ENVIRONMENTAL MODIFICATION OF CHEMOSENSORY INTERACTIONS BETWEEN PREDATORS AND PREY: THE WORLD ACCORDING TO WHELKS

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ENVIRONMENTAL MODIFICATION OF CHEMOSENSORY INTERACTIONS BETWEEN PREDATORS AND PREY: THE WORLD ACCORDING TO WHELKS

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To the memory of Esther Ferner, an exemplary teacher, grandmother, and friend

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d	characteristic length scale
f	frequency
I.D.	inner diameter
κ	von Karman's constant
v	kinematic viscosity
NGDR	net-to-gross-displacement ratio
O.D.	outer diameter
Pc	predation on control plots
Pt	predation on treatment plots
PI	predation intensity
Re	Reynolds number
Re_*	roughness Reynolds number
S	Strouhal number
TI	normalized turbulence intensity
U	net velocity
U_{rms}	root mean square velocity
U_{z}	velocity at height (z)
u_*	friction velocity
z	height above sediment
z_0	hydraulic roughness

SUMMARY

The effect of environmental modification of predator sensory abilities remains largely unknown, despite the importance of predators to ecosystem function. I conducted a series of experiments to investigate effects of hydrodynamics on the chemosensory search behavior and foraging success of two species of marine gastropods, knobbed whelks (*Busycon carica*) and channeled whelks (*B. canaliculatum*). This research consisted of laboratory studies of navigational performance in turbulent odor plumes, as well as field studies that related *in situ* patterns of foraging success to turbulent mixing.

Laboratory and field tests showed that whelks are effective foragers in turbulent flow. The search success of both whelk species was unaffected by changes in flow velocity and turbulence, whereas search efficiency (tracking speed, orientation towards the source) increased in the most turbulent conditions tested. Manipulative field experiments demonstrated the ecological consequences of whelk foraging proficiency in turbulent environments. When deployed in tidal channels, baited traps that increased turbulent mixing of bait odors captured twice the number of channeled whelks as unmodified control traps. Experimental plots of clams subjected to elevated turbulence experienced a 43% increase in knobbed whelk predation compared to unmodified control plots. The magnitude of turbulent mixing also alters the importance of nonlethal predator effects by reducing prey responses to predation risk. Avoidance responses to predator odor normally protect clams from consumers, but increased turbulence around clam plots exposed to predator cues counteracted avoidance responses of clams and resulted in increased whelk predation. Detailed flow measurements in the field indicated that background levels of turbulence may mediate the impact of hydrodynamics on chemosensory interactions between whelks and their prey. Collectively, this research suggests that slow-moving predators can continue foraging in turbulent conditions that are known to diminish the olfactory abilities of faster taxa, even when prey animals are given advance warning of a predatory threat. Environmental factors affecting animal sensory abilities can change the outcome of chemically mediated interactions and possibly could result in resource partitioning along a gradient of turbulence intensity. Further examination of diverse sensory strategies should help to refine expectations of predator-prey interactions in a variety of systems.

CHAPTER 1
INTRODUCTION

All organisms must sense information from their environment in order to survive, and knowledge about how organisms perceive and respond to meaningful signals has helped to illuminate basic ecological principles (Dusenbery 1992). Chemical signals provide information that mediates numerous biological interactions in both terrestrial (Alberts 1992) and aquatic (Brönmark & Hansson 2000) realms. Chemosensory ecology is an interdisciplinary field that encompasses the production and fate of chemical signals, their detection by receiving organisms, and the resulting behavioral responses that affect organism distribution and abundance. Chemical deterrents are widely used by plants and animals to defend against consumption (Paul 1992), and by doing so may help regulate species abundance and community composition (Hay 1996). In contrast, the ecological consequences of chemical attractants remain poorly understood and are only recently beginning to receive attention (Weissburg et al 2002b).

Following odor trails in search of food is a common foraging strategy employed by marine consumers of diverse taxa (Zimmer and Butman 2000, Stachowicz 2001). In most cases of olfactory orientation, hydrodynamics play a critical role in the transport and detection of waterborne molecules (Weissburg 2000). Brown and Rittschof (1984) found that a combination of flow and chemical stimuli was necessary for odor tracking by oyster drills, whereas either factor in isolation was ineffective. Similar constraints apply to foraging blue crabs, allowing these animals to orient to spatial aspects of chemical stimuli in turbulent flows (Zimmer-Faust et al. 1995). The ability of blue crabs to locate an odor source is proportional to the ambient current velocity (Finelli et al. 2000), although turbulent mixing of dilute cues will eventually limit crab tracking success and efficiency (Weissburg and Zimmer-Faust 1993, 1994).

Despite technological advances that allow quantification of three-dimensional flow velocities and odor concentrations (e.g., Crimaldi and Koseff 2001, Webster et al. 2003, Rahman and Webster 2005), establishing the ecological relevance of odor-tracking behavior is limited by the difficulties of testing animal responses within realistic flow regimes. A notable reason for this limitation is that habitats suitable for studies of chemically mediated foraging should be accessible for manipulation and characterized by periods of directed flow. These two characteristics are essential in order to match odor plume dynamics with those generated in laboratory flume experiments. Tidally driven estuaries meet these criteria by virtue of having periodic and often unidirectional flow, moderate water depth, and proximity to a range of intertidal habitats. Along the eastern coast of the United States, semidiurnal tidal currents reverse direction at regular intervals (~ 6 h) and allow chemical plumes to persist for relatively long periods, making these habitats particularly appealing for field tests of olfactory orientation.

Studies of marine crustaceans have yielded important insights into the mechanisms and implications of chemically mediated prey search (e.g., Atema 1985, Weissburg et al. 2002a, Koehl 2006). However, generalizations of these results to other taxa may be confounded by the narrow range of animal size and mobility represented in these studies (Weissburg 2000). Slow-moving marine gastropods offer an alternative model system in which to investigate chemosensory strategies of detection and avoidance in estuarine tidal flows. Knobbed whelks (*Busycon carica*) are large, non-visual gastropods that track chemical cues along the seafloor and have important effects on their bivalve prey

(Magalhaes 1948, Peterson 1982, Irlandi & Peterson 1991, Nakaoka 2000, Powers and Kittinger 2002). Channeled whelks (*B. canaliculatum*) are less well studied but appear to prey upon thin-shelled bivalves (Magalhaes 1948, Paine 1962) and carrion that accumulates in subtidal waters (Walker 1988). Preliminary studies in coastal Georgia confirmed that both of these whelk species coexist in similar estuarine habitats and are easily collected and maintained in the laboratory.

Basic observations of whelk behavior raise a number of interesting questions: How do whelks locate their prey? (Chapters 2,5) Do whelk search behaviors resemble those of other taxa? (Chapter 2) How are whelk search behaviors affected by environmental factors such as water flow and sediment characteristics? (Chapters 2,3,5) Do avoidance responses of prey alter whelk foraging success? (Chapter 4) How do environmental factors affect the lethal and nonlethal effects of whelks on their prey? (Chapters 3,4) Is whelk foraging activity affected by predator cues? (Chapter 5) In the following chapters, I address these and other questions by examining the chemosensory basis of whelk foraging behavior and its implications for predator-prey interactions in turbulent marine environments. Extensions of this work should lead to testable predictions regarding the strength and outcome of predator-prey interactions across a range of environmental conditions in a variety of systems.

CHAPTER 2

SLOW-MOVING PREDATORY GASTROPODS TRACK PREY ODORS IN FAST AND TURBULENT FLOW

Abstract

Olfactory searching by aquatic predators is reliant upon the hydrodynamic processes that transport and modify chemical signals. Using a laboratory flume, I investigated the odor-tracking behavior of a marine gastropod whelk (*Busycon carica*) to test the generalization that turbulence interferes with chemically mediated navigation. Individual whelks were exposed to turbulent odor plumes in free-stream velocities of 1.5, 5, 10, or 15 cm s^{-1}, or with one of two obstructions placed upstream of the odor source in an intermediate flow of 5 cm s^{-1}. Measurements of velocity and stimulus properties confirmed that obstruction treatments increased turbulence intensity and altered the fine-scale structure of downstream odor plumes. In all conditions tested, between 36 – 63 % of test animals successfully located the odor source from 1.5 m downstream with no significant effect of flow treatment. Cross-stream meander was reduced at higher flow velocities and in the presence of obstructions, allowing whelks to reach the odor source significantly faster than in slower, less turbulent conditions. These results demonstrate that whelks can respond to chemical information in fast and turbulent flow, and I suggest that these slow-moving predators can forage in hydrodynamic environments where the olfactory abilities of other taxa are compromised.

Introduction

Mobile predators often search for prey using chemical cues, particularly where visual or mechanical stimuli are obscured or unavailable (Zimmer-Faust 1989, Stachowicz 2001, Weissburg et al. 2002b). In hydrodynamic environments, dissolved chemicals that emanate from prey are mixed and transported downstream in a plume of filamentous odors interspersed with patches of clear water (Crimaldi and Koseff 2001). Studies of marine crustaceans have yielded valuable insights regarding the adaptations that enable animals to forage successfully in benthic habitats where the physical processes affecting odor transport are of central importance (Atema 1985, Derby and Atema 1988, Weissburg 2000, Koehl et al. 2001). One important conclusion from previous research with blue crabs (*Callinectes sapidus*), for example, is that turbulent mixing alters odor plumes in ways that interfere with olfactory navigation (Weissburg and Zimmer-Faust 1993, 1994). Turbulence breaks apart individual odor filaments and homogenizes chemical gradients, ultimately generating a Gaussian distribution of odor concentrations across a plume (Moore and Atema 1991, Zimmer-Faust et al. 1995, Finelli et al. 1999b). These physical alterations reduce the signal contrast available within an odor plume and blur the distinctiveness of plume boundaries, both of which are important cues guiding blue crab search behavior (Zimmer-Faust et al. 1995, Weissburg et al. 2002a). Consequently, olfactory foraging success by these animals should be reduced in regions of elevated turbulence, as was shown to be true in simple laboratory flows (Weissburg and Zimmer-Faust 1993).

Given that turbulent water flow is both a common feature of benthic environments and a major determinant of odor plume structure, it is necessary to test the importance of hydrodynamics for olfactory searching in a variety of taxa in order to elucidate the general constraints that foraging animals experience in nature. Gastropod molluscs offer an intriguing contrast to crustaceans in that these slow-moving animals hunt for similar prey in similar habitats while using an entirely different array of sensors and behavioral strategies. Although investigators rarely examine the impact of water flow on olfactory navigation, studies of gastropod chemosensation have been a productive area of research for more than half of a century (reviewed by Kohn 1961, Mackie and Grant 1974, Kats and Dill 1998). This rich research lineage has broadened our understanding of the mechanisms and importance of chemosensation by gastropods, and the chemical identity of feeding stimuli has been a common focus of investigation (Sakata 1989) leading to detailed studies of physiological responses (Elliot and Susswein 2002). A few researchers have considered how the strength and stability of water currents affect the olfactory behavior of gastropods (McQuinn et al. 1988; Lapointe and Sainte-Marie 1992; Rochette et al. 1997), and one recent study tested the effect of increased flow velocity on predation (Powers and Kittinger 2002). However, no studies to date have examined the impact of turbulence on the chemosensory responses of gastropods.

Successful olfactory predation should depend upon an individual's ability to detect chemical stimuli in the environment and to locate the source of prey odors faster than competitors. Weissburg (2000) proposed a theoretical framework that predicts how animal characteristics such as size and mobility might interact to dictate effective olfactory strategies. Body size is inherently related to the spatial scale of chemical information available to receiving organisms, in that larger animals may be capable of simultaneous odor sampling at different locations across a plume whereas spatial sampling by smaller individuals is more restricted. Highly mobile foragers seem to employ a strategy that relies upon intermittent bursts of chemical information in conjunction with spatial comparisons (Weissburg et al. 2002a). This sensory approach emphasizes rapid search at the expense of fine-grained sampling. On the other hand, slower animals might benefit by sampling more successfully in the temporal domain. Averaging odor concentrations at a single location over time could allow a slow-moving forager to accurately estimate its position within a plume or its degree of progress toward an odor source. This sampling strategy does not require reaction to instantaneous concentrations contained in discrete odor filaments and thus should avoid the apparently detrimental homogenization of plume structure associated with turbulent mixing. Within this context, marine gastropods possess relatively low capacity for spatial sampling but high potential for temporal integration, simply by virtue of their sluggish movement that provides numerous sequential sampling opportunities at each point within an odor plume. By responding to the time-averaged concentration, these slow-moving predators may be able to locate the source of dissolved prey chemicals even when the fine-scale structure of the odor plume has been eroded by turbulence.

In the present study, I examined the chemosensory behavior of predatory gastropods to test the hypothesis that turbulent water flow does not impair the odor-tracking ability of slow-moving benthic foragers. Knobbed whelks (*Busycon carica*) are common marine gastropods that consume bivalves such as oysters, scallops, and clams along the eastern coast of the United States (Magalhaes 1948, Carriker 1951, Peterson, 1982, Walker 1988). These predators forage on intertidal flats and creeks fringed by oyster reefs, as well as in subtidal channels that experience largely unidirectional flow (Li et al. 2004). I exposed knobbed whelks to prey chemicals under controlled laboratory flows and evaluated their ability to locate the stimulus source in different current velocities. I then introduced additional turbulent mixing near the stimulus source to decouple the effects of velocity and turbulence on the properties of downstream odor signals. Results from this study offer strong predictions about the relevance of the boundary-layer flow regime for trophic interactions in estuarine communities. Although it is generally accepted that physical forces diminish the severity and importance of benthic predation, I tested the notion that slow-moving olfactory predators could thrive in more vigorous flows and might actually benefit from the turbulent mixing of prey odors.

Materials and Methods

Collection and maintenance of whelks. This study was conducted at the Skidaway Institute of Oceanography (SkIO) between August and December 2001. Knobbed whelks were collected by hand from intertidal habitats of Wassaw Sound and returned to the laboratory where they were held under a continuous flow of gravel-filtered estuarine water (22 – 30 ‰). All holding tanks shared the same water source but no single tank contained more than 12 individuals to allow free movement within the tank. Whelks were fed an *ad libitum* diet of ribbed mussels (*Geukensia demissa*) and hard clams (*Mercenaria mercenaria*) for at least one week following the date of collection to standardize recent feeding history. Preliminary observations revealed that recently fed animals were less likely to respond to prey odors than those starved for 10 to 14 days, and therefore all whelks were starved for two weeks prior to experiments. Each individual was tested once in a single flow treatment and subsequently fed and released near its original capture location.

Characterization of laboratory flows. I conducted odor-tracking experiments in controlled hydrodynamic conditions generated in the SkIO flume facility. This oval-shaped racetrack flume is composed of polyvinylchloride (PVC) and powered by a paddle-wheel drive system capable of sustaining a wide range of flow velocities. The paddle system completely fills one of two parallel channels (7.3 m long, 1 m wide, and 0.75 m deep), and the opposite channel contains a clear Plexiglas™ working area where all experimental manipulations and observations were performed. The curved section upstream of the working area is vertically divided by four parallel partitions followed by a honeycomb baffle designed to dampen large eddies and cross-stream flows. The smooth bottom of the working area was covered with a 1-cm layer of graded sand (diameter = 803 ± 144 μm [mean ± 1 *SD*]; $n = 250$) to provide a more realistic sediment surface for whelk activity. The flume was filled to a depth of 25 cm with estuarine water (22 – 30 ‰) that was filtered through gravel, sand, and 5-μm polypropylene filter bags to remove incoming organisms and suspended sediments. One third of the flume water (approximately 2200 L) was exchanged each night to remove chemical compounds derived from odor solutions and to match water conditions with the holding tanks in which test animals were acclimated prior to experiments.

Hydrodynamic treatments consisted of unidirectional flow at four different free-stream velocities (U = 1.5, 5, 10 and 15 cm s^{-1}) with bulk flow Reynolds number ($Re = Ud/v$, where d is water depth and v is kinematic viscosity) ranging from 3800 to 38000.

These flow conditions are representative of natural whelk habitats, where velocity ranges from near zero at slack water to more than 30 cm s^{-1} during peak tidal flow (Chapter 3) and intertidal water depth ranges from 0 to 3 m. Additional treatments contained one of two obstructions intended to alter odor plume structure independent of changes in bulk flow speed. I tested obstructions at only one flow speed as an initial examination of whelk responses to enhanced mixing, and the intermediate velocity (U = 5 cm s^{-1}) selected for these obstruction treatments provided a substantial increase in boundary-layer turbulence that exceeded the level associated with the fastest flow condition (see Results). The first obstruction was one of the symmetric halves of a 1-m section of PVC pipe (*O.D.* = 4.8 cm) that was cut along its longitudinal axis, oriented perpendicular to the mean flow direction, and positioned on the sediment 1 cm upstream of the delivery nozzle with the open side facing downward to create a "bump treatment." The second obstruction was a 30-cm cylindrical section of PVC pipe (*O.D.* = 4.8 cm) oriented vertically and centered 1 cm upstream of the delivery nozzle. Based on an estimate of the cylinder Reynolds number (where d is the cylinder diameter) and previous examinations of fluid motion around circular cylinders (e.g., Taneda 1965, White 1991), I expected that this "cylinder treatment" should shed unstable vortices and introduce meander not present in unobstructed flows. The frequency (f) of vortex shedding downstream of the cylinder was estimated to be 0.2 Hz, based on the nondimensional Strouhal number ($S = fd/U$) which remains roughly constant over a wide range of Re spanning my test conditions (Kundu 1990).

The flume was operated for 20 minutes before beginning data collection to allow the flow to stabilize at each new treatment condition, and dye visualization confirmed that the flow was smooth and that wall effects were negligible throughout the central region of the working area. I used an acoustic Doppler velocimeter (ADV) to collect high-resolution, 3-dimensional-velocity data (± 0.01 cm s^{-1}) at various heights above the sediment surface in order to characterize boundary layer structure and to compare the different flow treatments quantitatively. The ADV probe (SonTek/YSI 16-MHz ADVField) was positioned in the center of the flume on an adjustable mount oriented to the nominal horizontal flow axis (x-direction), and measurement height was adjusted with a vernier sliding scale (± 0.25 mm). Velocity data were collected at a frequency of 10 Hz, and instantaneous measurements were averaged over four minutes to obtain velocity means and variances at each height.

Velocity profiles from unobstructed flow treatments were compared to the generalized Karman-Prandtl log-profile relationship used to describe the logarithmic increase in velocity above a boundary:

$$U_z = (u_*/\kappa)\ln(z/z_0)$$

where U_z is the mean velocity at height z above the bed, u_* is the shear velocity, κ is von Karman's constant, and z_0 is the hydraulic roughness determined by least-squares regression of $\ln(z)$ against mean velocity. Values of shear velocity were used to calculate a roughness Reynolds number (Re_*), where d is the mean diameter of sand grains (i.e., roughness scale). Re_* provides a description of the turbulent nature of boundary layer flows (Nowell and Jumars 1984) that is particularly relevant for olfaction by benthic foragers (Weissburg 2000). Similar characterization of obstruction treatments was inappropriate due to the absence of an equilibrium boundary layer. Previous studies have estimated u_* from the covariance between vertical and downstream velocities (e.g., Finelli et al. 1999b, 2000). However, these height-dependent approximations were not suitable for the present study because precise measurement heights were not replicated across flow conditions. Instead, root mean square velocity data (U_{rms}) served as a measurement of turbulence intensity and were compared to unobstructed flow at the same free-stream velocity (U = 5 cm s^{-1}) as a first-order assessment of the hydrodynamic effects of obstructions. Similar profiles of U_{rms} also provided an additional comparison of unobstructed flows.

Characterization of odor-plume structure. In order to quantify variation in odor plumes associated with different flow treatments, I used salt water as a proxy for prey chemicals and collected conductivity data describing the temporal structure of downstream stimulus concentrations. The flume was initially drained, rinsed, and refilled with fresh water (0 ‰) to provide a featureless background against which salt-water filaments could be resolved. A neutrally buoyant salt solution (50 ‰) was prepared by mixing concentrated salt water with anhydrous ethanol. Matching densities of the resulting salt solution and flume water were confirmed with a standard hydrometer and the solution then was introduced through a delivery nozzle at the same position and injection rate used for odor-tracking experiments (see below). Salt concentrations were measured with a microscale conductivity and temperature instrument (Precision Measurement Engineering, Model 125 MSCTI). This four-electrode sensor has a spatial resolution of approximately 1 mm and protrudes from the end of a thin aluminum shaft oriented upstream and aligned parallel to the sediment surface. Data were collected at a single point 1.5 m downstream from the stimulus source where test animals began searching, and the sensor was positioned 2.5 cm above the sediment surface because a typical whelk extends its siphon at about this height. Electrical conductivity of water passing between the electrodes resulted in voltage differences that were measured at a frequency of 10 Hz, amplified, and recorded using National Instruments™ software (LabVIEW™ 6).

A calibration curve (0 – 50 ‰) confirmed the linear relationship between salinity and voltage output across the expected range of salinities ($r^2 = 0.991$, $n = 5$). Three replicate data sets (30 s each) were collected to characterize diagnostic features of plume structure for each flow treatment, and background conductivity of the flume water was recorded for one minute as a control prior to beginning each subset of measurements. Data were analyzed to determine the number and average conductivity of stimulus peaks (filaments) detected by the sensor. Peaks were identified as discrete excursions above a baseline value that equaled the mean conductivity of the preceding control. Voltages were normalized by the conductivity of the source solution to facilitate comparison with other investigations.

Preparation and delivery of prey chemicals. I standardized preparation and delivery of prey chemicals to provide a consistent stimulus for foraging whelks. Initial tests confirmed that whelks exhibit feeding responses to mantle fluid from a variety of bivalves including ribbed mussels, which were selected as the source of prey chemicals for these experiments. Mussels were collected from Cabbage Island in Wassaw Sound, transferred to holding tanks in the SkIO flume facility, and held for up to one week prior to stimulus preparation. Mussels were frozen and thawed immediately before being opened to avoid shattering the shell and to reduce the extent of damage during tissue extraction. Approximately four liters of stimulus solution were prepared for each trial by soaking freshly thawed mussel tissue in filtered estuarine water drawn directly from the flume. Prey tissues were soaked for one hour at a concentration of 7.5 g of tissue per L of water, and solutions were filtered through a 60-µm screen before reintroduction to the flume. Preliminary trials with lower concentrations (1.5 g L^{-1}) or shorter soaking times failed to elicit a sufficient number of tracking responses, whereas higher concentrations would have introduced excessive quantities of prey chemicals into the flume and required more frequent exchanges of flume water.

Dissolved prey chemicals were injected into the flow using a gravity-driven delivery system suspended above the flume and upstream of the working area. The stimulus solution was recirculated through a 1.2-L tank fitted with a standpipe to allow excess solution to drain into an overflow reservoir. This arrangement maintained constant head pressure on a delivery tube (Tygon® 2275, *I.D.* = 6.35 mm) that exited the tank and passed through a flow meter (Gilmont® GF-2360). Solutions were released in the center of the flume at a constant rate of 52 mL min^{-1} through a small brass nozzle (*I.D.* = 4.7 mm; *O.D.* = 6.4 mm) modified with a fairing to reduce flow disturbances. The bottom edge of the nozzle rested at a height of 1 cm above the sand to permit sufficient downstream advection while ensuring that odors were retained near the sediment surface where whelks could encounter them. Injection rate was selected to be isokinetic with a free-stream velocity of 5 cm s^{-1} to reduce the mixing of odors by minimizing shear between the stimulus solution and ambient flow. Despite the benefits of isokinetic release, injection rate was not adjusted to match the other velocity treatments (U = 1.5, 10, and 15 cm s^{-1}) so as to avoid varying the flux of odor solution presented to test animals. Total flux of chemical attractants can be an important determinant of animal responses (Zimmer et al. 1999, Keller and Weissburg 2004), and thus, adjusting injection rate to preserve isokinetic release would have required extensive additional tests of the interactive effects of stimulus flux and flow velocity. The jet Reynolds numbers based on relative velocity and outlet diameter were less than 700 and dye visualization around the nozzle indicated that mixing due to shear was minor in all flows, suggesting that an intermediate injection rate (of 52 mL min^{-1}) was reasonable for the purposes of these experiments.

