Chemosensory guidance cues in a turbulent chemical odor plume

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Abstract

The characteristics of chemical odor plumes released into a turbulent open channel flow are evaluated in the context of chemical plume tracking. The objective is to assess the availability and usefulness of chemosensory cues to animals, such as benthic crustaceans, attempting to orient in the plume. Releasing fluorescent dye into the fully developed turbulent boundary layer of a large laboratory-scale flume created turbulent odor plumes. Flow visualization of odor fields created with varying release velocity, release distance from the bed, and nozzle diameter indicated that chemosensory cues in plumes depend on the release characteristics as well as the ambient flow conditions. Thus, to understand animal behavior, it is important to quantify the plume release properties and characteristics. We chose to quantify concentration fields for the case of isokinetic release using the planar laser-induced fluorescence technique. These measurements indicate that the time-averaged concentration converges far too slowly to be useful to a foraging animal. Similarly, resolving the rise slope of a concentration burst requires sampling rates unattainable by animals, and the spatial variation of rise slope is too mild to follow without lengthy sampling periods. In addition, only mild variation with distance from the source is observed in the concentration burst magnitude and duration. Thus, the time-averaged concentration, rise slope, and burst shape all appear to have limited usefulness for plume orientation for animals known to orient effectively to these types of odor sources.

Sensory systems in organisms translate spatial and temporal patterns of physical properties into electrical signals that mediate animal responses. Light, sound, pressure, and chemical concentration, among others, are stimuli that are used by animals to collect information on their external world, and which evoke various behaviors necessary for survival. Understanding the operation of perceptual systems provides information on ecological interactions mediated by various sensory modalities, as well as on basic neurological mechanisms of encoding and processing information.

A fundamental tenet in the analysis of sensory systems is that they are not fully interpretable until the appropriate sensory environment is characterized or defined. In other words, unless the nature of the input to a sensory system is known, the details and functions of its operation will be obscured. For instance, the elegant construction of the eyes of some insects allows them to use polarized light as a navigational aid. This design is contingent on the orientation of regions of the eye corresponding to the orientation of the e-vector of polarized light emanating from the sector of the sky scanned by each region. Thus, the map of the eye cannot be appreciated unless one has similarly obtained a map of the sky (Wehner 1989).

The physical cues used by many sensory modalities offer convenient dimensions for characterization of stimulus patterns, even in the spatial or temporal domain; understanding the Doppler frequency shifts from moving objects has proved a powerful way to probe the operation of the amazingly acute hearing of owls or bats (Schnitzler 1973).

In this regard, one particularly recalcitrant system is chemosensation. Many marine (and terrestrial) animals use odor to navigate toward the source of distant objects such as food or mates (reviewed in Weissburg 1997, 2000; Zimmer and Butman 2000). However, accurate spatial and temporal characterization of odor environments is possible under limited circumstances. Molecular diffusion models have lead to realistic pictures of chemically mediated navigation of bacteria, microorganisms, and small crustaceans (Yen et al. 1998; Weissburg 2000). Unfortunately, the diffusion models are not useful in environments where the mechanisms of odor dispersion include turbulent processes that produce substantial temporal and spatial variation in chemical concentration. Because many animals in these turbulent environments sample odor concentration relatively quickly, rapid fluctuations and small-scale spatial variation, which cannot be captured using diffusion models, appear to mediate their responses (e.g., Murlis et al. 1992; Weissburg and Zimmer-Faust 1994; Atema 1996). Characterization of odor environments relevant to macroscopic invertebrates can be achieved only by a comprehensive analysis of this spatial and temporal variation.

Sampling the instantaneous properties of plumes has been practical only in recent years and has been only rarely applied to situations relevant to the odor environment of aquatic animals such as benthic crustaceans. As expected, these studies have revealed that odor plumes are filamentous and sporadic, and their evolution reflects the initial plume size and ambient turbulent scales. Some attention has been paid to examining how the turbulent flow affects the resultant plume (Fackrell and Robins 1982; Jones 1983; Murlis 1986; Bara et al. 1992; Yee et al. 1993), and this has provided

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valuable insights into the possible effects of fluid physics on animal navigation and into potential constraints on the sensory system. Proceeding from this data, a number of hypotheses have suggested that animals may use changes in instantaneous properties, such as the onset slope of an odor filament or concentration peak shape, to orient in the plume (e.g., Moore and Atema 1991). Other proposals suggest that as chemical signals become entrained by turbulence, the coincidence of both flow and odor signals presents the searcher with “flavored eddies” that contain special information (Atema 1996). Although animals may use chemical and velocity signals to track an odor, there currently is little information on how the plume structure may be affected by the release characteristics of the source, particularly its initial momentum relative to the ambient flow. Odor may be released in a jet of considerable velocity (e.g., Moore and Atema 1991; Weissburg and Zimmer-Faust 1994) or leaking into the flow with almost no momentum relative to the source (i.e., modeling a decaying piece of flesh—e.g., Finelli et al. 1999; Crimaldi and Koseff unpubl.). The term “flavored eddy” implies a correlation between the vorticity and concentration fluctuations that is case dependent and remains poorly quantified.

