9. ELECTROCHEMICAL SENSORS FOR IN SITU SMALL-SCALE, FAST TEMPORAL MEASUREMENTS OF ORGANIC MOLECULES IN SEAWATER

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9.1 THE IMPORTANCE OF ORGANIC MOLECULES FOR AQUATIC ORGANISMS

Chemical cues are important in the natural history of virtually every aquatic organism. For example, for growth and reproduction, aquatic primary producers rely on chemical cues e.g., nitrogen and phosphorus. Many aquatic larvae use chemical signals to find suitable settlement sites. For macroscopic animals, chemical signals are used in predator-prey interactions, foraging ecology, and mate selection. Great inroads have been made by many scientists in identifying what chemicals are involved in these different interactions, but a complete ecological picture of these interactions is missing mainly due to the lack of knowledge about the fine-scale spatial and temporal distribution of chemicals in aquatic habitats.

For macroscopic animals there is considerable morphological, electrophysiological, and behavioral evidence for chemosensory location of prey and predators by marine organisms on scales of millimetres to metres (e.g. Carr and Derby, 1986; Legier-Visser \textit{et al.}, 1986; Price \textit{et al.}, 1988), and the importance of near-field chemosensory orientation is widely accepted. While the sensory basis of such behavior in laboratory settings is fairly well understood for some benthic marine organisms like lobsters (e.g. Atema, 1985; Derby and Atema, 1982; Moore \textit{et al.}, 1991), very little is known about chemosensory behavior in natural environments. Analogies from coastal species in the laboratory are not always applicable to the size and time scales of benthic or pelagic environments. Physical processes dispersing chemical signals are different for near-shore and deep benthic environments as compared with laboratory settings and these natural processes have rarely been measured and quantified. The water column and benthic environments offer several potential cues for behavioral orientation, ranging from large-scale gradients of pressure, temperature, and light through meso-scale changes in food and chemical concentrations to small-scale and transient visual, chemical, hydrodynamic, and electrical signals generated by
animals. Each of these sensory signals has properties and characteristics, which convey different types of information over different temporal and spatial scales (Atema et al., 1988). Phenomena, such as migration and swarming that involves large numbers of organisms over large distances, rely on large-scale sensory cues, while inter-individual events like predation, escape, and mating are mediated by short-range and short-lived biogenic signals (Maier and Müller, 1986; Atema and Engstrom, 1971; Gleeson et al., 1987; Miller, 1979).

Aquatic chemical signals can convey specific information over a long range, but have been shown to be highly patchy over short time and space scales (Atema, 1985; Moore and Atema, 1991; Atema et al., 1991; Moore et al., 1992). The importance of chemical signals to deep-sea animals has been amply demonstrated by numerous studies using baited traps to catch or photograph sparse and elusive scavengers (e.g. Hessler et al., 1972; Budosh et al., 1982; Hargrave, 1985; Ingram and Hessler, 1983; Sainte-Marie, 1986; Wilson and Smith, 1984). It is clear from these studies that chemical information can travel considerable distances and guide predators or scavengers quickly and accurately to a food source. On a smaller scale, Hamner and Hamner (1977) have demonstrated precise scent tracking by neritic sergestid shrimp. It is possible that the midwater and benthic environments are fared with plumes and trails of chemical signals left, for varying lengths of time, by passing individuals or groups. In addition to food odors, algal metabolites (e.g. Maier and Müller, 1986), pheromones (e.g. Atema and Engstrom, 1971; Gleeson et al., 1987) or sperm attractants (e.g. Miller, 1979) might play crucial roles in the biology of widely dispersed organisms, regulating feeding, aggregation, and spawning. In all of these instances, it has been shown quite convincingly that fine-scale chemical signals play an important role in the behavior of marine animals, but virtually nothing is known of the spatial and temporal characteristics of chemical signals in the open ocean environment. All of these studies show the importance of chemical signals, which are small organic molecules, to the ecology, physiology, and behavior of organisms.

