

Role of Chemical Signals in the Orientation Behavior of the Sea Star *Asterias forbesi*

PAUL A. MOORE AND DEBORAH M. E. LEPPER

Laboratory for Sensory Ecology, Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43403

Abstract. The importance of chemical signals as foraging and orientation cues has been demonstrated for many marine organisms. It is still unclear whether sea stars use chemical signals during orientation and whether chemoreception occurs in the absence of macroscale flow. To determine whether the sea star *Asterias forbesi* can perceive chemical signals in the absence of flow and what role such signals play in orientation and foraging behavior, we tested the orientation behavior of sea stars to prey and nonprey items under conditions of nondirectional flow. Prey items were whole and broken clams (*Mercenaria mercenaria*) and mussels (*Mytilus edulis*); the nonprey item was squid flesh. *Asterias forbesi* showed the ability to successfully locate odor sources irrespective of the type of odor. Only in trials with the broken clam did the animals reveal an initial directional choice towards the odor source. There were significant changes in the movement rates and heading angles during orientation for all three stimuli. In addition, orientation paths were different for each of the chemical stimuli tested. From these results, we conclude that sea stars can detect and respond to chemicals in the absence of macroscale flow. Orientation paths appear to be more of a taxis, in which heading is directly guided by the stimulus field.

Introduction

Asteroids are marine benthic invertebrates found in abundance in the littoral and subtidal zones of most shorelines. Most asteroids are carnivores and can play a significant role as keystone predators in these habitats (Feder and Christensen, 1966; Jangoux, 1982). Prey

items consist of large epifaunal species including gastropods, various bivalves, and some crustaceans, typically barnacles (Feder and Christensen, 1966; Jangoux, 1982). Some species show food preferences that are not due exclusively to prey availability (Christensen, 1957; Jangoux, 1982). The sensory mechanisms that asteroids use to forage for prey have been debated for a number of years.

Most of the previous research, focusing on the chemosensory or mechanosensory abilities of asteroids, has resulted in mixed conclusions. Sloan and Campbell (1982) have reported evidence for olfaction in some species, while concluding that others have no such abilities. Other researchers have shown that olfaction is important for foraging (McClintock and Lawrence, 1981; McClintock *et al.*, 1984; Valentincic, 1985; Valentincic and Ota, 1985). In addition, chemical orientation also has been seen in both field (Christensen, 1957) and laboratory settings (Castilla, 1972a; Castilla and Crisp, 1970; Rochette *et al.*, 1994). Conversely, it was noted that *A. rubens* showed an avoidance response to damaged or spawning prey and living predators in the static-flow Y-maze and the flow tank (Castilla and Crisp, 1970). *Crossaster papposus* was observed to be attracted to prey extracts by choosing the arm in a Y-maze in which the extract was added. They also avoided the extract of carnivorous conspecifics by moving downstream (Sloan and Northway, 1982). However, orientation to live oysters, mussels, and nudibranchs could not be demonstrated in other instances (Sloan and Campbell, 1982).

Many of these studies were done in flow tanks (Castilla, 1972b; Castilla and Crisp, 1970; Sloan and Northway, 1982; Zafiriou, 1972; Zafiriou *et al.*, 1972), to which sea stars show a positive rheotaxis (Valentincic, 1983). Observed movement toward the odor source may or may not have been mediated by chemical stimulation but

may have been strictly a response to water flow. Avoidance responses in these situations may be negative rheotaxis, initiated by the presence of the chemical signal. Behavioral trials with no macroscale flows can help eliminate the possibility of rheotaxis but may have some confounding factors due to small-scale water dynamics in the tank. Sea stars, when excited by a food item in the aquarium, often pass directly by it or turn away just as they near it (Feder and Christensen, 1966). These behavioral results could be interpreted as being a result of small-scale circulation patterns within the aquarium.

The spatial distribution of chemical signals in marine environments is determined by the hydrodynamics of the environment. In most marine habitats, turbulent diffusion is the major force that disperses chemicals. Whether in air or water, turbulent odor concentrations in plumes are heterogeneous when measured at fast temporal and small spatial scales (air: Murlis and Jones, 1981; Murlis *et al.*, 1991; water: Atema, 1985; Moore and Atema, 1988, 1991; Zimmer-Faust *et al.*, 1988). The exact nature of concentration fluctuations within any habitat depends on the interaction between the size of the turbulent eddies and the size of the odor plume. As a result of these interactions, animals using chemical signals to locate potential prey items will experience different stimulus patterns in different flow regimes (Moore *et al.*, 1994). Thus, if changes in behavior occur simultaneously with changes in flow, it is often difficult to determine whether those changes are due to the differences in the chemical signal or the mechanical signal. In previous work, mechanical and chemical signals were presented simultaneously (Castilla, 1972b; Castilla and Crisp, 1970; Rochette *et al.*, 1994; Sloan and Northway, 1982; Zafriou, 1972; Zafriou *et al.*, 1972). To determine which source of information is important in orientation behavior, it is important to separate these two sources of information during orientation trials.

