The Hydrodynamics of Chemical Cues Among Aquatic Organisms

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Abstract
Chemical cues mediate many critical life processes, such as feeding, reproduction, and benthic settling, for aquatic organisms. Depending on the fluid velocity and flow regime, released chemicals are transported via diffusion, laminar advection, or turbulent advection prior to organism reception. Here, we review transport mechanisms and ecological consequences in each regime. We discuss cue structures in terms of concentration gradients, concentration fluctuations, and spatial patterns and draw conclusions about strategies that animals use to acquire information. In some cases, chemical transport occurs through a combination of mechanisms, which requires a multiscale analysis. Regime and scaling are major themes that emerge from recent research. In particular, nondimensional parameters that combine biological and physical variables reveal general principles under which organisms respond to chemical cues and facilitate defining regimes of behavior.
1. INTRODUCTION

Dissolved chemicals are ubiquitous in aquatic habitats and provide a major source of information for animals immersed in water. Studies of marine and freshwater organisms have shown that nearly every critical activity in the life of an animal can be regulated by the perception of chemicals (Hay 1996, Zimmer & Butman 2000). Water-borne chemicals initiate feeding behaviors and play large roles in determining food choice (Hay 1996, Zimmer-Faust 1989), and organisms (including single cells, zooplankton, snails, urchins, crustaceans, and fish) find food using chemical trails or plumes (Koehl 2006, Weissburg 2000). Reproductive processes such as recognizing or locating potential mates also are mediated frequently by water-borne chemicals (e.g., Doall et al. 1998, Hardege et al. 1996). Organisms use chemicals to detect and recognize dominant versus subordinate individuals (Breithaupt & Atema 2000, Gherardi & Daniels 2003). Other processes controlled by water-borne chemicals include predator avoidance (Covich et al. 1994, Zimmer et al. 2006), chemical defense (Larsson & Dodson 1993), habitat choice (Gerlach et al. 2007, Pawlik 1992), and sibling and individual recognition (Brönmark & Hansson 2000, Gherardi et al. 2005). All these chemically mediated processes directly affect individuals and indirectly affect organism populations, community organization, and overall ecosystems.

An attempt to understand chemically mediated processes must consider fluid properties and flow because the fluid environment determines the spatial and temporal patterns of dissolved chemical concentration (Weissburg 2000). Meaningful patterns can result from incidental transmission (e.g., the release of waste or metabolic by-products), which are referred to as cues (Dusenbery 1992). Alternatively, the term signals refers to those patterns resulting from deliberate release, although it is sometimes used synonymously with cues. Regardless of the intent of the releasing entity, the specific spatial and temporal patterns critically mediate interactions. As a result, there has been increasing dialogue between researchers in fluid mechanics and biology as we attempt to determine where, when, and how animals use chemical cues to regulate behavior and physiological processes. Further progress will require a broadening and deepening of these collaborative efforts.

Describing the hydrodynamics of chemical cues is challenging because chemical signal transmission involves physical processes, biological processes, and their interaction. The large size range of organisms (micrometers to meters) that respond to chemical cues combined with the large range of flow and movement speeds means that diffusive, advective, and turbulent transport mechanisms are relevant. For the purposes of this review, we describe small organisms as those less than 0.1 mm, large organisms as those greater than 10 mm, and medium-sized organisms as those between the two ranges. Unicellular organisms, gametes (i.e., sperm and eggs), and small planktonic organisms generally exist in a regime in which diffusion or laminar advection is the predominant transport process that establishes the odorant field occurring around an egg, potential mate, or sinking food particle. Large creatures follow turbulent plumes (on the scale of centimeters to meters) emanating from a point source in flows that are often unpredictable in time and space. At even larger scales, a homing salmon may follow the chemical signature from its birth stream for many kilometers to reach its breeding site (Dittman & Quinn 1996). Furthermore, chemical cues may be transported and shaped by multiple transport modes (e.g., turbulent advection at relatively large scales between or surrounding organisms and laminar advection at smaller scales in the vicinity of sensory organs).

