

# CHEMOSENSORY-MEDIATED FORAGING IN A TURBULENT BOUNDARY LAYER

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## ABSTRACT

Concentration measurements of a chemical plume in a turbulent open channel flow are collected using planar laser-induced fluorescence (PLIF). The objective is to document the chemosensory cues that may be useful to a rapidly moving animal tracking the chemical odor. The plume is released isokinetically into the logarithmic layer of a fully developed turbulent boundary layer for two bed surfaces: fine gravel and painted steel. Of interest is the variation of the sensory cues, particularly a spanwise correlation function, with bed roughness. It has been hypothesized that animals, such as blue crabs, use a bilateral comparison of the chemosensory signal to steer toward the plume centerline. The current study represents the first step in understanding the effect of bed roughness on the turbulent transport and specifically addresses the usefulness of bilateral comparison to chemical plume tracking.

## INTRODUCTION

Many animal sensory systems respond to spatial and temporal patterns to mediate response. Humans are most familiar with visual, sound, and touch responses, but one particularly amazing system in many marine (and terrestrial) animals is chemosensation. Animals, such as crabs and lobsters, use odor to track distant objects such as food or mates. Figure 1 is an overhead photograph of a hungry adult blue crab tracking a plume of shrimp odor. Obviously, the success of such an activity is critical because food, reproduction, and predator avoidance are fundamental tenets of sustained life. A basic question is: *what chemosensory information are animals using to track an odor source in a turbulent flow?*

A fundamental stumbling block to understanding chemosensory-mediated behavior is a lack of understanding of the chemical signal and its information content. In a laminar flow, chemical transport is dominated by molecular diffusion and bacteria, microorganisms and small crustaceans can track along well-defined concentration gradients (Dusenbery, 1992). For larger animals in turbulent flows, the tracking ability becomes much more difficult to understand. The instantaneous concentration field fluctuates and does not possess a

clear instantaneous gradient toward the source. Nevertheless, animals such as moths, blue crabs, and lobsters are readily capable of tracking odors to their source (e.g. Murlis et al., 1992; Weissburg and Zimmer-Faust, 1993, 1994; Atema, 1996).

A variety of evidence suggests that benthic crustaceans use instantaneous properties during odor-guided navigation. First, these animals do not wait long enough at a particular location to accurately assess time-averaged quantities and their small spatial variations (Moore and Atema, 1991; Weissburg and Zimmer-Faust, 1994; Finelli, 2000). Typically, the animal finds the source within tens of seconds once it acquires the odor. Second, benthic crustaceans are rarely successful in locating the odor source in the absence of bulk flow and turbulent transport, in spite of the presence of well-developed odor gradients (Weissburg and Zimmer-Faust, 1993, 1994). Lastly, Weissburg and Zimmer-Faust (1994) varied the bed roughness and found that blue crabs had more difficulty for higher *turbulence intensity* with the same mean velocity. (Alternatively, Moore and Grills (1999) found that crayfish performance improved over rough beds.) These observations strongly suggest that many animals make tracking decisions based on an instantaneous assessment of the rapidly fluctuating, small-scale spatial variation in the odor plume.

One current hypothesis is that the animals are using a bilateral spatial comparison of the chemosensory signal to orient relative to the plume centerline. Zimmer-Faust et al. (1995) suggested that an animal spanning the "edge" of a plume would have enough contrast to steer into the plume. Weissburg (2000) refined this idea by defining the spatial integration factor (SIF) as the ratio of the sensor span to the plume width. He suggested that an animal with a large SIF would have sufficient sensory contrast to steer within the plume. Webster et al. (2001b) used the integral length scale of the spatial correlation function to properly define the width of the plume, and thus define the relative measure for the sensor spacing for a chemical plume over a smooth bed.

To further understand chemosensory-mediated behavior, concentration and velocity signals must be quantified for turbulent flows of interest. The purpose of this study is to examine the information content of the turbulent chemical signal. Of

particular interest is the variation of the integral length scale with increased bed roughness.