Clearly, we need more complete information on odor plume dynamics in order to ascertain the mechanisms used in chemically mediated guidance and to interpret the properties of the sensory system as they are currently understood. In particular, long-term records of chemical concentration fields would quantify the plume characteristics. As an initial step in this direction, we have used a noninvasive optical method to measure planar odor concentration fields in a turbulent plume. Our primary goals are to understand how release characteristics affect the resultant plume structure and to characterize the plume in time and space in order to determine the utility of current hypotheses regarding the information potentially available to a chemosensory forager.

Methods

Experiments were performed in a tilting flume 1.07 m wide by 24.4 m long with a rectangular cross-section and smooth bed. Figure 1 shows a sketch of the experimental apparatus. The working fluid was water at 20°C. The average velocity in the cross section was 50 mm s⁻¹, and the flow depth, H, was 200 mm. The bottom slope was adjusted to provide uniform flow for at least 12 m approaching the measurement location. In this region, the flow depth was constant to within 0.3 mm. These conditions agree well with the hydrodynamic environment in previous laboratory studies of odor-mediated tracking by crustaceans (e.g., Weissburg and Zimmer-Faust 1993, 1994).

Mean and root mean square (rms) profiles of velocity were measured using laser Doppler velocimetry (LDV). The mean boundary layer profile was fully developed at the measurement location and agrees well with the law-of-the-wall, as expected. The wall shear velocity, u*, was 3.55 mm s⁻¹. The
The turbulences fluctuations reach a local maximum of $u''/u^* = 2.5$ below $0.1H$, and $u''/u^*$ approaches unity near the free surface, where $u'$ is the velocity standard deviation.

Brass nozzles with inner diameters of 2.2 and 4.7 mm were used as the chemical plume source. A brass fairing was attached to the downstream face of each nozzle to minimize the wake disturbance. Preliminary flow visualization confirmed that the flow perturbation resulting from each nozzle was minimal. Effluent was pumped continuously from a 40-liter polyethylene tank, and the flow rate was measured with a rotameter.

Flow visualization images were obtained by releasing neutrally buoyant red dye and photographing with a Kodak color digital camera.

Quantitative measurements of the concentration field were performed with the planar laser-induced fluorescence (PLIF) technique (e.g., Ferrier et al. 1993). PLIF utilizes the fact that fluorescent dye emits light at intensity proportional to the species concentration and laser sheet intensity. As illustrated in Fig. 1, a laser sheet bisecting the flow causes the dye to fluoresce, and a digital camera captures the emitted light. Thus, after an in situ calibration of the laser sheet intensity, quantitative planar concentration fields can be calculated from the images.

In these experiments, a small amount of Rhodamine 6G was mixed into the plume effluent. The peak absorption wavelength of Rhodamine 6G is approximately 530 nm, and the peak emission is near 560 nm (Arcoumanis et al. 1990). Source concentration levels were carefully controlled such that the entire dynamic range of the camera is utilized at each distance from the source, resulting in the capacity to record the full range of concentration occurring in any given region. This also assured that the plume concentration in the measurement region was below 25 \( \mu \text{g L}^{-1} \), thus avoiding problems with absorption. The illumination sheet was formed by rapidly sweeping a 1-mm-diameter argon-ion laser beam horizontally through the flow.

A Kodak MegaPlus ES 1.0 CCD camera mounted above the test section captured eight-bit digital images with 1,008 by 1,018 pixels. Images were collected with magnification of 0.2 mm pixel\(^{-1}\) and 1.0 mm pixel\(^{-1}\). It should be noted that the laser sheet thickness was 1 mm in both cases, thus degrading the resolution in the third dimension for the higher resolution case. An optical filter on the camera lens isolated the fluoresced (yellow-orange) light so that stray illumination did not interfere with capturing the fluorescence intensity. To eliminate the optical distortion of photographing through the free surface, a thin acrylic sheet was located at the water surface, such that the bottom surface was wetted.