Marine animals use many different behavioral mechanisms to orient to a chemical source. Categories for orientation behaviors have been based on a variety of criteria, including locomotor output, distribution and number of sensory receptors, and information available to and used by the animal (Bell, 1984; Dusenbery, 1992; Kennedy, 1986; Preface for Bell and Cardé, 1984; Schöne, 1984). In a broad sense, it appears that chemical signals either play a direct guidance role (Johnson and Teeter, 1980; Moore *et al.*, 1991; Reeder and Ache, 1980; Rochette *et al.*, 1994), serve to initiate maneuvers that depend on nonchemical stimuli (Mafra-Neto and Cardé, 1994), or can be used in conjunction with mechanical signals (Weissburg and Zimmer-Faust, 1993).

From a sensory perspective, it is important to differentiate between potential sources of directional information. Y-mazes and other choice experiments demon-

strate that chemoreception can play a role in directional decisions, but under these conditions, reliable directional information is still provided by the unidirectional flow. Although there are problems of small-scale circulation, the reason for performing experiments in still water is the removal of any directional information provided by macroscale currents. Although it is highly unlikely that flow is completely absent in still-water trials, it is equally unlikely that reliable directional information on the odor source is provided by any small-scale circulation present within the tank.

Chemical cues are apparently important in orientation by *A. forbesi*, but it is still not clear whether chemical signals or mechanical and chemical signals mediate foraging and orientation. The purpose of this study was to demonstrate chemoreception by *A. forbesi* in the absence of directional information provided by macroscale flow and to investigate the role of chemical signals in orientation behavior. We hypothesize that this species of sea star has the ability to use chemical signals in the absence of macroscale flow to successfully orient to potential prey. Thus, still-water trials become crucial for determining the source of information controlling or guiding the orientation of the organism. A better understanding of the chemoreceptive abilities of this sea star and sources of sensory information used in foraging may lead to a broader understanding of intertidal foraging mechanisms in sea stars.

Materials and Methods

Animals

Sea stars, *Asterias forbesi*, were obtained from the Aquatic Resources Division of the Marine Biological Laboratory in Woods Hole, Massachusetts. The animals were wild caught off the coast of Woods Hole and remained in flow-through seawater tanks before shipping to our laboratory. The animals measured 7.5–15.25 cm in diameter and were kept in 35-gallon aquaria, maintained at a salinity of 25‰–30‰, a temperature of 15°–20°C, and a cycle of 12 h light and 12 h dark. An under-gravel filter was used for maintaining water quality in the tank, and filtered air was pumped into the system for aeration and circulation. Each sea star was isolated from the others in the aquarium by plastic crating, which allowed water movement between the chambers but separated animals for individual identification. No more than four individuals were housed in a single aquarium. The sea stars were fed once a week at a maintenance level, about 2 g of thawed squid flesh. Any uneaten food was removed from the aquarium after 2 h.

Hard-shelled clams (*Mercenaria mercenaria*) and blue mussels (*Mytilus edulis*) were obtained from the Aquatic Resources Division of the Marine Biological Laboratory

in Woods Hole. Both of these molluscs are common prey items of *A. forbesi* in this area. The clams (5–10 cm in width) and mussels (2–5 cm in width) were placed in a 35-gallon aquarium under the same conditions of salinity, temperature, and light as the sea stars. They were fed suspended algae twice a week for 4 h each time by placing them in beakers with the algae.

Experimental procedure

The testing arena was an acrylic plastic aquarium, dimensions 57.5 cm $\times$ 117.5 cm, with a water depth of 5 cm. It was located within the same room as the housing aquaria and under the same lighting conditions. The salinity of the tank was matched to the salinity of the housing aquarium. The bottom of the tank was marked off in a 5-cm grid with the origin (0, 0) at the center of the tank. Between each trial, the tank was rinsed with cold tap water to avoid any chemical contamination from the previous trial. After filling, the tank was allowed to sit for at least 1 h before orientation trials were started.

For every trial, the animal was placed at the origin, with its madreporite as a fixed point of reference. Previous observations indicated that handling did not adversely affect the behavior. In trials with a chemical stimulus, the source was placed in a position ($x = 0$ cm, $y = -45$ cm) that allowed the sea star to move both toward and away from the stimulus by several body lengths and prevented accidental contact with the source if the animal was only following the contours of the tank walls.

During each 25-min trial, the position of the sea star (determined using the madreporite as a reference) was recorded by eye every 30 s. Animals that did not move for a period of 6 min were rejected. For experimental trials, the chemical stimulus (squid, mussel, or clam) was placed in the tank before the sea star was added. If the animal walked within 5 cm of the stimulus source, the run was considered successful. If the madreporite of the animal was within 5 cm of the odor source, one of the arms would be in contact with the source. By accepting a distance of 5 cm for the madreporite, we had a criterion that was consistent between trials and independent of the arm size of the animals. Control studies were conducted in the same way as experimental trials except that no chemical stimulus was placed in the tank. After each trial, the sea star was returned to its chambered aquarium and any stimulus source discarded.

Stimulus preparation and distribution

In chemical stimulus trials, five stimulus sources were used: squid flesh (a broad-based amino acid source), whole live clam and mussel (potential prey items), and cracked clam and mussel (wounded potential prey items). For the squid stimulus, a 2-g piece of flesh was

cut from the body of the squid with a sharp blade. The frozen flesh had been obtained in bulk and was allowed to thaw before use. For whole prey trials, the bivalve was placed in the tank 5 min prior to an orientation run to allow it to begin filtering. For broken prey trials, the bivalve was crushed and left in the tank for 10 min prior to an orientation run. Mussels were prepared by holding the animal directly over the source point and crushing the shell with pliers; clams were placed on plastic wrap, hit with a hammer, and then transferred to the source point. Additional control trials used cleaned and dried empty shells from the clam or mussel. For these trials, an intact shell of each species was recovered from dead individuals in the holding aquarium. The shells were vigorously scrubbed with biodegradable soap and a nylon brush. The shells were then rinsed under tap water for 1 min, soaked in tap water for 1 h, and soaked in dilute bleach (1:10) for 10 min. After this the shells were rinsed under tap water for 1 min, soaked three times for 30 min each in distilled water, and rinsed between each period. Just prior to the trials, the shells were soaked for 30 min in 30‰ salt water.