Our goal in this review is to summarize recent progress in understanding hydrodynamic processes that influence chemically mediated biological interactions. We concentrate on characteristics of the overall flow environment that lend insight to the chemical cue structure, cue transmission, and the resulting influence of fluid mechanics processes on organismal and ecological properties.
2. TRANSPORT OF CHEMICAL STIMULI

Figure 1 describes the basic steps in chemically mediated interactions. Chemicals are released by the transmitting entity, transported through the fluid medium, and ultimately received by an organism that produces a physiological or behavioral response. The specific metabolites that mediate such interactions often are unknown, and their presence and transport are generally assumed based on responses of the receiver. Chemicals that induce responses include highly soluble compounds, such as amino acids, proteinaceous compounds, nucleic acid–related compounds, glycerolipids, and pheromones (Carr 1988, Dusenbery 1992). Diffusivity in water for molecules of this size is typically of the order of $10^{-5} \text{ cm}^2 \text{s}^{-1}$ (e.g., Lide 2008, Yen et al. 1998).

Recent advances in the ability to couple the analysis of cue structure with observations of animal responses have led to a new appreciation of the link between flow physics and organism ecology. The transmission and delivery of chemical cues are controlled by flow physics, and the mode of transport is dictated by a combination of Reynolds number,

$$Re = \frac{\rho U L}{\mu} = \frac{U L}{v},$$  \hspace{1cm} (1)

and Pécel number,

$$Pe = \frac{UL}{\Gamma},$$  \hspace{1cm} (2)

where $U$ is the characteristic velocity; $L$ is the characteristic length; $\rho$ is the fluid density; $\mu$ and $v$ are the dynamic and kinematic viscosities, respectively; and $\Gamma$ is the molecular diffusivity. Molecular diffusion is the dominant transport mode in the absence of fluid motion (Figure 1a). Fluid motion for small values of $Re$ (i.e., order of 100 and smaller) indicates that the flow is laminar and transmission is characterized by advective transport (Figure 1b). Large values of $Re$ (note that the transition $Re$ is case dependent) denote a regime in which the flow is turbulent, leading to random fluctuations of chemical concentration, with the pattern becoming an important aspect of the cue (Figure 1c). Analogously, the value of the Pécel number distinguishes the diffusion-dominated transport regime (small $Pe$) from the advection-dominated transport regime (large $Pe$). Understanding transport is critically important for interpreting behavioral or physiological responses to the chemical cue because the transport process greatly influences the spatial and temporal patterns of the chemical concentration field.

2.1. Diffusion

Chemicals in a motionless fluid environment are transported via molecular diffusion. Assuming that transport is described by Fickian diffusion, for which flux is proportional to the concentration gradient (i.e., $q = -\Gamma \nabla c$), the equation that describes diffusive transport is

$$\frac{\partial c}{\partial t} = \Gamma \nabla^2 c,$$  \hspace{1cm} (3)

where $c$ is the concentration of the chemical solute.

For $Re < 10^{-3}$, chemical transport from the surface of individual cells is dominated by diffusion because diffusive timescales are less than advective timescales. Hence, local stirring is ineffective. In the context of nutrient uptake, a minimum cell radius of 20 $\mu$m is needed before motion substantially increases the chemical flux. Organisms smaller than this limit cannot increase uptake by moving (Karp-Boss et al. 1996), but they can increase chemical flux by increasing cell radius or decreasing surface concentration.
**Release of chemicals**
Types:
- Waste products
- Leaking chemicals
- Pheromones

**Transport modes**
- Diffusion
- Laminar advection
- Turbulence

**Cue characteristics**
- Chemical compounds
- Concentration level
- Concentration spatial pattern
- Concentration temporal pattern

**Reception**

**Responses**
- Behavioral
- Physiological

Diffusive transport (no motion, $Re$ and $Pe << 1$). Cue structure is characterized by slowly evolving, smooth concentration gradients.

Laminar advection ($Re < \text{order of 100}$). Cue structure is characterized by small-scale spatial and temporal concentration gradients and can be affected by flow unsteadiness.

Turbulent advection ($Re >> 1$). Cue structure is characterized by chaotic spatial and temporal distributions of concentration filaments. The time-averaged field or filament properties are often inaccessible to the receiver.

**Figure 1**
Mechanisms of chemically mediated interactions among aquatic organisms and their implications for relevant signal structures. Examples of transport modes include (a) diffusion of a pheromone around a small spherically shaped organism, (b) laminar advection through a lobster’s aesthetascs array, and (c) turbulent plume tracking of prey by a shark.
**Figure 2**
Classification of guidance mechanisms in an odorant field. Kinesis occurs typically in smoothly varying chemical gradient fields, whereas taxis occurs in a variety of cue environments.

