ELSEVIER

Available online at www.sciencedirect.com
SCIENCE DIRECT®

Journal of Marine Systems 49 (2004) 55–64

JOURNAL OF
MARINE
SYSTEMS

www.elsevier.com/locate/jmarsys

Odor landscapes and animal behavior: tracking odor plumes in different physical worlds

Paul Moore[a,*], John Crimaldi[b]

[a] Laboratory for Sensory Ecology, Department of Biological Sciences, Bowling Green State University, Bowling Green, OH 43403, USA
[b] Department of Civil and Environmental Engineering, University of Colorado, Boulder, CO 80309-0428, USA

Received 24 October 2002; accepted 4 May 2003

Abstract

The acquisition of information from sensory systems is critical in mediating many ecological interactions. Chemosensory signals are predominantly used as sources of information about habitats and other organisms in aquatic environments. The movement and distribution of chemical signals within an environment is heavily dependent upon the physics that dominate at different size scales. In this paper, we review the physical constraints on the dispersion of chemical signals and show how those constraints are size-dependent phenomenon. In addition, we review some of the morphological and behavioral adaptations that aquatic animals possess which allow them to effectively extract ecological information from chemical signals.

Keywords: Turbulence; Odor plume; Animal behavior; Orientation; Hydrodynamics

---

1. Introduction

The basis of many ecological interactions ultimately depends upon an organism's ability to extract relevant spatial and temporal information about its environment. Information about an environment is carried by sensory signals present within a habitat. Because sensory signals have varying physical properties, different physical phenomena in habitats will set constraints upon the transmitted signals. As a result of this physical constraint, organisms have evolved a variety of habitat-specific sensory systems and mechanisms to gather ecological information (Dusenbery, 1992).

Among the many sensory systems that organisms have evolved, chemical senses are sources of ecological information for a variety of terrestrial and aquatic organisms (for excellent reviews, see Bell and Cardé, 1984; Atema, 1988). In particular, organisms in the marine environment have evolved elaborate mechanisms to extract information from chemical signals. Organisms use chemical cues to detect the presence of predators (Tomba et al., 2001; De Meester and Cousyn, 1997; Covich et al., 1994; Mathis and Smith, 1993), locate food resources (Thar and Fenchel, 2001; Zimmer and Butman, 2000; Crenshaw, 1996; Tamburri et al., 1996; McLeese, 1973), and find mates (Vickers, 2000; Yen and Strickler, 1996; Gleeson et al., 1987; Atema and Engstrom, 1971). One of the most challenging sensory tasks that organisms face when using chemical signals is a determination of the distance and orientation to the source (Webster et al., 2001).

---

* Corresponding author. Tel.: +1-419-372-8556; fax: +1-419-372-2024.
E-mail address: pmoore@bgnet.bgsu.edu (P. Moore).

0924-7963/$ - see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.jmarsys.2003.05.005

To appreciate the difficulties associated with this behavioral task, it is imperative to understand the interaction between a sensory signal and the physical constraints of an environment. This interaction structures environmental information and can limit or constrain the types of possible behaviors (Kikas et al., 2001). In regard to understanding chemoreception as a behavioral phenomenon, an understanding of the interaction between signal and environment requires knowledge of the physical processes that transport chemicals through environments and create structure in the form of spatial and temporal information in signals. For odor signals, these physical processes are turbulent advection and dispersion.

The purpose of this manuscript is threefold. First, we want to review the set of physical parameters that constrain or govern the transmission and movement of chemical signals within different environments. Second, we will describe qualitatively the sensory environments that are present in different physical environments. Third, we will review the various strategies that have evolved among organisms in order to effectively use chemical signals to solve important behavioral and ecological tasks. It is our hope that this approach will provide a broader understanding of how physical processes within an environment influence the strategies used by organisms to extract relevant spatial and temporal information from odor signals.

2. Physical constraints on signal transmission

In this section, we describe a set of parameters used to quantify physical characteristics of the turbulence and the chemical signal being transported. The descriptors are familiar non-dimensional parameters put in the context of turbulent plume transport. Two flows that share a common set of relevant non-dimensional parameters will share qualitatively similar plume transport characteristics; flows with differing parameters may exhibit dissimilar traits.

The transport and mixing of a chemical in a turbulent flow consists of two distinct physical processes: advection and dispersion. Advection consists of macroscopic, bulk chemical transport by the mean flow. Dispersion consists of the combined effects of turbulent intermingling of fluid parcels (*stirring*), molecular diffusion due to Brownian motion (*mixing*), and (at larger scales) spreading due to effects of shear in the mean velocity field (*shear dispersion*). Fluctuating velocity gradients in turbulent flows deform, or stir, the spatial structure of the chemical field into complex patterns consisting of thin filaments. This stirring does not directly produce chemical dilution, but it promotes molecular diffusion (and hence dilution) by greatly enhancing the interfacial area between intermingled parcels of fluids with differing chemical concentrations. The net effect of turbulent stirring, combined with subsequent molecular mixing, is termed *turbulent mixing*. By analogy with molecular mixing, turbulent mixing is often modeled as a diffusion process. As a general rule, stirring is a chemical redistribution process that operates at large scales, and mixing is a gradient-smearing process that operates at small scales. The distinction between large and small scales is quantified later.

