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Feeding and Distribution Study of the Sunflower Sea Star *Pycnopodia helianthoides* (Brandt, 1835)[1]

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ABSTRACT: Observations are reported on the feeding biology of *Pycnopodia helianthoides* (Brandt) in Barkley Sound, British Columbia, in areas of differing wave exposure. Three hundred asteroids were examined; 220 were feeding on prey representing 11 taxa, with heaviest predation on gastropods, bivalves, and crustaceans. *P. helianthoides* found on soft substrates were larger than those inhabiting hard substrates. Juvenile sea stars (< 5 cm diameter) were found primarily at protected sites often on kelp substrate. The observed size distributions of *P. helianthoides* may be the result of the nature of food resources available in different habitats. Significant positive correlations were obtained between sea star size and prey size except in the case of the gastropod *Tegula pulligo*. The possible importance of sea star predation on this snail is discussed.

THE FEEDING BIOLOGY OF ASTEROIDS is of considerable interest because these predators may play an important role in structuring marine communities (Paine 1974, 1980). In turn, they have the potential to influence production of stocks of commercially important invertebrates.

The sunflower sea star *Pycnopodia helianthoides* (Brandt, 1835) is the largest, heaviest, and most active of asteroids inhabiting the west coast of North America (Feder 1980). Although its range includes the coast from Alaska to southern California, it is especially common in the subtidal waters of British Columbia with densities of up to 20/m^2 in some areas (unpubl. obs.). *P. helianthoides* is known to be a generalist feeder, varying its diet according to locality and available prey (rev. by Sloan 1980, Herrlinger 1981, Lambert 1981). Feder (1980) has recently summarized the information on *P. helianthoides* indicating that sea urchins—*Strongylocentrotus purpuratus*, *S. franciscanus*, and *S. droebachiensis*—and bivalves such as *Pecten* spp. are preferred prey. Paul and Feder (1975) reported that *P. helianthoides* collected from the intertidal in Alaska were feeding most on the bivalve *Mytilus edulis* with much of the rest of the diet consisting of the bivalves *Protothaca staminea* and *Saxidomus giganteus* and various small unidentified gastropods. Collection by trawl or in crab pots of *P. helianthoides* in the subtidal indicated that the bivalve *Nuculana pernula* occurred most frequently in stomachs examined. In spite of these and other studies on *P. helianthoides*, Feder (1980) points out that no single aspect of this sea star's biology is well known.

Apart from Breen's report (1979) on the laboratory feeding of this asteroid, no information exists on its diet in British Columbia waters. Yet it is very abundant and may be responsible for limiting populations of bivalves like *Saxidomus giganteus* (pers. comm., N. Bourne and P. Breen, Fisheries and Oceans, Canada). In view of its potential to influence harvestable resources like the sea urchin and various bivalves, we investigated the diet and distribution of *Pycnopodia helianthoides* in

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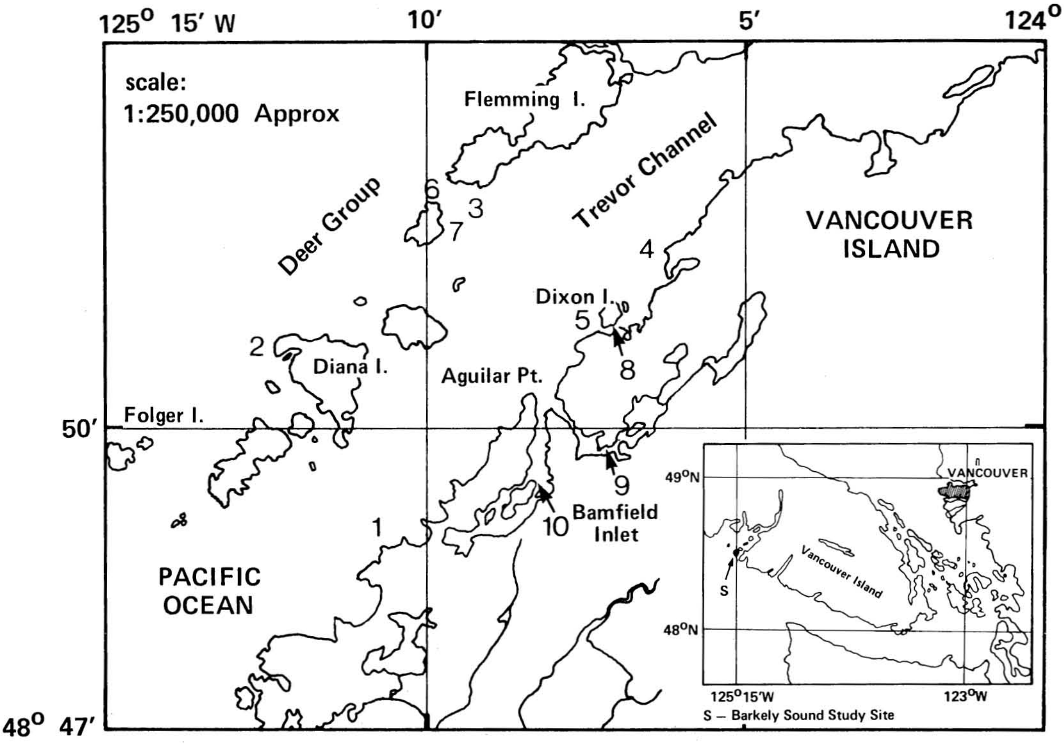

