

Slow-moving predatory gastropods track prey odors in fast and turbulent flow

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Summary

Olfactory searching by aquatic predators is reliant upon the hydrodynamic processes that transport and modify chemical signals. Previous studies indicate that the search behavior of some benthic crustaceans is hindered by rapid water flow and turbulent mixing of prey chemicals, but different sensory strategies employed by other taxa might offset such detrimental effects. Using a laboratory flume, we investigated the odor-tracking behavior of a marine gastropod whelk (*Busycon carica*) to test the generalization that turbulence interferes with chemically mediated navigation. We exposed individual whelks 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. Search behaviors, such as cross-stream meander were reduced at higher flow velocities and in the presence of obstructions, allowing whelks to reach the odor source significantly more quickly than in slower, less turbulent conditions. Our results demonstrate that whelks can respond to chemical information in fast and turbulent flow, and we suggest that these slow-moving predators can forage in hydrodynamic environments where the olfactory abilities of other taxa are limited.

Key words: boundary-layer flow, *Busycon carica*, chemosensation, foraging success, hydrodynamic, odor plume, predation, temporal integration, turbulence, velocity.

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*, Rathbun), 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 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. Conversely, 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 estimate accurately its position within a plume or its degree of progress towards 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. We therefore predict that these slow-moving predators can 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, we 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*, Gmelin) 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). We exposed knobbed whelks to prey chemicals under controlled laboratory flows and evaluated their ability to locate the stimulus source in different current

velocities. We 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. In contrast to the generally accepted notion that physical forces diminish the severity and importance of benthic predation, we propose that some 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 (*Busycon carica*, Gmelin) were collected by hand from intertidal habitats bordering 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*, Dillwyn) and hard clams (*Mercenaria mercenaria*, Linnaeus) for at least 1 week following the date of collection to control for differences in feeding history. Preliminary observations revealed that recently fed animals were less likely to respond to prey odors than those starved for 10–14 days and, therefore, all whelks were starved for 2 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

We 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 S.D.); 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 (Aquatic Eco-Systems, Inc., Apopka, FL, USA) to remove incoming organisms and suspended sediments. A 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 ($Re=Ud/\nu$, where d is water depth and ν is kinematic viscosity) ranging from 3800 to 38,000. These flow speeds are representative of natural whelk habitats, where velocity ranges from zero at slack water to as high as 30 cm s^{-1} during peak tidal flow (M.C.F. and M.J.W., unpublished). Additional treatments contained one of two obstructions intended to alter odor plume structure independent of changes in bulk flow speed. We tested obstructions at only one flow speed as an initial examination of whelk responses to enhanced mixing and the intermediate velocity ($U=5 \text{ cm s}^{-1}$) selected for these obstruction treatments provided a substantial increase in boundary-layer turbulence that exceeded the level associated with our 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 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), we 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 ($S=f d/U$), which remains roughly constant over a wide range of Re spanning our test conditions (Kundu, 1990).

The flume was operated for 20 min 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. We used an acoustic Doppler velocimeter (ADV) to collect high-resolution, three-dimensional-velocity data ($\pm 0.01 \text{ cm s}^{-1}$) at various heights above the sediment surface to characterize boundary layer structure and to compare the different flow treatments quantitatively. The ADV probe (SonTek/YSI 10 MHz ADVField; Sontek/YSI, Inc., San Diego, CA, USA) 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 ($\pm 0.25 \text{ mm}$). Velocity data were collected at a frequency of 10 Hz and instantaneous measurements were averaged over 4 min to obtain velocity means and variances at each height.

Velocity profiles from unobstructed flow treatments were compared with 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 our purposes because precise measurement heights were not replicated across flow conditions. Instead, root mean square (RMS) velocity data served as a measurement of turbulence intensity and were compared with unobstructed flow at the same free-stream velocity ($U=5 \text{ cm s}^{-1}$) as a first-order assessment of the hydrodynamic effects of obstructions. Similar profiles of RMS turbulence intensity also provided an additional comparison of unobstructed flows.