Dusenbery & Snell (1995) similarly analyzed pheromone transport from small spherical organisms. An individual's search rate for its mate depends on organism radius to the seventh power largely because of the diffusive rate of transport of pheromone molecules. Hence, the detectability and usefulness of pheromone release are strongly dependent on cell size. Pheromone release does not provide increased advantage for mate location below a critical size limit of 0.2–5 μm, which is consistent with observations on organism behavior.

Small organisms also exploit gradients in chemical concentration to locate food via guiding mechanisms (Figure 2). For instance, phytoplankton leak organic matter into solution, creating a high-concentration region around the organism, thereby allowing bacteria to employ chemoklinokinesis to locate the resource for feeding (Blackburn et al. 1998, Thar & Fenchel 2001). Chemoklinokinesis is a process of stimulus-induced movement in directions that are not correlated with the direction of the concentration gradient (Figure 2) (Dusenbery 1992). In this case, bacteria maintain motion in a straight line for longer periods when sensing an increase in concentration, and alternatively, they more frequently shift to randomly directed movement when sensing a decrease in concentration. Other small organisms such as ciliates (Verity 1988) and spermatozoa (Crenshaw 1996) also respond to chemical cues with attractive behavior. Spermatozoa of the purple-spined sea urchin, *Arbacia punctulata*, orient through a concentration gradient using a helical klinotaxis strategy that is particularly effective because it requires only that the angle between the direction of translation and rotation be controlled by the stimulus intensity (Crenshaw 1996). Medium-sized organisms, such as nematodes, also use chemoklinokinesis to orient in chemical gradients (Pierce-Shimomura et al. 2005).
Dusenbery (1997) found that organism size influences the ability to orient to chemical gradients, with a size greater than 0.58 μm needed to effectively employ a spatial comparison. Similarly, when employing sequential temporal comparisons, one finds that a minimum size of 0.65 μm is required for effective orientation. These thresholds represent a size limit below which location via chemosensation is not beneficial owing to physical constraints. The difference in threshold estimates results from the assumption that the time available to determine the stimulus direction is limited by Brownian motion, whereas the resolution of instantaneous spatial comparisons is constrained by the scale of the organism relative to the concentration gradient. Dusenbery (2003) noted that in addition to the advantages of larger span, increased size confers benefits by facilitating more numerous and larger sensors. In the context of two-dimensional orientation, spatial comparisons are the distinctly superior strategy, whereas elongated shapes with temporal comparison are most effective when organisms in the micrometer range orient in three dimensions, owing to improved signal-to-noise ratio (Dusenbery 2003).

### 2.2. Laminar Advection

Fluid motion, via movement of the organism or of the surrounding fluid, adds the advective flux of solute (i.e., \( q = uc - \Gamma \nabla c \)). At low \( Re \), the flow is laminar, and transport is described by the advection-diffusion equation

\[
\frac{\partial c}{\partial t} + u \cdot \nabla c = \Gamma \nabla^2 c. \tag{4}
\]

Phytoplankton larger than 20 μm can increase nutrient flux to their surface by swimming or sinking and hence inducing relative fluid motion (Karp-Boss et al. 1996). Typical \( Re \) for these phytoplankton during such motion is less than 1. The concentration distribution at low \( Pe \) is governed by molecular diffusion near the organism surface and is more sensitive to morphological features as the \( Pe \) increases. These features, such as spines and horns, influence the flow pattern and magnitude of advective transport. Similarly, motion in the fluid surrounding the organism increases nutrient transport and uptake and ultimately enhances the organism’s growth rate (Short et al. 2006, Waraars & Hondzo 2006). In either case, the Sherwood number (\( Sh = \frac{hL}{D} \), where \( h \) is the overall mass transfer coefficient) describes the ratio of flux in the presence of motion to purely diffusional flux and provides a measure of transport enhancement due to relative fluid motion.

