way analyses confirm the findings of the full two-way ANOVA with significant differences in overall predation rates based on distance ($H = 9.84$, $df = 2$, $P = 0.007$ via Kruskal-Wallis), with total predation rates being higher at 0 m and 5 m than at 10 m from the oyster reef (Figure 1.1A). Predation by blue crabs was significantly affected by distance ($F_{2,21} = 4.23$, $P = 0.029$ via ANOVA; Figure 1.1B), with predation being higher at 0 m than at 10 m. Similarly, predation rates by whelks were significantly affected by distance ($H = 7.57$, $df = 2$, $P = 0.023$ via Kruskal-Wallis), but in contrast to blue crabs, rates were higher at 5 m than at either 0 m or 10 m from the reef (Figure 1.1C).

All clams survived at all distance treatments ($N = 4$) in predator exclusion cages (1.5 cm^2 mesh) over a 24 hour period, confirming that bivalve loss was attributable to large mobile predators. Qualitative analysis of survival of blue crabs tethered at the three distance treatments showed no differences in blue crab survival (number surviving out of 6 replicates; 0 m = 4, 5 m = 3, 10 m = 3), suggesting biotic structure does not act as a refuge for blue crabs. Gut content analysis of bonnethead sharks (*Sphyrna tiburo*) caught near oyster reefs also indicated that predation on blue crabs is very high in these environments (J. Byers - *personal communication*). No additional hard clams were found in the sediment (via clam rake prior to experimentation), confirming that odor cues emanating from the experimental hard clam patches were the predominant source of associated prey odors during field experiments.

1.4.2 Flow Characteristics Near Biotic Structural Elements

Simultaneous measurements of three dimensional velocity fluctuations were taken in proximity to oyster reefs to determine the intensity and extent of influence that oyster reef structures have on flow parameters that impact the foraging efficiency

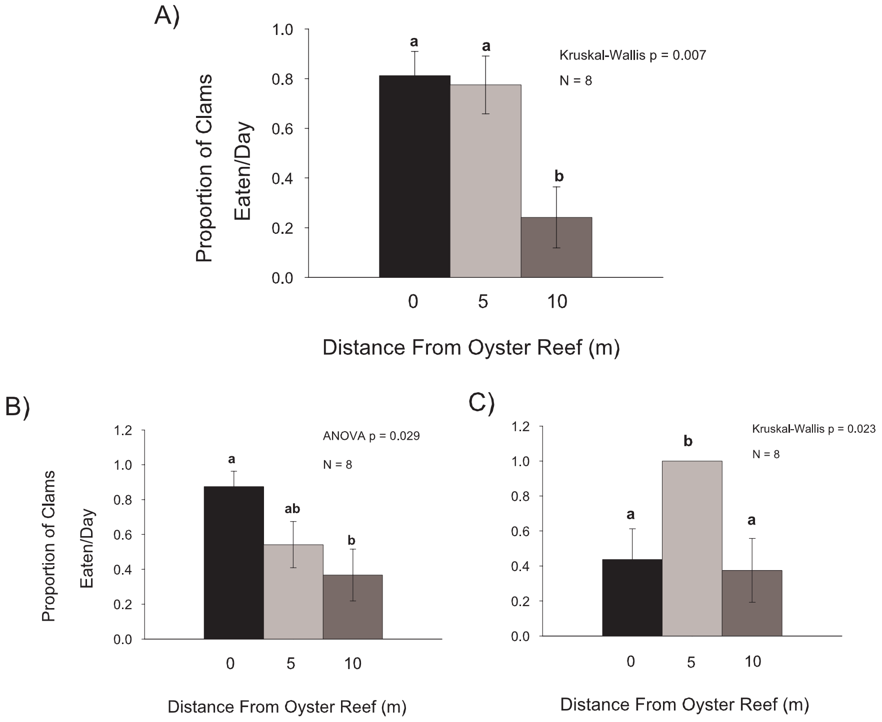

Figure 1.1: Predation rates, normalized to the reef-specific highest predation rate, on hard clams at 0 m, 5 m, and 10 m from oyster reefs in the field. Letters indicate significant differences between treatments via post-hoc tests (Tukey test [ANOVA] and a Nemanyi test [Kruskal-Wallis]). Error bars indicate one standard error. (A) Total predation rates. (B) Crab only predation rates. (C) Whelk only predation rates.

of odor-mediated predators. Both reefs measured showed similar trends. I found a significant effect of distance on net velocity at reef #1 ($F_{3,190} = 2.70$, $P = 0.047$; Figure 1.2A), with smaller net velocities at 0 m than at 6.6 m and 10 m from the oyster reef matrix. There also was a significant effect of distance on net RMS velocity at reef #1 ($F_{3,190} = 3.21$, $P = 0.024$; Figure 1.2B) that was characterized by relatively high net RMS velocities at all distances. Net RMS velocity values are approximately two times higher than those measured at other study sites over mud with no oyster reef nearby (calculated from data in Smee *et al.* 2008), indicating that all distances contain relatively high turbulence despite significant differences between those distances. I saw similar effects of distance on net velocity and net RMS velocity at reef #2 (net velocity: $F_{3,190} = 4.1$, $P = 0.001$; net RMS velocity: $F_{3,190} = 10.62$, $P = 0.001$), with lower net velocities closer to the oyster reef matrix and generally high net RMS velocities throughout the downstream area (data not shown).

1.4.3 Hydrodynamic and Chemical Influence on Predator Success

Flume experiments determined the influence of hydrodynamic and chemical cues of oyster reefs on the odor-mediated foraging efficiency of blue crabs and whelks. The proportion of successful predators was significantly different between oyster reef treatments ($G = 64.25$, *df* $= 2$, $P < 0.001$; Figure 1.3) with a higher proportion in treatments containing additional chemicals (C and CT) than in the treatment with structurally-induced turbulence only (T). Structurally-induced turbulence had a generally deleterious effect, as indicated by lower success rates in this treatment, but the presence of oyster reef chemicals ameliorated the negative impact of turbulence on tracking success. Patterns of predator success in control treatments were similar to those observed in previous experiments (Weissburg and Zimmer-Faust 1993).

Tracking by blue crabs was more efficient in treatments containing additional chemicals only (C) than those containing structurally-induced turbulence (T and CT).

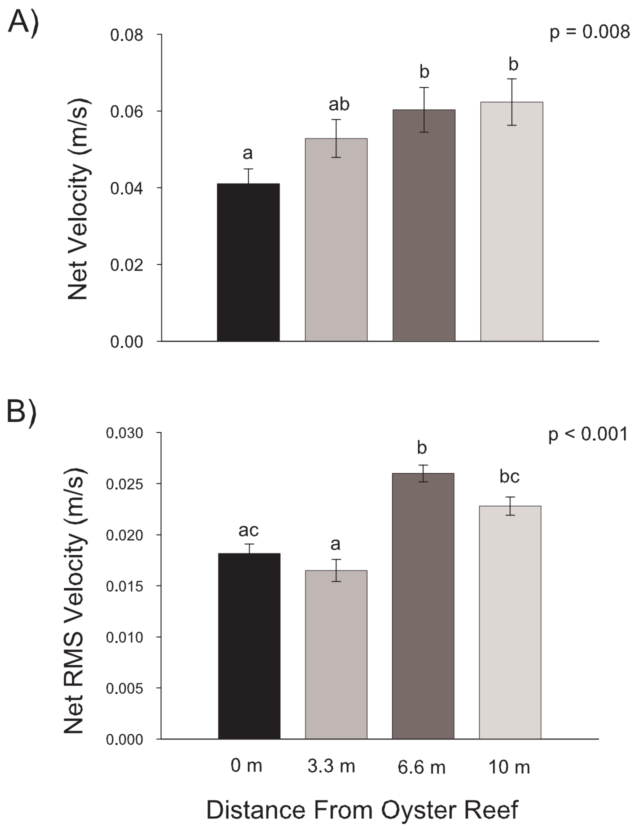

Figure 1.2: Net velocity (A) and net RMS velocity (B) at 0 m, 3.3 m, 6.6 m, and 10 m from oyster reef # 1 in the field as measured using simultaneously deployed ADVs. Significance was determined using one-way ANOVAs for (A) and (B) and letters indicate significant differences between treatments via post-hoc Tukey tests. Error bars represent one standard error

There were no significant effects of treatment on blue crab path linearity ($F_{2,60} = 0.65$, $P = 0.53$), but path linearity was significantly affected by section ($F_{2,120} = 3.05$, $P = 0.051$; Figure 1.4A), as demonstrated by lower path linearity in the section closest to the prey item. I also found a significant treatment by section interaction ($F_{4,120} = 2.69$, $P = 0.034$), showing that blue crabs in the chemical only treatment (C) increase their path linearity as they approach the prey item, whereas crabs in treatments containing structurally-induced turbulence decrease their path linearity as they approach the prey item. There was a significant effect of treatment on walking speed ($F_{2,60} = 3.27$, $P = 0.045$), with faster walking speeds in the chemical only

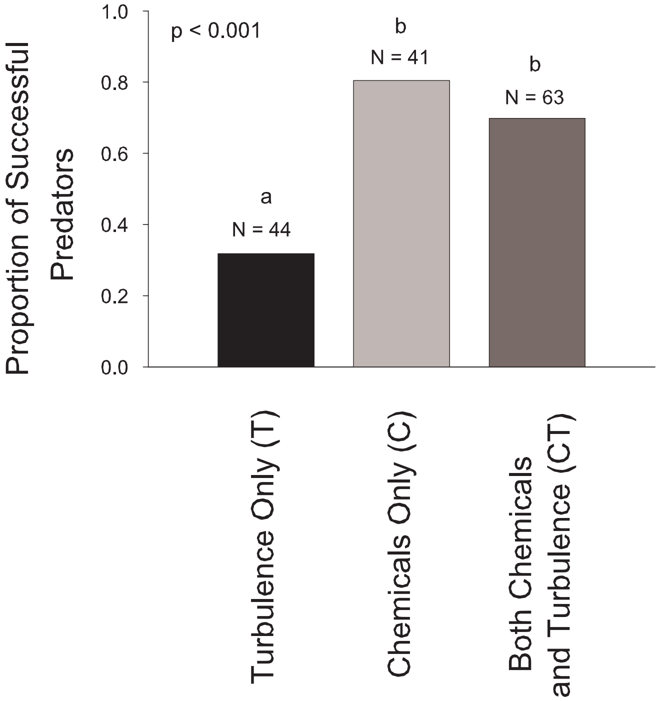

Figure 1.3: Proportion of predators (both blue crabs and whelks) that were successful in locating the injured prey clam downstream of oyster reef treatments. Successful individuals were those that contacted the injured prey clam first and started to feed (see methods). Significance was determined via G-Tests for independence. Different letters indicate significant differences between treatments. Both blue crabs and knobbed whelks show decreased foraging success in the structurally-induced turbulence only treatment. The presence of additional chemicals, regardless of structurally-induced turbulence, ameliorates the negative impact of turbulence.

treatment than in treatments containing structurally-induced turbulence (T and CT). There also was a significant effect of flume section on blue crab walking speed ($F_{2,120} = 14.04$, $P = 0.001$), with faster walking speeds in the middle section of the flume, but there was no treatment by section interaction ($F_{4,120} = 1.97$, $P = 0.10$; Figure 1.4B).

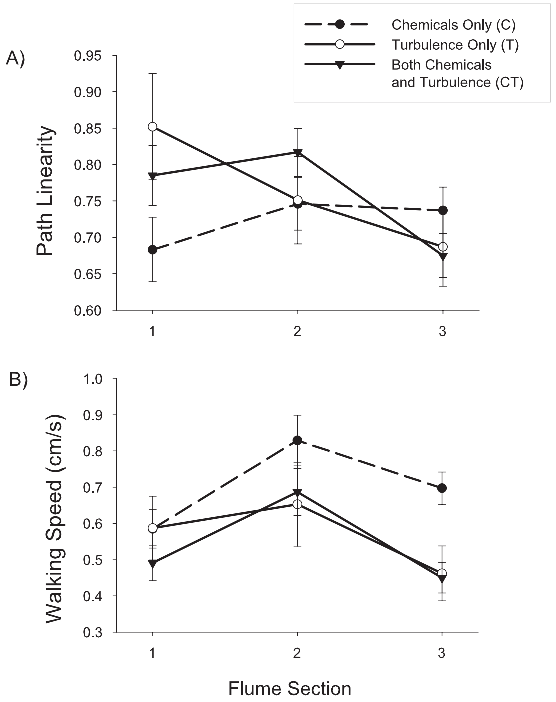

Figure 1.4: Path kinematics (path linearity [A] and normalized walking speed [B]) of successful blue crabs. Solid lines indicate treatments containing structurally-induced turbulence; dashed lines do not contain structurally-induced turbulence. All error bars represent one standard error. (A) There is no significant effect of treatment on path linearity ($F_{2,60} = 0.65, P = 0.53$), but there is significantly lower path linearity in the section closest to the prey item ($F_{2,120} = 3.05, P = 0.05$). A significant treatment by section interaction ($F_{4,120} = 2.69, P = 0.03$) indicates that blue crabs in treatments containing turbulence have higher path linearity at the beginning of tracks which decrease closer toward the prey item, whereas in the chemicals only treatment, blue crab path linearity increased closer toward the prey item. (B) There is a significant effect of treatment on blue crab walking speeds ($F_{2,60} = 3.27, P = 0.045$). Walking speeds are also significantly higher in the middle section of the test arena ($F_{2,120} = 14.04, P = 0.001$), but there is no significant treatment by section interaction ($F_{4,120} = 1.97, P = 0.10$).

Whelk movement speed and path linearity did not significantly differ between treatments or between sections of the test arena, indicating that whelks may not be as affected by turbulence as are blue crabs.

1.4.4 Flow Characteristics During Behavioral Assays

Treatments with structurally-induced turbulence (T and CT) had lower net velocities and higher net RMS velocities than the treatment with chemicals only (C). Specifically, net velocities were significantly affected by treatment ($F_{4,40} = 22.85$, $P < 0.001$; Figure 1.5A), as demonstrated by lower net velocities in treatments with structurally-induced turbulence (T and CT) than in the treatment with chemicals only (C). Net velocities also were significantly affected by distance from the reef matrix ($F_{3,40} = 19.44$, $P < 0.001$) and showed that lower net velocities could be found closer toward the oyster reef than farther away. There was a significant interaction between treatment and distance from the oyster reef ($F_{12,40} = 4.09, P < 0.001$), showing that treatments containing structurally-induced turbulence had depressed net velocities until 1.08 m downstream of the injured prey item, whereas treatments without structurally-induced turbulence maintained similar net velocities throughout the test arena (Figure 1.5A). There was a significant effect of treatment on net RMS velocity ($F_{4,40} = 5.57$, $P = 0.001$; Figure 1.5B), with higher net RMS velocities in treatments with structurally-induced turbulence (T and CT) than the treatment with chemicals only (C). There was no significant effect of distance on net RMS velocity ($F_{3,40} = 2.17$, $P = 0.11$), indicating that the net RMS velocity stayed consistent throughout the entire test arena. I also found no significant interactions between treatment and distance for net RMS velocity ($F_{12,40} = 1.13$, $P = 0.36$).

Flow dynamics in the vicinity of oyster reefs in the laboratory and the field were similar in magnitude and pattern. Net velocities ranged from 0.04 - 0.08 m/s downstream of both oyster reefs in the field and were approximately 0.05 m/s within 1 m downstream of oyster reef treatments in the laboratory. Net RMS velocities ranged between 0.016 - 0.03 m/s downstream of both oyster reefs in the field as compared

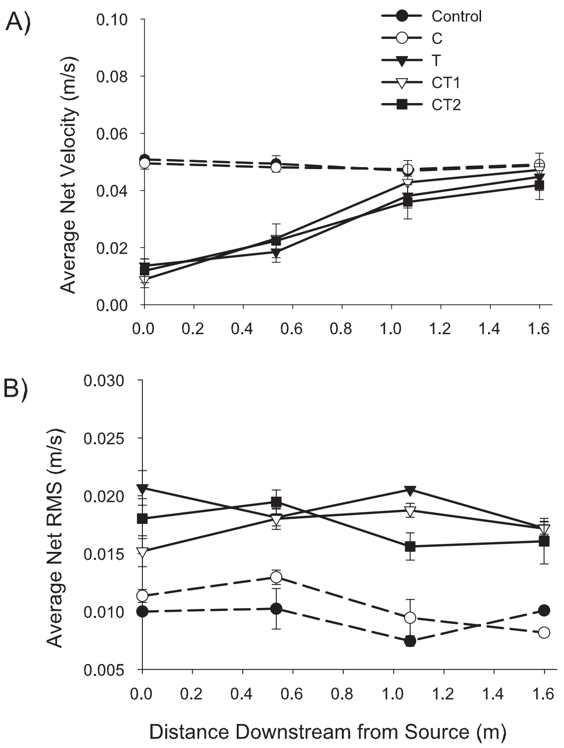

Figure 1.5: Net velocity (A) and net RMS velocity (B) measured in the flume at 6 cm above the substrate. Solid lines indicate treatments containing structurally-induced turbulence; dashed lines indicate treatments without structurally-induced turbulence. Each point represents the average of three cross-stream measurements and error bars represent one standard error. (A) There is a significant effect of both distance and treatment on net velocity ($F_{3,40} = 19.44, P < 0.001$; $F_{4,40} = 22.85, P < 0.001$, respectively). There is also a significant interaction between distance and treatment ($F_{12,40} = 4.09, P < 0.001$), showing that treatments containing structurally-induced turbulence have lower velocities near the source. (B) Net RMS velocity is significant higher for those treatments containing structurally-induced turbulence ($F_{4,40} = 5.57, P = 0.001$), but there is no significant effect of distance ($F_{3,40} = 2.17, P = 0.11$) or interaction term ($F_{12,40} = 1.13, P = 0.36$).

to 0.015 - 0.022 m/s downstream of oyster reefs in the laboratory This confirms that predators were exposed to roughly similar physical parameters in both laboratory and field experiments.

1.5 Discussion

Biotic structural elements, represented by oyster reefs, have negative indirect effects on associated prey as a result of changes in the sensory landscape that affect predator perception. Predation on hard clams close to oyster reefs is significantly higher than farther away from the oyster reef matrix (Figure 1.1A). This seems to be a result of high foraging success in the presence of oyster reef chemical cues despite enhanced turbulence downstream of structural elements (as seen in both field and flume measurements [Figure 1.2B and 1.5B, respectively]). The addition of oyster reef chemicals (CT) ameliorated the negative impact of turbulence and restored the percent of successful individuals to that in treatments without structurally-induced turbulence (C) (Figure 1.3). Large scale odor cues play important roles in mediating a variety of interactions in other systems including; guiding procellariiform sea birds to potential food patches from a distance (Nevitt 1999), aggregating coral reef fish to areas of potential food resources (DeBose *et al.* 2008), and aiding fish navigation to natal waters (Dittman & Quinn 1996). Success of both blue crabs and whelks is mediated by the presence of additional chemical cues, which may function to aggregate predators at larger scales and enhance tracking success at smaller scales, resulting in higher predation near the reef than farther away and creating a negative indirect effect on associated prey.

Studies on the indirect effects of structure generally focus on interactions occurring on or within the structure itself (Irlandi 1994; Hughes & Grabowski 2006); but rarely examine those occurring in the vicinity of structure. Structure is often seen as a refuge that results in a positive indirect effect on prey species (Micheli 1996). My study shows a negative impact on associated prey species, with oyster reefs enhancing predation on hard clams near biotic structure (Figure 1.1). Like other studies (Ogden *et al.* 1973; Sweatman & Robertson 1994), I see a "halo" around the oyster reefs. This halo is produced not by organisms that use structural elements for habitat or refuge and forage in areas nearby as has been documented, but because of enhanced foraging success in areas where biotic structural elements have modified the sensory landscape.

Although the presence of additional chemicals results in a positive impact on predator foraging success in the laboratory (Figure 1.3), the success of predators is dependent on both the odor and hydrodynamic landscape created by biotic structural elements. Modification of the hydrodynamic landscape by structurally-induced turbulence will mediate the concentration and homogeneity of those chemical cues downstream of biotic structural elements. Understanding the extent to which the hydrodynamic landscape modifies the intensity and distribution of chemical cues downstream increases our ability to determine the magnitude of indirect interactions, whether they will have positive or negative affects on associated prey, and how far away from biotic structural elements associated organisms will be impacted.

My study also shows that modification of the sensory landscape and the corresponding impact on predator foraging behavior near biotic structural elements may be much larger than predicted. Structural elements in many systems have been shown to modify the hydrodynamic landscape by increasing turbulence and lowering flow velocities directly downstream (Leonard & Luther 1995; Lenihan 1999; Finelli *et al.* 2000; Murlis *et al.* 2000), but rarely have these studies measured the spatial extent to which these properties are modified (i.e. extent of the wake; although see Murlis *et al.* 2000). Turbulence has also been shown to mediate predator success in many systems (Mafra-Neto & Carde 1994; Moore & Grills 1999; Ferner & Weissburg 2005; Jackson *et al.* 2007) by modifying the characteristics of odor plumes that predators use as guidance. My measurements confirm that flow velocities are depressed directly downstream of oyster reefs, but are still low 10 m downstream (Figure 1.2A). Turbulence (as measured by RMS velocity) stays relatively high over the entire region measured (Figure 1.2B), indicating that the influence of oyster reefs downstream may extend beyond my 10 m study scale. Biotic structural elements may be capable of influencing predator behavior and foraging success from a distance, making it important to consider the spatial scale at which experimentation should be conducted and interactions identified.

Our ability to understand how changes in the sensory landscape and the sensory capabilities of predators impact the strength of indirect interactions near biotic structural elements may allow us to predict and identify potential prey refuges and prey distributions in various systems. For example, parasitoids use host plant odor to improve their success in locating insect herbivores (Landolt & Phillips 1997). Host plant modification of the hydrodynamic landscape could result in spatially explicit refuges for insect herbivores, but to my knowledge this mechanism has not been incorporated into any studies to explain insect herbivore patch distributions. In the marine realm, predator refuge use has been cited to explain higher predation rates by blue crabs on oyster reefs right next to *Spartina alterniflora* stands than those farther away (Micheli & Peterson 1999). Based on my study, another mechanism that could explain this pattern is enhanced foraging success by blue crabs in areas near *S. alterniflora* stands. *S. alterniflora* stands could represent a source of food for blue crabs (many small invertebrate prey items use *S. alterniflora* as refuge) and function to attract predators and enhance foraging success in the area.

Although biotic structural elements have an overall negative effect on associated prey, my data shows predator-specific spatial patterns of predation that seem directly related to their unique sensory abilities. Blue crabs show significantly higher predation rates than whelks and significantly higher predation rates right next to the oyster reef than at 10 m distant (Figure 1.1). In contrast, whelk predation rates peak at an intermediate distance (5 m) from the reef rather than right next to or farther away from the reef matrix (Figure 1.1C). I suspect that these patterns result from differences in how the two predator species locate and successfully track prey odor plumes. Velocity and RMS velocity in the wake of reefs (Figure 1.2) suggest prey odor plumes right next to the reef should contain intermittent filaments of high odor concentration and plumes further away should be more homogeneous and with lower odor concentrations. Blue crabs may be generally attracted by the large odor signature from oyster reefs (e.g. Harding & Mann 2010), but may not be able to perceive individual odor plumes until very close to the reef where plume filaments contain higher odor concentrations (Weissburg & Zimmer-Faust 1993; Page *et al.* 2011). Their inability to successfully follow the homogeneous and/or low concentration plumes that are characteristic of intermediate and far distances can explain the significantly higher predation rates by blue crabs right next to oyster reefs. Blue crabs also show decreased walking speeds in treatments containing turbulence (T and CT) (Figure 1.4B; see Jackson *et al.* 2007 for similar results), indicating reductions in locomotory efficiency associated with more challenging plume conditions. Reductions in blue crab locomotory efficiency are unlikely associated with the hydrodynamic effects of turbulence in the absence of odor plumes (Jackson *et al.* 2007), although drag forces associated with increased flow velocity have been shown to mediate blue crab body angles relative to the direction of bulk flow (Weissburg *et al.* 2003). Spatial localization of the odor plume, essential for upstream navigation, was delayed in treatments containing turbulence until close to the source because of rapid cross-stream spreading of the plume. This is indicated by the significant decrease in path linearity in the section closest to the prey item where individuals detected plume edges and initiated turning back to the plume centerline (Page *et al.* 2011) (Figure 1.4A). I also saw a gradual decrease in path linearity toward the prey item in treatments containing turbulence (T and CT) (Figure 1.4A).

Whelks, on the other hand, are very slow moving predators, enabling them to time-average odor concentrations and track plumes of lower and more homogeneous concentrations than blue crabs, which is associated with better tracking in turbulent field conditions (Powers & Kittinger 2002; Ferner & Weissburg 2005). I did not see any significant differences in the path kinematics of whelks, most probably because of their slow movement and ability to time-average plume characteristics which makes them less susceptible to challenges associated with turbulent mixing (Weissburg 2000; Ferner & Weissburg 2005). However, whelks also may be tidal height limited because of their slow movement and may not be able to reach prey patches right next to the oyster reef within a complete tidal cycle. Both of these mechanisms may explain high predation rates by whelks at intermediate distances from oyster reefs. Thus, different perceptual mechanisms, combined with the sensory landscape in which predators are challenged to locate prey, result in predator-specific patterns of predation even in the same physical conditions.

Understanding the impact that the sensory landscape has on blue crabs and whelks gives insights into demographic impacts of predator-specific indirect effects on prey communities. For example, in areas dominated by blue crabs (e.g. upper marsh tributaries), hard clams may gain a refuge from predation in areas far away from biotic structural elements. In areas dominated by whelks, biotic structural elements may indirectly provide a refuge for those hard clams located right next to the structure. Walker & Tenore (1984) sampled hard clam distributions in Wassaw Sound and its tributaries (where these experiments were done) and found higher densities near oyster beds and higher densities closer towards the ocean which may show supporting evidence for my predictions. A more substantial sampling of hard clam populations in all areas of the estuary is necessary to determine if their distribution reflects patterns of predation based on predator-specific sensory abilities.

This study highlights four important consequences of predator-mediated indirect effects of biotic structural elements on associated prey. 1) Biotic structural elements can have negative indirect effects on associated prey species as opposed to the positive impacts they usually provide as refuge. Biotic structural elements may not necessarily function as refuge or habitat because they produce attractive cues that may function to aggregate predators and can enhance foraging success in their vicinity. 2) The impact of biotic structural elements on predator-mediated interactions may not be relegated to the area within or on the structure. The extent of potential impact on interactions may be much larger than considered in previous work and is dependent on the extent to which the sensory landscape is modified by biotic structural elements. 3) Predator-specific sensory capabilities result in different strengths and patterns of predation near biotic structural elements. 4) Predator sensory abilities and changes in the sensory landscape due to the presence of biotic structural elements can be used to generate predictions about the extent, intensity, and spatial distribution of indirect interactions in communities.

CHAPTER II

PREDATOR RESPONSES TO WITHIN-PATCH PREY DENSITY AND DISTRIBUTION RESULT IN PREDATOR-SPECIFIC REFUGE CHARACTERISTICS FOR PREY

2.1 Abstract

Predators are frequently challenged to locate multiple prey within patches and their ability to do so can mediate predator and prey population abundances and dynamics in the field. Predators that use chemical cues to detect and successfully locomote to prey from a distance (odor-mediated) may be particularly impacted by changes in the density and distribution of prey within patches, as prey density and distribution will mediate the concentration and spatial structure of patch-scale odor plumes. Species-specific sensory capabilities and foraging modes may influence the ability of predators to detect and encounter prey patches of differing density and distribution. I examined the ability of two odor-mediated predators (blue crabs [*Callinectes sapidus*] and knobbed whelks [*Busycon carica*]) to exploit patches of juvenile hard clam prey (*Mercenaria mercenaria*) with differing combinations of density (low [15 clams/m^2] and high [60 clams/m^2]) and distribution (aggregated and random) in the field. Highly mobile blue crabs had higher predation in clam patches containing high densities and aggregated distributions, whereas slow moving whelks had higher predation in patches containing randomly distributed prey. I then challenged both predators to detect, distinguish between, and track to clam patches of differing density or distribution in laboratory flume choice experiments to determine

whether patterns of predation in the field matched the ability of predators to detect and navigate efficiently toward prey patches. Laboratory experiments indicated that patterns of predation by blue crabs in the field matched closely with their detection and foraging efficiencies in the laboratory, suggesting that blue crabs had decreased ability to detect random and low density patches as a result of low concentration odor plumes. Patterns of whelk detection and navigational ability in the laboratory manifested as locating high density patches more frequently than low density patches and locating random and aggregated patches equally, which did not support their patterns of predation in the field. Instead they seemed to exploit patches in the field that produced odor landscapes spread over wider areas (random patches), which may have resulted in greater encounter rates with those patch types. Predators that move quickly and have a high capacity for spatial integration of prey odors (blue crabs) show patterns of predation related to their tracking efficiency, whereas slow moving predators that have a high capacity for the temporal integration of prey odors (whelks) show patterns of predation that seem to be related to their encounter rates with patches. Predator-specific patterns of predation as a function of prey density and distribution will likely result in differing abundance of specific patch types based on the dominant predator.

2.2 Introduction

Predators in natural environments are challenged to locate and consume prey in complex landscapes where they are seldom exposed to individual prey items. Instead they may encounter multiple prey in patchy distributions. The success of predators in locating patchy prey can mediate prey population density and distribution (Sih *et al.* 1985), determine the presence or absence of functional refuges (Huffaker 1958), and modify predator-prey patch dynamics (van Baalen & Sabelis 1993). A variety of foraging theories have been offered to explain how predators should exploit patchy resources to maximize energy intake (MacArthur & Pianka 1966; Fretwell & Lucas 1970; Charnov 1976; Bernstein *et al.* 1991). Models have expanded on these theories to make predictions about predator foraging efficiency as a function of prey spatial distributions (Nonaka & Holme 2007) and increased information about resource distributions (Byers 1996; Fortin 2002; Klaassen *et al.* 2006). Although these theories may be helpful in predicting general predator behavior at the population level, the mechanisms by which predators respond to prey density and distribution are needed to better understand and correctly scale-up individual-based foraging behavior models to explain patterns of predation in the field.

Predator ability to correctly locate patches and identify their quality may determine patterns of predation in patches containing differing densities and distributions. It has been shown in many systems that predation rates are higher in patches containing high prey densities (Bertness & Grosholz 1985; Turchin & Kareiva 1989; Sponaugle & Lawton 1990; Eggleston *et al.* 1992; Wellenreuther & Connell 2002; Micheli 1997; Heard 1998; Finn & Giller 2000; Seitz *et al.* 2001; Kuhlmann & Hines 2005) as a result of increased predator foraging efficiency. On the other hand, some studies have found that predator efficiency can plateau if prey densities are high enough (Holling 1959) and can result in lower individual risk (Aukema & Raffa 2004). Although there is a plethora of studies examining how predators respond to prey density, there are fewer that consider the impacts of within-patch prey distribution on predator foraging success and behavior. Studies with grazing ungulates show increased predation rates in patches where preferred plants are aggregated (Edwards *et al.* 1994; Dumont *et al.* 2000; Dumont *et al.* 2002), but others provide evidence for enhanced predation when resources were randomly distributed within patches (Edenius *et al.* 2002). The relationship between prey distribution and predator foraging success remains unclear, as does how prey patch density and distribution may interact to mediate predator foraging success and behavior.

Odor-mediated predators use prey chemical cues to detect and successfully locomote to prey from a distance. Previous studies have shown that predator success is dependent on the concentration and structure of prey odor plumes (Weissburg & Zimmer-Faust 1993; Mafra-Neto & Carde 1994), but observations and experimentation have been limited to interactions between individual predators and individual prey. Thus, little is known about how multiple prey within patches modify the sensory environment in which predators are challenged to forage. Patches containing high prey densities should produce plumes containing more chemicals than those containing low prey densities. Plumes from patches containing aggregated prey may be thinner and contain more chemicals per unit area than those generated by patches containing prey in more spread distributions. It has been hypothesized that thinner plumes may result in a smaller "zone of attractiveness", reducing plume encounter rates by predators (Cain 1985) and making these patches harder to find. The ability of predators to successfully locate specific patch types will be dependent on their foraging modality and perceptual abilities.

Differences in predator sensory capabilities may result in predator-specific patterns of predation on different prey patch types. For example, highly mobile animals that use spatial integration strategies, such as blue crabs, are more successful tracking plumes containing high concentrations and well-defined edges (Weissburg & Zimmer-Faust 1993; Page *et al.* 2011). Plumes with these characteristics are most likely to emanate from prey patches containing high densities and aggregated distributions. Slow moving animals, like gastropods, that have a high capacity to temporally average plume information to maintain search efficiency, can result in similar or enhanced foraging success when plumes are homogeneous and have low chemical concentrations (Ferner & Weissburg 2005) compared to when plumes are heterogeneous with high chemical concentrations. Therefore, time-averagers may be equally able to detect and locate prey in patches of high and low densities and in patches containing random or aggregated prey distributions, but encounter rates with different patch types may be a constraint for these slow-moving predators. Predator-specific responses based on sensory capabilities and foraging mode may also result in predator-specific patch characteristics that function as effective prey refuges.

In this study, I examined the effects of within-patch density and distribution characteristics on predator-specific foraging success and behavior in an effort to identify patterns of predation and elucidate the mechanisms by which predators perceive and interact with patchy resource landscapes. Specifically, I investigated the ability of two large predators (blue crabs [*Callinectes sapidus*] and knobbed whelks [*Busycon carica*]) to detect and locate patches of hard clams (*Mercenaria mercenaria*) containing different densities and distributions in an intertidal salt marsh system. Blue crabs are known to have strong impacts on infaunal prey species in intertidal salt marsh systems along the East coast of the United States (Virnstein 1977), with bivalves making up 50% of blue crab diets (Hines *et al.* 1990). Whelks also are common salt marsh predators whose diets are primarily composed of bivalves (Carriker 1951). Hard clams have patchy distributions at multiple spatial scales throughout salt marsh systems (Walker & Tenore 1984), making them ecologically relevant prey in which to investigate the impacts of within-patch characteristics on predator foraging.

Previous studies indicate that blue crabs have higher predation rates in prey patches containing high clam densities than those containing low clam densities (Sponaugle & Lawton 1990; Eggleston *et al.* 1992; Micheli 1997; Seitz *et al.* 2001; Kuhlmann & Hines 2005). To my knowledge, there is no information about blue crab foraging success in relation to within-patch prey distribution, but I would expect to see higher predation in patches containing aggregated distributions because these patches produce signal characteristics most favorable for rapidly moving foragers. Whelk foraging success in relation to density and distribution characteristics of prey patches is unknown, but their ability to time average dilute and homogeneous signal sources may allow them to successfully locate and consume individual prey, producing similar responses to patches with differing density and distribution characteristics. It also is unknown whether patterns of predation in the field are a result of predator perceptual ability to detect and follow prey odor plumes or predator encounter rates with prey plumes. Incorporating information about the perceptual abilities and sensory modalities of predators is essential to developing informed hypotheses concerning the spatial and temporal characteristics of prey refuges and the resulting impacts on prey population dynamics.

I addressed these specific questions in my efforts to explore the impact of within-patch prey density and distribution on predator foraging success and behavior: 1) How do changes in the sensory landscape because of within-patch prey density and distribution mediate predator foraging success and behavior? 2) How do predator responses to within-patch prey density and distribution differ from previous single-prey studies? Can single-prey studies be scaled up to accurately represent predator responses to multiple prey? 3) How are predator-specific patterns of predation related to the perceptual abilities and sensory modalities of predators? To explore these questions I first exposed patches of hard clams of four different combinations of within-patch density (high and low) and distribution (aggregated and random) to natural densities of predators in the field using a randomized block design to determine the ability of predators to detect and locate patches with differing density and distribution characteristics. To distinguish between predator responses based on prey patch detectability versus prey patch encounter rate, I then challenged predators in a laboratory flume to choose between patches of live clams containing differing densities or distributions.

2.3 Methods

2.3.1 Patterns of Predation in the Field

To determine the ability of predators to detect and locate prey patches in the field, I exposed 1 m^2 patches of hard clams (*Mercenaria mercenaria*), consisting of four combinations of density and distribution, to natural densities of predators (blue crabs [*Callinectes sapidus*]) in the field. Experiments were conducted in July 2008 and 2009 in the Skidaway Narrows, Savannah, GA and at Priest Landing, Wassaw Sound, GA.

Patch characteristics included combinations of two densities (high = 60 clams/m^2 and low = 15 clams/m^2; both within the range of natural densities [Walker & Tenore 1984]) and two within-patch distributions (aggregated or randomly distributed); for a total of four possible treatments (high density and aggregated [HA], high density and random [HR], low density and aggregated [LA], and low density and random [LR]). To maintain distribution treatments during experiments and to determine predator identity, juvenile clams (obtained from Bay Shellfish, Sarasota, FL; 15-25 mm in length) were tethered to pieces of 7.52 cm diameter × 8 cm in height pieces of polyvinyl chloride (PVC) using monofilament, super glue, and tape. Five individual clams were attached to each piece of PVC. Clams were then placed in 1 m^2 patches in the field to create differences in density and distribution (high density = 12 PVC/patch and 60 clams/m^2; low density = 3 PVC/patch and 15 clams/m^2). Each PVC pipe was pushed flush with the mud and all tethered clams were placed within the PVC pipe with the shell margins facing down. Aggregated patches were created by placing all PVC pieces right next to each other in a haphazard location within the patch, whereas random patches were created by haphazardly placing individual PVC pieces throughout the patch. Patches were deployed in a randomized block design, with each block containing all four treatment combinations (HA, HR, LA, and LR). Patches within each block were placed approximately 5 m apart in a random order parallel to the main channel at the low tide line, and blocks were separated by at least 10 m. Preliminary experiments showed no significant difference in predation rates on tethered clams attached to PVC and those attached to garden stakes (i.e. PVC did not inhibit predator foraging behavior: $t = -1.32, df = 12, P = 0.21$).

Blocks were left in the field until there had been evidence of predation but before all clams had been eaten, at which time the number of missing and eaten clams was counted and predator identity was confirmed based on shell chipping characteristics (Micheli 1997). All predation in 2008 and 2009, regardless of site, could be attributed to blue crab predators. I calculated the number of clams eaten per day and then standardized by the patch density. As there was no effect of year or site, data from both years and both sites were pooled for analysis. I ran a two-way analysis of variance (ANOVA) with a blocking factor to determine the effect of within-patch density and distribution on predation rates.

This experiment was repeated in April 2010 at Priest Landing, Wassaw Sound, GA in order to explore predator-specific patterns of predation on different patch types. The interval May to September represents the peak seasonal activity of blue crabs, whereas whelks are active from roughly February to July. Thus, April represents a time of peak activity for whelks but only moderate activity for blue crabs. Patches were exposed to natural densities of predators for 14 days (to allow for sufficient levels of predation as previously described). Preliminary analysis showed a significant effect of predator identity on predation rates, so I ran two-way ANOVAs with a blocking factor for each predator species to determine the effect of patch density and distribution on predator-specific predation rates.

2.3.2 Predator Ability to Detect and Locate Patch Types

All behavioral experiments were conducted in a paddle-driven racetrack flume at the Skidaway Institute of Oceanography, Savannah, GA (working section 4.8 m long, 1 m wide, 0.25 m water depth; see Ferner & Weissburg 2005 for a more detailed description of the flume apparatus). All experiments were conducted using a naturally representative flow speed of 0.05 m/s (Berry *et al.* 2011, Chapter 5). Predators were obtained from Wassaw Sound, GA and its tributaries. Blue crabs were caught using commercially available crab pots and knobbed whelks were collected by hand. Juvenile hard clam prey were obtained from Bay Shellfish, Sarasota, FL (15-25 mm in length). All animals were housed in flow-through sea tables using water pumped from the Skidaway River and filtered through both sand and gravel filters. Salinity and temperature ranged from 15 to 30 ppt and 25 to 30 °C, respectively. Animals were held in these tanks for at least 48 hours before being used in experiments; if held longer, predators were fed clams every three days and were starved for 48 hours before being used in experiments.

