

Habitat complexity alters lethal and non-lethal olfactory interactions between predators and prey

Matthew C. Ferner^{1,*}, Delbert L. Smee², Marc J. Weissburg³

¹University of California-Davis, Bodega Marine Laboratory, PO Box 247, Bodega Bay, California 94923-0247, USA

²Texas A&M University-Corpus Christi, Department of Life Sciences, 6300 Ocean Drive, Corpus Christi, Texas 78412, USA

³Georgia Institute of Technology, School of Biology, 310 Ferst Drive, Atlanta, Georgia 30332, USA

ABSTRACT: Habitat complexity often modifies rates of prey capture by visual predators, but little is known about how structural features affect non-visual olfactory consumers. Laboratory studies indicate that turbulent water flow over complex bedforms mixes chemical information in ways that confuse some olfactory foragers but improve the odor-tracking abilities of burrowing gastropods (whelks *Busycon* spp.). We augmented bottom roughness in a soft-sediment estuary to test the hypothesis that turbulent mixing of chemical attractants in the field increases whelk predation on hard clams *Merccenaria mercenaria*. Thin flat layers of shell fragments around the perimeter of experimental clam plots increased turbulent mixing of prey odors relative to those emanating from control plots. Assessment of prey mortality after 4 wk of exposure revealed that whelk predation on clams surrounded by shells was significantly higher than on clams surrounded by natural sediment. A second set of experiments showed that open prey plots containing a centrally caged (non-lethal) whelk experienced lower mortality due to avoidance responses of prey, but surrounding those plots with shells counteracted the non-lethal predator effect and led to significantly greater consumption by naturally foraging whelks. Shell treatments did not increase prey feeding or reduce predator interference. Results suggest that whelks hunt more successfully when bottom roughness increases turbulent mixing of prey chemicals or disrupts prey abilities to detect and respond to predator odors. When integrated over time, habitat-related differences in chemical transfer and olfactory behavior could have important implications for populations of both predators and prey.

KEY WORDS: Prey search · Predator avoidance · Sensory behavior · Hydrodynamics · Turbulence

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Ecological processes are inherently linked to the physical structure of local habitats where organisms interact with the environment and each other. Structurally complex habitats can benefit prey organisms by providing physical protection from predators (Menge & Lubchenco 1981, Peterson 1982) and by interfering with the abilities of predators to detect, capture and handle prey (Crowder & Cooper 1982, Sponaugle & Lawton 1990, Persson & Eklöv 1995). Many of these effects of habitat structure on consumer interactions result from a decrease in the abilities of visual predators to perceive and encounter prey (Main 1987, Diehl 1992, Beukers & Jones 1997). Such alterations of predator efficiency can subsequently influence the persis-

tence of prey populations as well as species richness and diversity (Summerson & Peterson 1984).

Just as habitat complexity hinders prey search and predator avoidance by visual animals, structural features that modify the spread of dissolved chemicals can alter cue detection and response by olfactory animals. Many benthic consumers adjust their behavior in response to chemical cues released by upstream organisms (Stachowicz 2001), and hydrodynamic processes that affect cue dispersal can have important effects on the performance of both predators and prey (Weissburg et al. 2002). For example, food resources become more detectable when gradual changes in current direction expose a greater number of downstream consumers to attractive odor plumes (Lapointe & Sainte-Marie 1992). Flow around vertical structures, like

*Email: mcferner@ucdavis.edu

submerged vegetation, mixes odor filaments and dilutes the information contained in waterborne cues (Finelli 2000). Even a relatively minor increase in bottom roughness generates turbulence that disrupts the transfer of chemical information along the seafloor (Rahman & Webster 2005) and can impair the ability of benthic predators to navigate effectively (Weissburg & Zimmer-Faust 1993, Jackson et al. 2007). Despite an abundance of carefully controlled laboratory studies examining olfactory behavior, little is known about how habitat structure interacts with benthic boundary-layer flow to affect natural foraging patterns. A few studies have explored effects of hydrodynamics on olfactory foraging using field enclosures (Powers & Kittinger 2002) or observation in small natural areas (Zimmer-Faust et al. 1995, Zimmer et al. 1999, Finelli et al. 2000), but large-scale field experiments that manipulate bottom roughness (and turbulent mixing) are still needed to determine the ecological importance of habitat features that modify chemical dispersion.

Intertidal molluscs living in soft sediments provide an excellent model system for investigating effects of bottom roughness on chemosensory interactions. Burrowing gastropods (whelks *Busycon* spp.) are not visual foragers and instead rely on olfaction to detect and locate prey such as hard clams *Mercenaria mercenaria*, which likewise use chemical cues to detect the threat of nearby predators. Previous research demonstrated that knobbed whelks *B. carica* have important lethal and non-lethal effects on their bivalve prey (Peterson 1982, Nakaoka 2000). In contrast to paradigms based on the behavior of fast-moving crustaceans (Weissburg 2000), laboratory experiments have shown that knobbed whelks exhibit substantial improvements in odor-tracking efficiency in the presence of bed-generated turbulence (Ferner & Weissburg 2005). If heightened searching ability translates into greater hunting success in the field, then whelks should locate and consume more prey in areas where bottom roughness increases ambient turbulence relative to that present above smooth sediments. Furthermore, the non-lethal (indirect) effects of whelks via avoidance responses of their prey should be suppressed by bottom roughness through increased attraction of whelks and/or diminished prey responses, as has been shown for clams responding to nearby predatory crabs (Smee et al. 2008).

The goal of this study was to examine how bottom roughness alters predation intensity in the field through modification of odor exchange between predators and prey. We established pairs of clam plots in intertidal soft sediments and then increased structural complexity (and turbulent mixing) around treatment plots to test the hypotheses that bottom roughness (1) increases rates of olfactory predation by naturally

foraging whelks, and (2) suppresses non-lethal effects of whelk presence on clams by disrupting or counteracting predator avoidance behaviors. We augmented bottom roughness only in a narrow region surrounding (but not within) prey plots to mix chemicals contained in near-bed flows without introducing physical barriers to predation or vertical structure that could interfere with predator movement. Whereas earlier research indicates that direct effects of predators are reduced in high-flow habitats (e.g. Leonard et al. 1998) or that turbulence provides a refuge from benthic predators (Weissburg & Zimmer-Faust 1993), results from our experiments suggest that turbulent mixing associated with bottom roughness can both interfere with non-lethal predator effects and increase predation intensity by whelks in soft sediments.

