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Defense mechanism and feeding behavior of Pteraster tesselatus Ives (Echinodermata, Asteroidea)

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DEFENSE MECHANISM AND FEEDING BEHAVIOR OF *PTERASTER TESSELATUS* IVES (ECHINODERMATA, ASTEROIDEA)

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INTRODUCTION

Pteraster tesselatus was first described by Ives (1888). It occurs on many types of substrata and has a geographic distribution winding from the Bering Sea south along the North American coast to Washington (Fisher, 1911). Bathymetrically it ranges from 15 to 540 m (Djakonov, 1951).

Rodenhouse & Guberlet (1946) described the morphology of *P. tesselatus* in great detail. Like other sea stars in the family Pterasteridae, *P. tesselatus* has a supradorsal membrane, supported over the true body wall by ossicles topped with paxilla (Fig. 1). The nidamental cavity formed beneath the membrane contains the dermal branchiae. Fresh sea water is drawn into the cavity by inflation of the disk through numerous small spiracula located in the supradorsal membrane (Fig. 2). The water is then forced out a centrally located osculum by contraction of muscles located in the body wall (Fig. 2). As these muscles relax overlapping plates located under the body wall force the disk to re-expand, forcing new water into the cavity.

Unlike other *Pteraster* species which brood their young (Djakonov, 1951; Martin, 1974; Brattstrom, 1976), *P. tesselatus* produces pelagic, lecithotrophic larvae which metamorphose into young sea stars in about 30 days (Chia, 1966).

In addition to reproductive activity the behavior of this sea star, as with most organisms, is centered around the procurement of food and escape from predators (Laverack, 1974; Mackie & Grant, 1974).

