Foraging strategy of the asteroid *Leptasterias polaris*: role of prey odors, current and feeding status

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ABSTRACT: We performed laboratory experiments to investigate the perception and localization of prey by the subtidal asteroid *Leptasterias polaris*. Motivation to eat greatly influences its responsiveness to current and waterborne odors from prey. Fed asteroids behave erratically, whereas asteroids starved for 2 mo exhibit predictable behaviors revealing the species' foraging strategy. In the absence of prey, starved asteroids search by moving cross-current which increases the probability of encountering odor plumes. In conditions of varying current velocities (differences of 0.5 to 1 cm s⁻¹), movement is cross-stream towards the stronger current and 2- to 3-fold faster in strong (ca 17 cm s⁻¹) than in weak (ca 0.7 cm s⁻¹) current. We hypothesize that strong currents are preferred because they increase the spatial definition of odor plumes which facilitates localizing prey. When starved *L. polaris* perceive prey, they move upstream towards the odor plume. Because this should reduce the predator's conspicuousness, it may increase its chances of capturing the prey.

KEY WORDS: Foraging strategy · Asteroid · *Leptasterias polaris* · Olfaction · Current · Starvation

INTRODUCTION

Asteroids are major predators in marine ecosystems, and many aspects of their feeding biology have been studied (see reviews by Feder & Christensen 1966, Sloan 1980a, Jangoux & Lawrence 1982). However, the means by which they detect and localize food resources in nature are poorly understood. Potential mechanisms are chance encounters with prey (e.g. Mauzey et al. 1968, Feder 1970, Menge 1972, Dayton 1973, Dayton et al. 1977) and foraging based on the use of olfactory cues (e.g. Valentincic 1973, Mootoza & Phillips 1979, McClintock & Lawrence 1981, McClintock et al. 1984). The ability of asteroids to detect prey from a distance may vary among species as Sloan & Campbell (1982) report positive evidence of distance chemodetection (olfaction) for 14 species, negative evidence for 5 species, and contradictory evidence for 4 species. For species with an ability to detect waterborne odors, the capacity only appears to be functional over short distances (Feder & Christensen 1966). An animal which detects a prey or food material from waterborne odors may localize this resource by moving upstream in response to the mechanical stimulation of the current (rheotaxis), by moving up the odor concentration gradient (chemotaxis) (Atema 1985), or by a combination of both mechanisms. In all cases, localization of the prey will be most effective if current flow is sustained in one direction. Consequently, subtidal asteroids are more likely to use olfaction to detect and localize prey than asteroids from the more turbulent (wave-washed) intertidal zone (Sloan 1980a). Although there are numerous studies which examine the effect of current on the feeding behavior of subtidal animals, most focus on scavengers and suspension feeders, and few examine predators. The movement of scavenging amphipods, crabs, gastropods and fishes towards bait is strongly affected by current direction, velocity, and directional stability (e.g. Miller 1978, Thurston 1979, Lampitt et al. 1983, Wilson & Smith 1984, Himmelman 1988, McQuinn et al. 1988, Lapointe 1991), and the orientation of food-capturing organs of suspension
Leptasterias polaris is a major predator of subtidal communities in the St. Lawrence Estuary (Himmelman 1991), eastern Canada. They were divided into 2 groups of 15 individuals. Each group was kept in 4 plastic baskets (45 × 25 cm) suspended in a 16 000 l holding tank which was maintained under constant conditions (5°C, 30 to 32‰ salinity and 12 h light : 12 h dark). For 2 mo, the asteroids in one tank were fed blue mussels Mytilus edulis ad libitum. Those in the other tank were kept without food to increase their motivation to eat. Neither group showed signs of deteriorating condition after 2 mo. Individuals deprived of food displayed consistent and reproducible behaviors during the experiments, which suggested that they had not been adversely affected by the fasting (Sloan 1980a). Previous observations indicate that asteroids can tolerate long (>3 mo) periods of starvation (Feder 1970, Valenticr 1973, McClintock & Lawrence 1984, author's unpubl. data on L. polaris). This is particularly likely for L. polaris because it is a cold-water species and because females routinely do not feed for >4 mo while brooding their young (Boivin et al. 1986).

We observed the behavior of Leptasterias polaris in a plexiglass aquarium (125 × 125 × 14 cm) which was uniformly lit by 2 fluorescent lights. The bottom was marked off in a grid (5 cm squares; Fig. 1) to facilitate monitoring of the movements of the asteroids. A current was generated across the aquarium using 2 pumps which fed water into both ends of a 135 cm straight current crossing the aquarium (pumps on) to straight current crossing the aquarium (pumps off). Currents were generated across the aquarium using 2 pumps which fed water into both ends of a 135 cm straight current crossing the aquarium (pumps on) to straight current crossing the aquarium (pumps off).

