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Chemosensory responses and foraging behavior of the seastar *Pycnopodia helianthoides*

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Abstract Chemical cues released by damaged or dead organisms can affect how and where benthic organisms feed. These cues may cause predators to act as opportunistic scavengers in lieu of their normal predatory role. A scavenger, as defined in this study, is an organism that consumes damaged and/or dead organisms. In-situ experiments were performed to determine how the seastar *Pycnopodia helianthoides* (Brandt) reacts in the presence of chemical cues from one of its prey species, the butter clam *Saxidomus giganteus* (Deshayes), using both intact and damaged individuals. The results of these experiments suggest that *P. helianthoides* use their chemosensory abilities to locate damaged/dead prey. The role of current in propagating chemical cues was paramount in this foraging activity. *P. helianthoides* chose damaged prey over live prey even when live prey was encountered en route to the damaged individual. This study suggests that chemical cues emitted from damaged or dead individuals may cause significant changes in foraging tactics of key predators, thus altering food-web dynamics.

Introduction

Seastars are among the most important predators in tropical, temperate and polar marine systems (e.g., Mauzey et al. 1968; Dayton et al. 1974; Paine 1974). Several seastar species are thought to be a controlling force in benthic communities due to their large appetite and ability to find food quickly. Aggregations of seastars can cause the decimation of food sources (Paul and Feder 1975; Shivji et al. 1983; Lourey et al. 2000), or the production of patchwork mosaics (Duggins 1983; Ninio et al. 2000). Predation by seastars has been shown to be the leading cause of juvenile (Ross et al. 2002) and adult (Flagg and Malouf 1983) bivalve loss, and in some instances, seastars can act as keystone species, having direct control over the equilibrium of the community (Dayton et al. 1974; Paine 1974).

Along the Pacific coast, *Pycnopodia helianthoides* is considered to be one of the most active and voracious subtidal invertebrate predators on echinoids (Mauzey et al. 1968; Breen 1979; Pearse and Hines 1987), gastropods (Herrlinger 1983; Shivji et al. 1983), and bivalves (Paul and Feder 1975; Lambert 1981). Many authors suggest *P. helianthoides* is a generalist predator that sweeps across the seafloor ingesting anything within its path (Mauzey et al. 1968; Wobber 1975; Moitsozoa and Phillips 1979; Sloan 1980; Shivji et al. 1983). Despite reports of *P. helianthoides* feeding on many different types of carrion, such as opalescent squid (*Loligo opalescens*; Wobber 1975), seabirds (Alcidae; Shivji et al. 1983), spiny dog-fish (*Squalus acanthias*; Shivji et al. 1983), herring (*Clupea pallasii*; Shivji et al. 1983), other seastars (Herrlinger 1983; Shivji et al. 1983), Pacific octopus (*Enteroctopus dofleini*; Shivji et al. 1983), Pacific hake (*Merluccius productus*; Herrlinger 1983), and sea otters (*Enhydra lutris*; personal observation), no quantitative published studies have established *P. helianthoides* as a scavenger.

Both predators and scavengers depend on the perception of food to orient their movements towards the

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food source (Moitzoa and Phillips 1979; Himmelman 1988; Lapointe and Sainte-Marie 1992). For scavengers, chemoreception is considered to be one of the most important means by which to locate food. Because radially symmetrical invertebrates receive chemical cues from all directions equally well, seastars should have an ideal shape for chemosensory perception. Some seastars also possess a tactile discriminatory ability, but are more motivated by chemical cues than by physical shapes (Sloan and Campbell 1982). The outer tips of seastar tube feet function as chemical, mechanical, and light sensors (MacGinitie and MacGinitie 1949; Valentincic 1983).

The specific role that *P. helianthoides* chemosensory abilities play in foraging is a subject of debate. Herrlinger (1983) stated that *P. helianthoides* feeds mainly by coming into contact with prey organisms, and that sensing prey at a distance plays no role in its foraging. Two other studies suggest that *P. helianthoides* probably does use distance chemoreception as the primary means of locating food (Greer 1961; Moitzoa and Phillips 1979), but its actual role in foraging is not well understood.