Diffusion acts to eradicate spatial gradients in chemical concentrations via the classic Fickian relationship

$$\vec{q} = -D_{\mathrm{m}} \nabla C \tag{1}$$

Diffusion produces a flux $\vec{q}$ in the direction of decreasing concentrations (direction of $-\nabla C$). A chemical's propensity to diffuse in a particular fluid is quantified by the molecular diffusivity D_{m}, with units $\mathrm{L}^2\mathrm{T}^{-1}$.

Since most relevant chemicals have a diffusivity on the order of 10^{-9} m^2 s^{-1} in water, molecular diffusion is a slow process whose effects are most prevalent where there are large changes in concentration over short distances (large ∇C). The Péclet number quantifies the relative rates of advection and diffusion. The average time required for a small particle (e.g. a molecule) to diffuse a distance L is $t_{\mathrm{d}}=L^2/2D_{\mathrm{m}}$. Notice that t_{d} is related to the distance L via a non-linear relationship; diffusion becomes increasingly slow at larger spatial scales. If the mean flow velocity is U, the time required for the same particle to advect the same distance is $t_{\mathrm{a}}=L/U$. The Péclet number is the ratio of times required for advection and diffusion to displace a particle a distance L. Ignoring the factor of 2 in t_{d}, we have

$$P\acute{e} = \frac{t_{\mathrm{a}}}{t_{\mathrm{d}}} = \frac{UL}{D_{\mathrm{m}}} \tag{2}$$

When $P\acute{e} \ll 1$ (typically for extremely low velocities, or at very small spatial scales), chemical dispersion is dominated by molecular diffusion. When $P\acute{e} \gg 1$, advection dominates, and the effect of molecular diffusion can be neglected at all but the smallest scales. If turbulent dispersion is modeled as a diffusion process (with an effective turbulent diffusivity D_t), then a turbulent Péclet number can be written that compares the effect of advection with the effect of turbulent dispersion.

The characteristics of the stirring processes are governed by the nature of the turbulence. The Reynolds number gives a bulk measure of the turbulent state by comparing inertial forces with viscous forces. The inertial forces represent the strength of the large, momentum-containing scales that sustain the turbulence (and stir any chemicals). The viscous forces constitute the damping effect of the small-scale viscous processes that dissipate momentum into heat. In the governing equations for fluid dynamics (the Navier–Stokes equations), the inertial term is $\vec{u} \cdot \nabla \vec{u}$, which scales as $U \cdot U/L$, and the viscous term is $\nu \nabla^2 \vec{u}$, which scales as $\nu U/L^2$ (where ν is the kinematic viscosity of the fluid). Taking the ratio of the scales for the inertial and viscous forces forms the Reynolds number,

$$Re = \frac{U^2/L}{\nu U/L^2} = \frac{UL}{\nu} \tag{3}$$

When $Re \gg 1$, momentum in the flow overpowers viscous damping, and the flow is turbulent. The higher the Reynolds number, the more turbulent the flow, the broader the range of temporal and spatial scales present. As Re decreases, the turbulence loses this richness of scales. For sufficiently low Re, the viscous forces dominate and the flow becomes laminar (hydrodynamically structure-free).

The form of the Péclet number and the Reynolds number is the same (compare Eqs. (2) and (3)), and the interpretations of the two numbers are analogous. The kinematic viscosity, $\nu = 1 \times 10^{-6}$ m^2 s^{-1}, is the molecular diffusivity of momentum within the fluid, making it the momentum analog to the molecular chemical diffusivity D_m or the turbulent chemical diffusivity D_t. The Péclet number compares the rate of advective transport of the chemical to the rate of smearing (smoothing or eradication) of gradients and spatial structures in the chemical field. The Reynolds number compares the rate of advective transport of momentum to the rate of molecular smearing of velocity gradients (spatial structures in the velocity field). The two numbers are related through the Schmidt number

$$Sc = \frac{P\acute{e}}{Re} = \frac{\nu}{D_m} \tag{4}$$

where Sc is the ratio of the molecular diffusivities of momentum and the chemical. Typical chemical odors have a Schmidt number in water on the order of 10^3, and are therefore referred to as weakly diffusive (relative to the diffusion of momentum). Note that only two of the three parameters $P\acute{e}$, Re, and Sc need be specified; the third parameter can be calculated from the other two.

Since diffusion acts to eradicate spatial gradients (and hence spatial structure in the chemical signal) at small scales, diffusive processes set a limit for the smallest possible spatial gradient. The scales of the smallest velocity and chemical structures are controlled by the diffusivities ν and D_m, respectively. The Kolmogorov microscale is the scale of the smallest velocity structures, given by

$$\eta = \left(\frac{\nu^3}{\varepsilon}\right)^{1/4} \tag{5}$$

where ε is the rate at which turbulent kinetic energy is dissipated into heat. Within the log layer of a turbulent boundary layer, the dissipation can be estimated as $\varepsilon \approx u_\tau^3/\kappa z$, where z is the distance from the bed, u_τ is the boundary layer shear velocity, and $\kappa \approx 0.41$. As Re increases (and the flow becomes more turbulent), the dissipation ε increases, and the smallest velocity structures in the flow η become smaller.