Kiørboe et al. (2001) performed numerical simulations around spherical particles for \( Re < 20 \) to gain a better appreciation of the chemical distribution and transport. A sinking particle (e.g., live or dead organism, organic particle) leaves a long, slender plume in its wake. For example, for a 0.5-cm-diameter sinking particle, the wake region defined by concentration levels exceeding a biologically relevant threshold extends for 80 cm behind the particle and lasts for 13 min after the organism passes in still water. Chemotactic bacteria may utilize the presence of chemicals in the wake plume to locate the odorant source via chemoklinokinesis (Jackson 1989). The persistence time period and spatial extent of the cue in comparison to scales of the searcher mediate the success of locating prey. Furthermore, Kiørboe & Thygesen (2001) found that the threshold required to explain the detection of sinking aggregates via chemosensation of the wake plume was consistent with the reported chemosensitivity of zooplankton, supporting the conclusion that the cue is chemical rather than hydromechanical.

Jumars et al. (2002) noted that flow unsteadiness influences chemical transport at low Reynolds number and is potentially important to suspension feeding, prey detection and capture, and fertilization. Sources of unsteady flow motions at low Reynolds number include periodic beating of appendages, interaction with neighboring organisms, and turbulent motion in the surrounding...
Figure 3
The mate-tracking trajectory of the male copepod *Temora longicornis*, which has a body length of approximately 2 mm, is shown via the thick line, with the color indicating swimming speed. The trajectory of the female, which is coincident with her pheromone trail, is illustrated by the thin black line. Male swimming speed increases after contacting the female trail, and his path accurately follows the female trajectory. Data courtesy of Jeannette Yen.

Chemotaxis: directed orientation through a chemical concentration field via either spatial or temporal sampling.
Aesthetascs: a major and well-studied class of hair-like chemosensors found on the antennules of crustaceans

Leakiness: a parameter that characterizes the effect of the physical presence of the hairs on the volumetric flow rate through a hair array

The female's morphological and kinematic properties determine the chemical structure of the trail. Bagøien & Kiørboe (2005) observed wake-plume-tracking behavior in male Centropages typicus and quantified plume length and width via a simple plume model. They observed that the plume was narrower for a faster swimming female, whereas the plume length was independent of female swimming speed. This observation is consistent with those of T. longicornis males, which move more slowly and display more chaotic paths when tracking slowly swimming females compared with males tracking swiftly swimming females (Doall et al. 1998, Weissburg et al. 1998). Alternatively, female Oithona davisae copepods create a plume with odorant gaps owing to intermittent jumps in swimming speed (Kiørboe 2007). Consequently, males of this species perform local search behaviors to bridge gaps between odorant segments. Similar relationships between swimming kinematics and chemical cue patterns exist in other copepod species (e.g., Pseudocalanus elongatus) (Kiørboe et al. 2005).

Laminar advective-diffusive transport is also important for large aquatic organisms, particularly for the transport of chemicals through the boundary-layer flow surrounding chemosensory appendages. Most large crustaceans, including lobsters (Gleeson et al. 1993), stomatopods (Mead et al. 2003), and crayfish (Humphrey & Mellon 2007), flick their antennules to sample the chemical environment in a process that is analogous to sniffing. This chemosensory appendage is composed of dense tufts of aesthetascs, which are hair-like structures that contain chemosensory receptors (Gleeson et al. 1993). Fluid motion is inhibited by the dense morphology; hence antennule flicking is critical to reduce boundary-layer thickness and increase chemical transport to the sensitive organ. The typical Re range for hairs during the flick is $10^{-4}$ to 10, hence in the laminar advective-diffusive regime (Koehl 1996).

Koehl (1996) defines the leakiness of the array of hairs as the ratio of the volumetric flow rate through an array to the ideal volumetric flow rate if the hairs did not influence the velocity distribution. Increased leakiness due to flicking may help increase the transport of chemicals to the aesthetascs, but it moves chemical filaments through the region rapidly, hence limiting the time period in which diffusion can act to transport chemicals transversely across the boundary-layer flow. Koehl (2001) observed that for a given array of hairs, there is a transition from nonleaky to leaky flow behavior as Re increases. Animals appear to take advantage of this transition by performing an asymmetric stroke sequence. A rapid down stroke with relatively large Re and high leakiness flushes out the old water sample and replaces it with a new sample. The return stroke is slower (lower Re and lower leakiness), which traps the new water sample in the hair array and allows sufficient time for diffusive transport to the surface (Stacey et al. 2002). The velocity gradient near the hairs, the morphology of the hair array, and the orientation during the flick also critically mediate the transport process (Gleeson et al. 1993, Koehl 2001).