To eliminate encounter rate issues and determine predator preference when exposed to multiple patch types, I challenged blue crab and whelk predators to detect and locate patches with differing characteristics (similar to those used in field experiments) in a laboratory flume choice assay. Analysis of predation patterns in the field showed no significant interaction effects between patch density and distribution, so I challenged predators to detect and locate patches of differing density (density experiment), and in separate experiments, differing distribution with the same density (distribution experiment). This choice experiment was designed such that differences in success rates in relation to patch characteristics could be discerned clearly. A factorial experimental design exposing predators to a single patch type at a time could result in very similar success rates, unreflective of small differences in predator perception as a function of patch type. Choice experiments could be especially important for distinguishing whelk responses to patch types, as they can successfully locate individual prey clams (MLW - unpublished data). This could result in similar whelk success rates in factorially designed experiments that are unreflective of differences between patch types. Patches were generated by placing live juvenile clams in sand-filled false bottoms within the test arena of the flume. The center of each patch was located 19.5 cm to either side of the flume centerline in the cross-stream direction.

Predators in the density experiment were simultaneously exposed to a low density patch (3 clams [40 clams/m^2]) and a high density patch (10 clams [125 clams/m^2]), with individual clams located no more than 3 cm from each other. The high density used in this experiment is approximately 1.5 times that of naturally occurring patches (Wells 1957; Walker & Tenore 1984), but was used to ensure that an adequate number of clams were providing odor cues throughout individual trials. Predators in the distribution experiment were exposed simultaneously to an aggregated patch (individuals placed approximately 3 cm apart) and a random patch (individuals placed randomly throughout the false bottom area), each containing 10 clams. The location of patch types relative to the flume centerline was chosen randomly for each trial.

Predators were introduced to the flume arena 1.6 m downstream of both patches when at least half of the clams within each patch were buried and actively pumping (see Smee & Weissburg 2006a). New clams were used for each trial. Preliminary dye studies indicated that odor plumes emanating from both patches had contacted each other and been mixed sufficiently within 1.6 m downstream.

Blue crabs were allowed 10 minutes to acclimate within a starting box prior to the starting box door being lifted upwards slowly to minimize disturbance. Individuals were allowed 10 minutes to exit the starting box and move either upstream or downstream. Individuals moving in an upstream direction had an additional 10 minutes to locate either prey patch.

Whelks were introduced into the flume when at least half of the clams were buried and actively pumping, but were not constrained by a starting box. Individuals were then given 30 minutes to initiate movement in an upstream or downstream direction and an additional 60 minutes to reach either patch if movement was upstream. Twenty minutes was then given to successful individuals to consume any desired clams.

Clam pumping was assessed at multiple points during trials (blue crab = introduction to starting box and immediately prior to opening the starting box door; whelk = introduction to the flume, movement initiation, and directly before patch contact) to confirm that patches maintained treatment differences. The average number of clams actively pumping during blue crab experiments was significantly different for patches in the density experiment (high density = 7.85 ± 0.36 clams, low density = 2.31 ± 0.17 clams; $t = 19.02$, $df = 12$, $P < 0.001$), but there were no differences for the distribution experiment (aggregated = 7.56 ± 0.16 clams, random = 7.84 ± 0.20 clams; $t = -1.54$, $df = 14$, $P = 0.16$). I found similar patterns for whelk trials (density: high = 4.95 ± 0.22 clams, low = 1.48 ± 0.08 clams, $t = 17.40$, $df = 21$, $P < 0.001$; distribution: aggregated = 5.3 ± 0.24 clams, random = 5.56 ± 0.28 clams, $t = -1.27$, $df = 17$, $P = 0.22$).

Both blue crabs and whelks that moved downstream were not included in future analyses. The number of animals excluded by this criterion was small (14.2 % of blue crabs and 0 % of whelks). For whelks, assays were terminated when individuals moved in a downstream direction, passed to the sides of either patch, or contacted a clam within the patch and started to feed. Assays were terminated for blue crabs when individuals moved in a downstream direction, passed to the sides of either patch, or demonstrated a variety of search behaviors while passing directly over the patch (visible pausing with substrate probing, digging, or consuming clams). Blue crabs rarely consumed clams within patches regardless of patch type and seemed skittish during flume trials, with some individuals darting in response to noises or shadows. Thus, I gave blue crab predators a piece of clam following an apparently successful patch location to confirm that individuals were properly food motivated. Blue crabs were considered not properly food motivated if they did not consume the clam within 3 minutes and were not included in future data analyses (21.1 %). The number of blue crabs that failed to consume prey following apparently successful patch location was similar for patch types in the density (high density = 1, low density = 0) experiment and for patch types in the distribution (aggregated = 3, random = 5) experiment. Predators were tested individually and no individual was tested more than once.

For each experiment (density and distribution), a binomial test was used to determine if the proportion of individuals successfully locating a patch type was significantly different from a null hypothesis of 50%.

Each trial was recorded using a video camera mounted approximately 2.5 m above the test arena (Fieldcam M370 mono camera, Furhman Diversified). Predator paths were then analyzed using motion analysis software (Motion Analysis Corp. Model VP110) according to Jackson *et al.* (2007) to determine differences in tracking efficiency for successful individuals. Blue crab paths were analyzed at 15 frames/second and whelk paths were analyzed at 1 frame/second. Walking speed (standardized to carapace width or shell length depending on predator species) and path linearity (arcsine transformed) for blue crabs and whelks within each experiment were calculated, and the effect of patch treatments determined using a t-test. I then divided the flume into three equal sections to determine how predator behavior changed with distance from the prey odor source. I calculated walking speed and path linearity for each section and then did a one-way repeated measures analysis of variance (ANOVA) with section as the repeated factor for each path kinematic and predator species separately. I did not statistically analyze path kinematics for blue crabs in the density experiment because only 2 individuals successfully located the low density patch.

2.4 Results

2.4.1 Patterns of Predation in the Field

Blue crab predation in the field in 2008 and 2009 was significantly affected by both clam density and distribution ($F_{1,108} = 9.56, P = 0.003$ and $F_{1,108} = 5.24, P = 0.02$, respectively), but there was not a significant interaction effect between patch density and distribution ($F_{1,108} = 0.043, P = 0.84$; Figure 2.1). Predation rates were higher in high density patches and in aggregated patches. I also saw a significant block effect ($F_{36,108} = 5.12, P < 0.001$), which is likely a result of high variability in predation rates throughout my study sites.

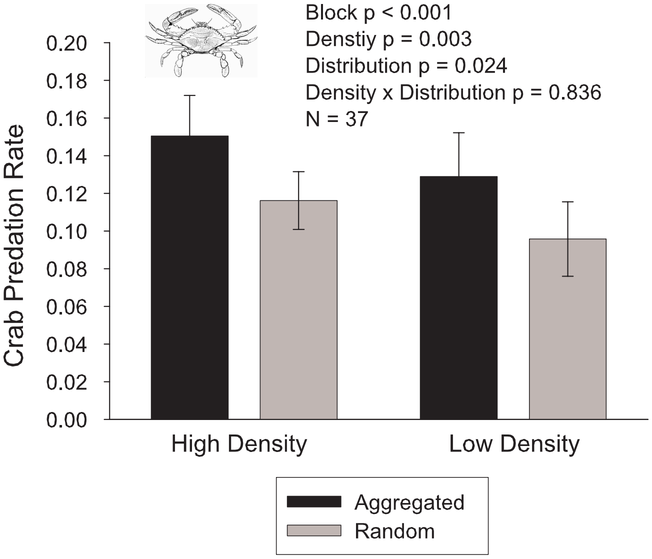

Figure 2.1: Blue crab predation rate (number of clams eaten per day), standardized by treatment density, at Skidaway Narrows and Priest Landing in 2008 and 2009. All predation was attributed to blue crab predators based on shell chipping characteristics. A randomized block design was used during experiments. Error bars represent standard error. Significance was determined using a two-way ANOVA with a blocking factor.

Similar trends in blue crab predation were seen in 2010 when both predators were present (density: $F_{1,24} = 3.82, P = 0.06$; distribution: $F_{1,24} = 2.74, P = 0.11$; density × distribution: $F_{1,24} = 0.047, P = 0.83$; block: $F_{8,24} = 4.17, P = 0.003$;

Figure 2.2A).

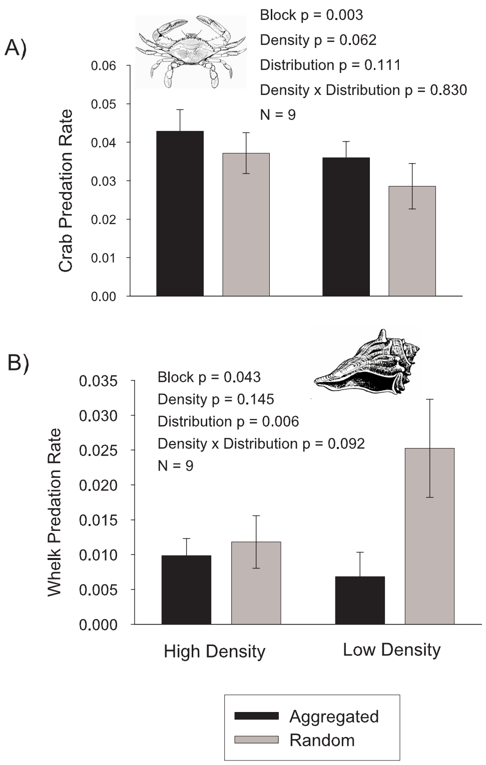

Figure 2.2: Predation rates (number of clams eaten per day) at Priest Landing in April 2010 when both blue crab and whelk predators were active. Predation rates are standardized by the treatment density. Error bars represent standard error. (A) Predation rates by blue crabs. (B) Predation rates by knobbed whelks. A two-way ANOVA with a blocking factor was used to determine significance within predator type.

Patterns of whelk predation in the field were similar to results from blue crabs in some respects only. There was a significant effect of clam distribution ($F_{1,24} = 9.07, P = 0.006$) on predation rates by whelks in the field and no interaction between density and distribution ($F_{1,24} = 3.09, P = 0.09$; Figure 2.2B). In contrast to results from blue crabs, I did not see a significant effect of clam density on whelk predation rates ($F_{1,24} = 2.27, P = 0.15$). Thus, whelks showed higher predation rates in random patches, regardless of density. I also saw a significant effect of block ($F_{8,24} = 2.45, P = 0.04$) on whelk predation rates.

I thought that highly mobile blue crabs may have consumed clams within high density patches to the extent that there were no differences between density treatments prior to patch exploitation by less mobile whelk predators. To test for this, I assumed that all predation by blue crabs occurred prior to whelk predation. Predation rates were re-calculated using the number of clams not consumed by blue crabs as the number of available prey, and then re-analyzed the data using a two-way ANOVA (preliminary analysis indicated a non-significant effect of block). I found similar patterns of whelk predation regardless of accounting for blue crab exploitation (density: $F_{1,32} = 1.32, P = 0.26$; distribution: $F_{1,32} = 5.05, P = 0.032$; density × distribution: $F_{1,32} = 3.31, P = 0.08$), indicating that patterns of whelk predation are not the result of prior exploitation by blue crabs and may instead be the result of predator-specific detection abilities.

2.4.2 Predator Patch Choice and Behavior

2.4.2.1 Density Experiments

Blue crabs challenged to detect and locate different density prey patches in choice assays successfully found high density clam patches significantly more often than expected ($P = 0.007, N = 12$; Figure 2.3). Whelks also found patches of high density significantly more often than expected ($P = 0.047, N = 23$; Figure 2.3).

Whelks displayed different movement patterns in response to patch density treatments and moved more quickly when tracking toward high density patches ($t = 2.10, df = 20, P = 0.049$). There was a marginally insignificant trend towards greater path linearity when successfully tracking toward high density clam patches ($t = 1.92, df = 21, P = 0.08$). Recall that there was an insufficient number of blue crabs successfully locating low density clam patches which prevented an analysis of locomotory efficiency as a function of patch density.

Locomotory efficiency (i.e. path linearity) of whelks, as a function of distance from the prey patches, was significantly affected by patch density ($F_{1,19} = 4.52, P =$

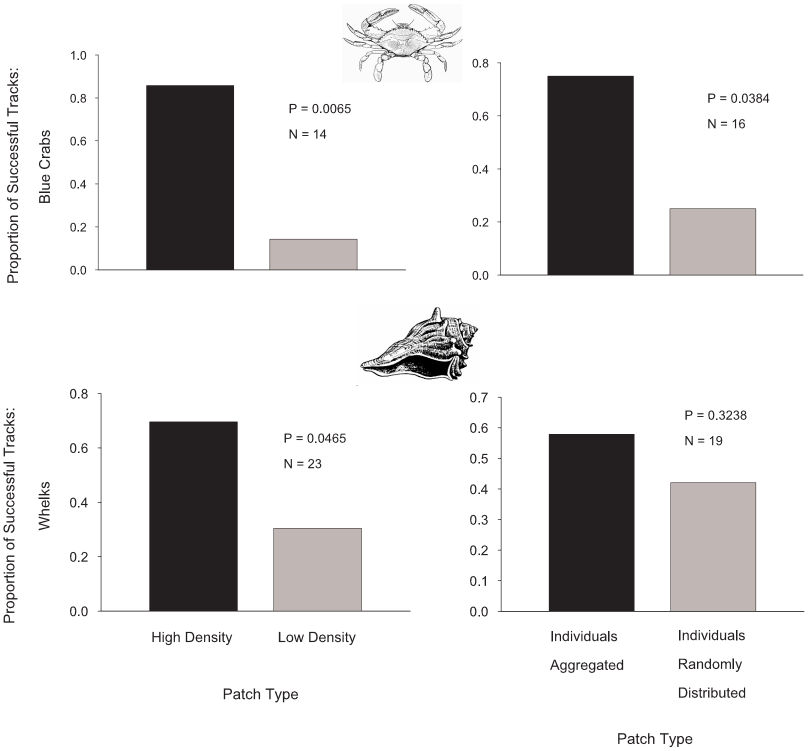

Figure 2.3: Proportion of successful tracks to different clam patch types by blue crabs (top) and knobbed whelks (bottom) in a laboratory flume. Predators were exposed to two densities (high [10 clams] versus low [3 clams]) or two distributions of individuals (aggregated versus randomly distributed, both with 10 clams). Statistical significance was determined using a binomial test that compared the distribution of success to a null hypothesis of 50:50.

0.047) and section ($F_{2,38} = 7.08, P = 0.002$), but there was no significant treatment by section interaction ($F_{2,38} = 0.71, P = 0.50$; Figure 2.4). Whelks successfully locating high density patches showed greater path linearity than those locating low density patches. There also was a significant effect of section on whelk movement speed ($F_{2,38} = 16.45, P < 0.001$); movement speed of whelks decreased as they approached the odor source regardless of which patch they successfully located during the density experiment. Whelk movement speed was not significantly affected by patch density ($F_{1,19} = 2.83, P = 0.11$) and there was no significant patch density by section interaction ($F_{2,38} = 0.07, P = 0.93$).

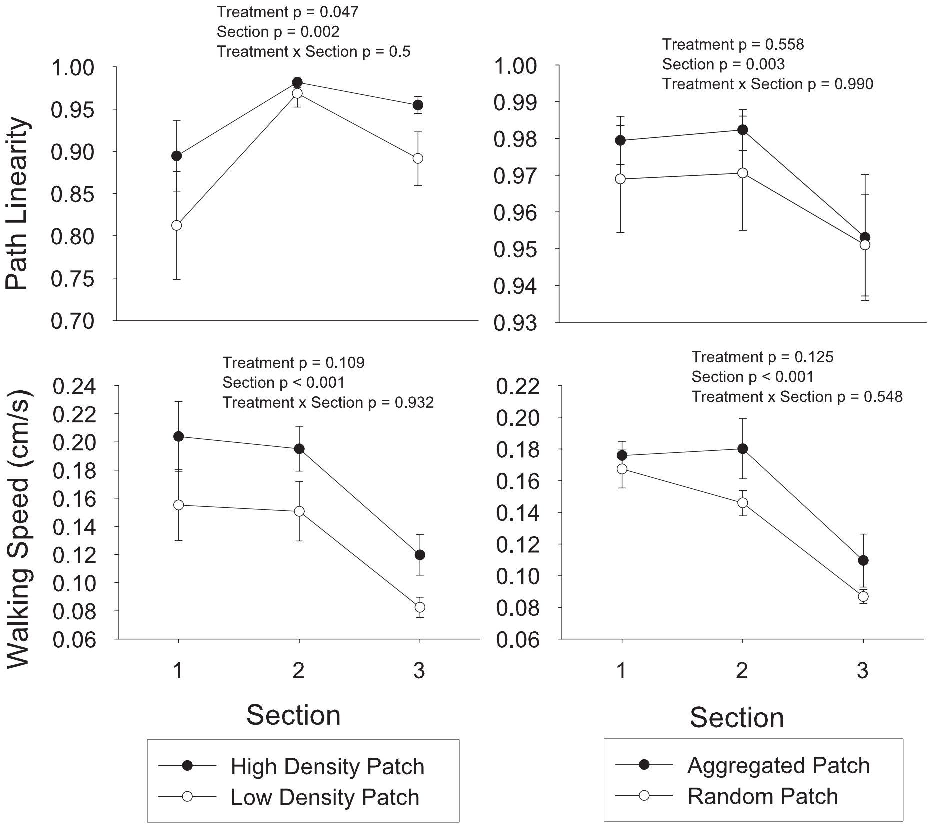

Figure 2.4: Path kinematics of successful whelks in the density experiment (left) and the distribution experiment (right). Error bars indicate one standard error. All statistics were determined using a repeated measures ANOVA with section as the repeated factor. Sample sizes = 15, 7, 10, and 8 for whelks successfully locating high density, low density, aggregated, and random patches, respectfully.

2.4.2.2 Distribution Experiments

Blue crabs found clam patches with aggregated distributions significantly more often than expected ($P = 0.04, N = 16$; Figure 2.3). In contrast to blue crabs, whelks did not find aggregated patches more often than expected ($P = 0.32, N = 18$; Figure 2.3), although there was a slight trend toward locating aggregated patches more frequently.

I did not see any effect of patch type (aggregated or random) on blue crab locomotory efficiency for distribution experiments (walking speed: $t = 0.73, df = 14, P = 0.48$; path linearity: $t = -0.67, df = 14, P = 0.53$). For whelks there also were no significant effects of patch type during distribution experiments for either movement speed ($t = 1.44, df = 16, P = 0.18$) or path linearity ($t = 0.74, df = 16, P = 0.47$).

Examining how tracking behavior changed as a function of distance from prey patches revealed that path linearity of blue crabs was significantly affected by section ($F_{2,26} = 9.86, P = 0.001$; Figure 2.5), with lower path linearity in the section farthest from the prey odor source. As in the previous analyses, there were no significant effects of patch distribution on blue crab path linearity ($F_{1,13} = 0.26, P = 0.62$), but there was a significant treatment by section interaction ($F_{2,26} = 4.86, P = 0.02$; Figure 2.5). Blue crab path linearity increased with distance to the patch for individuals that successfully located aggregated patches, but decreased for individuals successfully locating random patches. There was a marginally insignificant effect of section on blue crab walking speed for the distribution experiment ($F_{2,26} = 3.05, P = 0.06$) and a significant treatment by section interaction ($F_{2,26} = 6.26, P = 0.006$; Figure 2.5). Walking speed increased with distance to the odor source for blue crabs locating aggregated patches, but decreased with distance to the odor source for those individuals locating random patches. I did not see any significant effects of treatment on walking speed by blue crabs in the distribution experiment ($F_{1,13} = 0.015, P = 0.90$).

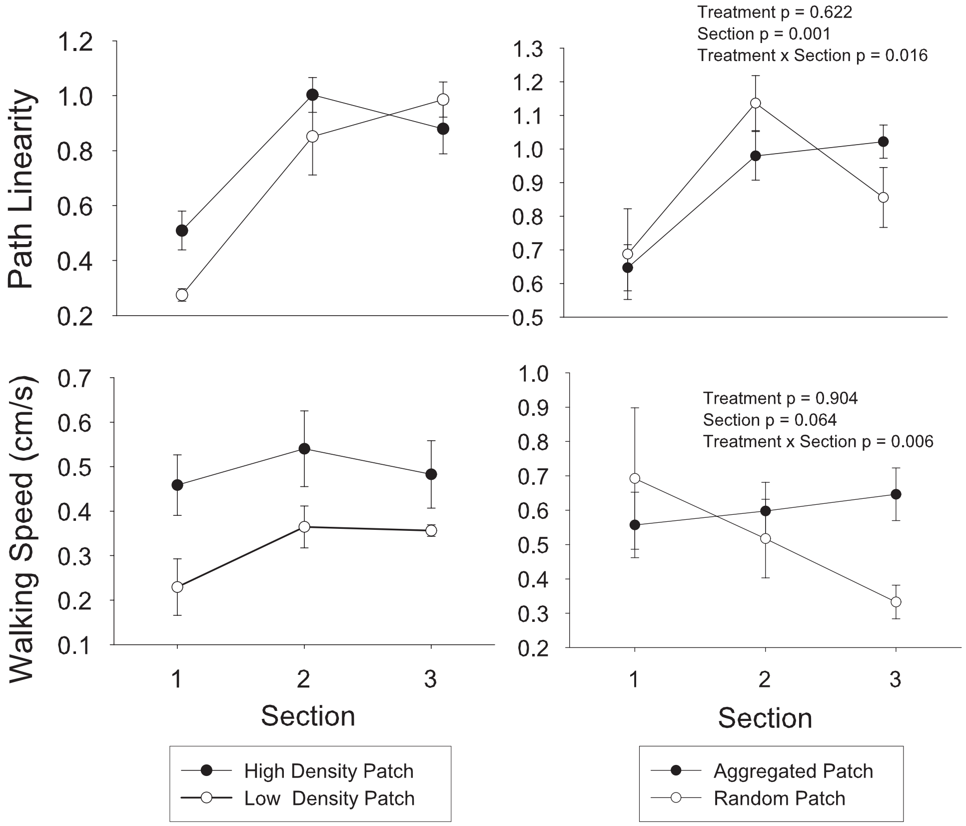

Figure 2.5: Path kinematics of successful blue crabs in the density experiment (left) and the distribution experiment (right). Error bars indicate one standard error. All statistics were determined using a repeated measures ANOVA with section as the repeated factor. Sample sizes = 12, 2, 12, and 4 for crabs successfully locating high density, low density, aggregated, and random patches, respectfully.

Whelks in the distribution experiment decreased their movement speed as they approached the odor source regardless of which patch they successfully located. There was a significant effect of section on movement speed ($F_{2,32} = 24.00, P < 0.001$), but no effect of patch distribution ($F_{1,16} = 2.66, P = 0.13$) or patch distribution by section interaction ($F_{2,32} = 0.61, P = 0.55$; Figure 2.4). There were no significant effects of patch distribution ($F_{1,16} = 0.31, P0.59$) or patch type by section interaction ($F_{2,32} = 0.01, P = 0.99$) on whelk path linearity, but there was a significant effect of section ($F_{2,32} = 6.95, P = 0.003$), with individuals showing reduced path linearity closer toward the odor source, regardless of patch distribution.

Laboratory studies may be summarized as follows. Blue crabs and whelks both located high density patches more successfully compared to low density patches. Blue crabs also had higher success in locating aggregated patches, whereas whelks showed no differences in tracking success between aggregated and random patches (Figure 2.3). Whelk foraging efficiency was not affected by prey distribution, but whelks did show reductions in walking speed and path linearity as they approached the odor source in distribution experiments (Figure 2.4). Whelk movement efficiency (path linearity) was greater when tracking toward high density patches. In contrast to whelks, blue crab foraging efficiency was affected by distribution treatment as a function of distance from the prey patch (Figure 2.5). Blue crabs tended to have greater locomotory efficiency (walking speed, path linearity) when locating high density patches, but trends were not analyzed because of low sample size. Blue crabs increased their locomotory efficiency (walking speed, path linearity) as they approached aggregated patches.

2.5 Discussion

My results show significant effects of within-patch prey density and distribution on predation rates by large mobile odor-mediated consumers in the field. The strength and pattern of these effects is mediated by predator-specific responses to distribution-dependent differences in odor landscapes based on predator's sensory capabilities and foraging modes. Blue crabs show higher predation rates on patches containing high prey density and patches containing aggregated distributions in the field (Figure 2.1 and 2.2A). Blue crabs also have greater foraging efficiency when locomoting toward patches containing high density and aggregated distributions in the laboratory (Figure 2.5), suggesting that navigational efficiency to patches of varying density and distribution is a major constraint on the foraging success of highly mobile predators. Less mobile whelk predators show higher predation rates in patches containing randomly distributed individuals in the field, despite the fact that predatory success and efficiency in laboratory settings are not higher for whelks in these conditions (Figures 2.3 and 2.4). Instead less mobile foragers like whelks may be limited by odor plume encounter rates in the field rather than their ability to navigate efficiently once patches have been detected.

Within-patch distribution of prey individuals (and the resulting odor landscapes) had a significant effect on predation rates by both predator species in the field (Figures 2.1 and 2.2). These effects were mediated by the ability of predators to efficiently navigate within odor plumes (for quick moving predators) or by predator encounter rates with odor plumes (for slowly moving predators). Patches with differing distributions seemed to produce odor landscapes that were not simple aggregates of odor plumes from individuals, or those that could be predicted by density alone (Salt 1979; Wilson 1990). Blue crabs had higher predation rates in patches containing aggregated prey and in patches containing high prey densities in the field and the laboratory (Figures 2.1 and 2.3) as a result of enhanced foraging efficiency when locomoting toward these patch types (Figure 2.5). Many studies have shown higher predation rates by blue crabs in patches of high prey density (Sponaugle & Lawton 1990; Eggleston *et al.* 1992; Micheli 1997; Seitz *et al.* 2001; Kuhlmann & Hines 2005), but my study indicates that the effect of within-patch distribution may result in a misinterpretation of the importance of density. Information about the distribution of prey individuals within patches needs to be incorporated into manipulative studies in order to correctly predict patterns of predation within resource patches and the mechanisms governing these interactions.

Predator responses to resource patch distribution, independent of patch density, have been seen previously in other communities including; dung beetle interactions with dung pads (Horgan 2005); cattle and sheep grazing in patches containing different distributions of preferred foods (Edwards *et al.* 1994; Dumont *et al.* 2000; Dumont *et al.* 2002); location of mushroom habitat by mushroom-breeding flies (Heard 1998); and moose foraging in patchy tree stands (Edenius *et al.* 2002). Dumont *et al.* (2002) found that sheep and cattle utilized patches containing preferred ryegrass significantly more when those patches contained aggregated distributions than when they contained randomly distributed resources. Blue crabs also showed similar preferences for patches containing aggregated individuals in the field (Figure 2.1), although the mechanisms by which the two species perceive resource patches are probably different.

Responses of predators to within-patch prey distribution seem to occur because differences in odor landscapes affect a predator's ability to perceive and efficiently locomote toward patches or affect their encounter rates with patches, resulting in differences in predation rates. Studies examining interactions between model bivalve excurrent plumes show that multiple individuals and individuals located closer together produce plumes that have increased mixing and are raised higher above the bed relative to plumes from individual bivalves (Monismith *et al.* 1990; Yu *et al.* 2006). Based on this, I suspect that patches containing aggregated distributions (with individuals spaced closer together) will produce plumes that are raised above the bed, contain more chemicals per unit area and have more readily identifiable edges relative to patches containing randomly distributed individuals. Patches containing randomly distributed individuals will produce plumes that are wider than aggregated patches of the same density, resulting in a larger area downstream that contains prey odors. Differences in the spatial spread and homogeneity of plumes emanating from random and aggregated prey patches may impact odor-mediated predators based on their foraging mode and ability to extract spatial and temporal information from odor signals.

The success and efficiency of quickly moving predators in locating patches containing different within-patch distributions seems to be related to their capacity to spatially integrate information from odor plumes. Plumes from random patches that are spread in the cross-stream direction, located closer to the substrate, and have poorly identifiable edges, may represent highly complex odor landscapes for blue crabs that use near-bed thoracic chemoreceptors to spatially localize odor plumes and guide cross-stream searching behavior (Keller *et al.* 2003; Page *et al.* 2011). Decreases in blue crab walking speed and path linearity while approaching random patches (Figure 2.5) indicate that predators may be slowing down and increasing their cross-stream movement to acquire adequate information about the location and spatial extent (edge detection) of plumes emanating from random patches in comparison to those from aggregated patches. Highly mobile foragers that use the spatial integration of plume information to successfully locate prey patches seem to be limited by their ability to navigate efficiently toward odor sources.

Patterns of foraging success by slow moving whelks in the field as compared to those in the laboratory suggest that differences in predation rates in the field were the result of encounter rates with patches containing different distributions, as opposed to the ability to efficiently navigate odor plumes. Whelks show higher path linearity when tracking to patches of high density that could be the result of enhanced odor concentrations (Figure 2.4), but I saw no changes in locomotory efficiency in response to different patch distributions in the laboratory. Whelks also had higher predation rates in patches containing randomly distributed prey in the field (Figure 2.2), which does not correspond to their sensory capabilities and patterns of foraging efficiency in the laboratory (Figures 2.3 and 2.4). Random patches that spread out farther in the cross-stream direction, relative to aggregated patches should create a larger "zone of attractiveness" (Cain 1985) and may enhance the encounter rates of slow moving predators with patches containing this distribution, accounting for patterns of whelk predation in the field (Figure 2.2). Slow moving predators that can temporally integrate (time-average) information from odor plumes may not be constrained by patch distribution effects on foraging efficiency like quickly moving predators are; instead they may be dependent on encounter rates with patch odor plumes, resulting in higher predation rates in patches with wider cross-stream distributions.

Patterns of predation on patches with differing density and distribution characteristics seems to be the result of predator-specific differences in mobility and sensory strategies, which shape predator constraints to foraging success (Figure 2.6A). Predator-specific responses to prey density and distribution suggest that differences in the dominant predator in estuaries, either spatially or temporally may determine the relative occurrence of different prey patch types (Figure 2.6B). These conceptual frameworks can be used to generate predictions about predator-specific patterns of predation as a function of predator mobility, sensory strategies, and foraging constraints. For example, in less salty tributaries where blue crabs are the dominant predator, clams may be found more frequently in patches of low density where prey individuals are randomly distributed. In saltier areas of the estuary where whelks are the dominant predator, clams should be found more frequently in aggregated patches, regardless of density. Current assessments of clam density are mainly limited to those areas closer to the ocean (Walker & Tenore 1984) and do not consider within-patch distribution. To assess the predictive ability of my conceptual framework, I recommend that future studies assess patch density and distribution in all estuarine locations to confirm my predictions.

Responses of predators to differences in odor landscapes based on prey patch density and distribution are dependent on predator species' sensory capabilities and foraging modes, resulting in prey refuge characteristics that are dependent on predominant predator identity. Predators utilizing quick movement and spatial integration (blue crabs) show patterns of predation that are related to their tracking efficiency, whereas patterns of predation by predators that are slow moving (whelks) and use

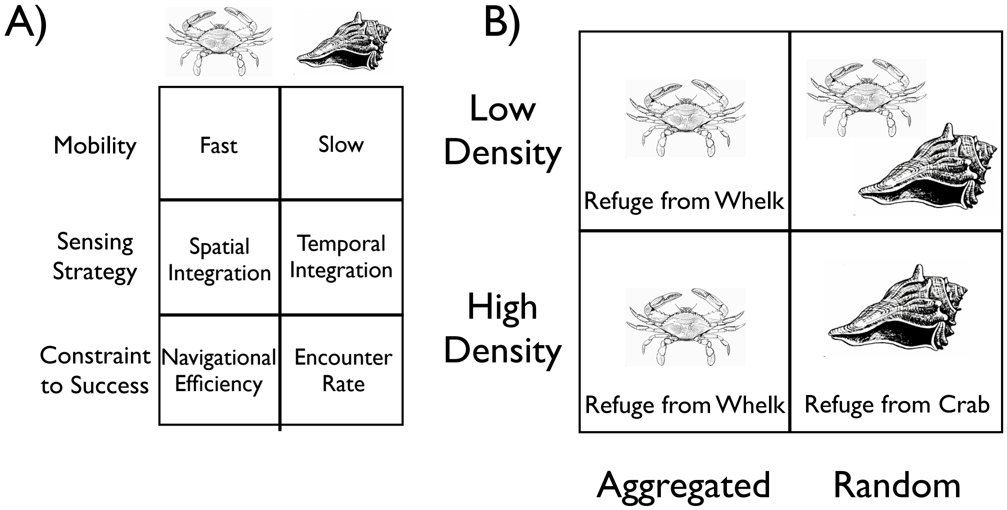

Figure 2.6: (A) Predator foraging behaviors and the resulting constraints on successful searching. (B) Graphical representation of within-patch prey characteristics resulting in possible refuges from predation. Each combination of density and distribution results in a specific combination of successful predators. For example, whelks show high predation rates in all patches where prey individuals were randomly distributed, whereas the success of crabs predators is limited in patches of low prey density and random distribution.

temporal integration of odor plume information for navigation seem to be mediated by their encounter rates with patches. I recommend that predator sensory capability and foraging modalities be included in individual-based foraging models in order to develop more predictive frameworks to assess predator-prey dynamics in patchy landscapes.

CHAPTER III

TEMPORAL AND SPATIAL SENSING STRATEGIES MAINTAIN TRACKING SUCCESS OF WHELKS TO PREY PATCHES OF DIFFERING CROSS-STREAM DISTRIBUTIONS

3.1 Abstract

Odor-mediated predators use a variety of mechanisms to efficiently navigate to prey within patches, including the spatial and temporal integration of chemicals from prey odor plumes. Predators that have a high capacity to time-average odor concentrations are successful at locating prey in odor landscapes characterized by homogeneous odor plumes of low concentration which are mediated by mixing through changes in turbulence (flow velocity, roughness elements, and structure). Odor plumes from individual prey also may interact with each other via mixing processes to create odor landscapes with the same characteristics as those generated by turbulence, but the ability of predators with a high capacity for temporal integration to navigate odor plumes from collections of prey has not been examined. I challenged knobbed whelk (*Busycon carica*) predators to detect and navigate to prey patches (hard clams; *Mercenaria mercenaria*) containing different configurations of individuals at two densities (3 clams/patch: parallel vs. perpendicular arrangement relative to the direction of bulk water flow; 10 clams/patch: aggregated vs. random distribution) in laboratory assays to better understand how prey-generated mixing conditions impact time-averaging predators. Whelks had decreased navigational efficiency (walking speed,

path linearity, tracking time) in treatments with individuals arranged perpendicularly to the direction of bulk water flow at low densities, but distribution-dependent differences in whelk foraging efficiency were not seen at high densities. Whelks also demonstrated increased spatial sampling behaviors in response to low-density, perpendicular treatments, presumably in a effort to enhance information about the spatial extent and structure of odor plumes to help maintain navigational success. These responses seem to be the result of increased mixing in high-density and low-density, parallel treatments, which may mitigate information about the configuration of prey individuals within patches. The ability of whelks to effectively utilize temporal integration mechanisms to extract information from prey patch odor plumes allows them to maintain foraging success despite differences in the distribution of individuals within aggregations and may enable whelks to occupy specific sensory niches that could reduce competition with other odor-mediated predators over resources.

3.2 Introduction

Odor-mediated predators use a variety of sensing strategies to successfully locate prey including both the temporal and spatial integration of chemical information from odor plumes. The effectiveness of using these sensory mechanisms is dependent on body size (or span between chemosensors) relative to the spatial extent of odor plumes, as well as predator mobility and chemosensory sampling rate (Weissburg 2000). Predators have been generally categorized into groups dependent on their capacity to both temporally and spatially integrate information from odor plumes. Organisms that have a high capacity for temporal integration but a low capacity for spatial integration are generally small and slow, enabling them to time-average odor plume concentrations but preventing them from making simultaneous comparisons of odor concentrations at distant locations. Predators that have a high capacity for spatial integration but a low capacity for temporal integration are generally large enough that they can simultaneously sample odors at different positions within odor plumes using distant chemosensors (e.g. bilateral comparison; Webster *et al.* 2001), but move too quickly to obtain average information about odor plume concentrations. Some predators, like sea stars, may have a high capacity to integrate odor plume information using both spatial and temporal mechanisms because of their large size and slow movement, whereas other predators like moths may have low spatial and temporal integration capabilities because of their quick movement and small size (Weissburg 2000). Numerous studies have examined the ability of predators that have a high capacity for spatial integration to successfully navigate toward prey in the laboratory (blue crabs - Weissburg & Zimmer-Faust 1993, Weissburg & Zimmer-Faust 1994; Page *et al.* 2011; lobsters Moore *et al.* 1991) and in the field (Zimmer-Faust *et al.* 1995; Powers & Kittinger 2002), but fewer have adequately done the same for predators that have a high capacity for temporal integration (whelk - Powers & Kittinger 2002; Ferner & Weissburg 2005; nudibranch Wyeth *et al.* 2006; sea stars Rochette *et al.* 1994).

It has been hypothesized that the ability to time-average information about odor concentration may allow predators to navigate successfully in low concentration, largely homogeneous odor landscapes. Average concentrations of turbulent odor plumes vary predictably with distance downstream of the odor source and with distance from plume centerlines in the cross-stream direction. The ability of predators to time-average odor concentrations is dependent on the collection of large numbers of odor samples which can be accomplished by moving slowly. Predators can use time averaging to navigate homogeneous, low concentration odor plumes by determining their position relative to the odor source and plume centerline as successfully as they can for odor plumes of high concentration. This pattern of navigational and foraging success has been shown for slow moving gastropod whelks in response to turbulent odor plumes produced by increases in velocity and turbulence (Powers & Kittinger 2002; Ferner & Weissburg 2005; Ferner *et al.* 2009). Turbulent odor plumes can be created by mixing processes and result in odor plumes that are homogeneous and contain low concentrations of odors. Understanding how time-averaging predators respond to other natural sources of turbulence is required to determine under what specific conditions predatory success and navigational efficiency are maximized or constrained, thus providing insight into the context-specificity of predator-prey interactions. Odor plumes from individual prey may interact with each other via mixing processes to create odor landscapes with the same characteristics as those generated by turbulence, but the ability of predators with a high capacity for temporal integration to navigate odor plumes from collections of prey has not been examined explicitly.

Predators in natural environments are rarely exposed to single prey individuals, and thus predator success is dependent on the ability to forage efficiently in response to patches containing multiple prey. Prey odor landscapes to which predators are exposed are mediated by the density and distribution of individuals within patches. Laboratory experiments using model bivalves suggest that patch-scale odor plumes undergo increased mixing when separation distances between individual prey excurrent plumes are smaller and when patches contain greater densities, resulting in slightly elevated (above the bed) and more homogeneous patch-scale odor plumes (Monismith *et al.* 1990; Yu *et al.* 2006). Prey patches containing closely spaced individuals should produce more homogeneous plumes in comparison to prey patches containing individuals separated by large distances, which should produce heterogeneous patch-scale plumes made up of highly concentrated filaments from individual prey. It is unknown how predators that have a high capacity for temporal integration respond to collections of spatially distinct odor plumes from individual prey. Predators that utilize simultaneous bilateral sampling can determine the extent and spatial distribution of odor plumes via concentration comparisons, but it is largely unknown what mechanisms time-averaging predators use to determine the spatial extent and distribution of odor plumes. Whelks may use siphonal movement in the cross-stream direction to gather information about the spatial distribution and extent of odor plumes (as suggested by Rhorkasse & Atema 2002; Ferner & Weissburg 2005), but to my knowledge this has not been examined as a mechanism to maintain foraging success in relation to different odor landscapes. Additional experimentation is needed to determine how these spatial sampling behaviors influence whelk navigational efficiency and success in odor landscapes that differ in their spatial extent and distribution. From this information, predictions can be made as to the context-dependency of spatial sampling behaviors in helping to maintain foraging success by time-averaging predators.