MATERIALS AND METHODS

Site characteristics. Intertidal field sites in coastal Georgia, USA (Fig. 1), were selected to target spatially distinct whelk populations. The upper region of these sites contained live oyster *Crassostrea virginica* reefs that served as habitat for a variety of benthic invertebrates and fish. Predation experiments were conducted in soft sediments 10 to 20 m away from these areas of intense biological activity to provide discrete odor sources for foraging whelks and to avoid effects of vertical structure and tightly packed shell hash. Relevant habitat features were quantified at the elevation of experiments in our 3 primary sites (Dead Man Hammock [DMH], House Creek [HC] and North Cabbage Island [NCI]).

Sediments: Samples of unconsolidated sediment ($n = 3$ per site, spaced 20 m apart) were collected from the upper 0.01 m of sediment at mean lower-low water (MLLW). Samples were wet-sieved to separate the sand fraction ($>63 \mu\text{m}$) from the mud fraction (silt plus clay, $<63 \mu\text{m}$). Retained sediment was dry-sieved and the filtrate was analyzed with a Sedigraph (Model 5100, Micromeritics). Sediment surface cover was documented using 0.5 m^2 quadrats ($n = 10$ per site) haphazardly positioned along the MLLW contour. Photographs taken from above each quadrat allowed determination of percent area occupied by sand or mud, shell fragments, algae and macrofauna (ImageJ 1.37). The height and wavelength of ripples were also measured in each quadrat because these features represent a scale of roughness that can influence olfactory behavior (Finelli et al. 2000).

Hydrodynamics: Current velocities were recorded at 10 Hz in 2 min bursts every 15 min at a height of 0.04 to 0.06 m above natural sediments at MLLW using an acoustic Doppler velocimeter (ADV) (10 MHz

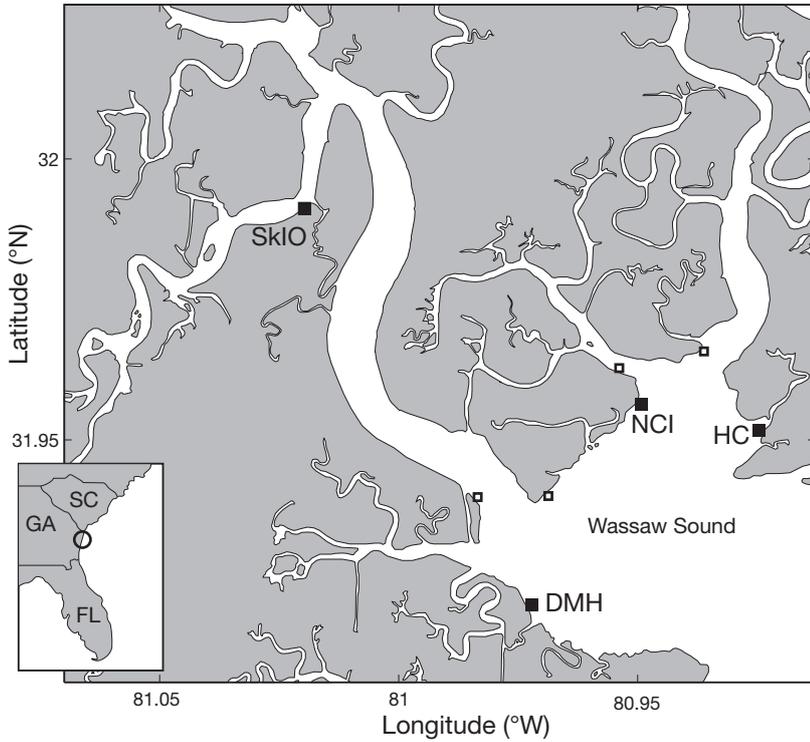


Fig. 1. Field sites bordering Wassaw Sound near the Skidaway Institute of Oceanography (SkIO) in Savannah, Georgia, USA. Prey plots were used to assess effects of bottom roughness on olfactory predation in Expt 1 at sites Dead Man Hammock (DMH), House Creek (HC) and North Cabbage Island (NCI). □: additional sites where prey plots and centrally caged predators were used to assess effects of bottom roughness on non-lethal predator effects in Expt 2

ADVField, Sontek/YSI). Measurements were repeated at each site on 6 different days scattered over 8 wk to incorporate a representative sample of conditions. Velocities were rotated onto principal axes, averaged in the x , y and z directions (u , v and w , respectively) and used to compute net velocity (U) for each burst. An index of turbulence intensity (TI) allowed comparison of mixing conditions across a range of velocities and was calculated as:

$$TI = \frac{\sqrt{(u_{rms})^2 + (v_{rms})^2 + (w_{rms})^2}}{\sqrt{u^2 + v^2 + w^2}} \quad (1)$$

where u_{rms} , v_{rms} and w_{rms} are root mean square velocities for each burst (e.g. Jonsson et al. 2006). Because velocity fluctuations associated with waves could compromise estimates of TI, a relative measure of wave action at each site was determined by calculating the root mean square wave amplitude (A_{rms}) or pressure signal measured with the ADV (Denny 1988).

Physical effects of shell treatments. Laboratory flow: Vertical velocity profiles were measured in a racetrack flume over both sand and shells using another ADV (16 MHz MicroADV, Sontek/YSI). The 1 m wide flume was filled to a depth of 0.25 m and free-stream velocity was

maintained at 0.06 m s^{-1} . Instantaneous velocities were recorded at 10 Hz for 2 min at various heights (0.01 to 0.14 m) above a 0.02 m layer of graded sand as well as a 0.02 m layer of the shell fragments used in predation experiments (mean \pm SD: shell length = $0.062 \pm 0.026 \text{ m}$, shell width = $0.020 \pm 0.006 \text{ m}$; $n = 100$). Values of TI were calculated for each velocity record as described previously.