Images were stored on the hard drive in real time using Video Savant RTD software. Several minutes of digital video were required to achieve statistically stationary data and to provide a long, continuous record of the concentration field. In this experiment, 6,000 PLIF images were captured at 10 frames s\(^{-1}\). The total period in each case was thus 10 min.

A calibration of the intensity versus concentration was performed in the flume. A concentrated solution of Rhodamine 6G was released uniformly across the flow near the head box at controlled flow rates to create the calibration concentration levels. In the measurement region (far downstream), the dye was uniformly mixed. The light emission was photographed, and corrections to the calibration images were made to account for the absorption of laser light through the dyed fluid (Ferrier et al. 1993). A least squares fit was calculated to yield a calibration slope and intercept at each of the 1,008 by 1,018 pixel locations. This calibration procedure accounts for nonuniformities in the laser sheet intensity and lens vignette and for pixel response variability (Webster et al. 2001).

The discussion of the measurements in a biological context requires some assurance that the length scales and dynamic range are relevant to benthic crustaceans. The spatial resolution of the concentration fields is similar to aquatic decapods, which have chemosensors that are generally 10 to 100 \( \mu \text{m} \) in length and width (e.g., Derby 1982; Hamilton 1983; Hamilton et al. 1985). The dynamic range of the measurements also preserves the basic functional characteristics of crustaceans as they are currently understood. Crustaceans possess a variety of chemosensors, often with individual sensors expressing fairly narrow dynamic ranges (e.g., 2–4 orders of magnitude—Derby and Atema 1985; Laverack 1985), but a range of sensor sensitivities equip the animal with an overall dynamic range of many orders of magnitude.

Analogously, in the current measurements, the source concentration was adjusted to utilize the full dynamic range at each camera location. Thus, at a particular location, the measurements are limited to two orders of magnitude (i.e., eight bits), but a much larger dynamic range is measured over the length of the plume. With this procedure, the variation in odor intensity is accurately preserved at each location.

Results

Qualitative plume characteristics—Figure 2 shows plumes released with the same velocity as the surrounding open channel turbulent flow (isokinetic release). In order to maintain a constant dye flux among the cases, the release velocity was matched to the average channel velocity. Four release heights above the bed are shown in Fig. 2 for the large nozzle. Because the effluent and channel velocities are matched, the velocity gradient produced by the release is very small, and the production of turbulence due to velocity shear is minimal. Thus, turbulence produced in the fully developed bed boundary layer is responsible for the turbulent transport of the chemical tracer. The release location for the plume shown in Fig. 2a corresponds to the outer region of the boundary layer above the logarithmic region. The turbulence intensity, $u''/u^*$, is 1.25 in this region.

The plume shown in Fig. 2a exhibits evidence of the stretching and distorting processes that are normally associated with turbulent stirring. Concentrated packets of dye are observed for long distances downstream owing to the relatively low turbulence intensity and mild local mean velocity gradient in this region. Even at the end of the field of view, concentrated packets of dye are observed.

One would expect the mixing characteristics to be differ-
ent for a release near the bed due to much higher mean velocity shear and turbulence intensity. Indeed, Figs. 2b–d each exhibit different characteristics because the release location is progressively closer to the bed. The plume, released at 25 mm (0.125H) above the bed as shown in Fig. 2c, is subject to significantly greater turbulent mixing, and at the end of the field of view the tracer has experienced significant dilution and is more homogeneous. This contrasts with the previous example, in which the plume appears as a twisted and folded filament of dye for several channel depths downstream of the nozzle. The tracer has spread over a slightly wider region despite being confined by the bed.

Figure 2d shows the plume released with the nozzle resting on the bed. The chemical plume in this case appears to be trapped initially in the viscous sublayer, as suggested by streaks of high tracer concentration close to the bed when observed from above (not shown here). The side view indicates that the dye is trapped near the bed until it first bursts away more than a channel depth downstream of the nozzle. The dye distribution at the end of the image is fairly homogeneous near the bed, but the plume is confined to a much smaller region than the other cases due to the physical constraint of the bed.

The variation with release height from the bed results from the variation in fluctuating eddy size and intensity. The success of the Prandtl mixing length model for a turbulent boundary layer ($l = \kappa z$, where $l$ is the size of the mixing eddy, $\kappa$ is the Karman constant, and $z$ is the distance from the bed) suggests that the integral eddy size is smaller near the bed. In addition, the fluctuation intensity is greater near the bed. Thus, more energetic, smaller eddies (presumably smaller than the nozzle diameter) distort and stir the patches of chemical tracer as seen in Fig. 2.

