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Chemically regulated feeding by a midwater medusa

Abstract—Planktonic cnidarians are principal predators in the vast habitats between the ocean’s surface and the deep-sea floor. Almost nothing is known, however, about the chemical ecology of these fragile midwater animals because of difficulties associated with collecting healthy specimens and conducting experiments in the field. With the use of a remotely operated vehicle, we found that the hydromedusa *Mitrocoma cellularia* is not a passive “drift-net” predator. This relatively simple gelatinous organism reacted to both the taste and smell of prey in the laboratory and in situ. Our results comprise the first definitive demonstration that a species of pelagic cnidarian responds behaviorally to chemical signals, and they lend new insight into the role of chemoreception in structuring midwater communities.

Gelatinous zooplankton are an integral part of oceanic midwater ecosystems. Predatory forms (including scyphomedusae, hydromedusae, cubomedusae, siphonophores, and ctenophores) often comprise up to 30% of the biomass in mesopelagic environments, which have no solid boundaries and little or no sunlight (Robison 1995; Pugh et al. 1997). As with all organisms, the success and distribution of gelatinous zooplankton is determined in large part by their ability to obtain food. Sensing molecules dissolved in fluids (distant

chemoreception or “smell”) and bound in solid materials (contact chemoreception or “taste”) have long been known to aid in the search for and selection of prey. Almost all organisms from bacteria (e.g., Adler 1969) to birds (e.g., Nevitt et al. 1995) have been found to acquire nutrition through the use of chemical signals.

Surprisingly, however, it has not been clearly demonstrated that any planktonic cnidarians or ctenophores utilize chemical cues. Most are thought to be relatively passive “drift-net” or random contact predators, relying either on active prey that swim into extended tentacles or on the predator moving through the water column for chance encounters with prey. Although it has been shown that mechanical stimuli are typically used by pelagic cnidarians and ctenophores when feeding, their ability to perceive chemical cues is largely a matter of speculation (see review by Purcell 1997).

A few studies have attempted to determine if various species of planktonic cnidarians or ctenophores respond behaviorally to compounds associated with prey (Loeb and Blanquet 1973; Swanberg 1974; Arai 1991; Falkehnaug and Stabell 1996). However, limitations in the methods used make the results of these studies difficult to interpret. Stronger support for the possibility that pelagic cnidarians may utilize chemical signals is found in the intracellular record-

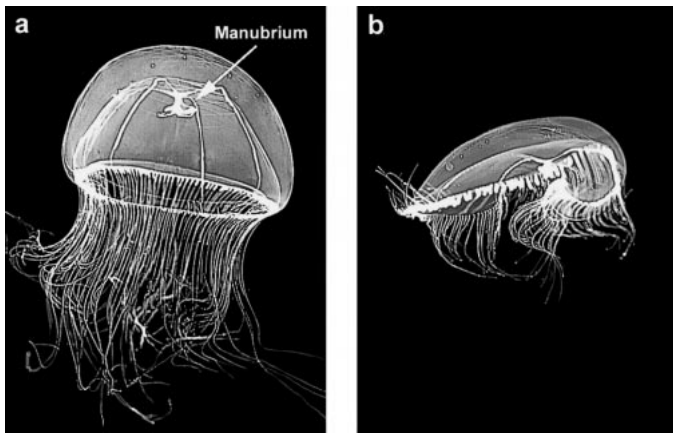


Fig. 1. Adult *Mitrocoma cellularia* (a) swimming with tentacles extended and (a) feeding with bell bent to the manubrium and tentacles retracted.

ings made from nematocyst-containing cells on tentacles of the Portuguese man of war, *Physalia physalia*, a cystonect siphonophore. Chemical extracts from fish mucus elicited electrical responses that might lower the threshold for nematocyst discharge after mechanical stimulation in this species (Purcell and Anderson 1995).