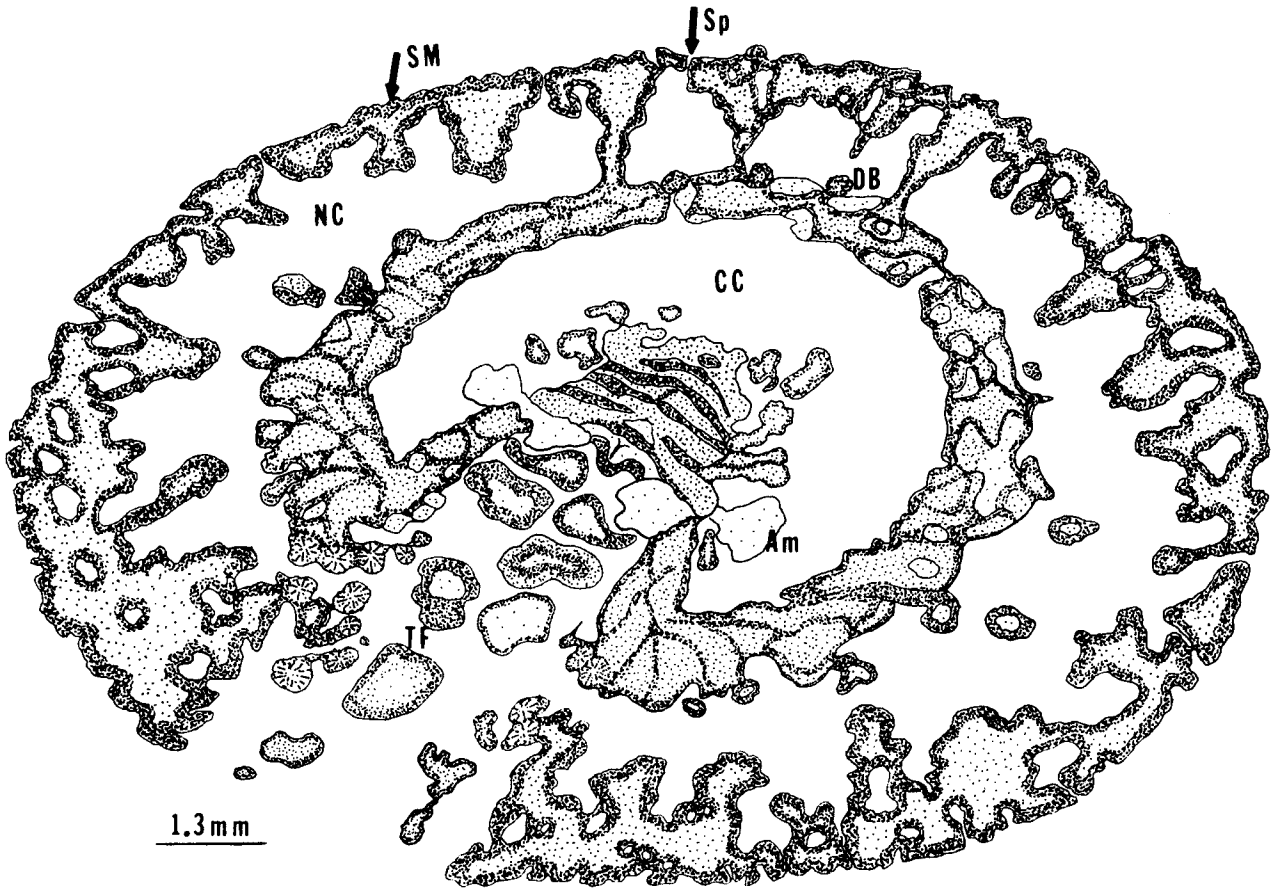


Fig. 1. *Pteraster tesselatus* ray cross section, illustrating the unique nidamental cavity and supradorsal membrane which are characteristic of the family Pterasteridae. Am, ampulla; CC, coelomic cavity; DB, dermal branchia; NC, nidamental cavity; Sp, spiraculum; SM, supradorsal membrane; TF, tube foot.

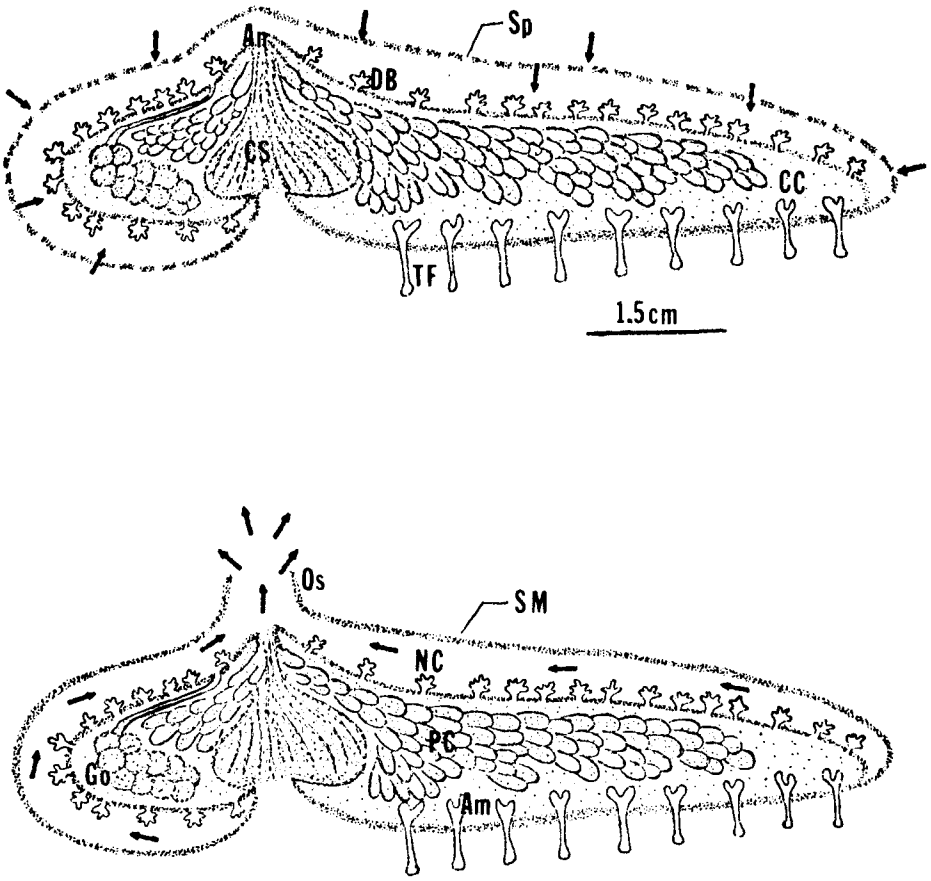


Fig. 2. Sections through the central disk and a ray of *Pteraster tesselatus* illustrating water circulation through the nidamental cavity, according to Rodenhouse & Guberlet (1946). An, anus; CS, cardiac stomach; Go, gonad; PC, pyloric cecum; Os, osculum.

Most asteroids use distance chemoreception to detect their prey. Romanes (1883) demonstrated that *Asterias rubens* has some type of olfactory perception, because it could be led around a sea water tank by pulling a piece of crab meat, tied to a thread, 5 cm in front of the leading ray. Some investigators repeated Romanes first experiments and had similar success (Preyer, 1886-1887; Galtsoff & Loosanoff, 1939). Other researchers have shown that sea stars can readily detect prey upstream in a current of water (Smith, 1940; Hancock, 1955; Fenchel, 1965; Feder & Christensen, 1966; Christensen, 1970).