The Batchelor microscale is the scale of the smallest chemical structures, given by

$$\eta_B = \left(\frac{\nu D_m^2}{\varepsilon}\right)^{1/4} \tag{6}$$

Eqs. (4), (5), and (6) can be used to relate η and η_B as

$$\eta_B = \eta Sc^{-1/2} \tag{7}$$

When $Sc \gg 1$, the scales of the smallest chemical structures are therefore significantly smaller than the smallest velocity structures. For a typical turbulent benthic boundary layer, the Kolmogorov microscale would be on the order of a millimeter, with the Batchelor microscale being approximately 30 times smaller (assuming Sc=1000).

The characteristics of turbulent mixing vary over the vertical extent of a boundary layer, due to physical variations over the depth of the flow. Vertical location is usually specified in terms of the coordinate z^+, defined as

$$z^+ = \frac{zu_\tau}{v}$$

where z is the distance from the bed. The shear velocity u_τ is a measure of the shear stress at the bed, and is defined as

$$u_\tau = \sqrt{\tau_\mathrm{w}/\rho}$$

where τ_w is the shear stress at z=0, and ρ is the fluid density. Very close to the wall (z^+<5), the mean velocity reaches its maximum vertical gradient, with a linear velocity profile given by

$$u^+ = z^+$$

where u^+=u/u_τ. Further from the wall, this velocity profile deviates from the linear relationship and asymptotes to a logarithmic relationship given by

$$u^+ = \frac{1}{k}\ln z^+ + 5.5$$

If near-wall eddies are assumed to have dimensions that scale with z, and velocities that scale with u_τ, then z^+ can be viewed as a local Reynolds number. Close to the wall (small z^+), viscous interactions become significant, suppressing turbulent motions (and turbulent mixing). However, the mean velocity gradient is at a maximum near the bed, so there is significant dispersion of chemicals in this region due to the mean shear. Chemicals in this near-wall region exhibit a streaky, persistent characteristic (Crimaldi et al., 2002b). Further from the wall (large z^+), turbulence intensities increase to a maximum before decreasing towards the edge of the boundary layer. In this region of larger eddies and higher turbulence intensities, chemicals are stirred rapidly by turbulent dispersion. The spatial distribution of the instantaneous chemical field in this region is characterized by high levels of intermittency (patchiness). The presence of a rough bed surface tends to enhance turbulence levels in the flow, and eradicates the viscous behavior in the near-wall region.

3. Odor landscapes at varying scales

Turbulent dispersion and molecular diffusion spread chemicals into a dynamic, three-dimensional distribution of odorant concentrations. This distribution can be visualized as an ‘odor-landscape’ (Atema, 1996; Nevitt et al., 1995) consisting of evolving peaks and valleys whose elevation represents the strength of a particular odorant concentration. The spatial characteristics of these peaks and valleys, as well as their evolution in time, depend on the physical nature of both the flow and odorant (Weissburg et al., 2002; Kiørboe et al., 2001; Webster and Weissburg, 2001; Moore et al., 2000; Westerberg, 1991).

Stirring caused by macroscopic structures in the turbulent velocity field introduces complexity into the odor landscape. At the same time, mixing caused by molecular diffusion at the microscopic level eradicates complexity by smoothing local features. Since stirring and mixing dominant over the other at different scales, perception of the resulting heterogeneous odor landscape depends greatly on the scale of observation (Kiørboe and Thygesen, 2001). Thus, organisms of different sizes experience different features of the heterogeneity (Crimaldi et al., 2002a).

In their 1977 paper, Berg and Purcell described the odor landscape for microscopic organisms. This odor landscape occurs in an environment that is dominated by very small spatial scales (relative to the Kolmogorov microscale). Since even the smallest turbulent motions are much larger than these organisms, turbulence is experienced as pure translation combined with strain from simple linear velocity gradients. At the low Reynolds numbers that define these environments, the flow is locally laminar. This causes a localized thinning of the boundary layer around cells, maintaining concentration gradients and increasing rates of diffusion for chemical signal molecules (Karp-Boss et al., 1996). At these scales, molecular diffusion controls the evolution of the odor field (Kiørboe et al., 2001). Chemical gradients in this world are small, and have spatial and temporal fluctuations that are smoother and less variable than those at more turbulent scales (Kiørboe and Thygesen, 2001; Moore et al., 1999).

At large spatial scales, both stirring and mixing are relevant. Stirring generally acts more rapidly than molecular mixing, so stirring can be more important than mixing at short time scales, especially when the spatial scales are large. But molecular mixing processes produce macroscopic changes in the odor landscape given sufficient time. The odor landscape perceived by organisms that are large relative to the Kolmogorov microscale is highly complex relative to that experienced by microscopic organisms (Crimaldi et al., 2002b; Webster and Weissburg, 2001; Zimmer and Butman, 2000; Moore et al., 1994). Stirring strains and elongates features in the odor field, creating chemical filaments with sharp concentration gradients. Most significantly, the odor field is chaotic at these scales, and changes occur rapidly and unpredictably (Kikas et al., 2001; Moore et al., 1999, 1994; Moore and Atema, 1988).