The principal reasons for our general lack of knowledge about gelatinous organisms in deep water are associated with the difficulties of collecting and maintaining healthy specimens for study in the laboratory and with the logistical problems of conducting observations and experiments in the field. However, recent advances in remotely operated vehicle (ROV) technology now allow us to more closely examine the biology and chemical ecology of these important but delicate midwater animals (Robison 1993). We were able to use an ROV not only to collect healthy individuals for laboratory assays but also to conduct controlled behavioral experiments on a gelatinous species in its natural midwater environment.

Our study focused on the ability of a small (up to 9-cm bell diameter) mesopelagic hydromedusa, *Mitrocoma cellularia*, to recognize potential prey by surface-bound and waterborne chemical cues. The nearly transparent *M. cellularia* occur at depths of 30 to 800 m, from the Bering Sea to the waters off the coast of central California (Kramp 1968; Widder et al. 1989). Their bell margin is lined with over 250 tentacles, which are used for prey capture, and a manubrium with four dexterous lips, which is located at the inner apex of the bell, delivers food to the mouth (Fig. 1a,b).

Materials and methods: Collection and maintenance of animals—The ROV *Ventana* was used to observe and gently collect adult *M. cellularia* from deep water in Monterey Bay, California. *Ventana* is a 3,000-kg, electro/hydraulic unmanned submersible operated by the Monterey Bay Aquarium Research Institute. The vehicle has the ability to carry up to eight low-impact detritus samplers and a suction sampler with 12 isolated collection containers. The main camera used for observing and recording the behavior of midwater

animals was a Sony DXC3000, which was mounted on a three-axis pan-and-tilt (Robison 1993).

Collected specimens were maintained in, and all laboratory experiments (excluding *consumption of live prey*, see below) were conducted, in 700-liter circular Kreisel tanks (Hamner 1990) with 8°C recirculating, sand-filtered natural seawater (collected nearshore from Monterey Bay). *M. cellularia* were fed *Artemia* nauplii twice a week but were isolated from food for 48 h prior to use in an experiment. Each individual was tested with any particular treatment only one time.

Consumption of live prey—Because little is known about their feeding behavior, our first set of laboratory experiments was designed to determine what types of organisms *M. cellularia* would consume and how they would respond to the presence of live prey. In three replicate trials, a single *M. cellularia* was placed in a jar containing 3 liters of filtered (1 μm) natural seawater and either 50 *Artemia franciscana* nauplii (young brine shrimp), 50 copepods (mixture of harpacticoid and cyclopoid species collected from Monterey Bay), or 50 juvenile *Aurelia aurita* (scyphozoa). Animals were closely observed, and video records were made during the first few hours of exposure to potential prey so that feeding behaviors could be characterized. After 24 h, the numbers of brine shrimp, copepods, or juvenile *A. aurita* remaining in each container were counted to determine the percent consumption of each prey type.

Test solutions and chemical analyses—Three solutions were created for the taste and smell experiments described below. One solution consisted of the natural seawater used to bathe (or hold) live *Artemia* nauplii (ABW). Bathwater solutions were prepared by maintaining 25 *Artemia* nauplii per 1 ml seawater for 24 h, then removing the *Artemia* (and other particulate matter) by filtering the solution to 0.45 μm . Another solution was prepared by homogenizing *Artemia* nauplii (AH). Two grams of wet tissue weight of *Artemia* nauplii per 25 ml of seawater were blended in a tissue homogenizer (model PT10/35, Brickmann), then filtered to 0.45 μm to remove all particulate matter. Although *Artemia* do not naturally co-occur with *M. cellularia*, we justified their use because they were consumed in proportions similar to the copepods collected from Monterey Bay (see results) and because large numbers of this single prey species could be cultured in the laboratory for this study.

The third solution used was simply filtered (0.45 μm) natural seawater as a control (SWC). A different food coloring was added to each of the three solutions as a visual marker. Assays conducted with and without food coloring confirmed that the visual markers alone did not influence the behavior of test animals.