**MATERIALS AND METHODS**

**Experimental design.** Thirty Leptasterias polaris, measuring 15 to 30 cm in diameter, were collected by SCUBA divers in November and December 1991 from Anse aux Basques, near Les Escoumins (48° 32’ N, 69° 41’ W), on the north coast of the St. Lawrence Estuary, eastern Canada. They were divided into 2 groups of 15 individuals. Each group was kept in 4 plastic baskets (45 × 25 cm) suspended in a 16 000 l holding tank which was maintained under constant conditions (5°C, 30 to 32‰ salinity and 12 h light : 12 h dark). For 2 mo, the asteroids in one tank were fed blue mussels Mytilus edulis ad libitum. Those in the other tank were kept without food to increase their motivation to eat. Neither group showed signs of deteriorating condition after 2 mo. Individuals deprived of food displayed consistent and reproducible behaviors during the experiments, which suggested that they had not been adversely affected by the fasting (Sloan 1980a). Previous observations indicate that asteroids can tolerate long (>3 mo) periods of starvation (Feder 1970, Valenticr 1973, McClintock & Lawrence 1984, author's unpubl. data on L. polaris). This is particularly likely for L. polaris because it is a cold-water species and because females routinely do not feed for >4 mo while brooding their young (Boivin et al. 1986).

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In tests with prey odor, we placed a 1 mm mesh box containing a common whelk (*Buccinum undatum* L., 6 to 7 cm in shell length), one of the asteroid's preferred prey (Dutil 1988, Himmler & Dutil 1991), 45 cm upstream from the asteroid. Dye tests showed that the odor plume did not flow straight across the tank but rather veered to the left side both when the pumps were on (strong current) and when they were off (weak current) (Fig. 1).

The rate of locomotion and direction of movements were first quantified in the absence of whelk odor by subjecting each asteroid to a strong current (ca 17 cm s⁻¹, pumps on), a weak current (ca 0.7 cm s⁻¹, pumps off), and then a strong current again (ca 17 cm s⁻¹, pumps on). No differences were detected in the rate of locomotion in the first and second current regimes and then in the second and third current regimes were compared using Wilcoxon matched-pairs, signed-ranks tests (Siegel 1956).

**RESULTS**

**Response of starved asteroids**

Starved *Leptasterias polaris* always reached the line indicating 20 cm from the starting point within 20 min.
regardless of current speed and presence or absence of whelk odor. When a food source was upstream, asteroids displayed arm curling and terminal tube-foot responses, as previously reported for *Crossaster papposus* (Sloan 1980b) and *Marthasterias glacialis* (Valentinić 1973). Furthermore, their movements were oriented (*p* < 0.05), not directly towards the whelk but towards its odors as indicated by the analysis of current direction using methylene blue (Figs. 1 & 2). In the absence of whelk odor, the movement of starved asteroids was still oriented (*p* < 0.001). As indicated earlier, current strength differed between the 2 sides of the experimental aquarium. Starved individuals consistently chose the side with the stronger current (the right side in strong current and the left side in weak current) and they moved cross-current (Fig. 2). Their orientation was not precisely perpendicular to the current but rather slightly downstream. Thus, the angle was > 90° for 35 of the 45 starved *L. polaris* tested in the 3 current conditions. Further, the 95% confidence interval about the average orientation angle included the 90° orientation only when the current was weak (118 ± 22°, 100 ± 22° and 119 ± 10°, for the first strong, weak and the second strong current regimes, respectively).

In both the presence and the absence of whelk odor, the locomotory rate of starved *Leptasterias polaris* varied markedly with current regime (*p* < 0.001; Fig. 3). It decreased sharply between the first strong current regime and the subsequent period of weak current (*p* < 0.001), and then increased 2- to 3-fold as strong current was reintroduced (*p* < 0.001).

**Response of fed asteroids**

The behavior of fed *Leptasterias polaris* differed strikingly from that of starved asteroids. Firstly, 18% of fed *L. polaris* did not reach the 20 cm radius circle within 45 min and several remained nearly stationary. Secondly, in all but 1 of the 6 tests fed *L. polaris* exhibited no specific orientation (Fig. 2). They were significantly oriented (*p* < 0.05) only during the first strong current regime in the presence of whelk odor. When returned to the center of the aquarium at the beginning of each current regime, the asteroids were randomly oriented and may have continued moving in the direction in which we placed the previously ‘leading arm’. This possibility was explored using 5 fed individuals. Each was allowed to move about in the aquarium in a strong current and on 3 occasions, when the asteroid was moving in a straight line, the orientation of its leading arm was changed by 90° to 180°. The 5 asteroids consistently changed direction according to the new orientation of the ‘leading arm’. In contrast, when 5 starved individuals were tested in the same manner, they consistently paused, during which time their terminal podia moved actively, and then resumed movement in the original direction relative to current flow. Thus, fed asteroids appeared to have a weak interest in feeding and their lack of orientation during the second and third current regimes was probably a result of the manipulations.
DISCUSSION