Odor transport: Effects of shells on odor transport were quantified in the flume at a free-stream velocity of 0.06 m s^{-1} using a neutrally buoyant ethanol/saltwater solution (Ferner & Weissburg 2005) released 0.2 m upstream of the leading edge of the shell layer. Downstream concentrations were measured with a conductivity probe (MSCTI Model 125, Precision Measurement Engineering) held 0.02 m above either sand or shells at the same location where velocity data were collected. This process was repeated 3 times over each sediment type to obtain the average number and concentration of stimulus peaks (i.e. odor filaments) that exceeded the baseline value recorded before each trial.

Field flow: Velocities over sand and shells were measured simultaneously in the field to confirm hydrodynamic effects of shell treatments in naturally varying flows. One randomly selected ADV was positioned over natural sediment on a tidal flat while the other ADV was positioned over the center of a 0.36 m^2 patch of shells placed approximately 5 m away at the same tidal height (0.0 to 0.2 m above MLLW). In each of 7 field locations, velocities were recorded at 10 Hz in 2 min bursts every 15 min for approximately 24 h. Daily averages of U and TI measured over shells and natural sediments were compared using paired t -tests.

Expt 1: Lethal predator effects. Expt 1 tested the hypothesis that turbulent mixing of prey chemicals increases predation intensity. Clams measuring 0.035 to 0.075 m in length were collected by hand and tethered with a 0.3 m piece of monofilament line tied to a 0.1 m metal staple to provide an anchor within the sediment while still allowing burial or readjustment by the clams. Tethered clams were evenly distributed within square plots measuring 0.5 m on a side (12 adult clams per 0.25 m^2) established 0.0 to 0.2 m above MLLW. This clam density (48 clams m^{-2}) was within the naturally occurring range (Walker & Tenore 1984) and provided a source of attractive odors for foraging whelks.

Oyster shells comprise natural roughness elements on tidal flats and were used in our experiments to alter fluid flow around prey. Approximately 0.03 m³ of sun-bleached shell fragments (dimensions stated above) were spread evenly until flush with the sediment surface to form a shell perimeter 0.3 m wide around a randomly selected treatment plot within each pair. Sediments surrounding control plots were treated similarly, but without the addition of shells. Treatment and control plots within each pair were spaced 3 m apart at the same tidal height, and adjacent pairs within a site were separated by at least 10 m. Initially, 3 pairs of plots were established at each site in May 2003. Plots were exposed to natural predators for 28 d and clams were then collected and classified as alive, dead or consumed. Residual feeding marks on dead clams enabled reliable assessment of whelk predation (Peterson 1982). This experiment was repeated the following year to determine the generality of shell treatment effects. Three runs were conducted in which 5 or 6 pairs of plots were established at each site ($n = 16$ pairs per site). In both 2003 and 2004, clam mortality in treatment versus control plots was evaluated using a paired *t*-test.

Observed physical differences between sites (see Table 1 in 'Results') prompted testing for a site effect using ANOVA. Absolute levels of predation varied between plot pairs within a given site, potentially obscuring differences across sites in the effect of our shell treatment. Thus, for each plot pair, we normalized predation level by determining the fraction of total predation that occurred only in the shell treatment plot. This was achieved using an index of predation intensity (PI):

$$PI = \frac{P_t}{P_t + P_c} \quad (2)$$

where P_t is the number of clams consumed in a treatment plot and P_c is the number of clams consumed in the paired control plot. A Cochran's test confirmed that sample variances were homogeneous (Underwood 1981) and a 2-way ANOVA was used to determine whether PI varied between sites and experimental runs (blocks). The block effect was insignificant ($p > 0.25$) and, therefore, data were combined and reanalyzed as a 1-way ANOVA examining PI as a function of site (Underwood 1981). The source of significant site differences was identified using a Tukey-Kramer post hoc test.

Expt 2: Non-lethal predator effects. The second set of experiments used caged whelks to elicit avoidance responses that limit clams' release of chemical attractants (Smee & Weissburg 2006) to test whether predation is diminished by non-lethal predator effects, and whether bottom roughness counteracts those effects.

Knobbed whelks measuring 0.13 to 0.16 m in length were collected by hand and fed clams for at least 10 d before experiments. Cylindrical cages were constructed out of 0.01 m polyethylene mesh and measured 0.20 m tall and 0.25 m in diameter. Initially, tethered clams (12 per plot) were evenly distributed within plots containing either a centrally positioned caged whelk (predator treatment) or an empty cage (control). Cages were buried to a depth of 0.1 m in the center of each plot and clams were accessible to naturally foraging whelks as before. Plot size (0.5 m²) was larger than in Expt 1 to accommodate the cages, but resulting prey density (24 clams m⁻²) was still well within the naturally occurring range. Each plot pair consisted of a predator treatment and control plot spaced 3 m apart at the same tidal height. Adjacent plot pairs within a site were separated by at least 10 m. Paired plots ($n = 21$ pairs) were established around Wassaw Sound (Fig. 1) in June 2004 and exposed to natural predators for 21 d. Clams and clam shells were then recovered and the effect of whelk presence on clam mortality was evaluated using a paired *t*-test.

Results demonstrated that caged (non-lethal) whelks increased clam survival. Therefore, we modified the experiment in May 2005 to test the hypothesis that bottom roughness counteracts non-lethal predator effects by either increasing whelk attraction or hindering clam avoidance responses. Paired plots ($n = 20$ pairs) were established as before, but with 2 notable differences: (1) both treatment and control plots contained a centrally caged whelk; and (2) a thin perimeter of shell fragments was spread around each treatment plot (Fig. 2) as in Expt 1. Clams and clam shells were recovered after 21 d and the effect of shell treatments on clam mortality was evaluated using a paired *t*-test.

Effect of shell treatments on prey growth. It was possible that turbulence generated by shell treatments increased food delivery to experimental clams, causing them to liberate more metabolic waste and thereby provide a more attractive odor source for foraging whelks. If clams increased feeding in this manner, then individuals in plots surrounded by shells should experience faster growth compared with control clams. To test for this potentially confounding treatment effect, pairs of clam plots were established on a tidal flat similar to previous sites but where surveys revealed predation to be minimal. This setting allowed us to test the effect of shells on clam growth without the added complication of predator influence. The longest dimension of each clam was measured to 0.01 mm and then 12 pairs of plots (shell treatments and controls) were established as in Expt 1. Clams were left in the field for 52 d before retrieval to provide for a detectable level of growth. Changes in shell length were evaluated using a paired *t*-test.