Our objective was to determine if *P. helianthoides* utilizes chemoreception to locate prey and how this affects its foraging. Three hypotheses were posed to determine the immediate responses of *P. helianthoides* to prey cues: (H₁) *P. helianthoides* uses chemoreception to pursue damaged/dead prey; (H₂) only when *P. helianthoides* is down-current of damaged/dead prey does it react to it; (H₃) *P. helianthoides* will forgo live prey to reach damaged/dead prey.

Materials and methods

Study sites were located in Kachemak Bay, southcentral Alaska at water depths of 5–20 m. The chemosensory ability and foraging behavior of *P. helianthoides* (Brandt, 1835) were studied using three types of choice experiments: Y-maze, cue propagation, and corridor. Each experiment was designed to observe a key component of the feeding behavior to test the hypotheses previously stated. All of the choice experiments were performed, in situ, in Jakolof Bay, where currents are strong due to a high tidal amplitude (9–10 m, Carroll 1994). Jakolof Bay has a relatively flat topographic gradient (Carroll 1994), with a substrate composed predominantly of medium-grain sand to cobble/rock (personal observations). *P. helianthoides* is found in dense concentrations (approximately seven seastars 25 m²) throughout the area, and sites for our experiments were selected based on similarities in substrate and current regime. To ensure adequate current flow, experiments were performed at least 1.5 h before or after slack tides. The current direction and speed were estimated by ejecting 1 ml lacteal fluid from the same height above the substrate as introduced prey cues (just above the bottom for the Y-maze and corridor, and 0.5 m

above the bottom for the cue propagation), and measuring the time needed to travel 1 m. Before each trial, current direction was confirmed. The prey item used in these experiments was the butter clam, *Saxidomus giganteus*, a locally abundant bivalve often consumed, sometimes preferentially, by *P. helianthoides* (Mauzey et al. 1968). No preferential relationships between prey size and seastar size were observed. Though the clams are found both intertidally and subtidally in Jakolof Bay, they were collected intertidally for logistical ease. After collection, clams were kept in a continuous-flow seawater tank at Kasitsna Bay Laboratory until they were used in experiments, but in no case were individuals held for more than 3 days. In the following experiments, a damaged clam refers to a living clam that was broken open with a lead dive weight to insure tissue damage. Clam-shell controls were empty clam shells collected in the local area that were also broken to control for prey shape and other possible factors associated with breaking a clam shell. In pre-study experiments, clams extended siphons and began processing water in less than 3 min. Divers always checked that this was occurring when using live clams. At the conclusion of each experiment, *P. helianthoides* were marked by clipping a small portion of one of the two arms located closest to the madreporite. *P. helianthoides* found with clipped, damaged, or missing arms were not used in any experiment to prevent pseudoreplication.

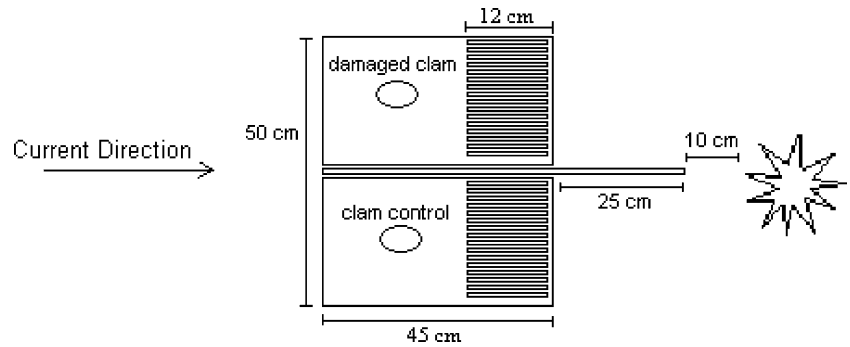
Y-maze

To determine if *P. helianthoides* uses chemoreception to pursue damaged/dead prey cues, a Y-maze (similar to Menge 1971; Moitzoa and Phillips 1979) was used to offer seastars a choice between experimental and control treatments. This Y-maze was portable so that it could be used in the field. The Y-maze measured 45 cm long×50 cm wide×30 cm high and had a Plexiglas divider separating the two sides of the maze that extended 25 cm beyond the end of the maze. To insure laminar flow, several thousand 12-cm plastic straws were arranged within the down-current end of the Y-maze (Fig. 1). Y-maze experiments were performed between July and September 2001 when water temperatures were 7–10°C.