Figure 3 shows five plumes released with increasing release velocity. The velocity is doubled between each successive image, whereas the dye concentration is halved so that the flux of dye remains constant across all images. In Fig. 3a, the release velocity matched the average velocity in the channel (isokinetic, as in Fig. 2). As discussed above, the turbulence in this case is due to the turbulent boundary layer, resulting in relatively large, low-intensity eddies that act to stretch and distort the filament of dye as observed.

Doubling the velocity (Fig. 3b) increases turbulence production due to the velocity shear between the jet and the ambient fluid. Although the turbulent eddies appear to affect the plume much closer to the nozzle, the overall effect at the end of the image is mild for this case. Doubling the velocity again (Fig. 3c) leads to a significant effect. The fluctuating eddies produced by the velocity shear are ideally sized to distort the plume and thus stir the tracer with the ambient fluid. The plume in this case still possesses a me-
andering appearance, but the filaments of high concentration have been diluted and spread.

Further increases in jet velocity continue to affect the character of the plume substantially. Doubling the velocity again (Fig. 3d) and again (Fig. 3e) leads to increasingly large turbulence intensity at increasingly small turbulent eddy scales. As a result, the plume concentration becomes more diluted and homogeneous, and the filamentous nature of the plume is nearly lost.

The nozzle diameter also has a significant effect on the plume mixing characteristics. Figure 4 shows the plume resulting from an isokinetic release from the small nozzle at middepth. The dye filament distortion is slight; a continuous filament of dye persists over much of the image. In fact, the dye filament is even less mixed than the isokinetic release from the large nozzle at middepth. It should be noted that the faring for this nozzle was slightly different than for the large nozzle; in each case the flow perturbation due the nozzle was very mild.

Quantitative measures—Although the flow visualization images are useful for a basic qualitative appreciation of the plume behavior, the integrated view through the plume prevents meaningful quantitative analysis. In this section, we present the quantitative aspects of the concentration fields obtained using the PLIF technique. We chose to examine the case of isokinetic release because this is characteristic of leaky odor sources crustaceans readily locate and consume. In nearly identical flow and source release conditions, behavior trials with adult blue crabs, *Callinectes sapidus*, reveal a success rate of 85–90% for animals locating the source (clam metabolites) located 1.5 m upstream. A typical successful search period is less than 30 s (Keller and Weissburg unpubl. data). Similar results are obtained for crabs
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Fig. 5. Concentration landscape in the neighborhood of 3H downstream of the nozzle. The chemical plume is released at 0.125H from the bed.

locating small pieces of flesh that release odor with minimal perturbation to the flow.

Figure 5 shows a sample instantaneous concentration field normalized by the source concentration, $C_0$, for the plume released at 0.125H from the bed. The measurement plane consists of the streamwise, $x$, and spanwise, $y$, directions, and the elevation corresponds to the local concentration level. The flow moves in the positive $x$ direction (i.e., from the upper right to the lower left). The conditions shown in Fig. 5 are the same as for Fig. 2c. The region shown in Fig. 5 is located roughly in the center of the field of view of Fig. 2c, although the perspective is now from above rather than from the side. The field consists mostly of concentration levels approaching zero. Most striking, however, are the sporadically located large peaks of high concentration. The largest peak in this particular image is roughly 20% of the source concentration. Because the PLIF images are limited to a single plane in the flow, it is important to realize that in addition to advection and turbulent transport within the plane, packets of chemical tracer move vertically in and out of the plane. The true peak values depend on the sampling scale and are actually larger than the peaks shown in Fig. 5. The Batchelor length scale is a measure of the length scale at which molecular diffusion is the dominant transport mechanism affecting the distribution of a chemical species and is defined as $L_B = (vD^2/\epsilon)^{1/4}$, where $v$ is the fluid kinematic viscosity, $D$ is the molecular diffusion coefficient of the chemical species in the fluid, and $\epsilon$ is the dissipation rate of the turbulent fluctuations (Batchelor 1959). For the flow discussed here, the Batchelor scale is about 0.02 mm. In contrast, the image resolution is 0.2 mm (with 1 mm depth corresponding to the laser sheet thickness). Thus, the image is roughly an order of magnitude too coarse to resolve the fine-scale structure and peak magnitude of concentration. This resolution limitation is not unique to our measurement technique since the size of a biological sensor may have similar spatial constraints (e.g., Moore and Atema 1991; Finelli et al. 1999).