To understand how organisms use chemical signals in their natural environment we must be able to "see" their odor world. With the development of new technology to investigate the fine-scale distribution of chemical signals in aquatic environments, it has been possible to further our understanding of the role of chemical signals in ecosystem dynamics. In order to do this, it is important to develop sensors and recording systems that sample at the same spatial and temporal scales used by these organisms.

9.2 APPROPRIATE SPATIAL AND TEMPORAL SCALES FOR MEASUREMENT

The physical processes involved in the distribution of chemicals in the aquatic habitat range from molecular diffusion to large-scale turbulence. Within this range, biologically relevant spatial and temporal scales must be estimated from behavioral and signals using 1980; Devine sensilla that a receptor cells gametes can microns (Maier with these org 8–150 μm). In well understudied responses to Christensen: americanus has pulses (Gome Atema, 1990), the order of I mate a tempo spectra of aqu (Moore and the situations lie be will give a bio- though underdispersal of cl

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behavioral and electrophysiological studies. Most arthropods orient to chemical signals using sensory input from antennae or antennules (Reeder and Ache, 1980; Devine and Atema, 1982). These appendages usually have small hairs or sensilla that are permeable to odors and contain the dendrites of the primary receptor cells (Ghiradella et al., 1968; Laverack, 1988). In addition, male algal gametes can track signals from female gametes over distances of 300–400 microns (Maier and Muller, 1986). To match the spatial sampling area associated with these organisms, we can choose electrochemical electrodes with diameters of 8–150 μm. In contrast, the temporal sampling scales for aquatic organisms is not well understood and must be estimated from a limited number of physiological studies. Neurons, both peripheral and CNS, in two moth species can give distinct responses to odor pulses presented as fast as 10 Hz (Kaissling et al., 1987; Christensen and Hildebrand, 1988). Similar studies in the lobster Homarus americanus have found some peripheral chemoreceptor cells that can follow 4 Hz pulses (Gomez et al., 1994) and others that begin to adapt in 500 ms (Voigt and Atema, 1990). Algal gametes have been shown to make behavioral decisions on the order of 100 ms (Maier and Muller, 1986). From these studies, we can estimate a temporal sampling scale between 100 and 500 ms. In addition, frequency spectra of aquatic odor signals measured at sampling rates of 10, 25, and 200 Hz (Moore and Atema, 1988; 1991) have shown that most of the odor signal fluctuations lie below 10 Hz. Thus, a sampling rate of 25–50 Hz in an aquatic medium will give a biologically realistic resolution of odor pulses, although a more thorough understanding of the temporal dynamics associated with the turbulent dispersal of chemical signals requires a much higher sampling rate.

9.3 BASIC THEORY OF ELECTROCHEMICAL MEASUREMENT OF ORGANICS IN SEAWATER

The techniques for electrochemical recordings in seawater are based on the principles of electrochemical measurements at solid electrodes (Adams, 1969). In general terms, the working electrode (described below) is polarized in an aqueous solution using a potentiostat. In solution, molecules that physically come into contact with the exposed surface of the working electrode can donate or receive electrons from the electrode’s surface, provided that the polarization is sufficient to cause the molecule to oxidize or reduce. If the molecule donates electrons, oxidation of the molecule has occurred and if the molecule receives electrons then reduction has happened. The resulting current flow due to the exchange of electrons at the working electrode surface is directly proportional to the number of molecules that contact the surface of the working electrode. A calibration of the electrode prior to in situ measurements is used to convert the current flow into concentration units.

This process is illustrated in Figure 9.1 for the detection of dopamine in seawater. Thus, in situ electrochemical measurements entail causing oxidation or reduction reactions at the surfaces of electrodes and measuring the amount of
current flow that results from these chemical reactions. By quantifying the current flow, it is possible to quantify the number of molecules that contact the electrode’s surface.