Fig. 2. Representative pair of prey plots used in Expt 2 to evaluate effects of bottom roughness on olfactory interactions between knobbed whelks *Busycon carica* and hard clams *Mercenaria mercenaria*. A single non-lethal whelk was confined in each of the 2 cages and surrounded by 12 adult clams evenly distributed throughout the remainder of each 0.5 m² plot. The treatment plot (foreground) was then surrounded with a thin layer of shell fragments designed to increase turbulent mixing across the plot without restricting the access or movement of naturally foraging whelks. Both cages measured 0.25 m in diameter for scale (photo: M. C. Ferner)

Table 1. Mean \pm SE of physical habitat characteristics and flow conditions at 3 intertidal study sites (DMH: Dead Man Hammock; HC: House Creek; NCI: North Cabbage Island). U : net velocity; TI: turbulence intensity; A_{rms} : root mean square wave amplitude

| | DMH | HC | NCI |
|--|-------------------|-------------------|-------------------|
| Percent sediment weight^a | | | |
| Sand | 86.5 \pm 4.4 | 50 \pm 8.3 | 85.6 \pm 5.5 |
| Silt | 3.6 \pm 1.2 | 18.6 \pm 3.7 | 3 \pm 0.9 |
| Clay | 9.9 \pm 3.2 | 31.1 \pm 5.0 | 10.8 \pm 4.2 |
| Percent surface cover | | | |
| Sediment | 97.5 \pm 0.6 | 97.1 \pm 0.8 | 89.9 \pm 1.4 |
| Shell | 0.7 \pm 0.3 | 0.2 \pm 0.1 | 8.6 \pm 1.5 |
| Biogenic | 1.8 \pm 0.3 | 2.7 \pm 0.7 | 1.5 \pm 0.2 |
| Ripples^b | | | |
| Height (m) | 0.018 \pm 0.001 | – | 0.017 \pm 0.002 |
| Length (m) | 0.054 \pm 0.001 | – | 0.056 \pm 0.002 |
| Flow conditions^c | | | |
| U (cm s ⁻¹) | 0.056 \pm 0.016 | 0.139 \pm 0.015 | 0.109 \pm 0.034 |
| TI | 0.867 \pm 0.238 | 0.376 \pm 0.070 | 1.641 \pm 0.936 |
| A_{rms} (dbar) | 0.008 \pm 0.002 | 0.007 \pm 0.000 | 0.022 \pm 0.007 |

^aGrain-size frequency distributions measured from upper 0.01 m of sediment surface. Values are average percentages (by weight) of 3 replicate samples collected at each site. Fractions not represented at HC and NCI consisted of tiny shell fragments (0.3 and 0.4 % by weight, respectively)

^bNo ripples were present in quadrats surveyed at HC

^cFlow data represent ensemble averages of 2 min sampling bursts collected 0.04 to 0.06 m above natural sediments every 15 min on 6 separate days at each site. Total numbers of bursts averaged were 453, 462 and 424 for DMH, HC and NCI, respectively

RESULTS

Site characteristics

A habitat comparison of the primary study sites is shown in Table 1. Surface cover was similar between DMH and HC, but NCI sediments were covered by an order of magnitude more shell material. Average U was highest at HC. Average TI was highest at NCI, reaching nearly twice that at DMH and more than 4 times the average TI at HC. Average daily maximums of all flow parameters were greatest at NCI, and TI at that site exceeded daily maximums at DMH and HC by more than a factor of 3. Variability in sea-surface elevation (A_{rms}) was negligible at all sites and indicated that wave action in these areas probably did not influence estimates of TI.

Physical effects of shell treatments

Shell fragments increased turbulent mixing compared with flow over smooth sand in the near-bed region where whelks and clams reside (Fig. 3). Velocity fluctuations induced by the shells homogenized and diluted chemicals in the overlying water. Shells resulted in a 17 % increase in the average number of odor filaments detected downstream (mean \pm SE, 1.50 \pm 0.03 peaks s⁻¹) compared with the number detected over sand (1.28 \pm 0.12 peaks s⁻¹), and variability in peak number also decreased as water passed over the shells. Relative concentration of odor filaments dropped from 0.62 (\pm 0.03) over sand to 0.13 (\pm 0.01) over shells.

Field measurements of flow over shells and natural sediments verified the mixing effect of shell treatments across sites and tidal conditions. Initial calibrations with ADVs held side by side in the flume confirmed that velocities recorded by the 2 instruments were similar (mean \pm SD, 5.66 \pm 0.58 [10 MHz] and 5.29 \pm 0.58 [16 MHz]). Paired t -tests comparing daily averages of U and TI over both sediment types in multiple field locations (Fig. 4) showed

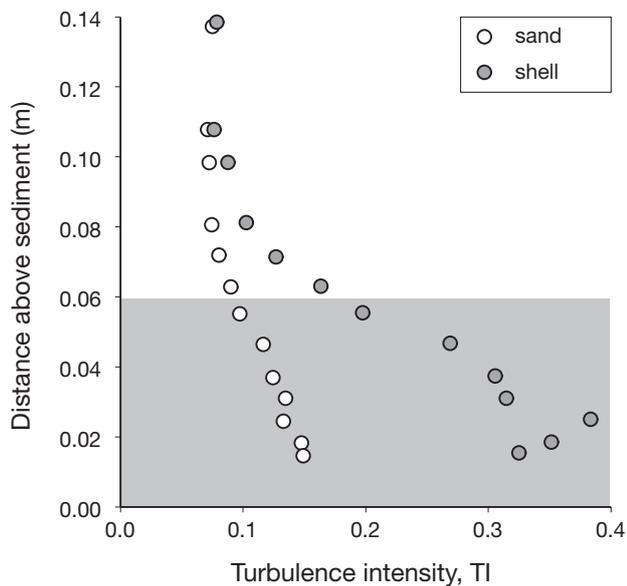


Fig. 3. Vertical profiles of turbulence intensity (TI) measured at various heights above sand and shells in a racetrack flume. Mean free-stream velocity was 6 cm s^{-1} over both substrates. Higher values of TI close to the bed (shaded region) reflect mixing due to bottom roughness and illustrate the hydrodynamic effect of shell treatments used in predation experiments

that U was similar above shells and natural sediments ($n = 7$, $t = 1.06$, $p = 0.330$), but TI was significantly greater over shells ($n = 7$, $t = 4.03$, $p = 0.007$).