By understanding the relationship between predators that have a high capacity for temporal integration and prey density and distribution within patches I can begin to make predictions about possible predatory impacts on the abundance of specific prey patch types in natural systems. The ability of time-averaging predators to successfully locate prey in low concentration, homogeneous odor plumes suggests that their success may not be impacted by the mixing effects produced by patches of differing prey density and distribution. If time-averaging predators are not impacted by density- and distribution-dependent changes in odor landscapes, it may result in similar abundances of different prey patch types in the field. It may also allow time-averagers to exploit prey patches that other predators, whose foraging efficiency is affected by prey patch density and distribution, cannot.

I used a gastropod, the knobbed whelk *Busycon carica*, as a model organism to explore the foraging behavior and efficiency of predators with high capacities for temporal integration, but potentially limited spatial sampling. I focused on navigational behavior and performance in relation to prey density and distribution within patches to examine the consequences of specific patterns of odor signal structure produced by prey demography. Whelks are important components of many intertidal salt marsh communities along the Atlantic Coast (Carriker 1951). Whelks feed mainly on bivalve populations (Carriker 1951) that are distributed patchily at a variety of spatial scales (Wells 1957; Walker & Tenore 1984), making this a good system to examine the impacts of prey patch density and distribution on predator foraging efficiency. Although other organisms that have a high capacity for temporal integration have been studied (nudibranch: Wyeth *et al.* 2006, sea stars: Rochette *et al.* 1994), the explicit behavioral impacts of changes in odor landscape due to water velocity and turbulence have already been elucidated for knobbed whelks (Powers & Kittinger 2002; Rhorkasse & Atema 2002; Ferner & Weissburg 2005; Ferner *et al.* 2009), and thus readily allow comparisons to be made.

I challenged knobbed whelk predators to detect and navigate to prey patches containing different distributions of individuals at two densities (3 bivalves/patch and 10 bivalves/patch) in laboratory assays. Using path analysis techniques I was able to compare foraging behavior and performance as a function of prey distribution and density. I predict that whelks will have high foraging efficiency and success regardless of density or distribution as a result of their ability to time-average information about odor plume characteristics.

3.3 Methods

3.3.1 Flume Characterization and Animal Collection/Maintenance

All odor-tracking experiments were performed in a paddle-driven racetrack flume at the Skidaway Institute of Oceanography during April 2010. The working section is approximately 4.8 m long by 1 m wide with approximately 1 cm of sand evenly distributed along the smooth Plexiglas bottom. The working section contains three circular false bottoms (each 30 cm in diameter) arranged in a triangle. Two of the false bottoms have centers located 19.5 cm from the left and right of the flume centerline and the third false bottom has a center located on the flume centerline approximately 40 cm upstream of the other two false bottoms (Figure 3.1). I created bivalve aggregations of different densities and spatial configurations within these areas (see below).

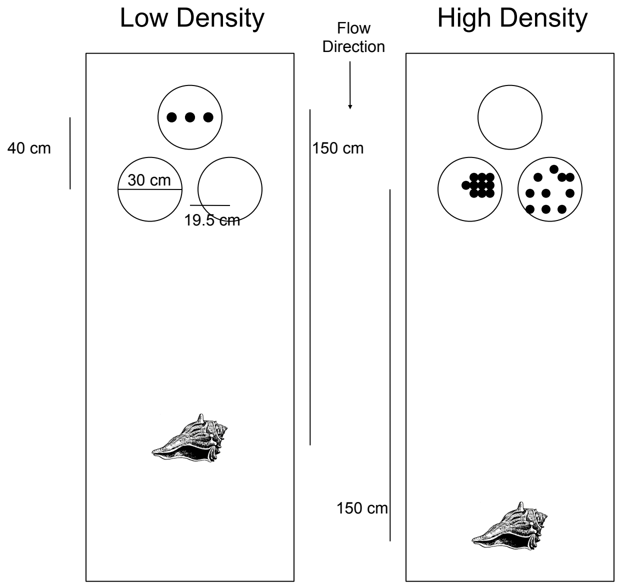

Figure 3.1: Experimental setup for low- and high-density experiments. Low density experiments contained three clams arranged perpendicular (shown) or parallel to bulk flow (from top to bottom of the figure), which whelks were exposed to in separate trials. Whelks in high density experiments were exposed to both aggregated and random patches simultaneously, but the side of the flume where patch types were located was randomized.

All experiments were conducted with a water depth of 0.25 m and at 5 cm/s flow speed (representative of natural flow environments where animals were collected [Berry *et al.* 2011; Chapters 5 and 6]). See Ferner & Weissburg (2005) for a more detailed description of the flume apparatus and the hydrodynamic environment. Knobbed whelks (*Busycon carica*) were collected by hand from Priest Landing and other intertidal habitats in Wassaw Sound, Georgia. Individuals were held in flow-through tanks with gravel-filtered water pumped directly from the Skidaway River. Whelks were starved for 1 week prior to experimentation to standardize hunger levels. Individuals were tested only once and then released near where they were collected. Juvenile prey clams (15-25 mm length) were obtained from Bay Shellfish, Sarasota, FL. Salinity and temperature in the flume and holding tanks ranged from 15 to 30 ppt and 25 to 30 °C, respectively.

3.3.2 Prey Configuration at Low Density

To investigate whelk foraging efficiency in response to collections of individual prey that varied in the sensory landscapes they create, I challenged knobbed whelks to locate and track to live juvenile hard clams (*Mercenaria mercenaria*) in patches that varied in the configuration of individuals relative to bulk water flow direction. Patch configuration treatments consisted of three clams separated by 7 cm placed parallel to the direction of bulk water flow (parallel configuration treatment) or three clams separated by 7 cm placed perpendicular to the direction of bulk water flow (perpendicular configuration treatment) (Figure 3.1). These two treatments will create patch-scale odor plumes that spread out in the cross-stream direction to different degrees. Clams were positioned in the upper false bottom such that the middle clam or all three clams were positioned along the centerline of the flume for both perpendicular and parallel configuration treatments, respectively. The order of treatments was randomly chosen and individual whelks were exposed to only one patch treatment.

Clams were placed in the sand with the shell margin facing down and allowed to bury and begin pumping (See Smee & Weissburg 2006b). A single knobbed whelk was introduced to the flume 1.5 m downstream of the clam patch when all three clams were pumping. Thirty minutes was then allowed for whelks to initiate movement in the upstream or downstream direction. An additional 60 minutes was given to contact the clam patch for whelks moving upstream. Individuals were given 20 minutes to consume any clams once they contacted the prey patch. Trials were terminated when individuals moved in a downstream direction, contacted the patch and the feeding period was completed (N = 9 for both configuration treatments), or moved upstream of the prey patch without contacting it (N = 2 for both configuration treatments). Clam pumping was assessed every 5 minutes from whelk introduction to contact with the patch to confirm that there were no significant differences in odor production between treatments ($t = 0.51$, $df = 7$, $P = 0.62$; perpendicular configuration = 2.84 ± 0.18 clams, parallel configuration = 2.78 ± 0.33 clams). New clams were used for each trial.

3.3.3 Prey Distributions at High Density

To determine how whelk foraging efficiency and success changed in response to differences in more realistic distributions of prey groups, I challenged knobbed whelks in a choice assay to distinguish between and locate two patches of juvenile hard clams in an aggregated distribution (10 individual clams with an approximately 3 cm separation distance) and a random distribution (10 individual clams placed randomly with 3 to 10 cm separation distances) (Figure 3.1). Patches were constructed by placing clams in the right and left side false bottoms. The location of patch types (i.e. which side of the flume) was chosen randomly for each trial. The clam density used in this experiment was approximately 1.5 times that in naturally occurring patches (Walker & Tenore 1984), but was used to ensure that an adequate number of clams were providing odor cues throughout individual trials. See Chapter 2 for a more detailed description of experimental methodology.

Clams were placed in the sand, shell margin down, and allowed to bury and begin pumping. A single knobbed whelk was introduced into the flume 1.5 m downstream of both patches when at least half the clams in each patch were pumping.

Individual whelks were then allowed 30 minutes to initiate movement in the upstream or downstream direction. An additional 60 minutes was given to reach either patch for whelks that moved in an upstream direction. Successful individuals were then given 20 minutes to consume as many clams as they wanted. Clam pumping was assessed at three points during trials: upon whelk introduction to the flume, initiation of movement, and immediately prior to contact with the patch. New clams were used for each trial. The average number of clams pumping throughout each trial was compared between patch types to confirm that there were no significant differences in odor production ($t = -1.268$, $df = 17$, $P = 0.222$; aggregated $= 5.30 \pm 0.24$ clams, random $= 5.56 \pm 0.28$ clams). Assays were terminated when individuals moved in a downstream direction, passed to the sides of either patch, or contacted a clam within the patch and started to feed.

3.3.4 Data Analysis

Trials for each experiment (low and high density) were recorded using a video camera mounted approximately 2.5 m above the test arena (Fieldcam M370 mono camera, Furhman Diversified). Video of each successful predators' path was then analyzed using motion analysis software (Motion Analysis Corp. Model VP110) to determine differences in tracking efficiency and behavior for individuals. Paths were analyzed at 1 frame/second and then a moving average was used to correct for any erroneous detection of movement due to scanning behavior. Scanning behavior can be characterized by the siphon moving in the cross-stream direction relative to the individuals center of mass. This may be a sampling strategy to help whelks assess the cross-stream spread of odors or identify plume edges, and has been seen in previous tracking experiments (Rhorkasse & Atema 2002; Ferner & Weissburg 2005). I defined a single scan as one cycle of the siphon moving in the cross-stream direction and returning to the origin. The average number of seconds between scans was determined for each whelk and this number was used as the number of seconds averaged in my moving average calculations.

3.3.4.1 Path Kinematics of Foraging Whelks

I calculated movement speed (standardized to shell length) and path linearity (arcsine transformed), and the effect of prey configuration or distribution was determined for each experiment (low or high density) using a t-test. I then divided the flume into three equal sections to examine how predator behavior changed with distance from the prey odor source. I calculated movement speed and path linearity for whelks in each section and then used a repeated-measures analysis of variance (ANOVA) with section as the repeated factor to determine differences in foraging kinematics based on distance from the odor source. I analyzed low and high density experiments separately. I also compared the total time needed to successfully locate prey for distribution treatments within each experiment using a t-test.

3.3.4.2 Scanning Behavior of Foraging Whelks

I calculated whelk scanning rates (as defined above) during each trial and for each section. For each experiment (i.e. low and high density) I compared scanning rates between configuration or distribution treatments and flume sections using a repeated-measures ANOVA with section as the repeated factor.

3.3.4.3 Direction of travel

The direction of movement relative to a straight path toward the patch should indicate whether whelks are heading away from the plume centerline or maintaining a straight course toward prey patches. I compared the distribution of angular headings for whelks tracking toward patches in different configuration or distribution treatments within each density experiment using a G-test of independence. Larger angular headings should be associated with whelks sampling odors farther from the plume centerline, presumably in an effort to gather information about the cross-stream spread and spatial configuration of the odor plume to help maintain foraging success. Thus, whelk angular headings should vary based on the spatial configuration or distribution of prey upstream.

3.3.4.4 Distance from Centerline While Foraging

Average odor plume concentration decreases predictably away from the plume centerline (Webster & Weissburg 2001). Sampling away from the plume centerline should provide time-averaging predators with information to determine the direction of the centerline and help maintain contact with the odor plume. This sampling scheme could be important in plumes that are heterogeneous or are more spread out in the cross-stream direction. I compared whelk distance from the plume centerline (also the centerline of the flume arena; see methods above) in three sections of the flume using a repeated-measures ANOVA with section as the repeated measure to help examine the extent to which whelks may be utilizing spatial sampling strategies as a function of distance to the odor source in low density configuration experiments.

The experimental design for the high density experiment (choice assay) prevented us from using the same analysis technique as in the low density experiment. Instead, I determined the position downstream of the prey patch at which whelks showed preferences for specific patch types by assessing their distance from the plume centerlines. I divided the flume into 5 equal sections and determined the distance of whelks from the centerline of each patch plume and then calculated the position of the whelk relative to these two centerlines as: $DD = D_{AP} - D_{CP}$, where DD = difference in distances, D_{AP} = distance from alternative plume centerline, and D_{CP} = distance from chosen plume centerline. Values of DD greater than zero indicate that whelks were closer to the plume centerline of the chosen patch (e.g. the patch the whelks moved to) than the plume centerline of the alternative patch. I compared values of DD for whelks successfully locating aggregated and random patches using a repeated-measures ANOVA with section as the repeated measure to determine the position downstream of the prey patch where whelks explicitly chose one plume over another.

3.4 Results

3.4.1 Responses of Whelks to Low Density Prey Patches with Differing Configurations

3.4.1.1 Tracking Efficiency and Success

There were no apparent differences in whelk tracking success based on prey configuration treatments in low density experiments; whelks successfully located prey patches 9 times out of 11 for both prey configuration treatments.

Whelks seemed to have overall greater foraging efficiency while navigating toward patches in the parallel configuration treatment. Whelks showed significantly greater path linearity when successfully tracking to patches in the parallel configuration treatment compared to the perpendicular configuration treatment ($t = -2.44$, $df = 16$, $P = 0.038$; Figure 3.2A). There also was a significant difference in overall whelk movement speed between prey configuration treatments ($t = -2.21$, $df = 16$, $P = 0.043$; Figure 3.2C), with whelks moving faster when successfully tracking to patches in the parallel configuration treatment. There was a significant difference in the amount of time that whelks took to successfully track to patches of differing configurations ($t = 2.31$, $df = 16$, $P = 0.036$; Figure 3.2E); whelks took longer to locate patches in the perpendicular configuration treatment than the parallel configuration treatment.

Analysis of whelk foraging efficiency as a function of distance to the odor source did not provide much additional information that was not elucidated by comparisons of average kinematic parameters for low density configuration experiments

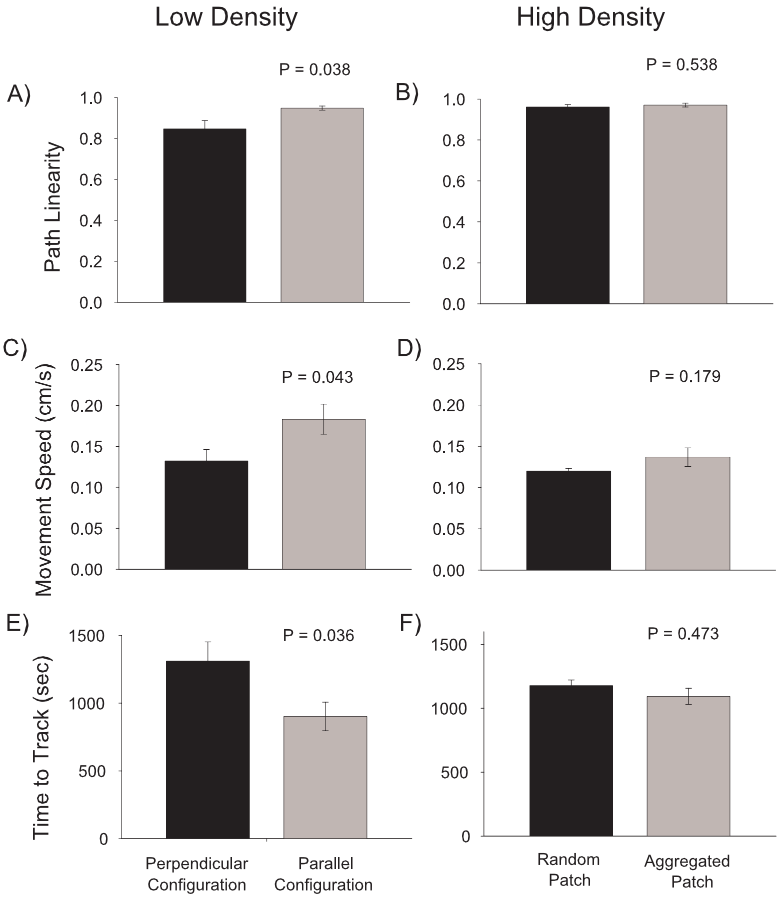

Figure 3.2: Increases in plume width result in reductions of predator foraging efficiency (path linearity [A, B] and movement speed [C, D], total tracking time [E, F]) of successful whelks navigating toward patches in low density experiments (left) but not patches in high density experiments (right). For low density, parallel and perpendicular refer to the configuration of the three clams within each patch relative to the direction of bulk water flow. For high densities, random and aggregated refer to the distribution of 10 clams within each patch. For each comparison, statistical significance was determined using a t-test. Error bars indicate standard error.

(see above). There were significant effects of section on whelk movement speed in low density configuration experiments ($F_{2,32} = 42.39$, $P < 0.001$) that showed decreases in whelk movement speed in the section closest to the odor source (Figure 3.3). This pattern has been seen previously for many organisms (blue crabs: Weissburg & Zimmer-Faust 1994; whelks: Ferner & Weissburg 2005) and did not seem to have any relation to patch density or prey configuration within patches.

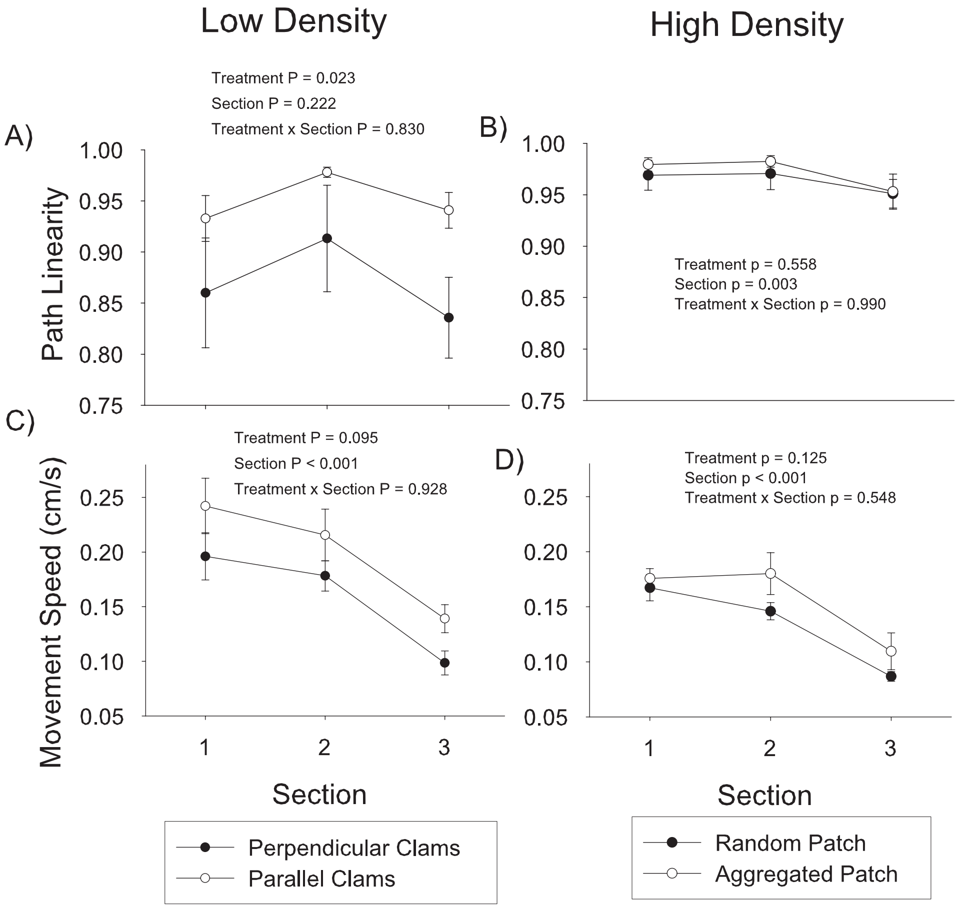

Figure 3.3: Path kinematics of whelks as a function of distance to the odor source. The flume was divided into three equal sections with section 1 including the whelk starting position and section 3 including the prey patch. Perpendicular and parallel refer to the configuration of clams relative to the direction of bulk water flow. Significance was determined using a repeated-measures ANOVA with section as the repeated measure. Error bars indicate one standard error.

3.4.1.2 Spatial Sampling Strategies

Whelks took between 10 and 100 seconds to complete each scan. Individual scans occurred anytime directly following another scan to approximately 40 seconds after the previous scan was completed (Figure 3.4). Note that scanning speed does not necessarily correspond to the scanning rate calculated since scans are not continuous. Whelks successfully navigating to patches showed higher scanning rates when challenged with perpendicular prey configurations ($F_{1,16} = 5.24$, $P = 0.036$; Figure 3.5A) in low density experiments. There also was a significant effect of section ($F_{2,32} = 3.39$, $P = 0.046$) and prey configuration by section interaction ($F_{2,32} = 3.72$, $P = 0.035$) on whelk scanning rates. Scanning rates for whelks navigating to patches with perpendicular prey configurations decreased as individuals approached the odor source, but stayed relatively constant for whelks navigating to patches with parallel prey configurations (Figure 3.5A).

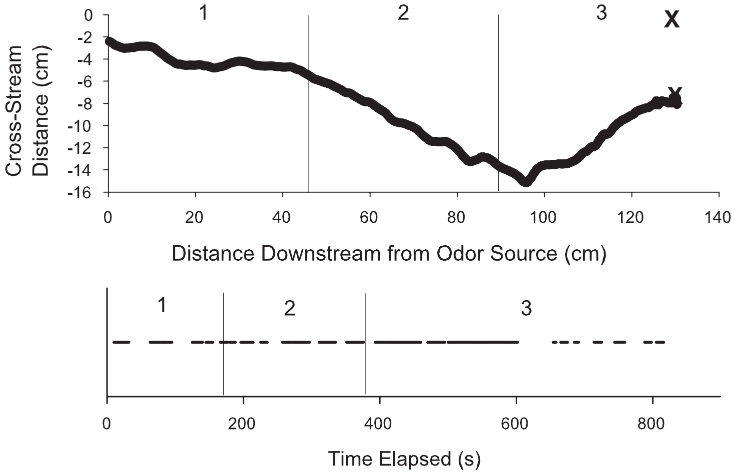

Figure 3.4: An example whelk track for the low density, perpendicular configuration treatment (top). Two of the three available clam prey are marked (X). Whelk scanning behavior (bottom) is shown as a function of the time elapsed since the beginning of the trial where each dash represents one scan. Numbers and the related divisions represent the three sections of the flume (top) and the corresponding time spent in each of the flume sections (bottom).

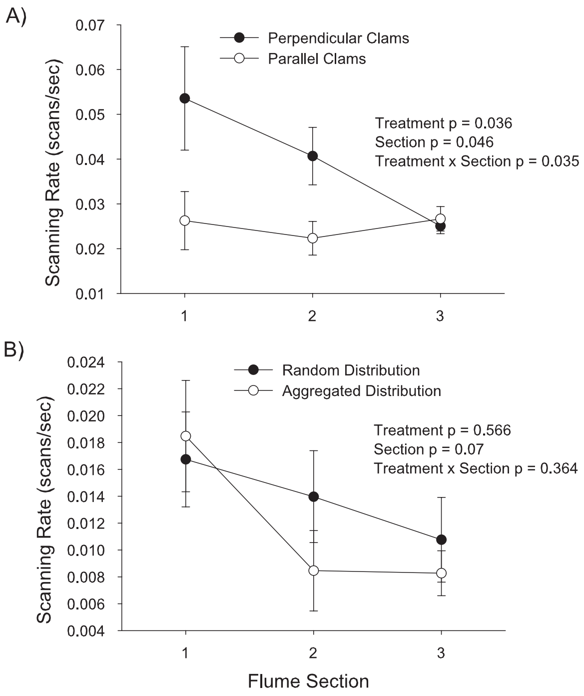

Figure 3.5: There were significant decreases in scanning rates as whelks approached prey patches for both low (A) and high density (B) experiments. Scanning rates were greater for patches with perpendicular prey configurations in low density experiments. Significance was determined using a repeated-measures ANOVA with flume section as the repeated factor. Flume section 1 contained the whelk starting position and flume section 3 contained the prey patch. Error bars indicate one standard error.

The distribution of angular headings by whelks in low density experiments was significantly different between prey configuration treatments (Pearson $\chi^2 = 28.46$, $df = 3$, $P < 0.001$), with a higher frequency of large angular headings for whelks navigating plumes from the perpendicular configuration treatment than for whelks navigating plumes in the parallel configuration treatment (Figure 3.6A). Whelks navigating toward clam patches also were closer to the plume centerline in the section closest to the odor source, regardless of prey configuration. There was a significant effect of section ($F_{2,32} = 6.39$, $P = 0.005$) on whelk distance from the plume centerline, but there were no significant effects of prey configuration ($F_{1,16} = 2.00$, $P = 0.18$) or prey configuration by section interaction ($F_{2,32} = 0.62$, $P = 0.53$; Figure 3.7A).

Clams in the center position in perpendicular configuration treatments were found more frequently than clams located to the right or left of the flume centerline (left = 1, right = 1, center = 7), suggesting that nearness to the centerline in these conditions reflects patterns of prey discrimination.

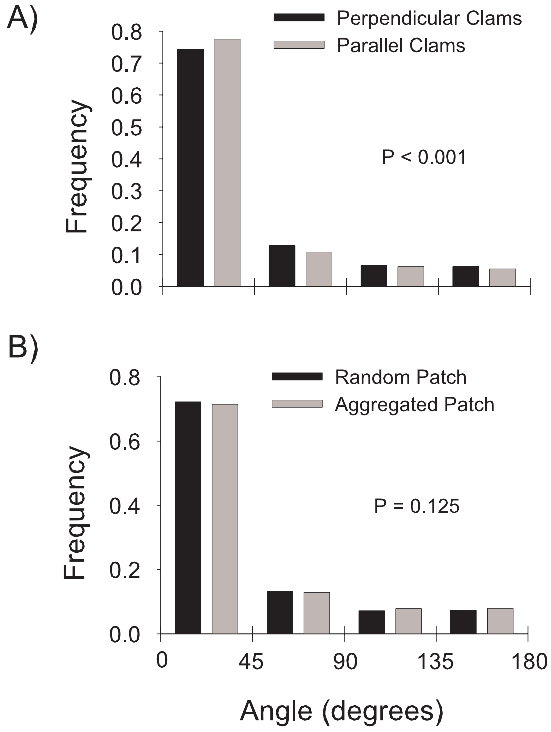

Figure 3.6: There were significant differences in angular headings between whelks tracking to patches containing prey individuals in different configurations in low (A) and high density (B) experiments. Angular headings were determined such that 0 degrees indicates no turning and 180 degrees indicates a complete reversal of direction. Magnitudes of angular headings are reported above. The numbers of samples used in determining distributions were: cross-stream = 11787, along-stream = 8011; random patch = 8966, aggregated patch = 10204. The distribution of angular headings was compared for each experiment using a G-Test.

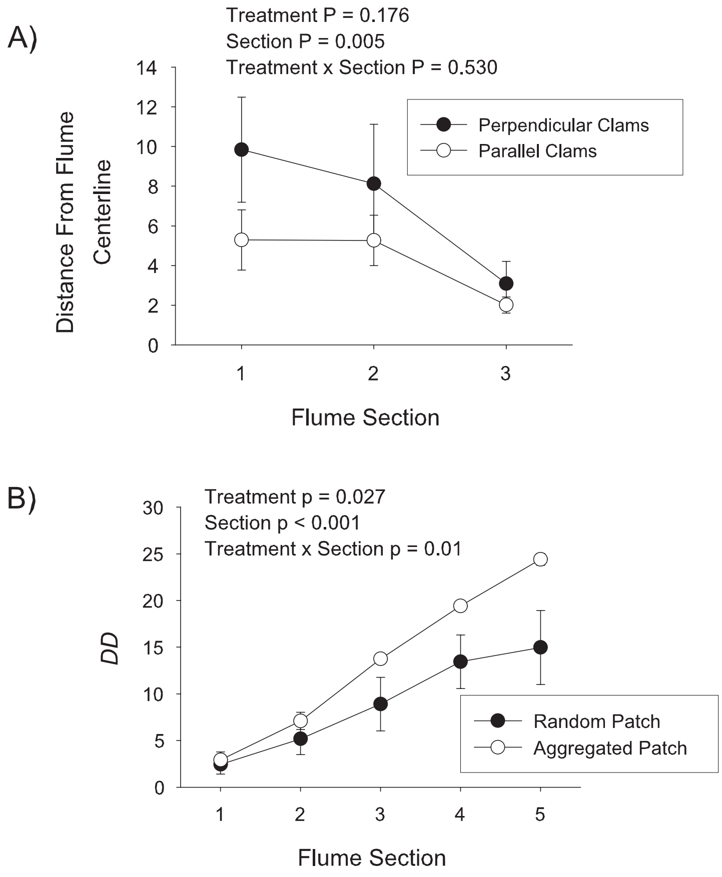

Figure 3.7: (A) Whelks in low density experiments decreased their distance from the plume centerline as they approached the prey patch ($N = 9$) (B) Whelks in high density experiments were closer to the plume centerline produced by their chosen patch than the alternative patch ($DD > 0$), but whelks tracking to aggregated patches were closer to their respective plume centerlines than whelks tracking to random patches (Random N = 8, Aggregated N = 11) $DD = D_{AP}D_{CP}$; where DD = difference in distances, D_{AP} = distance from alternative plume centerline, D_{CP} = distance from chosen plume centerline. Flume section 1 includes the whelk starting position for both (A) and (B). Section 3 and section 5 include the prey patches for low and high density experiments, respectively. Significance for both low and high density experiments was determined using a repeated-measures ANOVA with flume section as the repeated factor. Error bars represent one standard error.

3.4.2 Responses of Whelks to High Density Prey Patches with Realistic Distributions

3.4.2.1 Foraging Efficiency and Success

Whelks showed similar preferences for patches containing randomly distributed prey individuals and those containing aggregated individuals (random = 8 successful whelks, aggregated = 11 successful whelks; see Chapter 2). There were no significant differences in overall path linearity ($t = 0.74$, $df = 16$, $P = 0.471$) (Figure 3.2B) or overall movement speed ($t = 1.44$, $df = 16$, $P = 0.179$) (Figure 3.2D) between whelks tracking to aggregated versus random patches in high density experiments. There also were no significant differences in the time whelks took successfully tracking to random and aggregated patches ($t = -0.74$, $df = 16$, $P = 0.47$; Figure 3.2F).

Analysis of whelk navigational efficiency as a function of distance to the patch identified significant effects of flume section on whelk path linearity ($F_{2,32} = 6.95$, $P = 0.003$) and movement speed ($F_{2,32} = 24.00$, $P < 0.001$), but there were no significant effects of patch distribution on either path kinematic (Figure 3.3).

3.4.2.2 Spatial Sensing Strategies

Whelks took between 10 and 100 seconds to complete each scan. The time between scans ranged from immediately following the previous scan to 240 seconds after the previous scan was completed. Note that scanning speed does not necessarily correspond to the scanning rate calculated since scans are not continuous. There were no significant effects of patch distribution ($F_{1,16} = 0.34$, $P = 0.57$) or patch distribution by section interaction ($F_{2,32} = 1.04$, $P = 0.36$) on whelk scanning rates, but there was a significant effect of section ($F_{2,32} = 5.76$, $P = 0.007$) (Figure 3.5B). Whelks had reduced scanning rates as they approached prey patches, regardless of patch distribution.

Whelks in high density experiments showed no significant differences in the distribution of angular headings (Pearson $\chi^2 = 5.74$, $df = 3$, $P = 0.125$) while tracking toward random or aggregated patch types (Figure 3.6B).

Instead of examining whelk distance from the flume centerline for high density choice experiments, I calculated the difference between whelk distance from their chosen plume centerline and the alternative plume centerline (DD) (see Methods). I did this in an effort to determine at what point during tracking individuals showed an explicit preference for following plumes from a specific patch type. Recall that any difference greater than zero indicates that whelks were closer to the plume centerline of their chosen patch than the alternative patch ($DD > 0$). Differences in distance were greater than zero for all flume sections, indicating that whelks followed odor cues from one patch exclusively from the beginning of their tracks despite indications that plumes from both patch types started mixing 30 to 60 cm upstream of the whelk starting position based on dye visualizations.

There was a significant effect of patch distribution ($F_{1,13} = 6.22$, $P = 0.027$), section ($F_{4,52} = 49.59$, $P < 0.001$) and patch distribution by section interaction ($F_{4,52} = 3.70$, $P = 0.01$) on values of DD (Figure 3.7B). Whelks successfully tracking to aggregated patches were closer to plume centerlines than those successfully tracking to random patches. Whelks were similar distances from their chosen plume centerlines relative to alternative plume centerlines at the beginning of their tracks. Whelks were closer toward their chosen plume centerlines as they moved toward the odor source, but whelks tracking toward aggregated patches were closer to their respective plume centerlines than whelks tracking toward random patches. There were no apparent differences in the position of consumed clams within patches between whelks locating aggregated and random patches.

3.4.3 Summary of Comparisons Between Low and High Density Experiments

Overall, whelks in low density configuration experiments seemed to respond behaviorally to the spatial distribution of prey individuals, but these responses were diminished in whelks navigating toward more natural distributions of prey within groups. Whelks showed decreases in navigational efficiency (walking speed, path linearity, tracking time) in treatments with prey in perpendicular configurations in low density experiments, but distribution-dependent differences in whelk foraging efficiency were not seen in high density experiments (Figure 3.2). Whelks exhibited higher scanning rates in response to prey in perpendicular configurations in low density experiments. In contrast, whelks did not exhibit any distribution-dependent differences in scanning rates in high density experiments (Figure 3.5). In low density experiments whelks moved with headings shifted toward larger angles in response to perpendicular prey configurations than parallel prey configurations (Figure 3.6). There were no differences in the distribution of angular headings as a function of within-patch prey distribution for whelks navigating in high density experiments. Whelk distance to the centerline was not impacted by the spatial configuration of individuals within low density experiments, but whelks successfully locating aggregated patches in high density experiments were closer to the plume centerline than those locating random patches (Figure 3.7).

3.5 Discussion

Whelks demonstrated the ability to extract information from prey odor plumes using both temporal and spatial sampling strategies. Whelks responded to perpendicular prey configurations (relative to the direction of bulk water flow) in low density experiments with decreased foraging efficiency and increased spatial sampling behaviors. Prey in perpendicular configurations in low density configuration experiments produce a collection of spatially spread-out, high concentration, filamentous odor plumes that require increased sampling by whelks to assess average plume concentrations. Whelks did not show any differences in navigational efficiency or success as a function of prey patch distribution in high density experiments. Differences in odor landscapes between the perpendicular prey configuration at low density and both aggregated and random distributions at high density, reflect increased mixing in patches at high densities and where prey are closer together. This results in greater plume homogeneity that seems to mitigate information about prey distribution within patch-scale odor plumes. Differences in the configuration of individuals relative to bulk flow direction also produces patch-scale plumes of differing spatial coverage. The ability of whelks to effectively utilize temporal integration mechanisms to extract information from prey patch odor plumes allows them to maintain foraging success despite differences in the distribution of individuals within aggregations, and may enable whelks to occupy specific sensory niches that could reduce competition with other odor-mediated predators over resources.

3.5.1 Prey Distribution and Mixing Effects on Odor Landscapes

Within patch prey distribution seems to mediate whelk foraging efficiency via mixing processes that are dependent on prey configuration and density. Thus, the differences seen in responses of whelks to individual plumes created by different prey configurations do not translate into different foraging performance in larger aggregations with different distributions (Figure 3.2). Whelks exhibited decreased foraging efficiency in response to perpendicular prey configurations (relative to the direction of bulk water flow) in low density experiments, but did not show distribution-dependent differences in foraging efficiency in high density patches (Figures 3.2, 3.3). Interactions between individual prey plumes at high densities will create more homogeneous patch-scale odor plumes relative to low densities because of greater mixing (Monismith *et al.* 1990; Yu *et al.* 2006), which would mitigate apparent differences in prey distribution and result in similar foraging efficiencies to patches of differing prey distribution at high densities (Figure 3.2; although see Chapter 2 for differences in foraging success based on patch distribution in the field). In contrast, interactions between individual prey plumes in patches with individuals arranged perpendicularly to the direction of bulk water flow in low density experiments will not experience high mixing (Monismith *et al.* 1990), creating patch-scale plumes composed of a collection of spatially spread-out, highly intermittent, and high concentration odor filaments. Mixing, either through increases in density or orientation relative to bulk flow, seems to prevent whelk detection of clam individuals within plumes at high densities. This suggests that odor landscapes generated by low density collections of individuals are not necessarily predictive of odor landscapes generated by various prey distributions at high densities or in more natural distributions. Differences in foraging efficiency at low densities seem to be a result of responses to different odor landscapes based on prey configuration that are not apparent at large scales.

3.5.2 Utilization of Temporal and Spatial Sensing Strategies

Weissburg (2000) suggested that gastropods and other slow moving organisms may have a high capacity for temporal integration (temporal integration fraction [TIF]) of odor signals, allowing them to time-average odor plume characteristics and successfully navigate homogeneous and low concentration odor plumes (Ferner & Weissburg 2005). Foraging organisms must be able to perceive their position relative to the source (e.g. how far they are away from the patch) and their position relative to the plume to successfully navigate odor plumes. Average chemical concentrations within odor plumes decrease predictably as a function of downstream distance from the source and cross-stream distance from the plume centerline (Webster & Weissburg 2001). This suggests that time-averagers may easily be able to assess their position relative to odor sources regardless of their cross-stream position within an odor plume, but that cross-stream movement and scanning behaviors may be needed to assess the spatial extent of odor plumes and organism position relative to plume centerlines (Rhorkasse & Atema 2002; Ferner & Weissburg 2005). Based on my results, I suggest that whelks may use temporal integration in combination with sequential spatial sampling behaviors to determine both their position relative to the plume as well as the spatial extent and distribution of odors within the plume, which can help them maintain foraging success under a variety of odor plume conditions.

Whelks seem to be using time-averaging to obtain information about their position relative to the odor source and the plume centerline to different degrees in response to the challenging odor landscapes produced by differences in prey configuration and distribution at low and high densities. Whelks navigating toward patches containing perpendicular prey configurations (low density experiments) took longer to successfully locate those patches than patches containing prey in parallel configurations (Figure 3.2E). Longer tracking time seemed to be related to lower average concentrations and the increased spatial spread of odor plumes created by perpendicular prey configurations. Successful navigation in these conditions would require smaller movement speeds and path linearity (Figure 3.2) to collect adequate information about average concentrations to determine position relative to the odor source and plume centerline, respectively. Tracking time for whelks in high density experiments was intermediate to that of the two configuration treatments in low density experiments, but did not seem to be related to spatial sampling behaviors (i.e. path linearity was not different). My results support the idea that average odor concentrations should take longer to obtain in odor landscapes characterized by highly intermittent and high concentration filaments (low density, large plume width) in comparison to low concentration, homogenized odor landscapes (high density).

Whelks seem to use scanning behavior to gather information from odor plumes about the spatial distribution of prey, presumably in an effort to better determine position relative to the plume. Whelks have higher scanning rates and move with larger angular headings (Figure 3.5A and 3.6A, respectively) in response to patches of prey in perpendicular configurations at low densities compared to prey in parallel configurations. Scanning allows whelks to sample odors away from the plume centerline which should provide information about the centerline direction and spatial extent of odors to help maintain contact with odor plumes. Information about the spatial configuration of individual prey may be discernible in low density, perpendicular configuration treatments where odor landscapes contain intermittent filaments of high concentration, requiring increased sampling in order to determine accurate information about predator position relative to the plume centerline. Scanning rates in the high density experiment are similar between prey distribution treatments (Figure 3.5B), likely because greater mixing in high density patches results in homogeneous patch-scale odor plumes where information about the spatial distribution of individual prey are absent.