Forty *P. helianthoides* were tested for each of 3 clam manipulations ($n=40$ /manipulation): (1) a damaged clam (experimental) versus a clam shell (control), (2) a live clam (experimental) versus a clam shell (control), and (3) Y-maze controls (no clams or clam shells on either side of the Y-maze). Experimental and control treatments were placed in randomly determined sides of the Y-maze. In the second manipulation, clams in the experimental treatment were live clams that were placed in the Y-maze 3 min prior to experimentation so that they would extend their siphons and begin to process water (3 min based upon pre-study experiments).

The Y-maze was placed up-current of a *P. helianthoides* with approximately 10 cm separating the end of

Fig. 1 *Pycnopodia helianthoides*. Y-maze apparatus used to test the chemosensory ability of *P. helianthoides* ($n=40$ /manipulation). Y-maze was placed 10 cm up-current of the seastar being tested. Each replicate began with the introduction of experimental and control prey cues



the divider and the closest arm of the seastar (Fig. 1). This was done to insure the seastar being tested would receive flow from both sides of the Y-maze. Individual seastars were timed from the introduction of experimental and control treatments. Arm-curling and tube-foot extension were used as indicators of chemosensory detection (Valenticic 1983). The time to move was noted as the time for a seastar to begin to move from its original position (Valenticic 1983). Timing stopped when a seastar reached either side of the Y-maze or 15 min had elapsed. The results (experiment, control, or neither chosen) from each of the three treatments were analyzed with a one-way ANOVA followed by Tukey's post-hoc test (SAS statistical software, Delwiche and Slaughter 1996).

Cue propagation

To determine if only *P. helianthoides* located down-current of an introduced damaged/dead prey cue would respond, divers observed the activity of seastars in 25 m² plots (5 m×5 m) with centrally located prey cues (Fig. 2). Six replicates were conducted between August and September 2001. For each replicate, an experimental and a control plot were spaced 10 m apart. Each plot (experimental and control) was divided into two areas: down-current (45° to each side opposite the determined current direction) and up-current (the remaining 270° of each plot, Fig. 2).

Prey cues for experimental plots were six damaged *Saxidomus giganteus* placed in two perforated plastic boxes. The plastic boxes were hung inside the crab pots approximately 0.5 m above the substrate. Crab pots were necessary to: (1) insure that scavengers would not completely cover the prey cues, and (2) allow the prey signal to broadcast more effectively. The number of *Saxidomus giganteus* used was based on the mean density of clams found in 1 m², the area covered by the crab pot. Controls consisted of six damaged *Saxidomus giganteus* shells in similar boxes. Experimental and control plots were determined randomly. To determine the movement of *P. helianthoides* in response to experimental and control treatments, the position of each seastar was marked initially and then at 5-, 10-, 20-, 30-, and 60-min intervals with colored flagging tape tied to

metal stakes. After 60 min, the distances and azimuths from each flag to the center of each plot were measured.

Because each plot (experimental and control) and replicate varied in *P. helianthoides* density, activities (moving and reaching the center of the plot) were reported as percentage of the total seastars in each plot. A two-way ANOVA (location and treatment), using a Tukey post-hoc (SAS software), was performed to compare the mean percentage of seastars that moved to the center of the plot, and the mean percent of seastars that reached the center of the plot.

Corridor

To determine if *P. helianthoides* would bypass live prey to reach damaged/dead prey, a corridor with closed sides and open top was constructed (1 m long×0.8 m wide×0.5 m high) to direct down-current *P. helianthoides* through an area where a live clam was located down-current of a damaged clam (Fig. 3). Corridor experiments were conducted from June to September 2002 when temperatures ranged from 7°C to 12°C. The corridor was oriented parallel to the current flow and placed up-current of the seastar being tested. Fifteen *P. helianthoides* were tested for each of 4 clam manipulations ($n=15$ /manipulation): (1) a damaged *Saxidomus giganteus*