Expt 1: Lethal predator effects

Shell treatments significantly increased whelk predation over 28 d ($n = 9$, $t = 2.98$, $p = 0.017$). Total clam mortality in shell treatment plots (mean \pm SE, 5.89 ± 0.65) was 43% higher than in control plots (4.11 ± 0.35), and diagnostic feeding marks confirmed that whelks were responsible for all predation. No whelks were present in any plots at the conclusion of the experiment.

Repeating this experiment the next year confirmed that shell treatments consistently increased whelk predation relative to controls ($n = 48$, $t = 2.52$, $p = 0.015$). An ANOVA of PI values revealed that the ecological effect of shell treatments was different among the 3 sites (Fig. 5; $F_{2,45} = 4.410$, $p = 0.018$). Post hoc tests confirmed that shell treatments had a significant effect on PI at all sites except NCI. Overall, 18 whelks were discovered foraging in a total of 8 treatment plots and 7 control plots at the conclusion of this experiment. Treatment plots never contained more than a single whelk and the average number of whelks found in treatment versus control plots was not significantly different ($n = 48$, $t = 0.40$, $p = 0.69$).

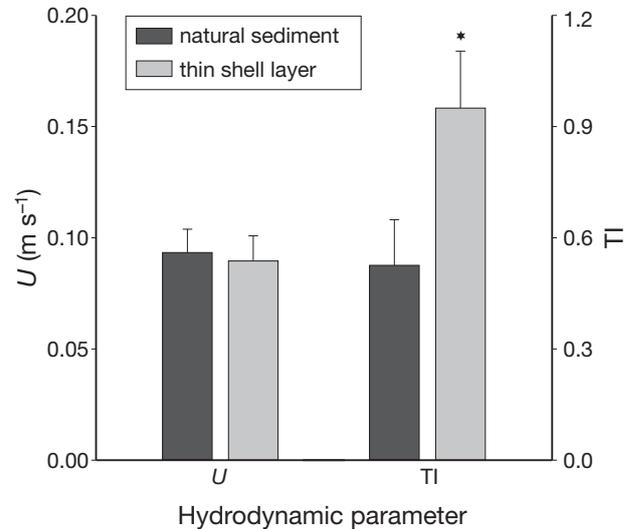


Fig. 4. Mean (\pm SE) net velocity (U) and turbulence intensity (TI) measured for 24 h periods over paired patches of natural sediments (control) and shells (treatment) at 7 intertidal locations. Asterisk (*) denotes a significant difference in TI ($p < 0.01$)

Expt 2: Non-lethal predator effects

Data from several plot pairs were discarded because currents washed away predator cages, but final sample sizes in both the first ($n = 19$) and second ($n = 17$) caging experiments were sufficient for statistical analysis. These clam plots initially were surrounded by natural sediment, and predator treatment plots containing a centrally caged whelk were paired with control plots containing an empty cage. Naturally foraging whelks consumed an average of 25% fewer clams (mean \pm SE, 5.11 ± 0.65) in predator treatment plots compared with paired control plots (6.79 ± 0.75), confirming a significant non-lethal effect of predator presence on prey survival (Fig. 6A; $n = 19$, $t = 2.31$, $p = 0.033$). Seven naturally foraging whelks were recovered from a total of 3 treatment plots and 3 control plots, with no significant effect of plot type ($n = 19$, $t = 0.44$, $p = 0.667$).

The final predation experiment exposed all clam plots to a centrally caged whelk, and treatment plots surrounded with shells were paired with control plots surrounded by natural sediment (Fig. 2). Whelk predation on clams in these shell treatments (7.06 ± 0.74) was 22% higher than predation on control clams (5.76 ± 0.87). This significant increase in consumer pressure (Fig. 6B; $n = 17$, $t = 2.68$, $p = 0.017$) demonstrated that shell treatments negated the non-lethal effects of caged whelks. Note that the average number of clams eaten in plots containing a caged whelk and surrounded by natural sediment was similar between the

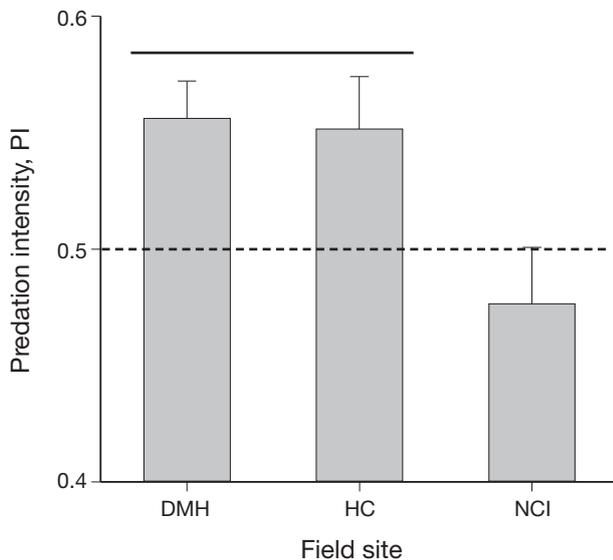


Fig. 5. *Mercenaria mercenaria*. Mean (\pm SE) proportion of clams consumed from the shell (treatment) plot within each plot pair established in Expt 1 in 2004. Means sharing the same solid line were statistically indistinguishable and represent sites where shell treatments significantly increased predation ($p < 0.05$). (----): an equal level of predation on clams in plots surrounded by natural sediments (control) or shells (treatment). DMH: Dead Man Hammock; HC: House Creek; NCI: North Cabbage Island