Experimental tests of odor-tracking behavior. Olfactory tracking experiments were conducted in groups of four to six consecutive trials at a given flow speed. Velocity for each group was chosen at random, and trials to be run at 5 cm s^{-1} then were randomly assigned to the cylinder, bump, or unobstructed treatment. Individual whelks for each trial also were randomly selected to receive either odor solution or flume water (control) as an experimental stimulus. The 1-cm layer of sand covering the working area of the flume was vigorously mixed after each trial to flush out porewater odors and to release chemicals adsorbed to sand grains. As many as three groups of trials were run in the same day, but no more than eight hours of odor release were permitted before the flume water was partially exchanged overnight.

A single whelk was transferred from its holding tank to a flow-through cage (30 x 21 x 17 cm) constructed of plastic grating and located 1.5 m directly downstream from the delivery nozzle. The upstream wall of the starting cage was lifted after an acclimation period of 10 min during which time the whelks were exposed to the stimulus plume, and whelks then were allotted up to 20 min to begin upstream movement followed by an additional 40 min to locate the stimulus source. Total allowable trial time was based on preliminary measurements of whelk movement speed, which was estimated to be as slow as 0.5 mm s^{-1} during active upstream searching. Trials were terminated and scored as a failed track if the whelk: (1) did not leave the cage within 20 min; (2) reached the side walls of the flume outside the lateral extent of the odor plume; or (3) did not track successfully within 60 min after the cage grating was lifted. Trials were terminated and scored as a successful track if the whelk moved to within 10 cm downstream of the odor source before halting upstream or lateral movement. Dye visualization revealed that waterborne chemicals impacted the shell at this close distance, accumulating around the animal's siphon, foot, and cephalic tentacles. Although most successful whelks (74 %) proceeded to make direct contact with the delivery nozzle, inundation with stimulus solution close to the nozzle sometimes caused an individual to begin persistent digging behavior, presumably in search of what it perceived to be nearby prey. Whelks rarely advanced toward the nozzle opening after this behavioral shift occurred and so further observations were uninformative. All whelks that failed to locate the source of treatment or control plumes were offered a freshly killed mussel to confirm an adequate level of feeding motivation. Most unsuccessful whelks (62 %) readily consumed the offered food, but those that did not begin ingestion within two hours were judged to be uninterested in foraging and were excluded from subsequent analysis. The influence of flow velocity and obstruction treatments on the proportion of animals that tracked successfully was evaluated using a G-test. Analysis of variance (ANOVA) was used to evaluate the effect of flow treatments on the search time required for whelks to locate the stimulus source.

Table 2.1. Shear velocity (u_*) and roughness Reynolds number (Re_*) for unobstructed flows that differed in free-stream velocity (U). Determination of hydraulic roughness (z_0) by regression of ln(z) against velocity yielded an $r^2 > 0.95$ in all four conditions.

U (cm s^{-1})	u_* (cm s^{-1})	Re_*
1.5	0.14	1.1
5	0.22	1.8
10	0.52	4.1
15	0.71	5.7

Results

Hydrodynamic conditions. Vertical velocity gradients (Figure 2.1A) recorded at the location of the delivery nozzle were used to derive hydrodynamic parameters. Flow speed in each unobstructed condition increased with distance above the bed until reaching the characteristic free-stream velocity. Data collected within 1 cm of the bed supported the existence of equilibrium boundary-layer conditions, but these velocities were not included in the estimation of u_* because ADV measurements in this region are susceptible to interference from the bed (Finelli et al. 1999a). Calculated values of u_* increased with flow speed and yielded Re_* of up to 5.7 (Table 2.1), suggesting that turbulent eddies began to penetrate the boundary layer in at least the fastest condition tested. Vertical profiles of turbulence intensity (Figure 2.1B) showed a characteristic peak close to the sediment as expected for equilibrium boundary layer flows (Schlichting

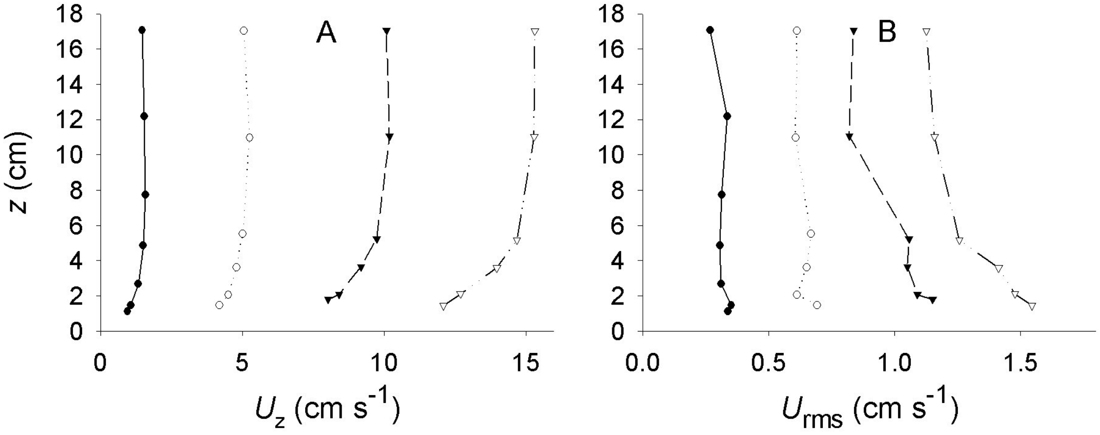

Figure 2.1. Hydrodynamic characteristics of the four unobstructed flow treatments. (A) Profiles of flow velocity (U_z) at various heights (z) above the sediment. ADV measurements were recorded in the center of the flume at the location of stimulus release. Each data point represents a four-minute average of instantaneous velocities collected at a frequency of 10 Hz. Precise replication of measurements heights was not possible due to slight differences in signal resolution across flow treatments. (B) Vertical profiles of turbulence intensity (U_{rms}) corresponding to each of the velocity records in the unobstructed flow treatments. Turbulence intensity increased with velocity, such that the slowest flow was least turbulent and the fastest flow most turbulent. In all four unobstructed conditions, turbulence intensity was greatest from 1 – 2 cm above the sediment and decreased with height (z) until boundary effects were negligible.

1987), further verifying that faster flows were more turbulent throughout the lower 17 cm of the water column.

Profiles of U_{rms} at the location of the delivery nozzle illustrated the effect of flow obstructions (Figure 2.2A). The bump treatment increased turbulence intensity by a factor of 2.5 relative to the unobstructed or smooth condition, whereas turbulence in the overlying water column was unaffected or even slightly diminished, possibly due to flow

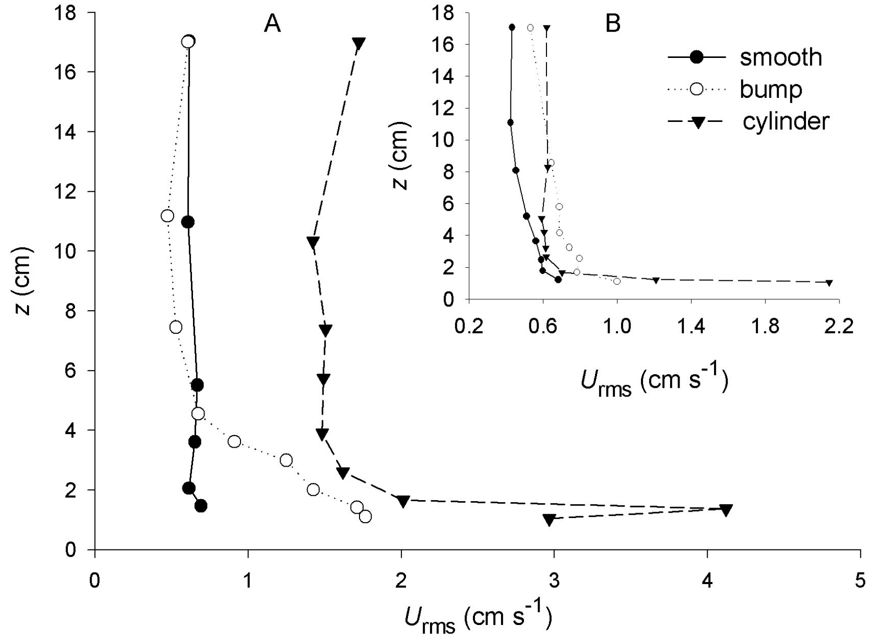

Figure 2.2. Vertical profiles of turbulence intensity (U_{rms}) in the three flow treatments having a free-stream velocity of $U = 5$ cm s^{-1}. Turbulence intensities were derived from ADV measurements of velocity at (A) the location of stimulus release and (B) the starting position of test animals, which was 1.5 m downstream from the stimulus source. Data for the smooth condition is the same as that shown in Figure 2.1 and is included here for the sake of comparison. The bump and cylinder obstructions increased turbulence intensity near the sediment surface relative to unobstructed flow.

impedance by the bump that extended across the entire width of the flume. The cylinder treatment disrupted flow at all depths, and at the height of stimulus injection it increased turbulence intensity by more than four times relative to the smooth condition and nearly twice the level generated by the bump treatment. Downstream profiles of turbulence intensity confirmed that the hydrodynamic effects of obstructions persisted throughout the entire length of the test section (Figure 2.2B). At the starting location of test animals, the bump treatment yielded a 50 % greater level of turbulence than the smooth condition, whereas the cylinder treatment produced a threefold increase in turbulence intensity. Although I maintained the same free-stream velocity of 5 cm s^{-1} across these treatments, the data in Figure 2.2 demonstrate that, relative to the smooth condition, both obstructions increased turbulent mixing in the near-bed region where prey chemicals were introduced and delivered to foraging whelks. Moreover, these increases in turbulence exceeded those present in even the fastest unobstructed flows (see Figure 2.1).

Stimulus properties. Conductivity data revealed distinct patterns of chemical signal structure associated with the various flow treatments. The slowest condition (1.5 cm s^{-1}) was not included in this characterization because accumulation of the salt solution hindered performance of the conductivity sensor and prevented reliable measurements of concentration changes over time. Differences in the number of stimulus peaks detected per second at the downstream limit of the test section confirmed that the greater shear associated with faster flow broke apart odor filaments and created more numerous peaks (Figure 2.3A), with 0.5 peaks per second detected in flows of 5 cm s^{-1}, compared to 0.9 peaks per second in the fastest flows of 15 cm s^{-1}. Greater numbers of peaks were accompanied by a concordant decrease in concentration (Figure 2.3A) because the stimulus injection rate was constant across treatments. Average peak concentration did not exceed 1.3 % of the source concentration in any of the conditions that I characterized, indicating that substantial dilution occurred during stimulus transport. Taken together, these results demonstrate that an increase in velocity alone disrupted odor signals in a manner consistent with previous investigations (e.g., Moore et al. 1994, Finelli 2000).

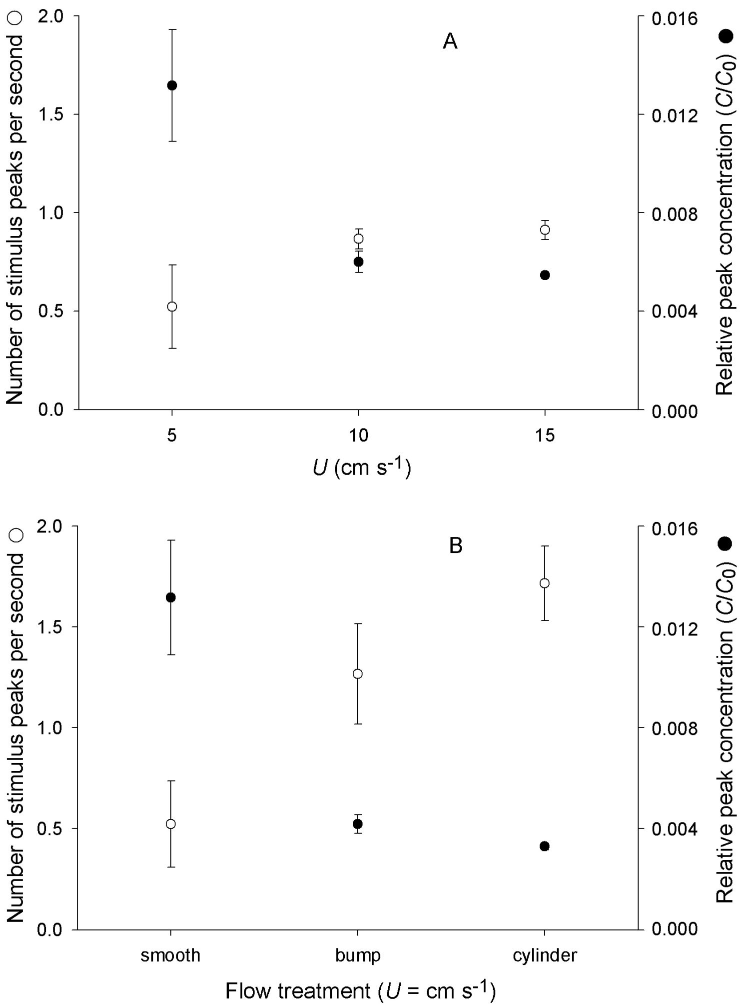

Figure 2.3. Conductivity data representing the number of stimulus peaks detected per second (open circles) and the relative peak concentrations (closed circles) for (A) the three fastest unobstructed flows and (B) the three flow treatments having a free-stream velocity of 5 cm s^{-1}. Values for the smooth condition ($U = 5$ cm s^{-1}) are included in both graphs for the sake of comparison. Data points represent an average of three replicates (± *SE*) in which conductivity was recorded for 30 s at a frequency of 10 Hz. Peaks were identified as bursts of concentration above a baseline that was established from background measurements collected prior to each trial. Peak concentrations (C) include all measurements that exceeded baseline and are normalized to source concentration (C_0).

Obstruction treatments were designed to enhance mixing and homogenize stimulus concentrations similar to that in faster flows but without the associated effects of higher velocity (e.g., increased drag on foraging whelks). Conductivity measurements downstream of the bump and cylinder treatments showed an expected increase in the number of peaks detected per second and a decrease in average peak concentration (Figure 2.3B). Compared to the 0.5 odor peaks detected per second in the smooth condition (Figure 2.3A, B), the bump treatment generated 1.3 peaks per second and the cylinder treatment 1.7 peaks per second. In addition, turbulence generated by both obstructions incorporated "clean" water into the stimulus plume and diluted average peak concentrations even below levels observed in the fastest unobstructed flows (see Figure 2.3A).

Tracking success. A total of 259 knobbed whelks were tested during the course of this study, and 179 of these individuals satisfied the post-trial criteria for feeding motivation. Considering only those motivated foragers exposed to the odor stimulus ($n = 102$), between 36 – 63 % of whelks tracked successfully in all six treatments (Figure 2.4). Tracking success was independent of flow speed (df = 3, $G = 2.46$, $P > 0.25$), confirming that whelks were able to detect and follow turbulent odor plumes in flows ranging from 1.5 to 15 cm s^{-1}. The apparent increase in tracking success at 5 cm s^{-1} (Figure 2.4A), although not statistically significant, could coincide with an optimal range of velocity in which knobbed whelks are particularly successful at navigating over smooth sand. At least 36 % of test animals also located the odor source when either one of the obstructions was present. Comparison of success rates between obstructed and unobstructed conditions confirmed that whelk tracking ability was independent of flow treatment (df = 2, $G = 2.55$, $P > 0.25$), although the bump obstruction slightly reduced the success rate of motivated searchers when compared to the cylinder treatment or smooth condition (Figure 2.4B).

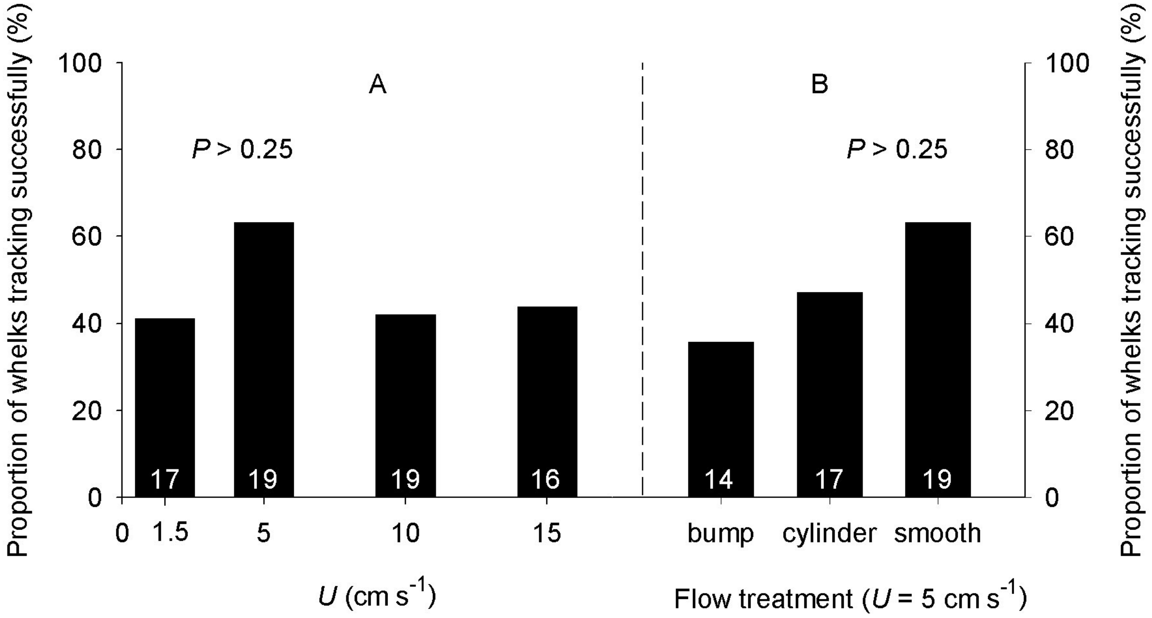

Figure 2.4. Proportion of motivated whelks (*Busycon carica*) that successfully tracked prey chemicals in each flow condition. Success rates were independent of flow treatment for both unobstructed and obstructed flows. Sample sizes are indicated at the bottom of each bar. No animals in any flow treatment tracked to the delivery nozzle in response to unscented control plumes.

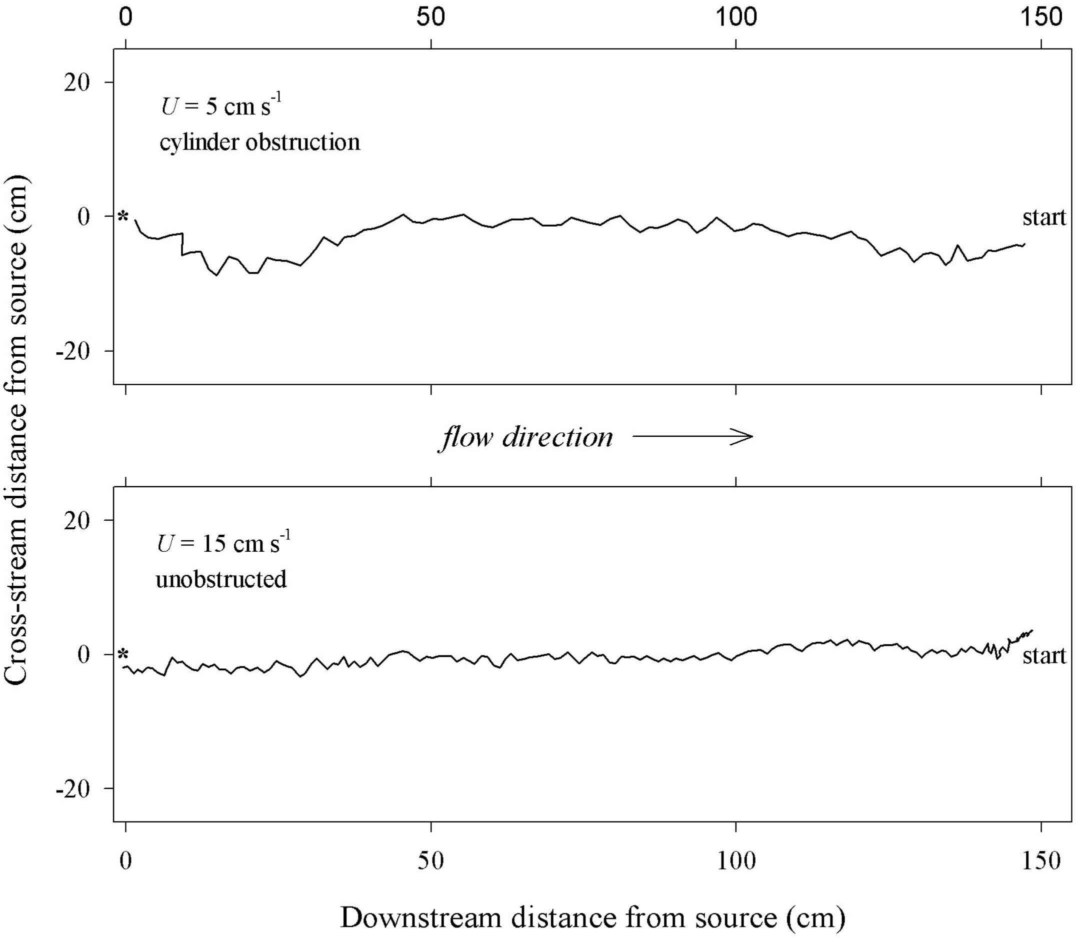

Figure 2.5. Examples of whelk tracking behavior in the two most turbulent treatments: the cylinder obstruction in a flow of 5 cm s^{-1} (top panel), and an unobstructed flow of 15 cm s^{-1} (bottom panel). Trials were filmed with a CCD camera mounted directly above the flume, and paths show motion of the anterior tip of an individual whelk (*B. carica*). Images of animal location were collected at a frequency of 2 Hz, smoothed over 8-s bins, and downsampled to a frequency of 0.125 Hz. Jagged lateral motions represent siphon casting as whelks tracked upstream, and asterisks represent the stimulus source.

Directed upstream movement was not simply a response to unidirectional flow or to disturbances associated with stimulus injection; no test animals in any flow treatment tracked to the delivery nozzle during control trials when unscented flume water served as a potential stimulus. Of the motivated foragers exposed to odorless control plumes (n = 77), 43 % showed no signs of activity and 38 % exhibited a short period of digging followed by apparent inactivity. Only the remaining 19 % left the starting cage and traveled to the edge of the test section or turned to move in a downstream direction, in contrast with the 68 % of motivated foragers that actively left the starting cage when exposed to prey odors.

Successful searchers moved upstream while casting back and forth with their siphon, apparently in order to maintain or confirm their continued presence within the attractive odor plume (e.g., Figure 2.5). Despite these casting motions, overall paths to the stimulus source were rather direct, particularly in comparison to behavior displayed by blue crabs searching in similar flows (Weissburg and Zimmer-Faust 1994).

Comparison of mean search times across flow treatments (Figure 2.6) showed that successful whelks reached the stimulus source more quickly in both faster (df = 3, F = 3.35, P = 0.036) and more turbulent flows (df = 2, F = 3.77, P = 0.049). Tukey-Kramer post-hoc tests revealed that search times in the two fastest treatments were significantly shorter than in flows of 1.5 cm s^{-1}, and search times in the cylinder treatment were significantly shorter than in unobstructed flows of the same free-stream velocity.