4. Sensing and orientation in odor landscapes

In this section, we provide a survey of sensor designs and orientation strategies that have evolved to allow organisms to effectively extract spatial and temporal information from odor landscapes. It is our hope that this section will provide a global picture of how physical constraints on odor transmission sets design limits on chemoreceptive appendages and influences the types of behavioral strategies animals have adopted.

4.1. Small-scale two-dimensional habitats

As outlined above, small-scale environments are dominated by molecular mixing alone. Consequently, odor landscapes are simple and less variable than at more turbulent scales (Visser, 2001; Peters and Marrasé, 2000; Kiørboe and Thygesen, 2001). Bacteria and algae are the typical example of organisms that rely heavily on chemoreception at these spatial scales. Bacteria use chemoreception for localizing nutritional sources and algal sperm use concentration gradients to localize eggs (Bell and Mitchell, 1972; Miller, 1979; Maier and Müller, 1986).

Relatively predictable and stable spatial gradients in an odor landscape exist at the scale of whole organisms which allows a true chemotaxis to be performed. (Although called a chemotaxis, it is really a chemokinesis; Dusenbery, 1992.) In chemotactic search strategies, spatial differences in chemical concentration are detected and organisms turn toward the higher concentration. For bacteria and algal gametes, chemical gradients are sensed across the whole body and, as such, there are no individual sensors at spatial distinct locations as seen at larger spatial scales (Berg, 1983). Even given the simple nature of the odor landscape, bacteria and algal gametes still have evolved different mechanisms to orient effectively to odor sources.

Bacteria perform a chemo-kinesis strategy that is commonly referred to as a “random walk” (Berg, 1983). In this strategy, bacteria have two modes of behavioral patterns. First, there is a “run” which consists of a straight line movement. Runs are interspersed with “tumbles.” During a tumble, the “run” is stopped and the bacterium rotates and starts to head off on a new run in a random direction. The length of the “runs” and hence, the time between the random tumbles is influenced by the chemical gradient. If the bacterium is moving toward an odor source and, thus, up the concentration gradient, tumbles become less frequent. If the bacteria is moving down the concentration gradient, the length of the run decreases and tumbles become more frequent. This simple pattern of tumbles and runs and the timing between the two behaviors moves the bacteria up concentration gradients and allows them to localize odor sources.

Algal gametes have a more straightforward behavior (Maier and Müller, 1986). Although they have a mechanism of turning and movement similar to bacteria, it appears as if the increasing concentration of algal pheromone causes a complete cessation of turning and movement toward the odor source. Both of these mechanisms work because there is a direct and stable spatial gradient of odor centered on the odor source. In environments where stirring becomes more important, these types of search strategies are ineffective.

More recent work has shown that microorganisms can actually sense gradients along their body and respond in a fashion that can truly be called a chemotaxis (Thar and Fenchel, 2001). The theory of helical klinotaxis (Crenshaw, 1996, 1993) provided a mechanism by which microorganisms could turn by actually steering rather than altering any “run and tumble” sequence as described above. These microorganisms alter their direction of motion by changing the direction of the rotational velocity vector (Crenshaw, 1996). Given a self-steering behavior, it was only a matter of time before others discovered that chemical distributions could guide the self-steering behavior (Fenchel, 2002). It was discovered that a prokaryote could detect the smooth concentration gradients that are present at these size scales and alter their swimming behavior in order to stay within the most favorable concentrations of chemicals (oxygen for example, Thar and Fenchel, 2001). In this manner, it is the smooth concentration gradients and their lower variability in space that allows a self-steering motion to keep cells within desired nutrient ranges (Thar and Fenchel, 2001).

4.2. Intermediate-scales, three-dimensional habitats

At intermediate spatial scales, diffusive mixing of chemical concentrations remains a distinctive feature of the odor landscape, but the complex topography imparted by turbulent stirring also comes into view. Copepods are an excellent example and probably the best-studied chemoreceptive animals at these scales. Copepods are relatively small crustaceans and range from microns to millimeters in size. Since they are often larger than the Kolmogorov microscale, copepods experience effects of small-scale turbulence (Visser, 2001). Copepods often forage on small algal cells in the water column or function as predatory animals feeding on other copepods. Chemoreception is important for both of these tasks. In addition, it appears as if they use mating pheromones to track females in the open ocean.

Copepods forage by generating a feeding current that draws potential food particles from the surrounding water to a capture zone (Alcaraz et al., 1980). When the food item enters the capture zone, the copepod actively reaches out and gathers in the food particle. To effectively capture food particles, the copepod redirects and moves the feeding current around to draw food particles into the capture zone. In order to perform this behavior, the copepod needs precise spatial and temporal information on the location and distance of the food particle. The spatial information is used to redirect the food particle into its capture area, whereas the temporal information is used to time the capture sequence.

The spatial and temporal information is gathered from the odor landscape by sensory receptor cells on the antennae of the copepod. In these environments, chemical sensors are spaced at the same spatial scale as the Batchelor microscale, approximately tens of microns. At a slightly larger spatial scale, the antennae of these organisms as a whole is at the same spatial scale of the smallest eddies, approximately tens to hundreds of microns.