3.5.3 Ecological Implications of Predators that Utilize Multiple Sensing Strategies

Utilization of temporal integration strategies to extract information on distance to the source and position relative to the plume may enable whelks to maintain high levels of foraging success regardless of within patch prey distribution or density in the field. This is in contrast to other odor-mediated predators like blue crabs that have drastic reductions in foraging efficiency in response to patches containing random distributions of prey (see Chapter 2). Whelks may occupy a sensory niche that allows them to reduce competition with other odor-mediated predators by exploiting resources undetectable by other predators. The ability of whelks to maintain navigational success to patches, regardless of prey distribution, suggests that whelks may not be impacted by large-scale changes (either anthropogenic or natural) in the abundance of patches containing certain prey distributions. The shellfish industry commonly collects infaunal bivalves from high density and aggregated patches, which could reduce the availability of detectable patches for blue crab, but not whelk predators.

Although utilization of time-averaging and spatial sampling behaviors enables whelks to locate patches with a wide variety of densities and distributions, whelks still will be subject to foraging interference dependent on their navigational efficiency to patches of differing prey density and distribution. For example, whelks that take longer to navigate to patches (Figure 3.2) could experience increased disruptions or interference while foraging. Organisms commonly are faced with interference from inter- or intra-specific competitors (Sih *et al.* 1998) or predators while foraging. For example blue crabs interfere with each other during foraging, resulting in decreased predation rates in the field (Clark *et al.* 1999; Hughes & Grabowski 2006) and changes to the spatial scales at which individuals forage (Hines *et al.* 2009). Physical processes such as tidal cycles and water flow direction will mediate the time available for slowly moving predators to follow odor plumes. Whelks are forced to stop foraging when they can no longer detect prey odor plumes because of changes in water flow direction (Lapointe & Sainte-Marie 1992). Whelks that take longer to navigate to an odor source will experience an increased chance of disruptions to foraging and subsequent decreases in foraging success.

CHAPTER IV

PREDATOR EFFECTS MODIFY WITHIN PATCH PREY DISTRIBUTION BY INCREASING PREY MOVEMENT

4.1 Abstract

Predators can shape prey population abundance, density, and distribution through a variety of consumptive and non-consumptive mechanisms. Prey distributions within patches can be mediated by predators through both direct removal of individuals and changes in prey behavior. The dynamic relationship between prey distribution and predators could result in feedback loops if predator-induced changes in prey distribution result in changes in subsequent foraging success. I exposed patches of juvenile hard clams (*Merenaria mercenaria*) to blue crab (*Callinectes sapidus*) predator exposure treatments in the field (predator odor cues only, no predator control, and access by naturally occurring predators) and assessed the resulting changes in within-patch distribution and clam growth to examine the role of predators in modifying prey distributions. I also completed a field survey of naturally occurring within-patch clam distributions to determine if predator impacts on prey distribution may be a mechanism helping shape prey distributions in the field. Clam movement was greater and distributions were significantly more random after exposure to actively foraging predators, but not after exposure to predator odor cues. Growth rates were lower when clams were exposed to predator odor cues and actively foraging predators, presumably in an effort to decrease patch apparency by reducing feeding activity. Also, an overwhelming proportion of patches in the field contained clams that were randomly distributed, suggesting that predators may be involved in shaping clam distributions in the field. My results also indicate that the prevalence of patches

containing randomly distributed clams in the field may be a product of a negative feedback loop between blue crab predators and clam distributions. Actively foraging blue crabs seem to mediate the formation of random clam distributions, which future blue crabs may have a hard time locating because of low foraging efficiency and success in locomoting to patches containing random prey distributions.

4.2 Introduction

Changes in prey distribution within patches can be a dynamic process regulated by predators that selectively remove individuals from the group, as well as by prey behaviors exhibited to minimize predation risk. Although predators are not the only things shaping prey distribution within patches (e.g. other factors include settlement, immigration/emigration, competition), predators have been shown to structure and regulate prey population abundance and dynamics in many systems (Holling 1959; Glasser 1979). For instance, predators have frequently been shown to restrict prey distributions to refuge habitats (Huffaker 1958; Grear & Schmitz 2005), which can result in prey population stability (van Baalen & Sabelis 1993).

The relationship between prey distribution and predator foraging can be divided into three parts of a possible feedback loop: 1) patch detection by predators, 2) predator impacts on prey individuals within the patch (either through predation or changes in prey behavior), which result in 3) changes to within-patch prey distribution that impact subsequent detection by predators. Much attention has been focused on predation rates within patches of differing density (Eggleston *et al.* 1992; Anderson 2001; Kuhlmann & Hines 2005), and described by numerous density-dependent foraging models (Holling 1959). Predator feedback loops are essential components driving theories about the distribution of predators relative to patches of varying density (MacArthur & Pianka 1966; Fretwell & Lucas 1970), where ideal predators should leave patches when they have depleted resources to less than is further profitable relative to other patches. Exploited patches, therefore, gain relative refuge from future predators which can result in ecological stability for prey populations (van Baalen & Sabelis 1993). Less is known about predator foraging patterns within patches of differing distributions (although see Cain 1985; Hankski & Cambefort 1991; Dumont *et al.* 2002; Chapter 2) and how those interactions could potentially result in predator mediated feedback loops. Additional study is needed to determine if distribution-dependent feedback loops occur and interact with predator foraging to influence the stability of prey populations.

Prey distribution within patches will mediate the ability of predators to detect and locate patches because of changes in the sensory landscape. Odor-mediated systems are ideal systems to examine the impacts of prey distribution on predator detection, as differences in prey distribution result in odor plumes that clearly vary in their chemical concentration, cross-stream spread, and spatial distribution of individual prey plumes. For example, prey patches containing random distributions create patch-scale plumes that have large cross-stream spreads and low chemical concentrations relative to aggregated distributions. It has been suggested that patches containing prey in random distributions will have large sized "zones of attractiveness" (Cain 1985) for foraging predators because of their large cross-stream spread. This may result in high encounter rates with odor plumes from random patches, but those odor plumes may also contain lower concentrations which could make plumes harder for predators to detect (Parrish & Edelstein-Keshet 1999). The ability of predators to successfully locate patches of differing distributions is dependent on their sensory ability and foraging mode (Chapter 2), which may provide the basis for species-specific predator feedback loops related to prey distribution.

Predators can change prey patch distributions through direct consumption of individuals; the resulting distribution being a product of predator selection patterns on individuals (Morrell & Romey 2008). Many studies have focused on predation rates in patches with various distributions (Turchin & Kareiva 1989; Heard 1998; Dumont *et al.* 2002; Edenius *et al.* 2002; Coleman *et al.* 2004; also see Chapter 2), but fail to account for changes in patch distribution upon removal of prey individuals. The selfish herd hypothesis and supporting studies suggest that removal of individuals on the periphery of groups should be the most common pattern of predation (Hamilton 1971; Okamura 1986; Morrell & Romey 2008), which could subsequently result in more highly aggregated distributions within patches. Removal of individuals from groups of prey via predation could result in changes to prey distributions that would make those groups subsequently harder or easier for predators to locate, suggesting the possibility for feedback loops to arise based on prey distribution.

The threat of predation (or predator detection) also may impact prey distributions by changing prey behavior or movement patterns within patches (Lima & Dill 1990). Movement by prey individuals can change distributions within patches and result in reductions in prey apparency by reducing encounter rates with predators (Courtney 1985; Uetz & Heiber 1994; Parrish *et al.* 2002). Many organisms can assume distributions that reduce the individual risk of predation if a predator attacks a patch (although this might be dependent on individual prey location within the patch; see above). For example, prey organisms in aggregated distributions may attain safety in numbers through dilution or predator confusion effects (Turchin & Kareiva 1989; Uetz & Heiber 1994; Parrish & Edelstein-Keshet 1999). Other prey behaviors that can reduce apparency include hiding (Bertness *et al.* 1981; Turner *et al.* 2000) and reduced feeding (Richardson & Brown 1992; Smee & Weissburg 2006a). These behaviors (movement, hiding, reduction of feeding) can be triggered by the detection of predator cues (kairomones) or alarm cues from conspecifics (Chivers & Smith 1998). Changes in prey behavior that mediate patch apparency to predators could result in changes to subsequent predation pressure or risk for prey individuals within patches.

The occurrence of negative feedback loops between predators and prey distribution is dependent on predator sensory ability and foraging mode. Negative feedback loops will arise when predator-dependent changes in prey distribution result in patches that are hard for subsequent predators to detect or navigate toward relative to other patch distributions. For example, blue crabs (*Callinectes sapidus*) are less successful locating bivalve prey in patches containing random distributions than patches containing aggregated distributions (Chapter 2). If predation by blue crabs on bivalves resulted in patches containing randomly distributed prey, it would reduce subsequent predation on those patches, and result in a negative feedback loop.

To explore the effect of predators on prey distributions within patches and the possibility of predator-dependent feedback loops, I assessed hard clam (*Mercenaria mercenaria*) prey responses to both direct (predation and disturbance) and indirect (predator odors) effects of their blue crab (*Callinectes sapidus*) predators in intertidal salt marsh systems along the Atlantic coast. Hard clams are found in patchy distributions at a variety of spatial scales (Wells 1957; Walker & Tenore 1984) throughout the salt marsh system, and can be found in mud, oyster shell hash, and near *Spartina* sp. stands. Specific information about small-scale clam distributions (i.e. within patches) is lacking; thus the within patch distributions of prey that predators are exposed to in this system is unknown. Hard clams are known to respond to predator odor cues from blue crabs by clamming up (Smee & Weissburg 2006b), which can reduce predation on clams next to caged blue crabs in the field at short time scales (Smee & Weissburg 2006a), but may decrease clam growth rates by inhibiting feeding behavior. Blue crabs have been shown to control bivalve populations (Virnstein 1977), with bivalves accounting for approximately 50 % of blue crab gut contents (Hines *et al.* 1990). Blue crab foraging success on clam patches also is dependent on within patch clam density and distribution, as demonstrated by decreased success in locating patches of low density and patches containing individuals in random distributions (see Chapter 2).

High predation pressure in my system (Virnstein 1977; Hines *et al.* 1990) suggests that predators may have large influences over clam distributions in the field. Two alternative, but unlikely, processes shaping clam distributions include settlement and competition. There is very little information about the influence of settlement on clam distributions at the within-patch scale (although see Butman *et al.* 1988 for larval substrate preferences). Regardless of the specific distribution characteristics mediated by settlement, the distribution of adult clams can be similar to those of newly settled larvae in the absence of post-settlement processes like predation (although this seems an unrealistic assumption in my system). It is also unlikely that clam distributions are mediated by competition, as resource depletion has only been documented for bivalve patches containing unrealistically high densities of individuals (Peterson & Black 1987).

I focused on these objectives: 1) To assess changes in prey distribution as a function of direct (predation) and indirect (predator odors and disturbance) effects of predators; 2) To explore possible tradeoffs between prey growth and behavioral responses related to the presence of direct and indirect predator effects; and 3) To examine natural distributions of prey within patches in the field in light of the mechanisms in 1) and 2). I accomplished these goals by exposing clam prey patches to predator exposure treatments in the field (predator odor cues only, no predator control, and access by naturally occurring predators) and then assessed growth and changes to the distribution of individuals within patches. I also completed a survey to determine natural distributions of prey in patches in the field. I predicted that clams will respond to predator odor cues and predator disturbance by reducing their movement and feeding behavior, resulting in little to no change in their distributions but large reductions in growth relative to no odor controls. Selfish herd theory indicates that prey individuals on the outside of patches are the most vulnerable to predation, suggesting that predation events themselves would not change the interior distribution of prey patches. Thus I hypothesized that predation events will not appreciably change the aggregation characteristics of patches from those of the original distribution.

4.3 Methods

4.3.1 Predator Effects on Clam Distributions

I assessed the influence of predator odor cues and actively foraging predators on clam distributions in the field (Skidaway River, Wassaw Sound, GA; Figure 4.1) using a caging experiment during June 2009. I exposed patches of 30 juvenile hard clams (28.16 ± 2.89 cm; obtained from BayShellfish, Sarasota, FL) in 1 m^2 quadrats to four predator treatments in a randomized block design. Clam densities were within the range of natural densities in Wassaw Sound (Walker & Tenore 1984). Predator treatments consisted of: a full cage, a full cage with blue crab (*Callinectes sapidus*) predators caged 0.5 m upstream and downstream (see Smee & Weissburg 2006a), a half cage (two sides open) that allowed predator entry, and a half cage (two sides open) with empty blue crab cages (placement similar to full cage treatment, but no predator present) that allowed predator entry. Both half cage treatments were included to account for differences in mixing produced by my caging design, as mixing can mediate the availability of food to infaunal organisms and consequently, alter distributions (e.g. Yakovis *et al.* 2004). Logistical concerns prevented the inclusion of a full cage with empty predator cages treatment, although it is likely that the addition of a small predator cage relative to the size of my full cage enclosures would not appreciably change the mixing environment experienced by clams.

Clam patches were created by placing individually labeled clams (FPN tag,

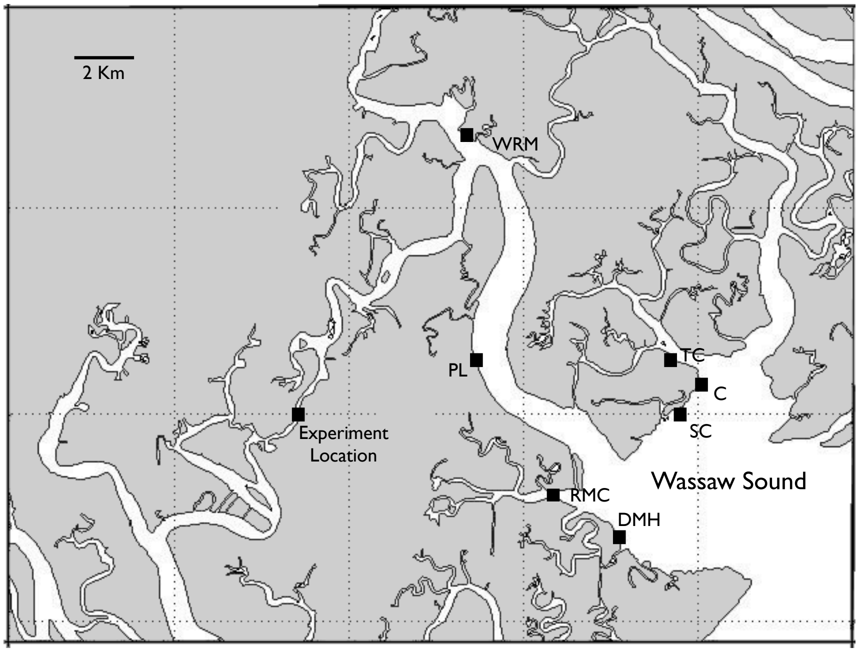

Figure 4.1: Locations in Wassaw Sound, GA where predator exposure experiments were conducted and naturally occurring clam patches were found. C = Cabbage Island, DMH = Dead Mans Hammock, PL = Priest Landing, RMC = Romerly Marsh Creek, TC = Tybee Cut, SC = South Cabbage Island, and WRM = Wilmington River Marina.

Hallprint) in an area 30 cm by 36 cm centered in the middle of the quadrat, with 6 cm separating individuals (uniform distribution). All patches, regardless of treatment, started the experiment with this distribution. Preliminary laboratory studies indicated that clams in this arrangement were unlikely to move beyond cage edges during the experiment (*MLW - unpublished data*). Patches were placed at the mean low tide level and surrounded by cages (1 m × 1 m × 0.25 m; mesh size of 1.5 cm^2). Cages used to hold predators in full cage and half cage treatments were approximately 20 cm diameter by 30 cm high and were stabilized in the field using stakes. Predators were fed clams every three days to ensure a continuous release of odor cues throughout the experiment.

Patches were left in the field for 10, 20, or 30 days ($N = 5$ blocks for each) to assess how clam movement, distribution and growth varied as a function of exposure time and predator treatment. Clams were retrieved by carefully probing the substrate by hand and the final x and y coordinates for each individual were recorded. Clams were measured (shell length and width, and clam thickness; accurate to 0.01 mm), and weighed (wet weight; accurate to 0.01 g) before and after exposure to predator treatments in the field to assess growth.

I calculated the distance that individual clams moved over the course of the experiment and their resulting nearest neighbor distances. Preliminary analysis indicated no significant effect of exposure time on predation rates, so I used a one way analysis of variance (ANOVA) with a blocking factor to determine the impact of predator treatment on predation rates (including data from all 15 blocks). Preliminary analysis also indicated no significant effect of exposure time on the distance clams moved or the average nearest neighbor distances between clams. Thus, I used one-way ANOVAs with blocking factors to determine the effect of predator treatment on clam movement and nearest neighbor distance. Entire blocks were removed for movement and nearest neighbor analyses if any treatment contained less than 2 clams for clam movement distance analysis (10 day exposure = 1 removed, 20 day exposure = 2 removed, 30 day exposure = 3 removed) and less than 5 clams for nearest neighbor distance analysis (10 day exposure = 1 removed, 20 day exposure = 3 removed, 30 day exposure = 4 removed). I performed post-hoc planned contrasts between full cage treatments with and without predator odors and between the full cage treatment without predator odor cues and the half cage treatment without predator cages when ANOVA analyses indicated significant differences between predator treatments. These comparisons allowed us to determine the influence of predator odor cues and actively foraging predators, respectively, on clam movement and nearest neighbor distance.

Normalized clam growth was calculated using $(S_F - S_B)/S_B$ where S_F is final clam size (length, width, thickness, weight) at the end of the experiment and S_B is clam size before being placed in the field. Growth rates were calculated as a function of exposure time. I used a multivariate analysis of variance (MANOVA) to test for differences in growth parameters between predator exposure treatments for clams in the 30 day exposure only. In this analysis, each growth parameter (length, width, thickness, weight) was treated as a response variable. Individual clam growth parameters may be correlated with each other, thus using a MANOVA analysis allows the response variables to be considered jointly and the power to detect differences between treatments is enhanced. Growth rates were highly variable within treatments in the first 20 days, often showing little or even negative growth, particularly for clams in 10 day exposures. Other studies examining bivalve growth in conditions similar to mine used a 30 day period (Nakaoka 2000). I examined the significance of univariate analyses (one-way ANOVAs) for each growth variable separately when multivariate analysis was significant (Zar 1999) and determined significant differences between treatments for each growth variable using post hoc Tukey tests. I paid particular attention to comparisons between full cage treatments with and without predator odors and between the full cage treatment without predator odors and the half cage treatment without predator cages. These comparisons should elucidate any predator avoidance behaviors (such as reduced feeding) that would result in differences in growth as a function of predator odors or active foraging by predators.

The within-patch distribution of clams was assessed using the x and y coordinates of each individual clam to calculate the distance to their nearest neighbor. Patch distributions based on nearest neighbor distance before and after exposure to predators in the field were both compared to that of a completely random distribution based on the methods of Clark & Evans (1954). The average nearest neighbor distance was calculated for each patch:

$$r_A = \frac{\Sigma r}{N}, \tag{4.1}$$

where r = distance from each individual to its nearest neighbor and N = number of individuals. The average nearest neighbor distance for the patch is then compared to the expected nearest neighbor distance (r_E) based on a random distribution of similar density according to:

$$R = \frac{r_A}{r_E}, \tag{4.2}$$

where $r_E = 1/(2\sqrt{\rho})$, and ρ is the density of the observed patch (# individuals/area of patch). R can range from 0 to 2.15; with $R = 0$ indicating complete aggregation, $R = 1$ indicating complete randomness, and $R = 2.15$ indicating a completely uniform distribution (Clark & Evans 1954). Significant differences from random can be assessed by comparison to a normal curve using:

$$c = \frac{(r_A - r_E)}{\sigma r_E}, \tag{4.3}$$

where σr_E for a population density of ρ is $0.26/(\sqrt{N\rho})$. A value of $c = \pm 1.96$ represents the 5% significance level (Clark & Evans 1954). Values of R were compared between full cage treatments with and without predator odors and between the full cage treatment without predator odors and the half cage treatment without predator cages using a Mann-Whitney U test to determine differences in distribution as a function of predator odors or actively foraging predators.

The scale of the distribution within patches was then assessed by examining the relationship between lacunarity and spatial scale. Lacunarity analysis uses a variable-sized sliding box method which assesses the number of individuals within a viewing box at each sliding step and box size to determine distribution patterns at different spatial scales (Plotnick *et al.* 1996; Fortin & Dale 2005). A box of side length r is placed at the origin of the plot (0, 0) and the number of individuals within the box is counted. The box is then moved one step (grain size of the patch; 1 cm in my case) in the x-direction and the number of individuals is again counted. This continues until the box reaches the other side of the plot (100, 0), at which point the box is moved one step in the y-direction. The box is then moved step-wise to the original side of the plot in the x-direction and this process is repeated until the entire plot has been assessed. This is repeated for boxes of size $r = 1$ to the number of steps along one side of the plot (1 cm to 100 cm in my case).

Lacunarity can be calculated by determining the first and second order moments for the sliding box model using:

$$Z_1(r) = \frac{\Sigma\Sigma x_j}{(n+1-r)} \; and, \tag{4.4}$$

$$Z_2(r) = \frac{\Sigma(\Sigma x_j)^2}{(n+1-r)}; \tag{4.5}$$

where x_j is the number of individuals in the jth step, n is the total number of individuals in the plot and r is the box length. These equations can be combined to calculate the lacunarity statistic via:

$$\Lambda(r) = \frac{Z_2(r)}{(Z_1(r))^2} \tag{4.6}$$

This can be simplified as:

$$\Lambda(r) = \frac{s_s^2(r)}{s^2(r)} + 1, \tag{4.7}$$

where $s_s^2(r)$ is the variance of the number of individuals per box and $s(r)$ is the mean number of individuals per box (Plotnick *et al.* 1996). The relationship between lacunarity and box size can then be visualized on a double log plot. The shape of the resulting plot can be used to determine the distribution characteristics of patches and the spatial scales at which they manifest (Plotnick *et al.* 1996; Seifan & Kadmon 2006; Imeson & Prinsen 2004; Malhi & Roman-Cuesta 2008). For example, aggregated distributions will manifest as convex curves whose values decrease with increasing box size, while random distributions manifest as concave curves whose values decrease with increasing box size (Figure 4.2). Uniform distributions can be characterized by relatively straight lines that intercept zero at values of r equal to the scale of uniformity (Figure 4.2). Relative comparisons of lacunarity under multiple conditions are generally recommended, as there is no exact curve shape that describes a particular dispersion pattern (Plotnick *et al.* 1996; Malhi & Roman-Cuesta 2008). The shape of the curve produced using lacunarity analysis was compared for patch distributions before and after exposure to predators in the field, as well as between full cage treatments with and without predator odor cues and between the full cage treatment without predator odors and the half cage control treatment without predator cages.

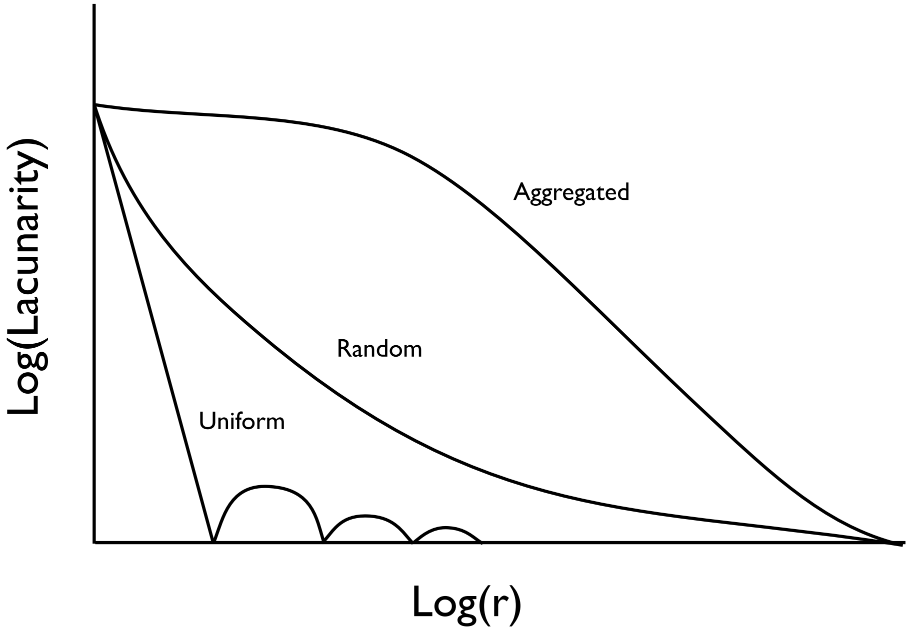

Figure 4.2: Visualization of Lacunarity as a function of gliding box size viewed in a log-log plot. Curves represent idealized situations of aggregated, random, and uniform distributions.

4.3.2 Within-Patch Distribution Survey

I assessed natural distributions of hard clam prey (*Mercenaria mercenaria*) within patches in seven sites in Wassaw Sound, GA and its tributaries (Cabbage Island [C], Dead Mans Hammock [DMH], Priest Landing [PL], Romerly Marsh Creek [RMC], South Cabbage Island [SC], Tybee Cut [TC], and Wilmington River Marina [WRM]) (Figure 4.1). I identified existing clam patches by placing a 1 m^2 quadrat on the substrate and carefully unearthing the top 5-10 cm of mud using rakes, which uncovered clams with minimal disturbance and allowed us to count them and record their x and y coordinate positions. I also unearthed approximately 10 cm of mud on all sides of the quadrat if possible (some had edges up against oyster reefs or *Spartina* sp. stands) to ensure that patches did not extend outside of the designated area. One m^2 quadrats containing at least 5 clams were defined as a patch (56% of patches sampled had at least 5 clams; within the range of reported natural densities [Walker & Tenore 1984]). This allowed for statistical comparisons of within-patch clam distribution, and was comparable to patch densities used in previous predation experiments (see Chapter 2 and 3). Identifying patches in this manner resulted in different numbers of identified patches between sites and substrate types.

I assessed patch distribution in the field using nearest neighbor distance and lacunarity analyses as described above.

4.4 Results

4.4.1 Predator Effect on Clam Distributions

There were significant differences between predator treatments in the number of clams eaten ($F_{3,42} = 37.71$, $P < 0.001$; Figure 4.3). Planned contrasts indicated significantly higher predation rates in half cage treatments lacking predator cages than full cage treatments without predator odor cues ($P < 0.001$), but not between full cage treatments with and without predator odor cues ($P > 0.99$). This confirms the efficiency of my caging methods and differences in predator exposure treatments. There also was a significant effect of block on clam predation ($F_{14,42} = 1.97$, $P = 0.045$), as a result of strong variability in predation intensity throughout my study site.

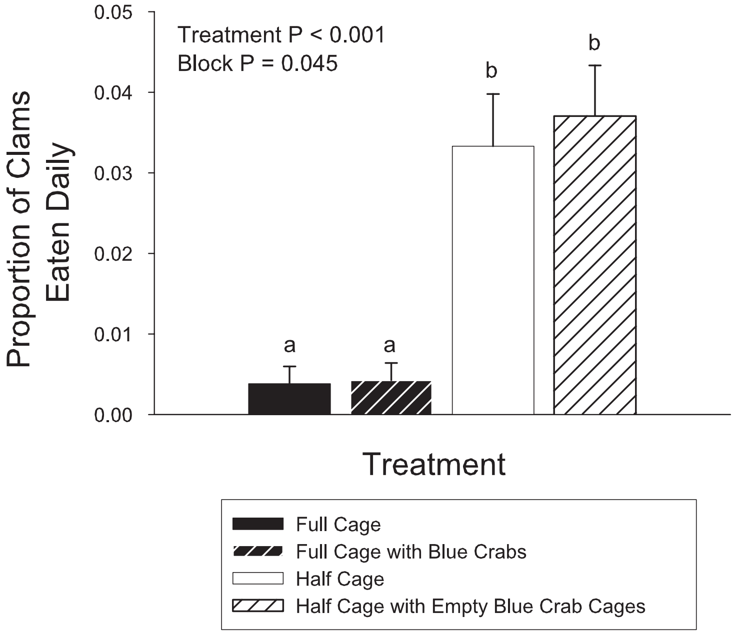

Figure 4.3: Proportion of clams missing from cages as a function of treatment confirms that full cage treatments suffered less clam loss than half cage treatments. Error bars represent one standard error. Statistical significance was determined using an ANOVA with a blocking factor. Data from all blocks was included.

There was a significant effect of predator treatment on the average distance that clams moved per day ($F_{3,24} = 6.13$, $P = 0.003$; Figure 4.4A). Planned contrasts indicated no significant difference in clam movement between full cage treatments with and without predator odors ($P = 0.99$), but did show clams in the half cage treatment lacking predator cages moved significantly more than clams in the full cage treatment without predator odors ($P = 0.023$). There was a significant effect of block ($F_{8,24} = 4.21$, $P = 0.003$) on the distance that clams moved per day.

Analysis also revealed a significant effect of predator treatment on average

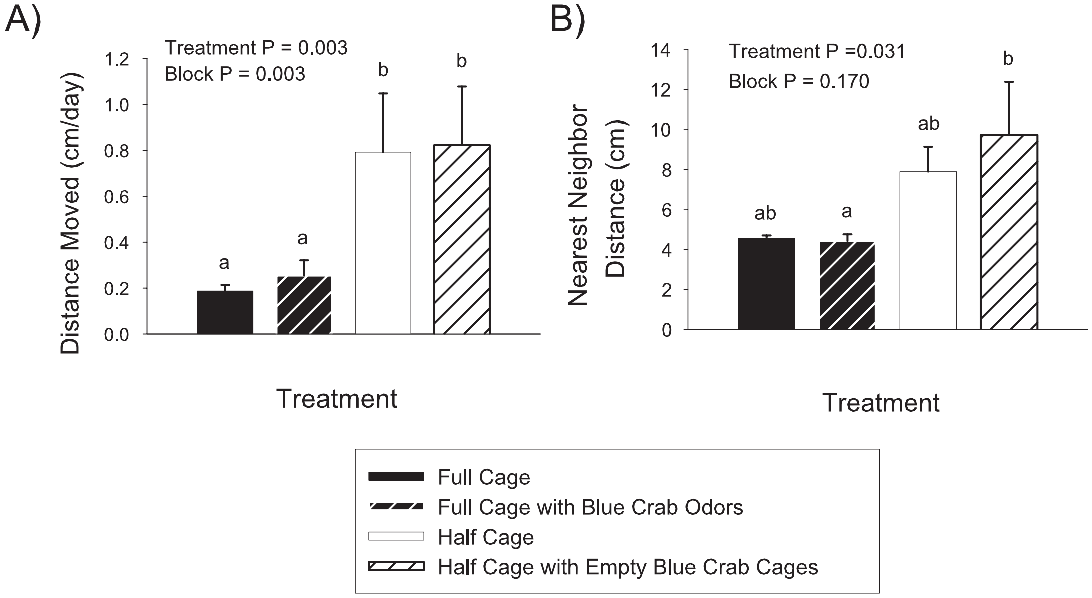

Figure 4.4: Average distance traveled by clams (left, standardized to exposure time) and the resulting average distance between neighboring individuals (right) is shown. Error bars represent one standard error. Statistical significance was determined for both analyses using an ANOVA with a blocking factor. Post-hoc tests did not reveal any significant pairwise comparisons. N = 9 for both analyses.

nearest neighbor distance ($F_{3,18} = 3.68$, $P = 0.031$; Figure 4.4B), with generally smaller nearest neighbor distances between clams in treatments that prevented predator access (regardless of predator odor cues) than between clams in treatments allowing predator access. Planned contrasts revealed no significant differences between full cage treatments with and without predator odor cues ($P = 0.99$) or between the full cage treatment without odor cues and the half cage treatment without predator cages ($P = 0.37$), although the latter is most likely because of high variance for half cage treatments. There was no significant effect of block on nearest neighbor distance ($F_{6,18} = 1.74$, $P = 0.17$).

Values of R were not significantly different between full cage treatments with and without predator odor cues ($U = 20$, $N = 7$, $P = 0.57$), but there were significant differences in the values of R between the full cage treatment without predator odor cues and the half cage treatment without predator cages ($U = 7$, $N = 7$, $P = 0.025$). Clam patches exposed to actively foraging predators had increased values of R relative to patches that denied predator access, indicating that clam distributions were less aggregated because of interactions between actively foraging predators and clam prey.

Clams exposed to actively foraging predators assumed random distributions, but clams in treatments that denied predator access maintained aggregated characteristics similar to the original patch distribution (Figure 4.5). A concave relationship between log(lacunarity) and log(box size), typical of a random distribution (Plotnick *et al.* 1996; Seifan & Kadmon 2006; Malhi & Roman-Cuesta 2008), was seen for clams exposed to actively foraging predators (Figure 4.5, arrow A). Lacunarity analysis for clams in full cage treatments that denied predator access showed a convex curve at a scale of approximately 30 cm (Figure 4.5, arrow B). This convex shape has been documented previously to indicate aggregated distribution characteristics (Plotnick *et al.* 1996; Seifan & Kadmon 2006). Lacunarity curves for clams in full cage treatments were similar to those for clams in the original distribution that consisted of individuals in a 36 × 30 cm patch, indicating that clams in full cage treatments did not significantly change their distribution relative to the original patch characteristics. Evidence of the original uniform spacing (6 cm; Figure 4.5, arrow C) was not retained in any experimental treatment. Similar patterns of patch distribution for predator exposure treatments were seen for all blocks examined.

4.4.2 Predator Effects on Clam Growth

Predator exposure treatments significantly affected clam growth (MANOVA, Wilks $\lambda = 0.69$, $F_{12,764} = 9.72$, $P < 0.001$), with significant effects of treatment on all four clam growth variables based on univariate analyses (length: $F_{3,288} = 31.11$, $P < 0.001$; width: $F_{3,288} = 26.13$, $P < 0.001$; thickness: $F_{3,288} = 17.25$, $P < 0.001$; wet weight: $F_{3,288} = 24.05$, $P < 0.001$; Figure 4.6). There also were significant block

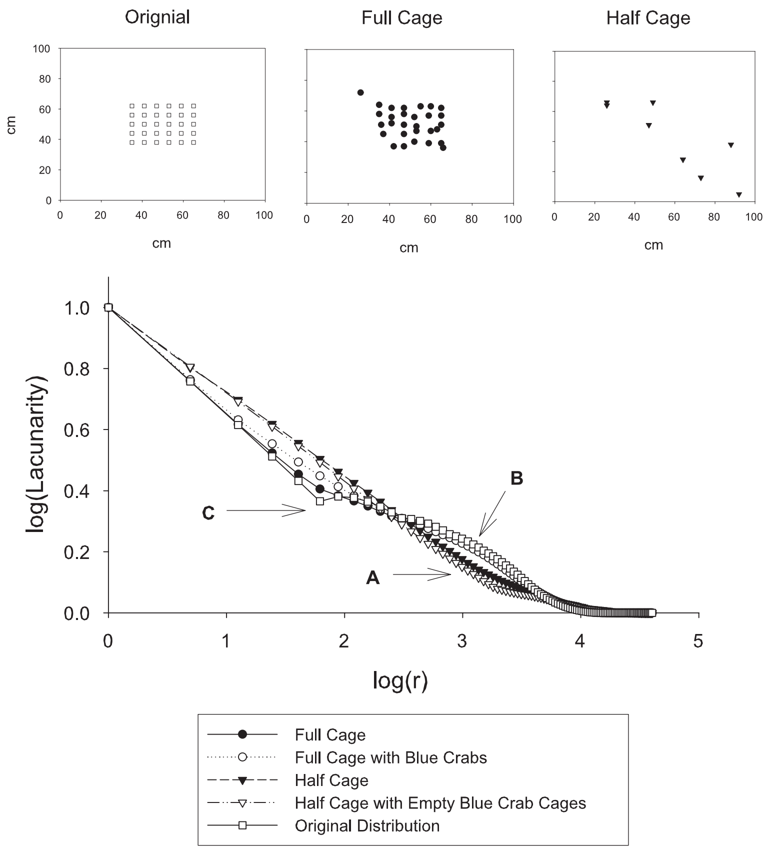

Figure 4.5: Visualization of lacunarity for patches after exposure in the field. Circles and triangles represent full and half cage treatments, respectively. The original distribution of clams for all treatments is plotted using squares. Example plots are shown for clams in the original, full cage, and half cage treatments in the top panels. A, B, and C refer to random characteristics, aggregation characteristics, and uniform characteristics of the curves, respectively (see Results for a complete description). All log(lacunarity) values are normalized to a maximum value of 1 for comparison.

effects for length, width, and thickness ($F_{4,288} = 3.47$, $P = 0.009$; $F_{4,288} = 2.63$, $P = 0.035$; $F_{4,288} = 4.80$, $P = 0.001$; respectively).

Clams had greater growth rates in full cage treatments where predator odors were absent, suggesting that predators tended to reduce clam growth rates via odor cues. Clam length and wet weight were significantly different between full cage treatments with and without predator odor cues (Tukey tests; $P = 0.023$ for length, $P = 0.035$ for wet weight), but there were no significant differences in clam width or thickness as a function of predator odor presence or absence (Tukey tests: $P = 0.23$

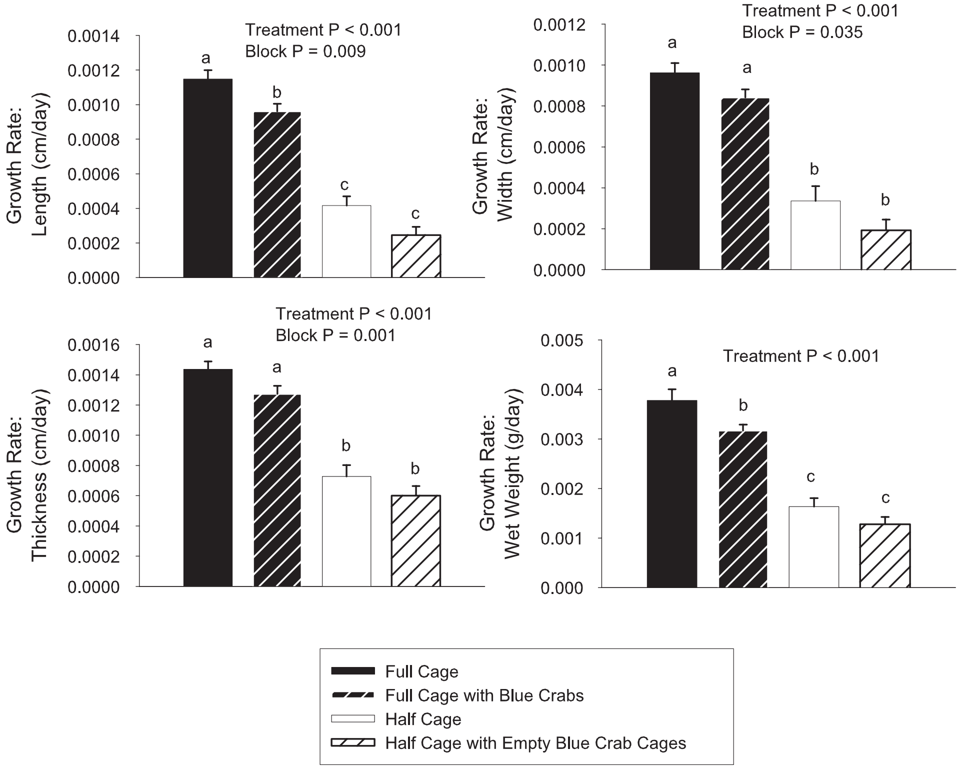

Figure 4.6: Clam growth rates (shell length, width, clam thickness, weight) as a function of treatment. Significance was determined using one-way ANOVAs with blocking factors. Data from all blocks were included in the analysis. Error bars represent one standard error.

for width, $P = 0.19$ for thickness), although the data display a trend toward reduced growth in the presence of predator odor.

Clams also had greater growth rates (all growth variables) in full cages than in cages where predators had access and could actively forage. In particular, clams grew more in the full cage treatment without odor cues than in the half cage treatment without blue crab cages for all growth variables (Tukey tests: $P < 0.001$ for length, width, thickness, and wet weight).

4.4.3 Within-Patch Clam Distributions in the Field

The majority of clam patches observed in the field contained clams in distributions that were not significantly different than random based on nearest neighbor distance analyses (79%; Table 4.1). The remaining patches (21%) contained clams in distributions that were significantly different than random (17% uniform distribution and 4% aggregated distribution). More patches that were located in oyster hash and mud contained distributions that were not significantly different from random (88%) than those located in *Spartina* sp. stands and mud (69%). Patches containing individuals that were uniformly distributed seemed to be more common in *Spartina* sp. stands then oyster hash (31% in *Spartina* sp. versus 6% in oyster hash).