The time-averaged concentration field and its standard deviation are shown in Figs. 6 and 7, respectively, for the plume released at 0.125H. Measurements are not shown for $x/H < 0.6$ because the peak concentration in that region is beyond the linear calibration range. The time-averaged concentration and standard deviation both decrease in the flow direction. In the spanwise direction, the mean profiles have a Gaussian distribution shape and collapse onto self-similar curves. The standard deviation profiles also collapse fairly well onto a self-similar curve, but the shape is not Gaussian. There appears to be a local maximum at roughly $y/H = 1$, which creates a profile reminiscent of that of a round jet (e.g., Webster et al. 2001). For this plume, the magnitude of the standard deviation is greater than the time-averaged concentration.

Comparison of the time-averaged versus instantaneous concentration shows large differences in signal intensity. The instantaneous peaks can be one to two orders of magnitude greater than the time-averaged concentration, and the difference would be greater with increased spatial resolution of the measurement (as discussed above in relation to the Batchelor length scale). This large disparity illustrates the danger in relying on the time-averaged value in a highly sporadic plume.

The centerline profiles of the concentration field are shown in Fig. 8. Close to the source ($x/H < 2$), the average concentration decreases faster than $x^{-1}$, indicating a regime of relative diffusion in which the patches of tracer are growing but are still smaller than the largest turbulent eddies. In
the range $2 < x/H < 5$, the centerline concentration decreases in proportion to $x^{-1}$, which agrees with the theoretical model of constant eddy diffusivity. This suggests that the patches have grown to the size of the largest eddies and a constant eddy diffusivity characterizes the mixing. Beyond $x/H = 5$, the decay is slower than $x^{-1}$, which indicates that the turbulent transport is attenuated in the vertical direction by the presence of the bed and free surface.

Close to the source, the standard deviation is larger than the time-averaged value because of the intense concentration fluctuations. Time records in this region consist of mostly zero or low concentrations with sporadic extreme peaks, thus
leading to relatively large standard deviation. As the concentration field becomes more homogeneous, the magnitude of fluctuations, and hence the standard deviation, decreases. The standard deviation is essentially equal to the time-averaged value around 10 channel depths downstream of the source.

It is important to realize that very long observation periods are required to achieve the converged statistics shown in these figures. Figure 9 demonstrates more clearly the necessity for taking a long time record to resolve the statistics. The time-averaged value and standard error are shown as a function of sampling period. For short periods, the scatter is enormous; the time-averaged value converges only beyond roughly 200 s. Shorter samples do not provide the accuracy required for an agent to assess the spatial variation shown in Fig. 6. Consistently, the standard error is very large for short time periods and also converges very slowly toward zero (Fig. 9b). Higher order statistics converge even more slowly than the time-averaged value.

For tracking, the time-averaged value and standard deviation are best observed over the entire field, as discussed above. Unfortunately, this perspective is unavailable to an animal or agent tracking a plume. An alternative is to monitor the characteristics of individual bursts of tracer concentration and use trends in burst properties to gauge relative location to the source. Atema (1996) and others have suggested that the burst characteristics reveal relative positional information and have identified three burst characteristics—slope, peak concentration, and duration—as possible sources of information used during tracking.

In Fig. 10a, an instantaneous centerline concentration profile has been converted to a temporal record by assuming that the concentration distribution is simply advected unchanged over short time scales (Taylor’s hypothesis). Thus, an agent would observe a time record similar to that in Fig.
Fig. 11. Time-averaged concentration slope and standard deviation along the centerline. Only negative slopes have been included in the statistics. (The slope is nondimensionalized by the source concentration and channel depth.)

The time-averaged concentration slope also is a slowly converging quantity. Shown in Fig. 12 is the variation of the average slope with sampling period. As with the time-averaged concentration, the time-averaged slope doesn’t converge until a sample time of approximately 200 s. The standard error also converges very slowly toward zero.

An alternative way for an agent to make use of information contained in bursts is to track the range or distribution of burst characteristics. If the likelihood of particular events changes in a systematic way along the length or breadth of the plume, the distribution of burst properties will contain information that may be more quickly discernible than changes in the time-averaged values.

The distribution of concentration does not resemble a Gaussian distribution along the centerline. The number of occurrences of concentration in this range is greatest at the closest location to the source ($x/H = 2.5$). With downstream distance, the entire distribution shifts to the left, which means that the concentration magnitudes are diminishing. This is consistent with the plume mixing and becoming more homogeneous.