FIGURE 1. Location of collection sites in Barkley Sound, British Columbia: (1) Execution Rock; (2) Kirby Point; (3) Ross Islets; (4) Ellis Islet; (5) Dixon Island; (6) North Sanford Island; (7) East Sanford Island; (8) Dixon Channel; (9) Grappler Inlet; (10) Burlo Island.

TABLE 1

SAMPLE SIZE AND PERCENTAGE OF *Pycnopodia helianthoides* FEEDING IN SITES OF DIFFERENT EXPOSURE IN BARKLEY SOUND, BRITISH COLUMBIA, 1977

		NUMBER OF SEA STARS COLLECTED AND PERCENT FEEDING (in brackets)†					
EXPOSURE RATING	COLLECTION SITES*	MARCH	APRIL	MAY	JUNE	JULY	AUGUST
Exposed	Execution Rock, Kirby Point	—	—	27(69–100)	14(86)	14(79)	26(65)
Intermediate	Ross Islets, Ellis Islet, Dixon Island, N. and E. Sanford Islands	65(68–100)	—	15(75–100)	18(83)	22(82)	9(78)
Protected	Dixon Channel, Grappler Inlet, Burlo Island	—	70(43)	10(70)	6(67)	3(67)	7(29)
TOTAL SAMPLES		65	70	52	38	39	42

* Not all sites were visited each month.
† Dash indicates no sample taken.

Barkley Sound, British Columbia. Population structure and predator–prey size relationships were also examined.

MATERIALS AND METHODS

Observations were made using SCUBA in the Barkley Sound region, west coast of Vancouver Island, British Columbia, from March to August 1977 (Figure 1). The *Pycnopodia helianthoides* collection sites were characterized by heterogeneous substrates and different degrees of wave exposure. Transects 30 or 60 m long, and 2 to 4 m wide depending on water visibility conditions, were established starting from zero datum and running perpendicular to the shoreline. Collection sites were categorized as exposed, intermediate, or protected depending on the degree of wave exposure (Figure 1, Table 1). Recorded for each asteroid were depth, substrate type, body diameter, and evidence of active feeding. Food items were removed from *P. helianthoides* on board a research vessel for subsequent identification and measurement in the laboratory. In cases where the feeding asteroid was very small or the digestion process advanced, the stomach contents were recorded as "unidentified organic material." Sea star diameter was measured to the nearest centimeter from tip to tip of opposite rays across the widest part of the animal.

Predator–prey size relationships were explored using Pearson product–moment correlation coefficients. The sizes of *Pycnopodia helianthoides* on soft and hard substrates were compared using a t test for unequal sample sizes (Sokal and Rohlf 1969). To compare the mean total diameter of *P. helianthoides* in exposed and intermediate sites, a t test was applied after a log transformation to correct for skewness in the histograms.

At two intermediate sites (Dixon Island and Ross Islets) airlift samples were taken in $0.5\ m^2$ quadrats to provide a measure of relative abundance of prey in the habitat. Time constraints prevented extensive use of this method, but some results are presented for comparison.