Patch distribution characteristics as determined using visualizations of the relationship between lacunarity and spatial scale in the field agreed with those determined using nearest neighbor distance methods. Random patches (as determined using nearest neighbor methods) all exhibited characteristic concave curves seen for random distributions at all spatial scales (Figure 4.2; Plotnick *et al.* 1996; see Figure 4.7A for an example using data from TC1). Patches designated as aggregated and uniform (via nearest neighbor analysis) were fairly similar, with more convex curves than those seen for patches with random distributions (as determined using nearest neighbor analysis) (Figure 4.7B and 4.7D). Although the lacunarity curves for aggregated and uniform patches showed similar non-random characteristics, uniform patches exhibited a characteristic dip in lacunarity followed by a convex hump that was not seen for the aggregated patch (Figure 4.7C; Plotnick *et al.* 1996). The characteristic dip in lacunarity represents the spacing between individual clams in a uniform distribution (approximately 30 cm; see letter A in the inset of Figure 4.7D).

4.5 Discussion

Blue crab predators are capable of changing prey distributions and growth within patches. These changes in clam distribution and growth are mediated by a variety of behavioral responses by clams to predator odors and actively foraging predators. Clams increase their movement in response to disturbance by actively

Table 4.1: Summary of average nearest neighbor distances and the resulting distribution after comparison to the expected nearest neighbor distance from a random distribution. Sites are labeled as follows: C = Cabbage Island, DMH = Dead Mans Hammock, PL = Preist Landing, RMC = Romerly Marsh Creek, TC = Tybee Cut, SC = South Cabbage Island, and WRM = Wilmington River Marina. Recall that $R > 1$ suggests uniform distributions, $R < 1$ suggests aggregated distributions, and $-1.96 > C > 1.96$ indicates a significant difference from random.

Site and Sample Number	Substrate	Density ($/m^2$)	Number Adults, Juveniles	NN Distance (cm)	R	C	Distribution
C1	Oyster	49	44, 5	6.93	0.97	-0.40	Random
C2	Oyster	21	20, 1	11.74	1.08	0.66	Random
C3	Oyster	9	9, 0	11.62	0.70	-1.74	Random
C4	Oyster	7	4, 3	15.67	0.83	-0.87	Random
C5	Oyster	59	56, 3	6.01	0.92	-1.13	Random
C6	Oyster	65	65, 0	6.03	0.91	0.43	Random
C7	Oyster	23	22, 1	11.16	1.07	-0.64	Random
C8	Oyster	13	12, 1	13.73	0.99	0.07	Random
C9	Oyster	57	52, 5	6.80	1.03	-0.40	Random
DMH1	Oyster	7	7, 0	23.36	1.24	1.20	Random
DMH2	Oyster	26	25, 1	8.26	0.84	-1.53	Random
DMH3	Oyster	10	10, 0	19.20	1.21	1.30	Random
DMH4	Oyster	13	12, 1	14.80	1.07	0.46	Random
DMH5	Oyster	37	34, 3	6.96	0.85	-1.79	Random
PL1	Oyster	8	7, 1	6.43	0.36	-3.44	Aggregated
PL2	Oyster	7	7, 0	31.61	1.67	3.40	Uniform
RMC1	*Spartina*	8	8, 0	24.00	1.36	-1.93	Random
RMC2	*Spartina*	5	5, 0	24.71	1.10	-0.44	Random
TC1	*Spartina*	61	56, 5	6.11	0.96	0.67	Random
TC2	*Spartina*	26	25,1	7.91	0.81	1.89	Random
SC1	*Spartina*	27	25, 2	10.24	1.06	-0.64	Random
SC2	*Spartina*	21	20, 1	11.76	1.08	-0.68	Random
SC3	*Spartina*	21	19, 2	9.86	0.90	0.84	Random
WRM1	*Spartina*	9	9, 0	18.81	1.13	-0.74	Random
WRM2	*Spartina*	9	9, 0	23.42	1.41	2.33	Uniform
WRM3	*Spartina*	9	9, 0	19.33	1.16	-0.92	Random
WRM4	*Spartina*	10	10, 0	22.12	1.40	2.41	Uniform
WRM5	*Spartina*	9	9, 0	25.44	1.53	3.02	Uniform
WRM6	*Spartina*	6	6, 0	33.67	1.65	3.04	Uniform

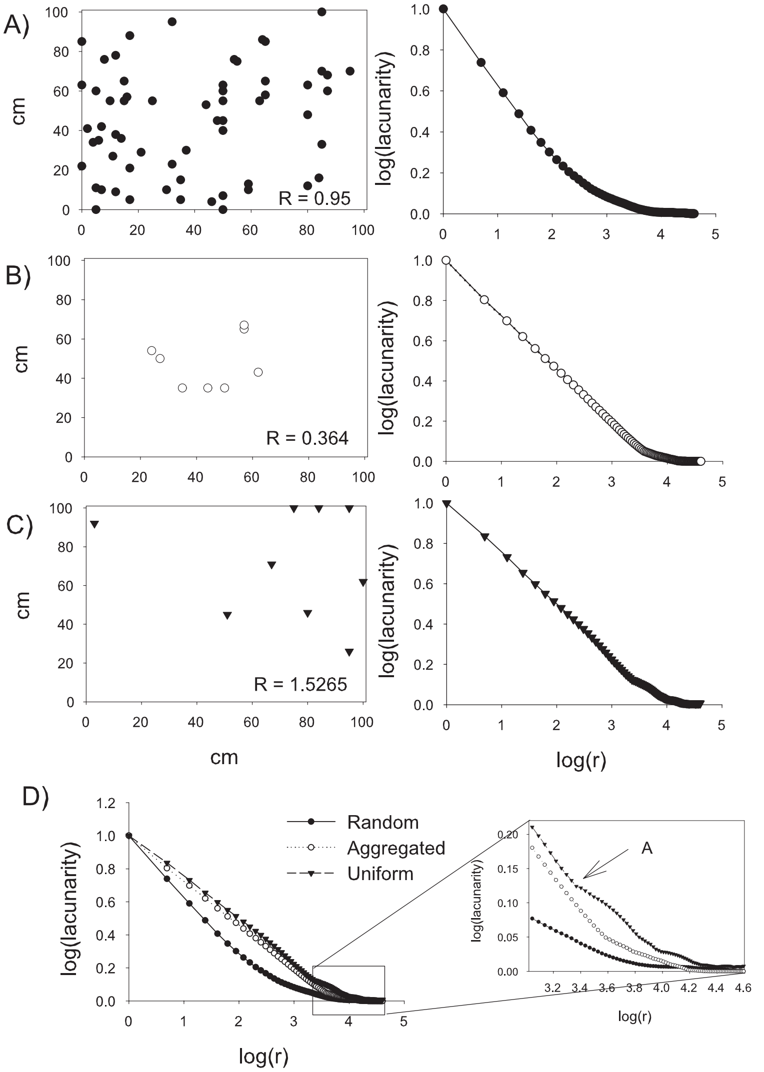

Figure 4.7: Examples of clam distributions within patches (left) and the corresponding visualization of lacunarity (right). Symbols represent the location of individual clams in each patch. Data from a random patch (as determined by nearest neighbor distance analysis) from TC1 (A), an aggregated patch from PL1 (B), and a uniform patch from WRM5 (C) are shown. All three patch types can be visualized on the same axis for comparison in (D). The arrow labeled “A” in the inset in (D) represents the characteristic dip in lacunarity seen for uniform distributions. All log(lacunarity) values are normalized to the highest value. Recall that $R = 1$ suggests a random distribution, $R < 1$ suggests an aggregated distribution, and $R > 1$ suggests a uniform distribution (all determined from the nearest neighbor analysis).

foraging predators, resulting in larger nearest neighbor distances (Figure 4.4) and random patch-scale distributions (Figure 4.5). Clams also have reduced growth in the presence of actively foraging predators and predator odor cues, but these responses seem to be independent from changes in clam movement and distribution. The resulting distribution of clams within patches exposed to actively foraging blue crabs matches closely to natural distributions in the field (Figures 4.5 and 4.7), suggesting that predation and behavioral responses of clams to predator presence may help shape clam distributions in the field.

Increases in clam movement seen in my study are likely a response to disturbance by actively foraging predators as opposed to an active escape mechanism or behaviors that reduce prey apparency. Clam movement was significantly greater in treatments with predator access relative to treatments where predator access was denied (Figure 4.4A). Organisms commonly respond to predator odor cues or disturbance by reducing feeding behavior (Smee & Weissburg 2006b) and horizontal movement (Kats & Dill 1998; Mitchell & Lima 2002; see Gilliam & Fraser 2001 for an example of increased movement) to reduce group apparency. My study suggests an opposite response where clams increase their movement in response to actively foraging predators (Figure 4.4A). Bivalves have been seen to increase their movement vertically in the substrate in response to predator disturbance, with greater burial depths conferring subsequent protection (Blundon & Kennedy 1982; Doering 1982; Griffiths & Richardson 2006). Increases in movement also do not seem to represent an active escape mechanism for clams, as differences in mobility between blue crab predators and clam prey in this study system suggest that movement by clams would be an ineffective escape strategy.

Changes in clam distribution seem to be a product of enhanced movement in response to actively foraging predators. Clams distributions are significantly more random in treatments exposed to predators than in caged controls, but exposure to predator odor cues did not result in differences in distribution relative to caged controls (see Results; Figure 4.5). This is in contrast to other studies showing that prey actively change their distribution in response to predator odor cues (Cote & Jelnikar 1999; Ishida & Iwasaki 2003; Kobak *et al.* 2010). Many organisms also assume aggregated distributions in response to predators as ways to reduce individual risk through prey dilution or predator confusion effects (Turchin & Kareiva 1989; Ioannou *et al.* 2008), although changes in prey distribution in response to predators did not result in aggregated distributions in my study. Observations of blue crab foraging and results from prey tethering studies suggest that blue crabs consume clams where they find them or carry them to deeper water to consume (Micheli 1996). There is no evidence to suggest that foraging blue crabs would remove clams from the sediment and move them without consuming them, indicating that changes in distribution likely result from active movement by individual clams and not predator manipulation.

Changes in the distribution of clams within patches exposed to actively foraging predators could mediate subsequent predation rates by predators, although specific patterns of predation will be dependent on predator sensory abilities and foraging modalities. Patches with random distributions create plumes that are more spread in the cross-stream direction relative to aggregated distributions, resulting in decreased foraging efficiency by quickly moving predators (see Chapter 2). Many organisms have been shown to locate patches of aggregated distributions more easily than random distributions (Dumont *et al.* 2002; Coleman 2008). Blue crabs are good examples of quickly moving predators that have increased success in locating patches containing aggregated distributions of prey than those with random distributions (Chapter 2). Blue crabs are key predators in many salt marsh systems that can regulate infaunal bivalve populations (Virnstein 1977), and thus will exert high predation pressure on clams. My study indicates that the formation of random clam distributions (mediated by predators) will have indirect negative effects on future foraging bouts by blue crabs. This negative feedback loop could reduce predation pressure on clam populations and mediate the abundance of patch types in natural settings.

Changes in clam distribution following exposure to predators results in random distributions similar to those occurring naturally in the field, suggesting that actively foraging predators may be involved in shaping clam distributions in the field. Natural distributions of clams in patches were overwhelmingly random (Figure 4.7, Table 4.1), with the few patches containing uniform distributions seen in connection with vegetation. The distribution of organisms within patches is mediated by a combination of settlement and post-settlement processes and is rarely attributable to a single process or interaction (Parrish *et al.* 2002). Uniform distributions of organisms can be created and maintained in an effort to limit competitive interactions between individuals (Yakovis *et al.* 2004), but this is unlikely to occur in my system as resources are only limiting at unnaturally high densities of bivalve prey (Peterson & Black 1987). Similarities between within patch distributions in the field and those after exposure to predators in my experiment suggest that predator impacts on prey populations may be one of the primary mechanisms shaping clam distributions in the field. The high prevalence of patches containing clams in random distributions also hints at the possibility that changes in clam distribution as a result of exposure to actively foraging predators may inhibit future detection of patches by blue crab predators.

Exposure to actively foraging predators and predator odor cues reduced clam growth rates relative to treatments where predator access was denied and where predator odors were absent (Figure 4.6). Changes in growth over long temporal scales were likely mediated by a reduction in feeding associated with reducing prey apparency. Prey commonly respond to predator odors by reducing feeding behaviors (Chivers &

Smith 1998; Nakaoka 2000; Smee & Weissburg 2006b), which can result in lowered predation rates in the field over short temporal scales (Smee & Weissburg 2006a). The long term impact of this behavior (30 days) is reduced growth (Figure 4.6), which can be corroborated by previous studies (Nakaoka 2000). Increased disturbance rates by experimenters (Walker 1984) and by predators (Irlandi & Peterson 1991) also have been shown to reduce the growth rates of clams in the field. Many prey organisms exhibit tradeoffs between growth and survival behaviors which can manifest as reduced growth during times of increased predation pressure (Lima & Bednekoff 1999; Trussell *et al.* 2006). Clams had smaller growth rates in response to actively foraging predators than in response to predator odor cues, suggesting that disturbance may be a more reliable indicator of predator threat than predator odors. Reduced growth rates because of predators, regardless of the mechanism, could delay the time it takes for individuals to reach a size refuge from blue crab predators and extend the amount of time individuals are vulnerable to predation (Arnold 1984).

Although my study suggests that prey responses to predators can result in changes to within patch distribution, additional studies are needed to determine if these prey responses are unique for blue crab predators or unique to my study system. Many studies have shown that predators create low density refuges for prey through predation and prey behavioral modifications, but my study on dynamic interactions between predators and prey distribution may result in a misinterpretation of the importance of density in previous studies. Predators in salt marsh systems interact with prey patch density and distribution independently (Chapter 2), indicating that the dynamic relationship between predators and prey distribution may have similar magnitude impacts on prey patch dynamics.

CHAPTER V

SITE- AND TIDE-SPECIFIC VARIATION IN THE HYDRODYNAMIC LANDSCAPE RELATIVE TO ODOR-MEDIATED PREDATORS IN SALT MARSH SYSTEMS

5.1 Abstract

Odor-mediated interactions in natural systems can be modified by local flow conditions which transport and disperse chemical cues. For example, the ability of odor-mediated predators to detect and navigate toward prey is dependent on local flow conditions which can modify the spatial distribution and concentration of odors. Flow conditions in natural intertidal estuary habitats where predators generally forage are likely to vary both spatially and temporally, but the extent of differences in flow conditions within and between experimental sites and over various time periods is largely unknown. I assessed spatial and temporal variation in values of turbulent flow parameters within and between four sites in Wassaw Sound, GA where information about predation rates is known using six acoustic Doppler velocimeters (ADVs). I also collected data across and within sites corresponding to different tidal types (neap, normal, and spring tide). Values of turbulent flow parameters were highly correlated and similar within sites at locations up to 20 m distant, but correlations of turbulent flow parameters between sites decreased as the distance between sites increased. There were site- and tidal type-specific effects on values of mean turbulent flow parameters, indicating that flow conditions need to be assessed separately for individual sites and during different tidal types. Differences in mean values, ranges,

and maximum values of flow parameters may have important effects on odor-mediated interactions, potentially creating site-specific impacts on predator foraging efficiency and, subsequently, prey population densities and distributions.

5.2 Introduction

Many physical processes in estuarine systems, such as the transportation of sediment, toxins, and wastewater runoff, are influenced by the turbulent characteristics of the water flow (Chanson *et al.* 2005). Flow and turbulence also mediate a variety of ecological interactions. For instance, flow and turbulence have been shown to mediate the distribution and intensity of larval settlement (Pawlik & Butman 1993; Abelson & Denny 1997), contribute to the erosion or smothering of infaunal communities (Miller *et al.* 2002), and impact odor-mediated predator-prey interactions (reviewed in Weissburg 2000; Webster & Weissburg 2009).

Odor-mediated predator-prey interactions are important in estuarine environments where suspended sediment and algal blooms increase the turbidity of water and prevent visual cues from being used to locate prey. The ability of predators to extract information from chemical cues entrained in flows mediates their ability to successfully locate prey individuals and hence affects prey populations. Variation in flow velocity, turbulence intensity, and Reynolds stresses affect predator tracking abilities in laboratory flume studies (Weissburg & Zimmer-Faust 1993; Jackson *et al.* 2007) and translate into changes in predatory success in the field (Zimmer-Faust *et al.* 1995; Finelli *et al.* 2000; Smee *et al.* 2010). The magnitude and effects of flow characteristics on predators, and subsequently prey populations, is predator-specific and directly related to their sensory capabilities and foraging modalities. For example, blue crabs (*Callinectes sapidus*) in the lab show decreased tracking success in swift flows (Weissburg & Zimmer-Faust 1993), and flows with large turbulence intensity (Jackson *et al.* 2007). The decrease in tracking success leads to reduced predation rates on infaunal bivalve populations in the field (Smee *et al.* 2008; Smee *et al.* 2010). It is hypothesized that the blue crabs' quick movement, consisting of cross-stream comparisons of chemical cues in conjunction with upstream movement in response to concentrated odor filaments, reduces their ability to gather adequate information from prey plumes in highly turbulent flows where odors are diluted, homogenized and spread out from the plume centerline fairly quickly. Knobbed whelks (*Busycon carica*), in contrast, show increased predation success in the field when roughness elements are placed around prey patches (Ferner *et al.* 2009) and in faster flow velocities (Powers & Kittinger 2002). Their slow movement may help them time-average information contained in dilute prey odor plumes and enhance foraging efficiency in turbulent environments.

The ability of predators to locate food can affect the abundance and distribution of prey populations, which is important in estuary systems along the East coast where blue crabs (Hines *et al.* 1990) and whelks (Carriker 1951) are two significant predators on infaunal bivalve populations. Predation rates by these two predators may likely be context-specific (both spatially and temporally) because local flow conditions may be dependent on site and bulk flow characteristics (Smee *et al.* 2010). By combining information about the fluid environment with corresponding biological behavior, informed hypotheses can be formulated as to the spatial and temporal patterns in predation success, and by extension, a better understanding of the ability of predators to control and shape prey populations can be created.

Thus far, information about flow characteristics in near-bed estuarine habitats has been sparse; relegated to short sampling time periods, irrelevant locations above the substrate (not in the near-bed environment where predators forage), arbitrarily-selected sampling time periods, and limited study sites (but see Smee *et al.* 2008; Ferner *et al.* 2009; Smee *et al.* 2010; Berry *et al.* 2011). Hence, information about turbulent flows experienced by benthic foragers is largely unknown, preventing adequate development of hypotheses as to how physical parameters may impact interspecific interactions over temporal and spatial scales that are relevant to odor-mediated predator and prey populations.

Relatively few studies have examined turbulent flow characteristics in the near-bed habitats of small-channel estuaries, or explored how processes like tidal forcing, wind generation of currents, and turbulence interact to affect large-scale estuarine dynamics as well as sediment entrainment and deposition processes (Kawanisi & Yokosi 1994; Bell *et al.* 1997; Collins *et al.* 1998; Le Hir *et al.* 2000; Voulgaris & Meyers 2004). Although these studies were not motivated to address ecological issues, they can be used to identify those processes and flow characteristics that may be important in estuarine dynamics. These studies provide essential information as to the variation and causes of turbulent flow characteristics, but information about temporal and spatial variation in turbulent flow characteristics (especially over long time-periods, in multiple sites, and in areas where concurrent information about predation is known) is lacking.

In order to understand how turbulent flows impact odor-mediated predation, the flow environments in which these predator-prey interactions occur must be assessed at relevant spatial and temporal scales. Specifically, the spatial variation in flow environments (at multiple scales) needs to be explored because it could result in spatially-explicit impacts on odor-mediated predator prey interactions. To do this I measured velocity time series at multiple locations within four sites across an intertidal estuary system. I also obtained measurements across and within multiple sites corresponding to variation in tidal forcing (neap tide, normal tide, and spring tide). Based on previous studies of intertidal estuary turbulent properties, I predict that tidal forcing will have a large effect on mean flow properties, with stronger forcing (spring tide) resulting in larger velocities and increased turbulence. I also predict that the values of turbulent flow parameters will vary within and between sites, although the extent to which these variations impact odor-mediated interactions should be greater between sites than within sites. I deployed multiple acoustic Doppler velocimeters (ADVs) over a three month survey period in Wassaw Sound, Georgia, USA to explore these hypotheses.

5.3 Methods

5.3.1 Data Collection

Time series of three-dimensional flow velocity were obtained during June-August 2010 at four sites in Wassaw Sound, GA and its surrounding tributaries including; Dead Man's Hammock (DMH), across from Priest Landing (APL), the Skidaway Narrows (SN), and Priest Landing (PL) (comparison site) (Figure 5.1). These sites are characterized by semi-diurnal tidally-driven flow with tidal ranges of 2-3 m. All sites are exposed to largely unidirectional flows during both ebb and flood tides. All sites have substrates consisting of a mix of mud and fine sand, are bordered by marsh grass (*Spartina alterniflora*) or oyster reefs (*Crassostrea virginica*), and range in salinity from 20-28 ppt (Smee *et al.* 2010).

Four acoustic Doppler velocimeters (ADVs; NortekUSA Vector) were simultaneously placed within each site, with each site measured over different dates during the sampling period. Instruments were placed 1 m, 5 m, and 10 m from a reference instrument within each site. Concurrent to measurements taken within each site, two ADVs were placed 1 m apart at the Priest Landing comparison site. All instruments were placed parallel to the water line at the mean low tide level. The sampling volume for each instrument was approximately 0.10 m above the substrate. This experimental protocol was repeated for each of the three other sites (not the PL comparison site) and for each of three tidal types (spring tide (SP), neap tide (NP), and normal tide (NL)). This facilitated within-site and between-site spatial comparisons of flows

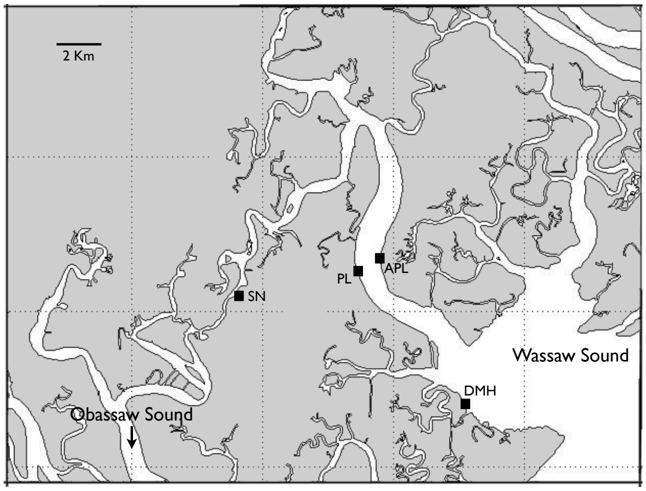

Figure 5.1: Map of Wassaw Sound, Georgia where instruments were deployed June-August 2010. DMH = Dead Man's Hammock, PL = Priest Landing, APL = Across from Priest Landing, SN = Skidaway Narrows.

in the context of large scale changes in tidal forcing. To examine patterns of flow at larger within-site spatial scales, within-site comparisons were also made for the Priest Landing comparison site during three tidal types using six ADVs located at 1 m, 5 m, 10 m, 15 m, and 20 m from a reference instrument.

All ADVs recorded three components of velocity, pressure, signal-to-noise ratios, and correlation coefficients over 4 consecutive complete tidal cycles (from low tide to subsequent low tide) for each tidal type deployment. Instruments were placed in the field such that the x-velocity was predominately the along-stream component and the direction upwards from the substrate was represented by a positive z-velocity. During data analysis, the x- and y-direction velocity components were rotated to maximize the magnitude of the x-velocity component and to ensure that the x-velocity was positive for flood tide and negative for ebb tide. Data were collected continuously at 16 Hz during 5 minute bursts, which were separated by 10 minutes.

5.3.2 Data Analysis

5.3.2.1 Data Filtering

Bursts were discarded if the mean correlation coefficient calculated was less than 70 %. Bursts also were discarded if they contained more than 500 consecutive points with a mean correlation coefficient less than 70 %. These two conditions occurred as a result of probe exposure to the atmosphere during low tides and resulted in removal of an average of 10 bursts for each tidal cycle data set.

5.3.2.2 Phase Filtering

"Spikes" commonly occur in ADV data because of aliasing of the Doppler signal, which results in erroneous data that still show good signal-to-noise ratios and correlation coefficients. To detect spikes I used the phase filtering method of Goring & Nikora (2002), which uses the first and second order differencing estimates to reveal non-physical spikes based on the universal threshold. Erroneous spikes were removed and replaced using a third-order polynomial fit including 12 points on either side of the spike, with an extended range in the presence of other nearby spikes (Goring & Nikora 2002).

5.3.2.3 Removal of Wave Energy

The presence of wind waves in shallow water estuaries can result in apparent wave motion contributions to turbulence parameters. Fluctuations from waves can also contribute to the turbulence signature when sensors are aligned improperly with the principal axis or when there is sloping bed geometry (Grant *et al.* 1984, Trowbridge 1998). The apparent contribution of wave motion to turbulent parameters should not be considered turbulence because of their low frequency ranges, periodicity, and orbital motion. Instantaneous velocity is decomposed into the mean component $\overline{u}$, the wave motion component $\tilde{u}$, and the turbulent fluctuation component u'

according to:

$$u = \overline{u} + \tilde{u} + u' \tag{5.1}$$

I used the coherence between the velocity and pressure measurements to identify and remove the wave portion of the kinetic energy and the Reynolds shear stress using methodology developed by Berry *et al.* (2011). The following is a brief description of the calculations involved in separating the wave component of the Reynolds shear stress. An analogous method is used for the normal stresses in order to separate the wave component of turbulent kinetic energy (see Berry *et al.* (2011) for a more thorough description of all calculations).

Trends due to a rising or falling tide were first removed from the velocity and pressure time series (each 5 minute burst) using a linear trend removal (Bendat & Piersol 2010). The mean value was then subtracted to obtain the fluctuating component of velocity and pressure. The notation employed below implies that the mean component is therefore zero. Following the methodology of Benilov & Filyushkin (1970), I calculated the coherence function for the u component of velocity and pressure (p), as a function of frequency:

$$\gamma^2(\omega) = \frac{S_{up}(\omega)S^*_{up}(\omega)}{S_{uu}(\omega)S_{pp}(\omega)} \tag{5.2}$$

where S_{up} is the cross-spectral density (CSD) of u and p, S_{uu} and S_{pp} are power spectral density (PSD) functions, ω is frequency, and * represents the complex conjugate.

Assuming that the coherence between velocity and pressure is due to wave influence, I then calculated the PSD for the turbulent portion of the signal by:

$$S_{u'u'}(\omega) = [1 - \gamma^2(\omega)]S_{uu}(\omega) \tag{5.3}$$

and used it to calculate the magnitude of the turbulent velocity fluctuation $|U'_j|$ as a function of discrete frequency (denoted with index j) via:

$$S_{u'u'j} = \frac{1}{d\omega}|U'_j|^2 \tag{5.4}$$

These steps were then repeated for the w component of velocity and pressure such that the magnitude of the turbulent velocity fluctuations for both the u and w velocity components were adjusted using the coherence of the respective velocity components with the pressure signal.

To calculate the Reynolds shear stress I then incorporated the phase of each velocity component with the magnitude of the turbulent velocity fluctuation. The velocity components can then be expressed using phasor notation of the Fourier coefficients:

$$U_j = |U_j|e^{i\angle U_j} \text{ and } W_j = |W_j|e^{i\angle W_j} \tag{5.5}$$

with the phases defined by:

$$\angle U_j = arctan\left[\frac{Im(U_j)}{Re(U_j)}\right] \text{ and } \angle W_j = arctan\left[\frac{Im(W_j)}{Re(W_j)}\right] \tag{5.6}$$

Using this, the CSD can be expressed as:

$$U_j^* W_j = |U_j||W_j|e^{j(\angle W_j - \angle U_j)} = |U_j||W_j|(\cos(\angle W_j - \angle U_j) - i\sin(\angle W_j - \angle U_j)) \tag{5.7}$$

Neglecting the imaginary part of the CSD, the Reynolds shear stress can be calculated using:

$$\overline{u'w'} = \sum_j U_j'^* W_j' = \sum_j |U_j'||W_j'|\cos(\angle W_j - \angle U_j) \tag{5.8}$$

where $|U_j'|$ and $|W_j'|$ are calculated from Equation (5.4) and $\angle U_j$ and $\angle W_j$ are calculated from Equation (5.6). The wave portion of the Reynolds shear stress then is calculated by subtracting the turbulent velocity fluctuation from the total covariance:

$$\overline{\tilde{u}\tilde{w}} = \overline{uw} - \overline{u'w'} \tag{5.9}$$

I used this methodology to calculate the wave contribution to turbulent kinetic energy and Reynolds shear stress for all bursts in each data set except the first two and last two bursts of each tidal cycle for data sets collected at Priest Landing. The two downward facing fixed stem ADVs at the Priest Landing site were mounted such that they were able to record velocity data while the pressure sensor was not immersed at the beginning and end of each tidal cycle, preventing the calculation of coherence between velocity and pressure for these bursts.

5.3.2.4 Calculation of Turbulent Parameters

Mean turbulence characteristics were calculated for each burst. Turbulence parameters calculated are as follows:

$$Turbulent\ Kinetic\ Energy\ (TKE) = 0.5(\overline{(u')^2} + \overline{(v')^2} + \overline{(w')^2}) \tag{5.10}$$

$$Reynolds\ Shear\ Stress = \overline{u'w'} \tag{5.11}$$

$$Turbulence\ Intensity\ (TI) = \frac{\sqrt{\overline{(u')^2} + \overline{(v')^2} + \overline{(w')^2}}}{\sqrt{\overline{u}^2 + \overline{v}^2 + \overline{w}^2}} * 100 \tag{5.12}$$

5.3.2.5 Statistical Analysis

To examine the spatial variability within sites, I performed a series of correlations between turbulence data from each ADV probe and the corresponding reference instrument within each site. Distance comparisons for the DMH, SN, and APL sites were 0×1 m, 0×5 m, and 0×10 m, and distance comparisons for the PL site were 0×1 m, 0×5 m, 0×10 m, 0×15 m, and 0×20 m, where zero represents the reference instrument. Burst-averaged data from four measured tidal cycles (approximately 140 bursts) was used to calculate correlation coefficients. Pearson correlations were used to calculate correlation coefficients for the burst-averaged absolute value of the u-component of velocity, and Spearman rank correlations were used for all other flow parameters (TKE, $|\overline{u'w'}|$, TI) because I was unable to achieve normality via transformation.

To determine correlation strengths between turbulent flow parameters at each site (DMH, APL, and SN) and the PL comparison site, I again utilized a series of

Pearson and Spearman rank correlation analyses for each turbulent flow parameter and each tidal type. Data used for between-site correlations were for time series taken simultaneously at PL and each individual site (approximately 135 bursts).

To determine the influence of site and tidal forcing (and any interactions) on mean turbulent flow parameters, I utilized a two-way analysis of variance (ANOVA), which is fairly robust to issues of non-normality (Zar 1999). Because I was unable to achieve normality via transformation for most of my turbulent parameters (TKE, TI, and $|\overline{u'w'}|$), non-parametric Kruskal-Wallis tests were also used to confirm significance of one-way comparisons. This was done for each flow parameter separately using burst-averaged data from the entire deployment period described above (approximately 140 bursts).

Regression analysis also was used to determine the relationship between values of $|\overline{u}|$, TKE, and $|\overline{u'w'}|$ using the ensemble-averaged values calculated for each site by tidal type combination for comparison.

5.4 Results

5.4.1 Flow Time Series and Comparison Within Sites

Similar values of $\overline{u}$, TKE and $\overline{u'w'}$ were obtained from the four simultaneously deployed instruments within a site (Figure 5.2 shows example data from the APL-NP data set). Similar patterns were seen for set comparisons within all sites. Overall, there is greater variation between instruments for values of TKE and $\overline{u'w'}$ than values of $\overline{u}$ and greater variation between instruments during ebb tide, regardless of the turbulent flow parameter. These patterns hold for the entire four tidal cycle sampling period (Figure 5.3).

5.4.2 Correlation within and between Sites

Correlation coefficients for within-site comparisons of all turbulent flow parameters were large and significantly different from zero for all distance comparisons

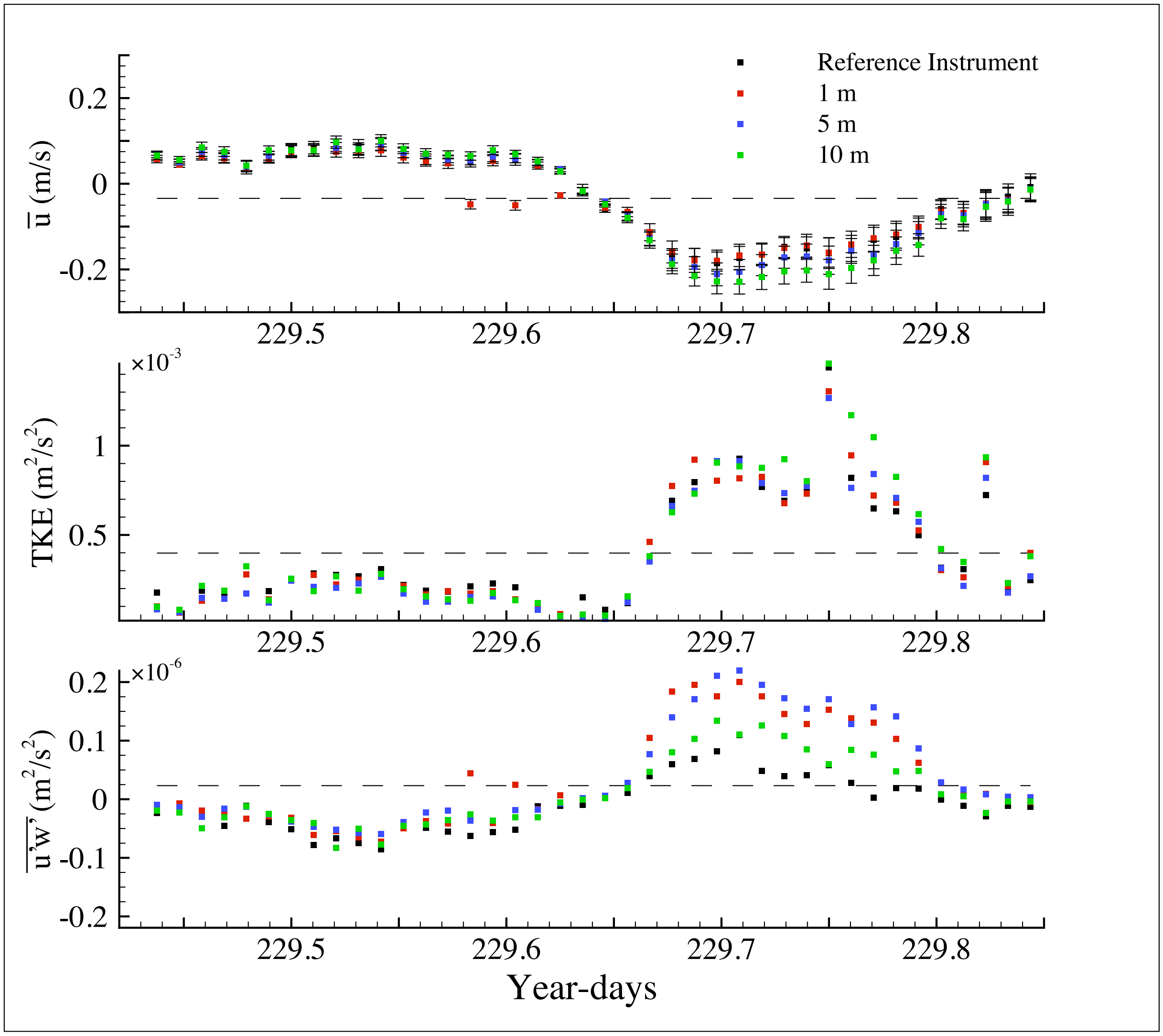

Figure 5.2: Time-series of flow parameters ($\overline{u}$ [top], TKE [middle], and $\overline{u'w'}$ [bottom]) from four simultaneously deployed ADVs within the APL site during neap tide for one tidal cycle. Error bars represent one standard deviation. Dashed lines represent the mean value for all instruments combined. Differently colored symbols represent the four instruments: Reference instrument = black, 1 m = red, 5 m = blue, and 10 m = green.

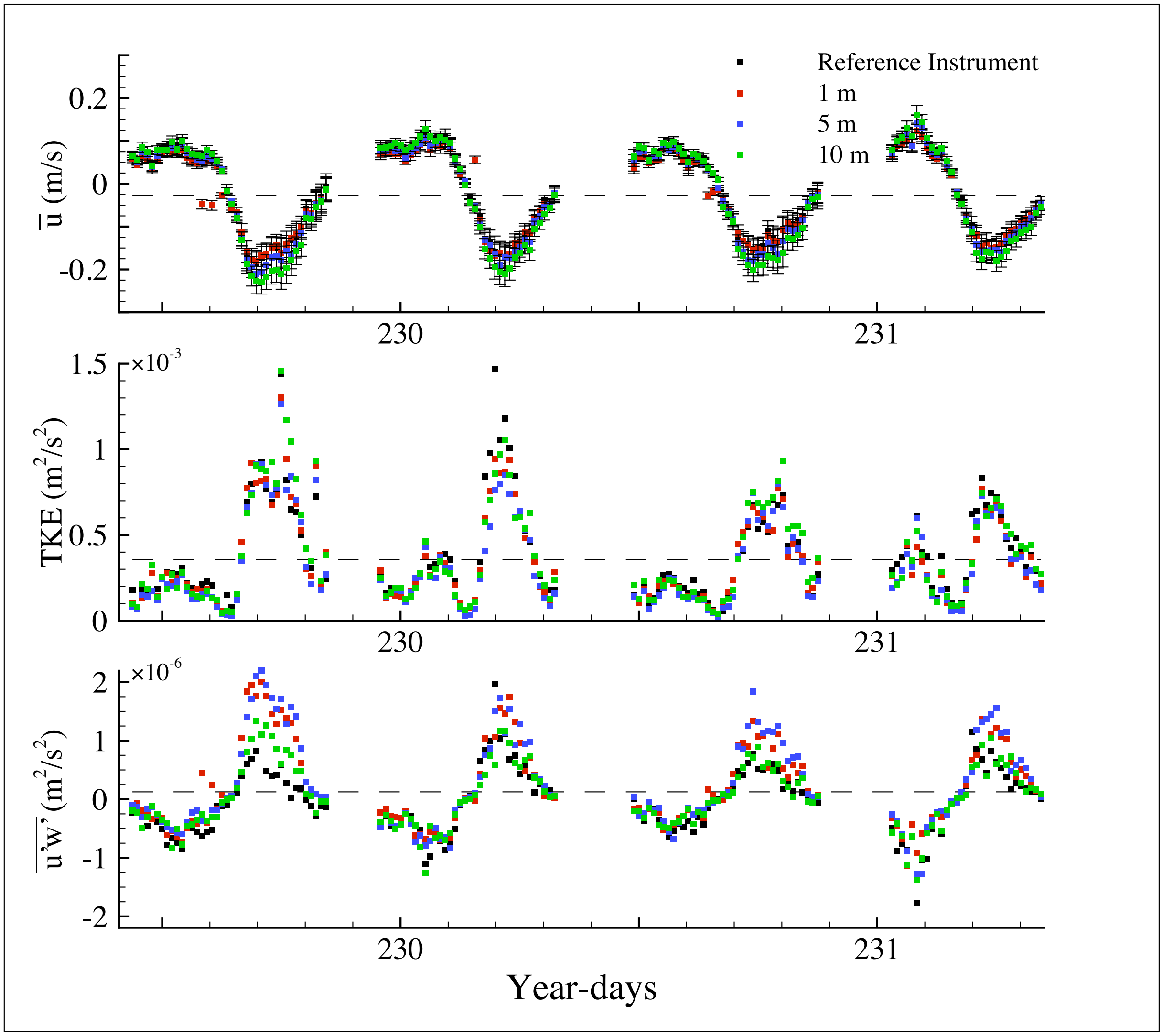

Figure 5.3: Time-series of flow parameters ($\overline{u}$ [top], TKE [middle], and $\overline{u'w'}$ [bottom]) from four simultaneously deployed ADVs within the APL site during neap tide for four tidal cycles. Error bars represent one standard deviation. Dashed lines represent the mean value for all instruments combined. Differently colored symbols represent the four instruments: Reference instrument = black, 1 m = red, 5 m = blue, and 10 m = green.

at the DMH, SN, and APL sites (Table 5.1, see Figure 5.4 for an example of correlations within the PL site). Correlation coefficients tended to decrease with separation distance, but statistics were not used to determine significant differences between correlation coefficients within each site. Comparisons of multiple correlation coefficients greater than 0.9 are discouraged because the z-transformation needed to normalize and stabilize the variance of the underlying correlation coefficient distribution is not reliable for coefficients greater than 0.9 (Zar 1999). Correlation coefficients ranged from 0.99 for $|\overline{u}|$ to 0.18 for $|\overline{u'w'}|$ (Table 5.1). For the DMH, SN, and APL sites, correlation coefficients for $|\overline{u}|$ were generally the highest and correlation coefficients for $|\overline{u'w'}|$ were generally the lowest, with the correlation coefficients for the other two turbulent flow parameters (TKE and TI) falling in between.