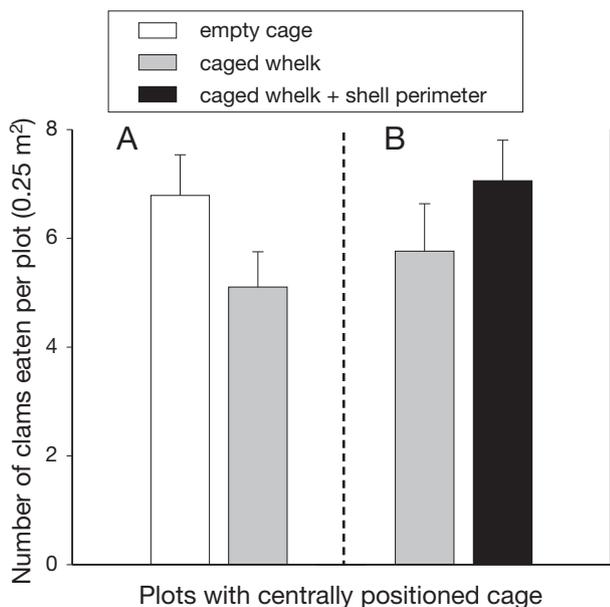


Fig. 6. *Mercenaria mercenaria*. Mean (\pm SE) number of clams consumed from paired plots in Expt 2 that (A) were surrounded by natural sediment and contained either an empty cage (control) or a centrally caged whelk (treatment), or (B) contained a centrally caged whelk within each plot and were surrounded by either natural sediment (control) or shells (treatment) as shown in Fig. 2. In both cases treatment effects were significant ($p < 0.05$)

2 phases of Expt 2, indicating that caged (non-lethal) whelks alone had a consistent effect on clam mortality. A total of 11 naturally foraging whelks were recovered from 4 treatment plots and 4 control plots, again with no significant effect of plot type ($n = 17$, $t = 0.77$, $p = 0.455$).

Effect of shell treatments on prey growth

Paired clam plots established in an area free of whelks allowed evaluation of shell effects on clam growth without the confounding influence of predator avoidance responses. Growth of clams in shell treatment plots (mean increase in length \pm SE, 0.46 ± 0.04 mm) versus control plots (0.47 ± 0.04 mm) was not significantly different ($n = 12$, $t = 0.33$, $p = 0.746$) and confirmed that shell treatments alone did not affect clam feeding activity. All clams were recovered alive and no whelks were present in any plots at the end of this experiment.

DISCUSSION

Prior conclusions from studies of olfactory behavior indicate that physical disruption of chemical cues can alter individual performance (Weissburg et al. 2002), but the ecological relevance of such alterations remains largely unknown. This study examined the effects of bottom roughness on olfactory interactions between predatory gastropods and their prey to determine whether bed-generated turbulence could modify these interactions in nature. We found that on tidal flats of unconsolidated sediment, patches of bottom roughness can increase predation by whelks (Fig. 5) and shift the effect of predators from non-lethal to lethal interactions (Fig. 6).

Mesocosm experiments have shown that habitat complexity can intensify predation by reducing interference between predators that display agonistic behavior or occur at high densities (e.g. Corkum & Cronin 2004, Grabowski & Powers 2004, Finke & Denno 2006, Hughes & Grabowski 2006). However, this mechanism does not appear to explain our results for several reasons. First, unlike more bellicose predators such as crabs (Clark et al. 1999), whelks do not display agonistic behavior and are often observed foraging independently in close proximity to other whelks in the field. It is possible that interference by stone crabs *Menippe mercenaria* reduced whelk foraging in control plots (Hughes & Grabowski 2006), although we never observed stone crabs in or around any plots and could conclusively attribute 100% of clam mortality to whelk predation. Second, whelk densities in our study area

are generally quite low (less than 0.03 ind. m^{-2} ; Walker 1988) and we have no evidence to suggest that shell treatments led to unnaturally high predator densities. Laboratory trials indicated that whelks crawl easily across a thin layer of shells and do not move toward sun-bleached shell fragments in the absence of prey odors (M. C. Ferner unpubl. data). A few whelks were occasionally discovered in clam plots, but these numbers were not significantly different between treatment and control plots and could not be construed as aggregative responses to shell layers. Lastly, in contrast to physical obstructions associated with sediment binding or vertical habitat structure (e.g. Peterson 1982, Grabowski & Powers 2004), our shell treatments provided a level of structural complexity that did not restrict whelk access to prey or interfere with whelk movements. Therefore, we expect that shell layers bordering treatment plots (e.g. Fig. 2) had negligible effects on predator–predator interactions, even if multiple individuals had decided to forage in the same plot.

We acknowledge that it is not possible to tease apart all potential mechanisms underlying our results, but observed increases in consumer pressure on clams surrounded by shells are consistent with the notion that turbulence generated by shells (Figs. 3 & 4) produced these patterns by modifying the dispersion of prey odors. Shell layers did not cause clams to release more metabolites, as would have been the case if turbulent mixing across the shells had increased food delivery to (and growth of) clams, but shells may have provided a more enduring source of attractive cues by trapping prey chemicals in low velocity regions between roughness elements (Moulin et al. 2007). In addition, bed-generated turbulence enhances solute exchange across the sediment–water interface (Huettel & Gust 1992, Dade 1993) and may have introduced clam effluents into sediment pore water where cue retention time exceeds that of the overlying flow. Whelks regularly encounter chemicals within the sediment matrix by virtue of their burrowing mode of locomotion. Thus, whelks could benefit from cues contained in pore water or adsorbed to sediment grains by continuing to track prey even after waterborne odors were washed away.

Shells also altered the information conveyed in attractive odor plumes (see 'Results'), and it is possible that whelks located clams more effectively when turbulent mixing changed the spatial and temporal features of waterborne cues emanating from shell treatment plots. Whelks exhibit relatively slow movement and long reaction times that may afford them the option of averaging sensory inputs over long periods (Weissburg 2000). Such a method of encoding information reduces the need for discrete stimulus bursts that

appear to underlie the 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 allow whelks 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 internal olfactory organ. Physical mixing and homogenization of odor filaments during transport through their siphons 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 across rough sediments might even facilitate whelk tracking by presenting individuals with more consistently mixed cues. Robust olfactory performance in response to well-mixed odors could have important ecological implications by extending the time periods or habitats in which whelks successfully search for prey, making them more effective consumers and competitors when turbulent mixing is high. The range over which turbulent mixing increases whelk predatory success is clearly finite; enhanced turbulence created by shells had no further effect at the ambient turbulence intensities present at NCI. Thus, some areas commonly inhabited by whelks may be near or at the limit where whelks are maximally effective foragers.