## EXPERIMENTAL EQUIPMENT AND PROCEDURE

Measurements were performed in a 1.07 m wide, 24.4 m long tilting flume, shown in Fig. 2, for two bed materials to examine the effect of bed roughness on the chemical transport and chemosensation signal. The hydrodynamically-smooth bed consisted of the painted steel floor of the flume. The rough bed consisted of  $d_{50} = 2.5$  mm gravel distributed with uniform depth of 25 mm. The flow in this case was in the transitional rough regime. In each case, the average flow rate was 50 mm/s and the channel depth was 200 mm. The bed slope was adjusted to create fully-developed, uniform flow conditions for at least 12 m approaching the measurement location. For each case, the water depth was uniform to within 0.3 mm. The wall shear velocity was 3.55 mm/s and 4.15 mm/s for the smooth and rough beds, respectively.

The plume was released iso-kinetically into the flow in order to simulate a leaky source. The release velocity matched the average channel velocity. A small amount of fluorescent dye, Rhodamine 6G, was added to the effluent such that the plume contained extremely low dye concentrations, of the order of 10  $\mu\text{g/L}$ .

The planar laser-induced fluorescence (PLIF) technique was used to collect long records of the concentration field. The horizontal laser sheet (created by sweeping an argon-ion beam with a scanning mirror in the same plane as the plume source) caused the dye to fluoresce and a digital CCD camera (1008 $\times$ 1018 pixels) captured the emitted light over a 1 m  $\times$  1 m region. The image capture rate was 10 frames per second and 6000 sequential images were collected. The light intensity emitted by the dye is directly proportional to the dye concentration and laser light intensity, so the planar concentration field can be calculated from the captured image. The sweep rate was non-uniform in order to have increasing incident light intensity with distance from the source. In this manner, the full dynamic range of the camera is utilized over the entire image despite the rapidly decaying dye concentration. Images were collected at four overlapping locations spaced 0.5 m apart along the plume axis. The source concentration was increased for each successive downstream location such that the dynamic range of the camera was continually optimized.

A careful calibration of the relationship of light intensity to the dye concentration is required for quantitative measurements. The calibration was performed by releasing a uniform dye concentration far upstream and imaging the *in situ* light emission. The calibration images were corrected for attenuation of the laser sheet passing through the

Rhodamine solution. The calibration procedure and measurement uncertainty are discussed in Webster et al. (2001a).

## RESULTS AND DISCUSSION

Figure 1 is a photograph of a blue crab tracking a food odor. Once the animal enters the plume, it moves upstream toward the source at speeds up to 200 mm/s. For the mildly meandering plume shown here, blue crabs identify the source at a success rate of 85-90% from a distance of 1.5 m. In those trials the odor was clam metabolites and the search typically was complete in less than 30 seconds (Keller and Weissburg, pers. comm.).

A sample instantaneous concentration distribution for the rough bed case is shown in Figure 3. The plume appears as patches (or filaments) of high concentration separated by odorless fluid. (Data are not shown closer to the source than  $0.6H$  because the concentration was beyond the range of the calibration procedure.) The peak concentration levels for this sample image are roughly 20% of the source concentration,  $C_o$ , and the peaks are intermittently even higher in this region. The peak values decrease rapidly with distance from the source due to turbulent stirring and mixing. The concentration gradients at the edges of the patches are very large, rising from essentially zero concentration to the peak within just a millimeter or two. An animation of a sequence of concentration fields suggests that advection dominates the transport, while variation in the patches due to turbulent mixing and out-of-plane motion occur relatively slowly.

It is important to remember the effect of sensor resolution to these observations. The camera resolution is about 50 times greater than the Batchelor scale and hence the true peak concentrations are not revealed in these data. However, the data are relevant to the biological context because chemosensors on benthic crustaceans are of a similar size to the image resolution (Derby, 1982).