In one of the most recent investigations, Castilla & Crisp (1970), using a Y-maze similar to the one used in this research, tested the chemoreceptive abilities of *Asterias rubens*. They were unable to confirm the findings of Milligan (1915), which suggested that *A. rubens* could locate dead prey, but did find that these sea stars were able to sense odors of living mussels and barnacles a few meters away. Carthy (1958) and Araki (1965) have shown that sea stars are attracted to the proteins given off by prey.

It is likely that *P. tesselatus* has similar chemoreceptive abilities; thus, one of the two major objectives of this research was to test this sea star's ability to detect prey and determine the prey which it normally feeds upon.

The second major objective of my research was to observe the mucous gland cells of the cushion star *P. tesselatus* histologically, as well as histochemically, to determine their positions and analyse their contents. Experiments were also conducted to test this star's

ability to avoid predation by the secretion of copious amounts of mucus.

Less research has been completed on the defense mechanisms employed by sea stars to avoid predation, than on their ability to detect food. The defense mechanism employed by *P. tesselatus* is thought to be its copious secretions of mucus (Rodenhouse & Guberlet, 1946), which it secretes when disturbed, as do other *Pteraster* species (Brattstrom, 1976; Nybakken, 1976).

Though many echinoderms secrete mucus by means of specialized gland cells in their integument (Hayashi, 1935; Smith, 1937; Hyman, 1955; Ward, 1965), only a few use it for defense (Fontaine, 1964) rather than for feeding (Nichols, 1960; Smith, 1962).

MATERIALS AND METHODS

Histology and Histochemistry

This aspect of the research was carried out at Brigham Young University. Nine *P. tesselatus* were flown in from Friday Harbor Laboratories, Friday Harbor, Washington, after being collected by use of SCUBA around Turn Island (Fig. 3). The sea stars were kept in large aerated aquaria containing artificial sea water at a constant temperature of 13°C.

Specimens were narcotized in a magnesium chloride solution (Pantin, 1948) to minimize the loss of mucus from the gland cells when the rays were cut into small sections. The sectioned rays were fixed in Bouin's for 24 hours, neutralized 10% formalin-sea water for 48 hours, Heidenhain's 'Susa' for 12 hours, Helly's for 12 hours, or Zenker's for 12 hours (Galigher & Kozloff, 1971). Fixed tissue samples were washed and progressively introduced to 70% Ethanol by means of an alcohol dripping technique. Skeletal ossicles in the tissue samples were decalcified over an 8 day period in a 3% Hydrochloric Acid - 70% Ethanol solution (Galigher & Kozloff, 1971). After decalcification, the tissues were dehydrated with increased alcohol concentrations, placed in xylene and embedded in paraplast (m.p. 56°C) with a vacuum infiltrater.

Tissues for histological observations were sectioned 6 to 8 μm thick and stained in Ehrlich's haematoxylin-eosine, Masson's trichrome, or Weigert's iron haematoxylin-eosine (Humanson, 1972).

Tissues used in histochemical analysis were sectioned 4 to 6μm thick and stained in alcian blue, aldehyde fuchsin, ninhydrin-Schiff, periodic acid-Schiff (PAS), or toluidine blue (Bancroft, 1967; Pearse, 1968).

Defense Mechanism

This and the next aspect of the research were conducted at the Friday Harbor Laboratories of the University of Washington. *Pteraster tesselatus* was collected by use of SCUBA around Cantilever Pier, Goose Island, Turn Island, and Yellow Island (Fig. 3). Some were collected by dredging around Fisherman's Bay, Point Caution, Point George, President Channel, and Spieden Channel (Fig. 3). All were placed in deep plexiglass aquaria supplied with fresh running sea water.

Pteraster tesselatus could be handled in the laboratory with relative ease if it were never allowed to come in contact with the air for more than a few seconds. If it had to be moved from its aquarium for a longer period of time, it was rapidly placed into a bucket of sea water and the move was made. In this way *P. tesselatus* could be kept from secreting copious amounts of mucus.

To study intake of water by *P. tesselatus* for respiration, sea stars were placed in a shallow plexiglass tank with a clear plexiglass bottom so that observations could be made from above and below with a long-arm dissection scope. With a micropipette fluorescien dye was placed near the aboral and oral surfaces of non-mucus covered, as well as mucus-covered sea stars. Dye intake and exit were observed through the microscope for each sea star used.