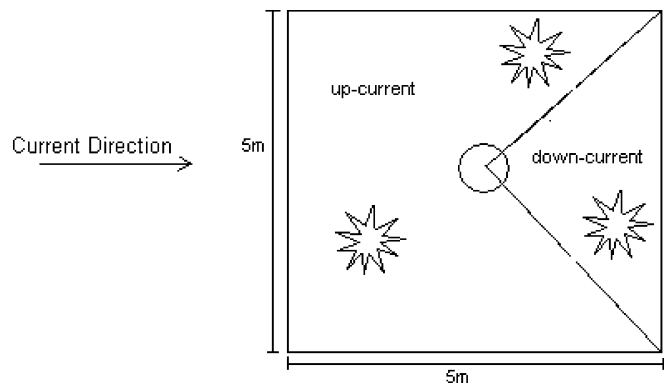


Fig. 2 *Pycnopodia helianthoides*. Cue propagation set-up used to test the role of predominant currents in propagating prey cues ($n=6$ experimental and control pairs). After the introduction of experimental and control prey cues, the position of seastars within each of the 25 m² plots was marked at 5-, 10-, 20-, 30-, and 60-min intervals

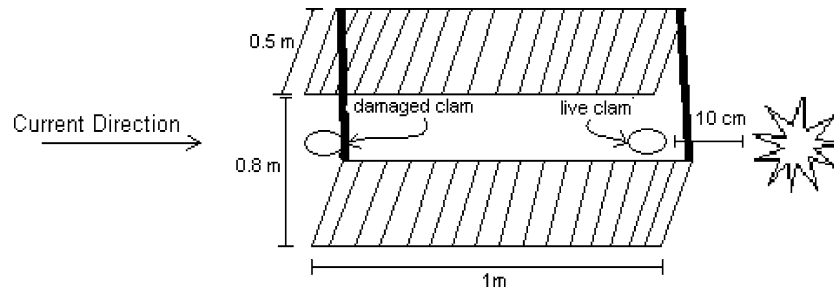


Fig. 3 *Pycnopodia helianthoides*. Corridor apparatus used to test if *P. helianthoides* will forgo live prey to reach damaged prey ($n=15$ /manipulation). Corridor was placed 10 cm up-current of the seastar being tested. After live clams were buried in the sediment (siphon side up, 10 cm from the seastar) and 3 min passed (time for live clams to begin processing water and extrusion of the siphon), damaged clams were introduced 1 m up-current of the live clam

teus up-current of a live undamaged *Saxidomus giganteus*, (2) a damaged *Saxidomus giganteus* up-current of a live *Saxidomus giganteus* when *P. helianthoides* were found in excavations, (3) only a damaged *Saxidomus giganteus*, (4) only a live *Saxidomus giganteus*. When live clams were used, they were positioned 10 cm up-current of the *P. helianthoides* being tested, buried siphon-side up so the top of the clam was even with the surface of the substrate, and were allowed 3 min to extrude their siphons and begin processing water before the introduction of the damaged clam. Damaged clams were placed 1 m up-current of the live clams. Experiments were concluded and time recorded when *P. helianthoides* either reached the damaged clam or 15 min elapsed. A one-way ANOVA followed by a Tukey post-hoc was performed to test for significant differences between the results of the manipulations (SAS software, Delwiche and Slaughter 1996).

Results

General

In the experiments described above, *P. helianthoides* densities ranged from 0.5 m^{-2} to 0 m^{-2} with an average of $0.022 \pm 0.005 \text{ m}^{-2}$ ($\pm \text{SE}$). The average size of *P. helianthoides* encountered (from arm tip to arm tip) was $52 \pm 1 \text{ cm}$ ($\pm \text{SE}$) ($n=594$). *Saxidomus giganteus* average weight was $0.13 \pm 0.006 \text{ kg}$ ($\pm \text{SE}$) and average length was $13.3 \pm 0.6 \text{ cm}$ ($\pm \text{SE}$) ($n=176$). The mean current speed observed in Jakolof Bay was $0.04 \pm 0.001 \text{ m s}^{-1}$ at 0.3–0.5 m above the substrate.

Y-maze

P. helianthoides showed a significantly greater response to damaged clams than to live clams, shell controls and Y-maze controls in the Y-maze experiments (Table 1, ANOVA, $F=72.54$, $P<0.0001$, $n=40$). Responses to live clams and clam controls and Y-maze controls were not significantly different from each other (ANOVA,

$F=1.30$, $P=0.26$, $n=40$). *P. helianthoides* detected, moved to and reached the damaged clams faster than the reaction of *P. helianthoides* to live clams, clam controls, or Y-maze controls (Table 2).