The local physical environment of the copepod exhibits moderate Reynolds numbers (order unity). This environment consists of a transition between flows where viscous effects dominate (small Re) and those where inertial effects dominate (large Re). Copepods exploit this transitional regime through behavioral responses. Small changes in either fluid flow or hair morphology can make appendages act like rakes or paddles (Cheer and Koehl, 1987). For paddles, water flows around the appendage, whereas with a rake the water flows through the hairs. Because small changes in morphology are important, sensory receptors are spaced at regular distances along the copepod’s first antennae. The relatively large spacing allows the antennae to act like a rake and odor signals will pass effectively through the array of receptors. The spatial arrangement of sensory hairs and the spatially stable gradients in the odor landscape allows the copepod to extract precise spatial and temporal information from its feeding current (Peters and Marrasé, 2000).

Not all copepods have the same feeding currents and, as stated above, small changes in flow velocity can have profound influences on the perception of odor landscapes (Peters and Marrasé, 2000). Thus, the odor landscape is a function of the hydrodynamics of a copepod’s feeding current (Moore et al., 1999). Odor landscapes located in high shear feeding currents (characteristic of the copepod *Pleuromamma xiphias*) have different spatial and temporal distributions than signals located in lower shear flow fields (characteristic of the copepod *Euchaeta rimana*; Moore et al., 1999). These differences in odor landscapes translate into differences in the sensory capabilities of these two copepods, which consequently mean different chemosensory behaviors, such as carnivory or herbivory.

4.3. Large-scale three-dimensional habitats

Most of the organisms studied to date detect and respond to odor signals at spatial scales 100–1000 times the Batchelor scale, yet also detect the patchy distribution of chemical signals with sensory appendages that function near the Batchelor scale. The interaction of these two distinct scales with the sensory structures dictates how odor signals are perceived and used by animals. Typical examples of such work include the homing of salmon (Dittman and Quinn, 1996; Døving et al., 1985) and the response of sharks to food cues (Hodgson and Matthewson, 1971). The best studied examples of orientation to chemical landscapes are the benthic crustaceans (Lobsters; Moore et al., 1991a,b; Blue crabs; Weissburg and Dusenbery, 2002; Finelli et al., 2000, 1999; Tamburri et al., 1996; Zimmer-Faust et al., 1995; Weissburg and Zimmer-Faust, 1993; and Crayfish; Kraus-Epley and Moore, 2002; Tomba et al., 2001; Keller et al., 2001; Moore and Grills, 1999).

Many of the animals at this scale detect odor landscapes with densely packed receptors either on external appendages (Gleeson et al., 1993; Moore et al., 1991a,b; Snow, 1973) or in internal cavities (Døving et al., 1977). The dense packing of receptor hairs increases the overall sensitivity of the system, but has a negative consequence of reducing flow to and between the hairs. Even at the scale of the receptor hairs, flow is important for delivering odor molecules to receptor sites (Stacey et al., 2002; Cheer and Koehl, 1987). Thus, a reduction in flow means a reduction in detectable odor. Organisms have solved this problem by creating artificial currents that either increase the flow of water to the receptor sites (as in the nasal cavities of fish; Døving et al., 1977) or by flicking the sensory appendage through the water at relatively high velocities (as in the flicking of crustacean antennules; Stacey et al., 2002; Gleeson et al., 1993; Moore et al., 1991a,b). These movement patterns temporarily alter the spatial structure of the hairs, increasing the local *Re* of the flow, and facilitating the delivery of odor to receptor sites (Stacey et al., 2002; Cheer and Koehl, 1987). As a result of the movement of the water or appendage, fine-scale spatial differences in the odor landscape are blurred and a form of a local temporal and/or spatial average of chemical concentration moving through the sensory appendage (Koehl et al., 2001).

At the scale of the whole organism, habitat differences (i.e. flow velocity, substrate, etc.) begin to play a larger role in the odor landscape and subsequently in the types of behavior observed in those habitats. In benthic invertebrates (crayfish, blue crabs, and lobsters), the fine-scale differences in the habitat alter the nature of the turbulence for that habitat. For example, in different sections of a river or near-shore environments, flow over sand substrate will have a different level of turbulent structure than flow over cobble or gravel (Hart et al., 1996). Even within a single substrate, topographical differences in habitat structure influence the level of turbulent flow. These can include riffles (faster flow), pools (slower flow), sandy substrates (smaller roughness elements), and cobble areas (larger roughness elements), which have been shown to greatly influence the turbulent nature of the flow (Hart et al., 1996). Since the turbulence is different, the odor landscape will be different (Moore et al., 1999). Consequently, odor landscapes will be habitat-specific (Moore et al., 1999; Westerberg, 1991).