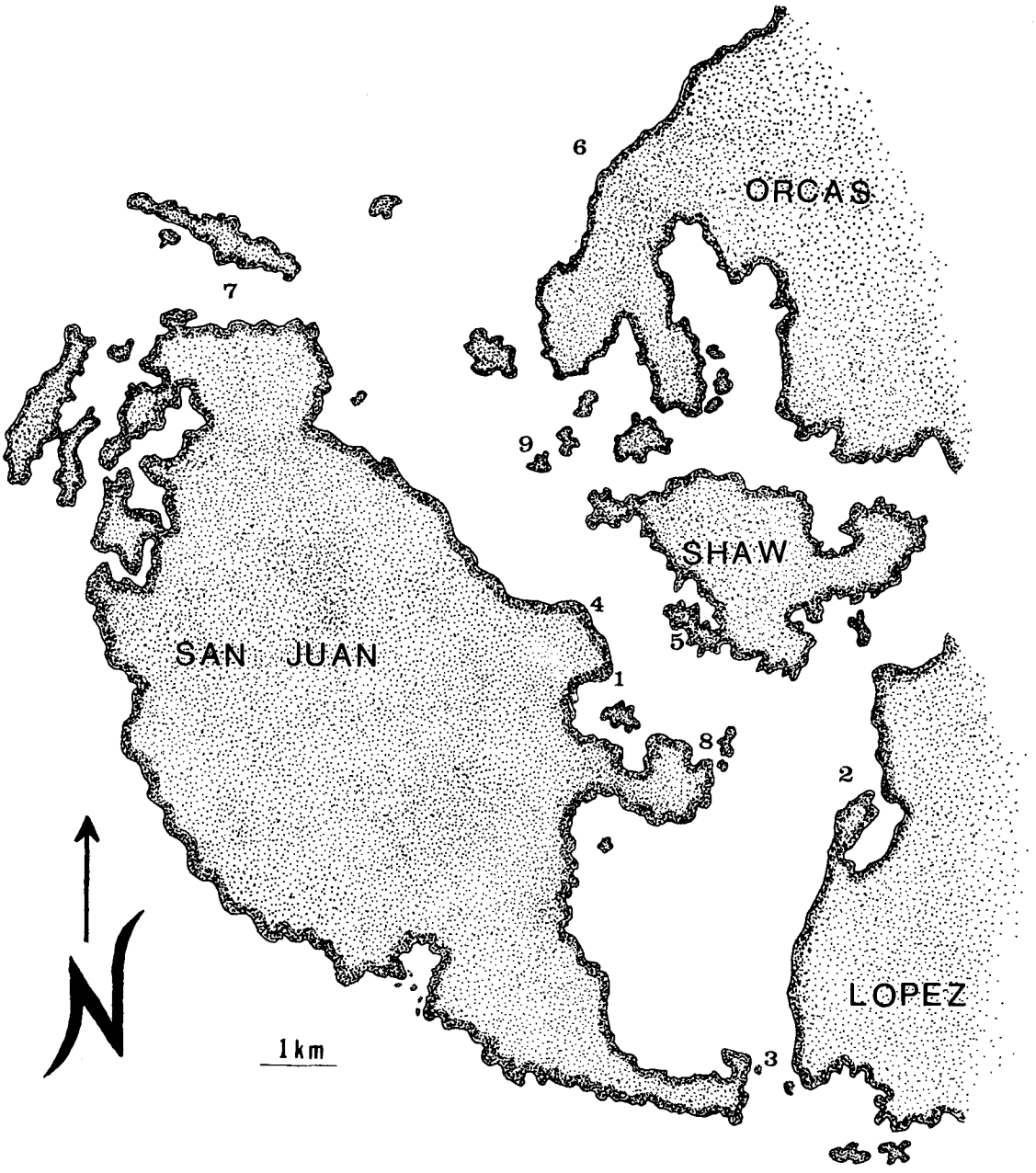


Fig. 3. Collection sites in the San Juan Archipelago, Washington. 1. Cantilever Pier, 2. Fisherman's Bay, 3. Goose Island, 4. Point Caution, 5. Point George, 6. President Channel, 7. Spieden Channel, 8. Turn Island. 9. Yellow Island.

Mucus from a freshly captured *P. tesselatus* was collected by running my hand along its aboral surface, pushing the copious secretion off and into a 1000 ml beaker. Several experiments were performed utilizing this mucus.

In the first experiment 25 aliquots of mucus were weighed and placed in crucibles in an oven at 250°C. After 5 hours when all the water had evaporated, the samples were weighed and the percentage water by weight was determined for each.

In the next experiment the harmful effects of the mucus were determined. Two 25 l aquaria, one containing 24 l of sea water and the other filled with 24 l of mucus, were placed in a large shallow aquarium containing fresh running sea water at 9 to 12°C.

Table I shows the death results of the animals that were added to each of the two experimental aquaria. Time of death was observed for each of the animals over a 14 day period.

The final experiment in which the freshly collected mucus was used was to observe the repelling effects of the mucus on asteroid eating sea stars such as *Pycnopodia helianthoides* and *Solaster dawsoni*. For testing the response of *P. helianthoides*, a freshly opened bivalve, *Saxidomus giganteus*, was placed in a tank with this multirayed sea star. A rubber tube was then inserted, with one opening placed in the interior of the valves and the other end leading to a 50 ml hypodermic syringe filled with either mucus or sea water. When the sea star began to feed on the bivalve's tissue, the contents of the hypodermic syringe were forced through the tube and into the valves. I simultaneously observed whether or not the star continued feeding once the liquid was purveyed.