Concentrations of total proteins, dissolved free amino acids (DFAAs), and ammonium in each solution (SWC, ABW, and AH) were determined in triplicate assays to indicate the quantity of potential chemical stimulants. Proteins and amino acids have been found to chemosensitize the cnidocytes on the tentacles of sea anemones (Lubbock 1979; Thorington and Hessinger 1988), whereas ammonium is a common catabolite release into seawater following the breakdown of

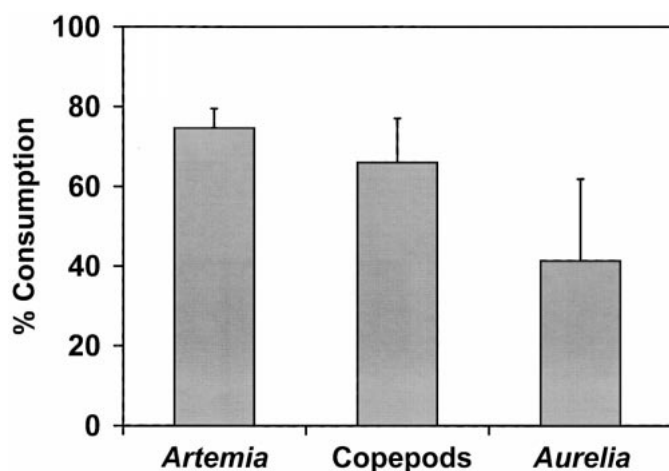


Fig. 2. Mean percentages and standard errors for three replicate trials of 50 *Artemia franciscana* nauplii, 50 copepods, and 50 juvenile *Aurelia aurita* consumed by *Mitrocoma cellularia* during 24-h feeding experiments.

proteins and amino acids by marine organisms. We therefore assumed that even if proteins, amino acids, or ammonium are not natural attractants, production of chemical stimuli that induce feeding behaviors might be coupled with their release.

Total protein and ammonium concentrations were determined by standard colorimetric techniques described by Bradford (1976) and Solorzano (1969), respectively. Levels of DFAAs in each solution were quantified by high-pressure liquid chromatography (see methods in Zimmer et al. [1998] and Tamburri and Barry [1999]).

Selection based on taste—To determine if prey selection is based on taste, three types of flavor treatments were presented to individual *M. cellularia*. One treatment comprised small cubes (approximately $2 \times 2 \times 2$ mm) made from low-melting point agarose (Sea-Plaque) and SWC (negative control). For the second treatment, similar agarose cubes were prepared, but with the AH solution rather than SWC. The final flavor treatment was adult *Artemia* (positive control), which served as a standard for behavioral responses to a live prey item. A single cube of the seawater agarose or *Artemia* agarose or a single live *Artemia* was delivered to the tentacles of eight replicate *M. cellularia* in separate trials, and their behavioral responses were monitored for 10 min.

Identification based on smell—To examine if *M. cellularia* is able to perceive prey from a distance using waterborne chemical cues, the three solutions were presented to individuals as they remained at rest in the center of the test tanks. In eight replicate trials, a single *M. cellularia* was exposed to either the SWC, ABW, or AH solution. Two milliliters of solution was delivered (at a constant rate), within 1 cm of the test animals, over a period of 30 s by syringe pump (KD Scientific, model KDS220, KD Scientific), and their behavioral responses were monitored for 10 min.

Table 1. Mean values for total protein, dissolved free amino acids (DFAAs), and ammonium (NH_4) concentrations determined in triplicate assays for the seawater control solution (Seawater), live *Artemia* bath-water solution (Bath water), and *Artemia* homogenate solution (Homogenate).

Solutions	Protein ($\mu\text{g ml}^{-1}$)	DFAA (nM)	NH_4 (μM)
Seawater (SWC)	0*	0.48	1.21
Bath water (ABW)	0*	0.63	58.75
Homogenate (AH)	533	51.91	259.66

* Below detectable levels.