RESULTS

Diet

Of 306 *Pycnopodia helianthoides* collected, 72 percent were feeding, although the percentage ranged from 28.6 to 100 between sites (Table 1). The mean number of food items per stomach in feeding *P. helianthoides* ranged from 1.3 to 8.7 items, excluding an individual which contained 110 *Diplodonta orbella*, 1 *Gari californica*, 1 *Candita* sp., and 1 *Humiliaria kennerlyi*.

Gastropod and bivalve prey were found to be taken with the greatest frequency, followed by crustaceans (Table 2). The sea urchin *Strongylocentrotus purpuratus* was found in seven stomachs and represented only 4.6 percent of prey items taken. The bivalve *Saxidomus giganteus* occurred in several sea stars at all exposure sites but formed only a small percentage of the diet (maximum 1.9 percent of items at the protected sites). Other taxa occurring in some stomachs at sites of three different exposures included the gastropods *Margarites* spp., *Nassarius mendicus*, and *Bittium* spp., and the crustaceans *Cancer productus* and *Pugettia* spp. Incidental observations include *P. helianthoides* feeding on carcasses of seabirds (Alcidae), spiny dogfish (*Squalus acanthias*), and Pacific herring (*Clupea harengus pallasi*), and in one case each on the asteroid *Pisaster ochraceus* and *Octopus dofleini*. Numerous juvenile asteroids were found in the protected sites apparently feeding mostly on detritus and microflora and fauna.

Distribution and Population Structure

No correlations were found between asteroid size and depth. A significantly larger size of asteroid inhabited soft substrates in sites of high and intermediate exposure (Table 3). No significant size difference was evident for populations inhabiting soft and hard substrates in protected sites ($P < 0.05$). However, if asteroids less than 5 cm in diameter are excluded from the calculations, the total diameter ($\pm$ s.d.) on soft substrates increases from 26.9 ± 20 to 39.9 ± 12.4 cm in diame-

TABLE 2

PARTIAL LIST OF PREY ITEMS CONSUMED BY *Pycnopodia helianthoides* IN AREAS OF DIFFERENT WAVE EXPOSURE

PREY SPECIES*	PERCENT OF PREY IN DIET (no. of that prey/no. of stomachs in which it occurred)		
	EXPOSED	INTERMEDIATE	PROTECTED
Gastropoda			
Over 19 genera including:			
Tegula pulligo	20(35/10)	22(82/29)	
Amphissa sp.	8.6(15/11)	3.8(14/11)	
Mitrella sp.	4.6(8/4)	0.8(3/1)	13.5(7/1)
Calliostoma ligatum	6.9(12/7)	0.5(2/2)	
Alvinia spp.			7.7(4/2)
Bivalvia			
Over 10 genera including:			
Diplodonta orbella†		10.2(38/8)	
Protothaca staminea	14.9(26/11)	3.8(14/7)	1.9(1/1)
Mytilus edulis		7.5(28/14)	
Macoma spp.		0.8(3/3)	9.6(5/3)
Crustacea			
Over 5 genera including:			
Balanus spp.	0.6(1/1)	1.3(5/5)	5.8(3/1)
Unidentified crabs	10.3(18/15)	6.2(23/23)	9.6(5/5)
Unidentified amphipods	2.3(4/3)		9.6(5/3)

*Other taxa occurring less frequently in stomachs included two species of polyplacophora, the sea urchins *Strongylocentrotus purpuratus* and *S. franciscanus*, polychaetes, ectoprocts, three types of vertebrates, and two plant species.
† Not included is one individual containing 110 *Diplodonta orbella*.

TABLE 3

MEAN TOTAL DIAMETER OF *Pycnopodia helianthoides* FOUND ON SOFT AND HARD SUBSTRATES IN AREAS OF DIFFERENT WAVE EXPOSURE

WAVE EXPOSURE RATING	MEAN SIZE IN CM ± S.D. (SAMPLE SIZE) ON		
	SOFT SUBSTRATES (sand/mud/shell/gravel)	HARD SUBSTRATES (rock/boulder)	*t* TEST
Exposed sites	35 ± 6.1 ($n = 12$)	27.5 ± 9.4 ($n = 69$)	−2.776*
Intermediate sites	43.5 ± 10.9 ($n = 30$)	33.0 ± 13.4 ($n = 99$)	−3.94*
Protected sites†	26.9 ± 20.8 ($n = 26$)	22.9 ± 16.7 ($n = 8$)	−0.4917 (not significant)

* Significant at $P < 0.01$.
† Not included are 62 individuals found on seaweeds (*Agarum* sp.).

ter ($n = 17$). This is significantly larger than starfish occupying hard substrates (22.9 ± 16.7 cm : $P < 0.01$).