Characterization of odor-plume structure

To quantify variation in odor plumes associated with different flow treatments, we 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 (Welch Scientific Co., Skokie, IL, USA) 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, MSC TI Model 125; Precision Measurement Engineering, Inc., Carlsbad, CA, USA). This four-electrode sensor has a spatial resolution of approximately 1 mm and extends 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 1 min 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

We 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 1 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 4 l 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 1 h at a concentration of 7.5 g of tissue per liter of water and solutions were filtered through a 60 μm screen before reintroduction to the flume. Lower concentrations (e.g. 1.5 g l^{-1}) or shorter soaking times failed to elicit a sufficient number of tracking responses, whereas higher concentrations (e.g. 15 g l^{-1}) 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; Barnant, Barrington, IL, USA). 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 (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 our 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 8 h 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 \times 21 \times 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 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 2 h 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 for heterogeneity. Analysis of variance (ANOVA) was used to evaluate the effect of flow treatments on the total search time required for whelks to locate the stimulus source.

Results

Hydrodynamic conditions

Vertical velocity gradients (Fig. 1A) recorded at the location of the delivery nozzle were used to derive hydrodynamic parameters. Horizontal 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 1), suggesting that turbulent eddies began to penetrate the boundary layer in at least the fastest condition tested. Vertical profiles of turbulence intensity (Fig. 1B) showed a characteristic peak close to the sediment as expected for equilibrium boundary layer flows (Schlichting, 1987), further verifying that faster flows were more turbulent throughout the lower 17 cm of the water column.

Table 1. Shear velocity and roughness Reynolds number for unobstructed flows that differed in free-stream velocity

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

Determination of hydraulic roughness (z_0) by regression of $\ln(z)$ against velocity yielded an $r^2 > 0.95$ in all four conditions; where u^* is shear velocity, Re^* is the Reynolds number and U is free-stream velocity.

Profiles of turbulence intensity at the location of the delivery nozzle illustrated the effect of flow obstructions (Fig. 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 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 (Fig. 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 we maintained the same free-stream velocity of 5 cm s⁻¹ across these treatments, the data in Fig. 2 demonstrate that, relative to the smooth condition, both obstructions increased turbulent mixing in the near-bed region

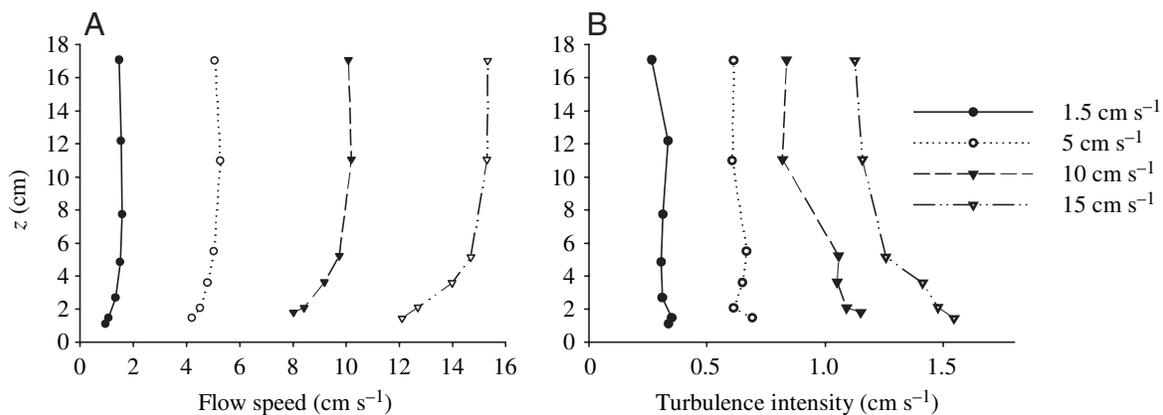
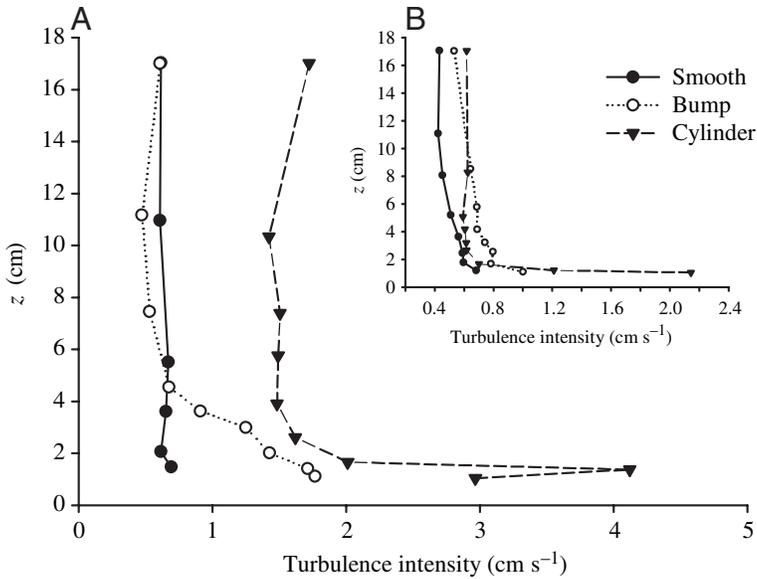