Clams are not passive odor sources, however, and survivorship of individuals exposed to caged whelks confirmed the ability of clams to detect and respond to predator cues so as to avoid consumption (Fig. 6A). This result is consistent with avoidance responses of hard clams described in other studies (Doering 1982, Irlandi & Peterson 1991, Nakaoka 2000, Smee & Weissburg 2006), and indicates that many clams stopped feeding when caged predators were detected. Such reductions in siphon pumping limit the release of chemical effluents by clams and consequently weaken the attraction of downstream predators (Doering 1982). As whelks move across the seafloor in search of prey, alerted clams will reduce their odor production and render themselves less detectable to predators hunting downstream. We found that bottom roughness around experimental plots of alerted clams counteracted the indirect effects of whelk presence and intensified predation (Fig. 6B). An interesting and unresolved issue involves the relative role of whelk versus clam responses in determining the effects of turbulent mixing on predation. Bottom roughness could have interfered with clam perception of caged whelks and encouraged a liberal release of attractive chemicals that may have rendered treatment plots more detectable than control

plots, as has been suggested by field experiments using a spatially separated predator (Smee et al. 2008). On the other hand, whelks can track chemical cues more efficiently when velocity or turbulent mixing is increased (Powers & Kittinger 2002, Ferner & Weissburg 2005) and clams in plots lacking a non-lethal predator still experienced greater predation when surrounded by shells (Fig. 5).

Environmental modulation of sensory behavior can occur before individuals experience physiological stress or movement restrictions, and constraints on information gathering may sometimes determine when animals can and cannot be effective consumers. In fact, our observations indicate that a moderate level of turbulent fluid motion (often considered a stressor at high levels) can result in elevated predation. Leonard et al. (1998) conducted a comparative study linking bulk flow to the relative importance of resource supply and consumer pressure on benthic community structure. Their findings signify that consumer pressure is reduced in high velocity environments where resource supply is maximal and where predators are impaired by strong fluid forces. Our results hold 2 caveats for these types of studies. First, the role of fluid motion cannot always be generalized; crustacean consumers seem particularly prone to show diminished foraging abilities in turbulent flow (Weissburg 2000; but see Moore & Grills 1999) whereas burrowing gastropods are clearly less inhibited by enhanced mixing of chemical cues. Second, our results suggest that flow speed in and of itself may not be the best indicator of the effect of fluid flow on predatory abilities, particularly in areas of high physical habitat heterogeneity. For example, predation by whelks was increased by the addition of bottom roughness at both low and high velocity sites that contained relatively low levels of pre-existing shells and boundary-layer turbulence (DMH and HC in Fig. 5, Table 1). Only at the site characterized by intermediate flow speeds did local elevation of bed-generated turbulence fail to enhance whelk predation (NCI in Fig. 5, Table 1). Importantly, this intermediate flow site also had the highest levels of pre-existing shell fragments and boundary-layer turbulence (Table 1). The lack of a significant treatment effect at this most turbulent site suggests that fluctuations in velocity may be more important than average flow speed in determining the outcome of chemosensory interactions between benthic predators and their prey. Earlier lab studies (e.g. Weissburg & Zimmer-Faust 1993) reached a similar conclusion, but field verification of this effect further supports the role of turbulence as a fundamental factor in mediating olfactory interactions.

Whelks targeted in the present study traverse a variety of sediment types in search of prey, ranging from

subtidal mud to frequently exposed oyster reefs in the upper intertidal zone, but these olfactory predators are primarily attracted to oyster reefs and spend the majority of their time foraging there (Walker 1988, Walker et al. 2004). Regions of shell hash fringing oyster reefs extended to as close as 10 m from experimental clam plots, and our shell treatments probably modified the local foraging behavior of whelks on their way to a bigger meal. The role of large-scale reef structures that enhance both mixing and odor intensity is unresolved. Even for individuals that are impaired by homogenization of odor cues, the detrimental effects of turbulence generated across complex structures like oyster reefs could be largely offset by the release of concentrated chemical attractants from oysters themselves. Given the formidable challenge of conserving and restoring structural habitats in soft-sediment estuaries (e.g. Lenihan et al. 2001, Grabowski et al. 2005), future research should address predator and prey olfactory responses to habitat complexity, the spatial scales over which chemically mediated prey search and predator avoidance are important, and the connections between these processes and other habitat effects on predator-prey and predator-predator interactions.

Acknowledgements. We thank the Skidaway Institute of Oceanography for providing space and resources necessary for completion of this work. Predation experiments were made possible by the enthusiastic efforts of numerous technicians and colleagues. We are especially grateful to S. Elston, A. Hollebhone, K. McCullough, T. Porter and U. Warttinger for their reliable field work. J. Pedersen and C. Vernheim assisted with sediment analysis, and K. Nickols helped process the field flow data. J. Blanton, S. Davies, D. Dusenbery, B. Gaylord, M. Hay, J. Jackson, D. Webster and several anonymous reviewers provided insightful comments on earlier versions of this paper. Funding was provided by National Science Foundation (NSF) IGERT, NSF-OCE #0424673 and NSF-OCE #0648433. Contribution 2443, Bodega Marine Laboratory, University of California at Davis.

LITERATURE CITED

- Beukers JS, Jones GP (1997) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114:50–59
- Clark ME, Wolcott TG, Wolcott DL (1999) Foraging and agonistic activity co-occur in free ranging blue crabs (*Callinectes sapidus*): observation of animals by ultrasonic telemetry. *J Exp Mar Biol Ecol* 233:143–160
- Corkum LD, Cronin DJ (2004) Habitat complexity reduces aggression and enhances consumption in crayfish. *J Ethol* 22:23–27
- Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813
- Dade WB (1993) Near-bed turbulence and hydrodynamic control of diffusional mass transfer at the sea floor. *Limnol Oceanogr* 38:52–69