To qualitatively analyze the spatial movement of chemicals within the testing arena, we used fluorescein dye in gelatin blocks to mimic the spatial distribution of chemicals emanating from the nonliving prey items. Gelatin blocks with 2 g/l of fluorescein dye were placed within the testing arena using the methods outlined above for broken prey items. After 10 min, the spatial distribution of the dye was mapped visually using four broad categories of dye concentration. This process was repeated six times. This qualitative analysis showed that each of the six replicates resulted in a different spatial distribution and that the lowest visible concentration of dye was 35 ± 0.2 cm (SEM) away from the odor source. For each replicate, the distance that 10 individual filaments of dye moved during a 1-min period was recorded as an estimate of the maximum water velocity within the tank. The estimate of the maximum water velocity was 3 ± 0.5 cm/min (SEM) or 0.05 ± 0.008 cm/s for all 60 samples.

Data analysis

The orientation paths from each run were recorded as a single point (x , y) every 30 s as previously described. From these paths, several orientation parameters were analyzed. These included walking speed, net-to-gross ratio (NGR), turning angles, and headings. NGR values were transformed using an arcsine method (specifically, $p' = \arcsine p^{1/2}$, Zar, 1984). Standard ANOVA techniques were used to compare the average value for each parameter between each of the trials. If the ANOVA was significant, it was followed by a *post-hoc* comparison us-

ing a Neuman-Keuls analysis. A linear regression analysis was used to correlate changes in parameter values with distance from source. Distance from the source for regression analysis was the Euclidean distance between the source point (0, 0) and the animal's position within the tank (described above). NGR was calculated by dividing the Euclidean distance from start to finish (net) by the total path length (gross). These values can range from 0 to 1, with 0 being a very circuitous path, and 1 being a linear path. Turn angle was defined as the angle between the path connecting the previous ($t = -1$) position to the present ($t = 0$) position and the path connecting the present to the next ($t = +1$) position (Moore *et al.*, 1991). A sea star's heading was defined as the angle between a straight line towards the source and the direction from the present position to the next position on the track, with an angle of zero pointing directly at the source (Moore *et al.*, 1991). All angles were calculated in a clockwise fashion.

The initial directional choice for each sea star was recorded as the heading angle for initial movement from the starting point. A modification of the Rayleigh's test (The V test) was used to determine whether the heading angles were uniformly distributed around the circle or if there was a significant directionality to the movement (Zar, 1984). For this test, we assumed *a priori* that an

angle of zero degrees towards the odor source was expected.

Results

General orientation results

Our criteria for successful orientation resulted in rejection of 52% of the total number of trials. Successful trials resulted in different paths that depended upon the odor source (Fig. 1). Most rejections were due to the animal's inability to locate the odor source; very few of the trials were rejected due to lack of movement by the animal. This high rate of rejection may be due to the unnatural experimental condition of no macroscale flow. Subsequent testing under flowing conditions may produce a higher success rate, but would not allow us to pursue the hypothesis proposed in the introduction.

Orientation to squid flesh

The odor of squid flesh in the test arena caused the animal to modify its walking behavior. This was shown by a significantly slower walking speed in the experimental animals compared with controls (t test, $P < 0.01$, Fig. 2). Sea stars in the presence of odor walked at 0.06 ± 0.01 (SEM) cm/s and control animals at 0.18 ± 0.02 cm/s. In