The time-average of the concentration field has a Gaussian profile and decays away from the source as shown in Figure 4. Figure 5 shows the self-similar Gaussian profiles non-dimensionalized by the centerline concentration and the standard deviation,  $\sigma$ , of the time-averaged profile. From the landscape plot, is easy to imagine a simple tracking strategy of moving up the concentration gradient to the centerline and then up the centerline gradient to the source. This strategy is generally referred to as chemotaxis and has been shown to be very effective for small animals (e.g. bacteria) in laminar environments in which long-term steady gradients are maintained (Dusenbery, 1992). In turbulent flows the instantaneous concentration field lacks a clear gradient in the source (Figure 3). Hence, to use

an analogous strategy the animal would need to collect a time record of concentration at each discrete location and then calculate the time-average value (and the distribution shown in Figure 4).

Because of the signal intermittency, the time-average converges extremely slowly for this plume. Figure 6 shows the convergence of the time average at a representative location in the plume. To create this figure, we split the 600-second record into finite divisions and then calculated and plotted the average for each segment. Converging to a well-resolved time-averaged value takes in excess of 200 seconds. For the shortest duration shown (4.7 seconds), the variation in the calculated average is enormous, i.e. more than  $\pm 100\%$  of the converged value. Attempting to assess the mild gradient in the time-average field (Figure 4) would be futile with this level of variation in the measurement. In fact, rapidly moving animals such as blue crabs do not hesitate and sample for even this short duration. Thus, we can easily conclude that benthic crustaceans do not track the concentration gradient. (Alternatively, slow moving animals such as gastropods or starfish may move slowly enough to sample the plume for significant durations and could conceivably use the variation in the time-averaged concentration.)

While we have used the time-average concentration to demonstrate the slow convergence properties of this plume, all time-averaged quantities at a point show similar or greater variability. Thus, to follow a trend in any sequentially sampled parameter requires time periods far in excess of the observed residence time (Webster and Weissburg, 2001).

Rapidly moving animals appear to be using guidance cues in the instantaneous structure of the odor plume. One spatial cue that has been suggested as useful is bilateral comparison, i.e. a spanwise comparison of the instantaneous concentration across the animal's body (e.g. Reeder and Ache, 1980; Atema, 1996). The photograph in Figure 1 illustrates at how this cue might be useful. Blue crabs have chemosensors on their eight walking legs, on their two front claws, and on antennules near their mouth. In the orientation shown in Figure 1, the right-hand side of the animal is immersed in the plume, while the left-hand side is receiving no significant chemosensory signal. Thus, by comparing the instantaneous signal from its right and left appendage chemosensors the animal could accurately identify the relative direction of the plume centerline. Coupling this information with an odor-gated rheotaxis strategy (i.e. moving upstream when in contact with odor) would lead to a highly successful approach. While the odor-gated rheotaxis strategy has been suggested based on blue crab behavioral experiments performed in the field (Zimmer-Faust et al., 1995; Finelli et al. 1999, 2000), recent simulations indicate that the strategy is

not effective if the animal doesn't correct its heading while moving through the plume (Dusenbery, pers. comm.).

The concentration fields collected in this study allow a detailed examination of the usefulness of a spanwise comparison. Figure 7 shows the correlation function between the absolute concentration at the centerline,  $c_o$ , and at a spanwise distance  $y$  from the centerline,  $c_y$ :

$$\overline{c_p c_q} = \frac{1}{T} \int_0^T c(y=p, t) \times c(y=q, t) dt \quad (1)$$

Four distances from the source are shown for the rough bed case (the smooth bed case has been previously reported in Webster et al., 2001b). As seen in the figure, the spatial correlation function is a strong function of sensor spacing and distance from the source. The correlation function is identically one at the centerline and decreases with increased sensor spacing. Close to the source the correlation function is small and approaches zero very near the centerline. This reflects the fact that the plume is narrow and that filaments of dye have not been spread extensively at this location. The correlation curve increases in magnitude and width as the plume grows and individual patches spread.

It should be noted that the correlation function defined by Equation (1) uses the absolute concentration rather than the fluctuation from the time-average,  $c'$ , as is typically calculated in turbulent flows. This is an important distinction for a couple of reasons. First, the correlation function based on concentration fluctuations does not demonstrate the clear spatial variation shown in Figure 7. Second, for a rapidly foraging animal the time-averaged concentration is unknown due to the slow statistical convergence as discussed above, thus the fluctuation cannot be readily calculated. While biological chemosensors can adapt to their ambient environment, there is insufficient time for the sensors to adapt to a well-resolved time-averaged concentration in this intermittent plume.