Laminar advection also characterizes internal transport in fish noses. Cox (2008) summarizes a variety of evidence that fish use both externally and internally generated flows to enable adequate rates of odorant delivery to olfactory sensors. Re varies from approximately 0.02 to 5, whereas Pe ranges from 20 to 3000. Bulk fluid flow dominates the delivery of odorants to the region of olfactory sensors, and diffusive transport to the substrate is enhanced by relatively steep boundary-layer profiles in the olfactory organ, particularly when flows are produced by ciliary movements.

2.3. Turbulent Transport

For larger values of Reynolds number, the flow is turbulent, and the flux of solutes is additionally influenced by advective transport owing to velocity fluctuations. In a time-averaged perspective, the additional turbulent flux of solutes is quantified by the covariance of velocity and concentration ($\mathbf{q} = \bar{\mathbf{u}} \bar{c} - \Gamma \nabla \tau + \bar{\mathbf{u}}' \mathbf{c}'$, where the overbar notation indicates time averaging). The time-averaged
concentration field is described by the Reynolds-averaged advection-diffusion equation:

\[
\frac{\partial \bar{c}}{\partial t} + \bar{\mathbf{u}} \cdot \nabla \bar{c} = \Gamma \nabla^2 \bar{c} - \nabla \cdot (\bar{\mathbf{u}} \bar{c}'),
\]

where \(c'\) and \(u'\) are the instantaneous fluctuations relative to time-averaged values of concentration and velocity, respectively (i.e., \(c = \bar{c} + c'\) and \(u = \bar{u} + u'\)). Equation 5 retains the unsteady term to allow for temporal variation over periods much longer than turbulent timescales. Although Equation 5 can provide insight into the time-averaged concentration field, we stress that many of the examples discussed in this section reveal the importance of unsteady turbulent stirring processes and instantaneous turbulent concentration fields for chemical cues and organism interactions. The instantaneous concentration field is described by the advection-diffusion equation (Equation 4) with a velocity field that varies unpredictably in both time and space.

Chemical cue transport among the small and medium-sized organisms discussed above can be affected by ambient turbulence. For example, ambient turbulence enhances mass transport to cells, such as diatoms or *Escherichia coli* (Hondzo & Al-Homoud 2007, Karp-Boss et al. 1996). Furthermore, the chemical plume in the wake of a small sinking particle is mixed into the surrounding fluid by turbulence despite the low Reynolds number of the flow around the particle. Ambient turbulence breaks the plume into discrete segments. The plume length, volume, and cross-sectional area are controlled by the product of the average turbulent shear rate and the diffusive timescale (Visser & Jackson 2004). The resulting plume characteristics influence the encounter rates of organisms and the ability of organisms to orient in the wake plume to locate the source particle.

Koehl et al. (2007) provide an example of the effects of turbulent stirring processes on small organisms, specifically the importance of incorporating unsteady spatial distributions to analyze organism behavior. In this case, larvae encountering filaments of chemical inducer quickly stop swimming and sink, but rapidly resume swimming upon exiting these filaments. Modeling this scenario predicts lower larval settling rates in a turbulent reef flow compared with the overestimate produced by considering the time-averaged concentration field. This occurs because the rapid responses to small-scale filamentous structure do not result in consistent downward movements produced in time-averaged fields, and larvae may consequently be advected out of the settlement region before they encounter the substrate. In another modeling effort, Crimaldi & Browning (2004) simulated stirring of two scalar quantities, representing sperm and eggs, by idealized vortex flows. The unsteady stirring process theoretically creates sufficient spatial coincidence of concentrated filaments at intermediate timescales, which explains observed fertilization rates better than a time-averaged diffusion modeling approach. Riffell & Zimmer’s (2007) recent work further suggests that sperm behavior and the ability to swim relative to the surrounding (turbulent) flow also are critical determinants of chemically mediated fertilization success.