To test the response of *Solaster dawsoni*, a small *Solaster stimpsoni* was placed in an aquarium with the predatory star. A rubber tube, with an opening placed near the mouth area, was wired onto one of the rays of the *S. stimpsoni*. The tube again led to a 50 ml hypodermic syringe containing either mucus or sea water. When feeding started to occur the liquid was discharged around the prey and the reaction of *S. dawsoni* was observed.

In another test, *Pteraster tesselatus* was placed in a shallow tank with a representative from most of the sea star species found in the San Juan Archipelago to observe which ones elicited an escape response from *Pteraster*. The amount of mucus given off by *Pteraster* when it was touched on its side by the leading ray of one of the intruder stars was noted, as well as the amount of mucus given off when one of the introduced sea stars crawled up onto the aboral surface of the *Pteraster*. The asteroids used in the experiment are listed in Table III.

To analyze how affective the mucous defense mechanism of *Pteraster* was against attacks from *S. dawsoni* and *Pycnopodia helianthoides, Pteraster tesselatus* was placed in aquaria with these sea stars along with their natural prey (Mauzey et al., 1968). In a large tank I placed 5 *S. dawsoni*, 5 normal *P. tesselatus*, and 5 *P. tesselatus* which had their supradorsal membrane removed by cutting the supporting ossicles under it. Without the membrane the *Pteraster* specimens still functioned normally, but were unable to secrete mucus for defense. In another tank with one small *Pycnopodia helianthoides* I introduced the same prey types, only substituting 5 *Saxidomus giganteus* for the 5 *Solaster stimpsoni*. The experiments were allowed

to continue until only one prey type remained uneaten. I also placed a *Pteraster*, which had its membrane removed, in a large aquarium containing the other local sea stars to observe if *Pteraster* would be consumed.

Feeding and Prey

In the field, using SCUBA, I observed one hundred *P. tesselatus* in the Cantilever Pier area; a locality with steep rock faces and sediment covered shelf-like slopes. The *Pteraster* specimens were checked to see if they were feeding, and if so, what they were feeding on.

Chemoreception experiments were performed using a Y-maze similar to one used by Castilla & Crisp (1970) (Fig. 4). My maze had a full length of 200 cm, a width at the end of the stem of 25 cm, and a width of only 13 cm at the entrance to the choice area. The width of each arm was 20 cm and the depth of the maze was 10 cm throughout. The maze was constructed of outside grade plywood with fiber glassed joint areas, and painted black with inert epoxy paint. Castilla & Crisp (1970) found that by constricting the aperature at the junction between the two branches of the Y their sea stars were able to differentiate between the two channels more effectively.

Water was introduced into the system by a single hose, which divided near the arms, so each arm was fed simultaneously with equal currents of water. Two 20 cm x 10 cm plexiglass sheets were placed, vertically in each arm of the maze to obstruct the current flow down them (Fig. 4). Each sheet, with numerous small holes drilled in it, allowed the current to flow slowly, in an even, nonturbulent manner to the choice area of the maze. A single stand pipe, 9 cm tall,