There are numerous recording techniques for carrying out electrochemical recordings *in situ*. These methods differ in the way in which the potential applied to the working electrode is varied. One method is called chronoaampedometry and involves varying the polarization or applied potentials to the electrode’s surface using a square-wave or voltage step (see below). The resulting chemical reactions at the electrode surface are measured as a function of time. Thus, chronoaampedometry is a time (chrono) versus current (amentometry) measurement.

9.4 CHRONOAAMPLEMETRY

Chromaapsedometry is the electrochemical method that uses a square-wave voltage to detect chemicals at the electrode surface (Figure 9.2). This can be explained best by describing the technique that is used to measure dopamine in seawater using the IVEC-10 electrochemical system at a sample rate of 10 Hz. A positive voltage is applied to a working electrode versus a Ag/AgCl reference electrode. The reference electrode is using a small gauge silver wire that has been plated with chloride. This is a common method for the construction of reference electrodes. For detection of dopamine, the oxidation voltage is set to +0.55 V for
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50 ms. During this phase of the measurement, analog-to-digital conversions of the current from the working electrode occur at 4,000 Hz. These 4,000 Hz samples are averaged for the entire 50 ms and stored as a single measurement of charge (integrated current) for this time epoch. The voltage is then stepped down to 0.0 V for the reduction phase of the measurement. Again, analog-to-digital conversions occur at 4,000 Hz and are averaged for the 50 ms epoch. The average is stored as the single measurement of charge for the reduction phase of measurement. The 50 ms oxidation step along with the 50 ms reduction step is repeated for the entire measurement period. This process results in a single time point for the oxidation measurement and a separate time point for the reduction measurement each measured at a rate of 10 Hz. The time length of the oxidation and reduction step sets the overall sampling rate of chemical signals. Currently, the IVEC-10 system can sample using this technique at an upper rate of 100 Hz.

Chronoamperometry has several advantages over other recording methods. The short time periods of the applied potential allow for rapid sampling of environmental signals (See examples of environmental signals below). In addition, the technique of stepping voltages decreases the possibility of chemicals adhering to the working electrode and compromising the sensitivity of the electrode. Using the currently available equipment, it is possible to measure nanomolar, micromolar, and millimolar levels of certain molecules in seawater.
9.5 AMPEROMETRY

Another method for electrochemical recordings involves applying a constant polarizing voltage to the electrode surface and is called amperometry (current monitoring). This approach is used when very high temporal resolution recordings are needed. This approach is very similar to the one outlined above except that a constant voltage is applied to the electrode instead of a square-wave. Only oxidation reactions occur when using the constant voltage technique at +0.55 V using most carbon electrodes. Analog-to-digital conversions occur at 4,000 Hz and are averaged for the time epoch appropriate for the desired sampling rate. The average is stored as the single measurement of charge for the oxidation measurements. Using the constant potential recordings, temporal resolutions of 10,000 Hz are easily achieved. We have used this type of recording method to measure aquatic tracer signals in the deep ocean (Atema et al., 1991) and the fine structure of aquatic tracer signals in a flume (Moore et al., 1992). An example of these high-resolution signals recorded from 2300 feet from the ocean surface is seen in Figure 9.3.

There are, however, several problems with this methodology. First, the constant application of the polarizing potential can cause the recording electrodes to adsorb reactive loss of sensitivity averaging the measurement. For example, if we have a that only 10 estimate.

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adsorb reaction products from the electrochemical reactions and this will result in
loss of sensitivity for the recordings. Second, the rapid measures preclude signal-
averaging methods from being used and therefore the method is less sensitive.
For example, a temporal resolution of 10,000 Hz means a sampling bin of 0.1 ms.
If we have analog-to-digital conversions at a rate of 100,000 Hz, this means
that only 10 oxidation measurements are averaged for the final concentration
estimate.

9.6 SELECTIVITY OF THE ELECTRODE AND FINGERPRINTING
OF THE SIGNAL MOLECULE

There are several techniques that can be used to either further identify signal
chemicals or to increase the specificity of the electrodes for target molecules. Each
of these techniques has advantages and disadvantages, and the selection of
whether the technique should be used is dependent upon the experimental
situation.