Large organisms often inhabit regions in which turbulence is present in the ambient flow, and the *Re* of the flow around the organism is often supercritical. A commonly studied chemically mediated process in turbulent flows is a forager’s tracking of an odorant plume to locate prey. The physical configuration typically consists of a point source of odorant located in a benthic boundary layer. The flow transports chemical compounds downstream while turbulence stirs and mixes concentration filaments to expand the plume and dilute the concentration. The result is a complex spatial and temporal pattern of concentration called a turbulent odorant plume (Figure 4) (Crimaldi et al. 2002, Webster et al. 2003). Within the plume, fine filaments of odorant concentration are separated by unscented fluid. From a sequential sampling perspective at a single location, the concentration record is highly fluctuating with intermittent bursts of large concentration (Finelli et al. 1999). Crimaldi et al. (2002) noted that the combination of the time average,
Overhead perspective of the concentration field measured via laser-induced fluorescence in the region surrounding an actively tracking blue crab, Callinectes sapidus. The plane shown is at a height near the crab antennules, 5.5 cm above the bed. Crabs use cues in the turbulent odorant plume to rapidly track upstream to the source (less than 30 s to track 1.5 m) with a high degree of success (75% success rate for the plume shown).
the sampling period required to perceive the subtle spatial variation in time-averaged quantities is much longer than the total tracking period for many organisms. All other cues that rely on sequential sampling, such as the average rising slope or the average shape of the concentration burst, have the same inherent problem. Many of these quantities vary systematically with the distance from the source location, but the extremely long sampling period required to assess the mild variation is far too long for a rapidly moving organism, rendering these trends inaccessible to the forager. Alternatively, organisms that move slowly, such as gastropods, may be able to acquire time-averaged measures of the plume structure. Hence, the relative timescale of sensory acquisition plays a critical role in determining the usefulness of the cue structure.

Many aquatic organisms appear to combine sensory modalities to evaluate tracking cues. For instance, combining flow direction and chemical stimulation reliably orients an organism to an upstream odorant source. Fish and blue crabs use this strategy to move upstream when stimulated by a desirable odor, which is called odor-gated rheotaxis (Baker et al. 2002, Keller et al. 2003, Zimmer-Faust et al. 1995). This forms the basis of a useful tracking strategy: the combination of odor-gated rheotaxis and the spatial comparison of chemical cue intensity (Keller et al. 2003). However, organisms are clearly extracting more information from the concentration field to increase the success and efficiency of their search. Simple simulations of these combined strategies in realistic odorant plumes predict some, but not all, features of animal navigation (Weissburg & Dusenbery 2002).

The physical conditions of the flow environment impact the turbulent plume structure and the cues available to foraging organisms. Ambient flow speed and release characteristics (i.e., height, orientation, and size) alter turbulence characteristics and the effectiveness of foraging (Finelli et al. 2000, Koehl 2006). The presence of bed roughness (Rahman & Webster 2005), emergent vegetation (Finelli 2000, Lightbody & Nepf 2006), and surface waves (Mead et al. 2003) greatly affects flow turbulence and mixing characteristics. In the case of blue crabs, increased bed roughness causes a decrease in walking speed and a decrease in source-finding success (Jackson et al. 2007). Concentrated odor filaments arriving at the antennules induce upstream walking, and decreased walking speed results from a reduced number of these filaments. The steering ability of blue crabs is less affected by bed roughness because moving to the edges of the plume enables them to utilize contrast across their chemosensory appendages to steer. However, the change in mixing characteristics over rough beds does not affect all organisms equally. For instance, whelks (Ferner & Weissburg 2005) and crayfish (Moore & Grills 1999) do not show diminished tracking performance in the presence of increased turbulence intensity.

An organism’s ability to access the fine-scale turbulent structure of the chemical filaments depends on local flow conditions surrounding the chemical sensors. As discussed above, many organisms employ a flicking mechanism to draw fluid into the region of the chemosensory organs. Koehl et al. (2001) noted that fine-scale filaments are drawn into the receptor area during the rapid down stroke, becoming only slightly blurred by the end of the stroke. The filament structure is largely maintained among the aesthetascs during the slow return stroke. Hence, the fine-scale concentration field structure created by turbulence in the ambient flow is transported near the antennules by laminar advection and diffusion. Preservation of these small-scale patterns potentially allows sensing of the turbulent chemical distribution, as long as the neural system retains that information at higher processing stages.