We show that the response of Leptasterias polaris to prey odors and current is strong and predictable for starved individuals but weak and variable for fed individuals. One explanation for the weak response of fed asteroids to whelk odor could be their exclusive consumption of mussels prior to the experiments (ingestive conditioning). However, the random movements of fed L. polaris when prey odors were absent suggest a general disinterest in feeding, likely the result of having been supplied with an excess of food for 2 mo prior to the experiments. This is supported by the observation that if their orientation is changed, fed individuals continue moving in the direction of the previously 'leading arm', whereas starved individuals reorient themselves relative to current flow. The way in which animals react to external stimuli is highly variable and often related to physiological condition (Schöne 1984, p. 57–58). An increased responsiveness to prey odors with increasing hunger may generally be true for asteroids since it has been reported for a number of other species (e.g. Brauer & Jordan 1970, Valentić 1973, 1975, Ribi & Jost 1978, McClintock & Lawrence 1984). Failure to take this factor into account might partly explain the controversy concerning olfactory capacities of asteroids.

Foraging strategy of Leptasterias polaris

Leptasterias polaris which are motivated to eat detect their prey from waterborne odors and their rate of movement, in both the presence and the absence of prey odors, is highly dependent upon current conditions. This supports the hypothesis that olfaction is used in detecting and localizing prey. The long terminal tube feet of asteroids are responsible for the detection of odors (Sloan 1980b) and the fact that those on several arms are active at the same time possibly provides the spatial and temporal resolution required for detecting and defining the structure of odor plumes. This type of sampling of the water may thus be analogous to ‘sniffing’ by fishes, ‘antennular flicking’ by lobsters, and ‘swinging of the siphon’ by gastropods (Atema 1985).

Animals which rely on odors to detect food may either wait or actively search for these odors. In the latter case, food intake must be increased to compensate for the additional energy invested into locomotion (Norberg 1977). Hughes (1980) points out that searching for prey will become a less advantageous strategy as their density decreases, because of the increased locomotory costs. Active search is probably advantageous for Leptasterias polaris as its prey are relatively

Locomotory rates of fed Leptasterias polaris differed significantly among the 3 current regimes only when prey odor was present (Fig. 3). Further, rates did not vary in a consistent manner with current velocity, rather, they tended to increase progressively through the 3 successive current regimes, in both the presence and the absence of whelk odor.

Olfactory stimulation of moving asteroids

In the tests where drops of water containing whelk odor were added upstream of starved Leptasterias polaris which were moving cross-current, all asteroids modified their trajectory and moved upstream. In contrast, all fed asteroids tested in the same manner did not modify their movements.

Fig. 3. Leptasterias polaris. Mean locomotory rates (cm min⁻¹) of 15 starved and 15 fed asteroids during the first strong current regime, the weak current regime and the second strong current regime, in both the presence and the absence of prey odor. Vertical bars represent standard errors. Locomotory rates in successive current regimes were compared using Friedman 2-way ANOVAs. When significant differences were detected (p < 0.05), locomotory rates in successive current regimes were compared by Wilcoxon matched-pairs signed-ranks tests. ns: not significant; *p < 0.05; **p < 0.001
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by a baited whelk trap is greater in weak (10 cm s⁻¹) than in strong (26 cm s⁻¹) current. A recent study by Lapointe & Sainte-Marie (1992) suggests that both strong and weak currents may enhance the localization of bait by scavenging whelks. They observed that the rate at which whelks arrived at bait is positively correlated to current velocities prevailing 0.5 to 3 h prior to their arrival but tends to be negatively corre-

lated for longer time lags. Since short time lags presumably reflect interactions which occur in the vicinity of the bait and longer time lags those occurring further away, it appears that strong currents may aid nearby whelks in localizing bait, whereas weak currents may increase the number of whelks detecting bait from further away. This does not imply that whelks are attracted from greater distances when currents are weak, only that the area from which they are attracted is greater because weak currents increase the width of odor plumes.

Whether weak or strong currents increase the foraging efficiency of marine animals probably depends upon factors such as the availability of food materials and the consumer's chemosensory and locomotory abilities. Scavengers exploit rare and often distant sources of food and this explains why scavenging fishes, amphipods and gastropods often possess well-developed olfactory and locomotory abilities. These permit them to detect such food materials, weak currents, which spread odors over a wide area, may be advantageous. On the other hand, asteroids generally exploit prey which are abundant and can be obtained over a distance of a few meters. Further, their chemosensory and locomotory abilities

abundant and also because most of them are not mobile. Three aspects of its behavior in relation to current conditions may increase foraging success: (1) cross-stream movements which increase the chance of detecting prey odors, (2) a preference for strong currents which enhances localizing a prey once detected and (3) approaching prey from downstream which renders the asteroid less conspicuous to its prey.