The size–frequency histogram for *Pycnopodia helianthoides* in protected sites (Figure 2) is skewed strongly toward the juvenile sizes (< 5 cm) with the other sizes being more uniformly represented. Very few juveniles were found in more exposed sites. The mean total diameter of *P. helianthoides* is significantly larger ($t = 3.433$, $P < 0.001$) in intermediate areas than in exposed sites (Figure 2).

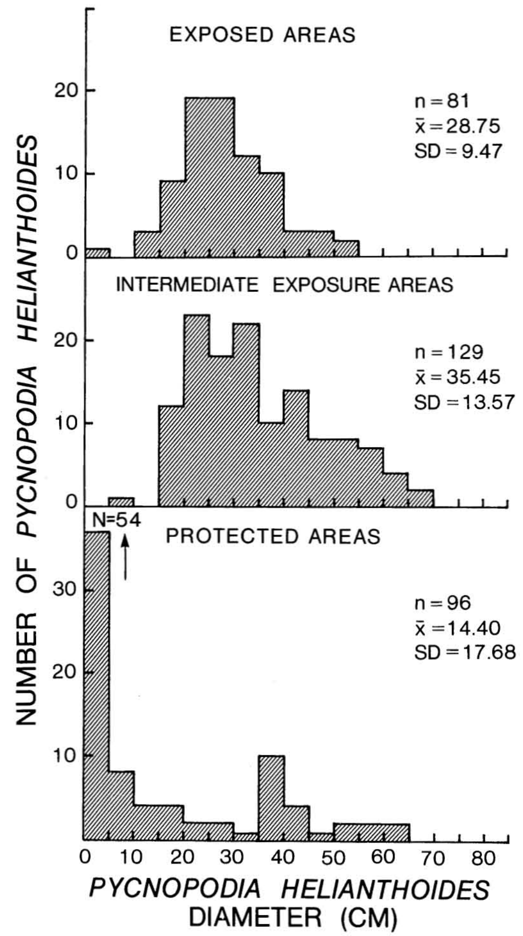

FIGURE 2. Size–frequency histograms for *Pycnopodia helianthoides* from areas of different wave exposure.

Predator–Prey Size Relationships

Significant positive correlations ($P < 0.05$) between sizes of *Pycnopodia helianthoides* and prey size were obtained in all cases examined, except for the herbivorous gastropod *Tegula pulligo* (Table 4).

Abundance of Prey in the Habitat

At Ross Islets (intermediate), the bivalve *Homapoloma* sp. formed 31.1 percent of the total organisms identified in six 0.5-m^2 quadrats, averaging 50.8 individuals per quadrat (s.d. = 60.7). This was followed by *Cardita* sp. (12.8 percent), *Tegula pulligo* (5.2 percent), and *Bittium eschrichtii* (4.5 percent). In each case, large variance was associated with the samples. In the same site, stomach analyses indicated that *Pycnopodia helianthoides* fed most on the bivalve *Diplodonta orbella*, followed by *T. pulligo*, *Homapoloma* sp., *Gari californica*, and *B. eschrichtii.*

Homapoloma sp. was also the most abundant item found in seven 0.5-m^2 quadrats at another intermediate site, Dixon Island. The bivalve made up 53.5 percent of the total organisms, averaging 74 individuals per quadrat (s.d. = 62.1). Other organisms occurring in the samples included *Tegula pulligo* (8.9 percent), *Cardita* sp. (6.8 percent), *Margarites* sp. (6.7 percent), and *Protothaca staminea* (4.7 percent). The samples were again characterized by large variance suggesting patchiness in prey distribution. Stomachs of *P. helianthoides* taken from all intermediate sites together indicated that the gastropod *T. pulligo* was fed on most, followed by the bivalve *Diplodonta orbella* (Table 2).