3. SCALE SIMILARITY IN BIOLOGICAL-PHYSICAL INTERACTIONS

The nondimensionalization of physical variables (e.g., $Re$, $Pe$) has revealed self-similarity that enables the identification of general principles in fluid mechanics. In contrast, the analysis of
chemically mediated biological principles often has proceeded in a case-based manner or has been organized along taxonomic groups (e.g., insects versus crustaceans). We suggest that the nondimensionalization of behavioral responses to odorant cue structure would allow easier identification of general aspects of organism responses to chemical fields. However, identifying nondimensional parameters is complicated because chemically mediated processes result from the relationship between organism spatial and temporal sampling abilities and the spatial and temporal characteristics of the cue structure. Thus, relevant characterizations of the sensory environment are functions of both biological and physical parameters. There are relatively few successful examples of nondimensional parameterization that characterize organism cues and behavior in relation to the physical environment. Our purpose here is to review these few cases and inspire the reader to seek analogous parameters in future research.

Weissburg (2000) introduced the temporal integration factor as

\[ TIF = \frac{Lf}{U_{\text{organism}}} \]  

where \( L \) is the length scale of the chemical cue, \( U_{\text{organism}} \) is the animal’s relative speed, and \( f \) is the animal’s sampling frequency. The relevant length scale is case dependent and is related to the dominant transport mechanism. For example, plume width is a relevant length scale for a large organism operating in a high \( Re \) environment (e.g., a crab). Alternatively, \( L \) may be the Batchelor scale for a small organism immersed in a turbulent concentration field (e.g., a larva) or the distance corresponding to a fixed change in stimulus concentration for a single cell organism in a smooth gradient environment. Similarly, a spatial integration factor was defined as

\[ SIF = \frac{A}{L} \]  

where \( A \) is the length span of the organism’s sensor. By identifying efficient sensing strategies in high and low combinations of these parameters, we can create a matrix of behavior patterns that explains (or predicts) behavior in the context of interactions between scale-dependent physical and biological properties. Ferner & Weissburg (2005) employed these concepts to predict that slowly moving gastropods may employ different sensing strategies than those of rapidly moving crustaceans in the same chemical cue environment. By operating in a different temporal-integration-factor regime, gastropods can use time averaging, and behavioral experiments show that they often locate an odorant source in environments that confuse crustaceans. Similarly, Jackson et al. (2007) employed the spatial-integration-factor concept to nondimensionalize the transverse position of foraging blue crabs relative to the width of the chemical plume in different turbulence environments. The normalized position is relatively constant regardless of flow-regime characteristics; blue crabs adjust to the local plume width by moving to the plume’s edge and hence maximize contrast among transversely separated sensors. Occupying a constant nondimensional transverse position suggests that blue crabs employ plume-tracking strategies that fix the contrast between sensor pairs solely as function of downstream distance from the source (i.e., effectively scaling the influence of the turbulence environment).

The unsteadiness of chemical transport has also received nondimensional treatment. Loudon & Tordesillas (1998) discuss the Womersley number in many biological applications, including chemical cues:

\[ Wo = \frac{L}{\sqrt{n} \sqrt{\nu}} \]  

where \( n \) is the frequency of flow unsteadiness. Transport near chemoreceptive organs during antennule flicking is an example of an unsteady flow influencing chemical cues. Estimates suggest that \( Wo \) is less than 1 in many chemically mediated aquatic interactions, which implies that analysis
can proceed in a quasi-steady approach. Crimaldi & Browning (2004) also discuss timescales of unsteadiness. In the context of the mixing of gamete patches, they define a timescale of dilution ($t^* = \frac{8Dt}{\ell^2}$, where $D$ is the effective diffusivity and $\ell$ is the distance between the sperm and egg sources). This effectively introduces a mixing timescale that can be compared with the timescale of fertilization. Although the authors did not include biological aspects in the modeling effort, they argue that fertilization may occur at intermediate timescales when dilution is minimal and the patches spatially overlap.

In the context of foraging to an isolated patch, Grünbaum (2002) defined the Frost number as

$$Fr = \frac{U_2}{\tau T L^2},$$

(9)

where $\tau$ is the interval between turns; and $L$ and $T$ are the length scale and timescale of the resource (chemical) patch, respectively. The combination of biological and environmental variables in the Frost number indicates whether foragers can locate patches of certain characteristics. In the case of $Fr \gg 1$, foraging movement is rapid across the resource distribution, and the patch is available to the forager. Alternatively for $Fr \ll 1$, the patch is relatively distant or ephemeral; hence the patch is unavailable to the forager. Gallager et al. (2004) examined a similar issue: the ability of an animal to respond to chemical (and other resource) patches. They defined the motility number, which parameterizes the ability of plankton to swim independent of ambient fluid motion:

$$Mn = \frac{U_{\text{swim}}}{q},$$

(10)

where $U_{\text{swim}}$ is the plankton swimming speed, and $q$ is the root mean square of turbulent velocity fluctuations. They conclude that $Mn = 3$ represents a transition value below which plankton are unable to swim against transport via turbulent fluid motion and hence cannot orient to resource patches (i.e., locate food via chemical cues). Riffell & Zimmer (2007) also examined the influence of swimming against ambient turbulent flow, specifically the role of swimming behavior in chemically mediated sperm fertilization of eggs. They defined a nondimensional ratio of the propulsive force generated by swimming ($F_{\text{swim}}$) divided by the shear force produced by fluid motion surrounding the egg ($F_{\text{shear}}$). If $F_{\text{swim}}/F_{\text{shear}} > 1$, then sperm swim toward the egg, and encounter and fertilization rates are high. Alternatively if $F_{\text{swim}}/F_{\text{shear}} < 1$, then fluid motion dominates behavior, and encounter and fertilization rates are correspondingly low.

In another example, Gross et al. (1992) employed the Rouse number to examine settling larvae:

$$Ro = \frac{w_f}{\kappa u^*},$$

(11)

where $w_f$ is the vertical velocity of the organism due to sinking or swimming, which is often mediated by chemical cues; $\kappa$ is the Kármán constant; and $u^*$ is the bed shear velocity. The authors identified a critical value of 0.75 that separates the well-mixed (small $Ro$) and near-bed concentrated (large $Ro$) regimes. Tamburri et al. (1996) later experimentally verified this transition value by observing that larval settling is not inhibited by turbulence in a high $Ro$ regime, whereas larvae remain suspended in a low $Ro$ regime.

The few examples here suggest that nondimensional parameters are valuable for defining regimes of biological-physical interactions. Additional parameter combinations that have not yet been defined could describe interactions that influence chemical capture mechanisms, the detectability of cue structure, biologically induced flow and turbulence, and other phenomena.
4. CONCLUDING REMARKS

The fluid mechanics community can make a potentially enormous contribution to ecology by confronting the challenge of quantifying and understanding flow and transport mechanisms in aquatic environments. Understanding the transport of chemicals in an aquatic environment is critically important to interpret behavioral and physiological responses of organisms or to predict the success by which organisms find resources. In particular, the spatial and temporal patterns of chemical concentration formed by transport processes usually are important aspects of the cue structure and strongly influence organismal properties and abilities. For instance, the concentration field is often smoothly varying and slowly evolving in a stagnant environment in which diffusion is the dominant transport mechanism. The concentration field, therefore, is well suited for organisms employing chemoklinokinesis to move efficiently toward high-concentration regions. Chemical plumes in the laminar advective regime of an organism’s wake provide a reliable roadmap to predators and mates owing to the smoothly varying distribution of concentration. Turbulence also potentially influences the chemical cues received by organisms of all sizes. The fluctuating and intermittent nature of the chemical concentration field in turbulent flows creates a challenging environment in which to interact via chemicals. Nevertheless, a wide range of organisms have adapted to the characteristics of turbulent chemical plumes and demonstrate successful tracking and other behaviors in these conditions. Based on these observations, a fundamental contribution of the fluid mechanics community is to measure and model the transport of chemicals in environments of ecological relevance. In collaboration with biologists and ecologists, quantification of the physical environment provides the ability to interpret observed organism responses, and, potentially, to extrapolate these responses to higher-order interactions (e.g., predation, mate finding) that govern the structure of populations and communities. Researchers have limited ability to understand the biological and ecological consequences of chemical signal transmission without this information.

Another contribution of the fluid mechanics community is to provide inspiration via the long-standing success of employing nondimensional parameters to define flow regimes. As discussed above, recent research has produced a few examples of nondimensional parameters that define regimes of biological-physical interaction and behavior. A challenge for researchers in the coming years is to identify parameters that combine biological and physical variables in a manner that provides general understanding of phenomena. A potentially greater challenge is to design experiments to verify that proposed nondimensional parameters correctly characterize the biological-physical interaction in nature. Although there is a great need for new and additional data to describe these biological-physical interactions, it is already apparent that the nondimensionalization of combined physical and biological parameters is useful for describing behavior and for defining scales of interaction.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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