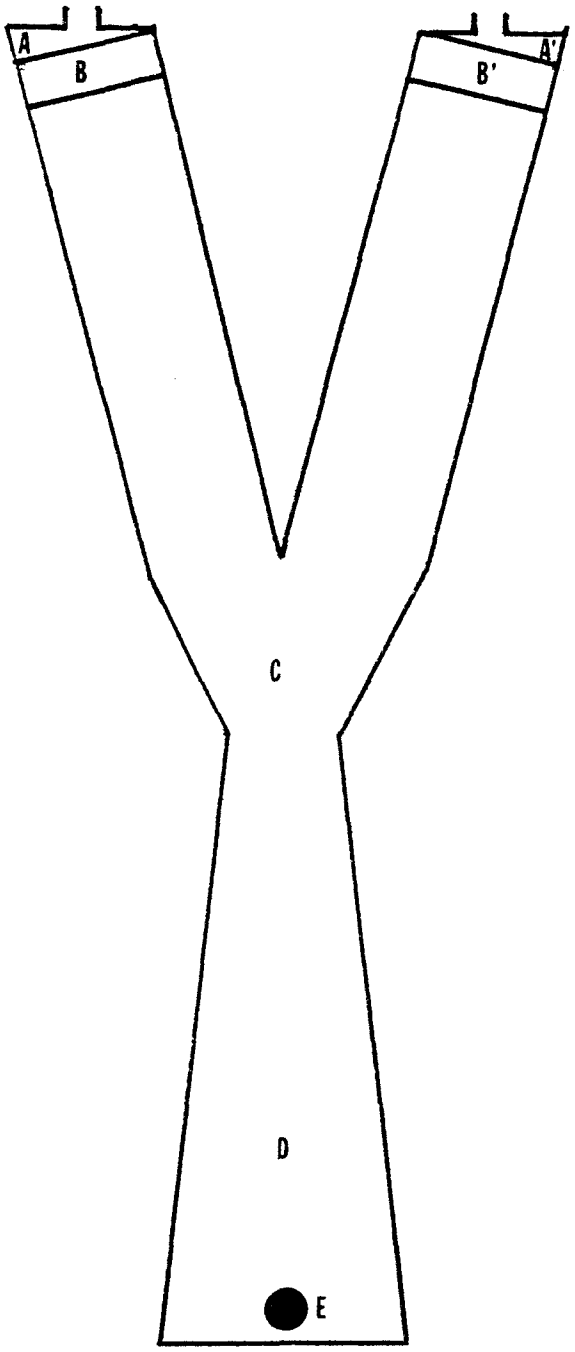


Fig. 4. Diagram of the Y-maze choice chamber. A,A', location of prey; B,B', plexiglass sheets used to buffer current; C, choice area; D, sea star starting position; E, drain plug.

was located at the end of the stem for the water to exit and to establish a water depth where the sea stars were completely covered, but were discouraged from climbing up the sides of the maze.

The Y-maze was placed in an area enclosed by a black plastic curtain to prevent light from entering into the test area. A red light within the enclosure allowed observations to be made, but did not affect the sea star's behavior (Rodenhouse & Guberlet, 1946).

Two types of chemoreception experiments were run in the maze. The first type was location of a single prey, and the second was a prey preference test. Forty *Pteraster* stars used in the chemoreception tests were collected with SCUBA from the same areas shown in Figure 3. Collection took place two weeks in advance of the experiments to allow all sea stars to be fed the same food, because selection of prey is influenced by the previous food taken in (Blake, 1960; Wood, 1968), and well fed animals are more selective in their choice of foods than starved ones (Feder, 1956; Emlen, 1966).

For the experiments involving the detection of a single prey, each of the 40 *Pteraster* specimens were placed, one at a time, into the stem of the Y. This took place 15 minutes after the prey had been introduced into one of the two arms. Two hours were given for the slow moving sea star to move up the Y-maze and into one of the two arms. A trial occurred each time a sea star was placed in the maze, but if the star failed to enter one of the two arms during the 2 hour period the trial was not counted in the results.

Between each trial the maze was cleaned with a brush and fresh sea water was run through the system for 10 minutes. After cleaning, the prey was reintroduced into the maze in the opposite arm it was in

the trial before, and a new sea star was placed in the stem to begin a new trial. The prey species used in this experiment are listed in Table V. The results of this test, and all others that called for statistical analysis, were tested for departure from expected values with a Chi-square test for significance involving one degree of freedom and the Yates correction factor (Edwards, 1955; Siegel, 1956; Bliss, 1967).

For the prey preference tests, the same procedure used in the single prey detection experiments was employed, with the exception that two different prey types were used for each trial; one type in each Y-maze arm. Only prey species that elicited a highly significant positive chemoresponse from *P. tesselatus* in the single prey experiments were used. The prey types used are listed in Table VI.

The next experiment concerned the feeding behavior of *P. tesselatus* towards the scallops *Chlamys hastata* and *C. rubida*. This test was undertaken because Bloom (1975) did not experiment on this scallop-eating aspect and Mauzey, et al. (1968) treated the subject superficially. The ratio of *Chlamys hastata* to *C. rubida* in the *Pteraster* collection areas was 9:1 and was constant in all experiments using scallops. The epizoic sponges *Myxilla incrustans* and *Mycale adhaerens* were found in equal abundance on both *Chlamys* species, and this ratio was also maintained for these experiments.

In order that my data could be compared with Bloom's (1975), scallops used in my experiments were prepared in a similar manner to his. The first variable type consisted of scallops which were rendered nonmotile by wiring their valves down upon a short piece of rubber tubing. The tubing produced a gape between the valves which allowed

Pteraster ready access to the prey's flesh. Some scallops of this experimental type were left with their epizoic sponge on both valves, whereas others were cleaned with a brush to remove all sponge tissue. The second basic type involved motile scallops that were also sponge-covered or sponge-free. The final basic experimental type consisted of sponge-covered *Chlamys* valves which had all the scallop tissues removed from between them. Different combinations of these 3 experimental types were placed in 3 aquaria, each containing 3 *Pteraster*, as the results in Figure 6 show.