In situ assays—To determine if the chemically mediated feeding behaviors found in our laboratory study also occur in situ, the ROV *Ventana* was used to release solutions near *M. cellularia* in the field and to record their subsequent behavior. In five replicate trials for each treatment, individuals encountered in the midwaters of Monterey Bay were presented with either SWC or AH. Solutions were delivered through a 6-mm (internal diameter) stainless-steel tube, within a few centimeters of the test animals by a hydraulically powered peristaltic pump controlled by the ROV.

Results: Consumption of live prey—Several individuals of all three prey types were eaten during the 24-h experiments (Fig. 2). More than one-half of both the *Artemia* nauplii and copepods presented were consumed, with few obvious differences in terms of the numbers eaten or how the prey were captured and ingested. *M. cellularia* also readily consumed the other gelatinous form (juvenile *A. aurita*), although in lesser numbers.

These first experiments also revealed clear feeding patterns. In the presence of all live prey, *M. cellularia* slowly drifted around the containers and would (1) extend and retract multiple tentacles, (2) contort the bell in an irregular manner to align or position prey on the margin (without forward propulsion and distinct from the uniform contractions used to swim), (3) bend the bell margin toward the manubrium for transfer of captured prey, and (4) manipulate the manubrium to grasp and deliver prey to the mouth. Although most of these indicators were observed during all feeding assays, each movement was distinct and was not necessarily sequential. These four behaviors were then used as criteria for a feeding response when we examined the ability of *M. cellularia* to taste and smell prey.

Chemical analysis of solutions—Large differences in the chemical concentrations were measured between the three solutions (Table 1). We found no measurable levels of protein in the seawater control and the live *Artemia* bathwater solutions, whereas the *Artemia* homogenate solution contained a large amount of protein. Levels of DFAAs and ammonium were lowest in the SWC, intermediate in ABW, and highest in the AH solution. The AH solution contained large concentrations of diverse organic compounds and was therefore useful as an initial stimulus to demonstrate chemoreceptive ability. The ABW solution, on the other hand, contained only dissolved compounds released from live,

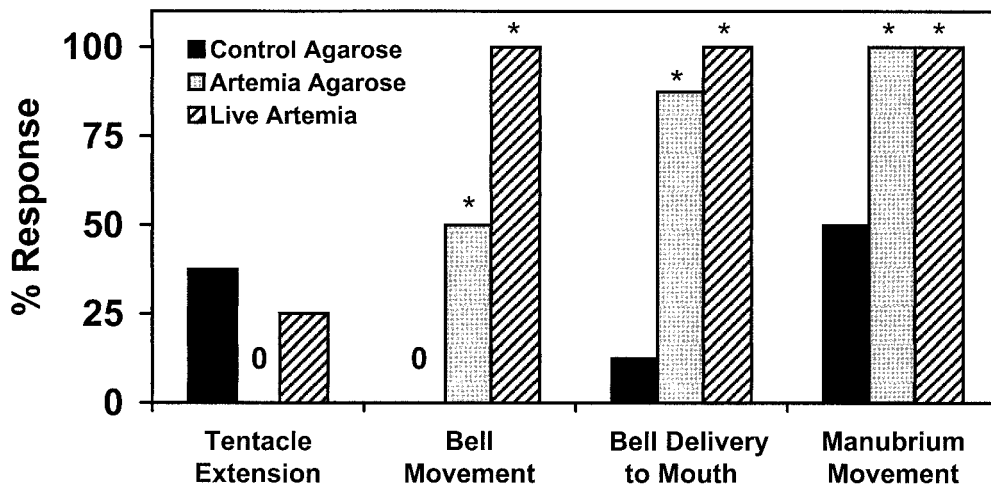


Fig. 3. Percentage of *Mitrocoma cellularia* that responded to a seawater control agarose cube, an *Artemia* homogenate agarose cube, or a live adult *Artemia* by extending or retracting their tentacles, contorting their bell, bending their bell for the delivery of food to the mouth, or manipulating their manubrium to grasp and ingest food. Eight replicate trials were conducted for each treatment. Asterisks designate values that were significantly greater than responses to the seawater control treatment.

undamaged animals at concentrations that might more closely resemble those encountered in dense, naturally occurring prey patches.