First, the specificity of the electrodes for dopamine or other compounds
depends on the electrical characteristics of their oxidation and reduction reac-
tions. Molecules are oxidized and reduced at different voltages depending upon
the surrounding conditions (pH, etc.) and type of sensor. These voltages can be
determined in laboratory trials, so that by selecting the optimal voltages, one can
include certain compounds and exclude others. For example, by selecting step-
ning voltages between 0.0 V and +0.55 V for dopamine, it is possible to create a
voltage window that will exclude all of those compounds that are oxidized at
higher voltages. This technique does not compromise the temporal or spatial
recording characteristics of the electrode and is the preferred first step to
increase electrode selectivity.

Second, the relative strength of the oxidation and reduction currents within
any one sampling epoch can be used as a characteristic signature of the chemical
species. By measuring this ratio (reduction to oxidation current ratio) during the
sampling of in situ chemical signals, it is possible to further identify the chemical
(or chemicals) that are contributing to the currents measured by the electrode.
Each organic chemical has a characteristic oxidation to reduction ratios recorded
using the IVEC-10 system. For example, using the graphite epoxy electrodes
(described below), dopamine has a characteristic ratio of 0.5–0.7 and serotonin
has a ratio of 0–0.1 at pH of 7.4. By determining these ratios in the laboratory
beforehand, it is possible to further identify the chemical composition of signals
during in situ measurements.

Finally, it is possible to coat the surface of the electrode with ion-selective
membranes. Nafion-coated electrodes have been used in the past to increase
selectivity for dopamine over other potentially inferring molecules within the
central nervous system (Gerhardt et al., 1984), but has not been needed for
oceanographic applications. Other membranes may be used to increase selectivity
for other compounds, but have not been extensively tested or employed (Friedemann et al., 1996). Surface membranes have a drawback of decreasing the temporal response of the electrode by adding another diffusional step to the detection process.

9.7 CURRENT INSTRUMENTATION

The present recording system that is being used to measure the spatial and temporal distribution of aquatic chemical signals is called the IVEC-10. The In Vivo Electrochemistry Computer system (IVEC-10) was developed by Dr. Greg A. Gerhardt at the University of Colorado Health Sciences Center and is currently being manufactured and sold by Medical Systems Corp. Greenvile, NY (800-654-5406). This system was originally developed and used extensively by Dr. Gerhardt to measure nanomolar to micromolar quantities of neurotransmitters within the CNS of mammalian systems (Adams, 1969; Adams and Marsden, 1982; Gerhardt and Adams, 1982; Gerhardt et al., 1984; 1987; Gerhardt and Palmer, 1987; Gratton et al., 1988). This system has been adapted for field use in conjunction with Dr. Gerhardt to measure concentrations of tracer compounds in seawater with very high temporal resolution (Moore et al., 1989; Moore and Atma, 1991; Atma et al., 1991; Moore et al., 1992). The electrodes were originally developed for the detection of monoamines (e.g., dopamine, norepinephrine and serotonin). Use of dopamine has the advantage that it does not occur naturally in seawater at levels detectable by our system and other chemicals do not interfere with its detection by the sensors. It has the drawback, however, of being a tracer and not a naturally occurring signal chemical. An additional drawback of the current system is that the methodologies to measure endogenous aquatic signal compounds (such as tyrosine, tryptophan, glutamate, glutathione, nitrates, or phosphates) have not been developed.

9.8 SENSOR CONSTRUCTION

The current electrodes are small glass capillary tubes either filled with a graphite epoxy (GEC) or with a single carbon fiber (Fiber) as small as 8 μm (Figure 9.4). The glass capillary for the electrodes is shaped on a common glass electrode puller using soda lime glass. For the carbon fiber electrodes, a single fiber is sealed in the glass capillary tube with an epoxy and baked to harden the epoxy. Both the GEC and Fiber electrodes are back-filled with graphite epoxy until the upper part of the capillary is filled with conducting epoxy. A copper wire is inserted into the epoxy for electrical connection and this assembly is baked again. The electrodes are connected to the IVEC-10 circuitry via a small connector for laboratory work. The sensors can currently be purchased through the Rocky Mountain Center for Sensor Technology and directly from Quanteon, Denver CO. (303-315-8650).