Cue propagation

P. helianthoides located in the experimental down-current areas moved to (Table 3, ANOVA, $F=18.12$, $P=0.0004$, $n=6$) and reached (Table 3, ANOVA, $F=15.94$, $P=0.0007$, $n=6$) the center of the plot significantly more than *P. helianthoides* located in the experimental up-current, control down-current, and control up-current areas. *P. helianthoides* located in experimental up-current, control down-current, and control up-current areas did not differ significantly from each other in seastars moving to the center of the plot (ANOVA, $F=0.05$, $P=0.953$, $n=6$) or reaching it (ANOVA, $F<0.0001$, $P=0.9999$, $n=6$). For the six replicates, the mean number of *P. helianthoides* observed in experimental and control plots was $6.8 \pm 0.4 \text{ SE}$ ($n=12$ plots).

Of the *P. helianthoides* that reached the center of the plot ($n=10$ seastars), the mean distance traveled was $1.8 \pm 0.2 \text{ m}$ ($\pm \text{SE}$), with seastars moving 1.2–2.5 m. The mean rate for seastars that reached the prey cue was $11.9 \pm 2.2 \text{ m h}^{-1}$ ($\pm \text{SE}$), with a range of 3.8–27.6 m h^{-1} . One seastar entered the plot 10 min after timing began and traveled 2.23 m to the prey cue, so it may have come from a greater distance than measured.

Corridor

Similar to the Y-maze experiments, *P. helianthoides* showed a significantly greater response to damaged

Table 1 *Pycnopodia helianthoides*. Chemosensory responses to different clam manipulations in Y-maze experiment ($n=40$ seastars/manipulation). In Y-maze controls, 3% of *P. helianthoides* moved to the right side of the Y-maze, 5% moved to the left side, and 92% did not move to either side ($n=40$ seastars)

Manipulation	Branch of Y-maze selected			
	Damaged clam	Live clam	Clam control	Neither
Damaged clams vs clam control	83%	n/a	2%	15%
Live clam vs clam control	n/a	5%	5%	90%

Table 2 *Pycnopodia helianthoides*. The means, ranges and the number of *P. helianthoides* (n) for the time to detect, time to move, and time to reach each of the experimental treatments in the Y-maze experiment (for the Y-maze controls, time to reach was calculated for either side of the Y-maze)

Treatment	Time to detect $\mu\text{s} \pm \text{SE}$ (range, n)	Time to move $\mu\text{s} \pm \text{SE}$ (range, n)	Time to reach $\mu\text{s} \pm \text{SE}$ (range, n)
Damaged <i>S. giganteus</i>	54 \pm 8 (4–160, 34)	158 \pm 30 (26–838, 33)	283 \pm 35 (72–865, 32)
Live <i>S. giganteus</i>	276 \pm 45 (25–605, 16)	304 \pm 56 (20–662, 14)	533 \pm 96 (250–658, 4)
Y-maze controls	210 \pm 42 (30–424, 10)	282 \pm 31 (144–470, 14)	500 \pm 109 (283–613, 3)

Saxidomus giganteus than to live *Saxidomus giganteus* in the corridor experiments (Table 4). Each of the three manipulations where damaged *Saxidomus giganteus* were offered to *P. helianthoides* resulted in significantly more seastars initiating a foraging response than in treatments without damaged *Saxidomus giganteus* (ANOVA, $F=62.52$, $P<0.0001$, $n=15$). The three manipulations that included the use of damaged *Saxidomus giganteus* were not significantly different from one another (ANOVA, $F=0.09$, $P=0.92$, $n=15$).

Discussion

When damaged/dead bivalves are available, *P. helianthoides* quickly finds and consumes them. When this type of prey is not available, *P. helianthoides* may act as a predator. Clearly it is easier for *P. helianthoides* to feed extra-orally on damaged or dying prey than on live prey that must be excavated, pulled apart, or swallowed whole. The results of all three experiments suggest that *P. helianthoides* is a facultative scavenger that depends on chemoreceptive abilities to locate damaged/dead prey. Moreover, these experiments suggest that the cue transmission mechanism is also important. Finally, there appears to be a fundamental preference for damaged/dead clams over live clams, even when a live clam is encountered on the way to damaged individuals. Since *P. helianthoides* has the ability to chemically sense damaged/dead organisms, we may need to rethink the role that this seastar plays in its benthic environment.