Each experiment was run until only one experimental prey type remained alive. Prey were counted as eaten when all the *Chlamys* tissue was gone and/or all of the sponge tissue was eaten.

Since *Pteraster* envelops its prey with its cardiac stomach during the feeding process, as does *Crossaster papposus* (Hancock, 1974) and other sea stars not in the family Asteridae (Feder & Christensen, 1966), I attempted to determine whether this sea star just "smothered its prey to death" by keeping it from respiring, or if some toxic substance were emitted by the stomach that killed the scallop and allowed feeding to begin.

To observe how long *Chlamys* could survive without access to oxygen, 20 *Chlamys* with valves held tightly closed with rubber bands were placed in ten 1000 ml beakers of sea water in a large aquarium bath at a temperature of 10 to 13 C. To check if water could seep between the scallop valves thus closed, 6 other prepared *Chlamys* were placed in three 1000 ml beakers of fresh-water in the same aquarium bath. The latter were used as controls, because unbound *Chlamys* died within one hour in this fresh-water environment (per. obs.). All

the *Chlamys* specimens were checked at 5 hour intervals to see when death occurred.

Other *Chlamys* specimens were placed in beakers containing *Pteraster* "stomach juice", to observe when death occurred. The cardiac stomachs of several *Pteraster* were removed, placed in a blender, and mixed until only a thin soup remained. One part soup was added to 20 parts sea water and placed in ten 1000 ml beakers. Twenty unbound *Chlamys* were placed in the beakers containing this mixture and checked each hour to see when death occurred. Five control beakers, containing only sea water and 2 scallops each, were also set up in the aquarium and checked.

To observe whether *Pteraster* would feed on diatoms, a sheet of glass covered on one side with *Biddulphia laevis* (Gran & Angst, 1931) was placed in a deep freshly cleaned tank in a vertical position next to the outer tank wall. The reaction of the sea stars within the tank to the diatom material was observed through the walls of the aquarium.

RESULTS

Histology and Histochemistry

Only two of the fixatives used in this research did not cause excessive swelling of the ectodermal tissues. The neutralized 10% formalin-sea water solution caused little or no swelling of the tissues, whereas Helly's fluid caused only slight swelling. Therefore, only *P. tesselatus* tissue sections fixed in these two solutions were used in determining the positions and contents of the mucous gland cells.

There were three types of mucous cells found in the tissues of *P. tesselatus*. Though all were unicellular in structure, they differed in size, location, and abundance.

The first type was a small (1.6 mm) gland cell found commonly only in the epidermis lining the dorsal surface of the supradorsal membrane (Fig. 7). It was stained deep red by the PAS reaction, but no other histochemical stain showed its presence. It therefore contained, as did the other two gland cells, a simple mucopolysaccharide compound without proteins (Hale, 1957; Bancroft, 1967). Ward (1960) made an analysis of the mucus of *Pteraster* and found it contained a monosaccharide (glucose) and a disaccharide believed to be cellobiose, but failed to find amino acids. My findings agree completely with Wards (1960) analysis in the cases of all three types of the mucous cells found.

The second type of mucous cell was similiar to the type found by Ward (1965) in the epidermis of *Dermasterias imbricata*. It was

found abundantly in the tall columnar cells which lined both the spiracula and the ventral surface of the supradorsal membrane. This gland cell, which is 110 µm long in most cases, was also found in the epidermis surrounding skeletal ossicles supporting the supradorsal membrane (Fig. 8). The fixatives used rendered the mucus in this gland, as well as in the first type, very grainy in appearance. The mucus found in these gland cells was stained a brilliant red with the PAS reaction.

The third type of mucous cell measured 80 µm in length and was abundant in the epidermal lining of the true body wall (Fig. 9). Though it stained red in color with PAS, it's appearance was unlike that of mucous gland cells found in invertebrate tissues (Pedersen, 1959; Nichols, 1960; Wells, 1961; Arcadi, 1963; Healy, 1963; Arcadi, 1965; Pedersen, 1965). The mucus contained in these glands appeared bubble-like from the process of fixation.

Defense Mechanism

In water intake experiments I found, as did Rodenhouse & Guberlet (1946) and Johansen & Petersen (1971), that when *P. tesselatus* is not mucus-covered, water was drawn into the nidamental cavity through the small spiracula in the supradorsal membrane. However, most of the water was taken in through another system, not discussed by these investigators. Large pores located along the lateral walls of the abulacral grooves (Fig. 10) were discovered to take in most of the water when the sea star was undisturbed. When *Pteraster* had any amount of mucus covering its supradorsal membrane, all of the water that the animal drew in for respiration was taken into the nidamental cavity

through the ambulacral pores. This action prevented unwanted mucus, which was covering the supradorsal membrane, and was not present on the oral surface, from entering the cavity. If mucus were allowed to enter this space, normal oxygen exchange through the dermal branchiae would cease. In sea stars not covered with mucus, water was ejected through only the osculum, but in mucus-covered *Pteraster*, water was forced through the numerous supradorsal spiracula, pushing large quantities of mucus, secreted by the interior mucous cells, out with it.