Selection based on taste—When presented with the SWC agarose cubes, almost all *M. cellularia* remained essentially motionless (Fig. 3). Although some manubrium movement was seen in one-half of the individuals tested, all but one merely let the small cubes drop after contact. Conversely, when presented with AH agarose cubes or live adult *Artemia*, nearly all individuals contorted their bells, transferred items from the bell margin toward the mouth, and manipulated the manubrium to grasp the item for ingestion (Fig. 3). Although no differences were found between responses to the two *Artemia* treatments, both induced significantly greater numbers of animals to begin feeding than did the SWC cubes (Fisher's exact test; $P < 0.01$; all comparisons).

Identification based on smell—As in the taste experiments, the seawater control treatment had no effect on *M. cellularia*. Almost all of the individuals tested remained nearly motionless after contact with the SWC solution (Fig. 4). However, when presented with dissolved compounds from either the ABW or AH solution, most *M. cellularia* instantly initiated at least some of their feed behaviors. A significant increase in the percentage of individuals responding with all four of the behavioral criteria was found in response to the AH solution (Fisher's exact test; $P < 0.01$; all comparisons). Although the same trends held true for responses to the ABW solution, the only statistically significant increase above seawater control was found in manubrium movement ($P = 0.03$). It is likely that a greater number of *M. cellularia* responded to the AH solution (than to the ABW) with the full set of behaviors because of larger stimulant concentrations. However, dilute cues emitted from live prey also induced some feeding responses.

In situ assays—As was the case with our laboratory results, *M. cellularia* in the field showed no behavioral response to SWC, whereas significantly greater numbers of individuals responded to the AH solution ($P = 0.005$). Although limitations of video imaging from the ROV did not allow for precise examination of tentacle or manubrium movement, the two other feeding criteria were obvious. Four out of five *M. cellularia*, which had never been handled or manipulated, immediately contorted their bells and then bent them to their mouths in response to dissolved compounds associated with prey.

Discussion—Although *M. cellularia* is a relatively simple, slow-moving organism, we found that it is not a passive “drift-net” predator. Signal molecules in the *Artemia* homogenate solution and bound within agarose cubes caused almost all of the individuals tested to begin feeding. Furthermore, no obvious differences were seen between the way *M. cellularia* responded to AH agarose cubes or to live adult *Artemia*. Therefore, although mechanoreception likely plays a role in the capture and ingestion of prey at some level, chemoreception alone regulated the feeding behaviors we observed in this experiment.

The one behavioral criterion only occasionally observed in the taste experiment was multiple tentacle extension, presumably because items were delivered directly to the test animals. Although *M. cellularia* were observed periodically extending and retracting individual tentacles without obvious stimulation, we only found multiple tentacle extensions when individuals were in the vicinity of several prey items (consumption of live prey experiment) or when they were presented with the ABW and AH solutions (smell experiment). This deployment of tentacles in a curtain below pelagic cnidarians or ctenophores dramatically increases the surface area for prey interception (Purcell 1981; Madin 1988). Our results, therefore, indicate that *M. cellularia* can