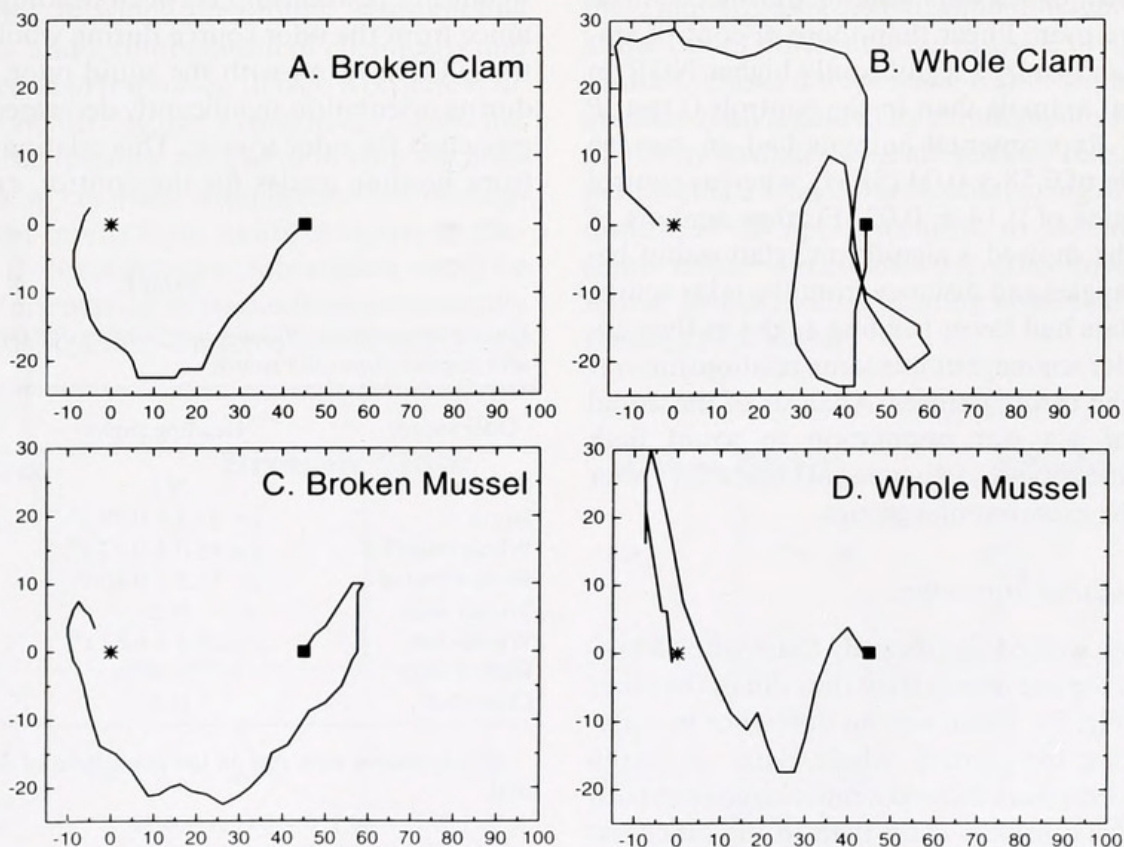


Figure 1. Randomly selected trials for four different sea stars for four different stimuli. Odor sources: (A) broken clam, (B) whole clam, (C) broken mussel, (D) whole mussel. Stimulus source is located at 0,0 (asterisk) and starting point of orientation path is at 45,0 (solid square).

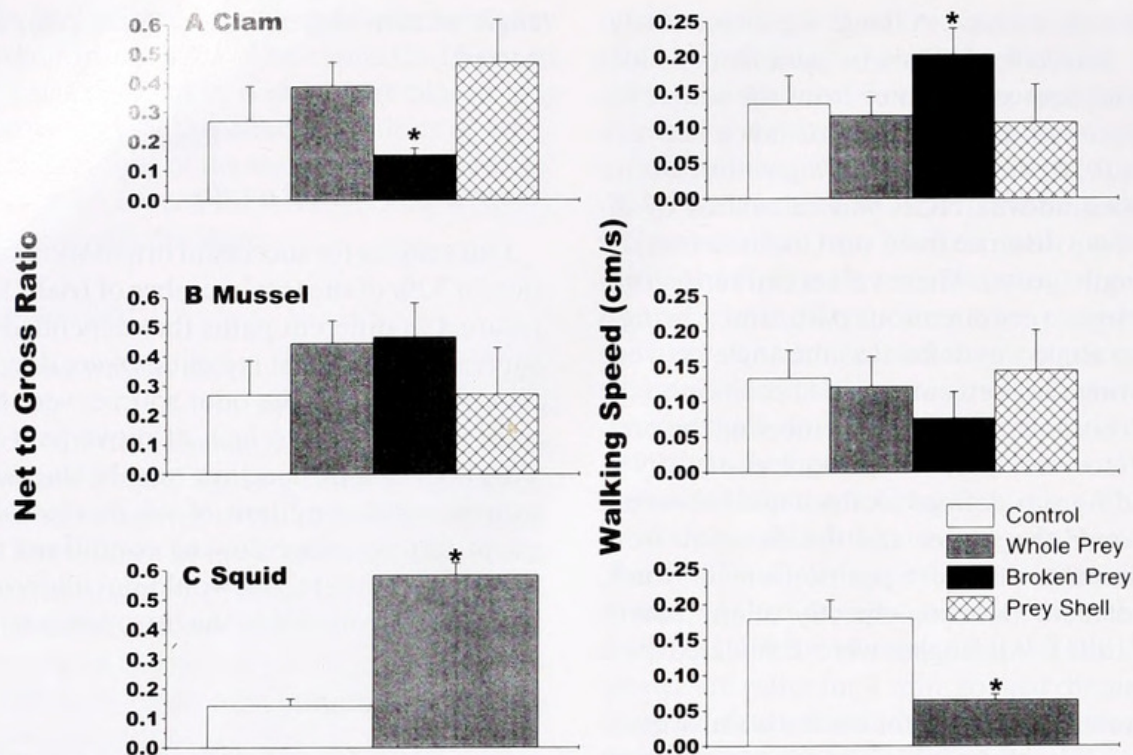


Figure 2. Average ($\pm$ SEM) net-to-gross ratio and walking speed of sea stars under no odor stimulation (control, blank bar), whole prey (gray bar), broken prey (black bar), and empty prey shell (hatched bar). Prey items: (A) clam, (B) mussel, (C) squid flesh. $n = 14$ for all trials for clam and mussel; $n = 22$ for squid. Asterisk indicates a value that is significantly different from all other values (ANOVA, then Newman-Keuls test, $P < 0.05$).

addition, the paths of sea stars walking during chemical stimulation were more linear than those of control animals. This was shown by a significantly higher NGR in the experimental animals than in the controls (t test, $P < 0.01$, Fig. 2). Experimental animals had an average net-to-gross ratio of 0.58 ± 0.04 (SEM), whereas control animals had ratios of 0.14 ± 0.02 . Further analysis of orientation paths showed a significant relationship between heading angles and distance from the odor source (Table I). Sea stars had lower heading angles as they approached the odor source, but this same relationship was not present in the turning angles. Analysis of the initial directionality of sea star orientation to squid flesh showed no significant initial directional choice for either the control or the experimental groups.