These habitat-specific landscapes also produce specific orientation behavior. Crayfish (*Orconectes rusticus*) exhibit different orientation behavior on diverse substrates (Moore and Grills, 1999). The changes in behavior are a result of the odor landscape and not just an effect of walking on alternative substrates. The ability of blue crabs (*Callinectes sapidus*) to effectively use chemical signals to forage is greatly impacted by local flow velocities (Finelli et al., 2000, 1999; Weissburg and Zimmer-Faust, 1993). Again, differences in the behavior have been attributed to how fluid flow structures the odor landscape. In general, both organisms respond well and are capable of locating odor sources in a variety of flows, but the exact nature of the behavior is altered by the different odor signals. In fact, both organisms show similar orientation behaviors. A detailed description of the behavior indicates that some aspects of the upcurrent movement are modified by the increased intermittency of signals in higher turbulent environments. Interestingly, crayfish are more efficient in higher turbulent environments (Moore and Grills, 1999), whereas blue crabs are more efficient in locating odor sources in lower turbulent flow (Weissburg and Zimmer-Faust, 1993). These results clearly show that orientation behavior is a habitat-dependent phenomenon.

At larger scales, both salmon and shark are known to use chemical signals to orient over great distances. At these scales, the behavior transpires several orders of magnitude beyond the Batchelor and Kolmogorov microscales. The salmon's olfactory goal is the large-scale, diffuse odor source of its home river (Døving et al., 1985; Dittman and Quinn, 1996). Its odor landscape is the coastal environment that contains many layers of water from different freshwater origins that lie in a vertical stratification due to density differences. These layers contain the odors of the many rivers that empty their waters into the ocean. Salmon move through these layers in a vertical pattern and, by doing so, sample very large scale differences in odor landscapes (Johnsen, 1983; Døving et al., 1985).

In contrast, sharks try to localize a point source (food item) as opposed to the large, diffuse source of a river in the salmon example. Sharks have been seen to swim in a small zigzag pattern that may allow them to sample odor landscapes at a spatial scale that corresponds to the largest eddy structure in the flow (Johnsen, 1983). For example, bonnet-head sharks have been found to use behaviors such as a circling behavior that halts the shark's forward movement and allows them to relocate the odor signal (Johnsen and Teeter, 1985). Both the salmon's vertical movement patterns and the side-to-side sampling behavior of the sharks appear to be directly due to the odor landscape which is structured by the types of flows within those environments.

5. Summary

Environments have unique physical features that influence the dispersion of chemical signals within them. As a result, unique physical habitats have distinctive odor landscapes with particular regard to intensity, spatial distribution, and temporal fluctuations of signal chemicals. These distinctive odor landscapes can set constraints on the types of sensor arrays, their behavioral sampling and the orientation behavior that is most effective for localizing odor sources. Small-scale habitats (those smaller than the Batchelor scale) have spatially and temporally stable odor distributions with smooth and less variable concentration gradients. In these habitats, simple behaviors, spatially distinct sensor arrays, and common search strategies are readily apparent. In larger habitats (those larger that the energetic eddies), spatial and temporal distribution of odors form a complex, dynamic odor landscape. In these habitats, densely packed arrays of sensors that force water through the array and complex movement patterns are common place. From an evolutionary perspective, we would predict that sensory systems and sensory-mediated behavior should be adapted to the particular constraints of different habitats. Thus, to begin to understand why organisms perform certain behaviors or why sensor arrays have a distinct morphology, it is imperative to understand the physical dynamics of the habitat in question.

References

Alcaraz, M., Paffenhofer, G.-A., Strickler, J.R., 1980. Catching the algae: a first account of visual observations on filter-feeding calanoids. In: Kerfoot, W.C. (Ed.), Evolution and Ecology of Zooplankton Communities. Special Symposium III American Society of Limnology and Oceanography. Univ. Press, New England, pp. 241–248.

Atema, J., 1988. Distribution of chemical stimuli. In: Atema, J., Popper, A.N., Fay, R.R., Tavolga, W.N. (Eds.), Sensory Biology of Aquatic Animals. Springer-Verlag, Berlin, pp. 29–56.

Atema, J., 1996. Eddy chemotaxis and odor landscapes: exploration of nature with animal sensors. Biological Bulletin 191, 129–138.

Atema, J., Engstrom, D.G., 1971. Sex pheromone in the lobster, *Homarus americanus*. Nature 232, 261–263.

Bell, W.J., Cardé, R.T., 1984. Chemical Ecology of Insects. Sinauer Associates, Sunderland, MA.

Bell, W., Mitchell, R., 1972. Chemotactic and growth responses of marine bacteria to algal extracellular products. Biological Bulletin 143, 265–277.

Berg, H.C., 1983. Random Walks in Biology. Princeton Univ. Press, Princeton, NJ.

Berg, H.C., Purcell, E.M., 1977. The physics of chemoreception. Journal of Biophysics 20, 193–219.

Cheer, A.Y.L., Koehl, M.A.R., 1987. Paddles and rakes: fluid flow through bristled appendages of small organisms. Journal of Theoretical Biology 129, 17–39.

Covich, A.P., Crowl, T.A., Alexander, J.E., Vaughn, C.C., 1994. Predator-avoidance responses in freshwater decapod–gastropod interactions mediated by chemical stimuli. Journal of the North American Benthological Society 13, 283–290.

Crenshaw, H.C., 1993. Orientation by helical motion. III. Microorganisms can orient to stimuli by changing the direction of their rotational velocity. Bulletin of Mathematical Biology 55, 231–255.

Crenshaw, H.C., 1996. A new look at locomotion in microorganisms: rotating and translating. American Zoologist 36, 608–618.