DISCUSSION

Our observations of *Pycnopodia helianthoides* substantiate that it is a generalist feeder and opportunistic predator (Mauzey, Birkeland, and Dayton 1968, Wobber 1975, Sloan 1980). Future studies may reveal an even more diverse diet. The inherent problems associated with identification of stomach contents (due to variable digestion rates) and the fact that *P. helianthoides* is a carrion feeder (Wobber 1975, pers. obs.) probably make our list of prey organisms a conservative one.

Observations from the Washington coast suggest that *Pycnopodia helianthoides* is an important predator of echinoderms (Mauzey, Birkeland, and Dayton 1968, Dayton 1975). Our observations in Barkley Sound do not support this particular role of *P. helianthoides*, as urchins formed only a very small part of its diet even though two species, *Strongylocentrotus purpuratus* and *S. franciscanus*, were abundant in areas of high and intermediate exposure. Breen (1979) came to the same conclusion about *P. helianthoides* control of *S. droebachiensis* populations.

TABLE 4

CORRELATION COEFFICIENTS RELATING *Pycnopodia helianthoides* SIZE TO PREY SIZE

Tegula pulligo	*Protothaca staminea*	ALL BIVALVES TOGETHER	ALL PREY TOGETHER (exposed sites)	ALL PREY TOGETHER (intermediate sites)	ALL PREY TOGETHER (protected sites)
−0.02204 n.s.*	0.4473†	0.2842†	0.5606†	0.3759†	0.5059‡
n = 103	n = 40	n = 101	n = 63	n = 80	n = 16

* n.s. = not significant at $P < 0.05$.
† Significant at $0.01 > P > 0.001$.
‡ Significant at $0.05 > P > 0.01$.

Tegula pulligo, *Protothaca staminea*, and *Mytilus edulis* were preyed upon with relatively high frequency where they were available. Whether this reflects numerical abundance, ease of capture, or high caloric/nutritional value of the prey organisms is not clear. Air lift samples in intermediate habitats indicated that *T. pulligo* was abundant but not as numerous as *Homapoloma* sp. *Diplodonta orbella*, which, along with *T. pulligo*, formed a significant part of the diet, did not show up in great abundance in the quadrat samples. The large number of *D. orbella* in one sea star, when considered in relation to their infrequent occurrence in habitat samples, may indicate that the sea star will feed heavily in clumps of this bivalve when such clumps are found. At this time we would have to say that our habitat sampling was inadequate. We are unable to provide good information on relative abundance and dispersion patterns of the various potential prey in the habitat.

Observations by Sharp (1976) in Barkley Sound indicate that *Tegula pulligo* is the numerically dominant invertebrate herbivore in the kelp beds characteristically found in our exposed and intermediate study sites. Sharp has suggested that *T. pulligo* may be responsible for the greatest continuous grazing pressure on *Macrocystis integrifolia* beds. Grazing, and incidental loss of plant tissue due to erosion caused by grazing and water movement, causes a loss of 55 ± 38.5 percent of lamina production. Since *Pycnopodia helianthoides* feeds extensively on *T. pulligo* where it is present, it is conceivable that the asteroid controls the herbivore's population. If so, *P. helianthoides* may have an enormous influence on the production of detrital material originating from the kelp bed.

Mauzey, Birkeland, and Dayton (1968) and Breen (1979) report with reference to bivalve prey that *Saxidomus giganteus* were taken preferentially over *Protothaca staminea*. Our data indicate the reverse trend, emphasizing the asteroid's dietary breadth. The evolution of a generalist feeding strategy confers some advantages to a predator in that unpredictable spatial and temporal availability of prey organisms will have little effect (Menge 1972, Birkeland 1974). Also, *Pycnopodia helianthoides* is probably not subject to the cyclical population oscillations that a monospecific predator might show if the prey resource were overexploited. The generalist feeding strategy may contribute to the abundance and ubiquity of *P. helianthoides*.

The size distribution of *Pycnopodia helianthoides* may be influenced by the nature of food resources available. The asteroid inhabits varied substrata and is able to exploit different prey occupying these habitats. On soft substrates *P. helianthoides* often feeds on burrowing bivalves for which it digs (Mauzey, Birkeland, and Dayton 1968, Breen 1979). *Pisaster brevispinus* also digs for bivalves, and only the larger asteroids are able to obtain large-sized, deeper burrowing prey (Van Veldhuizen and Phillips 1978). This is due to the physical limitations of smaller asteroids, which cannot dig deep enough. Similar limitations probably occur for small individuals of *P. helianthoides*.