Orientation to natural prey items

Clam. Sea stars walked significantly faster when a broken clam was in the test arenas than they did in the other test situations (Fig. 2). There was no difference in walking speeds among the control, whole clam, or empty clam shell trials. Sea stars showed a more circuitous path in the presence of a broken clam than in the other test situations (Fig. 2). There was no difference in NGR among the control, whole clam, or empty clam shell trials. Regression analysis of orientation paths showed a

significant relationship between heading angles and distance from the odor source during whole clam stimulation (Table I). As with the squid odor, heading angles during orientation significantly decreased as sea stars approached the odor source. This relationship was absent from heading angles for the control, empty shell, and

Table I

Regression summary of changes in heading and turning angles with distance from odor source

Odor source	Heading angles	Turning angles
Control	N.S.	N.S.
Squid	$y = 37.7 + 0.59 x^A$	N.S.
Whole mussel	$y = 46.0 + 0.52 x^B$	N.S.
Broken mussel	$y = 31.8 + 0.86 x^C$	N.S.
Mussel shell	N.S.	N.S.
Whole clam	$y = 26.2 + 0.82 x^D$	N.S.
Broken clam	N.S.	N.S.
Clam shell	N.S.	N.S.

All regressions were run on the population of sea stars within each trial.

^A $F(1,393) = 20.1$, $P < 0.05$, $r = 0.22$.

^B $F(1,348) = 12.5$, $P < 0.05$, $r = 0.18$.

^C $F(1,194) = 16.4$, $P < 0.05$, $r = 0.28$.

^D $F(1,120) = 11.4$, $P < 0.05$, $r = 0.30$.

All nonsignificant results had $P > 0.10$.

broken clam situations and was absent from all turning angle analysis. Analysis of the initial directional choices of sea stars during clam stimulation showed a significant directional choice towards the odor source for the broken clam only (The V test, $\mu_0 = 0^\circ$, $u = 2.0$, $P < 0.05$, Fig. 3). All other heading angles were uniformly distributed around the circle, indicating no significant initial heading angle.

Mussel. Sea stars did not alter either their walking speed or the NGR in any of the trials involving either mussels, broken mussels or empty mussel shells when compared to control values (Fig. 2). There was a significant change in heading angles for both the whole and broken mussel trials. Sea stars significantly decreased their heading angles as they approached the odor source (Table I). This relationship was absent from heading angles for the control and empty mussel shell and was absent from all turning angle analysis. Analysis of the initial directional choices of sea stars during mussel stimulation showed that there was not a significant directional choice towards the odor source for any of the odor stimulations (Fig. 4).

Discussion

In previous orientation studies using sea stars, it has been difficult to differentiate between a true chemically mediated response, in which the animal is responding only to the odors, and a combination of chemically and mechanically mediated responses. In fact, Rochette *et al.* (1994) showed conclusively that *Leptasterias polaris* has a strong orientation response to current in both the presence and absence of chemical stimulation. The orientation behavior that results from multiple inputs of chemosensory and mechanosensory information could be due to a range of orientation strategies from a chemically triggered rheotaxis to a flow-triggered chemotaxis (for a

review of different orientation strategies, see Shöne, 1984). This study demonstrates three results concerning the chemosensory abilities of *A. forbesi*. First, this species perceives and responds to chemical signals in the absence of macroscale flow. Many previous studies on both the foraging and orientation behavior of other sea stars have been in flow tanks (Castilla, 1972b; Castilla and Crisp, 1970; Sloan and Northway, 1982; Zafiriou, 1972; Zafiriou *et al.*, 1972). In many of these situations, the sea stars show a positive rheotaxis (Valenticic, 1983), and it is not clear whether they are responding to the macroscale flow, to the chemical, or to both.

Second, we demonstrate that *A. forbesi* is capable of locating odor sources without the aid of external directional cues provided by macroscale flow. The analysis of the orientation paths shows that orientations are probably a response to information from the chemical signal within the experimental arena. Several features of the orientation paths reveal an orientation strategy that may be a taxis (as defined in both Dusenbery, 1992, and Schöne, 1984). Using these definitions, a taxis is an orientation that is a result of biased or directed turns with respect to some aspect of the stimulus field. This would result in decreased heading angles as the organism approached the odor source. As has been demonstrated for other sea stars (Rochette *et al.*, 1994), and suggested for *A. forbesi* under different flow conditions (Dale, 1996), these animals use concentration differences as measured at the tips of different arms to guide orientation to food sources. This is a tropotactic response, in which the orientation path is guided by simultaneous information obtained by spatially separate sensory cells. If *A. forbesi* is performing a tropotaxis by comparing different concentrations at the tips of its arms, we would expect to find some initial directional decisions towards the odor source and decreased heading angles as the animal approached the source.