While the variation in the correlation function with sensor spacing and downstream distance is dramatic (Figure 7), animals cannot readily access or exploit this information directly because of the slow convergence of the time integration. In fact, the convergence of the correlation function is similar to that of the time-average shown in Figure 6. Nevertheless, Figure 7 suggests that a bilateral comparison may indeed be useful to a foraging animal. In fact, the integral length scale for the correlation function provides a measure of the plume width and may provide useful insight into the biological sensor spacing.

An integral length scale,  $L$ , based on the area under the correlation function curve grows rapidly with distance from the source (Figure 8). The growth rate of  $L$  is faster than that of  $\sigma$ , the standard deviation of the time-averaged concentration profile.

The bed roughness affects the integral length scale mildly, apparently increasing  $L$  slightly at any distance from the source. The fine gravel used in this study changes the wall shear stress only slightly compared to the smooth bed case, thus it is consistent that the plume growth is mildly affected as well.

The correlation function shown in Figure 7 maintains the inner sensor at the centerline of the plume. This is obviously an unrealistic constraint on the sensor location and we would like to generalize the correlation function for any position in the plume. Shown in Figure 9 is the correlation function between two sensors with fixed spacing  $L$ . The abscissa corresponds to the location of the inner sensor non-dimensionalized by  $\sigma$ . The choice of non-dimensionalization appears to be correct because the curves collapse onto the same trend. Similar collapse is observed for the smooth bed case (Webster et al., 2001b). Thus, the sensor spacing scales on the integral length scale of the spatial correlation function, while the sensor location scales on the time-averaged plume width. The peak value of the correlation with spacing of  $L$  is about 0.3 near the plume centerline. While this provides some contrast between the sensors, even better contrast is observed for larger spacing.

Increasing the sensor spacing to  $4L$  confirms the collapse onto a single trend and hence the scaling arguments (Figure 10). Now the peak value of the correlation is about 0.05 near the centerline. Therefore the contrast between the left and right sensor is very strong. The correlation function is so small for this sensor spacing that even an instantaneous or brief bilateral comparison provides significant contrast. Thus, we conclude that a bilateral contrast is useful provided the sensor spacing is "wide enough," which we can define relative to the integral length scale of the correlation function.

## CONCLUSION

Animals demonstrate a wide range of foraging behavior. While a number of aquatic animal studies have been reported in recent years (e.g. Moore and Atema, 1991; Weissburg and Zimmer-Faust, 1994; Breithaupt et al., 1999; Finelli et al., 2000), the use of bilateral comparison has not been definitively shown in those trials. The detailed measurements of the chemical plume fields reported here suggest that a bilateral comparison may indeed be a useful sensory cue to an animal moving rapidly in the plume provided the sensor spacing is wide relative to the plume. The parameter that defines the width of the plume in this context is the integral length scale of the spanwise correlation function. Animals with sensor spacing larger than the integral length scale have significant contrast between their left and right chemosensors and can steer toward the plume centerline. Since the integral length scale is a

function of distance from the source, there appears to be an advantage to animals that can adjust their sensor spacing or possess an array of sensors so they can continually have an optimum chemosensor separation. Whether blue crabs or other animals actually use this information needs to be established through controlled behavior trials, but it appears that a bilateral comparison can provide useful information about the relative position of the plume.

In this study we have provided the first measurements of a chemical odor plume released iso-kinetically into a turbulent boundary layer over a rough bed. For the transitional bed roughness examined here, there is a mild increase in the wall shear velocity and corresponding small increase in the integral length scale,  $L$ . The next phase of this study will include much larger roughness elements to establish flow in the fully-rough regime.

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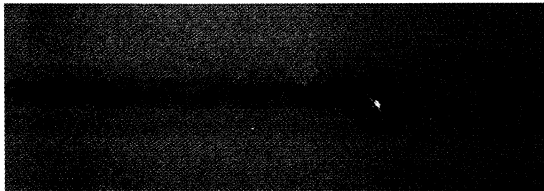


Figure 1 : Blue crab tracking a food odor plume. (Photograph courtesy of Keller and Weissburg.)