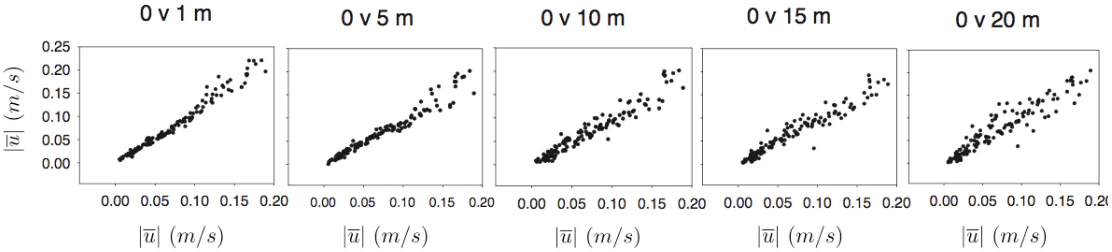

Figure 5.4: Within-site correlations of the absolute value of burst averaged u-velocity at Priest Landing site during normal tide. Correlation coefficients are shown for comparisons between each instrument and the reference instrument that was simultaneously deployed. Data included in the correlation calculation consisted of 128 bursts collected over 4 tidal cycles.

Correlation coefficients for within-site comparisons at PL also were large and significantly different from zero (Table 5.2). Correlation coefficients at PL ranged from 0.99 for $|\overline{u}|$ to 0.25 for TI, with generally the highest correlation coefficients for $|\overline{u}|$ and the lowest for $|\overline{u'w'}|$. Average correlation coefficients for PL (including all tidal types) showed a general decrease with distance for all flow parameters except TI, which were relatively similar for all distance comparisons.

Correlation coefficients for within-site comparisons at the PL, DMH, SN, and

Table 5.1: Correlation coefficients for comparisons of spatially-separated simultaneous data (0×1 m, 0×5 m, and 0×10 m) within each tidal type and site for each turbulent parameter ($|\overline{u}|$, TKE, TI, and $\overline{u'w'}$). "No. Bursts" indicates the number of bursts that were compared to calculate the correlation coefficients. Sites are named using the following convention; SN = Skidaway Narrows, APL = Across from Priest Landing, DMH = Dead Man's Hammock. All correlation coefficients are significantly different from zero.

Site	Tidal Type	No. Bursts	$\lvert\overline{u}\rvert$			TKE		
			0×1 m	0×5 m	0×10 m	0×1 m	0×5 m	0×10 m
SN	Normal	141	0.99	0.95	0.88	0.90	0.80	0.82
SN	Neap	173	0.99	0.97	0.92	0.86	0.84	0.85
SN	Spring	126	0.99	0.96	0.91	0.97	0.93	0.88
APL	Normal	149	0.91	0.99	0.97	0.99	0.94	0.94
APL	Neap	145	0.99	0.98	0.97	0.96	0.97	0.95
APL	Spring	137	0.94	0.92	0.91	0.77	0.76	0.76
DMH	Neap	129		0.92	0.94		0.84	0.88
DMH	Spring	143	0.98	0.96	0.95	0.95	0.96	0.95
All	All		0.97 ± 0.03	0.96 ± 0.03	0.93 ± 0.03	0.91 ± 0.08	0.88 ± 0.08	0.88 ± 0.07

Site	Tidal Type	No. Bursts	TI			$\overline{u'w'}$		
			0×1 m	0×5 m	0×10 m	0×1 m	0×5 m	0×10 m
SN	Normal	141	0.93	0.83	0.77	0.81	0.73	0.80
SN	Neap	173	0.88	0.78	0.70	0.86	0.61	0.72
SN	Spring	126	0.85	0.78	0.71	0.70	0.81	0.74
APL	Normal	149	0.87	0.85	0.72	0.94	0.93	0.92
APL	Neap	145	0.78	0.76	0.84	0.72	0.68	0.79
APL	Spring	137	0.49	0.37	0.45	0.54	0.83	0.54
DMH	Neap	129		0.85	0.87		0.20	0.18
DMH	Spring	143	0.95	0.95	0.94	0.44	0.63	0.50
All	All		0.82 ± 0.16	0.77 ± 0.17	0.75 ± 0.15	0.72 ± 0.18	0.68 ± 0.22	0.65 ± 0.23

Table 5.2: Correlation coefficients for comparisons of spatially-separated simultaneous data (0×1 m, 0×5 m, 0×10 m, 0×15 m, and 0×20 m) within each tidal type at Priest Landing (PL) and for each turbulent parameter ($|\overline{u}|$, TI, TKE, and $\overline{u'w'}$). "No. Bursts" indicates the number of bursts that were compared to calculate the correlation coefficients. All correlation coefficients are significantly different from zero.

Site	Tidal Type	No. Bursts	$\lvert\overline{u}\rvert$					TI				
			0×1 m	0×5 m	0×10 m	0×15 m	0×20 m	0×1 m	0×5 m	0×10 m	0×15 m	0×20 m
PL	Normal	128	0.99	0.98	0.97	0.96	0.88	0.48	0.79	0.49	0.61	0.51
PL	Neap	134	0.99	0.83	0.95	0.92	0.88	0.81	0.65	0.89	0.88	0.78
PL	Spring	136	0.99	0.99	0.97	0.92	0.88	0.31	0.52	0.42	0.40	0.25
PL	All		0.99	0.93 ± 0.09	0.96 ± 0.01	0.93 ± 0.02	0.53 ± 0.25	0.88	0.65 ± 0.14	0.6 ± 0.25	0.63 ± 0.24	0.51 ± 0.27

Site	Tidal Type	No. Bursts	TKE					$\overline{u'w'}$				
			0×1 m	0×5 m	0×10 m	0×15 m	0×20 m	0×1 m	0×5 m	0×10 m	0×15 m	0×20 m
PL	Normal	128	0.97	0.97	0.89	0.93	0.90	0.84	0.74	0.76	0.78	0.59
PL	Neap	134	0.94	0.89	0.90	0.88	0.87	0.74	0.70	0.43	0.29	0.59
PL	Spring	136	0.71	0.69	0.73	0.68	0.70	0.78	0.81	0.81	0.73	0.68
PL	All		0.87 ± 0.14	0.85 ± 0.14	0.84 ± 0.1	0.83 ± 0.13 for	0.82 ± 0.12	0.79 ± 0.05	0.75 ± 0.06	0.67 ± 0.21	0.6 ± 0.27	0.62 ± 0.05

APL sites were similar for all flow parameters except for TI. Data at the PL site showed smaller correlation coefficients for TI for all distance comparisons when compared to the other three sites. Average correlation coefficients for all turbulent flow parameters (except TI) for the PL 0×20 m and DMH, SN, and APL 0×10 m distance comparisons were similar and large, indicating that flow parameters are still highly correlated at 20 m separation distance. I did not see any clear effects of tidal type on correlation coefficients for any site.

For between-site comparisons I found larger correlation coefficients for all turbulent parameters for sites that are located closer to each other (Table 5.3 and Figure 5.1), but I did not see a clear effect of tidal type on correlation strength. The largest correlation coefficient was seen for the neap tide comparison of $|\overline{u}|$ between data for the APL and PL site (0.77), and the smallest was for the normal tide comparison of data for the SN and PL sites for both $|\overline{u}|$ and TI with a value of 0.02. As seen for within-site correlation coefficients (Table 5.1), comparisons of $|\overline{u}|$ between sites generally resulted in larger correlation coefficients than for other turbulence parameters. Negative correlations were seen for many between-site comparisons, possibly resulting from local bed topography (DMH is bordered by extensive mudflats) or in the case of SN, tidal influence from the adjacent Obassaw Sound (Figure 5.1). As expected, correlation coefficients are generally larger for within-site comparisons than between-site comparisons (largest within-site correlation coefficient = 0.99; largest between-site correlation coefficient = 0.77).

5.4.3 Site and Tide Comparisons

I found a significant effect of site ($F_{3,1537} = 72.08, P < 0.001$), tidal type ($F_{2,1537} = 38.62, P < 0.001$), and interaction between site and tidal type ($F_{6,1537} = 2.88, P = 0.008$) on $|\overline{u}|$ (Figure 5.5). Kruskal-Wallis tests confirmed significance of one-way interactions (site: $H = 190.64, df = 3, P < 0.001$, tide: $H = 44.31, df =$

Table 5.3: Correlation coefficients for comparisons between data at each site and simultaneous data at the Priest Landing (PL) comparison site for each tidal type and for each turbulent parameter calculated ($|\overline{u}|$, TKE, KE_{wave}, TI, $\overline{u'w'}$, and $\overline{\tilde{u}\tilde{w}}$). "Bursts" indicates the number of bursts compared to calculate correlation coefficients. * indicates non-significant correlation coefficients.

Site Comparison	Tide Type	Bursts	$\lvert\overline{u}\rvert$	TKE	KE_{wave}	TI	$\overline{u'w'}$	$\overline{\tilde{u}\tilde{w}}$
APL × PL	Normal	140	0.74	0.63	0.62	0.27	0.64	0.51
APL × PL	Neap	145	0.77	0.70	0.66	0.29	0.45	0.36
APL × PL	Spring	130	0.72	0.58	0.72	0.26	0.63	0.38
SN × PL	Normal	61	0.02*	-0.08*	0.17*	0.02*	-0.04*	0.10*
SN × PL	Spring	98	0.28	0.16*	0.15*	0.15*	0.08*	0.13*
DMH × PL	Normal	137	-0.41	-0.23	0.34	0.34	-0.19	0.33
DMH × PL	Spring	140	-0.36	-0.46	-0.15*	0.39	-0.31	0.15*

$2, P < 0.001$). Data at the DMH site showed the smallest $|\overline{u}|$ for all tidal types which may be related to the extensive mudflats located near the sampling site. $|\overline{u}|$ generally increased from neap tide to normal tide, with spring tide showing larger velocities than either other tidal type. The lone exception was data at the SN site where neap tide and normal tide show no apparent differences in velocity. Patterns of $|\overline{u}|$ confirm that increases in tidal forcing, with spring tide having a larger tidal range than neap tide, correspond to increases in flow velocity.

TKE was significantly affected by site ($F_{3,1537} = 17.71, P < 0.001$) and tidal type ($F_{2,1537} = 20.97, P < 0.001$), but there was not a significant interaction between site and tidal type ($F_{6,1537} =, P = 0.153$) (Figure 5.6). One-way analyses confirmed significant effects of site and tide (site: $H = 154.48, df = 3, P < 0.001$ tide: $H = 58.24, df2, P < 0.001$). Data for APL and PL sites had greater TKE than data for the DMH and SN sites (almost two times greater for some sites). All sites had greater TKE during spring tide than during either neap or normal tides (Figure 5.6).

Turbulence intensity (TI) was significantly affected by site ($F_{3,1537} = 63.52, P <$

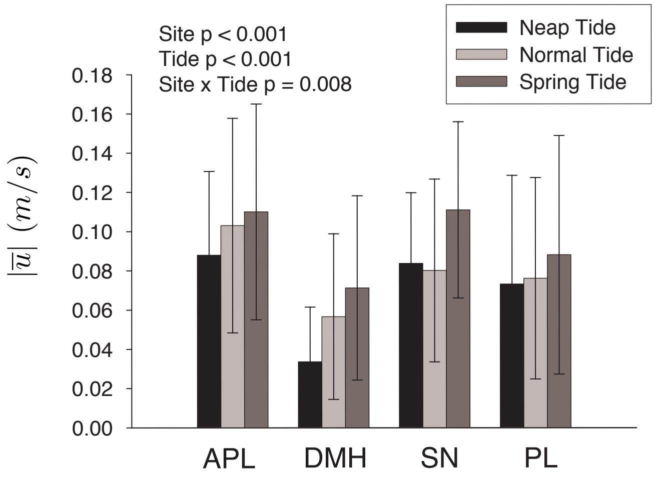

Figure 5.5: Ensemble average of the absolute value of burst-averaged values of u-velocity (m/s). Error bars represent one standard deviation. For the number of bursts included in calculating ensemble averages see Tables 5.1 and 5.2. APL = Across from Priest Landing, DMH = Dead Man's Hammock, SN = Skidaway Narrows, and PL = Priest Landing. Statistical significance was determined using a two-way ANOVA.

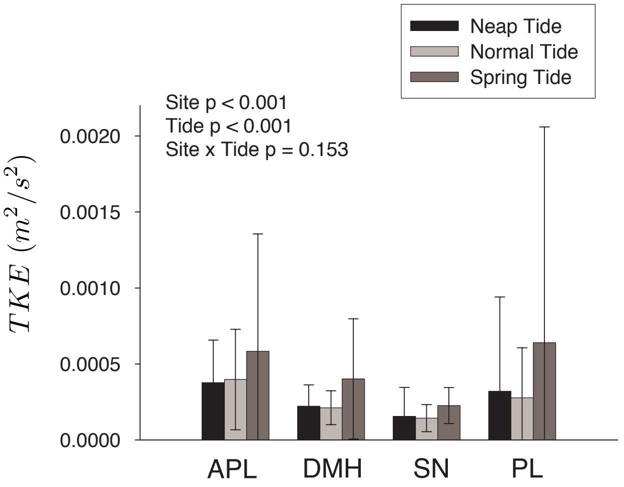

Figure 5.6: Ensemble average of burst-averaged values of TKE (m^2/s^2). Error bars represent one standard deviation. For the number of bursts included in calculating ensemble averages see Tables 5.1 and 5.2. APL = Across from Priest Landing, DMH = Dead Man's Hammock, SN = Skidaway Narrows, and PL = Priest Landing. Statistical significance was determined using a two-way ANOVA.

0.001) and tidal type ($F_{2,1537} = 3.19, P = 0.041$) (Figure 5.7), with DMH having greater TI than the other three sites. On average, there was lower turbulence intensity during spring tide than other tidal types, the result of large u velocities during spring tide (See Equation 5.12 and Figure 5.5). One-way analyses confirmed significance of site and tidal type (site: $H = 455.46, df = 3, P < 0.001$ tide: $H = 7.67, df = 2, P = 0.022$). There also was a significant interaction between site and tidal type ($F_{6,1537} = 3.52, P = 0.002$). At the PL and APL sites, the data reveal greater TI during neap and spring tides, but the data at the SN site show greater turbulence intensity during normal tide. Turbulence intensity at the DMH site was greater during neap and normal tides than spring tide.

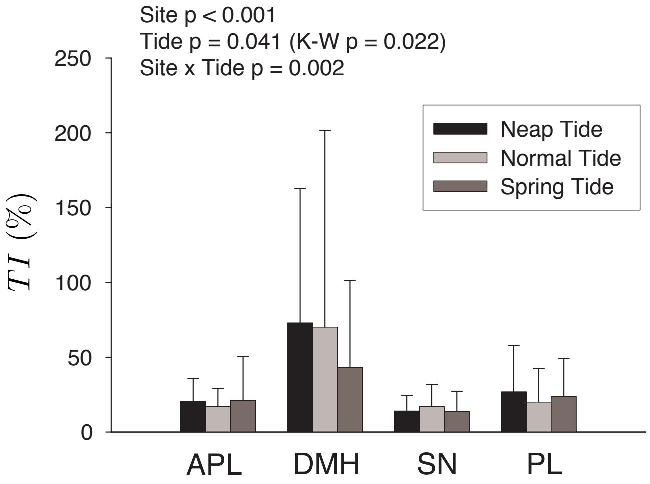

Figure 5.7: Ensemble average of burst-averaged values of Turbulence Intensity (TI, %). Error bars represent one standard deviation. For the number of bursts included in calculating ensemble averages see Tables 5.1 and 5.2. APL = Across from Priest Landing, DMH = Dead Man's Hammock, SN = Skidaway Narrows, and PL = Priest Landing. Statistical significance was determined using a two-way ANOVA.

There also was a significant effect of site ($F_{3,1433} = 10.02, P < 0.001$) and tide ($F_{2,1433} = 8.38, P < 0.001$) on Reynolds shear stress (Figure 5.8), with greater Reynolds shear stress at the APL site than the other three sites and greater Reynolds shear stress during normal tides (although this seems to be driven by large Reynolds shear stress for the APL site only). Kruskal-Wallis tests confirm significance of one-way analyses (site: $H = 51.85, df = 3, P < 0.001$, tide: $H = 20.48, df = 2, P < 0.001$). There also was a significant interaction between site and tidal type ($F_{6,1433} = 9.761, P < 0.001$), with APL showing greater Reynolds shear stress during normal tide as opposed to the other three sites that show smaller Reynolds shear stress during normal tide.

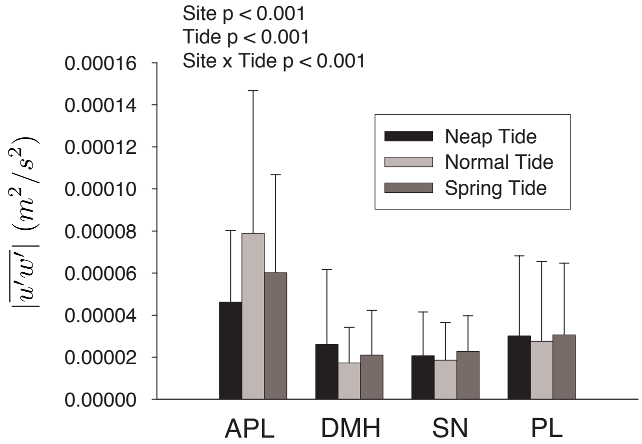

Figure 5.8: Ensemble average of the absolute value of the burst-averaged values of the Reynolds shear stress ($|\overline{u'w'}|\ (m^2/s^2)$). Error bars represent one standard deviation. For the number of bursts included in calculating ensemble averages see Tables 5.1 and 5.2. APL = Across from Priest Landing, DMH = Dead Man's Hammock, SN = Skidaway Narrows, and PL = Priest Landing. Statistical significance was determined using a two-way ANOVA.

Regressions between ensemble-averaged values of $|\overline{u}|$ and TKE ($F_{1,10} = 1.957$, $P = 0.19$), $|\overline{u}|$ and $|\overline{u'w'}|$ ($F_{1,10} = 3.78$, $P = 0.08$), and TKE and $|\overline{u'w'}|$ ($F_{1,10} = 4.09$, $P = 0.07$) for all site by tidal type combinations were marginally non-significant (Figure 5.9). Values of $|\overline{u}|$ were only able to explain 14 % of the variance in values of TKE and 27 % of the variance in values of $|\overline{u'w'}|$. Values of TKE explained 21 % of the variance in values of $|\overline{u'w'}|$. Relationships between values of turbulent flow parameters within sites are more similar to each other than relationships between values of turbulent flow parameters within each tidal type (i.e. values of turbulent flow parameters group together by site and not tidal type; Figure 5.9).

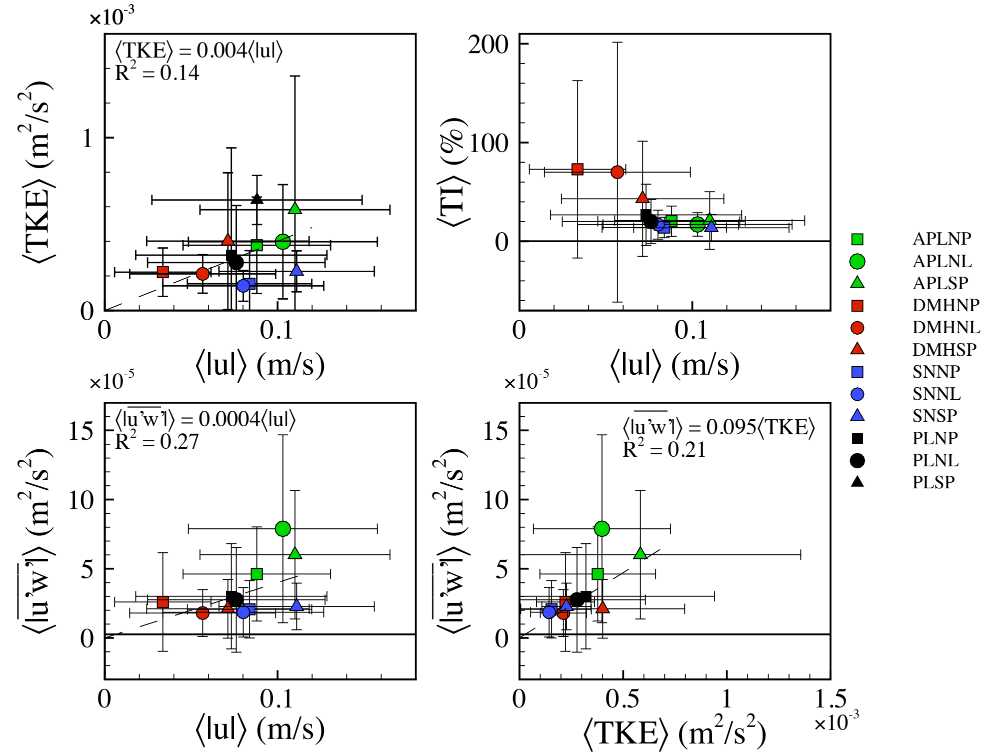

Figure 5.9: Relationships between values of turbulent flow parameters for ensemble averages of all sites by tidal type combinations. Data sets are named using the convention of site followed by tidal type: APL (green) = Across from Priest Landing, DMH (red) = Dead Man's Hammock, SN (blue) = Skidaway Narrows, PL (black) = Priest Landing; NP = neap tide, NL = normal tide, and SP = spring tide. Dashed lines show the line of best fit for a linear trend. Significance was determined using linear regression analysis. Brackets around each turbulent flow parameter axis label indicates the ensemble averaged (approx. 140 bursts) value. Error bars represent one standard deviation.

5.5 Discussion

Results from my within- and between-site comparisons of turbulent flow dynamics indicate that there is significant predictive ability (based on correlation strengths) within sites using limited instrument locations. However, the predictive ability between sites seems to be dependent on site separation distance, where differences in channel topography may be greater than within sites. This indicates that characterization of flow environments needs to be done for each site where experiments occur, but may not need to be obtained for multiple locations within sites (at least up to 20 m separation distance). There also are significant differences in mean values of flow parameters between sites and for different strengths of tidal forcing. There were significant interaction effects between sites and tidal types, indicating that tidal forcing may operate in a site-dependent manner to influence turbulent flow. This prevents large-scale generalizations concerning the influence of site and tidal forcing on turbulent flow parameters and suggests that observations need to be conducted within sites during different tidal forcing strengths to understand the variability in turbulent flow that organisms may be exposed to in natural environments. Differences in mean values, ranges, and maximum values of flow parameters may have important effects on odor-mediated interactions, potentially creating site-specific impacts on predator foraging efficiency and, subsequently, prey population densities and distributions.

5.5.1 Variation of Flow within Sites

My study indicates that values of within-site turbulent flow parameters are very similar for simultaneously deployed instruments (Figure 5.2) and are well correlated up to 20 m distant, regardless of tidal type (Tables 5.1 and 5.2). This suggests that large scale tidal forcing may overwhelm small differences in substrate or local topography within sites that could affect turbulent flow parameters. Still, I do see generally smaller correlation coefficients for turbulent flow parameters that are more dependent on small-scale substrate differences or bed topography (TKE and $\overline{u'w'}$) than those that are dependent on large-scale tidal forcing (Table 5.1). There are few studies that have measured turbulent flow properties at multiple locations within a single site, although to my knowledge none have taken simultaneous measurements.

Both Chanson *et al.* (2005) and Collins *et al.* (1998) measured flow at multiple locations within single sites during subsequent sampling periods (separated by up to a month), possibly confounding differences between microsites and differences in large scale flow patterns. Simultaneous sampling within my sites confirms that measurements of turbulent flow parameters from one instrument can be highly predictive of turbulent flow parameters up to 20 m distant and that this predictive ability is not dependent on tidal type. Larger-scale comparisons (20 m plus) need to be made to confirm the ability of single-location measurements to predict values of turbulent flow parameters at larger distances within sites. I do not see a break-point in the relationship between distance and correlation coefficients with distance, suggesting correlations will continue to decline with much the same slope observed from 0 to 20 m. In the absence of other studies, it is impossible to determine whether the patterns I observe characterize other estuaries as well.

The area defined as a single site also varies drastically among studies. Sites range in separation distance from approximately 200 m (Chanson *et al.* 2005) to multiple kilometers (Collins *et al.* 1998). Studies examining turbulent flow parameters at multiple within-site locations have done so at separation distances of approximately 80 m (Chanson *et al.* 2005) to 200 m (Collins *et al.* 1998). My data suggest that these larger separation distances may comprise sites that exhibit substantial differences in flow properties. For ecological applications of flow monitoring, I suggest that the scale of sampling within-sites should be relevant to the ecology of the focal organism (sensu Levin 1992). Odor-mediated predators in my study system are highly varied in their mobility, with blue crabs moving at greater than 3 cm/s (Weissburg & Zimmer-Faust 1994) and knobbed whelks moving at 0.15 cm/s (calculated from Ferner & Weissburg 2005). Blue crab movement in the field has been reported as slower than in the laboratory at approximately 20 m/hr (0.5 cm/s) (Hines *et al.* 1995). The scale of my survey seems ecologically-relevant, as both predator species would spend ample time in my survey area.

5.5.2 Variation of Flow between Sites

The strength of between-site correlations for turbulent flow parameters seems dependent on the distance between sites, but not on tidal type (Table 5.3). Sites that are closer in proximity may be subject to more similar large-scale tidal forcing processes than those farther apart. There were also site- and tide-specific impacts on all mean turbulent flow parameters, indicating that flow impacts on odor-mediated interactions may be highly context-specific.

Other studies comparing multiple intertidal sites within Wassaw Sound, GA (Smee *et al.* 2010; Berry *et al.* 2011) have shown site-specific differences in mean turbulent flow parameters. Both $|\overline{u}|$ and TKE at DMH and SN in my study are similar to those measured by Berry *et al.* (2011) for the DMH16 and Skidaway14/19/20 sets, but $|\overline{u'w'}|$ for these two sites is an order of magnitude larger in my data set than reported in Berry *et al.* (2011). This may be due to differences in the respective wave contributions for the two data sets (See Chapter 6), substrate properties due to erosion or sedimentation in the four years between sampling, or distance of the sampling volume from the bed. Velocities reported by Smee *et al.* (2010) for the Skidaway River (my SN site) are approximately 20% larger than my measured velocities, which can be accounted for by differences in my data filtration processes and sampling volume height.

Relationship trends between values of average turbulent flow parameters measured at each site and for each tidal type match those described in Berry *et al.* (2011) (Figure 5.9). Values from my study represent only the lower values of those measured in Berry *et al.* (2011), which may account for the different numerical relationships between the variables within the two studies and the marginal non-significance in my study. The relationships between values of average turbulent flow parameters measured in my study seem to group together based on site rather than tidal type, indicating that variation between sites drives the overall relationship between turbulent flow parameters (Figure 5.9). Berry *et al.* (2011) utilized more sites characterized by greater variability in bulk flow, exposure to Wassaw Sound, and sediment composition than my study, possibly accounting for differences in the linear relationships and significance of relationships between turbulent flow parameters in my two studies.

Differences in turbulent parameters between sites could have large spatial impacts on odor-mediated interspecific interactions throughout estuary systems. Using information about predator foraging efficiency under different flow regimes in combination with my observed vales of turbulent flow parameters (Figures 5.5, 5.6, 5.8) I can make predictions about temporal and spatial patterns of predation in the field. When turbulent properties such as $|\overline{u}|$ and TKE follow similar patterns in relation to tidal type or site, similar predictions of predation rates in the field would be made based on each turbulent flow parameter. Predators such as blue crabs, seem to be more sensitive to changes in turbulence than velocity in the laboratory (Jackson *et al.* 2007), suggesting that if patterns in $|\overline{u}|$ and TKE differ based on site or tidal type it could result in different predictions being made as to the impacts of these two turbulent flow parameters on predation efficiency. For example, higher $|\overline{u}|$ and TKE during spring tide both suggest a reduction in foraging efficiency by blue crabs during spring tide relative to neap and normal tides, but high values of $|\overline{u}|$ and low values of TKE at the SN site suggest opposing influences on blue crab foraging efficiency. Field assessments of blue crab predation rates also need to be made to confirm site and tidal forcing predictions, as there have not been any large-scale experiments comparing predation rates or bivalve prey densities (Walker & Tenore 1984) in my specific sites (although see Smee *et al.* (2010) for predation rates at other sites in Wassaw Sound, GA).

5.5.3 Variation in Flow as a Function of Tidal Forcing

Some studies have shown that the influence of tidal forcing on turbulent flow parameters at different sites is dependent on the balance between freshwater and marine inputs (Chanson *et al.* 2005; Chanson *et al.* 2008). This effect did not seem to be a factor in my study, as all of my sites are distant from freshwater inflow (Figure 5.1). Differences in turbulent flow characteristics between sites can be due to channel topography (Collins *et al.* 1998), substrate characteristics (Shiono & West 1987), tidal lag, or variation in tidal forcing (Le Hir *et al.* 2000). Other studies support my findings that u-velocity (Figure 5.5) (Bell *et al.* 1997; Le Hir *et al.* 2000; Trevethan *et al.* 2008; Trevethan & Chanson 2009) and TKE (Figure 5.6) (Trevethan & Chanson 2009) are greater during spring tide than neap tide. Trevethan *et al.* (2008) also recorded 2 to 4 times more variability in values of u-velocity during spring tides than during neap tides, which I confirmed for my DMH, APL, and PL sites, but not at my SN site (Figure 5.5).

There was a 3 to 4 cm/s increase in $|\overline{u}|$ between neap and spring tides in data for all my sites (Figure 5.5). In laboratory studies, a 2.8 cm/s increase in flow velocity (from 1 cm/s to 3.8 cm/s) resulted in a 50% reduction in predatory success by blue crabs (Weissburg & Zimmer-Faust 1993). Increases in turbulence (due to increased bed roughness) also resulted in an approximately 50% reduction in blue crab foraging success (Jackson *et al.* 2007). Independent of other processes, differences in turbulent flow parameters between neap and spring tide could result in significant differences in blue crab predation rates in the field, although additional field surveys and experimentation are needed to confirm this.

5.5.4 Summary

Based on large within-site correlation coefficients, I suggest that a limited number of sampling locations are necessary to accurately predict variation in turbulent flow parameters that an organism may encounter over distances of 1 to 20 m. Based on distant-dependent correlation strength between sites, I suggest that additional between-site comparisons be made to determine the distance at which predictive capabilities are maintained. Differences in turbulent flow parameters between sites and during different tidal types suggest that odor-mediated interactions should vary both spatially and temporally within the estuary system. This could have important consequences for predator-prey population dynamics via the creation of flow-mediated refuges from predation (as suggested by Smee & Weissburg (2006a) and Smee *et al.* (2010)) and vary based on the dominant predator species.

CHAPTER VI

TIDE AND WIND EFFECTS ON THE FLUCTUATING FLOW PARAMETERS IN SHALLOW INTERTIDAL SALT MARSH HABITATS

6.1 Abstract

Fluctuating flow parameters can influence a variety of ecological interactions in intertidal near-bed habitats in salt marsh systems, making characterization of the hydrodynamic environment essential in understanding the processes mediating interactions. Ecologists rarely have the equipment or technological know-how to adequately assess fluctuating flow parameters in the field, thus it would be beneficial if easily collectable and interpretable surrogate data could be identified that would serve as a proxy for estimating fluctuating flow parameters in natural settings. I assessed the predictive ability of wind speed and tidal range for estimating values of fluctuating flow parameters in intertidal salt marsh systems, as these parameters are known to influence values of wave and turbulent components of fluctuating flow parameters in shallow aquatic habitats. I also characterized the wave and turbulent components of fluctuating flow parameters at 4 sites and over a variety of temporal scales (48 hrs to 35 days) in intertidal habitats in Wassaw Sound, GA using six acoustic Doppler velocimeters (ADVs) in an effort to understand the spatial and temporal variability in fluctuating flow parameters that could influence ecological interactions. Wave components of fluctuating flow parameters varied by site and tidal type, making generalizations about the influence of wave components of fluctuating flow parameters at the estuary scale impossible. Wind speed correlates well with the wave components of fluctuating flow parameters using data from more than 9 complete tidal cycles,

whereas tidal range correlates well with all fluctuating flow parameters (except turbulence intensity) using data from more than 4 complete tidal cycles. The strength of correlations is site- and time-scale-dependent. Although wind speed and tidal range may be good predictors of values of fluctuating flow parameters, I recommend that they only be applied to time scales similar to those used in ecological experiments.

6.2 Introduction

The ability of predators to locate food can affect the abundance and distribution of prey populations. This is especially important in estuary systems along the East coast of the United States where blue crabs (Hines *et al.* 1990) and whelks (Carriker 1951) are two key odor-mediated predators on infaunal bivalve populations. Odor-mediated predators extract information from chemical cues that are transported and shaped by the flowing environment to locate resources. Their ability to do this efficiently determines their impact on prey populations in natural environments. Species-specific predation rates by these predators appear to be dependent on spatially- and temporally-specific local flow conditions, which vary with site and bulk flow characteristics (Smee *et al.* 2010, also see Chapter 5). By combining information about the fluid environment with corresponding biological behavior, informed hypotheses can be formulated as to the spatial and temporal patterns in predation success. By extension, we gain a better understanding of the ability of predators to control and shape prey populations.

To date, information about turbulent flow characteristics in near-bed estuarine habitats has been relegated to short sampling time periods, irrelevant locations above the substrate (i.e. not in the near-bed environments where odor-mediated predators forage), arbitrarily-selected sampling time periods, and few study sites. A handful of recent studies have provide limited data, however (Smee *et al.* 2008; Ferner *et al.* 2009; Smee *et al.* 2010; Berry *et al.* 2011, see Chapter 5). Some studies have investigated energy and momentum transport processes in estuaries, but have failed to adequately account for wave contributions to fluctuating velocity (although see Shaw & Trowbridge 2001 and Bricker & Monismith 2007) or spatial and temporal differences in the wave component of fluctuating flow parameters throughout estuary systems. To my knowledge, no study of the flow environment of the intertidal zone of small-scale estuary systems has examined the wave components of fluctuating flow parameters (turbulent kinetic energy and covariance) over large spatial and temporal scales (although see Berry *et al.* (2011) for wave contributions during single tidal cycles). Hence, information about turbulent flows experienced by benthic foragers is largely unknown, preventing adequate development of hypotheses as to how physical parameters may impact interspecific interactions over temporal and spatial scales that are relevant to odor-mediated predator and prey populations.

Turbulence in the water column can be mediated by tidal forcing (Grant *et al.* 1984), the presence of whitecapping and breaking waves caused by wind forcing (Terray *et al.* 1996), and waves transferring energy and momentum to the water column through orbital motion (discussed in Jones & Monismith (2008)). Wave motion and tidal forcing enhance the transport of energy and momentum to the near-bed environment by increasing the thickness of the wind-affected surface layer relative to the bed stress log layer (Jones & Monismith 2008) and enhancing the dissipation rate of turbulent kinetic energy from surface layers toward the near-bed environment (Agrawal *et al.* 1992).

Despite the importance of flow conditions in shaping interactions between organisms, many ecologists fail to measure water flow during field experiments or reproduce natural flow regimes in laboratory trials (Zimmer & Zimmer 2008). This prevents an understanding of how ecological interactions may vary naturally under different hydrodynamic conditions and inhibits the scope of processes used to understand patterns in data. Adequately measuring and reproducing natural hydrodynamic conditions (flow velocity and turbulence) requires expensive equipment and technological expertise that are not normally included in the typical ecologists' repertoire. It would be helpful for ecologists if adequate surrogate data that were easily collected and interpreted could be identified that would serve as a proxy for estimating flow velocity and turbulence characteristics in natural settings.

Wind speed and tidal range may be good candidates for surrogate data to make predictions about hydrodynamic environments, as these two parameters are known to have large influences on wave motion and bulk velocity characteristics, respectively. My objective is to understand how wind and tidal forcing influence the distribution of wave and turbulent components of fluctuating flow parameters between sites and at large temporal scales to assess the predictive ability of these parameters in estimating velocity and turbulence characteristics. Information about the wave and turbulent components of the fluctuating kinetic energy and covariance also can help make predictions as to the distribution and temporal patterns of wind and tidal forcing effects on these fluctuating flow parameters and ultimately, their influence on odor-mediated predator-prey interactions. If wind speed and tidal range correlate well with the wave and turbulent components of fluctuating flow parameters, ecologists should be able to use them to supplement difficult measurements of flow when generating hypotheses and explaining patterns of interactions that are mediated by hydrodynamic processes.

I measured velocity-time series at multiple sites in Wassaw Sound, GA over a variety of different tidal forcing strengths (neap, normal, and spring tides) and naturally occurring wind speeds. I calculated the wave components of fluctuating kinetic energy and Reynolds shear stress as a function of site and tidal type. I also calculated correlation coefficients for comparisons of values of fluctuating flow parameters and wind speed or tidal range to assess their predictive capacities. Based on prior knowledge of this system (Berry 2009; Berry *et al.* 2011), I predict that the wave components of fluctuating kinetic energy and covariance will be greater in sites that have larger fetch (allowing generation of wind waves) and during neap tides when the transfer of energy and momentum generated from wave motion can penetrate further into the near-bed environment because of shallower water depth. I also expect to see large correlation coefficients for comparisons between tidal range and flow velocity and between wind speed and the wave component of fluctuating flow parameters (kinetic energy and covariance). I deployed multiple acoustic Doppler velocimeters (ADVs) in four sites over a three month period to assess these hypotheses.

6.3 Methods

6.3.1 Data Collection

Time-series of flow velocity were collected from June to August 2010 at four sites in Wassaw Sound, GA and its tributaries: Dead Man's Hammock (DMH), Skidaway Narrows (SN), across from Priest Landing (APL), and Priest Landing (PL) (comparison site) (Figure 6.1). Sites are similarly characterized by semi-diurnal tidal flow with ranges of 2 to 3 m. All sites are exposed to largely unidirectional flows during ebb and flood tides. Sites all contain substrates of mud and fine sand, are bordered by marsh grass (*Spartina alterniflora*) or oyster reefs (*Crassostrea virginica*), and range in salinity from 20 to 28 ppt (Smee *et al.* 2010).