The distribution of concentration does not resemble a
Gaussian distribution, as demonstrated by the PDF shown in Fig. 15. The highly skewed (skewness ≈ 10) and very flat (kurtosis ≈ 100) distribution is consistent with the observations above. Close to the source, concentration bursts are rare; thus, there is a high probability of a zero or near zero concentration level. The probability of a high concentration value is small because it is an inherently rare event. As the tracer mixes, the probability of encountering zero concentration decreases. At the farthest downstream location shown (x/H = 9.9), there is a local maximum in the distribution around c/c~ ≈ 0.6, which means it is more probable to encounter low concentration than zero concentration as the volume of the tracer patches expands and the field becomes more homogeneous. A local maximum also may be present at x/H = 7.4, although at lower concentration.

Figure 16 is the PDF of the burst duration at four locations along the centerline. The burst duration is defined as the length of time that a continuous concentration burst is above the local time-averaged value. The data scatter masks any
clear trend, but it appears that there may be a subtle trend consisting of an increasing probability of pulses longer than 1 s with distance from the source. The specifics of this trend are not readily assessed from this data set because of the finite length of the record and rarity of long bursts. The mild trend is not surprising, however, given the expansion of patch volume during mixing. These data are consistent with Murlis (1986) who observed that the burst duration was a weak function of distance from the source.

The autocorrelation function (Fig. 17) also shows a mild trend with distance from the source. As the plume evolves downstream, tracer patches expand over a larger area, increasing the span over which concentrations are similar and leading to greater signal autocorrelation. Converting the longitudinal spatial correlation function to the autocorrelation using the advection speed yields nearly identical curves with increased resolution, thus confirming the trend in Fig. 17.

Discussion

It is easy to imagine from the flow visualization images that an observer in the flow, such as a blue crab, would receive widely different signals depending on the release location, release velocity, and release diameter. For instance, releasing odor at middepth produces a signal where the concentration would be zero or low with brief high fluctuations. In contrast, for a release closer to the bed or at high relative velocity, the signal would be more homogeneous with less extreme peak fluctuations.

Increasing jet velocity (Fig. 3) reveals characteristics that are consistent with that of a turbulent jet into a still ambient fluid (e.g., Tennekes and Lumley 1972). Such experiments indicate that the fully developed boundary layer turbulence is overwhelmed by the shear turbulence of the jet. Increasing the jet velocity above the ambient flow increases the velocity shear and, hence, the shear production of turbulent kinetic energy, which results in faster and more effective mixing. This affects the degree of odor plume dilution and increases the homogeneity of the signal. Because both odor intensity (or flux) and intermittence are important for odor-guided navigation, the degree of shear-induced mixing will have important consequences for animals attempting to orient in the plume.

The effects of nozzle diameter on plume characteristics may be given context by conceptual models of plume development. Csanady (1983), among others, describes the mixing as a twofold process in which turbulent eddies that are larger than a tracer patch convect the patch, whereas smaller eddies distort the patch surface and ultimately stir and dilute the chemical tracer. The nozzle diameter for the plume shown in Fig. 2 is 4.7 mm; thus, the eddies, which act to mix and distort the plume, must be smaller than that dimension. The Kolmogorov microscale for the fully developed open channel flow is 0.7 mm; thus, eddies smaller than 4.7 mm will contain little energy (for a description of the energy cascade, see, e.g., Tennekes and Lumley 1972). This conceptual picture is consistent with the filamentous nature of the plume observed in Fig. 2a, which results from the relatively large eddies twisting the plume, while the weak smaller eddies only mildly distort the surface of the filaments. For the smaller nozzle (2.2 mm diameter), fluctuating eddies smaller than the nozzle dimension contain even less energy and thus do not significantly distort and mix the filaments (Fig. 4).

In each example there is net transport of tracer away from the plume centerline, which suggests that the correlation between the fluctuating velocity and fluctuating concentration is nonzero. In fact, the cross-correlation, $v'c'$, has been quantified for a jet by Webster et al. (2001), among others, and for a plume by Liao et al. (2000). The term “flavored eddy,”
however, is a poor descriptor of the plume behavior. There is no evidence that high concentrations of tracer are correlated with the fluctuating turbulent eddies (this relationship is not inherently implied by a nonzero $v'c'$). In fact, the location and concentration of a particular patch of tracer is the result of the complex time evolution beginning with the release. Thus, it is unlikely that high-concentration patches would be correlated at an instant to the fluctuating eddies, particularly far from the source.