Fig. 1. Hydrodynamic characteristics of the four unobstructed flow treatments. (A) Profiles of horizontal flow speed (U_z) at various heights (z) above the sediment. ADV measurements were recorded in the center of the flume at the location of stimulus release. Each data point represents a 4 min average (mean) 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 treatments. (B) Vertical profiles of RMS turbulence intensity corresponding to each of the velocity records in the unobstructed flow treatments. Turbulence 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.



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 Fig. 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

Fig. 2. Vertical profiles of RMS turbulence intensity in the three flow treatments having a free-stream velocity of $U=5 \text{ cm s}^{-1}$. Turbulence intensities were derived from ADV measurements of horizontal 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 Fig. 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, an effect that persisted throughout the test section.

odor filaments and created more numerous peaks (Fig. 3A), with 0.5 peaks per second detected in flows of 5 cm s^{-1} , compared with 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 (Fig. 3A) because the stimulus injection rate was constant across treatments. Average peak concentration never exceeded 1.3% of the source

concentration in any of the conditions that we 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).

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 (Fig. 3B). Compared with the 0.5 odor peaks detected per second in the smooth condition (Fig. 3A,B), the

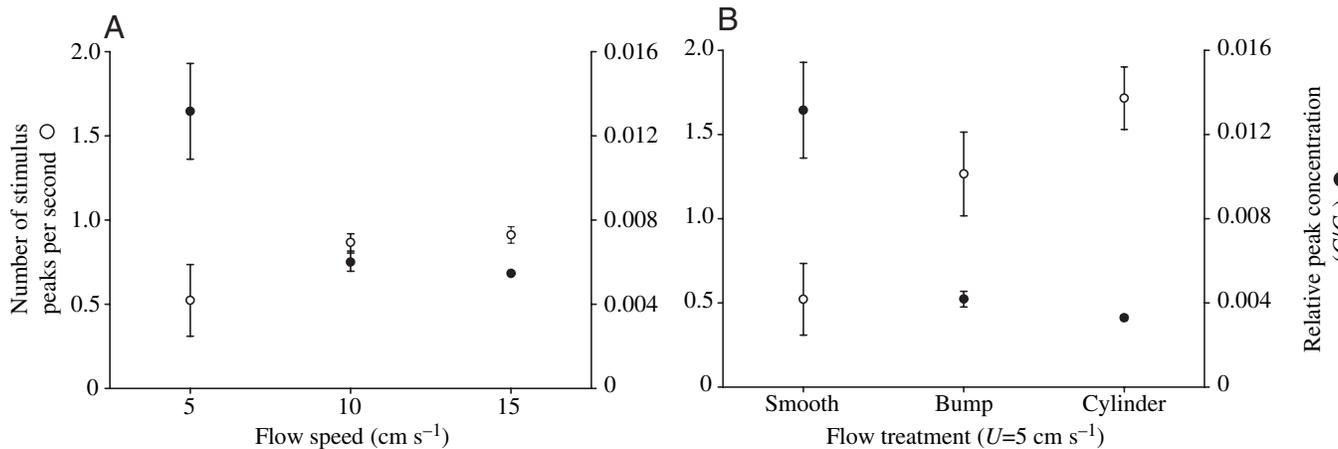


Fig. 3. Conductivity data representing the number of stimulus peaks detected per second (open circles) and the relative peak concentrations (closed circles) for (A) the three fastest unobstructed flows and (B) the three flow treatments having a free-stream velocity of 5 cm s^{-1} . Values for the smooth condition ($U=5 \text{ cm s}^{-1}$) are included in both graphs for the sake of comparison. Data points represent an average of three replicates (\pm S.E.M.) 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).