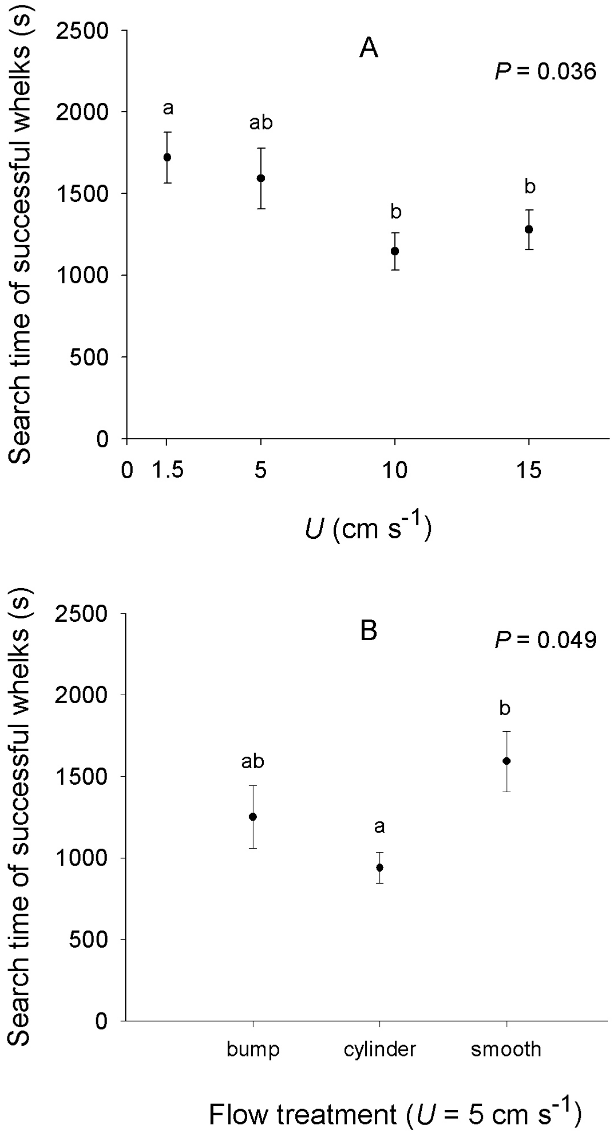

Figure 2.6. Average search time (± *SE*) required for successful whelks (*B. carica*) to navigate from the starting cage to the odor source located 1.5 m upstream. Letters indicate significant differences revealed by post hoc tests. (A) Compared to search times in the slowest unobstructed flow, whelks tracked more efficiently (i.e., reduced search time) in the two fastest flows. Seven tracks were analyzed for each of the unobstructed treatments. (B) Compared to search times in unobstructed flow of the same velocity, whelks tracked more efficiently when the cylinder obstruction introduced turbulent mixing at the odor source. Five tracks were analyzed for each obstruction treatment.

Discussion

Results of this study confirm that slow-moving whelk predators successfully track prey chemicals in turbulent flows that are known to confuse faster crustaceans. Increasing current velocity by an order of magnitude yielded no significant change in the success rate of searching whelks, and flow obstructions near the odor source did not significantly diminish tracking success relative to unobstructed conditions (Figure 2.5). Compared to whelk performance in slow and unobstructed flow, total search time was significantly reduced in the fastest and most turbulent conditions tested (Figure 2.6), suggesting that turbulence can facilitate odor tracking by these animals. Similarly, crayfish foraging in flows of up to 5 cm s^{-1} had improved search efficiency in more turbulent conditions (Moore and Grills 1999) or when signal structure was modified by increasing spatial complexity at the location of odor release (Keller et al. 2001). In contrast, flow speed and bed-generated turbulence suppressed the ability of blue crabs to locate the source of attractive odor plumes (Weissburg and Zimmer-Faust 1993). These authors recorded success rates of 33 % for crabs tracking bivalve prey odors from 1 m downstream in slow flow (1 cm s^{-1}), comparable to the responses that I measured for whelks in similar conditions. However, only 10 % of foraging crabs were successful when flow velocity was increased to 14.4 cm s^{-1}, compared to the 44 % of knobbed whelks that tracked successfully in the fastest flow treatment. It is important to note that whelks began their search 1.5 m downstream from the odor source, thereby tracking over a 50 % greater distance than that previously required of blue crabs. Mixing and dilution of odors over this additional distance combined with the limited mobility of knobbed whelks make the heightened success and efficiency of these slow-moving predators even more remarkable.

According to Weissburg and Zimmer-Faust (1993), reduction of crab tracking success in more turbulent flows may be due to erosion of the viscous sublayer or homogenization of odor plume structure, both of which reduce the presence and intensity of discrete, concentrated odor filaments that blue crabs use to locate a stimulus source. In comparison, a relatively large proportion of whelks appear to overcome or even benefit from these same disturbances. One explanation for whelk tracking success depends upon their potential for collecting a temporal average of chemical concentrations. Integrative sampling over a sufficient period of time would facilitate detection of dilute odors or estimation of the mean concentration of a rapidly fluctuating signal. This strategy should allow foragers to move up a gradient of mean concentration and track chemical signals that have been modified by mixing due to shear and turbulent diffusion, particularly for slow animals such as whelks that have a limited capacity for spatial sampling. As opposed to the discrete and concentrated odor filaments that help to guide fast-moving blue crabs, a more continuous signal of lower concentration may be suitable for whelks that are predisposed for temporal integration. This notion is strengthened by the observation that whelks tracked more efficiently when prey chemicals were disrupted by a cylindrical obstruction. A recent study of blue crab responses to pulsed odor plumes has shown that periodic odor release (on for 1 s, off for 4 s) degrades both tracking success and search kinematics of blue crabs (Keller and Weissburg 2004). This time course of stimulus release is similar to the 0.2-Hz signal modulation predicted from the Strouhal number for the cylinder treatment, further indicating that search strategies are different and that whelks are integrating over a longer period.

The persistent tracking ability of knobbed whelks also could relate to their intrinsic capacity for stimulus detection across the sediment-water interface. These gastropod molluscs use their muscular foot to push through sediments, glide over obstacles, and envelop and consume bivalve prey. Gastropod foot tissue is sensitive to a large number of stimulatory chemicals and mixtures (Nielsen 1975, Harvey et al. 1987, Dix and Hamilton 1993), and the presence of prey chemicals within the matrix of sediment grains and porewater should play a critical role in informing whelks of the quality, quantity, or proximity of potential food resources. Both unidirectional flow and bed-generated turbulence facilitate advective exchange of solutes across the sediment-water interface (Huettel and Webster 2001), potentially enriching the stimulus environment surrounding whelks. Subsequent adsorption to sediment grains or incomplete flushing of porewater could retain attractive odors within the range of whelk perception, and the ability to detect and respond to chemicals in this region should enhance whelk navigational abilities in areas where waterborne cues are less accessible. I thoroughly mixed sediments in the flume before and after each trial to remove any chemicals that had become entrained, but future experiments could be designed to tease apart the relative importance of dissolved versus adsorbed cues for animal navigation.

The benefits of living in unconsolidated sediments are not restricted to chemosensory processes. Vertical movement within mud or sand provides animals with an option for refuge from adverse physical conditions as well as from predation. Knobbed whelks must dig downward when pursuing infaunal prey and often are found partially or completely buried within natural intertidal sediments. In my flume experiments, whelks routinely displayed digging and plowing behaviors rather than merely gliding across the sediment surface. This partially submerged movement should allow whelks to maintain their body position lower in the sediments in order to reduce the drag imposed on their shell by high-velocity flows, a physical constraint that has clear ramifications for foraging blue crabs (Weissburg et al. 2003). It was difficult to interpret these behaviors, however, because I provided only a 1-cm layer of sand for animals to move through. Previous experiments with a smaller deposit-feeding gastropod indicate that burial is a common response to rapid flow velocities (Levinton et al. 1995), and future studies using deeper sediments could clarify the importance of whelk burial and subsurface movement within the context of chemically mediated predation.

Importantly, knobbed whelks often leave soft sediments to forage on the harder surfaces associated with intertidal oyster reefs where burrowing is not possible (M. C. Ferner, *personal observation*). The relative advantages of hunting on shell substrates still need to be evaluated, although it is unlikely that individuals remain on the same reef over multiple tidal cycles. Oyster reefs along coastal Georgia are restricted to the middle intertidal zone (Bahr 1976), and whelks that move onto an inundated reef are quickly exposed as the tide recedes. Particularly during daylight hours in summer months, this exposure provides incentive for whelks to retreat into deeper water or softer sediments where they can bury themselves to avoid desiccation and thermal stress. Surveys of collection sites over four successive low tides in August 2003 revealed that whelks were visibly foraging on clams and oysters at night, whereas no individuals were found exposed during daylight (M. C. Ferner, *unpublished data*). It is therefore reasonable to assume that a substantial proportion of whelk foraging effort is dedicated to navigating through soft sediments during the approach to and departure from oyster reef habitats. If turbulent mixing of prey odors is indeed beneficial to foraging whelks, then water flow over oysters and other shell substrates could play an important role in guiding whelks to regions of profitable foraging areas.

The notion that physical forces can weaken the importance of predation has aided the development of theories about factors that regulate community structure. Connell (1975) and Menge and Sutherland (1976) predicted that the relative importance of predation should decrease as the foraging ability of consumers is suppressed along a gradient of increasing environmental harshness. This concept of physical stress affecting the strength of trophic interactions led to some interesting research (e.g., Menge 1978, Power et al. 1988, Peckarsky et al. 1990, Hart 1992, Rilov et al. 2004) and has proven to be especially productive in studies of marine rocky intertidal habitats (Menge 2000). For example, comparison of benthic community dynamics between different flow regimes in a Maine estuary showed that crab predation was most important in low-flow sites, whereas recruitment and particle delivery dominated the high-flow sites (Leonard et al. 1998). In contrast with the knobbed whelks that I investigated, predators that live and forage primarily on hard surfaces do not have the option for vertical retreat and therefore are faced with a different suite of challenges in the search for prey and the tolerance of hydrodynamic forces. Mobile predators in high-energy environments risk dislodgement due to both wave action and the drag associated with persistent exposure to rapid flow. Furthermore, the vigorous and often violent hydrodynamic forces in rocky habitats should quickly disperse dissolved prey chemicals, thus limiting the spatial extent of olfactory navigation.

Compared to rocky intertidal habitats, less attention has been given to the regulatory role of hydrodynamic forces within soft-sediment communities, perhaps in part due to the difficult task of quantifying the spatial and temporal distributions of resident organisms. The importance of boundary layer flow is acknowledged in processes such as larval settlement (Butman et al. 1988), suspension and filter-feeding (Wildish and Kristmanson 1993), sediment transport (Hill and McCave 2001), and biogeochemical cycling (Boudreau 2001), but only a few studies have directly investigated the impact of hydrodynamics on predator-prey interactions in sedimentary environments (e.g., Rochette et al. 1994; Finelli et al. 2000). Powers and Kittinger (2002) modified current velocity on an intertidal sand flat and found that faster flow suppressed foraging by blue crabs but had no apparent effect on the ability of knobbed whelks to locate and consume hard clams. Interestingly, whelk predation on scallops was enhanced in the high-velocity condition, suggesting that faster flow either facilitated whelk behavior or impaired the ability of scallops to detect and respond to approaching predators. Although Powers and Kittinger (2002) did not explicitly consider the role of turbulence in their study, recent evidence from laboratory experiments confirms that turbulent mixing alters the perceptual abilities of hard clams in ways that affect their susceptibility to predation (Smee and Weissburg 2006a). Particularly in areas where regular flow patterns are established, such as estuarine tidal channels, sedimentary habitats that routinely experience more turbulent flows may provide a refuge for some animals and a foraging opportunity for others. Field studies that decouple the effects of turbulent mixing and advection should help to clarify the importance of hydrodynamic forces for trophic interactions within these benthic habitats.

In general, the effectiveness of sensory or navigational strategies may have significant impacts on competitive interactions. Odor-tracking abilities largely determine olfactory search success within a specified chemical and physical environment, and hydrodynamic forces that disrupt chemical signals may provide an underappreciated mechanism for resource partitioning among consumers that differ in their chemosensory potential. For example, fast-moving crustaceans should benefit from their rapid behavioral responses and locate odorous food more quickly than gastropods where flow velocity and shear are low. On the other hand, sensory strategies employed by fast animals may limit their performance in turbulent conditions where stimulus plumes are homogenized. Slower predators therefore might have an advantage in turbulent flows due to their ability to continue pursuing prey in areas where odors are rapidly mixed and diluted. The observation that whelks track prey odors successfully in flows that inhibit olfactory searching by blue crabs suggests the need to refine generalizations about how physical factors affect trophic interactions within benthic communities. The impact of hydrodynamic variability on chemosensory interactions could mediate patterns of organism distribution and abundance, but more realistic field investigations are needed to assess the ecological implications of flow variation and its interaction with animals of different sensory capabilities.

CHAPTER 3

HABITAT HETEROGENEITY FACILITATES OLFACTORY PREDATION ON INTERTIDAL BIVALVES

Abstract

Coarse sediments in benthic environments introduce turbulence into the overlying flow and promote the mixing of informative chemicals. I modified sediment roughness in the field around experimental plots of bivalves (hard clams, *Mercenaria mercenaria*) to test the hypothesis that turbulent mixing of prey chemicals does not diminish predation by gastropods (whelks, *Busycon* sp.). Velocity measurements near the bed confirmed that shell treatments increase turbulent mixing in the region where whelks actively search for prey. Whelk predation on treatment plots was significantly higher than on control plots and suggested that whelks actually benefit from turbulent mixing of prey chemicals. However, one field site (North Cabbage Island, NCI) yielded no significant difference in clam mortality between paired shell and control plots. Simultaneous measurements of velocity over shells and natural sediments at NCI showed no significant mixing effect of the shells, in contrast with corresponding data from a nearby site. Based on time-averaged estimates of flow parameters in all sites, I conclude that high background levels of turbulence at NCI overwhelm the impact of shell fragments on chemical dispersion and render treatment and control plots indistinguishable to foraging whelks. Results of this study suggest that sediment roughness or other physical habitat features that affect animal perception may shift predator-prey encounters toward a predictable outcome and influence the community impacts of predation.

Introduction

Ecological processes are inherently linked to the physical structure of local habitats. Both abiotic and biotic habitat structure can provide spatial resources such as surface area for sessile organisms (Dayton 1971), refuges for prey (Sih 1987), and foraging grounds for consumers (Estes and Palmisano 1974). In aquatic habitats, structural features also interact with ambient fluid motion to affect the movement of gases, nutrients, and propagules (Mann and Lazier 1991), the physical stress imposed upon organisms (Vogel 1994), and the transfer of sensory information (Weissburg 2000). Local habitats have strong impacts on an organism's struggle for survival, and an important goal of ecologists is to understand how environmental factors affect individual performance and success.

Resource acquisition and predator avoidance are universal requirements for organism survival. Attainment of these goals depends not only on an organism's intrinsic abilities, but also on features of the environment that facilitate or impede activities of predators and prey. Animal encounters are inherently related to the relative densities of both predators and prey, although certain habitats may be better suited than others for foraging or avoidance behaviors. For example, structural complexity can provide cover for intermediate predators (Summerson and Peterson 1984, Prescott 1990), potentially exposing resident prey animals to greater predation risk (Micheli 1996, 1997). Certain prey species avoid detection through camouflage in complex habitats (Saidel 1988), but at the same time prey may be more vulnerable in areas where predators are difficult to detect. Predicting the impact of habitat structure on predator-prey interactions requires knowledge about how specific habitat features affect those interactions.

Coastal marine habitats encompass a wide range of bathymetry and hydrodynamic regimes, and one understudied implication of these physical features is their combined effect on the transmission of chemical cues along the seafloor. Many benthic marine animals utilize olfactory information to guide behavioral decisions related to foraging and predator avoidance (Weissburg et al. 2002b). Detailed investigations of chemosensory behaviors have revealed that turbulent mixing of chemicals can impair the ability of animals to extract sufficient information from dissolved odors (Weissburg and Zimmer-Faust 1993), and yet animals forage in complex habitats where the net effect of such mixing may not always be detrimental (Moore and Grills 1999, Mead et al. 2003). A few studies have explored the effects of hydrodynamics on olfactory foraging using field enclosures (Powers and Kittinger 2002) or small observation arenas (Zimmer-Faust et al. 1995, Zimmer et al. 1999, Finelli et al. 2000), but large-scale field experiments that manipulate turbulence are still needed to determine the importance of odor disruption for animals in nature.

The goal of this study was to examine how bed-generated turbulence alters the direct effects of predators by modifying the transmission of sensory information. Marine gastropod whelks (*Busycon* spp.) forage in soft-sediment habitats and served as a model system for investigating the effects of physical forces on chemically mediated prey search. In particular, predatory knobbed whelks (*Busycon carica*) have important direct and indirect effects on their bivalve prey (Peterson 1982, Nakaoka 2000) and continue to hunt successfully when flow velocity is increased within experimental field enclosures (Powers and Kittinger 2002). Recent laboratory experiments verified that knobbed whelks track prey chemicals over a range of hydrodynamic conditions and demonstrated significant improvements in whelk tracking efficiency in more turbulent flows (Ferner and Weissburg 2005). Understanding the ecological implications of whelk olfactory abilities requires experimental manipulation of turbulence in the field. I established prey patches in the field to test the hypothesis that turbulent mixing associated with sediment roughness does not reduce predation intensity by naturally foraging whelks. Whereas previous studies suggest that direct effects of predators are reduced in high-flow habitats (e.g., Leonard et al. 1998) or that turbulent mixing provides a refuge from benthic predators (Weissburg and Zimmer-Faust 1993), results from my manipulative field experiments suggest that elevated turbulence can increase lethal predation by facilitating chemically mediated prey search.

Materials and Methods

Animal collection and handling. Hard clams (*Mercenaria mercenaria*) were used to evaluate predation intensity by gastropod whelks (*Busycon* spp.) and were collected by hand from intertidal sediments near Savannah, Georgia (Figure 3.1). Clams were held in the laboratory for up to one week under a continuous flow of sand-filtered estuarine water (20 – 30 ‰) prior to beginning field experiments. Only adult clams ranging from 3.5 – 7.5 cm in length were included as prey animals because whelks do not typically consume clams outside this size range (Peterson 1982). Each clam was tethered to prevent empty shells from washing away before recollection. Adapting methods used by Micheli (1996), a 30-cm piece of polyvinylchloride monofilament (20-lb test) was attached to each clam with a drop of cyanoacrylate glue and then was secured with a 0.5-cm^2 strip of electrical

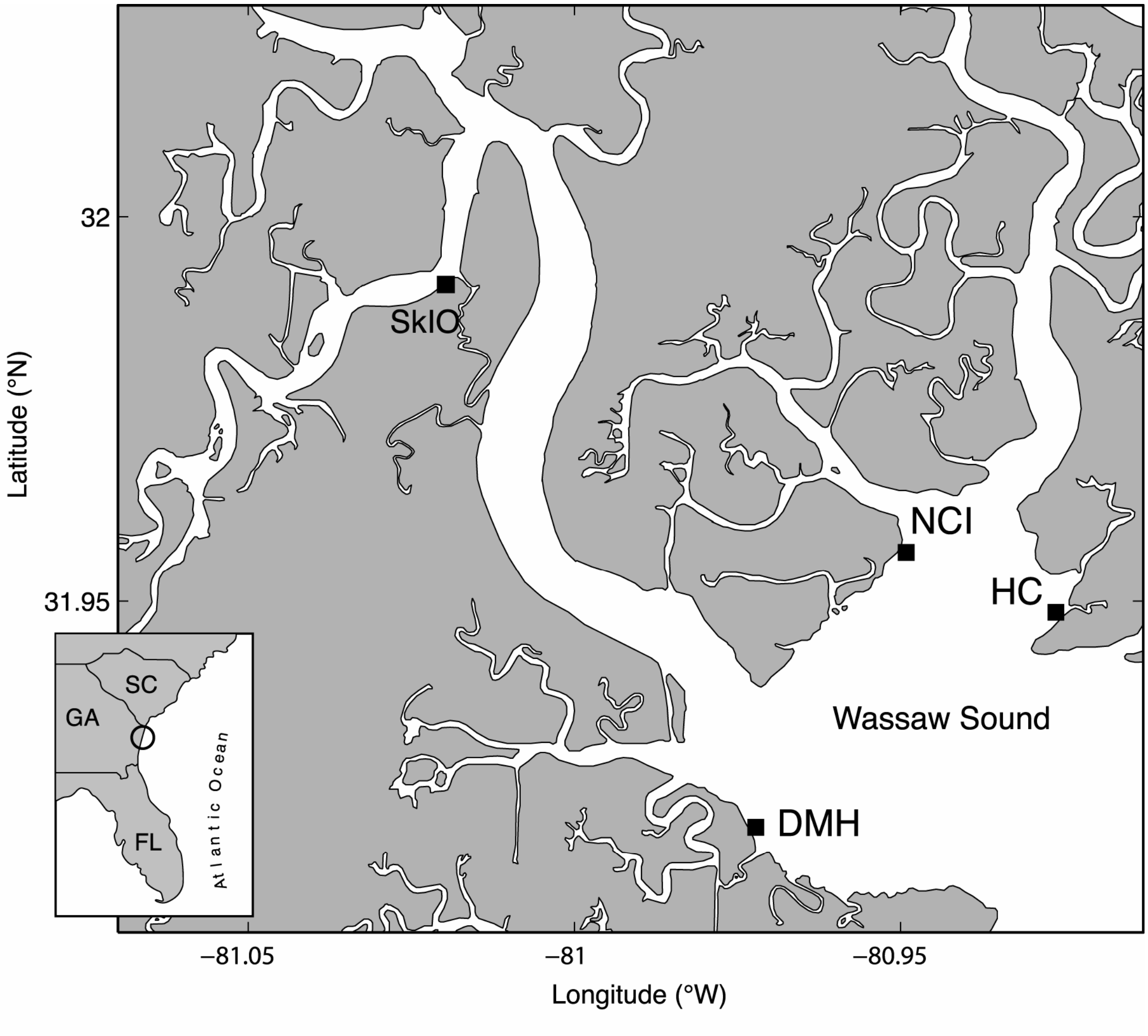

Figure 3.1. Map of field sites bordering Wassaw Sound near the Skidaway Institute of Oceanography (SkIO) in Savannah, Georgia: DMH = Dead Man Hammock, HC = House Creek, NCI = North Cabbage Island.

tape to allow the glue to dry completely without slipping. The opposite end of the tether was tied to a 10-cm metal staple that provided an anchor within the sediment while still allowing the animal to bury or readjust its position in response to the threat of predation or desiccation. Clams were transported to intertidal field sites and placed in experimental plots within 3 h of being tethered. Residual feeding marks on dead clams enabled determination of predator identity (Peterson 1982).

Predation experiments. A preliminary survey of whelk predation was conducted during March and April 2003 in a variety of soft-sediment intertidal habitats near Savannah, Georgia (Figure 3.1). Sites initially were selected based on accessibility and on the presence of unconsolidated sediments through which whelks could burrow. The upper intertidal region of each of my primary study sites contained live reefs of the eastern oyster (*Crassostrea virginica*) that were fringed by scattered patches of clams and provided habitat for a wide variety of benthic invertebrates and fish. Experimental clams were positioned 10 – 20 m from these areas of intense biological activity to avoid exposing clams to extreme levels of predatory activity. After clearing sediments of preexisting animals and shells, tethered clams were evenly distributed within square plots measuring 0.5 m on a side (12 adult clams per 0.25 m^2). This clam density (48 m^{-2}) was within the range of naturally occurring densities (Walker and Tenore 1984, Walker 1989) and provided a source of attractive prey odors for foraging whelks. Between 2 and 5 plots were placed in each of 11 different sites and harvested after 3 – 5 weeks to determine the degree of whelk predation. Subsequently, I targeted only sites where at least 50 % of established clams had been consumed by whelks during the preliminary survey.

Field experiments were conducted during 2003 and 2004 using pairs of clam plots to test the hypothesis that turbulent mixing of prey chemicals does not diminish olfactory predation by gastropod whelks (*Busycon* spp.). Plots were established during the spring tide in order to access the lower intertidal region. The placement of clams within this zone (0.0 – 0.5 ft above mean-lower-low water) afforded the slow-moving whelks a maximal period for foraging due to the extended immersion time at this tidal height. A randomly selected treatment plot within each pair was surrounded with a layer of sun-bleached oyster shells intended to generate turbulence by increasing sediment roughness, thereby mixing chemical effluents released from the clams. Approximately 0.1 m^3 of shell fragments were spread evenly and compressed until flush with the sediment surface to form a shell perimeter 0.3 m wide around the treatment plot. Sediments around control plots were treated similarly but without the addition of shells. The treatment and control plot within each pair were spaced 3 m apart at the same tidal height. Initially, 3 pairs of plots were placed in each field site on consecutive days. Adjacent pairs within a site were separated by at least 10 m to avoid interference between replicates. Plots were exposed to natural predators for 28 d and clams were then recollected and classified as alive, dead, or predated. Average clam mortality as a function of shell treatment was compared using a paired t-test.