We observed *Pycnopodia helianthoides* digging over the same pit for several days before finally obtaining the buried prey. The act of digging and length of time involved in pursuit of such prey may represent a major energetic expense to the asteroid. Assuming the importance of efficient exploitation of prey and minimization of the cost-benefit ratio to the predator (Emlen 1966, Pyke, Pullian, and Charnov 1977 for review), the capture of many infaunal prey is probably beyond the physical and energetic capabilities of small sea stars. Efficient exploitation is only possible for larger sized asteroids, restricting the distribution of small *P. helianthoides* to substrates where epifaunal prey organisms are abundantly available. Our results indicating a larger mean size of *P. helianthoides* inhabiting soft substrates compared with hard (Table 3) lend support to this hypothesis. The possibility remains that juvenile *P. helianthoides* dig for recently metamorphosed bivalves, but this was not indicated in our observations.

The lack of significant size difference between asteroids on soft and hard substrata in protected areas is noteworthy. Of the 96 animals collected, 54 were less than 5 cm in diameter. Of these, 9 were on mud bottom, reducing the mean starfish size computed for soft substrates. The remaining juveniles occurred on kelp. We suggest that the paradoxical presence of small starfish on soft substrate and the abundance generally of juvenile *Pycnopodia helianthoides* in protected areas can be attributed to the nature of food resources available. These areas are subject to little wave action and current, as is evident by the high degree of siltation on the kelp blades. Such conditions may favor the settlement of benthic diatoms, the retention of settled detrital material, and the corresponding proliferation of microbial and other detritivore meiofauna. Many of the juveniles were found with their stomachs extruded on the substrate, and analysis of their stomach contents revealed mainly organic material and some small amphipods (Table 2). These juveniles are most likely feeding on the above food resources, being too small to efficiently capture larger motile prey. Several cases of juveniles of other asteroid species feeding on detrital and micro-organism films have been documented in the literature (Sloan 1980). This leads to some interesting speculations on the recruitment potential of different habitats. Very few juvenile *P. helianthoides* were found in more exposed habitats, suggesting that the protected sites may function as a nursery for newly metamorphosed individuals. Birkeland (1974) has suggested that availability of appropriate food resources may be very important for the survival of newly metamorphosed asteroids. After they grow to a certain size, juveniles can migrate to new areas and feed on larger prey size classes or different prey altogether. The absence of juvenile *P. helianthoides* in more exposed areas may reflect a higher mortality rate for postmetamorphosed individuals caused mainly by a lack of appropriate food resources. The size partitioning of prey resources by individuals of different size classes has the added advantage of reducing intraspecific competition (Sloan 1980).

Predator–Prey Size Relationships

Our attempt at correlating size of *Pycnopodia helianthoides* with prey size indicates that larger asteroids consume larger prey (Table 4). The absence of significant correlation between asteroid size and *Tegula pulligo* size, however, suggests that larger *P. helianthoides* also eat small individuals as reported by Paul and Feder (1975). Predators may eat a food type with greater frequency if that food is relatively abundant, even though richer alternative food resources are present. The observed predation on a wide range of sizes of *T. pulligo* by *P. helianthoides* may be a response to high prey densities.

It is not clear from our data whether any prey items enjoy a size refuge from *Pycnopodia helianthoides* predation, such as *Mytilus californianus* does from predation by *Pisaster ochraceus* (Paine 1976). Such a size refuge may exist for certain clam species that grow large and can burrow deeply. Since *P. helianthoides* can digest prey extraorally, it may not be limited to sizes of prey that can be ingested. This suggests the epifaunal prey organisms will only enjoy a size refuge if they possess more effective escape/defense responses at certain size ranges (Mauzey, Birkeland, and Dayton, 1968, Menge 1972, Markowitz 1980). A case in point is *P. helianthoides* predation of *Parastichopus californicus*. The asteroid elicits a strong escape response in this holothurian (Margolin 1976) and readily feeds on juveniles in aquaria (L. Cameron, pers. comm.). No *P. californicus* were found in the stomachs examined here, which suggests that the adult holothurians may possess very effective escape responses.

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