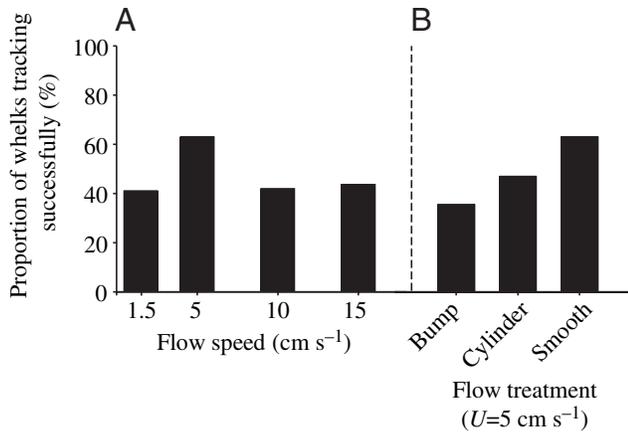


Fig. 4. Proportion of motivated whelks that successfully tracked prey chemicals in each flow condition. Success rates were independent of flow treatment for both unobstructed and obstructed flows ($P>0.25$). (A) Sample sizes for the four unobstructed treatments of 1.5, 5, 10 and 15 cm s⁻¹ were 17, 19, 19 and 16, respectively. (B) Sample sizes for the bump and cylinder obstruction treatments (at $U=5$ cm s⁻¹) were 14 and 17, respectively. No animals in any flow treatment tracked to the delivery nozzle in response to unscented control plumes.

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 Fig. 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 (Fig. 4). Tracking success was independent of flow speed (d.f.=3, $G=2.46$, $P>0.25$), confirming that whelks were able to detect and follow turbulent odor plumes equally well in flows ranging from 1.5 to 15 cm s⁻¹. The apparent increase in tracking success at 5 cm s⁻¹ (Fig. 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 (d.f.=2, $G=2.55$, $P>0.25$), although the bump obstruction slightly reduced the success rate of motivated searchers when compared with the cylinder treatment or smooth condition (Fig. 4B).

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

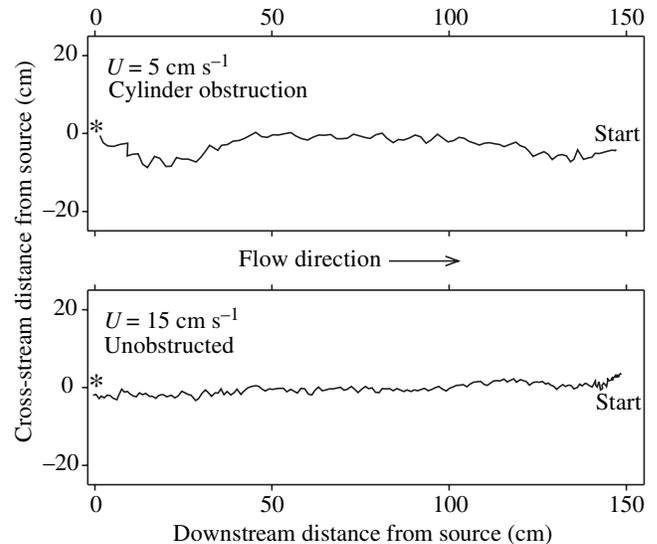


Fig. 5. Examples of whelk tracking behavior in the two most turbulent treatments: the cylinder obstruction in a flow of 5 cm s⁻¹ (top panel) and an unobstructed flow of 15 cm s⁻¹ (bottom panel). Trials were filmed with a CCD camera mounted directly above the flume and paths show motion of the anterior tip of an individual knobbed whelk. 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 followed odor plumes upstream and asterisks represent the stimulus source.