This experimental approach was repeated during May, July, and October 2004 to determine the generality of the shell effect between field sites and seasons. During each month (representing spring, summer, and autumn), either 5 or 6 plot pairs were established for 28 d in each site. Clam mortality between treatments and controls was evaluated as before using a paired t-test, although this analysis did not test for potential site effects. An explicit comparison of the treatment effect across sites (and seasons) required preservation of the paired nature of plot deployments because predation rates varied between plot pairs within a given site. I therefore calculated an index of predation intensity (*PI*),

$$PI = P_t / (P_t + P_c)$$

where P_t is the number of clams consumed in the treatment plot, and P_c is the number of clams consumed in the paired control plot. Each pair of clam plots was assigned a single PI value representing the proportion of predated clams that originated from the treatment plot in that pair. Values of *PI* greater than 0.5 indicated that treatment clams suffered greater predation than paired control clams. A Cochran's test confirmed that sample variances were homogeneous (Underwood 1981) and a two-way analysis of variance (ANOVA) was used to determine whether or not *PI* varied between field sites and seasons. Pair-wise post hoc tests identified the source of significant differences.

Characterization of treatment effects. Previous research has verified that increasing sediment roughness acts to increase turbulence and the homogenization of odor-plume structure (Rahman and Webster 2005). Although hydrodynamic effects of rough surfaces apply logically to my shell treatments, I collected simple laboratory and field measurements of near-bed velocities to confirm that shells were an effective method of elevating turbulence within the velocity range present in the field. Initially, vertical velocity profiles were measured in a racetrack flume (Ferner and Weissburg 2005) over both sand and shells using an acoustic Doppler velocimeter (SonTek/YSI 16-MHz MicroADV) and vendor supplied software. The flume is housed at the Skidaway Institute of Oceanography (SkIO) and is capable of sustaining current speeds up to 15 cm s^{-1}. The flume was filled with estuarine water to a depth of 25 cm and the drive system was adjusted to maintain a free-stream velocity of approximately 5 cm s^{-1}. Preliminary measurements confirmed that boundary layer conditions were stable throughout the central region of the working section where all data were collected. Instantaneous velocities were recorded at 10 Hz for 2 min at various heights above graded sand and a layer of the clean shell fragments used in my field experiments. The magnitude of turbulence was represented as the root mean square of the instantaneous velocities (U_{rms}) and was calculated along with average net velocity (U) for each 2-min record.

To examine the hydrodynamic effect of shells in the field, I collected simultaneous measurements of velocity over natural sediments and shell layers within the same field site using paired ADVs (Sontek/YSI 16-MHz MicroADV and 10-MHz ADVField). The vertical extent of the sampling volume was determined in the laboratory for each probe according to methods described by Finelli et al. (1999a). Spatial resolution of the ADVs was too coarse to resolve Kolmogorov scales of turbulence in our field sites. The backscatter sampling volume for velocity measurements was a cylinder of approximately 0.3 cm^3, which is larger than typical Kolmogorov scales produced in flows similar to those in our field conditions (Mann and Lazier 1991). Probes were positioned such that the lower limits of the sampling volumes were aligned to prevent the inclusion of velocity measurements too close to the bed. Initial calibrations with probes placed side by side in the flume (for 90 s at 2 Hz) confirmed that velocities recorded by the two instruments were similar (mean ± *SD*; 5.66 ± 0.58 (10-MHz) and 5.29 ± 0.58 (16-MHz)). In all subsequent field measurements the 16-MHz probe was positioned over natural sediments while the 10-MHz probe was positioned over a 0.5-m^2 patch of shells to avoid biases when comparing sites. Each probe was mounted on a steel frame and rotated to orient the x-component receiver with the predominant flow axis and to minimize interference from the frame. The probes were spaced approximately 5 m apart at the same tidal level and vertically adjusted to the appropriate height above the sediment before beginning data collection. Instantaneous velocities were recorded onto a data logger at 10 Hz for 2 min, and sampling bursts were repeated every 10 min for approximately 24 h. Similar paired ADV data were then collected in the remaining 2 sites to confirm the consistency of shell effects in different flow regimes. Additional velocity measurements were collected above natural sediments in each field site to describe the range of flow conditions across sites. These background measurements were repeated on multiple days in each site to incorporate a representative sample of tidal ranges and weather conditions, both of which strongly affect boundary-layer hydrodynamics throughout the study area.

Prior to analysis, field flow data were extracted and filtered to remove unreliable bursts in which average velocity correlations dropped below 70%, or bursts in which the standard deviation of velocity correlations was at least an order of magnitude greater than the median value for the entire 24 h period. These corrupt bursts often reflected times when the ADV transmitter or receivers were exposed to the air, either due to the receding tide or to wave action at the level of the probe. Remaining data were used to calculate U and U_{rms} for each burst, as well as an index of normalized turbulence intensity (*TI*), which is simply the ratio of U_{rms} to U. In order to judge whether or not hydrodynamic properties were statistically distinguishable between flows over shells and control sediments, I used

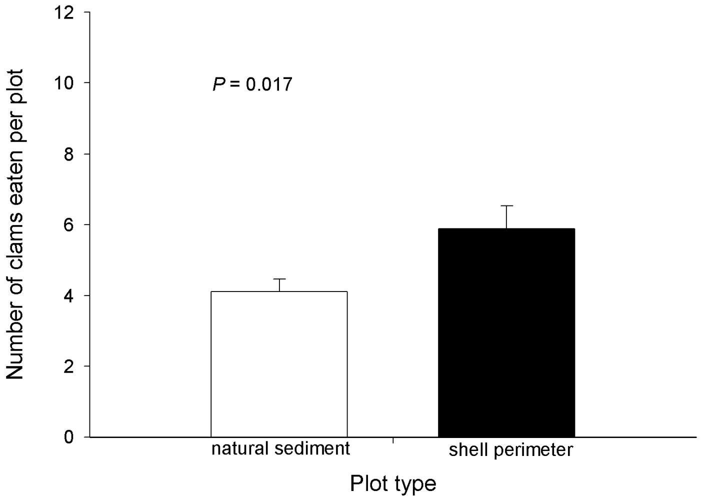

Figure 3.2. Mean number (± *SE*) of clams (*Mercenaria mercenaria*) consumed over 28 d from paired plots (*n* = 9 pairs) surrounded by either natural sediment (control) or shells (treatment).

nonparametric Mann-Whitney tests to compare burst values of both *U* and *TI* between shell and control plots within each site.

Results

Effects of surface roughness on predation intensity. Results from the initial experiment demonstrated that shell patches significantly increased whelk predation over 28 d (Figure 3.2; $n = 9$, $t = 2.98$, $P = 0.017$). Clams in treatment plots surrounded with shells experienced a 43 % increase in average mortality compared with clams in paired control plots, and diagnostic marks on the shells of deceased animals confirmed that whelks were responsible for all clam mortality. At least 3 out of 12 clams were consumed in every plot, and the maximum number of clams eaten per plot ranged from 5 in controls to 9 in treatments.

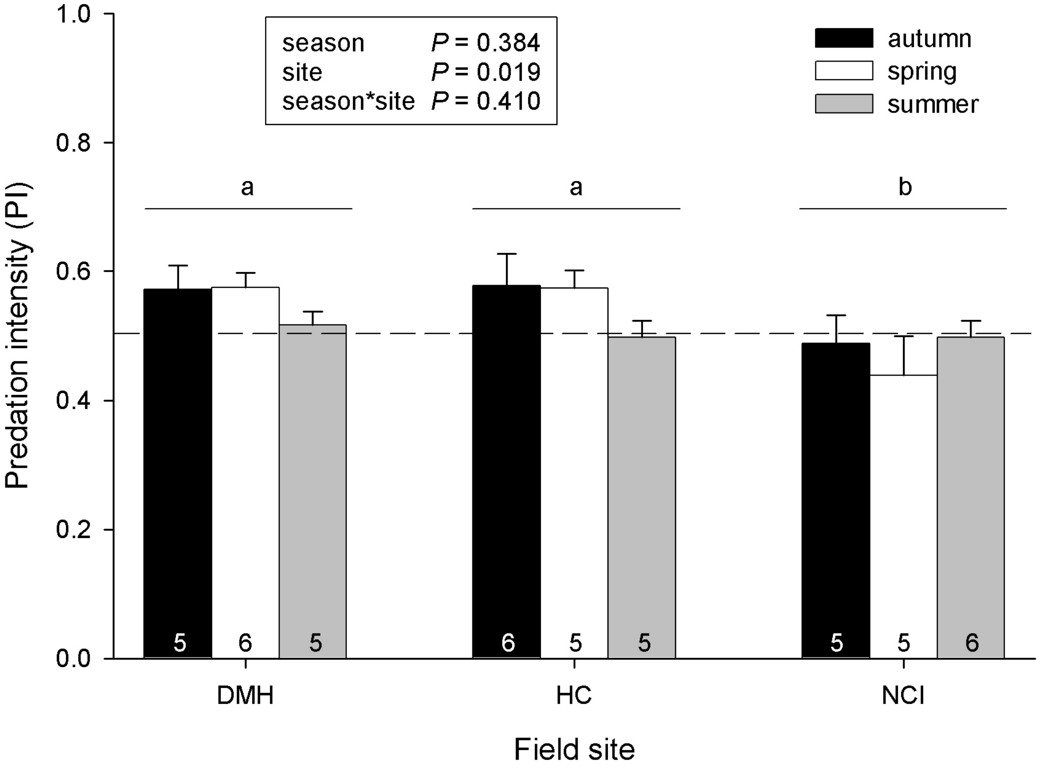

Figure 3.3. Mean proportion (± *SE*) of clams (*Mercenaria mercenaria*) consumed from the treatment plot within each plot pair. The dashed line at a value of 0.5 indicates equal predation on control and treatment clams, whereas higher values indicate greater predation on treatment clams. Sample sizes for each site and season combination are indicated at the bottom of each bar. Letters above bars denote statistical differences between sites. DMH = Dead Man Hammock, HC = House Creek, NCI = North Cabbage Island.

I repeated this predation experiment the following year to determine whether the attractive effect of shell patches was robust enough to persist between sites and across seasons. A total of 16 plot pairs were tested in each site and analysis of the combined data reconfirmed that shell treatments increased whelk predation relative to controls ($n = 48$, $t = 2.51$, $P = 0.015$). Total clam mortality in treatment plots (mean ± *SE*; 8.08 ± 0.41) was 13 % higher than in control plots (7.17 ± 0.37). A maximum of 12 clams (100 %) were consumed from treatment plots in all 3 sites, whereas no more than 11 clams (92 %) were consumed in any control plot. Of the 32 plots established at Dead Man Hammock (DMH), predation on treatment clams (9.38 ± 0.69) was 24 % greater than on control clams (7.56 ± 0.66). Similarly, at House Creek (HC) predation on treatment clams (7.56 ± 0.68) was 25 % greater than on control clams (6.06 ± 0.54). The third site, North Cabbage Island (NCI), showed an opposite pattern in which the number of clams eaten in control plots (7.88 ± 0.67) exceeded the number eaten in treatment plots (7.31 ± 0.69) by a margin of 8 %.

The index of predation intensity (*PI*) reflects the relative clam mortality in the treatment plot within each pair, thus condensing predation data for each plot pair into a single value (Figure 3.3). Results from an ANOVA of *PI* values revealed that season (spring, summer, or autumn) did not significantly affect preferential foraging on treatment clams ($F_{2,39} = 0.981$, $P = 0.384$). However, the ecological effect of shell treatments was significantly different between the 3 field sites ($F_{2,39} = 4.353$, $P = 0.019$), and Tukey-Kramer post hoc tests confirmed that shell treatments had a significant effect on *PI* at DMH and HC, but not at NCI. There was no significant interaction between site and season on *PI* ($F_{4,39} = 1.018$, $P = 0.4101$).

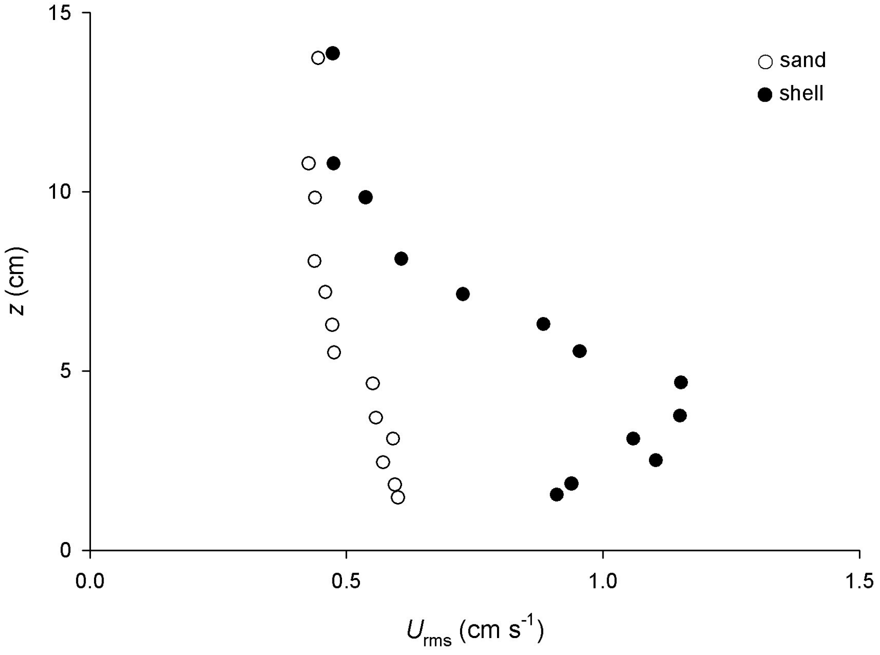

Figure 3.4. Vertical profiles of turbulence (U_{rms}) measured at various heights above sand and shells in a racetrack flume. Mean free-stream velocity was 6.1 cm s^{-1} in both conditions. Higher values of U_{rms} close to the bed reflect the turbulence associated with bed roughness, verifying the mixing effect of shells used in predation experiments.

Hydrodynamic effects of sediment roughness. Laboratory measurements of boundary layer velocities confirmed that a uniform layer of shells increases turbulent mixing compared to flow over graded sand (Figure 3.4). Measurement heights could not be precisely duplicated in each profile, but U_{rms} over shells exceeds that over sand in the near-bed region of the flow where whelks and clams reside. This physical mixing will act to homogenize and dilute any chemicals contained in water passing over the shells (Rahman and Webster 2005), effectively eroding the odor plume structure thought to be important for mediating olfactory search behavior. Thus, attractive compounds released from actively feeding clams in treatment plots should be more thoroughly mixed than those emanating from control plots.

Hydrodynamic differences between sites. Simultaneous 3-dimensional velocities were measured at 6 cm above shells and natural sediments at HC to verify that the mixing effect of shells was detectable in a natural hydrodynamic setting (Figure 3.5). The result of Mann-Whitney tests comparing net velocity and turbulence intensity (*TI*) over the 2 sediment types at HC showed that velocity was similar between conditions ($P = 0.140$) but TI was significantly greater over shells ($P < 0.001$). Even though tidal flow in this site was aligned with the channel and largely unidirectional, except during slack water periods, some variation in near-bed velocity was expected because the two probes were positioned several meters apart. Given the negligible difference in velocity over the two sediment types, the significant increase in *TI* over shells suggests that relative to flow over natural sediments, surface roughness had an even greater mixing effect in lower regions of the water column (< 6 cm above bed).

Subsequent efforts to characterize the hydrodynamic effect of shell treatments in the other 2 sites were less successful. Unfortunately, subsidence of the probe mount or erosion and deposition of sediments at DMH prevented me from obtaining paired ADV measurements at similar heights over shells and natural sediments. Matching measurement heights is critical for a meaningful analysis of these data because velocities and turbulent scales of motion vary substantially within the logarithmic region of the boundary layer. Probe heights were matched correctly at the third site (NCI), and as was the case for the data from HC, net velocity over shells and control sediments was similar at NCI (Figure 3.6; $P = 0.730$). However, a comparison of *TI* over the 2 sediment types did not show the expected mixing effect of shells ($P = 0.536$), despite the undeniable

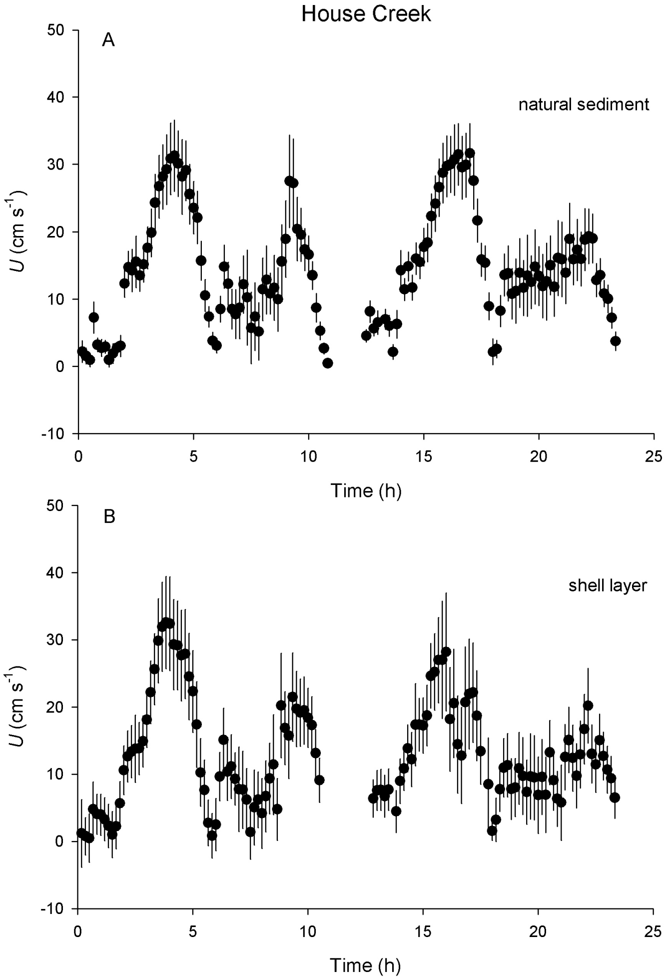

Figure 3.5. Mean velocity (± *SD*) for each 2-min sampling burst over shells and control sediments at House Creek where shell treatments significantly enhanced whelk predation.

physical effects of surface roughness on boundary-layer flow. The lack of an apparent increase in turbulence over shells at this site suggests that the mixing of water over control sediments was similar to that over shells and may help to explain why shell treatments did not enhance whelk predation at this site.

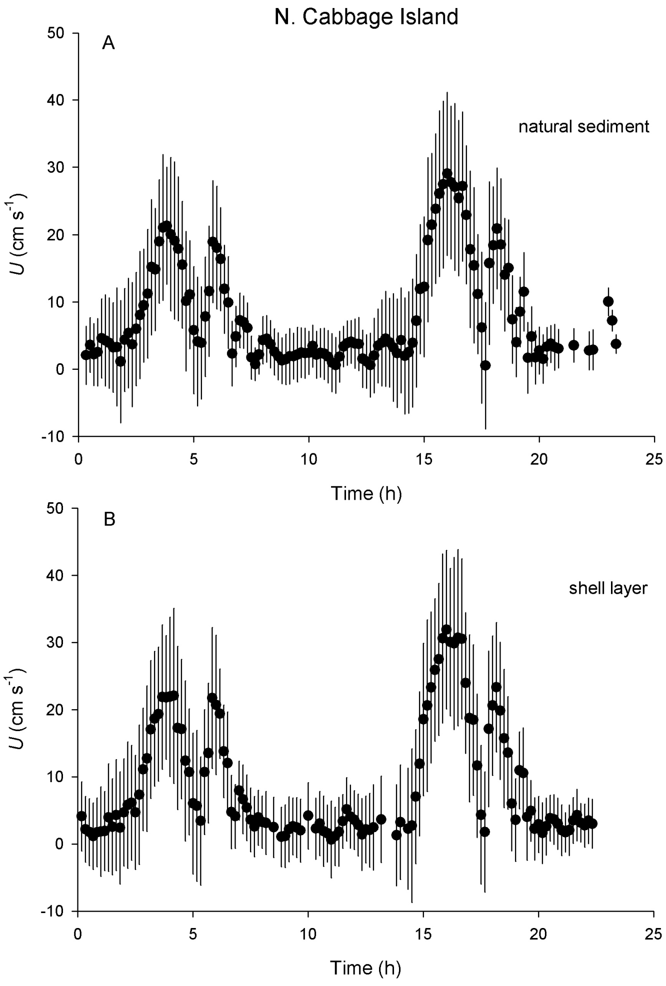

Figure 3.6. Mean velocity (± *SD*) for each 2-min sampling burst over shells and control sediments at North Cabbage Island where shell treatments had a negligible effect on whelk predation.

Finally, 5 separate days of velocity data collected over natural (control) sediments were combined to provide a general comparison of hydrodynamic conditions between the 3 field sites (Table 3.1). Including slack water periods when the probes were submerged, overall average velocity was consistently highest at HC. However, both average U_{rms} and average TI were highest at NCI, as were the maximum burst values of all 3 parameters. Another qualitative example of site differences is illustrated by a simultaneous comparison of free-stream velocity (> 18 cm above the bed) in each site (Figure 3.7). Tidal patterns within each site were not necessarily consistent from week to week and undoubtedly varied with local and regional weather patterns during the period in which predation experiments were conducted.

Discussion

The purpose of the present study was to explore the impact of habitat heterogeneity on interactions between predatory gastropods and their prey and to evaluate if sensory constraints might affect these interactions. Results from these field experiments showed that plots of infaunal clams surrounded by shell fragments were significantly more susceptible to predation than nearby control plots (Figure 3.2), indicating that isolated shell patches magnify the lethal effects of whelk predators on their prey. The observed increase in consumer pressure on treatment clams is consistent with the notion that turbulence generated by shells produces these patterns via changes in the sensory capabilities of burrowing whelks.

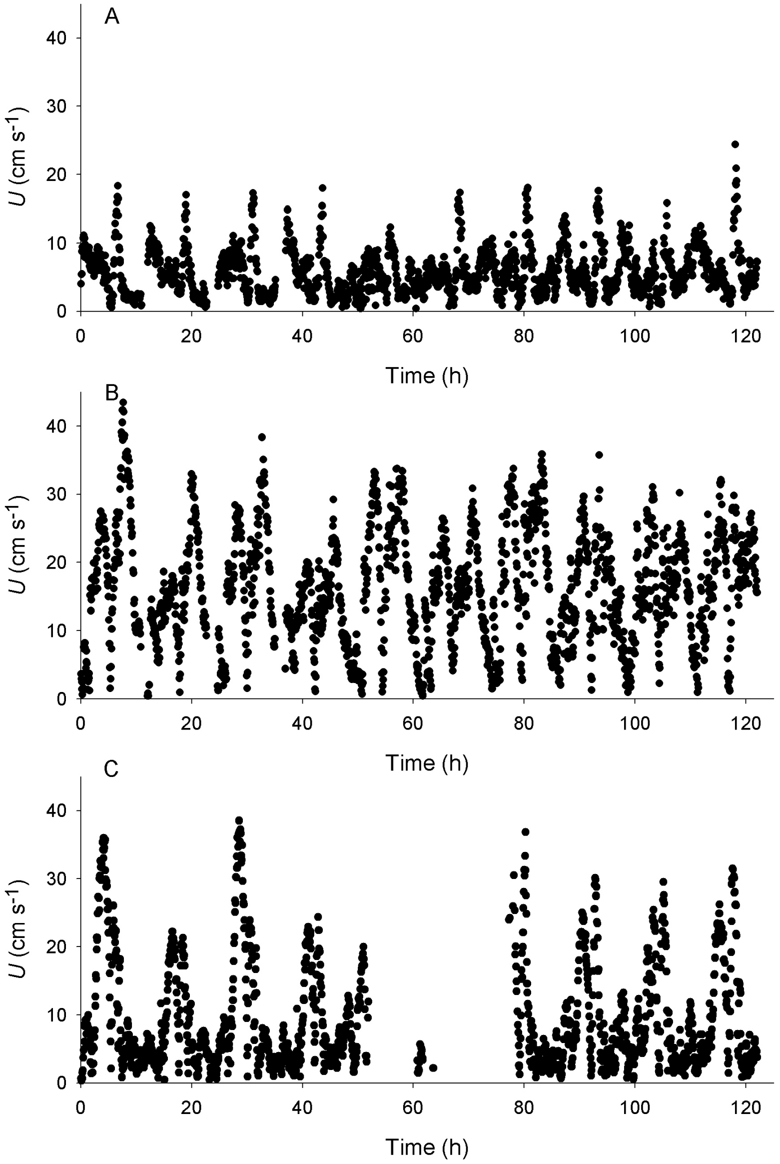

Figure 3.7. Simultaneous records of free-stream velocities collected for 5 d at a height of 18 – 20 cm above natural sediments in all 3 sites: (A) Dead Man Hammock, (B) House Creek, (C) North Cabbage Island. Missing data in (C) represent periods of extreme wave action and associated probe movement that prevented accurate velocity measurement.