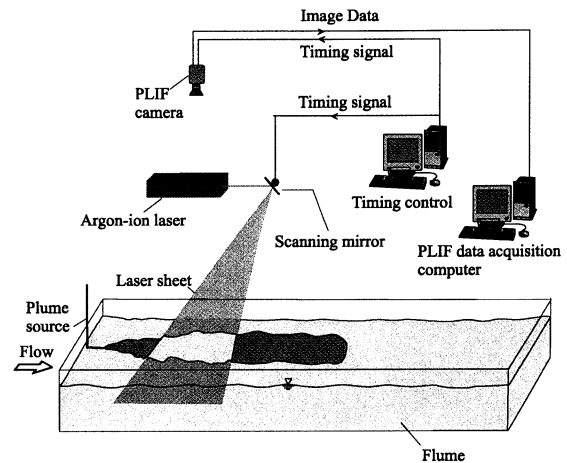


Figure 2 : Experimental apparatus.

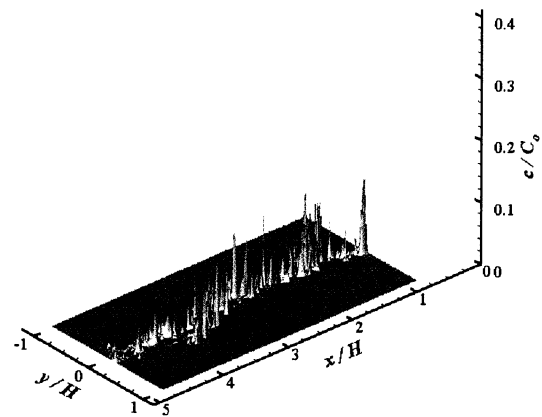


Figure 3 : Instantaneous concentration landscape for the rough bed case.

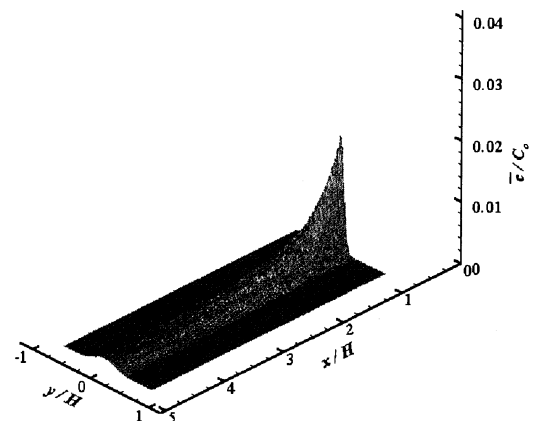


Figure 4 : Time-averaged concentration landscape for the rough bed case.

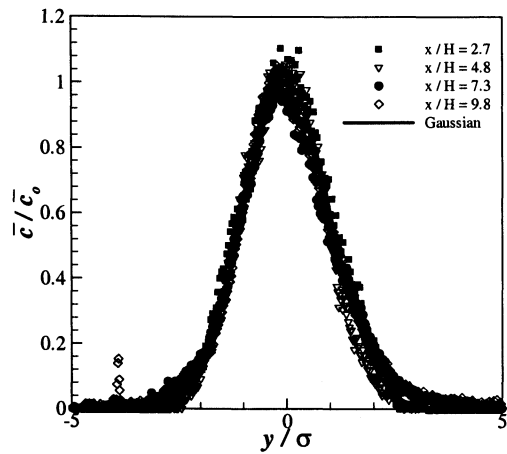


Figure 5 : Self-similar Gaussian profiles of the time-averaged concentration field for the rough bed case.