Four acoustic Doppler velocimeters (ADVs) (NortekUSA Vector) were simultaneously placed within each site, with each site measured over different dates during the sampling period. Instruments were placed 1 m, 5 m, and 10 m from a reference instrument within each site. Concurrent to measurements taken within each site, two ADVs were placed 1 m apart at the Priest Landing comparison site. Flow velocity at the Priest Landing comparison site was also recorded for an additional 35 days, independent of the other three sites. All instruments were placed parallel to the water

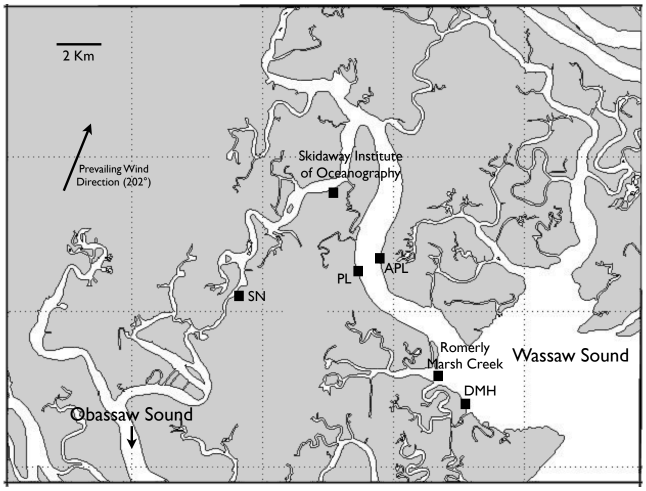

Figure 6.1: Map of Wassaw Sound, Georgia where instruments were deployed June-August 2010. DMH = Dead Man's Hammock, PL = Priest Landing, APL = Across from Priest Landing, SN = Skidaway Narrows. Also shown are the locations of the Skidaway Institute of Oceanography (site of wind speed measurement) and Romerly Marsh Creek (site of tidal range data).

line at the mean low tide level. The sampling volume of each instrument was approximately 0.10 m above the substrate. This experimental deployment was repeated for each of the four sites and for each of three tidal types (spring tide [SP], neap tide [NP], and normal tide [NL]).

All ADVs recorded three components of velocity, pressure, signal-to-noise ratios, and correlation coefficients over 4 consecutive complete tidal cycles (from low tide to subsequent low tide) for each tidal type deployment. Instruments were placed in the field such that the x-velocity was predominately the along-stream component and the direction upwards from the substrate was represented by a positive z-velocity. During data analysis, the x- and y-velocity components were rotated to maximize the magnitude of the x-velocity component and to ensure that the x-velocity was positive for flood tide and negative for ebb tide. Data were collected continuously at 16 Hz during 5 minute bursts, which were separated by 10 minutes.

Tidal ranges were obtained during the sampling period for Romerly Marsh Creek (Figure 6.1) from published tables (http://www.tidesandcurrents.noaa.gov). Tidal ranges from only one location were used because published data from Romerly Marsh Creek are highly similar to other sites in Wassaw Sound and its tributaries. Average and maximum wind speeds were obtained from the Skidaway Institute of Oceanography weather station (Figure 6.1) at 5 minute intervals (corresponding to the 5 minute bursts of recorded water velocity time-series).

6.3.2 Data Analysis

6.3.2.1 Data Filtering

ADV data were filtered to remove erroneous samples by discarding individual bursts if the mean correlation coefficient calculated was less than 70 % and if bursts contained more than 500 consecutive points whose mean correlation coefficients were less than 70%. I also filtered out erroneous data that manifested as "spikes" because of aliasing of the Doppler signal. I used the phase filtering method of Goring & Nikora (2002) to identify, remove and replace spikes throughout my data set (see Chapter 5 for more detailed information about data filtering).

6.3.2.2 Identification of the Wave Component of Fluctuating Flow Paramters

The presence of wind waves in shallow water estuaries results in wave motion contributions to fluctuating flow parameters. Fluctuations from waves also can contribute to the turbulence signature when sensors are aligned improperly with the principal axis or when there is sloping bed geometry (Grant *et al.* 1984; Trowbridge 1998). The contribution of wave motion to fluctuating flow parameters should not be considered turbulence because of their low frequency ranges, periodicity, and orbital motion.

I used the coherence between the velocity and pressure measurements (as seen in Benilov & Filyushkin (1970)) to identify and separate the wave component of the fluctuating kinetic energy and the covariance using the methodology developed by Berry *et al.* (2011). Fluctuations in the velocity components due to wave motions are coherent to simultaneously measured fluctuations in the water surface level (recorded as pressure in my data; Benilov & Filyushkin 1970). Correspondingly, the component of the fluctuating velocity that is not coherent with the fluctuating pressure can be attributed to turbulence. The following is a brief description of the calculations involved in separating the wave component of the covariance (and analogously the variance of each velocity component to separate the wave component of the fluctuating kinetic energy). See Chapter 5 and Berry *et al.* (2011) for a more thorough description of the calculations.

Instantaneous velocity can be decomposed into the mean component $\overline{u}$, the wave motion component $\tilde{u}$, and the turbulent fluctuation component u':

$$u = \overline{u} + \tilde{u} + u' \tag{6.1}$$

Trends due to rising or falling tides were first removed from the velocity and pressure time series (each 5 minute burst) using a linear trend removal (Bendat & Piersol 2010), and the mean was subtracted to obtain the fluctuating component of velocity and pressure. The notation employed below imples that the mean component is therefore zero. The coherence function for the u component of velocity and pressure (p) was then calculated as a function of frequency (following the methodology of Benilov & Filyushkin (1970)):

$$\gamma^2(\omega) = \frac{S_{up}(\omega)S^*_{up}(\omega)}{S_{uu}(\omega)S_{pp}(\omega)} \tag{6.2}$$

where S_{up} is the cross-spectral density (CSD) of u and p, S_{uu} and S_{pp} are power spectral density (PSD) functions, ω is frequency, and $*$ represents the complex conjugate.

The PSD for the turbulent portion of the signal was then calculated (assuming that the coherence between velocity and pressure is due to wave influence) using:

$$S_{u'u'}(\omega) = [1 - \gamma^2(\omega)]S_{uu}(\omega) \tag{6.3}$$

which was then used to calculate the magnitude of the turbulent velocity fluctuation $|U_j'|$ as a function of discrete frequency (denoted with index j) via:

$$S_{u'u'j} = \frac{1}{d\omega}|U_j'|^2 \tag{6.4}$$

The above calculations were repeated for the w component of velocity and pressure. The Reynolds shear stress was then calculated by incorporating the phases of each velocity component with the magnitude of the turbulent velocity fluctuation. Velocity components can be expressed using phasor notation of the Fourier coefficient according to:

$$U_j = |U_j|e^{i\angle U_j} \text{ and } W_j = |W_j|e^{i\angle W_j} \tag{6.5}$$

where the phases are defined by:

$$\angle U_j = arctan\left[\frac{Im(U_j)}{Re(U_j)}\right] \text{ and } \angle W_j = arctan\left[\frac{Im(W_j)}{Re(W_j)}\right] \tag{6.6}$$

Using this the CSD can be expressed as:

$$U_j^* W_j = |U_j||W_j|e^{j(\angle W_j - \angle U_j)} = |U_j||W_j|(\cos(\angle W_j - \angle U_j) - i\sin(\angle W_j - \angle U_j)) \tag{6.7}$$

and the Reynolds shear stress can be calculated using:

$$\overline{u'w'} = \sum_j U_j'^* W_j' = \sum_j |U_j'||W_j'|\cos(\angle W_j - \angle U_j) \tag{6.8}$$

where $|U_j'|$ and $|W_j'|$ are calculated from Equation (6.4) and $\angle U_j$ and $\angle W_j$ are calculated from Equation (6.6).

I used this methodology to calculate the wave component of the fluctuating kinetic energy and covariance (KE_{wave} and $|\overline{\tilde{u}\tilde{w}}|$, respectively) for all bursts in each data set except the first two and last two bursts of each tidal cycle for data sets collected at the Priest Landing comparison site. Two downward facing, fixed stem ADVs at the Priest Landing site were mounted such that they were able to record velocity data while the pressure sensor was not immersed at the beginning and end of each tidal cycle, which prevented the calculation of coherence between velocity and pressure for these bursts.

Mean total fluctuating characteristics also were calculated for each burst. The parameters calculated are as follows:

$$Total\ Fluctuating\ KE = 0.5(\overline{(u-\overline{u})^2} + \overline{(v-\overline{v})^2} + \overline{(w-\overline{w})^2}) \tag{6.9}$$

$$TKE = 0.5(\overline{(u')^2} + \overline{(v')^2} + \overline{(w')^2}) \tag{6.10}$$

$$KE_{wave} = Fluctuating\ KE - TKE \tag{6.11}$$

$$Total\ Fluctuating\ Covariance = \overline{(u-\overline{u})(w-\overline{w})} \tag{6.12}$$

$$Reynolds\ Shear\ Stress = \overline{u'w'} \tag{6.13}$$

$$\overline{\tilde{u}\tilde{w}} = \overline{(u-\overline{u})(w-\overline{w})} - \overline{u'w'} \tag{6.14}$$

$$Turbulence\ Intensity\ (TI) = \frac{\sqrt{\overline{(u')^2} + \overline{(v')^2} + \overline{(w')^2}}}{\sqrt{\overline{u}^2 + \overline{v}^2 + \overline{w}^2}} * 100 \tag{6.15}$$

I also calculated the percent contribution of the respective wave contributions to total fluctuating KE and total fluctuating covariance.

6.3.3 Statistical Analysis

To determine the influence of site and tidal type (neap, normal, and spring tide; and any interactions) on values of wave components of fluctuating flow parameters (KE_{wave} and $|\overline{\tilde{u}\tilde{w}}|$) and their percent contribution to the total, I utilized a two-way analysis of variance (ANOVA), which is fairly robust to issues of non-normality (Zar 1999), with site and tidal type as factors. I also utilized non-parametric Kruskal-Wallis tests to confirm significance of one-way comparisons because I was unable to achieve normality via transformation for my fluctuating flow parameters. This was done for each fluctuating flow parameter separately (KE_{wave}, $|\overline{\tilde{u}\tilde{w}}|$, % KE_{wave}, and % $|\overline{\tilde{u}\tilde{w}}|$) using burst-averaged data from the reference instrument at each site and for each deployment period described above (approximately 140 bursts).

I calculated correlation coefficients for comparisons between maximum wind speed and values of fluctuating flow parameters ($|\overline{u}|$, TKE, KE_{wave}, $|\overline{u'w'}|$, and $|\overline{\tilde{u}\tilde{w}}|$) to examine the relationship between wind speed and values of fluctuating flow parameters by using a non-parametric Spearman correlation for each site separately, including all tidal types. I used burst-averaged data from each site-specific reference instrument to calculate correlation coefficients (approximately 140 bursts). A Spearman correlation also was used to determine if site-specific relationships were similar to comparisons using data from all four sites.

The relationship between wind speed and values of fluctuating flow parameters as a function of sampling duration was further elucidated using long term time-series data from Priest Landing. I assessed comparisons between wind speed (average and maximum) and values of fluctuating flow parameters ($|\overline{u}|$, TKE, KE_{wave}, $|\overline{u'w'}|$, $|\overline{\tilde{u}\tilde{w}}|$, and TI) by calculating correlation coefficients (Spearman correlation) using tidal-cycle-averaged data for each variable. The number of tidal cycles used to calculate correlation coefficients ranged from 4 to 79. Data from individual tidal cycles was sequenced randomly to achieve the desired number of tidal cycles for calculation.

I also assessed comparisons between tidal range and values of fluctuating flow parameters at Priest Landing ($|\overline{u}|$, TKE, KE_{wave}, $|\overline{u'w'}|$, $|\overline{\tilde{u}\tilde{w}}|$, and TI) by calculating correlation coefficients (Spearman correlation). I utilized tidal-cycle-averaged data for all fluctuating flow parameters, with the range of tidal cycles used to calculate correlation coefficients. Again, the number of tidal cycles used to calculate correlation coefficients ranged from 4 to 79 and the sequence was random. Tidal range was calculated by taking the difference between the height above mean low water for the high tide and the average of the height above mean low water for the previous and subsequent low tides using published records (see above).

I also investigated the impact of tidal type and flow direction (flood and ebb) on values of turbulent flow parameters ($|\overline{u}|$, TKE, and $|\overline{u'w'}|$), because there seemed to be intrinsic asymmetries in values of fluctuating flow parameters between flood and ebb tides. The effect of tidal type and flow direction on values of fluctuating flow parameters was determined using a two-way ANOVA with tidal type and tide direction as factors. Ensemble-averaged values corresponding to flood and ebb tide from the PL site were used for the analysis.

6.4 Results

6.4.1 Velocity Data Associated with Wave Motions

There was a significant effect of site ($F_{3,1474} = 67.79, P < 0.001$; Figure 6.2) on KE_{wave}, with the greatest values of KE_{wave} at the DMH site and the smallest at the SN site. There also was a significant effect of tidal type ($F_{2,1474} = 9.25, P < 0.001$) and interaction between site and tidal type ($F_{6,1474} = 11.37, P < 0.001$), with greater values of KE_{wave} during neap and spring tide at all sites except for the PL site which had the greatest values of KE_{wave} during neap tide only (Figure 6.2). Non-parametric Kruskal-Wallis tests (site: $H = 745.72$, *df* $= 3$, $P < 0.001$; tide: $H = 28.58$, *df* $= 2$, $P < 0.001$) confirmed significance of one-way interactions. The percent wave contribution to total fluctuating KE showed similar patterns to the dimensional values of KE_{wave}. There was a significant effect of site ($F_{3,1474} = 588.38, P < 0.001$) and tidal type ($F_{2,1474} = 16.03, P < 0.001$) on the percent wave contribution to total fluctuating KE (Figure 6.2). The wave contribution to total fluctuating KE was greatest for the DMH site and smallest for the SN site. Overall, the greatest wave contribution to total fluctuating KE was during neap tide, but there was a significant interaction between site and tidal type ($F_{6,1474} = 10.67, P < 0.001$). Both the APL and DMH sites had greater wave contributions to total fluctuating KE during neap and spring tide, but the PL site had the smallest contributions during spring tide and there were negligible differences in wave contributions to total fluctuating KE between tidal types at the SN site (Figure 6.2). Non-parametric Kruskal-Wallis tests (site: $H = 785.66$, $df = 3$, $P < 0.001$; tide: $H = 6.58$, $df = 2$, $P = 0.037$) again confirmed significance of one-way analyses.

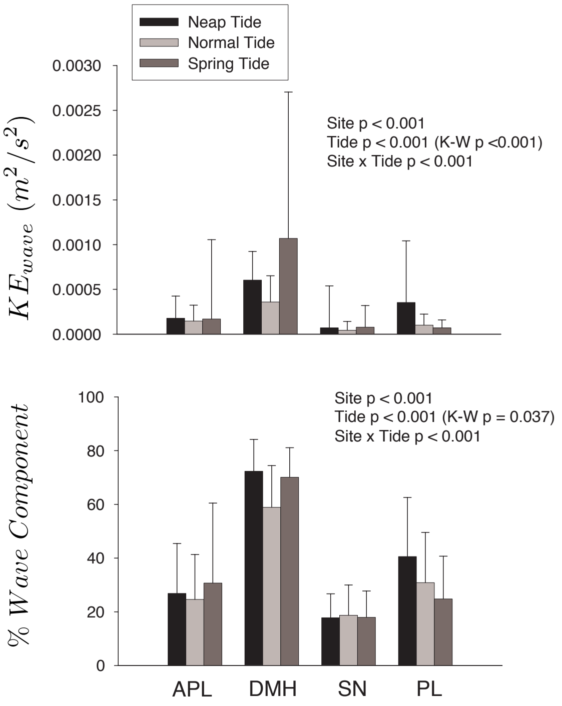

Figure 6.2: Ensemble average of burst-averaged values of KE_{wave} (m^2/s^2; top) and percentage of the total fluctuating kinetic energy attributable to the wave component (bottom). Error bars represent one standard deviation. The number of bursts included was: 149, 145, and 137 (APL; neap tide, normal tide, spring tide, respectively); 129, 144, 143 (DMH; neap, normal, spring, respectively); 141, 173, 126 (SN; neap, normal, spring, respectively); 128, 134, 136 (PL; neap, normal, spring, respectively), where APL = Across from Priest Landing, DMH = Dead Man's Hammock, SN = Skidaway Narrows, and PL = Priest Landing. Statistical significance was determined using a two-way ANOVA, with confirmation of one-way comparisons shown using a Kruskal-Wallis test (K-W).

Values of $|\widetilde{u}\widetilde{w}|$ showed similar patterns to KE_{wave} based on site and tidal type relationships: there was a significant effect of site ($F_{3,1367} = 98.94, P = 0.001$) and tidal type ($F_{2,1367} = 37.36, P < 0.001$) on values of $|\overline{\tilde{u}\tilde{w}}|$ (Figure 6.3). There also was a significant interaction between site and tidal type ($F_{6,1367} = 79.90, P < 0.001$). Non-parametric Kruskal-Wallis tests (site: $H = 287.69$, $df = 3$, $P < 0.001$; tide: $H = 8.55$, $df = 2$, $P = 0.017$) confirmed significance of one-way analyses. The SN site had the smallest values of $|\overline{\tilde{u}\tilde{w}}|$, and values of $|\overline{\tilde{u}\tilde{w}}|$ were greater during neap and spring tide at all sites except at the APL site where $|\overline{\tilde{u}\tilde{w}}|$ was greater during the normal tide (Figure 6.3). The percent wave contribution to total fluctuating covariance also had similar patterns to the wave contribution to total fluctuating KE based on site and tidal type. There was a significant effect of site ($F_{3,1367} = 86.08, P < 0.001$) on the wave contribution to total fluctuating covariance with the greatest percentage of wave contribution at the DMH site (Figure 6.3). Significance of this one-way interaction was confirmed using a Kruskal-Wallis test ($H = 227.08$, $df = 3$, $P < 0.001$). There also was a significant effect of tide ($F_{2,1367} = 3.52, P < 0.03$) on the percent wave contribution to total fluctuating covariance based on a two-way ANOVA, but this was not confirmed using a one-way non-parametric Kruskal-Wallis test ($H = 2.00$, $df = 2$, $P = 0.367$). There was no significant site by tidal type interaction ($F_{6,1367} = 1.21, P = 0.297$) on the percent wave contribution to total fluctuating covariance.

6.4.2 Correlation of Wind Speed and Fluctuating Flow Parameters

There were significant correlations between burst-averaged values of fluctuating flow parameters and maximum wind speed, but significance was site and parameter specific. Comparisons between values of fluctuating flow parameters and average wind speed resulted in similar relationships between correlation coefficients to those calculated using maximum wind speed, although a lower number of correlation coefficients were statistically significant when using average wind speed for comparisons. Therefore, I chose to report results only for comparisons using maximum wind speed.

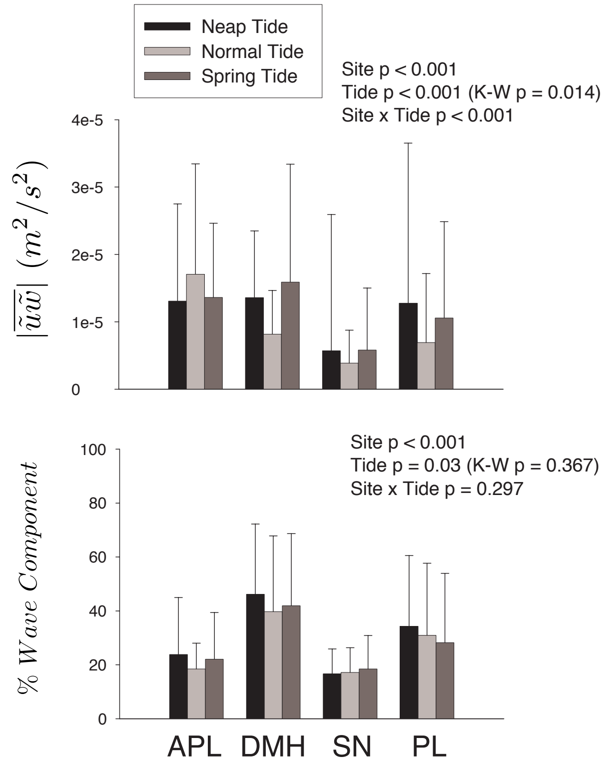

Figure 6.3: Ensemble average of burst-averaged values of $|\overline{\tilde{u}\tilde{w}}|$ (m^2/s^2; top) and the percentage of the total covariance attributable to the wave component (bottom). Error bars represent one standard deviation. The number of bursts included is the same as reported in Figure 6.2. APL = Across from Priest Landing, DMH = Dead Man's Hammock, SN = Skidaway Narrows, and PL = Priest Landing. Statistical significance was determined using a two-way ANOVA, with confirmation of one-way comparisons shown using a Kruskal-Wallis test (K-W).

There were significant correlations between values of TKE, KE_{wave}, and $|\overline{\tilde{u}\tilde{w}}|$ with maximum wind speed at the APL site (Table 6.1). There were similar patterns of significant correlations at the DMH site as at the APL site, with the exception of the correlation between $|\overline{\tilde{u}\tilde{w}}|$ and maximum wind speed, which was not significant. There were no significant correlations between values of any fluctuating flow parameter and maximum wind speed at the PL site, although the correlation coefficient for the comparison between KE_{wave} and maximum wind speed was only marginally

Table 6.1: Correlation coefficients for comparisons between maximum wind speed and values of fluctuating flow parameters. Data used for comparisons consist of burst averaged values for individual fluctuating flow parameters collected during all tidal type deployments. Wind speed data were acquired from the Skidaway Institute of Oceanography weather station. "Burst No." indicates the number of bursts that were used to calculate correlation coefficients. * indicates correlation coefficients significantly different from zero. Data sets are labeled using site names; APL = Across from Priest Landing, DMH = Dead Man's Hammock, SN = Skidaway Narrows, PL = Priest Landing.

Site	Burst. No	$\|\overline{u}\|$	TKE	KE_{wave}	$\|\overline{u'w'}\|$	$\|\overline{\tilde{u}\tilde{w}}\|$
APL	430	0.07	0.13*	0.30*	-0.03	0.15*
DMH	287	0.12	0.15*	0.12*	0.09	-0.03
PL	280	-0.02	0.01	0.10	-0.003	0.05
SN	325	-0.15*	-0.17*	-0.08	-0.14*	-0.14*
All	1322	0.03	0.03	0.08*	-0.01	-0.01

insignificant. There were significant correlations between all fluctuating flow parameters (except KE_{wave}) and maximum wind speed at the SN site, but as maximum wind speed increased, values of the fluctuating flow parameters decreased (i.e. correlation coefficients were negative). This relationship cannot be explained by errors in the raw or filtered data. There was a significant correlation for the comparison of KE_{wave} with maximum wind speed (Table 6.1) when data from all sites were combined (APL, DMH, SN, and PL).

Long-term time-series indicate a close relationship between values of fluctuating flow parameters and maximum wind speed at the PL site (Figure 6.4). To quantify the apparent relationship, the correlation coefficient was calculated as a function of the number of tidal cycles. Correlations between wind speed (maximum and average) and $|\overline{\tilde{u}\tilde{w}}|$ at the PL site were significantly different from zero for correlations using sample sizes greater than 9 tidal cycles (Figure 6.5). More than 43 and 55 tidal cycles were needed to achieve correlation coefficients significantly different from zero for correlations between KE_{wave} and maximum and average wind speed, respectively. Values of $|\overline{u'w'}|$ and TI were never significantly correlated with maximum or average wind speed. Marginally significant correlations between $|\overline{u}|$ and maximum or average wind speed were seen only comparisons using data from more than 55 tidal cycles (Figure 6.5).

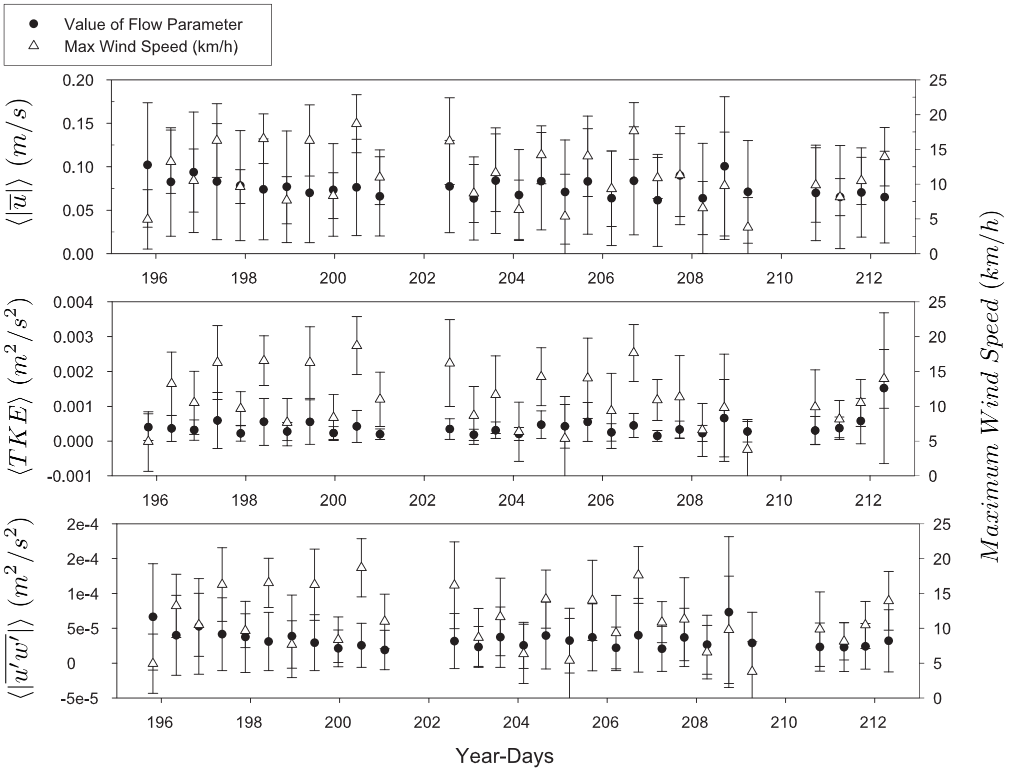

Figure 6.4: Long-term time-series of $\langle|\overline{u}|\rangle$ (top), $\langle TKE\rangle$ (middle), and $\langle|\overline{u'w'}|\rangle$ (bottom) at Priest Landing (filled circles). Maximum wind speed data (open triangles) are overlaid on each turbulent flow parameter to visually show the correlation. Values represent the tidal-cycle-average for all turbulent flow parameters and maximum wind speed (as denoted by angle brackets). Wind speed data were obtained from the Skidaway Institute of Oceanography weather station (see Figure 6.1). Error bars for turbulent flow parameters and maximum wind speed represent one standard deviation.

6.4.3 Correlation of Tidal Range and Fluctuating Flow Parameters

Long-term time-series at Priest Landing indicate the tight relationship between values of fluctuating flow parameters and tidal range (Figure 6.6). Correlations

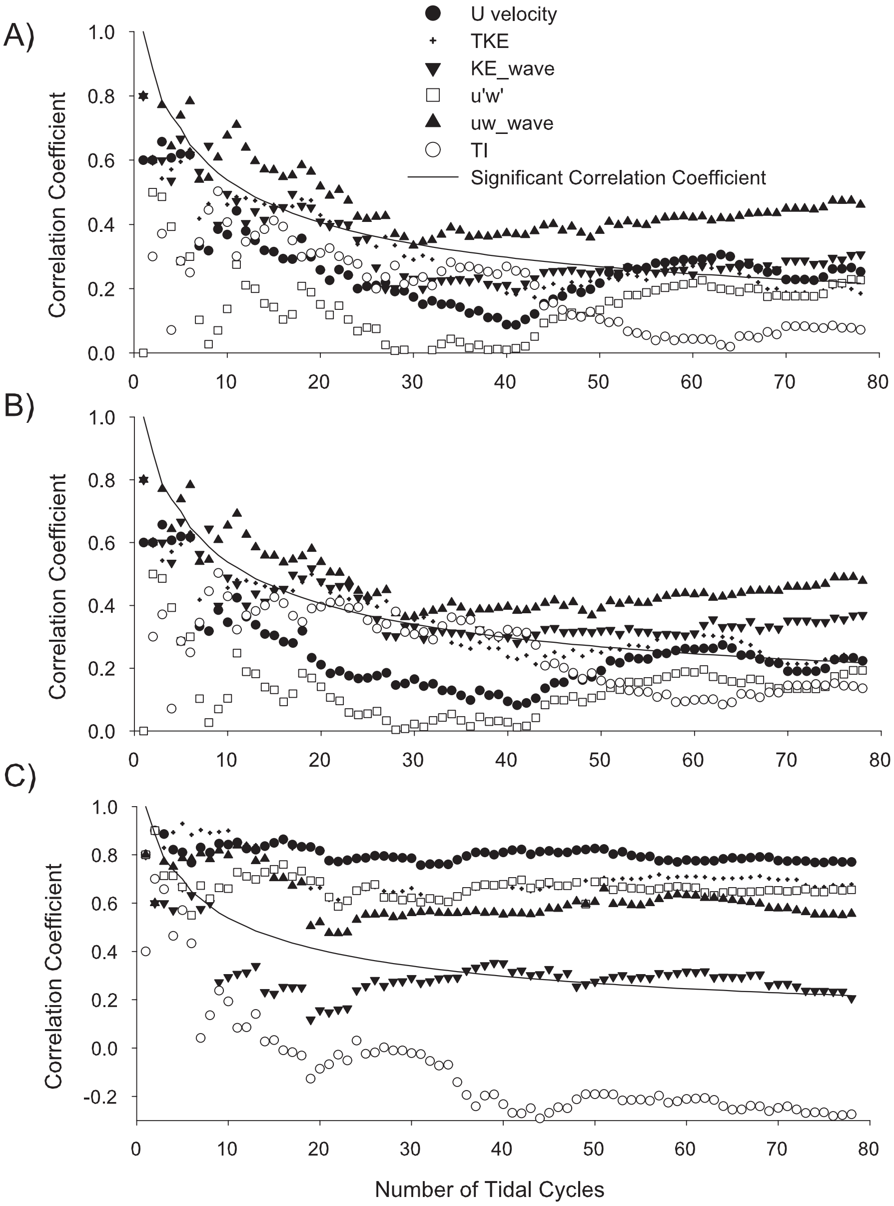

Figure 6.5: Correlation coefficients with (A) maximum wind speed, (B) average wind speed, and (C) tidal range as a function of the amount of data (number of tidal cycles) included in the calculation. Correlation coefficients shown for comparisons between $|\overline{u}|$ (closed circles), TKE (plus), KE_{wave} (closed inverted triangle), $|\overline{u'w'}|$ (open square), $|\overline{\tilde{u}\tilde{w}}|$ (closed triangle), or TI (open circle). Minimum values of significant correlation coefficients are shown by the solid line. Correlation coefficients above this line are significantly different from zero.

between $|\overline{u}|$, TKE, and $|\overline{\tilde{u}\tilde{w}}|$ and tidal range at the Priest Landing site were all significantly different from zero using data from more than 4 tidal cycles (Figure 6.5). Correlations between $|\overline{u'w'}|$ and tidal range were significantly different from zero using data from more than 9 tidal cycles. Correlations between KE_{wave} and tidal range were marginally significant using data from more than 37 tidal cycles. Values of TI were never significantly correlated with tidal range.

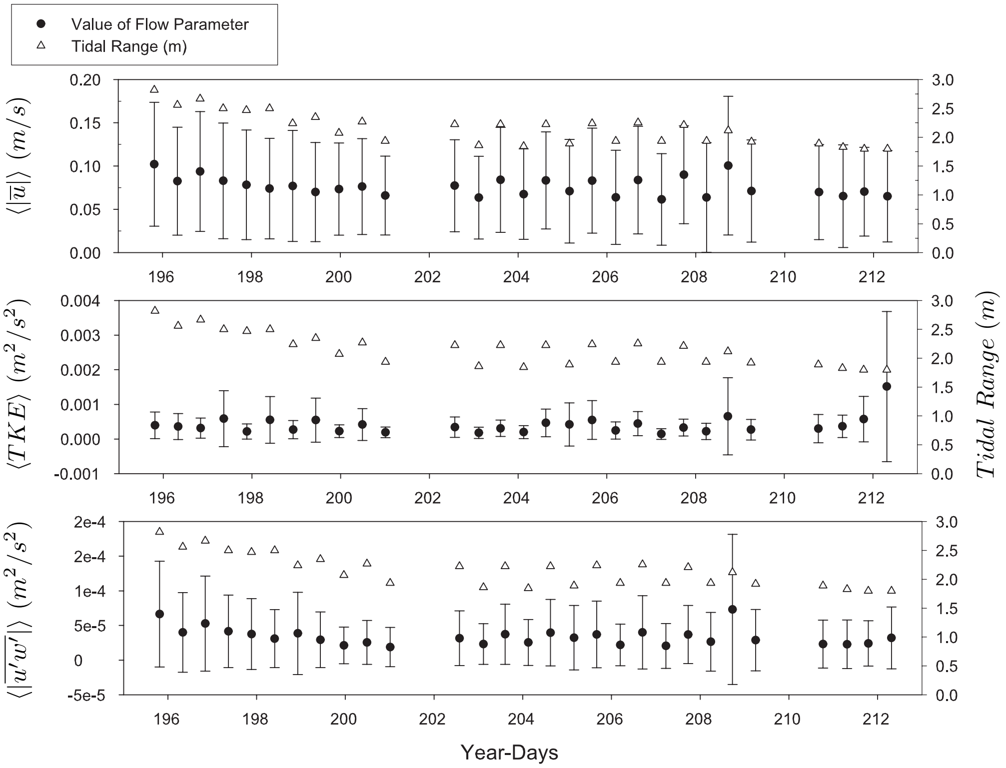

Figure 6.6: Long-term time-series of $\langle|\overline{u}|\rangle$ (top), $\langle TKE\rangle$ (middle), and $\langle|\overline{u'w'}|\rangle$ (bottom) at Priest Landing (filled circles). Tidal range data (open triangles) are overlaid on each turbulent flow parameter to visually show the correlation. Values represent the tidal-cycle-average for all turbulent flow parameters (as denoted with angle brackets). Tidal range was calculated as the difference between the height above mean low water for the high tide and the average of the height above mean low water for the previous and subsequent low tides. Tidal heights were obtained from published records for Romerly Marsh Creek (see Figure 6.1). Error bars for turbulent flow parameters represent one standard deviation.

Values of $|\overline{u}|$ were greater during spring tides and during ebb tides (Figure 6.7).

There was a significant effect of flood versus ebb tide on values of the $|\overline{u}|$ component at the PL site ($F_{1,18} = 123.36, P < 0.001$), and a marginally insignificant effect of tidal type ($F_{2,18} = 3.20, P = 0.065$). There was not a significant interaction between tidal type and flood/ebb tide status on values of $|\overline{u}|$ ($F_{2,18} = 0.15, P = 0.86$). There was a significant effect of tidal type on TKE ($F_{2,18} = 3.59, P = 0.049$), with greater values of TKE during spring tides (Figure 6.7). There also was a significant effect of flood/ebb tide status on TKE ($F_{1,18} = 6.24, P = 0.022$), but no significant interaction between tidal type and flood/ebb tide status ($F_{2,18} = 1.78, P = 0.19$). Values of $|\overline{u'w'}|$ were greater during ebb tides than during flood tides (Figure 6.7). There was a significant effect of flood/ebb tide status on values of $|\overline{u'w'}|$ ($F_{1,18} = 113.23, P < 0.001$), but no significant effects of tidal type ($F_{2,18} = 0.20, P = 0.82$) or tidal type by flood/ebb tide status interaction on $|\overline{u'w'}|$ ($F_{2,18} =, P = 0.42$). Similar asymmetries were observed in the values of fluctuating flow parameters for all other sites, with greater values during the ebb portion of the tide compared to the flood portion.

6.5 Discussion

6.5.1 Context-specificity of Wave Components of Fluctuating Flow Parameters

Wave contributions to total fluctuating KE and total fluctuating covariance in my study agree well with previous data reported by Berry *et al.* (2011) for the same estuary system. The magnitude of wave components of fluctuating turbulent parameters seems site dependent for data from both studies. Wave contributions to total fluctuating KE at my SN site and the Skidaway River site of Berry *et al.* (2011) were $17 - 19\%$ and $15 - 18\%$, respectively. At my DMH site and the DMH16 site of Berry *et al.* (2011), wave contributions to total fluctuating KE were $59 - 72\%$ and 56%, respectively. Another study in the same estuary system (Ferner *et al.* 2009), estimated the contribution of wave activity to values of fluctuating flow parameters as small, although these results may be accounted for by the relatively simple calculation

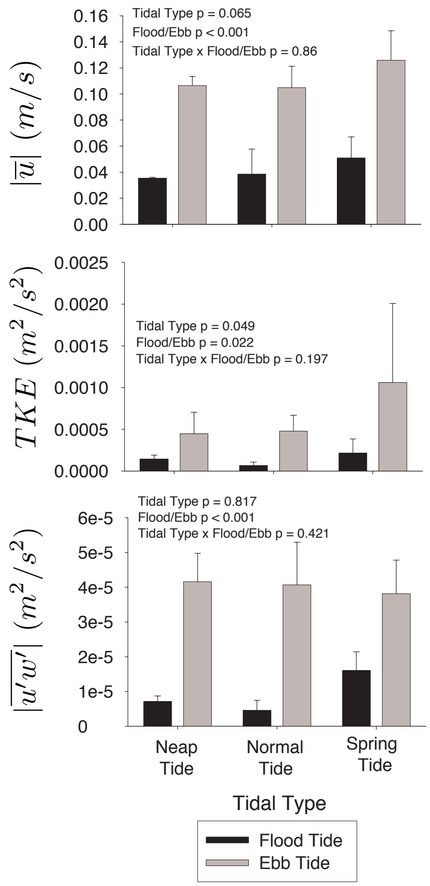

Figure 6.7: Effect of tidal type and ebb or flood flow on values of the turbulent flow parameters at the Priest Landing site. Values of turbulent flow parameters were calculated based on averages for flood and ebb portions of the tidal cycle ($N = 8$ for each tidal type). Error bars indicate one standard deviation. Statistical significance was determined using a two-way ANOVA.

of wave contributions using the root mean square of wave amplitude as compared to the spectral-based method employed in the current study. Studies focusing on wave contributions to fluctuating flow parameters primarily focus on decomposition techniques (Trowbridge 1998; Shaw & Trowbridge 2001; Bricker & Monismith 2007) and lack discussion of the distribution of wave contributions to values of turbulent flow parameters in different locations or systems, hence preventing comparisons with my study. In the shallow intertidal environments that are of interest in the current study, it is essential to account for wave contributions to values of fluctuating flow parameters to fully assess the turbulent environment that odor-mediated predator may be exposed to while foraging.

Unlike the study of Berry *et al.* (2011), which compared the wave contribution to values of total fluctuating KE and total fluctuating covariance in a variety of sites in Wassaw Sound, GA using data from one tidal cycle, I was able to collect information about wave contributions to fluctuating flow parameters at a variety of sites over longer periods (4 tidal cycles) of different tidal types (neap, normal, and spring tides). Spatially-explicit patterns of the wave contributions to the fluctuating flow parameters (Figures 6.2 and 6.3) suggest that wave contributions may be mediated by the area available for the generation of wind waves (i.e., the fetch). For example, the DMH site, which is exposed to Wassaw Sound and has a fetch that ranges from approximately 5 km to 20 km depending on wind direction (Figure 6.1), has the largest measured value of KE_{wave} and $|\overline{\tilde{u}\tilde{w}}|$ (Figures 6.2 and 6.3). The SN site, in comparison, has the smallest values of KE_{wave} and $|\overline{\tilde{u}\tilde{w}}|$ as well as the smallest fetch ($< 1\ km$), regardless of wind direction. Prevailing wind orientation (202.5° for my study; 204° from Powell & Rinard (1998); with 0° indicating winds from due north [Figure 6.1]) supports the idea of greater wave generation at the APL site, but greater exposure to Wassaw Sound may contribute to the influence of waves at the DMH site (Figure 6.1). Waves generally slow down and steepen in shallow environments which allows more transfer of energy from wind to wave motion (Holthuijsen 2007), suggesting that the DMH site also may have a greater influence of wave motion on fluctuating flow parameters because of the extensive mudflats that border the site. Data from Berry *et al.* (2011) support these patterns of wave influence as a function of exposure to Wassaw Sound, but additional sites with significant exposure need to be assessed for comparison.