Table 3.1. Summary of hydrodynamic parameters measured at 5 – 6 cm above natural sediments in field sites. The first 3 data columns represent ensemble averages of 2-min sampling bursts collected on 5 separate days. The last 3 data columns represent maximum burst values within each site. *n* = total number of sampling bursts.

Field site	mean velocity (cm/s)	mean RMS velocity (cm/s)	mean normalized turbulence intensity	maximum burst velocity (cm/s)	maximum RMS velocity (cm/s)	maximum normalized turbulence intensity	*n*
DMH	5.57	3.25	0.91	12.54	8.97	4.77	546
HC	14.01	3.71	0.38	31.79	8.13	3.04	576
NCI	10.59	7.62	1.59	34.66	14.86	9.31	520

The sun-bleached oyster shells used in these experiments do not attract whelks in and of themselves, but shells do modify the dispersion of dissolved chemicals released by their filter-feeding prey. Clams feed by actively pumping water across their gills and out an excurrent siphon that opens just above the sediment surface. Advective water motion broadcasts the location of clams to consumers by transporting chemical effluents downstream. As these dissolved cues move through space they are mixed and diluted according to local scales of turbulent diffusion (Weissburg 2000). Roughness elements on the bed, such as shell fragments, homogenize the spatial structure of chemical information and accelerate convergence to the mean concentration (Rahman and Webster 2005). Although changes in the quality and intensity of sensory information reduce the effectiveness of chemically mediated search strategies in other organisms (see Weissburg et al. 2002b), knobbed whelks are surprisingly adept at hunting in rapid flows (Powers and Kittinger 2002) and can even track chemical cues efficiently in the presence of turbulent mixing (Ferner and Weissburg 2005). The higher predation rate that I observed on clams in shell treatment plots suggests that this manipulation facilitated whelk hunting behavior, effectively increasing the attraction of whelks to treatment plots.

Relative to their fast-moving crustacean counterparts, whelks exhibit slow movement and long reaction times. One benefit of this sluggish existence is that averaging sensory inputs over long time periods could become a viable sensory strategy (Weissburg 2000). This method of encoding information reduces the need for discrete stimulus bursts that appear to underlie search strategies of faster moving consumers. From an olfactory perspective, this type of temporal sampling should avoid some of the detrimental effects of turbulent mixing (e.g., homogenization of odor filaments) and potentially broaden the time periods or habitats in which whelks can successfully search for prey by allowing them to “climb” up a gradient of mean concentration in the absence of spatial odor structure. Furthermore, much of the sensory information available to whelks is obtained by pumping water over the osphradium, an internally held olfactory organ. Physical mixing and homogenization of fine-grained odor structure associated with this internal transport could prevent whelks from responding to discrete stimulus bursts even if they moved through odor filaments more quickly. Whelks therefore may be preadapted to detect and respond to well-mixed chemical information, and turbulent homogenization of odors might even facilitate whelk tracking by presenting the animals with a more consistently mixed signal.

Another promising explanation for the observed treatment effect relates to the potential for prey chemicals to either adsorb to sediment grains or become entrained in subsurface flows. Bed-generated turbulence enhances solute exchange across the sediment-water interface (Dade 1993, Huettel and Gust 1992, Huettel and Webster 2001) and will introduce clam effluents into sediment porewater where cue retention time exceeds that of the overlying flow. Whelks regularly encounter chemicals within the sediment matrix and could benefit from porewater cues by continuing to track prey odors even after waterborne chemicals had been washed away. Similarly, the retention of prey chemicals within experimental plots could have been accentuated by shell treatments, thus providing a more enduring source of attractive cues. Although whelks most likely exploit a combination of sediment-associated and waterborne cues, a reliable determination of the relative importance of these sensory modes would require further experimentation.

Regardless of the exact mechanism, shell patches had a positive effect on whelk foraging and a negative effect on clam survivorship. Working concurrently with the same predator-prey system, Smee and Weissburg (2006a) found that clams respond to upstream whelks by “clamming up” to curb the release of chemical attractants. Even though whelks generally hunt by following clam effluents upstream, clam avoidance behaviors should be beneficial if other potential predators are foraging nearby. As whelks move across the benthos in search of prey, responses of alerted clams will modify the cues that they release and thus render the clams less detectable. Bed-generated turbulence is unlikely to deter chemosensory searching by whelks (Figures 3.2, 3.3), although the surface roughness in my experiments also could have interfered with clam perception of nearby predators, thereby encouraging a liberal release of attractive chemicals that could render treatment plots more detectable than control plots. Because related flume experiments showed that clams respond to upstream whelks even in highly turbulent flows (Chapter 4), it appears that shell treatments in the current study acted primarily to modify whelk attraction. Smee and Weissburg (2006a) propose a hierarchal scheme for predicting the net outcome of whelk-clam interactions along a gradient of turbulence intensity, and more thorough field experiments are needed to accurately assess limitations on the relative perceptual abilities of whelks and clams in a variety of conditions.

Early research in rocky intertidal habitats revealed that wave forces, physical disturbance and desiccation stress regulate the importance of predation on benthic invertebrates by interfering with predator abilities (Dayton 1971, Menge 1978). Insights from these and other studies lead to generalizations about the role of environmental stress as a determinant of community structure (Menge and Sutherland 1987), but unanticipated effects of environmental factors on sensory abilities could alter predictions of where predator effects might be important. Leonard et al. (1998) conducted a comparative study linking bulk flow regime to the relative importance of resource supply and consumer pressure on benthic community structure. Their findings suggest that consumer pressure should be reduced in high-flow environments where resource supply is maximal and where predators are impaired by strong fluid forces. However, simply comparing bulk flow between sites may not be sufficient to predict the importance of slow-moving predators such as those examined in the present study. For example, elevation of bed-generated turbulence enhanced lethal predation in sites having the fastest and slowest average velocities, but not in the site with intermediate flow (Table 3.1). Regardless of the inhibitory effects of high velocity flows, background levels of turbulence coupled with local habitat features may be largely responsible for limiting the sensory behaviors of many benthic animals.

Because foraging decisions are based on information about local resources, factors that modify predator behavior could have important ecological implications. Predators play an important role in determining patterns of community structure by directly consuming prey (Sih et al. 1985), initiating trophic cascades (Paine 1980, Carpenter et al. 1985), or altering prey characteristics in ways that indirectly affect other trophic levels (Turner and Mittelbach 1990, Schmitz et al. 1997, Trussell et al. 2003). It is necessary to understand the factors that influence chemosensory responses if we hope to predict variability in the strength of direct and indirect predator effects. Whelks targeted in the present study traverse a variety of substrates in search of prey, ranging from subtidal muds to frequently exposed oyster reefs in the upper intertidal. The primary cues that guide whelk foraging decisions are likely to be chemical, either through dissolved odors transmitted through the water or compounds entrained in interstitial pore water. Local variation in hydrodynamics has an important effect on the sensory battles between whelks and clams, and it is reasonable to expect that habitat features affecting information transfer will help to determine the strength of species interactions in a variety of systems.

CHAPTER 4
MIXING IT UP: STRUCTURAL COMPLEXITY COUNTERACTS INDIRECT EFFECTS OF A BENTHIC PREDATOR

Abstract

Predators exert direct pressure on lower trophic levels through consumption and indirect pressure by eliciting changes in prey behavior. Using clams and whelks as a model predator-prey system, I examined the possibility that increased sediment roughness reduces indirect predator effects by mixing odor cues and compromising the abilities of clams and whelks to detect and respond to each other. Initially, clams were exposed to upstream whelks in slow and fast flows over coarse sediments using a laboratory flume. Clams decreased feeding in response to whelks in both flow conditions, indicating that clams could detect whelks over a range of turbulence intensities. I then performed separate field experiments to determine if (1) clam reactions to whelks in the field increases their survival, and (2) turbulence related to sediment roughness does not interfere with this indirect effect. My general approach was to establish pairs clam plots in intertidal sediments and assess mortality after 21 d of exposure to foraging whelks. Diagnostic feeding marks on shells of deceased allowed identification of predation due specifically to whelks. In the first experiment, treatment plots contained a caged whelk at their center and paired control plots contained only an empty cage. Reduced clam mortality in treatment plots confirmed that avoidance behaviors indirectly benefited clams by reducing their susceptibility to whelk predation. In the second experiment, all plots contained a caged whelk but treatment plots were also surrounded with a ring of shell fragments that increased turbulent mixing across the plots. Greater clam mortality in

shell plots indicated that surface roughness impaired clam perception of risk and facilitated lethal predation by whelks. Results of this study suggest that environmental factors could help to explain the prevalence of lethal versus nonlethal predator effects via changes in information transfer between animals. Particularly in systems where predators initiate trophic cascades, knowledge of the relative sensory abilities of predators and prey could help to generate testable predictions of the spatial and temporal scales of predator impacts on community structure.

Introduction

Evidence from numerous ecosystems suggests that consumer pressure commonly drives the ecological processes that determine organism distribution and abundance (Pace et al. 1999, Schmitz et al. 2000, Shurin et al. 2002). Predators affect prey by direct consumption (lethal effect) and by altering prey traits such as behavior or habitat selection (nonlethal effect). Traditionally, ecologists focused on the roles of lethal predator effects in regulating community composition (Paine 1980, Sih et al. 1985), but more recent studies have shown that nonlethal predator effects can structure communities to an equivalent extent (Schmitz et al. 1997, Trussell et al. 2003).

In many cases the strength of predator effects may be dependent on habitat characteristics that reduce predator efficiency or facilitate prey avoidance behaviors. For example, structurally complex habitats often benefit prey by providing spatial refuges from predation (e.g., Menge and Lubchenco 1981, Summerson and Peterson 1984, Sih and Kats 1991, Diehl 1992, Beukers and Jones 1997). Not all habitat complexity has similar effects, however, and physical structure can also assist predators by reducing interference between individuals (Grabowski and Powers 2004, Griffen and Byers 2006, Hughes and Grabowski 2006). In a recent mesocosm study of tri-trophic interactions within oyster reefs, Grabowski (2004) demonstrated that increased structural complexity reduced the strength of lethal predation while having relatively little impact on the nonlethal effects of top predators. Similar experiments using only two trophic levels showed that at high predator densities, more complex reef structure actually increased the strength of lethal predation (Grabowski and Powers 2004). These studies highlight the difficulties in making assumptions about the role of habitat complexity within natural communities and suggest the need for careful experimentation using a variety of predator-prey combinations.

Environmental conditions may be as important as habitat structure in determining the mechanisms by which predators affect prey. For example, physical forces associated with breaking waves or rapid water flow can limit the ability of mobile predators to handle and ingest prey, thereby diminishing the lethal effects of predators on resident prey populations (Menge 1976, Leonard et al. 1998). Hydrodynamics can also modify predator effects in less obvious ways by altering the sensory abilities of predators and prey. Smee and Weissburg (2006a) suggested that reductions in prey perception caused by stimulus mixing could diminish nonlethal predator effects by reducing prey ability to detect and react to consumers. Likewise, the hydrodynamic distortion of prey chemicals also affects predator perception and could modify lethal predator effects (Weissburg et al. 2002b). Given the behavioral complexity underlying predator-prey interactions, experimental evidence from a variety of systems is needed to assess the relative importance of lethal and nonlethal predator effects on prey.

I conducted a series of experiments to evaluate how increased habitat complexity (i.e., surface roughness) affects the outcome of chemosensory interactions between marine gastropods (knobbed whelk, *Busycon carica*) and their bivalve prey (hard clam, *Mercenaria mercenaria*). In marine sedimentary environments, surface roughness provides structural complexity that affects biological and biogeochemical processes (Sternberg 1970, Eckman et al. 1981, Huettel and Gust 1992, Dade 1993). Roughness elements also generate turbulent mixing that homogenizes odor-plume structure (Rahman and Webster 2005), and I employed these properties of sediment roughness to alter the transfer of chemical information between whelks and clams. Previous research has shown that knobbed whelks can successfully hunt prey in a variety of hydrodynamic environments (Powers and Kittinger 2002, Ferner and Weissburg 2005), including those in which surface roughness elevates turbulent mixing of prey chemicals (Chapter 3). Hard clams respond to whelk chemicals by reducing their filter feeding activity (Irlandi and Peterson 1991, Smee and Weissburg 2006a), although the effect of turbulence on these avoidance responses is not well understood. The present study examines lethal and nonlethal effects of whelks on clams and the influence of turbulence on those interactions. Initial tests of clam responses to upstream whelks in turbulent laboratory flows over rough sediments revealed that turbulent mixing did not compromise avoidance responses of clams. Subsequent field experiments then addressed two related hypotheses: (1) predator avoidance behaviors of clams will lower the hunting success of whelks, and (2) turbulent mixing associated with surface roughness will not diminish these nonlethal predator effects. Results indicate that hydrodynamics and sensory capabilities interact to affect the outcome of predator-prey interactions between whelks and clams. One conclusion from this study is that efforts to predict the strength of species interactions in this and other systems should explicitly consider how environmental factors related to sensory detection alter behavioral responses of both consumers and their prey.

Materials and Methods

Laboratory tests of prey responses. Laboratory flow measurements and behavioral trials were performed over gravel sediments in a racetrack flume housed at the Skidaway Institute of Oceanography (SkIO) in Savannah, Georgia, USA. This flume is useful for simulating natural flow environments and can sustain currents of up to 15 cm s^{-1} (Ferner and Weissburg 2005). The 4x1 m working section was filled with estuarine water to a depth of 33 cm and covered with an even layer of gravel (mean diameter ± *SD*; 7.6 ± 1.7 mm; $n = 25$) to generate higher turbulence intensities than those present in flows over finer-grained sediment (as used by Ferner and Weissburg [2005] and Smee and Weissburg [2006a]). Flow speed was maintained at either 3 cm s^{-1} or 14 cm s^{-1} and an acoustic Doppler velocimeter (Sontek/YSI 16-MHz MicroADV) was used to record flow speed at a height of 5 cm above the bed in both conditions. Instantaneous velocities were measured at 10 Hz for 5 min and the root mean square of the velocity time series (U_{rms}) was used as a measure of turbulence that reflects the extent to which chemical odors are diluted and homogenized (e.g., Finelli 2000).

Knobbed whelks and hard clams were collected by hand from intertidal sediments and maintained under flow-through estuarine water in the SkIO flume facility. Previous flume experiments demonstrated that clams respond to upstream predators by retracting their feeding siphons (Doering 1982, Irlandi and Peterson 1991, Smee and Weissburg 2006a), presumably to limit the release of cues that could attract other nearby predators. I examined whether bed-generated turbulence associated with sediment roughness inhibits clam responses to whelks under controlled laboratory flows. Trials were conducted over gravel in the SkIO flume at a free-stream velocity of either 3 cm s^{-1} (slow) or 14 cm s^{-1} (fast). In both flow conditions, groups of 5 clams were acclimated in the flume for 30 min and allowed to bury in a recessed pot (diameter = 30 cm) filled with sand and positioned in the center of the working section. The number of clams with extended siphons was used as a proxy for feeding activity and was first recorded at the end of the acclimation period. Within each flow condition, replicate groups of clams were randomly assigned either to treatments in which a knobbed whelk was positioned 1 m directly upstream, or to controls in which clams were exposed only to flume water. Siphon extension was noted every 5 min for an additional 30 min after the initial observation, resulting in a total of 7 observations of feeding activity for each active clam. A nested analysis of variance (ANOVA) confirmed that the behavior of clams in this experimental setup is not biased by the responses of surrounding individuals (Smee and Weissburg 2006a), and therefore each individual clam was treated as an independent replicate. A total of 10 groups of clams were tested in slow flow (n = 50 clams) and 6 groups of clams were tested in fast flow (n = 30 clams). Individuals that did not bury or feed at the end of the acclimation periods were disqualified from the experiment, even if they were observed feeding at a later time. I used a two-way ANOVA to assess the effect of odor (whelk stimulus or odorless control) and flow (slow or fast) on the number of feeding observations per clam. Data were arcsine transformed prior to analysis to meet assumptions of normality (Sokal and Rohlf 1995).

Field tests of predator effects. Predation experiments were conducted using pairs of clam plots deployed along the edges of tidal channels and on intertidal mudflats bordering Wassaw Sound (Figure 4.1). All sites were dominated by fine-grained sediments and were bordered by salt marsh (*Spartina alterniflora*) and live oysters (*Crassostrea virginica*). In the upper and middle intertidal regions of these study sites, beds of shell hash typically extended several meters away from oyster bars. I conducted experiments in lower intertidal regions in order to maximize clam immersion time and to separate clam

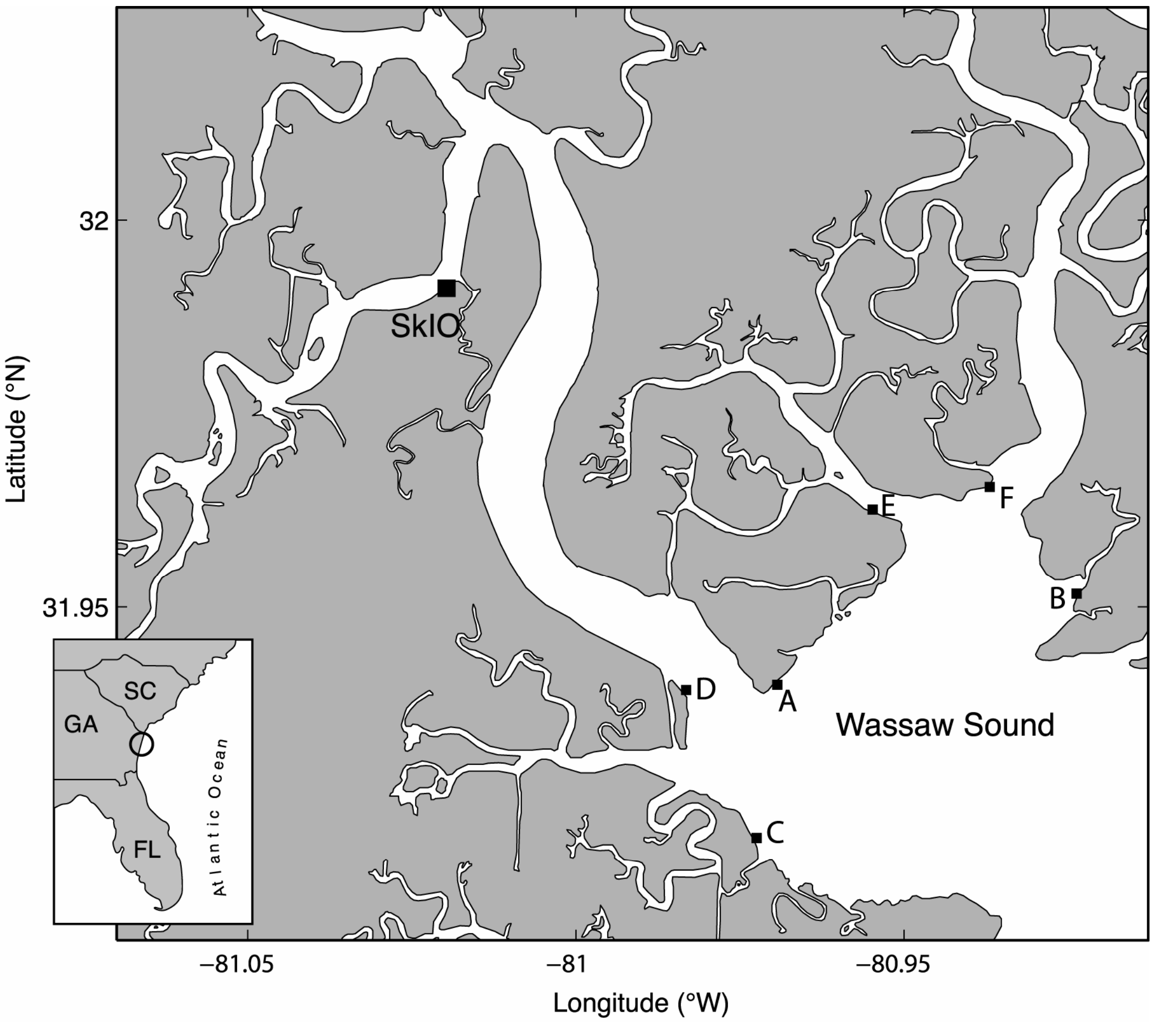

Figure 4.1. Map of study area. Prey plots were established at sites A, B and C in Experiment 1 and sites B, C, D, E and F in Experiment 2. SkIO = Skidaway Institute of Oceanography.

plots from nearby regions of shell hash. Preliminary surveys of predation intensity allowed selection of sites where hard clams consistently experienced natural whelk predation and where shell layers were not eroded or buried during the 3 week study period (M. C. Ferner, *unpublished data*). To characterize the hydrodynamic effects of shell treatments, I deployed paired ADVs (Sontek/YSI 16-MHz MicroADV and 10-MHz ADVField) and collected simultaneous measurements of U_{rms} over natural sediments and shells within the same field site. These instruments yield similar measurements of velocity and turbulence (Chapter 3).

Freshly collected clams were held in the laboratory for up to 1 week prior to experiments. Only adult clams (longest axis > 3.5 cm) were used because whelks rarely consume clams below this size (Peterson 1982). A monofilament tether (30 m length; 20-lb test) was glued to each clam and tied to a 10 m metal staple that was buried beneath the sediment when clams were placed in the field. This technique allowed recollection of empty shells after clams had been consumed while permitting living clams to freely adjust their burial depth. Whelks were fed an *ad libitum* diet of clams for at least 10 days prior to field experiments to encourage a liberal release of metabolic wastes necessary for inducing prey responses (Smee and Weissburg 2006b). Caged whelks were not fed during the 21 d of cage confinement, but immediately after experiments they were fed to satiation for at least 1 week before reintroduction to their natural habitat.

The first experiment (Experiment 1) was conducted from May-June 2003 to evaluate indirect effects of non-feeding whelks on clam survival in the field. Tethered clams (n = 12 per plot) were evenly distributed within 0.5-m^2 plots containing either a caged whelk (treatment) or an empty cage (control). Prey density in each plot (24 clams m^{-2}) fell within the natural range previously reported for this geographic region (Walker 1989). Cylindrical predator cages were constructed out of 10-m polyethylene mesh and measured 20 cm tall and 25 cm in diameter, following the basic method used by Nakaoka (2000). Cages were buried to a depth of 10 cm in the center of each plot so that whelks caged in treatment plots could retreat underground to avoid desiccation during low tide. This technique offered a conservative source of predator cues for two reasons. First, whelks that remained buried when plots were submerged would limit the release of predator cues. Second, whelks that surfaced within their cage should be apparent only to downstream clams, and since current direction shifted with the tides, only a portion of each treatment plot could be exposed to cues from whelks caged in the center of the plot at one time. Each pair of clam plots consisted of a treatment and control plot established 3 m apart at the same tidal height. Adjacent plot pairs within the same site were separated by at least 10 m to avoid interference between replicates. All plot pairs (n = 21) were established during the same spring tide and exposed to natural predators for 21 d. Tethered clams were recovered following this experimental period and the effect of whelk presence on clam mortality was evaluated using a paired t-test. Diagnostic feeding marks on shells allowed *post mortem* determination of predator identity (Peterson 1982).