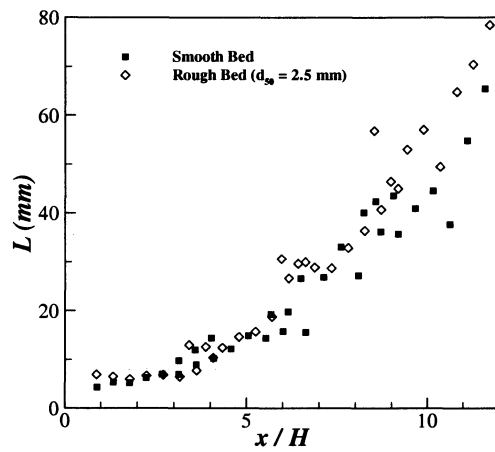


Figure 8 : Integral length scale of the spanwise correlation function.

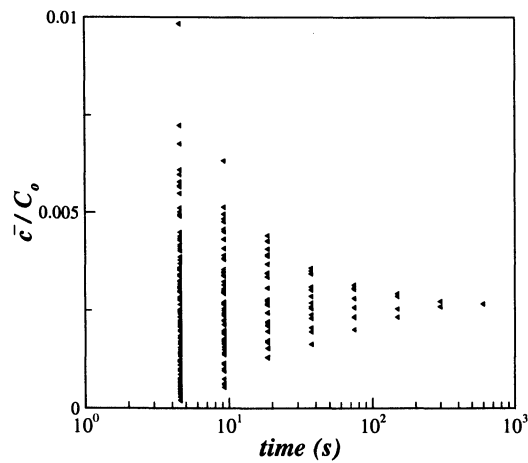


Figure 6 : Time-averaged concentration as a function of sampling period at one location for the rough bed case.

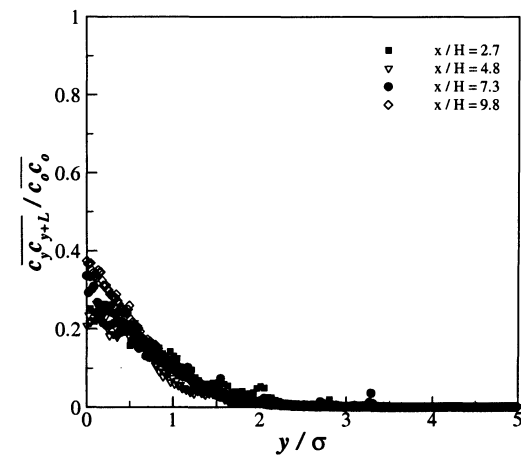


Figure 9 : Correlation function for sensors spaced at  $L$  for the rough bed case.

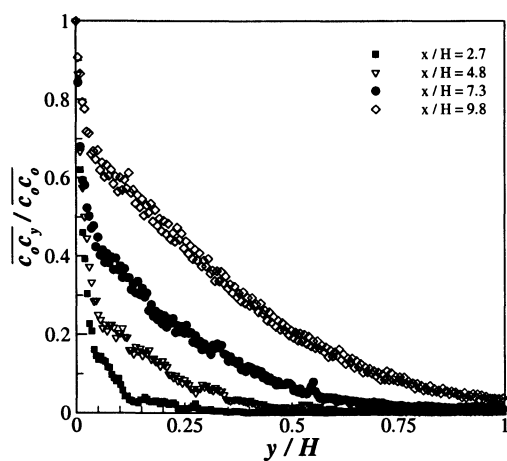


Figure 7 : Spanwise correlation function for the rough bed case.

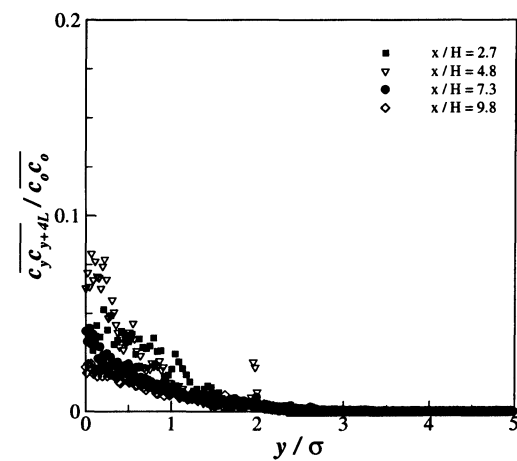


Figure 10 : Correlation function for sensors spaced at  $4L$  for the rough bed case.