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 to maintain or confirm their continued presence within the attractive odor plume (e.g. Fig. 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 (Fig. 6) showed that successful whelks reached the stimulus source more quickly in both faster (d.f.=3, $F=3.35$, $P=0.036$) and more turbulent flows (d.f.=2, $F=3.77$, $P=0.049$). Single degree of freedom *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. These increases in search efficiency can be explained by the observation that cross-stream meandering decreased in faster and more turbulent flows, and a more detailed kinematic analysis of whelk search behavior is in progress (M.C.F. and M.J.W., unpublished).

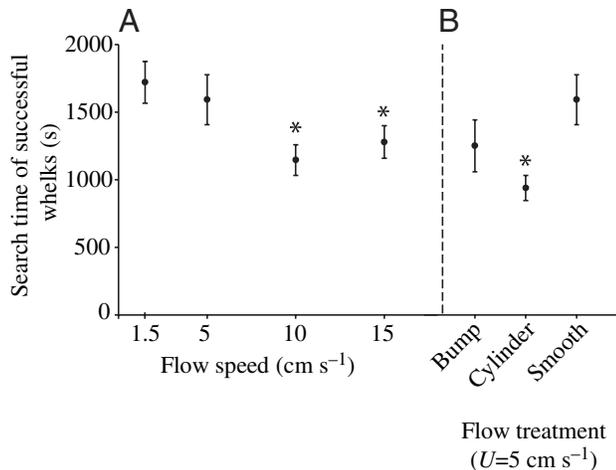


Fig. 6. Average search time (\pm S.E.M.) required for successful whelks to navigate from the starting cage to the odor source located 1.5 m upstream. (A) Compared with search times in the slowest unobstructed flow, knobbed whelks tracked more efficiently (i.e. reduced search time) in the two fastest flows. Seven tracks were analyzed for each of the unobstructed treatments and asterisks indicate a significant reduction in search time compared with the 1.5 cm s^{-1} treatment ($P < 0.05$). (B) Compared with search times in unobstructed flow of the same velocity, knobbed whelks tracked more efficiently when the cylinder obstruction introduced turbulent mixing at the odor source. Five tracks were analyzed for each of the obstruction treatments and asterisks indicate a significant reduction in search time compared with the unobstructed (smooth) condition ($P < 0.05$).

Discussion

Our results 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 (Fig. 5). Compared with whelk performance in slow and unobstructed flow, total search time was significantly reduced in the fastest and most turbulent conditions tested (Fig. 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 with the responses that we 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} in contrast to the 44% of knobbed whelks that tracked successfully in our 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 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 our 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. We 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 our 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 to reduce the drag imposed on their shell, a physical constraint that has clear ramifications for foraging blue crabs (Weissburg et al., 2003). It was difficult to interpret these behaviors, however, because we 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 sometimes leave soft sediments to forage on the harder surfaces associated with intertidal oyster reefs where the benefits of burrowing ability are reduced (M.C.F., unpublished). 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 our 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.F., unpublished). 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 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 we 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 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 with 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 (D. L. Smee and M.J.W., unpublished). 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. Conversely, 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. Our 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.

List of symbols and abbreviations

d	characteristic length scale
f	frequency
i.d.	inner diameter
κ	von Karman's constant
ν	kinematic viscosity
o.d.	outer diameter
Re	Reynolds number
Re^*	roughness Reynolds number
S	Strouhal number
U	free-stream velocity
U_z	velocity at height (z)
u^*	shear velocity
z	height above sediment
z_0	hydraulic roughness

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