Results from the first experiment suggested that caged whelks indirectly benefit clam survival. Therefore, I conducted a second experiment (Experiment 2) in May 2005 to determine whether bed-generated turbulence disrupted the indirect effect of caged whelks on experimental clams. Pairs of clam plots (n = 20) were established as before, but with two notable differences. First, both control and treatment plots contained a caged whelk, and second, I added a ring of sun-bleached oyster shells 30 cm wide around one (treatment) plot in each pair. Shells were pressed into the sediment and created a rougher surface than that surrounding control plots, allowing me to assess the effect of bed roughness on clam-whelk interactions. Preliminary flume trials indicated that whelks do not move towards shell fragments in the absence of prey odors (M. C. Ferner, *unpublished data*), and I therefore assumed that shell rings only served to alter the transmission of chemical cues released by caged whelks or by clams within the treatment plot. As in Experiment 1, both live and dead clams were recovered after 21 d and the effect of shell treatments on clam mortality was evaluated using a paired t-test.

Results

Effects of sediment roughness on turbulent mixing. Measurements of U_{rms} at 5 cm over sand and gravel in the flume confirmed that turbulence increased with both sediment roughness and velocity (Table 4.1). Of the 2 velocities over gravel in which clam behavior was observed, the fast flow of 14 cm s^{-1} produced a 51 % increase in turbulence compared with that in the slow flow of 3 cm s^{-1}. This upper level of turbulence surpassed those tested in a previous study of clam responses to predator cues (Smee and Weissburg 2006a) and represents the most turbulent conditions in which clam behavior has been examined to date. Paired ADV measurements in the field showed that shells increased the daily mean level of turbulence by 45 % relative to flow over natural sediments (Table 4.1), justifying the use of shells to increase mixing over treatment plots in Experiment 2.

Clam responses to whelks in turbulent laboratory flows. In flume experiments, upstream whelks caused clams to reduce feeding in both slow and fast flow over gravel (Figure 4.2;

$F_{1,56} = 15.89$, $P < 0.001$), indicating that turbulence associated with coarse sediments did not limit the perceptual abilities of clams. Siphon pumping behavior was not affected by either flow speed ($F_{1,56} = 0.32$, $P = 0.573$) or the interactive effects of flow and odor ($F_{1,56} = 0.001$, $P = 0.982$). Relative to siphon pumping in the absence of predator cues, clams exposed to upstream whelks reduced feeding time by 49 % in flows of 3 cm s^{-1} and 56 % in flows of 14 cm s^{-1}. The significant avoidance responses observed in these turbulent flows illustrates the acute sensitivity of clams to predator cues and suggests that clams should be capable of responding to whelk chemicals across a wide range of natural hydrodynamic conditions.

Table 4.1. Turbulence (U_{rms}) measured at 5 cm over smooth and rough sediments in a laboratory flume and on the bank of a tidal channel. Instantaneous velocities were measured at a frequency of 10 Hz using acoustic Doppler velocimetry. Sampling period for each value was 4 min in the flume and 24 h in the field. Field values represent an ensemble average of 130 (sand) and 125 (shell) measurement bursts recorded every 15 min. Corrupt bursts were filtered to avoid including times when the probes were exposed to air at low tide. Location of field measurements was site B (see Figure 4.1).

	Flow	Sediment	U_{rms} (cm s^{-1})**
Laboratory	slow	sand*	0.36
	slow	gravel	0.84
	fast	gravel	1.27
Field	variable	sand	3.38
	variable	shell	4.91

* Sand condition in the flume was characterized by Smee and Weissburg (2006a)
** U_{rms} = root mean square of velocity time series

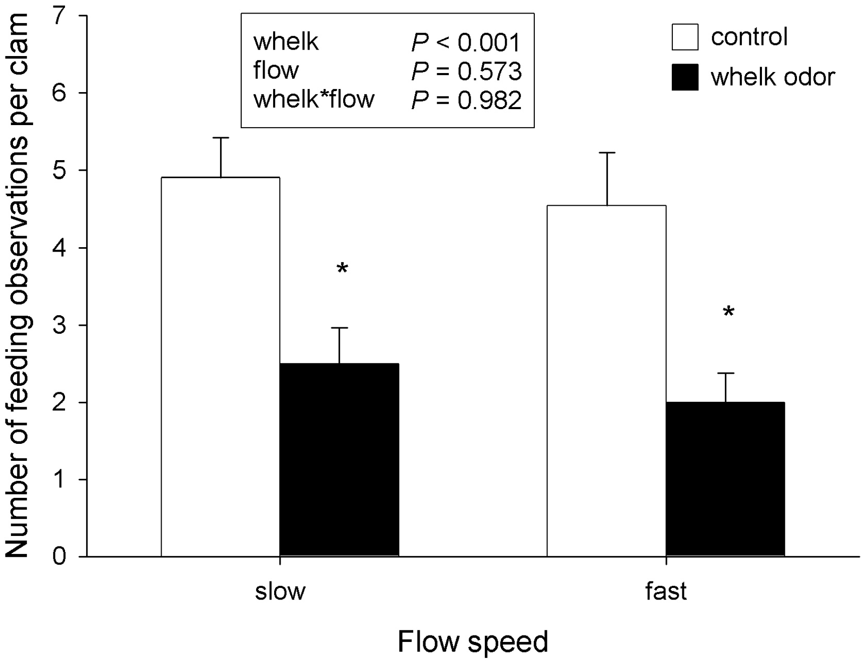

Figure 4.2. Mean number (± *SE*) of siphon pumping observations for clams (*Mercenaria mercenaria*) in slow flows of 3 cm s^{-1} and fast flows of 14 cm s^{-1} over a bed of gravel in a laboratory flume. Whelk odor trials contained a whelk positioned 1 m directly upstream from the clams, and control trials contained no predator or predator cues. Clams showed significant avoidance responses to whelks in both slow (n = 41) and fast flow (n = 19).

Lethal and nonlethal predator effects and the impact of surface roughness. All pairs of clam plots were excavated after 21 d of exposure to natural predators. All observed clam mortality was attributed to whelk predation, but 1 – 3 clams occasionally were not recovered from a given plot. A thorough search of the surrounding area often uncovered clams that had been scored as missing, but time restrictions associated with the tide sometimes prevented complete recovery from all plots. Live experimental clams were never found outside of established plots, and every clam that was recovered outside of plots had been predated by whelks and separated from its tether. Because these events were rare and an apparent consequence of tethers that had been severed during the act of predation, counts of missing clams were combined with counts of mortality attributed to whelk predation. Data from several plot pairs were discarded because predator cages had disappeared from treatment plots (or from control plots in Experiment 2). Wave action or vigorous currents most likely dislodged and washed away the missing cages. Final sample sizes in both Experiment 1 ($n = 19$) and Experiment 2 ($n = 17$) were sufficient for statistical analysis.

Treatment plots in Experiment 1 contained a caged whelk and were paired with control plots containing an empty cage. Clam mortality ranged from 0 – 92 % on both types of plots, but lower average predation on treatment plots demonstrated an indirect effect of caged predators on prey survival (Figure 4.3A). Naturally foraging whelks consumed an average of 25 % fewer clams from treatment plots than from paired control plots ($t = 2.31$, $P = 0.033$), suggesting that a nonlethal effect of predator presence significantly reduced clam mortality over the 3 week experimental period.

In Experiment 2, every clam plot contained a caged whelk and paired treatment plots also were surrounded with a shell layer that increased turbulent mixing. Clam mortality ranged from 8 – 100 % on treatment plots and 8 – 92 % on paired control plots. The hypothesis of robust clam responses was not supported since average whelk predation on treatment plots was 22 % higher than on control plots (Figure 4.3B). The increase in consumer pressure associated with shell treatments was statistically significant ($t = 2.68$, $P = 0.017$) and indicated that turbulence negates the indirect effect of predator presence observed in Experiment 1. It is important to note that the average number of clams eaten

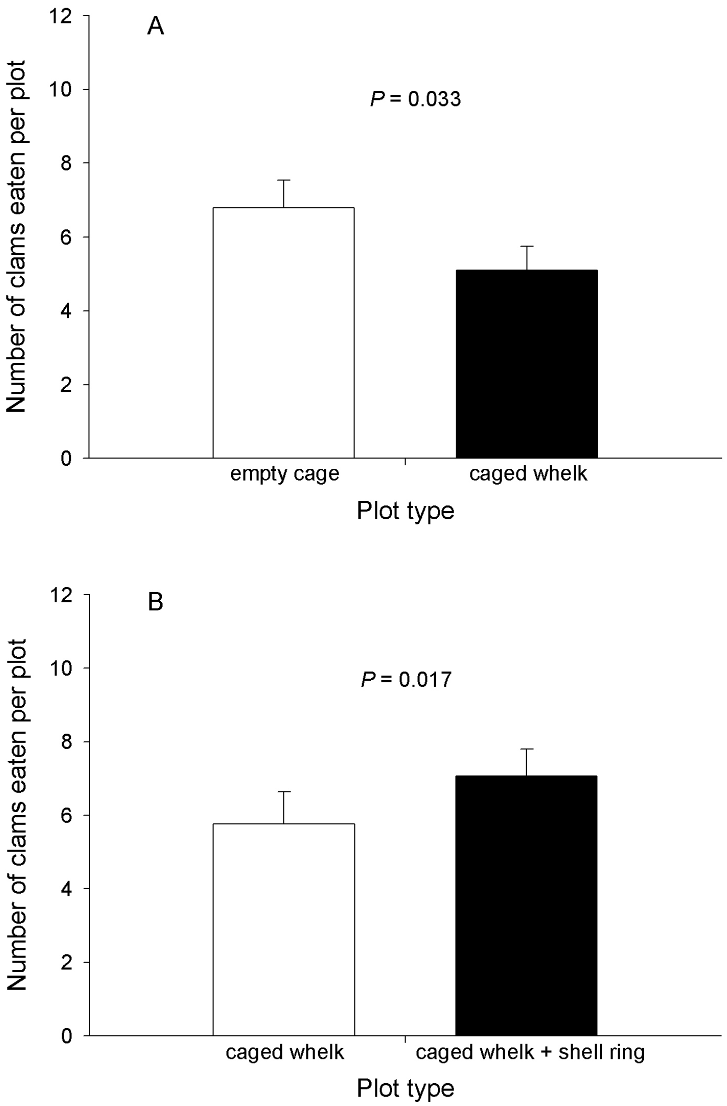

Figure 4.3. Mean number (± *SE*) of clams (*Mercenaria mercenaria*) consumed per plot. (A) Experiment 1 ($n = 19$). Treatment plots containing a caged (non-feeding) whelk were paired with control plots containing an empty cage. Reduced predation on treatment plots verified that whelk presence increased clam survival via predator avoidance responses. (B) Experiment 2 ($n = 17$). Treatment plots contained a caged (non-feeding) whelk and were surrounded with a layer of shells, whereas paired control plots contained only a caged whelk with natural sediments surrounding the plot. Increased predation on treatment plots revealed that surface roughness counteracted the effect of whelk presence.

in plots containing a caged whelk and surrounded by natural sediments was very similar in Experiment 1 (5.11 ± 0.65 clams) and Experiment 2 (5.76 ± 0.87 clams), indicating that caged whelks alone had a similar effect on clam mortality in both years.

Discussion

Lethal and nonlethal predator effects can have substantial impacts on prey populations (Lima 1998) and can cascade to affect even lower trophic levels (Schmitz 1998, Trussell et al. 2003). Knowledge of how environmental factors modify predator effects will help generate testable predictions about when and where various predator effects should be important. In the present study, a strong lethal effect of whelks on clams was illustrated by substantial levels of whelk predation on all clam plots established in the field. Whelks also affected clams indirectly by inducing behaviors that reduced subsequent losses to predation (Figure 4.3A). This result is consistent with avoidance responses of *Mercenaria mercenaria* described in other studies (Doering 1982, Irlandi and Peterson 1991, Nakaoka 2000, Smee and Weissburg 2006a), and indicates that many clams stopped feeding when caged predators were detected. These reductions in siphon pumping have been shown to limit the release of chemical effluents by clams and consequently weaken the attraction of downstream predators (Doering 1982). Smee and Weissburg (2006a) also found that caging predators near clam plots decreased predation on clams by blue crabs. The lower apparency of alerted clams provides an undeniable benefit in terms of survival, but feeding cessation also limits access to new chemical information and incurs a cost of reduced growth (Nakaoka 2000). Balancing tradeoffs between foraging and predator avoidance is a problem that many animals face (Lima and

Dill 1990), and the ecological consequences of these interactions can extend to lower trophic levels and consequently affect patterns of community structure (Werner and Peacor 2003).

Results from the present study illustrate how habitat characteristics can alter the relative importance of lethal and nonlethal predator effects on prey. Hydrodynamic data confirmed that roughness elements increase turbulent mixing in the region where chemical cues are transported (Table 4.1), and are in agreement with previous studies of roughness effects on boundary layer flow and resultant odor plume properties (Chapter 3, Weissburg and Zimmer-Faust 1993, Rahman and Webster 2005, Smee and Weissburg 2006a). Despite the acute abilities of clams to detect and respond to whelks in turbulent flow (Figure 4.2), turbulence associated with surface roughness counteracted the indirect effects of whelk presence and intensified lethal whelk predation (Figure 4.3B). This result is noteworthy because it demonstrates that environmental factors can mitigate the relative importance of lethal and nonlethal predator effects, a phenomenon that has recently received increased attention (e.g., Grabowski 2004). Roughness elements protruding from the sediment surface extract momentum from the overlying flow through hydrodynamic drag and introduce turbulence by disrupting flow streamlines. This physical mixing has irreversible effects on odor plume structure (Rahman and Webster 2005) and is known to modify olfactory search behaviors of benthic foragers (Weissburg and Zimmer-Faust 1993, Moore and Grills 1999, Mead et al. 2003, Ferner and Weissburg 2005). Previous field experiments within this model system revealed that surface roughness enhanced whelk predation on clams (Chapter 3), an effect that probably contributed to the observed increase in whelk predation on shell plots in this study (Figure 4.2B).

It is reasonable to assume that every predator will eventually become undetectable over some threshold distance within a given flow, and I propose that multiple sensory mechanisms act together to increase whelk attraction and reduce clam perception under natural hydrodynamic conditions. Although laboratory trials failed to generate enough turbulence to significantly impair clam detection of whelks (Figure 4.2), it is certainly possible that turbulence associated with the shells in Experiment 2 decreased avoidance behaviors of clams and rendered treatment plots more apparent to foraging whelks. On the other hand, turbulent mixing facilitates whelk tracking in the flume (Ferner and Weissburg 2005) and turbulence associated with shells can increase whelk predation on clams in the field (Chapter 3). Regardless of the precise mechanism, my findings are consistent with the hypothesis that some interplay between the sensory capabilities of whelks and clams drives the observed increase in predation on shell plots.

This explanation supports a previously described conceptual framework for predicting the net effect of turbulence on sensory interactions between clams and their predators (Smee and Weissburg 2006a). In highly turbulent flows, whelks are predicted to have a sensory advantage over clams due to a combination of physical interference with clam responses and facilitation of whelk tracking behavior. Results from Experiment 2 indicate that turbulence treatments increase intensity of whelk predation despite the potential for avoidance responses by clams. Whelks foraging in this study area apparently have the sensory advantage when the mixing of chemical information is augmented by an increase in sediment roughness. Turbulent mixing associated with surface roughness in very slow or very fast flows instead might favor the sensory abilities of clams, thereby intensifying the importance of nonlethal predator effects in those flows. I acknowledge that behavioral explanations applying to one set of environmental conditions may not adequately explain the outcome of other scenarios, and thus it is necessary to investigate these sensory interactions across a wide range of habitats and animal distributions before making broad conclusions.

This study demonstrated that environmental conditions help to determine the strength of lethal and nonlethal predator effects by altering relative sensory abilities of predator and prey. One implication of this study is that consumer pressure and prey survival in benthic marine communities should vary between areas of markedly different flow or along a gradient of turbulence intensity. The ecological relevance of this structuring process will depend on several factors: (1) relative sensory abilities of predators and prey in various flows, (2) spatial and temporal distribution of sediment and hydrodynamic features, and (3) density and spacing of both species within their shared habitat. A useful investigation of these factors should consider chemosensory interactions within a realistic community context. For example, preliminary surveys revealed that intensity of whelk predation within this study area was linked to the presence of established oyster reefs or scattered clumps of oysters (Chapter 3). Whelk presence within a given habitat may depend primarily on the abundance (or chemical apparency) of oysters rather than clams, and clam effluents may be relevant to whelks only in close proximity.

Experiments that test specific hypotheses about the strength of lethal and nonlethal predator effects within a sensory context will improve our ability to predict the impacts of predators on natural communities. Environmental factors affecting sensory interactions between predators and prey should be especially important in systems where nonlethal predator effects extend to lower trophic levels. For example, Trussell et al. (2003) demonstrated the cascading effects of predator cues on two parallel food chains in rocky intertidal communities. In this system, green crabs (*Carcinus maenas*) prey upon two common gastropods: carnivorous dog whelks (*Nucella lapillus*) that consume barnacles, and herbivorous periwinkles (*Littorina littorea*) that graze on fucoid algae. Crabs provide an indirect benefit to barnacles and algae through lethal predation on gastropods as well as by altering gastropod feeding activity and refuge use (Trussell et al. 2003). These behavioral interactions are chemically mediated (Palmer 1990) and will therefore depend on factors affecting chemical transport. Quantifying the effects of environmental conditions on animal sensory abilities may allow ecologists to predict the occurrence and strength of nonlethal predator effects in a variety of systems, including those in which visual or auditory cues comprise the dominant sensory modality.

CHAPTER 5
CHEMICAL ATTRACTION AND DETERRENCE OF A BENTHIC SCAVENGER IN TURBULENT FLOW

Abstract

Aquatic animals often exhibit chemically mediated behaviors that contribute to their search for resources or avoidance of predators. I used a combination of laboratory and field approaches to examine the olfactory search behavior of the channeled whelk (*Busycon canaliculatum*), a rarely investigated benthic gastropod found in subtidal waters along the eastern coast of North America. Foraging experiments conducted in controlled flow conditions of a laboratory flume revealed that odor-tracking efficiency of whelks increased in both faster and more turbulent flows. I then quantified whelk attraction to baited traps in the field to test the ecological significance of tracking responses in flow. Unmodified control traps were paired with treatment traps that had been baffled with polyethylene mesh to increase turbulent mixing of bait odors. Significantly more whelks were captured in treatment traps, confirming that hydrodynamic modification of odor dispersal can indeed have a positive effect on scavenging whelks. In a separate experiment, I used baited traps to test the hypothesis that predator cues reduce the attraction of whelks to carrion. Unmodified control traps were paired with treatment traps containing a confined predatory stone crab (*Menippe mercenaria*) in each of the trap corners. The capture of significantly more whelks in predator-free control traps indicated that the perceived threat of predation deterred whelks from entering treatment traps. Whelks that did enter treatment traps were significantly larger than those entering control traps, suggesting that large individuals may be less vulnerable to predation by stone crabs

and, thus, less deterred by stone crab odor. The results of this series of experiments suggest that channeled whelks benefit from hydrodynamic transport of attractants and can make sense of conflicting odors in stimulus-rich environments.

Introduction

Olfactory search behaviors are common among mobile organisms, particularly in aquatic systems where cue availability is prolonged by the slow rate of chemical diffusion in water (Dusenbery 1992, Stachowicz 2001). Early studies of chemical navigation by benthic marine invertebrates (e.g., Kohn 1961, Atema and Burd 1975, Hamner and Hamner 1977) quickly established the ecological significance of distance chemoreception and led to a vibrant field of investigation (Atema 1985, Zimmer-Faust 1989, Stachowicz 2001). Recent experimental and technological developments have enabled a more holistic examination of the processes driving chemical communication and the relevant scales over which these processes affect aquatic communities (Hay and Kubanek 2002, Weissburg et al. 2002b).

It is now widely acknowledged that chemical compounds released into the environment undergo important physical modifications during transport (Atema 1996, Weissburg 2000, Vickers 2000, Zimmer and Butman 2000). For example, aquatic organisms benefit from advective flows that increase the distance over which chemical cues are carried away from their source (Lapointe and Sainte-Marie 1992, Weissburg and Zimmer-Faust 1993, Finelli et al. 2000). Some researchers have observed that odor plumes can attract animals from tens of meters away (Himmelman 1988, McQuinn et al. 1988, Skaaja et al. 1998, Lapointe and Sainte-Marie 1992), but attractive distance is limited by physical changes in the concentration and distribution of dissolved odors, which eventually render them uninformative. Even in the absence of flow perturbations associated with eddies or waves, relatively small scales of turbulent mixing act to erode the fine-grained structure of odor plumes (Webster and Weissburg 2001) and may thus limit the distances over which animals can detect and respond to chemical information. Although some studies of marine crustaceans have highlighted the negative consequences of turbulent mixing (Weissburg and Zimmer-Faust 1993, Weissburg et al. 2002b), recent experiments suggest that physical mixing of odor plumes is less detrimental to other benthic animals (Moore and Grills 1999, Mead et al. 2003, Ferner and Weissburg 2005) and may actually facilitate hunting success in the field (Chapter 3, Powers and Kittinger 2002).

In addition to advantages and disadvantages associated with hydrodynamic transport of dissolved cues, aquatic animals typically benefit from chemical information related to the presence of predators (Kats and Dill 1998) or the plight of injured conspecifics (Chivers and Smith 1998). Numerous studies have explored the identity and function of alarm chemicals (Mathis et al. 1995, Chivers and Smith 1998), the effects of predator diet on their apparency to prey (e.g., Chivers et al. 1996, Crowl and Covich 1990, Huryn and Chivers 1999), and other factors affecting prey responses to predator cues (Kats and Dill 1998). Surprisingly, only a few studies have addressed the behavioral responses of mobile animals that rely on chemical information for both foraging and predator avoidance (e.g., Tomba et al. 2001, Ferner et al. 2005). It is important to understand these phenomena because chemically mediated tradeoffs between feeding and predator avoidance are costly to individuals (Ball and Baker 1996, Eklov 2000, Nakaoka 2000) and can alter community structure (Schmitz 1998, Trussell et al. 2003).

Marine gastropods are prime candidates for studies of chemically mediated foraging and predator avoidance (e.g., Rochette et al. 1995, 1997, Yamada et al. 1998), due in part to their slow movement and ease of capture. Channeled whelks (*Busycon canaliculatum*) are carnivorous gastropods that forage actively in subtidal waters along the coast of the southeastern United States (Ruppert and Fox 1988). The thin shell of *B. canaliculatum* limits their consumption of live bivalve prey to species that are also thin shelled (Paine 1962), but these whelks may also consume soft-bodied invertebrates and bivalves that are unable to close their shells tightly (Magalhaes 1948). Commercial fishermen frequently catch channeled whelks using baited traps (Walker 1988) and behavioral observations indicate that these opportunistic scavengers are stimulated by the scent of distant carrion (Copeland 1918, M. C. Ferner, *unpublished data*), but no studies to date have examined the environmental factors that affect channeled whelk foraging.

I performed a series of laboratory and field experiments to examine the olfactory behavior of channeled whelks in response to both physical and chemical factors. Initially, I exposed individual whelks to attractive chemicals in a laboratory flume to assess the effects of velocity and turbulence on whelk tracking performance. In order to test predictions originating from this flume study, I then conducted a field experiment using baited traps that were modified to enhance turbulent mixing of attractive chemicals. This approach of testing laboratory predictions in the field is critically important but rarely adopted in studies of olfactory foraging (but see Zimmer-Faust et al. 1995, Finelli et al. 2000). Given the plethora of laboratory research linking chemical cues to animal behavior, verification of the ecological relevance of these phenomena is overdue. Finally, I exposed naturally scavenging whelks to a mixture of bait and predator cues to evaluate how conflicting stimuli affect foraging responses in natural flow environments. Results from these efforts highlight the importance of considering how both chemical and physical factors interact to mediate the olfactory search behavior of aquatic consumers.