- Denny MW (1988) Biology and the mechanics of the wave-swept environment. Princeton University Press, Princeton, NJ
- Diehl S (1992) Fish predation and benthic community structure: the role of omnivory and habitat complexity. *Ecology* 73:1646–1661
- Doering PH (1982) Reduction of attractiveness to the sea star *Asterias forbesi* (Desor) by the clam *Mercenaria mercenaria* (Linnaeus). *J Exp Mar Biol Ecol* 60:47–61
- Ferner MC, Weissburg MJ (2005) Slow-moving predatory gastropods track prey odors in fast and turbulent flow. *J Exp Biol* 208:809–819
- Finelli CM (2000) Velocity and concentration distributions in turbulent odor plumes in the presence of vegetation mimics: a flume study. *Mar Ecol Prog Ser* 207:297–309
- Finelli CM, Pentcheff ND, Zimmer RK, Wetthey DS (2000) Physical constraints on ecological processes: a field test of odor-mediated foraging. *Ecology* 81:784–797
- Finke DL, Denno RF (2006) Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. *Oecologia* 149:265–275
- Grabowski JH, Powers SP (2004) Habitat complexity mitigates trophic transfer on oyster reefs. *Mar Ecol Prog Ser* 277:291–295
- Grabowski JH, Hughes AR, Kimbro DL, Dolan MA (2005) How habitat setting influences restored oyster reef communities. *Ecology* 86:1926–1935
- Huettel M, Gust G (1992) Impact of bioroughness on interfacial solute exchange in permeable sediments. *Mar Ecol Prog Ser* 89:253–267
- Hughes AR, Grabowski JH (2006) Habitat context influences predator interference interactions and the strength of resource partitioning. *Oecologia* 149:256–264
- Irlandi EA, Peterson CH (1991) Modification of animal habitat by large plants: mechanisms by which seagrasses influence clam growth. *Oecologia* 87:307–318
- Jackson JL, Webster DR, Rahman S, Weissburg MJ (2007) Bed-roughness effects on boundary-layer turbulence and consequences for odor-tracking behavior of blue crabs (*Callinectes sapidus*). *Limnol Oceanogr* 52:1883–1897
- Jonsson PR, van Duren LA, Amielh M, Asmus R and others (2006) Making water flow: a comparison of the hydrodynamic characteristics of 12 different benthic biological flumes. *Aquat Ecol* 40:409–438
- Lapointe V, Sainte-Marie B (1992) Currents, predators, and the aggregation of the gastropod *Buccinum undatum* around bait. *Mar Ecol Prog Ser* 85:245–257
- Lenihan HS, Peterson CH, Byers JE, Grabowski JH, Thayer GW, Colby DR (2001) Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. *Ecol Appl* 11:764–782
- Leonard GH, Levine JM, Schmidt PR, Bertness MD (1998) Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* 79:1395–1411
- Main KL (1987) Predator avoidance in seagrass meadows: prey behavior, microhabitat selection, and cryptic coloration. *Ecology* 68:170–180
- Menge BA, Lubchenco J (1981) Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecol Monogr* 51:429–450
- Moore PA, Grills JL (1999) Chemical orientation to food by the crayfish *Oreonectes rusticus*: influence of hydrodynamics. *Anim Behav* 58:953–963
- Moulin FY, Guizien K, Thouzeau G, Chapalain G (2007) Impact of an invasive species, *Crepidula formicata*, on the hydrodynamics and transport properties of the benthic boundary layer. *Aquat Living Resour* 20:15–31
- Nakaoka M (2000) Nonlethal effects of predators on prey populations: predator-mediated change in bivalve growth. *Ecology* 81:1031–1045
- Persson L, Eklöv P (1995) Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology* 76:70–81
- Peterson CH (1982) Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. *Mar Biol* 66:159–170
- Powers SP, Kittinger JN (2002) Hydrodynamic mediation of predator-prey interactions: differential patterns of prey susceptibility and predator success explained by variation in water flow. *J Exp Mar Biol Ecol* 273:171–187
- Rahman S, Webster DR (2005) The effect of bed roughness on scalar fluctuations in turbulent boundary layers. *Exp Fluids* 38:372–384
- Smee DL, Weissburg MJ (2006) Clamming up: environmental forces diminish the perceptive ability of bivalve prey. *Ecology* 87:1587–1598
- Smee DL, Ferner MC, Weissburg MJ (2008) Alteration of sensory abilities regulates the spatial scale of nonlethal predator effects. *Oecologia* 156:399–409
- Sponaugle S, Lawton P (1990) Portunid crab predation on juvenile hard clams: effects of substrate type and prey density. *Mar Ecol Prog Ser* 67:43–53
- Stachowicz JJ (2001) Chemical ecology of mobile benthic invertebrates: predators and prey, allies and competitors. In: McClintock JB, Baker BJ (eds) *Marine chemical ecology*. CRC Press, New York, p 157–194
- Summerson HC, Peterson CH (1984) Role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Mar Ecol Prog Ser* 15:63–77
- Underwood AJ (1981) Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr Mar Biol Annu Rev* 19:513–605
- Walker RL (1988) Observations on intertidal whelk (*Busycon* and *Busycotypus*) populations in Wassaw Sound, Georgia. *J Shellfish Res* 7:473–478
- Walker RL, Tenore KR (1984) The distribution and production of the hard clam, *Mercenaria mercenaria*, in Wassaw Sound, Georgia. *Estuaries* 7:19–27
- Walker RL, Smith JH, Power AJ (2004) Movement and behavioral patterns of whelks on intertidal flats in Wassaw Sound, Georgia. *Univ Georgia Mar Ext Bull* 29
- Weissburg MJ (2000) The fluid dynamical context of chemosensory behavior. *Biol Bull (Woods Hole)* 198:188–202
- Weissburg MJ, Zimmer-Faust RK (1993) Life and death in moving fluids: hydrodynamic effects on chemosensory mediated predation. *Ecology* 74:1428–1443
- Weissburg MJ, Ferner MC, Pisut DP, Smee DL (2002) Ecological consequences of chemically mediated prey perception. *J Chem Ecol* 28:1953–1970
- Zimmer RK, Commins JE, Browne KA (1999) Regulatory effects of environmental chemical signals on search behavior and foraging success. *Ecology* 80:1432–1446
- Zimmer-Faust RK, Finelli CM, Pentcheff ND, Wetthey DS (1995) Odor plumes and animal navigation in turbulent water flow: a field study. *Biol Bull (Woods Hole)* 188:111–116