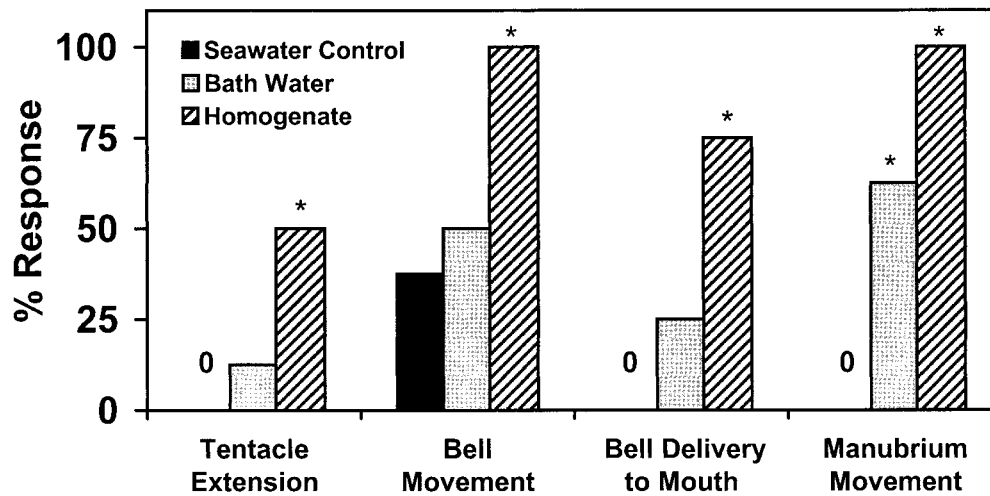


Fig. 4. Percentage of *Mitrocoma cellularia* that responded to the seawater control solution, the *Artemia* bathwater solution, or the *Artemia* homogenate solution by extending their tentacles, contorting their bell, bending their bell for the delivery of food to the mouth, or manipulating their manubrium to grasp and ingest food. Eight replicate trials were conducted for each treatment. Asterisks designate values that were significantly greater than responses to the seawater control treatment.

in fact identify the presence of prey remotely using purely waterborne chemical signals and can respond in a manner that will enhance their probability of capturing prey.

Although *M. cellularia* increased their chances of encountering prey perceived from a distance, we found no evidence that they would move toward the cue source. Individuals would drift slowly during the experiment and would only swim (by contracting their bell in pulses) when disturbed by contact with a wall or test equipment (the behavior of disturbed *M. cellularia* was not considered). It is likely that no tracking behavior was seen because the test animals were encircled by odor clouds. This study was designed simply to demonstrate chemoreceptive ability. Clearly, further work on movements toward cue sources or prey patches is needed, but some anecdotal evidence does exist for this type of behavior in other species of planktonic cnidarians (Arai 1991) and ctenophores (Swanberg 1974; Falkehnaug and Stabell 1996).

There are obvious difficulties in predicting the responses of animals in nature based on behavioral experiments conducted in the laboratory. This is particularly true for fragile gelatinous zooplankton that are studied in relatively small aquariums (DeLaFontaine and Leggett 1987; Gibbons and Painting 1992). Thus, a field experiment was required to confirm the results found in our aquarium assays. Remarkably, *M. cellularia* that had never been handled or manipulated in any way, immediately responded to the AH solution with the same types of behavior observed in the laboratory.

Detecting and locating food by chemoreception is common in most major phyla (e.g., Rittschof et al. 1983; Jones 1986; Zimmer-Faust 1989; Nevitt et al. 1995), and several species of benthic cnidarians (anemones and hydra) have long been known to utilize a variety of chemical signals (see review by Lenhoff et al. 1976). The results of this study, however, comprise the first definitive demonstration that any species of planktonic cnidarian alters its behavior in response

to chemical cues, either substrate-bound or waterborne. With the capacity to both smell and taste, *M. cellularia* may dramatically increase the probability of contact with prey perceived from a distance, and may select or reject captured items based on flavor or nutritional value.

Gelatinous zooplankton are dominant predators at two trophic levels in highly dilute midwater habitats. They are important competitors of predatory fish, squid, and crustaceans and are themselves a source of nutrition for many other pelagic animals (Robison 1995; Pugh et al. 1997; Purcell 1997). The mechanisms that regulate these interactions, however, are very poorly understood. Our results indicate that chemical signals can mediate predation by gelatinous zooplankton and may thus play a critical role in structuring communities within the largest habitat on earth.

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