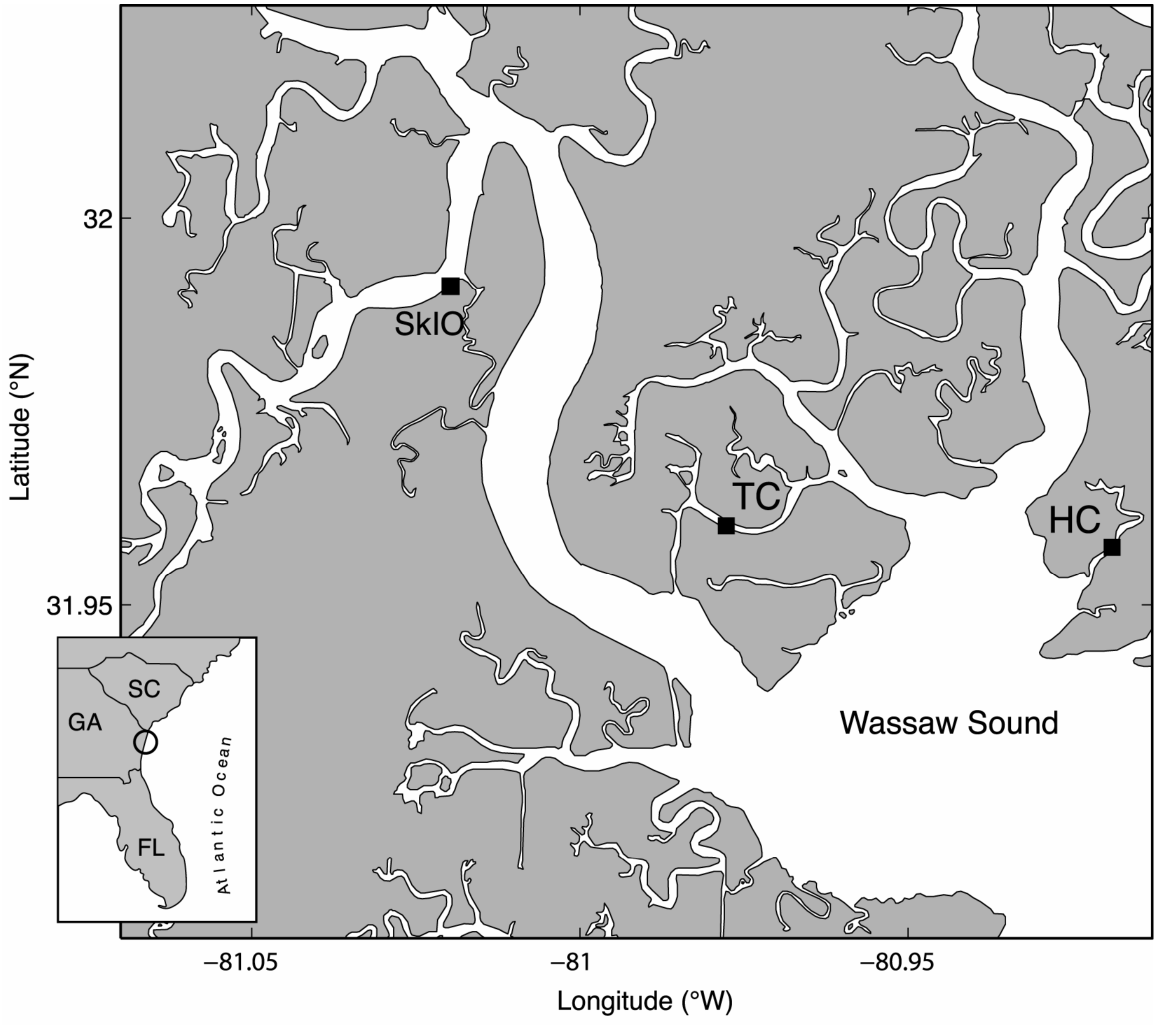

Figure 5.1. Map of study area. Channeled whelks were collected from subtidal waters of Wassaw Sound and associated tributaries using baited traps. Field experiments were conducted in 2 tidal channels: Tybee Cut (TC) and House Creek (HC). SkIO = Skidaway Institute of Oceanography.

Materials and Methods

Examination of whelk olfactory behavior. Foraging responses of channeled whelks were investigated in controlled laboratory flows to ascertain the effects of velocity and turbulence on their odor-tracking abilities. Adult whelks ranging in size from 6 – 14 cm in length were collected using commercial traps baited with dead menhaden fish (*Brevoortia* sp.) and deployed for 24 or 48 h in the subtidal waters and associated tributaries of Wassaw Sound, Georgia, USA (Figure 5.1). Traps consisted of a weighted box (61 x 61 x 50 cm) of rubber-coated 4 cm wire mesh with an entry hole on the bottom of each side. Captive whelks were transferred to laboratory tanks where they were held under flow-through estuarine water for up to 5 weeks. Whelk diet consisted of ribbed mussels (*Geukensia demissa*) and hard clams (*Mercenaria mercenaria*) that were collected by hand from intertidal sediments bordering Wassaw Sound. Mussels and clams were frozen and thawed because channeled whelks would not kill and consume these prey species in the laboratory. Whelks were fed *ad libitum* for at least 1 week after collection and then starved for 2 weeks to standardize hunger levels before trials.

Behavioral experiments were conducted in a racetrack flume housed at the Skidaway Institute of Oceanography (SkIO) in Savannah, Georgia, USA. This large flume generates smooth unidirectional flows as fast as 15 cm s^{-1} and contains a large working section (1 x 4 m) in which all manipulations were performed. Details of flume operation, hydrodynamic treatments and stimulus preparation are described in Chapter 2. Essentially, each test animal was exposed to 1 of 6 hydrodynamic conditions that included 4 unobstructed flows (U = 1.5, 5, 10, or 15 cm s^{-1}) and 2 obstructed flows (both at U = 5 cm s^{-1}). The effects of flow treatments on boundary layer turbulence (Table 5.1) and odor plume structure were previously characterized by Ferner and Weissburg (2005). In obstructed flows, a piece of polyvinylchloride (PVC) pipe was placed just upstream from the experimental odor source. One obstruction consisted of a “bump” or longitudinal half pipe of PVC (*O.D.* = 4.8 cm) placed on the sediment opening downward and aligned perpendicular to the nominal flow direction. The second obstruction was a complete “cylinder” of PVC pipe oriented vertically in the center of the flume. These impermeable obstructions served as a repeatable method to increase turbulence without changing bulk flow speed.

Hydrodynamic treatment for each group was randomly selected and test animals within each group were randomly assigned to receive either odor solution (treatment) or unaltered flume water (control). Trials began when a single whelk was transferred to a small cage 1.5 m downstream from the delivery nozzle. The cage was opened after whelks acclimated to stimulus conditions for 10 min, and whelks were given 20 min to begin upstream movement and an additional 40 min to locate the odor source. Tracking efforts were judged to be unsuccessful if whelks did not reach the delivery nozzle within 60 min of being released from the starting cage. Whelks that failed to track in response to treatment or control plumes were offered a dead mussel to confirm an adequate level of feeding motivation and individuals that did not eat the mussel within two hours were excluded from analysis. Sand was vigorously mixed after each trial to clear the working section of residual odors, and no more than 8 h of odor release were permitted before a third of the flume water (approximately 2200 L) was exchanged. Preliminary tests revealed that whelks behaved differently upon reintroduction to the flume, and so each whelk was tested only once in a single flow treatment before being released to the field.

Trials were filmed with a CCD camera mounted directly above the flume to document tracking success and to characterize search path trajectories. Images of animal location were collected at a frequency of 2 Hz, smoothed over 8 s bins and downsampled to a frequency of 0.125 Hz. Tests of flow velocity and obstruction treatments represent two different experiments and therefore were analyzed independently. Effects of velocity and obstruction treatments on the proportion of whelks that tracked successfully were evaluated using separate G-tests. Single-factor analysis of variance (ANOVA) was used to assess the effects of flow velocity and obstruction treatments on movement speed, search time, and net-to-gross-displacement ratio (*NGDR*) of successful whelks. The *NGDR* parameter represents the straightness of a path trajectory and equals the ratio of along-stream distance traveled to total distance traveled, including cross-stream meander. Prior to analysis, *NGDR* values were arcsine transformed and speed and search times were log transformed to satisfy ANOVA assumptions (Sokal and Rohlf 1995).

The effect of hydrodynamics on whelk scavenging activity was investigated in the field using pairs of baited traps in which one trap was modified to enhance turbulent mixing of chemical attractants. Extensive trapping in preparation for flume trials revealed that channeled whelks were consistently present in House Creek and Tybee Cut (Figure 5.1), and therefore I conducted the experiment in those 2 tidal channels. All traps were baited with a dead menhaden fish after the caudal fin was removed to standardize bait mass (350 ± 30 g) and provide a consistent source of attractants. Treatment traps were tightly wrapped with 1.3-cm polyethylene mesh to distinguish them from unmodified control traps having a 4-cm mesh size (described above). The smaller mesh size around treatment traps served as a baffle to break apart chemical filaments and homogenize odor plumes emanating from treatment traps, resulting in a more thoroughly mixed stimulus for whelks to track (M. C. Ferner, *unpublished data*). Over a period of 19 d, traps were deployed together in pairs (*n* = 83) such that a baffled trap and a control trap were placed in similar water depths about 5 m from opposite banks of a tidal channel. The distance between paired traps in this experiment varied with location within the tidal channels and ranged from about 10 – 20 m (the approximate width of tidal channels). Relative placement of traps was randomized within each pair and adjacent trap pairs were separated by at least 100 m to reduce interference between replicates. Traps were deployed in straight channel sections to maximize the occurrence of unidirectional flow and minimize asymmetry between the traps resulting from cross-channel flows (Li et al. 2004). Traps were retrieved after 24 h and the number of whelks captured in baffled and control traps was compared using a paired t-test. Trap pairs in which neither trap captured any whelks (*n* = 63) provided no useful information regarding the treatment effect and were excluded from analysis, resulting in a final sample size of *n* = 20.

Field test of whelk responses to predator cues. Pairs of baited treatment and control traps also were used to investigate the effect of predator odors on whelk attraction to bait. Stone crabs (*Menippe mercenaria*) are known predators of whelks (Magalhaes 1948, Kent 1983) and provided a source of predator cues for this experiment. Crabs collected from within the study area were transferred to holding tanks at SkIO and conditioned on a diet of hard clams for at least 3 d prior to experiments. All traps were baited with a dead menhaden fish after the caudal fin and posterior portion were removed to standardize bait leakiness and mass (250 ± 10 g). Average bait mass was less than in the previous experiment in an effort to reduce the concentration of attractant chemicals and increase the relative impact of predator cues. Each treatment trap was modified to contain 4 stone crabs before deployment. A single conditioned crab was imprisoned on the bottom level of each trap corner using a barrier of 1.3-cm polyethylene mesh anchored to the trap with cable ties. Confined crabs could turn around to adjust their body position but they were unable to access any animals that entered the trap. Individual crabs were used only once in these treatments before being released. Control traps were outfitted with mesh barriers in the same way as treatment traps but without crabs to control for predator presence.

Traps were deployed in the same tidal channels as before, although the experimental design differed from the previous experiment in that traps within a pair were spaced about 5 m apart on the same side of the channel and aligned perpendicular to the nominal flow direction. This closer pairing of traps (versus the 10 – 20 m separation between channel banks) was developed in a previous study of blue crab responses to conflicting cues (Ferner et al. 2005) and was intended to provide natural scavengers with a choice between treatment and control stimuli. Relative trap placement was randomized within each pair and adjacent trap pairs were spaced at least 100 m apart to reduce interference between replicates. A total of 26 trap pairs were tested in this manner over a period of 3 weeks during March and April 2003. Traps were retrieved 24 h after deployment and the number and shell length of captured whelks was recorded. Animals were then released at least 500 m outside of the active study site to reduce retesting of the same animals in subsequent trials. A paired t-test was used to compare the number of whelks captured in treatment and control traps. Because of unequal catch between trap types, an unpaired t-test was used to examine the effect of trap type on the shell length of captured whelks.

A modified version of this experiment was repeated to examine whether the physical presence of stone crabs changed odor stimulus dynamics in ways that interfered with the attraction of whelks to baited traps. Fragments of concrete blocks were substituted for stone crabs in the corners of treatment traps to provide odorless obstacles to the dispersion of bait chemicals, whereas baited control traps again contained only mesh barriers. Trap pairs were deployed as before and effect of obstruction traps on the number of whelks captured after 24 h was evaluated using a paired t-test.

Table 5.1. Summary of hydrodynamic parameters in various flow speeds and obstruction conditions characterized by Ferner and Weissburg (2005). Friction velocity (u^*) was estimated from regression of ln(z) against velocity for measurements conducted at multiple heights within the logarithmic region of the boundary layer ($r^2 > 0.95$). Note that u^* was not calculated for obstructed flows due to the lack of a well-developed log layer. Height (z) depicted here represents the measurement location of root mean square velocity (U_{rms}), an indication of turbulence intensity.

Flow speed	*Condition*	*u^* (cm s^{-1})*	*U_{rms} (cm s^{-1})*	*z (cm)*
1.5	smooth	0.14	0.35	1.46
5	smooth	0.22	0.69	1.47
10	smooth	0.52	1.15	1.81
15	smooth	0.71	1.55	1.45
5	bump	N/A	1.71	1.41
5	cylinder	N/A	4.12	1.37

Results

Odor-tracking in controlled turbulent flows. Previous characterization of flow treatments showed that turbulence increased with current velocity and was highest in obstruction treatments (Table 5.1), and that these hydrodynamic changes altered the fine-scale properties of odor plumes (Ferner and Weissburg 2005). Behavioral experiments allowed me to evaluate the effects of velocity and turbulence on tracking responses of channeled whelks. A total of 190 whelks were tested during the course of this study and 138 of these individuals satisfied the post-trial criteria for feeding motivation. Only 1 of 51 whelks exposed to control plumes tracked to the delivery nozzle, and although this single control trial also contained the cylinder obstruction, the apparent incidence of tracking behavior was probably associated with general upstream movement. Considering only those motivated foragers exposed to the odor stimulus (n = 87), a total of 62 % successfully located the upstream odor source (Figure 5.2). Tracking success rates varied from 56 – 67 % in smooth flows and from 50 – 83 % in the presence of flow obstructions. Evaluation of treatment effects revealed no significant effects of velocity treatment on tracking success rates (df = 3, $G = 0.36$, $P > 0.90$). The lack of statistically significant differences due to obstruction treatments (df = 2, $G = 3.34$, $P > 0.10$) indicated that effects of obstructions on tracking success could not be detected by the sample size used here.

Successful whelks generally proceeded directly upstream while casting their siphon back and forth in the odor plume (Figure 5.3). A total of 37 search paths were digitized and used to calculate movement speed, search time, and *NGDR* in each flow condition. Whelk movement speed across all conditions ranged from 0.19 – 1.08 cm s^{-1} and was

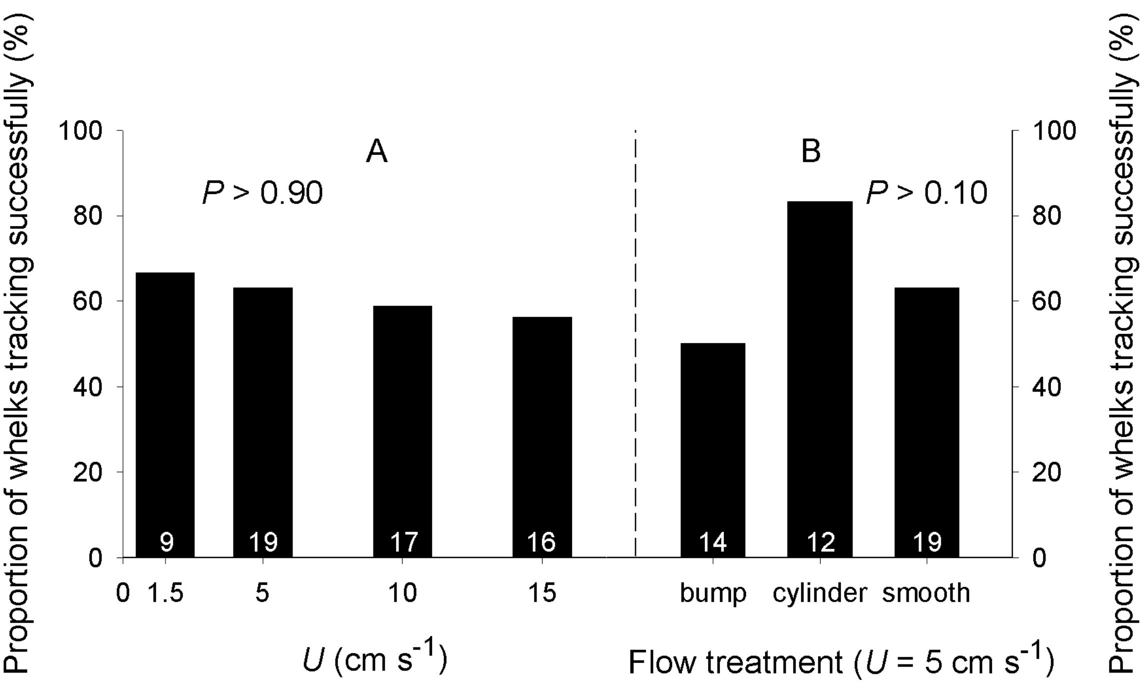

Figure 5.2. Proportion of motivated whelks (*Busycon canaliculatum*) that successfully tracked chemical odors in each flow condition. Success rates were independent of flow treatment for both unobstructed and obstructed flows. Sample sizes are indicated on the bottom of each bar.

independent of both velocity ($F_{3,21} = 0.67$, $P = 0.582$) and flow obstructions ($F_{2,15} = 0.04$, $P = 0.957$). Total search time ranged from about 3 – 16 min and was significantly affected by flow velocity (Figure 5.4A; $F_{3,21} = 6.63$, $P = 0.003$) but not by obstruction treatments (Figure 5.4B; $F_{2,15} = 0.24$, $P = 0.791$). Tukey-Kramer post hoc comparisons revealed that whelks searching in flows of 1.5 cm s^{-1} required significantly more time to reach the odor source than individuals searching in the two fastest flows of 10 and 15 cm s^{-1}. Tracking efficiency of whelks (represented by *NGDR*) ranged from 0.45 – 0.99 and

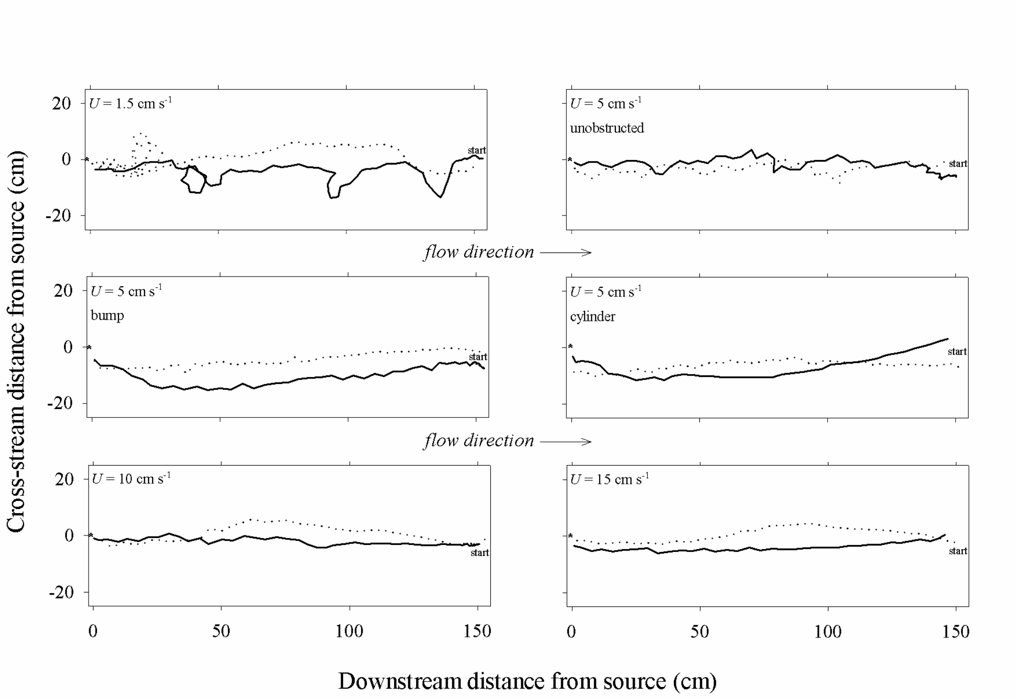

Figure 5.3. Paths representing whelk tracking behavior in each of the flow conditions tested. Trials were filmed with a CCD camera mounted directly above the flume and paths show motion of the anterior tip of an individual whelk (*B. canaliculatum*). The two paths shown for each condition represent paths having values of *NGDR* closest to the median value for that condition. Flow direction is from left to right and the stimulus source was located at 0 on the cross-stream (y) axis. Whelks began searching 150 cm downstream from the stimulus source, at the approximate coordinate of 150, 0.

was significantly affected by both velocity (Figure 5.5A; $F_{3,21} = 21.51$, $P < 0.001$) and flow obstructions (Figure 5.5B; $F_{2,15} = 7.15$, $P = 0.007$). Post hoc comparisons found that path trajectories in the two slowest flows were significantly different from each other and from the two faster flows, although trajectories in the two faster flows were statistically indistinguishable. Bump obstructions did not have a significant effect on whelk tracking, but post hoc analysis showed that cylinder obstructions caused whelks to follow a more

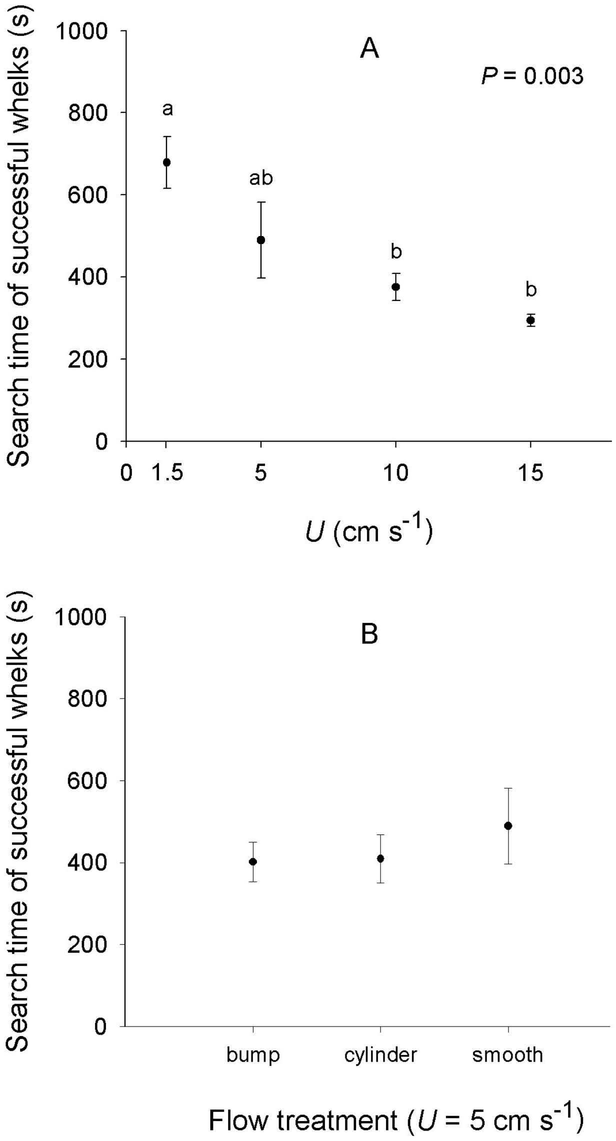

Figure 5.4. Average search time (± *SE*) required for successful whelks (*B. canaliculatum*) to navigate from the starting cage to the odor source located 1.5 m upstream. (A) Compared to search times in the slowest unobstructed flow, channeled whelks tracked more quickly in the two fastest flows. Number of paths analyzed for the unobstructed treatments of U = 1.5, 5, 10 and 15 cm s^{-1} were 4, 7, 8 and 6, respectively. Letters denote significant differences revealed by post hoc tests. (B) Number of paths analyzed for the bump, cylinder and smooth treatments were 4, 7 and 7, respectively.