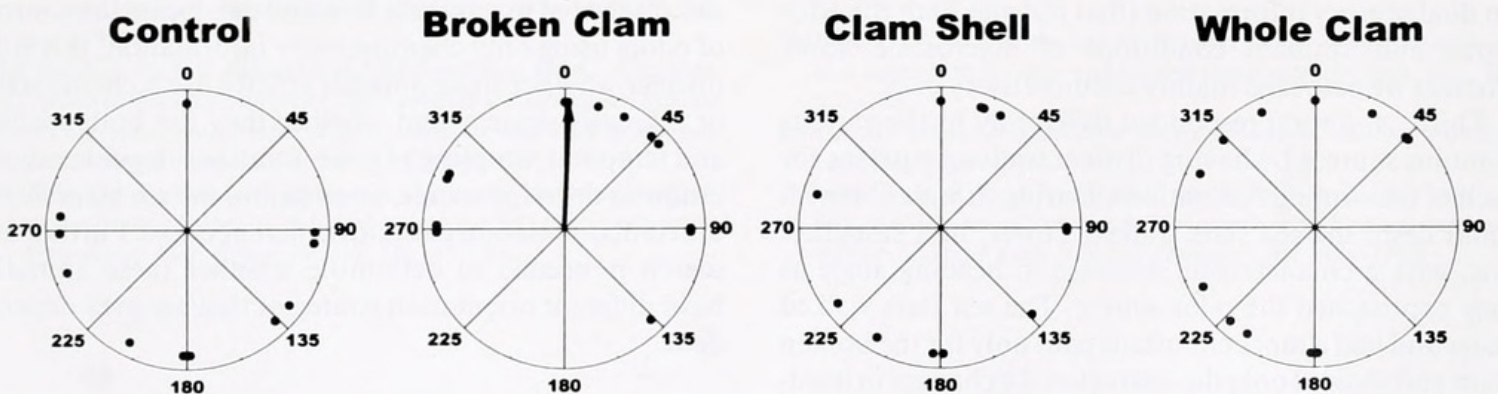


Figure 3. Initial directional choices for sea stars during different odor stimulations for clam sources. Solid dots represent heading angle in relation to odor source for the first movement of the animal. Significant mean angles are indicated by a solid black arrow, V test. All other groups were uniformly distributed around the circle; $n = 14$ for all groups.

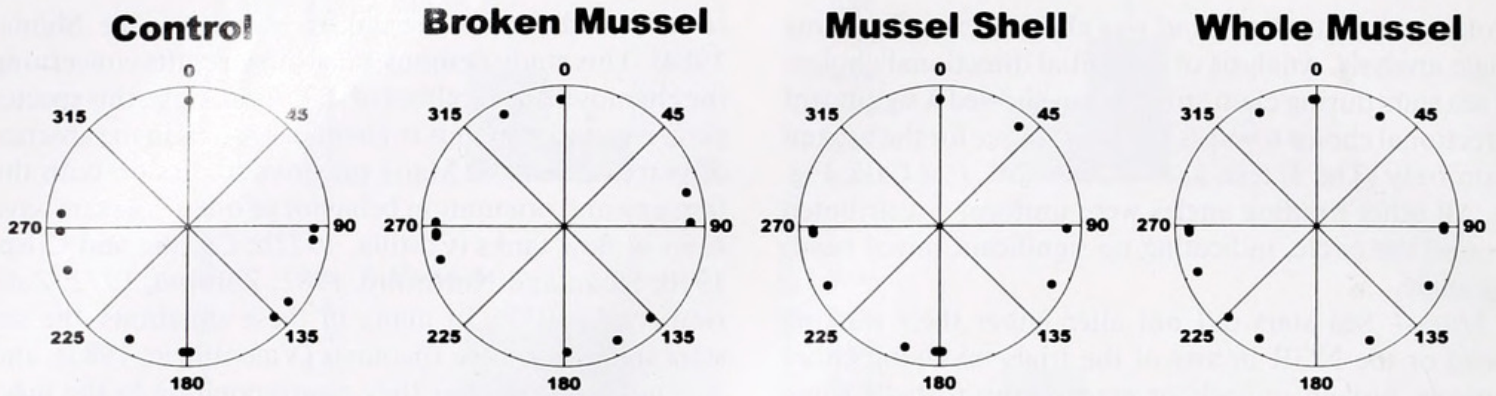


Figure 4. Initial directional choices for sea stars during different odor stimulations for mussel sources. Solid dots represent heading angle in relation to odor source for the first movement of the animal. There were no significant mean angles in any of the groups, indicating that the initial headings were uniformly distributed around the circle; $n = 14$ for all groups.

We found changes in the orientation paths to be a function of distance from the odor source. For all of our stimulus conditions except one, we found that the heading angle relative to the odor source decreased as an animal approached the odor source. In other words, as it approached the odor source, the animal began to walk in a straighter line towards the source. Since we did not find similar results with the control or shell studies, we conclude that the locomotory output of the animal is influenced by the chemical stimulus whether it is perceived spatially or temporally. In addition, walking speed and turning angles did not change as a function of distance. Although these results are consistent with either orientation mechanism, we feel that the behavioral patterns of our animals in the absence of macroscale flow are more compatible with a taxis-based orientation strategy than with a kinesis strategy (as defined by Dusenbery, 1992). This finding is similar to that of Rochette *et al.* (1994), who convincingly demonstrated that other species of sea stars were capable of showing directed responses, but that these directional choices were dependent upon their physiological state (starved vs. fed) and the ambient current flow. Their finding may be due to decisions based on dual sensory information (that is, from both the odor signal and ambient conditions of macroscale flow), whereas we provided mainly chemosensory cues.