Crimaldi, J.P., Koehl, M.A.R., Koseff, J.R., 2002a. Effects of resolution and kinematics of olfactory appendages on the interception of chemical signals in a turbulent odor plume. Environmental Fluid Mechanics 2, 35–63.

Crimaldi, J.P., Wiley, M.B., Koseff, J.R., 2002b. The relationship between mean and instantaneous structure in turbulent passive scalar plumes. Journal of Turbulence 3, 1–23.

De Meester, L., Cousyn, C., 1997. The change in phototactic behaviour of a *Daphnia magna* clone in the presence of fish kairomones: the effect of exposure time. Hydrobiologia 360, 169–175.

Dittman, A.H., Quinn, T.P., 1996. Homing in Pacific salmon: mechanisms and ecological basis. Journal of Experimental Biology 199, 83–91.

Døving, K.B., Dubois-Dauphin, M., Holley, A., Jourdan, F., 1977. Functional anatomy of the olfactory organ of fish and the ciliary mechanism of water transport. Acta Zoologica (Stockholm) 58, 245–255.

Døving, K.B., Westerberg, H., Johnsen, P.B., 1985. Role of olfaction in the behavioral and neuronal responses of Atlantic salmon, *Salmo salar*, to hydrographic stratification. Canadian Journal of Fisheries and Aquatic Science 42, 1658–1667.

Dusenbery, D.B., 1992. Sensory Ecology: How Organisms Acquire and Respond to Information. W. H. Freeman, San Francisco.

Fenchel, T., 2002. Microbial behavior in a heterogeneous world. Science 296, 1068–1071.

Finelli, C.M., Pentcheff, N.D., Zimmer-Faust, R.K., Wethey, D.S., 1999. Odor transport in turbulent flows: constraints on animal navigation. Limnology and Oceanography 44, 1056–1071.

Finelli, C.M., Pentcheff, N.D., Zimmer, R.K., Wethey, D.S., 2000. Physical constraints on ecological processes: a field test of odor mediated foraging. Ecology 81, 784–797.

Gleeson, R.A., Adams, M.A., Smith, A.B., 1987. Hormonal modulation of pheromone-mediated behavior in a crustacean. Biological Bulletin 172, 1–9.

Gleeson, R.A., Carr, W.E.S., Trapido-Rosenthal, H.G., 1993. Morphological characteristics facilitating stimulus access and removal in the olfactory organ of the spiny lobster, *Panulirus argus*: insight from the design. Chemical Senses 18, 67–75.

Hart, D.D., Clark, B.D., Jasentuliyana, A., 1996. Fine-scale field measurement of benthic flow environments inhabited by stream invertebrates. Limnology and Oceanography 41, 297–308.

Hodgson, E.S., Matthewson, R.F., 1971. Chemosensory orientation in sharks. Annals of the New York Academy of Science 188, 175–182.

Johnsen, P.B., 1983. New directions in fish orientation studies. In: Hernnkind, W.F., Thistle, A.B. (Eds.), Signposts in the Sea. Florida State Univ. Press, Tallahassee, FL, pp. 85–101.

Johnsen, P.B., Teeter, J., 1985. Behavioral responses of bonnethead sharks (*Sphyrna tiburo*) to controlled olfactory stimulation. Marine Behaviour and Physiology 11, 283–291.

Karp-Boss, L., Boss, E., Jumars, P.A., 1996. Nutrient fluxes to planktonic osmotrophs in the presence of fluid motion. Oceanography and Marine Biology 34, 71–107.

Keller, T., Tomba, A., Moore, P.A., 2001. Orientation in complex chemical landscapes: spatial arrangement of chemical sources influences crayfish food-finding efficiency in artificial streams. Limnology and Oceanography 46 (2), 238–247.

Kikas, T., Ishida, H., Webster, D.R., Janata, J., 2001. Chemical plume tracking: 1. Chemical information encoding. Analytical Chemistry 73, 3662–3668.

Kiørboe, T., Thygesen, U.H., 2001. Fluid motion and solute distribution around sinking aggregates: II. Implications for remote detection by colonizing zooplankers. Marine Ecology. Progress Series 211, 15–25.

Kiørboe, T., Ploug, H., Thygesen, U.H., 2001. Fluid motion and solute distribution around sinking aggregates: I. Small-scale fluxes and heterogeneity of nutrients in the pelagic environment. Marine Ecology. Progress Series 211, 1–13.

Koehl, M.A.R., Koseff, J.R., Crimaldi, J.P., Cooper, T., McCay, M., Wiley, M.B., Moore, P.A., 2001. Lobster sniffing filters the spatio-temporal information in a turbulent odor plume. Science, Nov. 30, 1948–1951.

Kraus-Epley, K.E., Moore, P.A., 2002. The effects of antennal lesions on orientation behavior of the crayfish, *Orconectes rusticus*. Chemical Senses 27, 49–55.

Maier, I., Müller, D.G., 1986. Sexual pheromones in algae. Biological Bulletin 170, 145–175.

Mathis, A., Smith, R.J.F., 1993. Fathead minnows, *Pimephales promelas*, learn to recognize nothern pike, *Esox lucius*, as predators on the basis of chemical stimuli from minnows in the pike's diet. Animal Behavior 46, 645–656.