Cross-current movement

In both strong and weak current, hungry *Leptasterias polaris* search for prey by moving cross-stream. At spatial and temporal scales pertinent to this predator, the dispersion of odor molecules depends mainly on the dynamics of the carrier medium and substrate topography and is little affected by diffusive processes at the molecular level (Okubo 1980, Atema 1988). Patchy odor plumes, which form downstream from foodstuffs (Lam et al. 1983, Atema 1988, Denny 1988), will most likely be encountered if animals move cross-

stream. The slightly downstream orientation indicated by our data, if not an artifact caused by nonuniform current flow throughout the aquarium, might be an adaptation to minimizing turbulence around the tube feet. This would facilitate determining from where prey odors originate.

Our study is the first documentation of a cross-

stream search path for an asteroid. However, cross-

stream movements have been observed for the whelk *Buccinum undatum* (Sainte-Marie 1991). An analogous situation is the movement of insects flying to locate mate, host or prey odors. Cross-wind movement is considered to be optimal (Bell & Cardé 1984) but has not been clearly demonstrated by field studies. This may be due to the lack of studies simultaneously evaluating wind direction and the path of the insect (Murlis et al. 1992). Nevertheless, flying insects have been shown to fly across the wind when they momentarily lose odor plumes (David 1986).

Preference for increased current velocity

The search strategy of *Leptasterias polaris* appears to be finely tuned to current velocity. Thus, *L. polaris* detects even small differences in current velocity (differences as little as 0.5 to 1 cm s⁻¹), moves cross-stream in the direction of the stronger current and increases it's locomotory rate by 2- to 3-fold in strong current. Turbulent diffusion and thermal agitation cause mole-

ules to wander about the main stream direction of the current and the average distance of departure from this axis increases moving downstream (Denny 1988). This can be visualized as a general widening of the odor plume in the downstream direction. An increase in current velocity decreases the width of the odor plume by limiting the drift of molecules from the main stream direction (Okubo 1980, Denny 1988). Consequently, stronger currents will generally increase the spatial definition of odor gradients and this enhances the capacity of animals to locate food materials perceived from exuded chemicals (Kleerekopper et al. 1975).

Although identifying the origin of an odor plume may be easier in strong current, the ability of animals to encounter prey or food materials using olfaction is probably not always enhanced by strong currents. Since decreased current velocity increases the width and thus the area of the odor plume, it also increases the number of individuals which are in a position to detect it. This is supported by field studies of McQuinn et al. (1988) which show that the effective area fished by a baited whelk trap is greater in weak (10 cm s⁻¹) than in strong (26 cm s⁻¹) current. A recent study by Lapointe & Sainte-Marie (1992) suggests that both strong and weak currents may enhance the localization of bait by scavenging whelks. They observed that the rate at which whelks arrived at bait is positively correlated to current velocities prevailing 0.5 to 3 h prior to their arrival but tends to be negatively corre-

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are weak. Whereas the area covered by an odor plume may have little importance in determining prey intake for asteroids, strong current may be critical, because it enhances the ability to localize prey.

Approaching prey from downstream

We studied how *Leptasterias polaris* detects and locates epibenthic prey such as the whelk *Buccinum undatum*. Similar mechanisms may be employed in the search and capture of clams and other endobenthic prey. Adult *L. polaris* frequently feed on large bivalves which they extract from the sediments using their podia, in a manner similar to that described by Smith (1961) for *Pisaster brevispinus*. As suggested by Smith, it is likely that infralittoral prey are detected prior to digging to prevent useless expenditures of energy. However, whelks and endobenthic bivalves also use waterborne odors to detect their predators and they possess defensive mechanisms to decrease the probability of being captured: whelks flee from *L. polaris* and bivalves bury themselves so that they are less readily found and captured (Legault & Himmelman 1993). Irrespective of the type of prey being consumed, *L. polaris* likely increases its feeding efficiency by approaching prey from a downstream direction, since this should make its presence less apparent and could permit taking the prey by surprise, particularly under conditions of regular and rapid current flow.

Our laboratory studies indicate that the detection of waterborne prey odors is a key element in the foraging strategy of *Leptasterias polaris*. Further investigations, and especially field studies, are required to elucidate how prey are detected and localized in natural habitats where current conditions are highly variable, where prey are abundant and frequently patchily distributed, and where the energy requirements of *L. polaris* vary among individuals and over time.

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