Third, *A. forbesi* responded differently to the various stimulus sources by having distinct walking patterns for each of the stimulus conditions. During stimulation with squid flesh, the sea stars walked slower, in a straighter line, with a characteristic decrease in heading angle as they approached the odor source. The sea stars walked faster and had a more circuitous path only for the broken clam and showed only the characteristic changes in heading angles for the mussel stimulus. Different locomotory outputs may indicate either that these animals can perceive and identify different prey items or that the outputs are responses to concentration differences between stim-

ulus sources. Since we neither quantified the stimulus patterns nor analyzed the chemical composition under the different treatments, it is difficult to make any definite conclusions based on the differences in locomotion.

Many researchers have studied chemical orientation in marine animals. Animal models include fish (Kleerekoper, 1967; Kleerekoper *et al.*, 1969) and decapod crustaceans (Moore *et al.*, 1991; Reeder and Ache, 1980; Weissburg and Zimmer-Faust, 1993). These studies have shown that the spatial and temporal distribution of chemical signals plays an important part in the orientation ability of these animals. It has also been shown that animals can have different responses to different odors. Certainly, for sea stars, some odors trigger an attraction and other odors an avoidance (Castilla and Crisp, 1970; Sloan and Northway, 1982). Similar findings have been recorded for the mud snail (Atema and Burd, 1975). All of these results taken together show that marine organisms can have different behavioral responses for different chemical sources, but it has yet to be shown whether a single animal has distinct orientation strategies for different odors.

In summary, *A. forbesi* has chemosensory responses in the absence of macroscale flow and can locate the source of odors using only chemosensory information. It is still unclear whether these animals strictly use a chemotaxis or a kinesis strategy and whether they use both spatial and temporal sampling of concentrations to guide orientation to the odor source. In addition, the sea stars show different orientation paths for different odors. Further research is needed to determine whether these animals have different orientation strategies that are prey dependent.

Acknowledgments

The authors thank Dr. Steve Vessey for reading an earlier version of this manuscript and three anonymous re-

viewers for insightful comments. This research is supported by NSF grant OCE-9596270.