In each of the experiments discussed above, *P. helianthoides* used chemoreception to actively pursue damaged prey cues. Other scavenging echinoderms are attracted to chemicals released by damaged tissues and will aggregate around injured invertebrates (Warner

1979; Kaiser and Spencer 1996; Veale et al. 2000). Damaged or dead organisms, including bivalves, fish, polychaetes, and echinoderms, may be the result of natural processes, such as incomplete consumption or death by natural causes or anthropogenic processes, such as commercial fishing. Sea otters often excavate prey, leaving behind damaged or partially eaten organisms (personal observation). Trawls and dredges that disturb the sediment damage or destroy many benthic organisms (Groenewold and Fonds 2000; McConnaughey et al. 2000; Mensink et al. 2000). A scavenger that is able to survive the passage of a beam trawl, or move into a disturbed area quickly, clearly has a competitive advantage because of the increased amount of food locally available (Kaiser and Spencer 1996). As with trawling, the practice of dumping fish waste selects for organisms that scavenge (Dayton et al. 1995).

The chemical cues released when clams were damaged initiated a foraging response from *P. helianthoides*, but the natural effluent from live clams did not. This may be due to the type or intensity of the two types of cues. Like *P. helianthoides*, many other scavengers react more strongly to damaged/dead prey than to live prey (Zimmer-Faust and Case 1982; Miller 1990; Zhou and Shirley 1997). The chemical cues released by the damaged clam tissues may provide a continuous source that seastars can follow, while the natural effluent released by live clams may be intermittently released due to the nature of respiratory pumping, or may be too dilute. The costs associated with locating suitable prey may be high, so it may be energetically more efficient for the seastar to search for continuous cues like damaged or decaying organisms, or a contact cue such as a clam bed.

In areas where current flow and tidal exchange are enough to transport prey cues, scavengers that can detect the cue at some distance and move quickly are more

Table 3 *Pycnopodia helianthoides*. Number of seastars that moved and reached the center of the plot for six replicates of cue propagation experiment

Treatment	Total number of seastars	Seastars moving to center of plot	Seastars reaching center of plot
Experimental down-current	14	12	10
Experimental up-current	30	2	0
Control down-current	10	1	0
Control up-current	27	1	0

Table 4 *Pycnopodia helianthoides*. Chemoreceptive response of *P. helianthoides* to four clam manipulations in corridor experiment ($n=15$ seastars/manipulation)

Manipulation	Result
Damaged clam up-current of live clam	13/15 reached damaged clam
Damaged clam up-current of live clam in an excavation	13/15 reached damaged clam
Damaged clam only	14/15 reached damaged clam
Live clam only	15/15 no reaction in 15 min

likely to reach the cue source. Many mobile predators with well-developed chemosensory abilities use water-borne signals to locate prey (Himmelman 1988). Although it was not possible to control damage levels of each clam or the amount of potential prey cue released, this study supports the idea that currents are needed to transport cues to a downstream scavenger (Himmelman 1988; Veale et al. 2000).

This study also suggests that *P. helianthoides* will bypass live prey to reach damaged prey. Optimal foraging theory predicts that organisms should seek prey that have a low search/handling time, low assimilation time and high energy content (Beddingfield and McClintock 1993; Hines et al. 1997). In all three experiments, *P. helianthoides* detected, moved to, and acquired damaged prey, while live prey was left alone. In the corridor experiment, each *P. helianthoides* passed over a live clam to reach an up-current damaged clam. In almost every case, the *P. helianthoides* being tested bypassed the live clam for the damaged clam. Even when *P. helianthoides* were found in excavations for live clams, they quickly abandoned their quarry when they received chemical cues from a damaged clam. When a *P. helianthoides* reacts to the presence of damaged/dead prey, it may decrease the search/handling time and the assimilation time, and increase the amount of energy gained per unit of effort.

The overall objective of this study was to determine if *P. helianthoides* utilizes chemoreception to locate prey and to what extent these abilities affect *P. helianthoides'* foraging techniques. The three experiments suggest that *P. helianthoides* uses chemoreception to quickly pursue damaged/dead prey, only individuals located down-current of damaged/dead prey react to it and, in most cases, *P. helianthoides* forgoes live prey to reach damaged/dead prey. Clearly, *P. helianthoides* has several foraging strategies to best accommodate a changing and complex ecosystem.

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