The essential conclusion from these flow visualization experiments is that odor source characteristics (relative velocity to ambient flow, release height, source diameter) strongly influence the odor signal properties (concentration, intermittence, pulse shape) that may provide information to a searcher. Even under similar ambient flows, variation in release characteristics may so substantially alter the resulting odor signal that animals could display completely different behavior as odor source properties change. It is the interaction between the source and the ambient environment that imparts a particular character to the plume, and although investigators have begun to appreciate the importance of defining the ambient environment (Zimmer and Butman 2000), only cursory attention has been paid to properties of the source. Future investigations need to carefully consider, and define, the source properties as well as the ambient fluid dynamic environment. Without such information, it will be difficult to interpret the resulting behavioral observations, and we run the risk of confusing differences in strategies across taxa or environments with artifacts created by an incomplete understanding of the relevant flow dynamics.

Understanding the variability in the plume characteristics may be of key importance for animals estimating the relative source location. It is unlikely that traditional statistical quantities such as the time-averaged value and variance are useful to an observer trying to deduce the relative position and distance of a chemical plume source. It is indeed easy to imagine a rather simple approach to plume tracking that involves following the time-averaged concentration gradient, such as that proposed for small organisms in low Reynolds number flows (e.g., Dusenbery 1998; Yen et al. 1998). From Fig. 6, this appears theoretically possible since the time-averaged concentration increases toward the centerline and toward the source. However, to reasonably resolve the time-averaged value, an observer needs to sample the concentration for a long period of time. Even after a 37-s sampling period, time-averaged estimates of odor concentration vary by almost ±40% of the converged value (Fig. 9a). In fact, it takes more than 200 s for estimates to converge at a given location. Thus, an animal in the flow would have to wait at each discrete location for several minutes to resolve the statistical quantities to the accuracy required to track the time-averaged gradients.

The long sampling periods necessary for accurate assessment of time-averaged concentration suggests that reliance on this quantity is impractical for many animals. There has been some skepticism that animals in turbulent environments track the time-averaged concentration, and trials with a variety of crustaceans in both lab and field environments do not reveal this type of behavior (Weissburg and Zimmer-Faust 1994; Zimmer-Faust et al. 1995; Moore and Grills 1999). Adult blue crabs typically locate this source configuration in less than 30 s from a distance of 1.5 m. Elkinton et al. (1984) and Murlis et al. (1992) observed similar slow convergence of the time-averaged concentration in airborne plumes and concluded that insects do not use the time-averaged concentration distribution to track airborne odor plumes.

The most readily available information to an animal tracking the flow is the instantaneous plume characteristics. The instantaneous plume shape is very different from the Gaussian distribution observed in the time-averaged concentration field and, in fact, doesn’t resemble a smooth distribution of any type (see Fig. 5, also see the description by Murlis et al. 1992). Gleaning directional information from such a field is far from a trivial task, and invites the question: What information is available in the instantaneous field?

Moore and Atema (1991) noted that the slope of the leading edge of a high concentration peak (i.e., a rising slope) is a function of the distance from the source and suggested that an animal could use it as a tracking cue. Measurements of isokinetically released odor into field environments also indicate a systemic decrease in the rising slope away from the source (Finelli et al. 1999), as do measurements of a jet source released into a cross-flow (e.g., a bivalve siphon, Moore et al. 1994) and a leaky source that disrupts the flow (Keller et al. 2001). However, for the slope to be a useful parameter, it must be perceptible by the animal and yield predictable patterns within the sampling period available to a searcher. Our evidence suggests neither condition is likely to exist for the case of isokinetic release into the log-layer region of a benthic boundary layer.

The temporal resolution required to adequately sample such pulses is beyond the range of aquatic animals as it is currently known. The sample burst shown in Fig. 10 is only well-resolved at a high frequency (data points shown correspond to 250 Hz), whereas crustacean olfactory neurons seem to be capable of sampling only at less than 10 Hz (Gomez and Atema 1996). Sampling at a slower frequency, such as that of a typical crustacean chemosensor, would fail to resolve a meaningful rising slope or may miss the slope entirely. The distribution in Fig. 16 shows that the example bursts shown in Fig. 10 are typical for this plume; the majority of bursts are less than 0.2 s in duration. A further complication is that molecular diffusion acting at the Batchelor scale controls the shape of the rising and falling slopes; thus, the slope is a continuously varying value (see example in Fig. 10b). Presuming that animals can detect concentration differences and roughly characterize the slope magnitude, we have calculated the time-averaged conditionally sampled negative slopes and standard deviation to learn if there is a trend to follow in the plume. Figure 11 verifies the decrease in the conditionally sampled time-averaged concentration slope with distance from the source. However, the standard deviation is larger than the time-averaged value, which means that the instantaneous values are highly fluctuating. Indeed, Fig. 12 shows that unrealistically long sampling periods are required in order to resolve the time-averaged concentration slope.