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Figure 9.4 Drawing showing the two basic types of electrodes used with the IVEC-10 electrochemical system. The length of the electrodes is not drawn to the same scale as the width and the middle section of the electrode (white strip) has been removed for clarity. The graphite-epoxy electrode (A) consists of a glass capillary that is back-filled with graphite epoxy. A copper wire, which is inserted into the epoxy before hardening, is used to connect the electrode to the main IVEC-10 system. The detecting surface of the electrode is a flat disk. The carbon-fiber electrode (B) has a carbon fiber that is used as the surface of the electrode. The carbon fiber can be extended out from the end of the capillary, so that the detecting surface of the electrode is a cylinder.

For fieldwork, we have connected the electrodes to submersible cables and then sealed all of the connections using silicon and epoxy. These are connected to a submersible headstage, which amplifies the signal. This signal is fed through a submersible cable that connects it to the IVEC-10 system.

9.9 EXAMPLE OF USES

The present detection system has been used in a number of laboratories for both laboratory and field measurement of chemical signals in seawater. The main
emphasis of all of these examples is measuring organic signals in flowing seawater at small spatial scales and high temporal resolutions.

### 9.9.1 Measurement of Chemical Signals in Aquatic Field Settings

We have performed a number of studies using the electrochemical recording techniques and the IVEC-10 system to measure concentrations of potential signal molecules (Moore et al., 1989; Moore and Atema, 1991; Atema et al., 1991; Moore et al., 1992; Moore et al., 1994). These studies have provided insight into the fine-scale structure of chemical signals dispersed by turbulent flow and allowed us to make predictions on the role of chemical signals in guiding behavior and foraging. Results from previous studies (Moore and Atema, 1991; Moore et al., 1992; Moore et al., 1994) have demonstrated three major consequences of different flow velocities and flow regimes on the distribution of chemical signals. First, slower flow velocities allow the initial energy of an odor plume to carry the main axis of the odor plume farther into the water column before the carrier flow begins to transport the chemical downcurrent. The main axis of an odor plume contains the most odor pulses and exhibits the largest fluctuations in concentration. Second, there is a general relationship between plume microstructure and the magnitude and degree of penetrants of turbulence into the boundary layer. Increased turbulence serves both to disperse odors and to distribute odor molecules into smaller and more discrete patches. Conversely, less turbulent flows result in greater average odor concentrations and more uniform distribution of odor further downstream from the source. Third, increased turbulence generally results in more predictable relationships between microscale plume structure and distance to the odor source. At higher flow velocities, plumes remain patchier as they are advected downstream as compared to slower velocities. These smaller and more discrete patches will have higher concentration gradients between patch/non-patch boundaries. In general, odor pulses will have higher slopes at higher flow velocities. At slower speeds, odor patches take a longer time to move downcurrent. This increase in transport time is correlated with a smoothing of the concentration gradient at patch boundaries, resulting in decreased slope values. Thus, the distribution of pulse slopes, and to a lesser extent pulse heights, shows a stronger correlation at higher flow speeds with downstream distance from the odor source within all boundary layer regions. At slower flow velocities, there is rarely any relationship between distance and plume microstructure.

### 9.9.2 Measurements in the Open Ocean Using Submersibles

The first field measurements of odor plume structure were made at a site 900 m deep near St. Croix, U.S. Virgin Islands with a field version of the IVEC-10 called "Subrose 1". The study mapped the concentration fluctuations within an odor plume at a sampling rate of 10 Hz (Atema et al., 1991). Subrose-1 was mounted on high microeddies within tests to source the spatial information. An update May, NJ that high frequency previous field apart revealed important signalings were detected the redox rate hypothesis th

### 9.9.3 Measurements in the Open Ocean Using Submersibles

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mounted on the Johnson Sea-Link and used to map the concentration of a dopamine-labeled plume at distances up to 50 m from its source. It recorded very high micro-scale variability in concentration due to the distribution of small eddies within the fluid flow. The high degree of patchiness seen in laboratory tests was confirmed by the in-situ electrode measurements. Many patches near the source had steep patch gradients and onset slopes, which may be important spatial information for orienting animals.