Literature Cited

- Atema, J. 1985.** Chemoreception in the sea: adaptation of chemoreceptors and behavior to aquatic stimulus conditions. *Soc. Exp. Biol. Symp.* **39**: 387–423.
- Atema, J., and G. D. Burd. 1975.** A field study of chemotactic responses of the marine mud snail *Nassarius obsoletus*. *J. Chem. Ecol.* **1**: 243–251.
- Bell, W. J. 1984.** Chemo-orientation in walking insects. Pp. 93–106 in *Chemical Ecology of Insects*, W. J. Bell and R. T. Cardé, eds. Sinauer Associates, Sunderland, MA.
- Bell, W. J., and R. T. Cardé. 1984.** *Chemical Ecology of Insects*. Sinauer Associates, Sunderland, MA.
- Castilla, J. C. 1972a.** Responses of *Asterias rubens* to bivalve prey in a Y-maze. *Mar. Biol.* **12**: 222–228.
- Castilla, J. C. 1972b.** Avoidance behavior of *Asterias rubens* to extracts of *Mytilus edulis*, solutions of bacteriological peptone, and selected amino acids. *Mar. Biol.* **15**: 236–245.
- Castilla, J. C., and D. J. Crisp. 1970.** Responses of *Asterias rubens* to olfactory stimuli. *J. Mar. Biol. Assoc. U.K.* **50**: 829–847.
- Christensen, A. M. 1957.** The feeding behavior of the seastar *Eva-sterias troschelii* Stimpson. *Limnol. Oceanogr.* **2**: 180–197.
- Dale, J. H. 1996.** Co-ordination of chemosensory orientation in the starfish, *Asterias forbesi*. *Chem Senses Abstr.* (in press).
- Dusenbery, D. B. 1992.** *Sensory Ecology: How Organisms Acquire and Respond to Information*. W.H. Freeman, New York.
- Feder H., and A. M. Christensen. 1966.** Aspects of asteroid biology. Pp. 87–127 in *Physiology of Echinodermata*, R. A. Boolootian, ed. Interscience, New York.
- Jangoux, M. 1982.** Food and feeding mechanisms: Asteroidea. Pp. 117–159 in *Echinoderm Nutrition*, M. Jangoux and J. M. Lawrence, eds. Balkema, Rotterdam.
- Johnsen, P. B., and J. H. Teeter. 1980.** Spatial gradient detection of chemical cues by catfish. *J. Comp. Physiol. A* **140**: 95–99.
- Kennedy, J. S. 1986.** Some current issues in orientation to odour sources. Pp. 11–25 in *Mechanisms in Insect Olfaction*, T. L. Payne, M. C. Birch, and C. E. J. Kennedy, eds. Clarendon Press, Oxford.
- Kleerekoper, H. 1967.** Some aspects of olfaction in fish, with special reference to orientation. *Am. Zool.* **7**: 385–295.
- Kleerekoper, H., A. M. Timms, G. F. Westlake, F. B. Davy, T. Malar, and V. M. Anderson. 1969.** Inertial guidance system in the orientation of the goldfish (*Carassius auratus*). *Nature* **223**: 501–502.
- Mafra-Neto, A., and R. T. Cardé. 1994.** Fine scale structure of pheromone plumes modulates upwind orientation of flying moths. *Nature* **369**: 142–144.
- McClintok, J. B., T. S. Klinger, and J. M. Lawrence. 1984.** Chemoreception in *Lucidia clathrata* (Echinodermata: Asteroidea): qualitative and quantitative aspects of chemotactic responses to low molecular weight compounds. *Mar. Biol.* **84**: 47–52.
- McClintok, J. B., and J. M. Lawrence. 1981.** An optimization study on the feeding behavior of *Lucidia clathrata* Say (Echinodermata: Asteroidea). *Mar. Behav. Physiol.* **10**: 167–181.
- Moore, P. A., and J. Atema. 1988.** A model of a temporal filter in chemoreception to extract directional information from a turbulent odor plume. *Biol. Bull.* **174**: 355–363.
- Moore, P. A., and J. Atema. 1991.** Spatial information in the three-dimensional fine structure of an aquatic odor plume. *Biol. Bull.* **181**: 408–418.
- Moore, P. A., N. Scholz, and J. Atema. 1991.** Chemical orientation of lobsters, *Homarus americanus*, in turbulent odor plumes. *J. Chem. Ecol.* **17**: 1293–1307.
- Moore, P. A., M. J. Weissburg, J. M. Parrish, R. K. Zimmer-Faust, and G. A. Gerhardt. 1994.** Spatial distribution of odors in simulated benthic boundary layer flows. *J. Chem. Ecol.* **20**: 255–279.
- Murlis, J., and C. D. Jones. 1981.** Fine-scale structure of odour plumes in relation to insect orientation to distant pheromone and other attractant sources. *Phys. Ent.* **6**: 71–86.
- Murlis, J., M. A. Willis, and R. T. Cardé. 1991.** Odour signals: patterns in space and time. Pp. 6–17 in *Proceedings of the Tenth International Symposium on Olfaction and Taste*, K. Døving, ed. Graphic Communication System, Oslo.
- Reeder, P. B., and B. W. Ache. 1980.** Chemotaxis in the Florida spiny lobster, *Panulirus argus*. *Anim. Behav.* **28**: 831–839.
- Rochette, R., J.-F. Hamel, and J. H. Himmelman. 1994.** Foraging strategy of the asteroid *Leptasterias polaris*: role of prey odors, current and feeding status. *Mar. Ecol. Prog. Ser.* **106**: 93–100.
- Shōne, H. 1984.** *Spatial Orientation*. Princeton University Press, Princeton, NJ.
- Sloan, N. A., and A. C. Campbell. 1982.** Perception of food. Pp. 3–23 *Echinoderm Nutrition*, M. Jangoux and J. M. Lawrence, eds. Balkema, Rotterdam.
- Sloan N. A., and S. M. Northway. 1982.** Chemoreception by the asteroid *Crossaster papposus* (L.). *J. Exp. Mar. Biol. Ecol.* **61**: 85–98.
- Valenticic, T. 1983.** Innate and learned responses to external stimuli in asteroids. Pp. 111–137 *Echinoderm Nutrition*, M. Jangoux and J. M. Lawrence, eds. Balkema, Rotterdam.
- Valenticic, T. 1985.** Behavioral study of chemoreception in the sea star *Marthasterias glacialis*: structure-activity relationships of lactic acid, amino acids, and acetylcholine. *J. Comp. Physiol. A* **157**: 537–545.
- Valenticic, T., and D. Ota. 1985.** Comparison of chemical senses in the sea star *Marthasterias glacialis* with chemical senses in some fishes. Pp. 563–569 in *Echinodermata: Proceedings of the Fifth International Echinoderm Conference*, B. F. Keegan and B. D. S. O'Connor, eds. Balkema, Rotterdam.
- Weissburg, M. J., and R. K. Zimmer-Faust. 1993.** Life and death in moving fluids: hydrodynamic effects on chemosensory-mediated predation. *Ecology* **74**: 1428–1443.
- Zafiriou, O. 1972.** Response of *Asterias vulgaris* to chemical stimuli. *Mar. Biol.* **17**: 100–107.
- Zafiriou, O., K. J. Whittle, and M. Blumer. 1972.** Response of *Asterias vulgaris* to bivalves and bivalve tissue extracts. *Mar. Biol.* **13**: 137–145.
- Zar, J. H. 1984.** *Biostatistical Analysis*, second edition. Prentice Hall, Englewood Cliffs, NJ.
- Zimmer-Faust, R. K., J. M. Stanfill, and S. B. Collard, III. 1988.** A fast, multichannel fluorometer for investigating aquatic chemoreception and odor trails. *Limnol. Oceanogr.* **33**: 1586–1595.



Moore, P A and Lepper, Dme. 1997. "Role of Chemical Signals in the Orientation Behavior of the Sea Star *Asterias forbesi*." *The Biological bulletin* 192, 410–417. <https://doi.org/10.2307/1542750>.

View This Item Online: <https://www.biodiversitylibrary.org/item/17361>

DOI: <https://doi.org/10.2307/1542750>

Permalink: <https://www.biodiversitylibrary.org/partpdf/32098>

Holding Institution

MBLWHOI Library

Sponsored by

MBLWHOI Library

Copyright & Reuse

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: University of Chicago

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.