An alternative hypothesis is that the probability of certain slope values varies with distance from the source, so that
the PDF could be used as a directional cue (Moore and Atema 1991). PDFs of the concentration rise slope show that although there is a trend, it is mild. In fact, a broad range of slopes is observed at each of the four locations shown in Fig. 13. The most obvious effect is for the slopes to be quite steep close to the source, but the probability of these events occurring is so small that they would be unlikely to occur during a typical tracking episode. In conclusion, the rising slope is difficult to measure accurately and is highly fluctuating; hence, it doesn’t appear to be a useful orienting cue for this plume.

It also appears that the burst shape is not terribly useful for tracking the plume. The concentration magnitude distribution shows a trend with distance from the source (Figs. 14, 15), but a wide range of concentration magnitudes can be expected at any location in the plume. In addition, the burst duration shows little, if any, variation in Fig. 16. Although there is a mild variation in the autocorrelation function, to resolve the variation takes an extremely long time record.

The underlying problem with all of these time-integrated quantities is the same. Although there may be weak spatial variation within the plume, resolving these subtle trends requires sampling the concentration distribution at a single point for time periods that exceed, by a large margin, the total time that animals spend tracking through several meters to the source. Figures 9 and 12 demonstrate the slow convergence of the time-averaged concentration and slope; higher order statistics and the other quantities presented here converge even slower. Thus, assessing these quantities and utilizing the information requires prohibitively long sampling periods for foragers such as blue crabs. In the current example the converged time-averaged concentration requires over 200 s, whereas an adult blue crab typically requires less than 30 s to locate the source from 1.5 m. It is important to remember that the temporal and spatial characteristics and hence time required to resolve the time-averaged quantities depend on the release properties (Figs. 2–4). Thus, the quantitative conclusions regarding the required sampling period should be considered case dependent (for instance, a less intermittent plume, such as that shown in Fig. 3e, will converge more rapidly).

Continued laboratory and field measurements (e.g., Finelli et al. 1999) are clearly necessary, yet it seems reasonable to conclude that macroscopic animals such as crabs and lobsters cannot glean much information from sequential sampling of odor properties. Although our results apply most directly to isokinetic release, the fact that the general characteristics of odor pulses produced by this method resemble that produced in situations with substantially different release properties, both in air and in water (Elkinton et al. 1984; Moore and Atema 1991; Murlis et al. 1992; Moore et al. 1994; Finelli et al. 1999; Keller et al. 2001), suggests that the futility of relying on temporal sampling is a widespread phenomenon.

The evidence presented here strongly suggests that the spectacular success that these animals display when tracking plumes must be due largely to other mechanisms. In fact, the tracking ability of male moths, perhaps the quintessential example of chemosensory tracking, appears to rely on a very simple set of behavioral rules that depend little on the properties of the odor itself. In response to the presence of female pheromones, males move upstream guided by their perception of flow, which ultimately results in efficient locomotion to the source (reviewed most recently in Vickers 2000). Up-current movement in response to odor is a common behavior in the repertoire of marine creatures (Weissburg 1997, 2000), and this mechanism, often referred to as odor-gated rheotaxis, has been hypothesized to occur in crustaceans (Weissburg and Zimmer-Faust 1993, 1994; Zimmer-Faust et al. 1995). Although sequential sampling may not be informative, simultaneous spatial sampling can allow animals to resolve their spanwise position in the plume (Webster et al. 2001) and has been suggested as an important element in olfactory navigation (Basil and Atema 1994; Zimmer-Faust et al. 1995). Odor-gated rheotaxis in combination with spatial sampling may be sufficient to explain the impressive abilities of marine crustaceans without the need to invoke measurement of other odor properties that we find convey little information.

It is essential to keep in mind that the information content of the signals we have analyzed depends not only on the signal itself, but also on the time available to the searcher to compile the information contained in the odor field. Whereas animals such as blue crabs may not rely on time-averaged signal intensity or burst properties, slowly moving creatures may sample the plume accurately enough to use these types of quantities. Using very conservative assumptions, sequential sampling is revealed to be a potentially effective strategy for creatures such as echinoderms and gastropods even in environments where this same mechanism fails for crabs and lobsters (Weissburg 2000). Sorting out the implications of animal size and scale, as well as continued investigation of signal structure, remains necessary for devising and testing the hypothesis of odor-guided navigation.

References


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