McLeese, D.W., 1973. Orientation of lobsters (*Homarus americanus*) to odor. Journal of the Fisheries Research Board of Canada 30, 838–840.

Miller, R.L., 1979. Sperm chemotaxis in the Hydromedusae: II. Some chemical properties of the sperm attractants. Marine Biology 53, 115–124.

Moore, P.A., Atema, J., 1988. A model of a temporal filter in chemoreception to extract directional information from a turbulent odor plume. Biological Bulletin 174, 355–363.

Moore, P.A., Grills, J., 1999. Chemical orientation to food by the crayfish, *Orconectes rusticus*: influence by hydrodynamics. Animal Behavior 58, 953–963.

Moore, P.A., Atema, J., Gerhardt, G.A., 1991. Fluid dynamics and microscale odor movement in the chemosensory appendages of the lobster, *Homarus americanus*. Chemical Senses 16, 663–674.

Moore, P.A., Scholz, N., Atema, J., 1991. Chemical orientation of the lobster, *Homarus americanus* in a turbulent odor plume. Journal of Chemical Ecology 17, 1293–1307.

Moore, P.A., Fields, D.M., Yen, J., 1999. Physical constraints of chemoreception in foraging copepods. Limnology and Oceanography 44, 166–177.

Moore, P.A., Weissburg, M.J., Parrish, J.M., Zimmer-Faust, R.K., Gerhardt, G.A., 1994. Spatial distribution of odors in simulated benthic boundary layer flows. Journal of Chemical Ecology 20, 255–279.

Moore, P.A., Grills, J., Schneider, R.W.S., 2000. Habitat specific signal structure for olfaction: an example from artificial streams. Journal of Chemical Ecology 26, 565–584.

Nevitt, G.A., Veit, R.R., Kareiva, P., 1995. Dimethyl sulphide as a foraging cue for Antarctic Procellariiform seabirds. Nature 376, 680–682.

Peters, F., Marrasé, C., 2000. Effects of turbulence on plankton: an overview of experimental evidence and some theoretical considerations. Marine Ecology. Progress Series 205, 291–306.

Snow, P.J., 1973. The antennular activities of the hermit crab, *Pagurus alaskiensis* (Benedict). Journal of Experimental Biology 58, 745–766.

Stacey, M.T., Mead, K., Koehl, M.A.R., 2002. Molecule capture by olfactory antennules: Mantis Shrimp. Journal of Mathematical Biology 44, 1–30.

Tamburri, M.N., Finelli, C.M., Wethey, D.S, Zimmer-Faust, R.K., 1996. Chemical induction of larval settlement behavior in flow. Biological Bulletin 191, 367–373.

Thar, R., Fenchel, T., 2001. True chemotaxis in oxygen gradients of the sulfur-oxidizing bacterium *Thiovulum majus*. Applied and Environmental Microbiology 67, 3299–3303.

Tomba, A.M., Keller, T.A., Moore, P.A., 2001. Foraging in complex odor landscapes: chemical orientation strategies during stimulation by conflicting chemical cues. Journal of the North American Benthological Society 20, 211–222.

Vickers, N.J., 2000. Mechanisms of animal navigation in odor plumes. Biological Bulletin 198, 203–212.

Visser, A.W., 2001. Hydrodynamic signals in the plankton. Marine Ecology. Progress Series 222, 1–24.

Webster, D.R., Weissburg, M.S., 2001. Chemosensory guidance cues in a turbulent chemical plume. Limnology and Oceanography 46, 1034–1047.

Webster, D.R., Rahman, S., Dasi, L.P., 2001. On the usefulness of bilateral comparison to tracking turbulent chemical odor plumes. Limnology and Oceanography 46 (5), 1048–1053.

Weissburg, M.J., Dusenbery, D.B., 2002. Behavioral observations and computer simulations of blue crab movement to a chemical source in a controlled turbulent flow. Journal of Experimental Biology 205, 3387–3398.

Weissburg, M.J., Zimmer-Faust, R.K., 1993. Life and death in moving fluids: hydrodynamic effects on chemosensory-mediated predation. Ecology 74, 1428–1443.

Weissburg, M.J., Dusenbery, D.B., Ishida, H., Janata, J., Keller, T., Roberts, P.J.W., Webster, D.R., 2002. A multidisciplinary study of spatial and temporal scales containing information in turbulent chemical plume tracking. Journal of Environmental Fluid Mechanics 2, 65–94.

Westerberg, H., 1991. Properties of aquatic odour trails. In: Døving, K. (Ed.), Proceedings of the Tenth International Symposium on Olfaction and Taste. Graphic Communication System, Oslo, pp. 45–65.

Yen, J., Strickler, J.R., 1996. Advertisement and concealment in the plankton: what makes a copepod hydrodynamically conspicuous? Invertebrate Biology 115, 191–205.

Zimmer, R.K., Butman, C.A., 2000. Chemical signaling processes in the marine environment. Biological Bulletin 198, 168–187.

Zimmer-Faust, R.K., Finelli, C.M., Pentcheff, N.D., Wethey, D.S., 1995. Odor plumes and animal navigation in turbulent water flow: a field study. Biological Bulletin 188, 111–116.