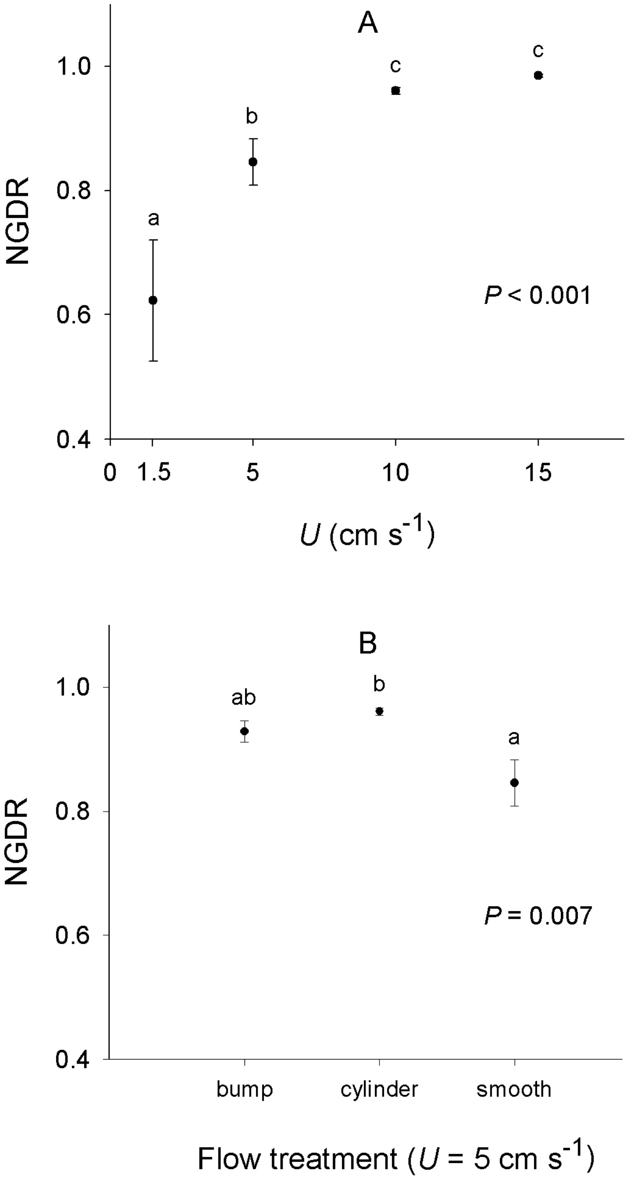

Figure 5.5. Average net-to-gross-displacement ratio (*NGDR*; ± *SE*) reflecting the straightness of search path trajectory for successful whelks (*B. canaliculatum*). A value of 1.0 would indicate a completely straight path between the starting position and odor source. Letters denote significant differences revealed by post hoc tests. (A) *NGDR* increased with flow speed, with significant differences among all but the two fastest flows. Number of paths analyzed for the unobstructed treatments of $U = 1.5$, 5, 10 and 15 cm s^{-1} were 4, 7, 8 and 6, respectively. (B) *NGDR* was significantly higher in the presence of a cylinder, relative to the unobstructed flow condition. Number of paths analyzed for the bump, cylinder and smooth treatments were 4, 7 and 7, respectively.

direct path than that followed by individuals searching in unobstructed flows of the same velocity. This result is an important illustration that whelk search behavior is affected by turbulent modifications of odor plume structure independent of differences in free-stream velocity.

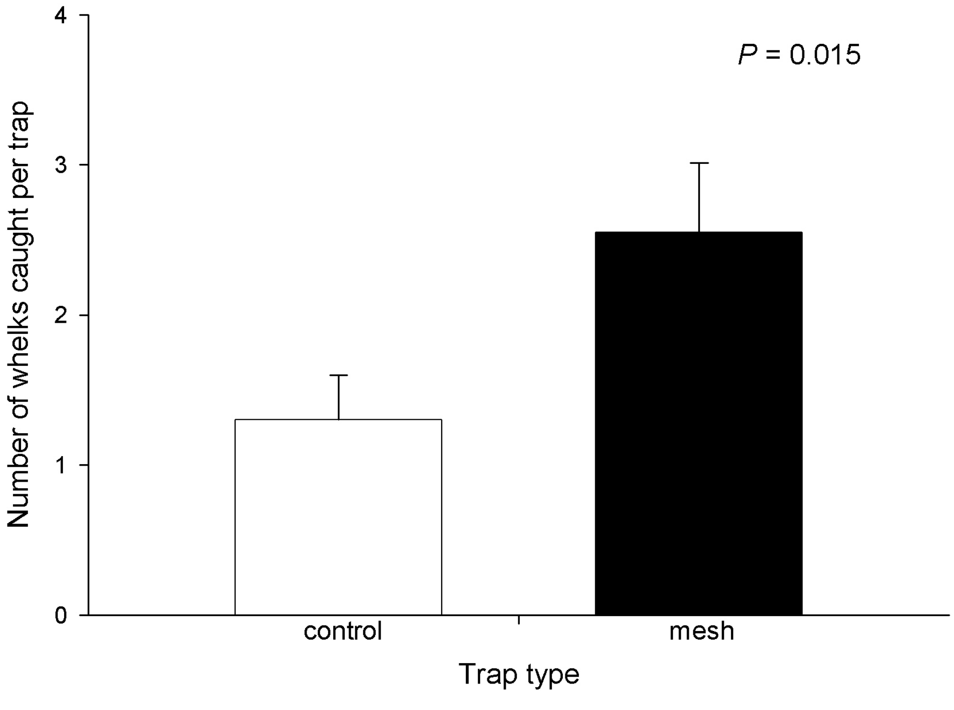

Figure 5.6. Mean number (± *SE*) of whelks (*B. canaliculatum*) that entered baited traps subjected to different hydrodynamic conditions for 24 h. Mesh (treatment) traps baffled to increase turbulent mixing of bait odors caught significantly more whelks than unmodified control traps deployed on opposite channel banks (n = 20 pairs).

Turbulent mixing enhances attraction to baited traps. The first field experiment compared the number of whelks captured in baited traps that were subjected to different levels of turbulence. Traps that were baffled to increase mixing of bait odors attracted twice as many whelks as unmodified control traps deployed on the opposite channel bank (Figure 5.6; $n = 20$, $t = 2.66$, $P = 0.015$). I purposefully selected the 2 study sites in which I captured the most consistent numbers of scavenging whelks in preliminary trap surveys, but even within these sites 76 % of trap pairs failed to attract any whelks.

Predatory crabs deter whelks from entering baited traps. The second field experiment used pairs of baited traps to test whelk responses to conflicting chemical cues emanating from bait and predatory stone crabs. Treatment traps containing stone crabs captured only 33 % of the mean number of whelks entering paired control traps (Figure 5.7; $n = 19$, $t = 3.32$, $P = 0.004$), indicating that the presence of stone crabs deterred whelks from entering baited traps. Stone crabs also had a significant effect on the size of the whelks that did enter traps (df = 62, $t = 2.19$, $P = 0.033$), as illustrated by comparing the mean shell length of whelks captured in treatment (14.4 ± 0.6 cm) vs. control traps (12.9 ± 0.3 cm). A follow-up experiment using concrete blocks in place of stone crabs confirmed that corner obstructions alone did not reduce whelk attraction to treatment traps ($n = 14$, $t = 1.24$, $P = 0.232$), with a trend towards more whelks entering obstructed traps (3.0 ± 1.0) relative to paired control traps (1.6 ± 0.3). This result suggests that chemical cues released by stone crabs were responsible for the observed decrease in whelk responses to attractive bait odors.

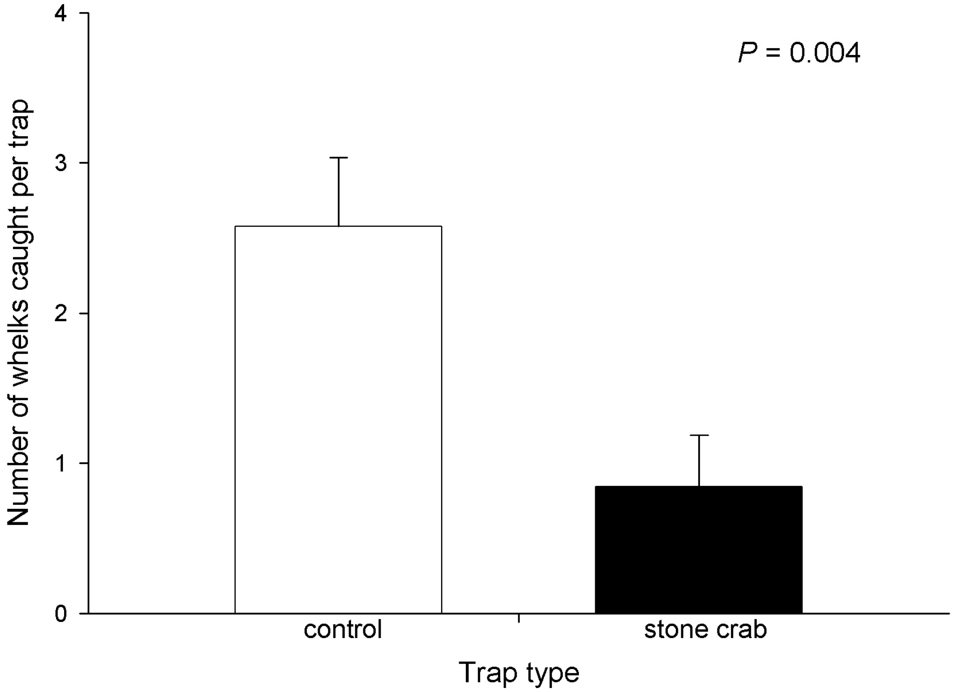

Figure 5.7. Mean number (± *SE*) of whelks (*B. canaliculatum*) that entered traps containing bait and predatory stone crabs (treatment) or only bait (control). Treatment traps presented scavengers with conflicting chemical cues and captured significantly fewer whelks than paired control traps deployed only 5 m away (*n* = 19 pairs).

Discussion

Behaviors that facilitate resource acquisition and predator avoidance are critically important for animal survival. This study investigated how environmental conditions modify chemically mediated search and avoidance behaviors of channeled whelks. Results of laboratory and field experiments indicate that physical and chemical factors have important effects on the olfactory responses of these benthic marine gastropods.

Exposing whelks to plumes of attractive chemicals in a laboratory flume showed that they can track odors successfully over a range of hydrodynamic conditions (Figure 5.2). Average search time was highest in the slowest and least turbulent flow of 1.5 cm s^{-1} and decreased significantly in the two fastest flows (Figure 5.4). Locating the odor source more rapidly resulted from improvements in tracking efficiency rather than an increase in movement speed. Path trajectories tended to be more direct (i.e., more efficient) in faster flows, as shown by an increase in *NGDR* with flow velocity (Figure 5.5).

One explanation for the observed reduction in cross-stream deviations could relate to the increase in hydrodynamic drag that whelks will experience in more rapid flows. Both cross-stream movement and shell rotation associated with siphon casting will increase the surface area exposed to oncoming flow, thereby magnifying drag forces experienced by the animal. Reduction of turning behaviors should minimize drag effects and could lead to more direct search paths. Drag forces have been shown to affect chemically mediated foraging by blue crabs (Weissburg et al. 2003) and could certainly influence whelk search behavior in similar ways. However, drag-induced changes in whelk posture cannot fully explain my results because improvements in tracking efficiency also occurred when turbulent mixing was increased without a change in bulk flow velocity. Compared with search behavior in unobstructed flows of 5 cm s^{-1}, search paths were significantly more direct when a cylinder obstruction was placed just upstream from the odor source (Figure 5.5). Turbulence associated with bed roughness shortens the time needed to obtain estimates of mean concentration within an odor plume (Rahman and Webster 2005), and thus, whelks could benefit from turbulent mixing by responding to temporal averages of odor properties. Siphon casting and meandering behaviors do suggest that some spatial information may be useful to foraging whelks, however, and further studies are needed to convincingly demonstrate the relative importance of these different sampling methods.

Field tests with both species showed that whelk olfactory capabilities have important implications for foraging success in natural habitats, verifying laboratory observations of improved whelk performance in the presence of turbulent mixing. Increased bed roughness showed that turbulence can facilitate whelk predation on clams (Chapter 3), and the use of baffled traps in the present study suggests similar benefits of turbulence for the scavenging behavior of channeled whelks (Figure 5.6). The greater number of whelks captured in baffled traps supports results of the flume study in that turbulent mixing of bait chemicals appears to facilitate odor-tracking behavior across a wide range of natural hydrodynamic conditions. Few researchers have tested laboratory predictions of olfactory search behavior in natural hydrodynamic conditions (e.g., Zimmer-Faust et al. 1995, Finelli et al. 2000), in spite of the fact that controlled laboratory flows do not capture all of the environmental factors that influence stimulus structure and animal behavior. Visual observations of another soft-sediment gastropod (*Buccinum undatum*) suggest that large-scale current fluctuations limit foraging and predator avoidance behaviors of downstream animals (McQuinn et al. 1988, Lapointe and Sainte-Marie 1992, Rochette et al. 1997), and future efforts to test the ecological relevance of olfactory search behaviors should be productive.

Based on results of the baffled trap experiment, it is difficult to reach conclusions about the spatial or temporal scales over which flow-induced changes in the structure of chemical information will be important. One confounding factor relates to temporal variation in the magnitude and direction of tidal flows within the study area. Maximum current velocities of 72 cm s^{-1} were measured near the mouth of Tybee Cut (unpublished data), and the 6 h cycle of flow reversal with the tides will produce a wide range of velocities with substantial periods of little or no flow. The periodicity of these tidal changes could offset the apparent challenge that they present by allowing animals to anticipate a regular cycle of favorable and unfavorable conditions. If whelk foraging effort is concentrated during specific times or in areas characterized by suitable flow conditions, then variation in hydrodynamic parameters could help to explain patterns of resource use and consumer pressure. For instance, flow through tidal channels interacts with local bathymetry to generate secondary circulation patterns (Elston 2005, Li et al. 2004) that might lead to persistent large-scale eddies or vertical flows. Channeled whelks living on the bottom of sinuous tidal channels could perceive certain regions of the benthos as profitable foraging tracts, whereas other areas might be avoided due to restricted availability of chemical information. Despite variability in boundary-layer turbulence associated with tidal forces or bathymetric features, the relatively unidirectional flows present in estuarine tidal channels (Li et al. 2004) should have a cumulative and beneficial effect on the chemosensory foraging efforts of whelks and other benthic macrofauna.

It is important to consider how different species respond to physical modification of odor cues if we hope to predict patterns of consumer pressure in these variable environments. For example, scavengers should experience strong selective pressure to detect and locate food resources as quickly as possible. Stockton and DeLaca (1982) proposed the idea that scavengers should only respond to concentrated carrion odors that represent a nearby odor source. Their rationale was that animals closest to nutritious food falls would be the first to detect and respond, particularly in environments such as the deep sea where ambient current velocities are sluggish or nonexistent. In most oceanic environments carrion is a limited commodity, but it would be counterproductive to expend valuable energy moving towards distant odor sources that are likely to be consumed first by other individuals. Gastropod whelks move more slowly than most scavengers, averaging top velocities of only 0.52 cm s^{-1}. One way of offsetting this disadvantage might relate to their ability to continue pursuing carrion in flow conditions that confuse faster moving scavengers. Blue crabs (*Callinectes sapidus*) are voracious carnivores that commonly enter baited traps and move quickly towards upstream carrion. Advective transport of food odors is critical for crab foraging success in the field (Zimmer-Faust et al. 1995, Finelli et al. 2000), although turbulent mixing can inhibit their olfactory abilities and reduce subsequent tracking success (Weissburg and Zimmer-Faust 1993, Weissburg et al. 2002a). In turbulent conditions where crabs are unable to forage efficiently, whelks may be able to continue searching upstream for small pieces of carrion, thereby reducing competition with other scavengers.

Whelks, like all attentive animals, are interested not only in the spatial and temporal characteristics of chemical information, but also in the composition and quality of that information. The dynamic interaction between positive and negative stimuli should dictate foraging behavior of many animals, and yet studies of chemically mediated tradeoffs in marine systems are relatively rare (e.g., Rochette et al. 1995, Tomba et al. 2001, Ferner et al. 2005). The second field experiment tested the interactive effects of odors derived from carrion and predatory stone crabs in order to determine how scavenging whelks respond to conflicting stimuli within their natural habitat. Stone crabs are known predators of channeled whelks (Magalhaes 1948, Kent 1983) and the survival benefits of whelk avoidance behaviors are supported by my own observation that stone crabs readily attack and consume whelks in laboratory holding tanks. Relative to predator-free control traps, significantly fewer whelks entered baited traps containing stone crabs (Figure 5.7). I found no significant difference in whelk attraction to traps when treatment crabs were replaced with concrete blocks of equivalent size, confirming that crabs did not impede the dispersal of bait odors and suggesting that dissolved predator cues were responsible for whelk responses. Recent flume experiments demonstrated that whelks terminate search behaviors when chemical cues from stone crabs are introduced just upstream of a food source (M. C. Ferner, *unpublished data*), further supporting a chemosensory mechanism for whelk avoidance behavior. Some prey animals respond most intensely to predators that have recently eaten individuals of closely related species (e.g., Jacobsen and Stabell 1999, Chivers and Mizra 2001), but this tactic may only be useful in response to specialist predators. In my field study, whelks responded to stone crabs even though the crabs had been fed a diet of clams, suggesting that these thin-shelled gastropods may be wary of cues released by a variety of generalist predators.

The importance of avoidance behaviors should extend from a subset of the population rather than from every alerted individual, and not all prey animals will reduce their foraging effort when exposed to threatening cues. Results from the experiment with stone crabs reinforce the notion that after animals achieve a size refuge from predation, their incentive to avoid predators diminishes and consequently their patterns of consumption and avoidance differ from what is observed for smaller individuals (e.g., Harvey et al. 1987, Harvey and Brown 2004). The chemosensory and behavioral mechanisms underlying differential whelk responses to predators have yet to be examined, and hypotheses targeted at the benthic macrofauna hold promise for ecological investigations of chemical signaling processes, particularly when the role of complex stimuli are considered within a realistic hydrodynamic context.

For animals such as whelks that rely upon chemosensation, physical and chemical factors affecting conspecific attraction should parallel those that modify foraging behavior. Therefore, it is reasonable to extend conclusions of the present study to chemically mediated processes of mate attraction. During their reproductive season, whelks tend to form mating aggregations with multiple males (< 6 cm) gathered around a single, large female (≈ 20 cm). I have observed several such mating aggregations in shallow subtidal waters along the edge of a broad mud flat in Wassaw Sound. Males presumably locate females using waterborne pheromones, and a seasonal migration onto tidal mud flats may be a mechanism for facilitating this search effort. Hydrodynamic disturbances or persistent predator presence in these habitats could interfere with the pheromone-tracking behavior of small males, potentially disrupting the formation of successful mating aggregations. Careful investigation of chemosensory interactions among consumers and potential mates should consider the impact of physical processes and the role of predator cues within an ecologically relevant context.

CHAPTER 6
CONCLUSION

Research combining theory, laboratory experiments, and field verification form a powerful tool for approaching interdisciplinary questions. In this dissertation, initial motivation was drawn from theoretical predictions of Weissburg (2000) that animal size and speed of movement should relate to spatial and temporal strategies of chemosensation. Departing from traditionally popular studies of benthic crustaceans, I began by examining the search behavior of whelks under controlled laboratory conditions that were dynamically similar to simple flows in the field. I then conducted a series of manipulative field experiments in order to explicitly test laboratory predictions about the foraging capabilities of whelks and the avoidance behaviors of their prey. I am now revisiting the flume to test the importance of hydrodynamics sensory cues in other predator-prey interactions. Continued iterations between laboratory and field approaches should generate insights that will expand our theoretical understanding of the environmental context of sensory behavior and predator-prey dynamics. Ultimately, I hope to broaden these studies to explore how physical factors affecting sensory interactions could be interpreted on landscape scales as a function of the distribution of “favorable” and “unfavorable” habitats.

An important ecological implication of my research lies in the evidence for environmental modification of interactions between predators and prey. Predators play a critical role in regulating community structure through lethal consumption (Paine 1966, Estes and Palmisano 1974, Carpenter et al. 1985) as well as through nonlethal changes in prey behavior (Turner and Mittelbach 1990, Trussell et al. 2003). The net impact of predator activities can generate direct and indirect trophic cascades in communities (Abrams et al. 1996), but a realistic understanding of these processes is limited by our ability to predict spatial and temporal patterns of various predator effects (Werner and Peacor 2003). By quantifying the relationship between environmental conditions and sensory abilities, we can begin to understand when and where foraging and avoidance behaviors of different taxa might be most successful. For example, if the perceptual abilities of a dominant predator are limited in certain habitats, then prey animals could gain a large enough advantage to survive there. Apparently disadvantaged foragers, such as the slow-moving whelks examined in this study, might search for food resources in areas or during times when environmental conditions render odor cues useless to faster-moving consumers. The persistent tracking ability of whelks in turbulent flows also could provide an additional advantage in areas where turbulence limits the ability of prey to detect the presence of nearby predators. In general, sensory interactions (e.g., chemical, visual, or auditory) among a wide variety of predators and prey could be better understood by applying the approach that I followed in this dissertation.

Given the ecological and economic significance of many estuarine animals, including clams (Arnold 2001), gastropods (Anderson & Eversole 1984), and crabs (Ehrhardt 1990), knowledge of how these species' sensory interactions are regulated by environmental conditions might aid in the conservation and management of these populations. For example, if humans altered hydrodynamic conditions through dredging or widening of tidal channels, then foraging and predator avoidance abilities might be compromised enough to jeopardize local populations. Through the study of species interactions across a variety of natural flow conditions, we could develop models to predict the biological consequences of proposed changes to hydrodynamic regimes.

Perhaps the most far-reaching and broadly important benefit of interdisciplinary research lies in its use as an educational tool. The realm of sensory ecology provides educators with an opportunity to entice students of all ages into the exploration of diverse scientific topics. Fascinating examples of animal sensation that operate within definable physical constraints and that involve familiar signals and sexy behaviors can capture the imagination of even the most restless pupil. Given that we live in a highly educated and informed society, the remedial level of scientific literacy in our country is a clear limitation to global progress. Fields such as marine chemosensory ecology should be used broadly as tools with which we can connect the fields of physics, chemistry, oceanography, biology, geology and environmental science. Following from the principles and suggestions of the recent National Oceanic and Atmospheric Association educational guidelines (NOAA 2004), we, as scientists, should strive to facilitate the integration of real experimental science into K-12 and undergraduate education. Sincere efforts to bring the excitement of scientific process to our schools will create a public that is more willing to financially support basic scientific research and encourage bright, motivated students to consider a career in research science. I genuinely hope that interdisciplinary research such as that described in this document will inspire and assist educators in their struggle to tempt students with real world examples of the links between physical, chemical and biological principles.

The functioning of ecological communities is ultimately dependent on the decisions and activities of individual organisms. Scaling up from studies of sensory behavior can lead to useful predictions of large-scale processes, but there will always be more to learn by narrowing our focus back to the organism. After all, careful examination of individuals is often what allows us to explain the patterns that we find in nature. Considering how fluid mechanics affects animal development, functional morphology, and sensory behavior should paint a realistic picture of animal capabilities that will hopefully lead to meaningful ecological conclusions. Whatever the scale or discipline of investigation, listening to the world with a vision of odors and sensations should illuminate the connections that echo ecosystem function.

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