Differences between sites in the wave contribution to the fluctuating flow parameters may have significant effects on odor-mediated foraging that could not be predicted from examining the turbulent portion of fluctuating flow parameters only. For example, based on values of KE_{wave} (Figure 6.2), blue crabs would have reduced foraging efficiency and success in the more turbulent environments at the DMH site than the other three sites, but based on values of TKE (See Chapter 5), blue crabs would have reduced foraging at the APL and PL sites relative to the DMH and SN sites. Combining values of KE_{wave} and TKE indicate that the DMH site has greater total fluctuating kinetic energy than the other three sites, suggesting that blue crabs may have reduced foraging in the DMH site relative to the other three sites. Whelk foraging success is less affected by turbulence than blue crabs (Powers & Kittinger 2002; Ferner & Weissburg 2005), suggesting that their dominance at the DMH site (Ferner *et al.* 2009) may be related to their maintenance of foraging success relative to blue crabs. The wave component of fluctuating kinetic energy represents a larger portion of the total fluctuating kinetic energy at the DMH site than at the SN site (Figure 6.2), possibly making this site less attractive to foraging blue crabs and more attractive to whelks. Correlations between maximum wind speed and values of wave components of fluctuating flow parameters at different sites over 4 tidal cycles (Table 6.1) support site-specific influences of the wave contributions to values of total fluctuating flow parameters. Thus far, no experiments have been done to explicitly connect wave characteristics with plume dispersion and subsequent impacts on chemically-mediated predator-prey interactions. Additional studies are needed to describe wave impacts on odor plume dispersion to better predict predatory behaviors under conditions of wave motion.

Significant differences in the wave components of fluctuating flow parameters, generally and as a function of tidal type, indicate that large-scale tidal forcing may influence the transfer of energy and momentum to the near-bed environment (Figures 6.2 and 6.3). The magnitude of wind impacts to near-bed environments will increase as water depth decreases (Agrawal *et al.* 1992; Terray *et al.* 1996; Holthuijsen 2007; Jones & Monismith 2008), suggesting that greater wave contributions to values of total fluctuating KE during neap tide (Figure 6.2) may be attributed to water-depth-specific patterns of TKE. Patterns of wave contributions to values of fluctuating flow parameters also suggest greater contributions during spring tides. This may be associated with increases in Reynolds shear stress throughout the water column, which would increase the size of the wave-affected surface layer and increase momentum flux to the near-bed environment (Jones & Monismith 2008).

The larger the contribution of the wave component to total fluctuating flow parameters, the greater influence any patterns in tidal type dependence will have on values of total fluctuating flow parameters. Specific patterns of mean values of total fluctuating flow parameters based on tidal type will be dependent on corresponding patterns in the wave and turbulent components of total fluctuating flow parameters. Values of total fluctuating flow parameters suggest that foraging efficiency and success of odor-mediated predators will vary over a roughly weekly time scale (the scale at which tidal types change). It also suggests that care should be taken when designing sampling schema for ecological experiments; taking into account possible variation in predation rates concurrent to changes in tidal type.

Tidal asymmetries are a common component of flow patterns in small-scale estuaries, but the relationship between values of turbulent flow parameters during flood and ebb tide are not dependent on large-scale tidal forcing in my system (neap, normal, and spring tides) (Figure 6.7). Asymmetries in the $|\overline{u}|$ velocity component, TKE and $|\overline{u'w'}|$ that favor ebb tides (Chanson *et al.* 2005; Collins *et al.* 1998) are usually associated with freshwater input, whereas asymmetries that favor flood tide result from local channel topography that acts to slow down tidal propagation (Le Hir *et al.* 2000). My sites have very little freshwater input (Walker & Tenore 1984) despite very large asymmetries in $|\overline{u}|$ favoring ebb tide. Although there are differences in $|\overline{u}|$ and TKE based on tidal type, there were no changes in the strength and direction of the flood/ebb asymmetry (although this has been seen in other estuary systems [Trevethan *et al.* 2008]). The asymmetry of $|\overline{u}|$ between flood and ebb tide in my system is comparable to that for laboratory experiments challenging blue crabs to locate prey odors under different hydrodynamic conditions (Weissburg & Zimmer-Faust 1993). Weissburg & Zimmer-Faust (1993) observed that an increase in flow velocity by 10.6 cm/s (from 3.8 cm/s to 14.4 cm/s), which closely mirrors differences in my study between $|\overline{u}|$ during flood and ebb tides (Figure 6.7), resulted in a roughly 50% decrease in foraging success (from 22% to 10% success). To my knowledge, no studies have examined differences in predatory success between ebb and flood tidal periods in the field.

6.5.2 Ability to Predict Fluctuating Flow Parameters

Ecologists often have limited or no ability to make detailed flow and turbulence measurements of the environments used in their field studies. Hence, it is useful to make connections between surrogate information, such as tidal range and wind speed, and mean and fluctuating flow parameters. If robust correlations can be identified for the intertidal zone, then surrogate data will provide insightful characterization of the flow environment when detailed assessment is impossible or impractical.

There are site-dependent differences in the predictive capacity of maximum wind speed to estimate values of fluctuating flow parameters (Table 6.1). Wind speed is directly related to the formation of whitecapping waves (Jones & Monismith 2008), which increases orbital motion in the water column and helps transfer energy and momentum to near-bed environments. The relationship between maximum wind speed and values of fluctuating flow parameters is not related to the distance between each site and the location where wind speed was measured (Figure 6.1). The wind speeds recorded during my observation period were relatively small compared to others examining the relationship between wind speed and fluctuating flow parameters (my study = 0 to 8 m/s, Jones & Monismith (2008) = 0 to 15 m/s, Bricker *et al.* (2005)

= 0 to 12 m/s), which decreases the range of my comparisons and the power needed to detect a significant relationship.

Wind speed (both maximum and average) and tidal range are correlated to values of fluctuating flow parameters at the Priest Landing Site, but the amount of data needed (tidal cycles) to achieve significant predictive ability varies as a function of specific fluctuating flow parameter. Wind speed is significantly correlated with $|\overline{\tilde{u}\tilde{w}}|$ when more than 9 tidal cycles are used to calculate correlation coefficients, but KE_{wave} is significantly correlated with maximum wind speed only when more than 43 tidal cycles are used. The majority of fluctuating flow parameters ($|\overline{u}|$, TKE, $|\overline{u'w'}|$, and $|\overline{\tilde{u}\tilde{w}}|$) are significantly correlated with tidal range using data from more than 4 tidal cycles. Values of fluctuating flow parameters track more closely with those of tidal range than wind speed (compare Figures 6.4 and 6.6), thus I suggest that tidal range is a better predicator at some temporal scales than wind speed for values of fluctuating flow parameters.

The predictive capacity of tidal range and wind speed to values of fluctuating flow parameters, should only be used at temporal scales similar to those of ecological experimentation. Most ecological experiments occur over short time scales (e.g. 48 hrs in Smee & Weissburg 2006a, see Chapter 1; although see Ferner *et al.* 2009 for experiments on the scale of 28 days) where correlations between wind speed or tidal range and values of fluctuating flow parameters are not significant. Tidal range seems to be a good predictor of a wide range of fluctuating flow parameters ($|\overline{u}|$, TKE, $|\overline{u'w'}|$, and $|\overline{\tilde{u}\tilde{w}}|$) at time scales greater than 4 complete tidal cycles, whereas wind speed seems to be a good predictor of $|\overline{\tilde{u}\tilde{w}}|$ and KE_{wave} at time scales greater than 9 and 43 complete tidal cycles, respectively.

6.5.3 Summary Comments

Fluctuating flow parameters have the capacity to influence ecological interactions in intertidal near-bed habitats in salt marsh systems, making characterization of the hydrodynamic environment essential in understanding the processes mediating interactions. The predictive capacity of both tidal range and wind speed can give some insight to the mean and fluctuating flow parameters organisms are exposed to, but I suggest that these relationships only be utilized if the temporal scale of ecological experimentation matches that of significant correlations between wind speed or tidal range and fluctuating flow parameters. I also caution that the influence of wind speed on values of fluctuating flow parameters can vary between sites at small temporal scales, suggesting that the outcome of ecological interactions may be site-specific. Additional site-specific information about wind speed, tidal range, and values of fluctuating flow parameters needs to be assessed to determine relationships between these parameters for longer temporal scales throughout estuary systems.

References

Abelson, A., & Denny, M. 1997. Settlement of Marine organisms in flow. *Annual Review of Ecology and Systematics*, **28**, 317–339.

Agrawal, Y. C., Terray, E. A., Donelan, M. A., Hwang, P. A., Williams, A. J., Drennan, W. M., Kahma, K. K., & Kitaigorodskii, S. A. 1992. Enhanced dissipation of kinetic energy beneath surface waves. *Nature*, **359**, 219–220.

Anderson, T. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology*, **82**, 245–257.

Arnold, W. S. 1984. The effect of prey size, predator size, and sediment composition on the rate of predation of the blue-crab, *Callinectes sapidus* Rathbun, on the hard clam *Mercenaria mercenaria* (Linne). *Journal of Experimental Marine Biology and Ecology*, **80**, 207–219.

Aukema, B., & Raffa, K. F. 2004. Does aggregation benefit bark beetles by diluting predation? Links between a group-colonisation strategy and the absence of emergent multiple predator effects. *Ecological Entomology*, **29**, 129–138.

Bell, R. G., Hume, T. M., Dophin, T. J., Green, M. O., & Walters, R. A. 1997. Characterisation of physical environmental factors on an intertidal sandflat, Manukau Harbour, New Zealand. *Journal of Experimental Marine Biology and Ecology*, **216**, 11–31.

Bendat, J. S., & Piersol, A. G. 2010. *Random data: Analysis and measurement procedures. 4^{th} Edition.* Hoboken, N. J.: John Wiley and Sons.

Benilov, A. Y., & Filyushkin, B. N. 1970. Application of methods of linear filtration to an analysis of fluctuations in the surface layer of the sea. *Izv Atmospheric and Ocean Physics*, **6**, 810–819.

Bernstein, C., Kacelnik, A., & Krebs, J. R. 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. *Journal of Animal Ecology*, **60**, 205–255.

Berry, W. A., Webster, D. R., Wilson, M. L., Ferner, M. C., Smee, D. L., & Weissburg, M. J. 2011. Characterization of turbulent hydrodynamics in the intertidal zone of a small estuary with respect to predator-prey chemical signaling. *Submitted.*

Berry, W. A. B. 2009. *A hydrodynamic characterization of tidal ecosystems with respect to predation.* M.Phil. thesis, Georgia Institute of Technology, Atlanta, Georgia.

BERTNESS, M. D., & GROSHOLZ, E. 1985. Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distriution. *Oecologia*, **67**, 192–204.

BERTNESS, M. D., GARRITY, S. D., & LEVINGS, S. C. 1981. Predation pressure and gastropod foraging: a tropical-temperate comparison. *Evolution*, **35**, 995–1007.

BLUNDON, J., & KENNEDY, V. S. 1982. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology*, **65**, 67–81.

BONSALL, M. B., & HASSELL, M. P. 1997. Apparent competition structures ecological assemblages. *Nature*, **338**, 371–373.

BRICKER, J. D., & MONISMITH, S. G. 2007. Spectral wave-turbulence decomposition. *Journal of Atmospheric and Oceanic Technology*, **24**, 1479–1487.

BRICKER, J. D., INAGAKI, S., & MONISMITH, S. G. 2005. Bed drag coefficient variability under wind waves in a tidal estuary. *Journal of Hydraulic Engineering-ASCE*, **131**, 497–508.

BUTMAN, C., GRASSLE, J. P., & WEBB, C. M. 1988. Substrate choices made by marine larvae settling in still water and in a flume flow. *Nature*, **333**, 771–773.

BYERS, J. A. 1996. An encounter rate model of bark beetle populations searching at random for susceptible host trees. *Ecological Modelling*, **91**, 57–66.

CAIN, M. L. 1985. Random search by herbivorous insects: a simulation model. *Ecology*, **66**, 876–888.

CARRIKER, M. R. 1951. Observations on the penetration of tightly closing bivalves by *Busycon* and other predators. *Ecology*, **32**, 73–83.

CHANSON, H., BROWN, R., FERRIS, J., RAMSAY, I., & WARBURTON, K. 2005. Preliminary measurements of turbulence and environmental parameters in a subtropical estuary of Eastern Australia. *Environmental Fluid Mechanics*, **5**, 553–575.

CHANSON, H., TREVETHAN, M., & AOKI, S. 2008. Acoustic Doppler velocimetry (ADV) in small estuary: field experience and signal post-processing. *Flow Measurement and Instrumentation*, **19**, 307–313.

CHARNOV, E. L. 1976. Optimal foraging, marginal value theorem. *Theoretical Population Biology*, **9**, 129–136.

CHIVERS, D. P., & SMITH, R. J. F. 1998. Chemical alarm signalling in aquatic predator-prey systems: a review and prospectus. *Ecoscience*, **5**, 338–352.

Clark, M., Wolcott, T. G., Wolcott, D. L., & Hines, A. H. 1999. Foraging and agonistic activity co-occur in free-ranging blue crabs (*Callinectes sapidus*): observation of animals by ultrasonic telemetry. *Journal of Experimental Marine Biology and Ecology*, **233**, 143–160.

Clark, P. J., & Evans, F. C. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology*, **35**, 445–453.

Coen, L. D., Brumbaugh, R. D., Bushek, D., Grizzle, R., Luckenbach, M. W., Posey, M. H., Powers, S. P., & Tolley, S. G. 2007. Ecosystem services related to oyster restoration. *Marine Ecology Progress Series*, **341**, 303–307.

Coleman, R. A. 2008. Overestimations of food abundance: predator responses to prey aggregation. *Ecology*, **89**, 1777–1783.

Coleman, R. A., Browne, M., & Theobalds, T. 2004. Aggregation as a defense: limpet tenacity changes in response to simulated predator attack. *Ecology*, **85**, 1153–1159.

Collins, M. B., Ke, X., & Gao, S. 1998. Tidally-induced flow structure over intertidal flats. *Estuarine, Coastal and Shelf Science*, **46**, 233–250.

Cote, I. M., & Jelnikar, E. 1999. Predator-induced clumping behaviour in mussels (*Mytilus edulis* Linnaeus). *Journal of Experimental Marine Biology and Ecology*, **235**, 201–211.

Courtney, S. P. 1985. Apparency in coevolving relationships. *OIKOS*, **44**, 91–98.

DeBose, J. L., Lema, S. C., & Nevitt, G. A. 2008. Dimethylsulfoniopropionate as a foraging cue for reef fishes. *Science*, **319**, 1356.

Dittman, A. H., & Quinn, T. P. 1996. Homing in Pacific salmon: mechanisms and ecological basis. *Journal of Experimental Biology*, **199**, 83–91.

Doering, P. H. 1982. Reduction of sea star predation by the burrowing response of the hard clam *Mercenaria mercenaria* (Mollusca: Bivalvia). *Estuaries*, **5**, 310–315.

Dumont, B., Maillard, J. F., & Petit, M. 2000. The effect of the spatial distribution of plant species within the sward on the searching success of sheep when grazing. *Grass and Forage Science*, **55**, 138–145.

Dumont, B., Carrerre, P., & D'Hour, P. 2002. Foraging in patchy grasslands: diet selection by sheep and cattle is affected by the abundance and spatial distribution of preferred species. *Animal Research*, **51**, 367–381.

Edenius, L., Ericsson, G., & Naslund, P. 2002. Selectivity by moose versus the spatial distribution of aspen: a natural experiment. *Ecography*, **25**, 289–294.

Edwards, G. R., Newman, J. A., Parsons, A. J., & Krebs, J. R. 1994. Effects of the scale and spatial distribution of the food resource and animal state on diet selection: an example with sheep. *Journal of Animal Ecology*, **63**, 816–826.

Eggleston, D. B., Lipcius, R. N., & Hines, A. H. 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. *Marine Ecology Progress Series*, **85**, 55–68.

Estes, J. A., & Palmisano, J. F. 1974. Sea otters: their role in structuring nearshore communities. *Science*, **185**, 1058–1060.

Ferner, M. C., & Weissburg, M. J. 2005. Slow moving predatory gastropods track prey odors in fast and turbulent flow. *Journal of Experimental Biology*, **208**, 809–819.

Ferner, M. C., Smee, D. L., & Weissburg, M. J. 2009. Habitat complexity alters lethal and non-lethal olfactory interactions between predators and prey. *Marine Ecology Progress Series*, **374**, 13–22.

Finelli, C. M., Pentcheff, N. D., Zimmer, R. K., & Wethey, D. S. 2000. Physical constraints on ecological processes: a field test of odor-mediated foraging. *Ecology*, **81**, 784–797.

Finn, J. A., & Giller, P. S. 2000. Patch size and colonization patterns: an experimental analysis using north temperate coprophagous dung beetles. *Ecography*, **23**, 315–327.

Fortin, D. 2002. Optimal searching behaviour: the value of sampling information. *Ecological Modelling*, **153**, 279–290.

Fortin, M-J., & Dale, M. R. T. 2005. *Spatial analysis: a guide for ecologists.* Cambridge, New York: Cambridge University Press.

Fretwell, S. D., & Lucas, H. L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheory*, **19**, 16–36.

Fulford, R. S., Breitburg, D. L, Newell, R. I. E., Kemp, W. M., & Luckenbach, M. 2007. Effects of oyster population restoration strategies on phytoplankton biomass in Chesapeake Bay: a flexible modeling approach. *Marine Ecology Progress Series*, **336**, 43–61.

Gilliam, J. F., & Fraser, D. F. 2001. Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. *Ecology*, **82**, 258–273.

Glasser, J. 1979. The role of predation in shaping and maintaining the structure of communities. *American Naturalist*, **113**, 631–641.

Goring, D. G., & Nikora, V. I. 2002. Despiking acoustic Doppler velocimeter data. *Journal of Hydraulic Engineering-ASCE*, **128**, 117–126.

Grabowski, J. H. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology*, **85**, 995–1004.

Grant, W. D., Williams, A. J., & Glenn, S. M. 1984. Bottom stress estimates and their prediction on the Northern California continental shelf during CODE-1: the importance of wave-current interaction. *Journal of Physical Oceanography*, **14**, 506–527.

Grear, J. S., & Schmitz, O. J. 2005. Effects of grouping behavior and predators on the spatial distribution of a forest floor arthropod. *Ecology*, **86**, 960–971.

Green, J. C. 2005. Velocity and turbulence distribution around lotic macrophytes. *Aquatic Ecology*, **39**, 1–10.

Griffiths, C. L., & Richardson, C. A. 2006. Chemically induced predator avoidance behavior in the burrowing bivalve *Macoma Balthica*. *Journal of Experimental Marine Biology and Ecology*, **331**, 91–98.

Hamilton, W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology*, **31**, 295–311.

Hankski, I., & Cambefort, Y. 1991. *Dung Beetle Ecology*. Princeton, New Jersey: Princeton University Press.

Harding, J. M., & Mann, R. 2010. Observations of distribution, size, and sex ratio of mature blue crabs, *Callinectes sapidus*, from Chesapeake Bay tributary in relation to oyster habitat and environmental factors. *Bulletin of Marine Science*, **86**, 75–91.

Heard, S. B. 1998. Resource patch density and larval aggregation in mushroom-breeding flies. *OIKOS*, **81**, 187–195.

Hines, A. H., Haddon, A. M., & Wiechert, L. A. 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Marine Ecology Progress Series*, **67**, 105–126.

Hines, A. H., Wolcott, T. G., Gonzalez-Gurriaran, E., Gonzalez-Escalante, J. L., & Freire, J. 1995. Movement patterns and migrations in crabs: telemetry of juvenile and adult behaviour in *Callinectes sapidus* and *Maja squinado*. *Journal of the Marine Biology Association of the U. K.*, **75**, 27–42.

Hines, A. H., Long, W. C., Terwin, J. R., & Thrush, S. F. 2009. Facilitation, interference, and scale: the spatial distribution of prey patches affects predation rates in an estuarine benthic community. *Marine Ecology Progress Series*, **385**, 127–135.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation by European pine sawfly. *Canadian Entomology*, 293–320.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, **12**, 197–229.

Holt, R. D., & Lawton, J. H. 1994. The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics*, **25**, 495–520.

Holthuijsen, L. H. 2007. *Waves in Oceanic and Coastal Waters*. Cambridge, New York: Cambridge University Press.

Horgan, F. G. 2005. Aggregated distribution of resources creates competition refuges for rainforest dung beetles. *Ecography*, **28**, 603–618.

Huffaker, C. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia*, **27**, 343–383.

Hughes, R. A., & Grabowski, J. H. 2006. Habitat context influences predator interference interactions and the strength of resource partitioning. *Oecologia*, **149**, 256–264.

Imeson, A. C., & Prinsen, H. A. M. 2004. Vegetation patterns as biological indicators for identifying runoff and sediment source and sink areas for semi-arid landscapes in Spain. *Agriculture, Ecosystems and Environment*, **104**, 333–342.

Ioannou, C. C., Tosh, C. R., Neville, L., & Krause, J. 2008. The confusion effect - from neural networks to reduced predation risk. *Behavioral Ecology*, **19**, 126–130.

Irlandi, E. A. 1994. Large- and small-scale effects of habitat structure on rates of predation: how percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia*, **98**, 176–183.

Irlandi, E. A., & Peterson, C. H. 1991. Modification of animal habitat by large plants: mechanisms by which seagrasses influence clam growth. *Oecologia*, **87**, 307–318.

Ishida, S., & Iwasaki, K. 2003. Reduced byssal thread production and movement by the intertidal mussel *Hormomya mutabilis* in response to effluent from predators. *Journal of Ethology*, **21**, 117–122.

Jackson, J. L., Webster, D. R., Rahman, S., & Weissburg, M. J. 2007. Bed roughness effects on boundary-layer turbulence and consequences for odor-tracking behavior of blue crabs (*Callinectes sapidus*). *Limnology and Oceanography*, **52**, 1883–1897.

Jones, N. L., & Monismith, S. G. 2008. The influence of whitecapping waves on the vertical structure of turbulence in a shallow estuarine embayment. *Journal of Physical Oceanography*, **38**, 1563–1580.

Karban, R. 1997. Neighbourhood affects a plant's risk of herbivory and subsequent success. *Ecological entomology*, **22**, 433–439.

Kats, L. B., & Dill, L. M. 1998. The scent of death: chemosensory assessment of predation risk by animals. *Ecoscience*, **5**, 361–394.

Kawanisi, K., & Yokosi, S. 1994. Mean and turbulence characteristics in a tidal river. *Estuarine, Coastal and Shelf Science*, **38**, 447–469.

Keller, T. A., Powell, I., & Weissburg, M. J. 2003. Role of olfactory appendages in chemically mediated orientation of blue crabs. *Marine Ecology Progress Series*, **261**, 217–231.

Klaassen, R. H. G., Nolet, B. A., van Gils, J. A., & Bauer, S. 2006. Optimal movement between patches under incomplete information about the spatial distribution of food items. *Theoretical Population Biology*, **70**, 452–463.

Kobak, J., Kakareko, T., & Poznanska, M. 2010. Changes in attachment strength and aggregation of zebra mussel, *Dreissena polymorpha* in the presence of potential fish predators of various species and size. *Hydrobiologia*, **644**, 195–206.

Kuhlmann, M. L., & Hines, A. H. 2005. Density-dependent predation by blue crabs *Callinectes sapidus* on natural prey populations of infaunal bivalves. *Marine Ecology Progress series*, **295**, 215–228.

Landolt, P., & Phillips, T. W. 1997. Host plant influences on sex pheromone behavior of phytophagous insects. *Annual Review of Entomology*, **42**, 371–391.

Langellotto, G. A., & Denno, R. F. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia*, **139**, 1–10.

Lapointe, V., & Sainte-Marie, B. 1992. Currents, predators, and the aggregation of the gastropod *Buccinum undatum* around bait. *Marine Ecology Progress Series*, **85**, 245–257.

Le Hir, P., Roberts, W., Cazaillet, O., Christie, M., Bassoullet, P., & Bacher, C. 2000. Characterization of intertidal flat hydrodynamics. *Continental Shelf Research*, **20**, 1433–1459.

Lenihan, H. S. 1999. Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. *Ecological Monographs*, **69**, 251–275.

Leonard, L. A., & Luther, M. E. 1995. Flow hydrodynamics in tidal marsh canopies. *Limnology and Oceanography*, **40**, 1474–1484.

Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.

Lima, S. L., & Bednekoff, P. A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist*, **153**, 649–659.

Lima, S. L., & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

MacArthur, R. H., & Pianka, E. R. 1966. On optimal use of a patchy environment. *American Naturalist*, **100**, 603–609.

Mafra-Neto, A., & Carde, R. T. 1994. Fine-scale structure of pheromone plumes modulates upwind orientation of flying moths. *Nature*, **369**, 142–144.

Malhi, Y., & Roman-Cuesta, R. M. 2008. Analysis of lacunarity and scales of spatial homogeneity in IKONOS images of Amazonian tropical forest canopies. *Remote Sensing of Environment*, **112**, 2074–2087.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs*, **65**, 21–74.

Micheli, F. 1996. Predation intensity in estuarine soft bottoms: between habitat comparisons and experimental artifacts. *Marine Ecology Progress Series*, **141**, 295–302.

Micheli, F. 1997. Effects of predator foraging behavior on patterns of prey mortality in marine soft bottoms. *Ecological Monographs*, **67**, 203–224.

Micheli, F., & Peterson, C. H. 1999. Estuarine vegetated habitats as corridors for predator movements. *Conservation Biology*, **13**, 869–881.

Miller, D. C., Muir, C. L., & Hauser, O. A. 2002. Detrimental effects of sedimentation on marine benthos: what can be learned from natural processes and rates? *Ecological Engineering*, **19**, 211–232.

Mitchell, W. A., & Lima, S. L. 2002. Predator-prey shell games: large-scale movement and its implications for decision-making by prey. *OIKOS*, **99**, 249–259.

Monismith, S. G., Koseff, J. R., Thompson, J. K., O'Riordan, C. A., & Nepf, H. M. 1990. A study of model bivalve siphonal currents. *Limnology and Oceanography*, **35**, 680–696.

Moore, P. A., & Grills, J. L. 1999. Chemical orientation to food by the crayfish *Orconectes rusticus*: influence of hydrodynamics. *Animal Behavior*, **58**, 953–963.

Moore, P. A., Scholz, N., & Atema, J. 1991. Chemical orientation of lobsters, *Homarus americanus*, in turbulent odor plumes. *Journal of Chemical Ecology*, **17**, 1293–1307.

Morrell, L. J., & Romey, W. L. 2008. Optimal individual positions within animal groups. *Behavioral Ecology*, **19**, 909–919.

Murlis, J., Elkinton, J. S., & Carde, R. T. 1992. Odor plumes and how insects use them. *Annual Review of Entomology*, **37**, 505–532.

Murlis, J., Willis, M. A., & Carde, R. T. 2000. Spatial and Temporal structures of pheromone plumes in fields and forests. *Physiological Entomology*, **25**, 211–222.

Nakaoka, M. 2000. Nonlethal effects of predators on prey populations: predator-mediated change in bivalve growth. *Ecology*, **81**, 1031–1045.

Nevitt, G. G. 1999. Olfactory foraging in Antarctic seabirds: a species specific attraction to krill odors. *Marine Ecology Progress Series*, **177**, 235–241.

Newell, R. I. E. 2004. Ecosystem influence of natural and cultivated populations of suspension feeding bivalve mollusks: a review. *Journal of Shellfish Research*, **23**, 51–61.

Nonaka, E., & Holme, P. 2007. Agent-based model approach to optimal foraging in heterogeneous landscapes: effects of patch clumpiness. *Ecography*, **30**, 777–788.

Ogden, J. C., Brown, R. A., & Salesky, N. 1973. Grazing by the Echinoid *Diadema antillarus* Philippi: Formation of halos around west Indian patch reefs. *Science*, **182**, 715–717.

Okamura, B. 1986. Group living and the effects of spatial position in aggregations of *Mytilus edulis*. *Oecologia*, **69**, 341–347.

Page, J. L., Dickman, B. D., Webster, D. R., & Weissburg, M. J. 2011. Staying the course: chemical signal spatial properties and concentration mediate cross-stream motion in turbulent plumes. *Journal of Experimental Biology*, **214**, 1513–1522.

Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist*, **100**, 65–75.

Parrish, J. K., & Edelstein-Keshet, L. 1999. Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science*, **284**, 99–101.

Parrish, J. K., Viscido, S. V., & Grunbaum, D. 2002. Self-organized fish schools: an examination of emergent properties. *Biological Bulletin*, **202**, 296–305.

Pawlik, J. R. 1992. Chemical ecology of the settlement of marine benthic invertebrates. *Oceanography and Marine Biology*, **30**, 273–335.

Pawlik, J. R., & Butman, C. A. 1993. Settlement of a marine tube worm as a function of current velocity: Interacting effects of hydrodynamics and behavior. *Limnology and Oceanography*, **38**, 1730–1740.

Peterson, C., & Black, R. 1987. Resource depletion by active suspension feeders on tidal flats: influence of local density and tidal elevation. *Limnology and Oceanography*, **32**, 143–166.

Peterson, C. H., Grabowski, J. H., & Powers, S. P. 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. *Marine Ecology Progress Series*, **264**, 249–264.

Plotnick, R. E., Gardner, R. H., Hargrove, W. W., Prestegaard, K., & Perlmutter, M. 1996. Lacunarity analysis: a general technique for the analysis of spatial patterns. *Physical Review E*, **53**, 5461–5468.

Powell, M. D., & Rinard, S. K. 1998. Marine forecasting at the 1996 Centennial Olympic Games. *Weather and Forecasting*, **13**, 764–782.

Powers, S. P., & Kittinger, J. N. 2002. Hydrodynamic mediation of predator-prey interactions: differential patterns of prey susceptibility and predator success explained by variation in water flow. *Journal of Experimental Marine Biology and Ecology*, **273**, 171–187.

Price, P. W., Bouton, C. E., Gross, P., McPheron, B. A., Thompson, J. M, & Weis, A. E. 1980. Interaction among three trophic levels: influence of plants on interaction between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, **11**, 41–65.

Rand, T. A. 1999. Effects of environmental context on the susceptibility of *Atriplex patula* to attack by herbivorous beetles. *Oecologia*, **121**, 39–46.

Rhorkasse, S., & Atema, J. 2002. Tracking behavior of Buysconinae whelks. *Biological Bulletin*, **203**, 235–236.

Richardson, T. D., & Brown, K. M. 1992. Predation risk and feeding in an intertidal predatory snail. *Journal of Experimental Marine Biology and Ecology*, **163**, 169–182.

Rochette, R., Hamel, J., & Himmelman, J. H. 1994. Foraging strategy of the asteroid *Leptasterias polaris*: role of prey odors, current and feeding status. *Marine Ecology Progress Series*, **106**, 93–100.

Salt, G. W. 1979. A comment on the use of the term emergent properties. *American Naturalist*, **113**, 145–148.

Schmitt, R. J. 1987. Indirect interactions between prey: apparent competition, predator aggregation, and habitat segregation. *Ecology*, **68**, 1887–1897.

Seifan, M., & Kadmon, R. 2006. Indirect effects of cattle grazing on shrub spatial pattern in a mediterranean scrub community. *Basic and Applied Ecology*, **7**, 496–506.

Seitz, R. D., Lipcius, R. N., Hines, A. H., & Eggleston, D. B. 2001. Density dependent predation, habitat variation, and the persistence of marine bivalve prey. *Ecology*, **82**, 2435–2451.

Shaw, W. J., & Trowbridge, J. H. 2001. The direct estimation of near-bottom turbulent fluxes in the presence of energetic wave motions. *Journal of Atmospheric and Oceanic Technology*, **18**, 1540–1557.

Shiono, K., & West, J. R. 1987. Turbulent perturbations of velocity in the Conwy Estuary. *Estuarine, Coastal, and Shelf Science*, **25**, 533–553.

Sih, A., Crowley, P., McPeek, M., Petranka, J., & Strohmeier, K. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics*, **16**, 269–311.

Sih, A., Englund, G., & Wooster, D. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution*, **13**, 350–355.

Smee, D. L., & Weissburg, M. J. 2006a. Claming up: environmental forces diminish the perceptive ability of bivalve prey. *Ecology*, **87**, 1587–1598.

Smee, D. L., & Weissburg, M. J. 2006b. Hard clams (*Mercenaria mercenaria*) evaluate predation risk using chemical signals from predators and injured conspecifics. *Journal of Chemical Ecology*, **32**, 605–619.

Smee, D. L., Ferner, M. C., & Weissburg, M. J. 2008. Alteration of sensory abilities regulates the spatial scale of nonlethal predator effects. *Oecologia*, **156**, 399–409.

Smee, D. L., Ferner, M. C., & Weissburg, M. J. 2010. Hydrodynamic sensory stressors produce nonlinear predation patterns. *Ecology*, **91**, 1391–1400.

Soniat, T. M., Finelli, C. M., & Ruiz, J. T. 2004. Vertical structure and predator refuge mediate oyster reef development and community dynamics. *Journal of Experimental Marine Biology and Ecology*, **310**, 163–182.

Sponaugle, S., & Lawton, P. 1990. Portunid crab predation on juvenile hard clams: effects of substrate type and prey density. *Marine Ecology Progress Series*, **67**, 43–53.

Sweatman, H., & Robertson, D. R. 1994. Grazing halos and predation on juvenile Caribbean surgeonfishes. *Marine Ecology Progress Series*, **111**, 1–6.

Tamburri, M. N., Zimmer-Faust, R. K., & Tamplin, M. L. 1992. Natural sources and properties of chemical inducers mediating settlement of oyster larvae – a reexamination. *Biological Bulletin*, **183**, 327–338.

Terray, E. A., Donelan, M. A., Agrawal, Y. C., Drennan, W. M., Kahma, K. K., Williams, A. J., Hwang, P. A., & Kitaigorodskii, S. A. 1996. Estimates of kinetic energy dissipation under breaking waves. *Journal of Physical Oceanography*, **26**, 792–807.

Tompkins, D. M., Draycott, R. A. H., & Hudson, P. J. 2000. Field evidence for apparent competition mediated via the shared parasites of two gamebird species. *Ecology Letters*, **3**, 10–14.

Trevethan, M., & Chanson, H. 2009. Turbulent mixing in a small estuary: detailed measurements. *Estuarine, Coastal and Shelf Science*, **81**, 191–200.

Trevethan, M., Chanson, H., & Brown, R. 2008. Turbulent measurements in a small subtropical estuary with semidiurnal tides. *Journal of Hydraulic Engineering-ASCE*, **134**, 1665–1670.

Trowbridge, J. H. 1998. On a technique for measurement of turbulent shear stress in the presence of surface waves. *Journal of Atmospheric and Oceanic Technology*, **15**, 290–298.

Trussell, G. C., Ewanchuk, P. J., & Matassa, C. M. 2006. The fear of being eaten reduces energy transfer in a simple food chain. *Ecology*, **87**, 2979–2984.

Turchin, P., & Kareiva, P. 1989. Aggregation in *Aphins varians*: an effective strategy for reducing predation risk. *Ecology*, **70**, 1008–1016.

Turner, A. M., Bernot, R. J., & Boes, C. M. 2000. Chemical cues modify species interactions: the ecological consequences of predator avoidance by freshwater snails. *OIKOS*, **88**, 148–158.

Uetz, G. W., & Heiber, C. S. 1994. Group size and predation risk in colonial web-building spiders: analysis of attack abatement mechanisms. *Behavioral Ecology*, **5**, 326–333.

van Baalen, M., & Sabelis, M. W. 1993. Coevolution of patch selection strategies of predator and prey and the consequences for ecological stability. *American Naturalist*, **142**, 646–670.

VanVeen, F. J. F., Morris, R. J., & Godfray, H. C. J. 2006. Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology*, **51**, 187–208.

Vickers, N. J. 2000. Mechanisms of animal navigation in odor plumes. *Biological Bulletin*, **198**, 203–212.

Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in CHesapeake Bay. *Ecology*, **58**, 1200–1217.

VOULGARIS, G., & MEYERS, S. T. 2004. Temporal variability of hydrodynamics, sediment concentration and sediment settling velocity in a tidal creek. *Continental Shelf Research*, **24**, 1659–1683.

WALKER, R. L. 1984. Effects of density and sampling time on the growth of the hard clam, *Mercenaria mercenaria*, planted in predator-free cages in coastal Georgia. *Nautilus*, **98**, 114–119.

WALKER, R. L., & TENORE, K. R. 1984. The distribution and production of the hard clam *Mercenaria mercenaria* in Wassaw Sound, Georgia. *Estuaries*, **7**, 19–27.

WEBSTER, D. R., & WEISSBURG, M. J. 2001. Chemosensory guidance cues in a turbulent chemical odor plume. *Limnology and Oceanography*, **46**, 1034–1047.

WEBSTER, D. R., & WEISSBURG, M. J. 2009. The hydrodynamics of chemical cues among aquatic organisms. *Annual Review of Fluid Mechanics*, **41**, 73–90.

WEBSTER, D. R., RAHMAN, S., & DASI, L. P. 2001. On the usefulness of bilateral comparison to tracking turbulent chemical odor plumes. *Limnology and Oceanography*, **46**, 1048–1053.

WEISSBURG, M. J. 2000. The fluid dynamical context of chemosensory behavior. *Biological Bulletin*, **198**, 188–202.

WEISSBURG, M. J., & ZIMMER-FAUST, R. K. 1993. Life and death in moving fluids: hydrodynamic effects of chemosensory-mediated predation. *Ecology*, **74**, 1428–1443.

WEISSBURG, M. J., & ZIMMER-FAUST, R. K. 1994. Odor plumes and how blue crab use them in finding prey. *Journal of Experimental Biology*, **197**, 349–375.

WEISSBURG, M. J., JAMES, C. P., SMEE, D. L., & WEBSTER, D. R. 2003. Fluid mechanics produces conflicting constraints during olfactory navigation of blue crabs, *Callinectes sapidus*. *Journal of Experimental Biology*, **206**, 171–180.

WELLENREUTHER, M., & CONNELL, S. D. 2002. Responses of predators to prey abundance: separating the effects of prey density and patch size. *Journal of Experimental Marine Biology and Ecology*, **273**, 61–71.

WELLS, H. W. 1957. Abundance of the hard clam *Mercenaria mercenaria* in relation to environmental factors. *Ecology*, **38**, 123–128.

WILSON, W. H. 1990. Competition and predation in marine soft-sediment communities. *Annual Review of Ecology and Systematics*, **21**, 221–241.

WOODIN, S. A. 1978. Refuges, disturbance, and community structure: a marine soft-bottom example. *Ecology*, **59**, 274–284.

Wyeth, R. C., Woodward, O. M., & Willows, A. O Dennis. 2006. Orientation and navigation relative to water flow, prey, conspecifics, and predators by the nudibranch mollusc *Tritonia diomedea*. *Biological Bulletin*, **210**, 97–108.

Yakovis, E. L., Artemieva, A. V., & Fokin, M. V. 2004. Spatial pattern indicates an influence of barnacle and ascidian aggregations on the surrounding benthic assemblage. *Journal of Experimental Marine Biology and Ecology*, **309**, 155–172.

Yu, D. Y., Ali, M. S., & Lee, J. H. W. 2006. Multiple tandem jets in cross-flow. *Journal of Hydraulic Engineering-ASCE*, **132**, 971–983.

Zar, J. H. 1999. *Biostatistical Analysis*. New Jersey: Prentice Hall.

Zimmer, R. K., & Zimmer, C. A. 2008. Dynamic scaling in chemical ecology. *Journal of Chemical Ecology*, **34**, 822–836.

Zimmer-Faust, R. K., Finelli, C. M., Pentcheff, N. D., & Wethey, D. S. 1995. Odor plumes and animal navigation in turbulent water flow: A field study. *Biological Bulletin*, **188**, 111–116.