An updated version, “Snubose-II”, was used for a second study east of Cape May, NJ that included concentration mapping at 50 Hz, simultaneous recordings from dual sensors at 200 Hz, and searching for naturally occurring chemical signals (Moore et al., in press). Recordings made at 50 Hz showed additional high frequency concentration fluctuations not seen in laboratory tests or the previous field study. Simultaneous recordings from two electrodes spaced 4 cm apart revealed microscale differences within the odor structure that may be an important source of information for aquatic animals. In addition, several recordings were made in which naturally occurring (non-dopamine) chemical signals were detected. Exact identification of the molecular species was not possible, but the redox ratio combined with the use of high oxidation potentials support the hypothesis that the signals were composed of low levels of tyrosine.

9.9.3 Measurements Around Chemosensory Appendages

Other studies have mounted the electrodes on organisms or within a particular appendage (Moore et al., 1991; Schneider et al., in press). A preliminary study demonstrated that the boundary layers around the chemosensory appendages of the lobster, Homarus americanus, significantly alter the spatial distribution of chemical signals arriving at the sensory hairs and that the distinct morphology of different sensory organs has a differential effect on the filtering of incoming odor signals. The electrode placed within the boundary layer of the lateral antennule detected lower concentrations as compared to recordings in either the medial antennule or the walking leg. This was true for all flow velocities, although it was more apparent at the lower flow rates. This demonstrates that the distinct morphology of each receptor structure results in a distinct boundary layer (Moore et al., 1991). Previous studies on other relevant flow situations (Vogel, 1983; Cheer and Koehl, 1987) have also shown that the fluid flow around and through sensory appendages is significantly altered by the morphology of the appendage. Under stationary conditions, odor access to all parts of the sensory sensillum is limited in the lateral antennule. Under active sampling conditions, the fluid dynamic conditions are changed and chemical signals have equal odor access to all regions of the aesthetasc hairs. The boundary layer surrounding a sensory organ acts as a smoothing filter for odor signals; temporal aspects of the signal are changed by the boundary layer. Since the thickness and structure of the boundary layer will depend upon the morphology of the chemoreceptor appendage and the relative fluid velocities, identical odor pulses in the environment will
be different in the microscale environment of morphologically different chemosensory appendages. Each of the lobster’s appendages, lateral and medial antennule and walking legs, has a distinct morphology and therefore each appendage will have a unique boundary layer.

9.10 FUTURE DEVELOPMENT

The current IVEC-10 system is constantly under development for implementation in oceanographic work. Future development of additional techniques and hardware are expected to make the current system easier to use and to broaden its application. The new developments fall into three categories. First, given the constant advances in microcircuitry, the system will probably be redesigned to be smaller and more portable, on-board battery sources of power will be added, and smaller and faster A-to-D cards will be used. This will increase the number of different field uses for the current system. Second, electrodes are currently being developed that are multisite electrodes (Figure 9.5), which will allow for multiple measures: molecular, functional, and structural levels.

References

Atema, J. (1985) Aquatic sti
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Busdosh, M., R
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Figure 9.5 Examples of 10 s chemical records measured at two sensors on a multisite semiconductor-based probe. Sensors used in these recordings are spaced 600 microns apart. This probe had five sensors in a linear array. Each sensor was 200 microns apart. (A) Sensor #1 and (B) Sensor #4.
multiple measurements at electrodes 100–200 microns apart. Finally, additional methods are being developed that will allow for a larger range of organic molecules to be detected with high sensitivity and selectivity against background levels.

References


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