The mucus which *Pteraster* secreted when disturbed contained 97% water by weight, making only 3% actual mucus secretion. The results in Table I indicate that the mucus was nevertheless viscous enough to congest the respiratory organs of an animal and even cause death if contact, between the mucus and the animal, was maintained for a long period of time. The *Modiolus* specimen (listed in Table I) did not die in the 14 day period, because, when it was placed in the tank, the valves closed tightly, thus preventing mucus from entering. Some of the other organisms also had this advantage of closing up to prevent intake of mucus, but their metabolism did not allow them to last through the 2 week trial. Most of them however, died much later than the other organisms without this advantage. None of the animals in the control tank died during the 14 day time interval.

Table II shows that the two sea stars that prey on other asteroids in the San Juan Archipelago, *Solaster dawsoni* and *Pycnopodia helianthoides*, will avoid mucus-covered prey.

Pteraster tesselatus had a very strong defense reaction toward two of the sea stars found in the region, and a moderate response with another (Table III). These results are in harmony with Mauzey's et al.

Table I

Comparative lethal death times for organisms placed in mucus of *Pteraster tesselatus*

Organisms	Time (hours)
Strongylocentrotus droebachiensis	15
Cancer oregonensis	21
Chlamys hastata	30
Triopha carpenteri	31
Henricia levinscula	31
Pteraster tesselatus	33
Notoacmea scutum	68
Balanus nubilus	84
Fusitriton oregonensis	86
Modiolus rectus	--

Table II

Responses of *Solaster dawsoni* and *Pycnopodia helianthoides* to prey experimentally covered with mucus from *Pteraster tesselatus*

Asteriod	Response	Control (sea water)	Treatment (mucus)	ΣX^2
Solaster dawsoni	continued to feed	37	10	37.6*
	left prey	3	30	
Pycnopodia helianthoides	continued to feed	39	3	65.0*
	left prey	1	37	

*$\ll$.01

Table III

Defense reactions of *Pteraster tesselatus* in relation to other asteroids in the San Juan Archipelago

Asteriod	Simple touch	Star placed on
Crossaster papposus	-	-
Dermasterias imbricata	-	-
Evasterias troschelii	-	-
glass rod	-	-
Henricia leviuscula	-	-
Hippasteria spinosa	-	-
Leptasteris hexactis	-	-
Luidia foliolata	-	-
Mediaster aequalis	-	-
Orthasterias koehleri	-	-
Patiria miniata	-	-
Pisaster brevispinus	-	-
Pisaster ochraceus	-	-
Pteraster tesselatus	-	-
Pycnopodia helianthoides	+	++
Solaster dawsoni	+	++
Solaster stimpsoni	-	+

- no mucous, + moderate amount of mucous, ++ copious amount of mucous

(1968) research, because both *S. dawsoni* and *Pycnopodia helianthoides* are known predators on a large variety of prey.

Experiments showed that, if *S. dawsoni* or *P. helianthoides* came into contact with *Pteraster tesselatus*, a moderate amount of mucus, 2 to 3 cm thick, was secreted to repel the predator. If these two sea stars attacked the *Pteraster* by attempting to crawl upon its aboral surface the *P. tesselatus* responded with a violent discharge of mucus, 6 to 7 cm thick, which extended over the supradorsal membrane and prevented the predatory star's tube feet from attaching to it. The attacking sea star then moved off the *Pteraster* and traveled away at a rapid pace. The fact that *S. stimpsoni* caused a moderate amount of mucus to be given off when it crawled over the aboral surface of *Pteraster* was possible due to its biochemical similarity to its predatory relative *(S. dawsoni)*, and it was therefore hard for *P. tesselatus* to distinguish between these two related asteroids by chemoreception (Mauzey et al., 1968).

Only *S. dawsoni* and *Pycnopodia helianthoides* preyed upon *Pteraster* with its supradorsal membrane removed. The other sea stars found in the region did not show any desire to do so or even attempt to feed on *P. tesselatus*. Figure 5 shows the rates at which *P. tesselatus* was consumed by *S. dawsoni* and *Pycnopodia helianthoides* along with their natural prey.

When *S. dawsoni* attacked an unprotected *Pteraster* it touched the intented prey first, and, while raising its leading rays, moved rapidly forward. It then lowered its rays onto the surface of the *P. tesselatus* and attached its tube feet. It pulled itself over the sea star with its tube feet and placed its rays between the rays of the

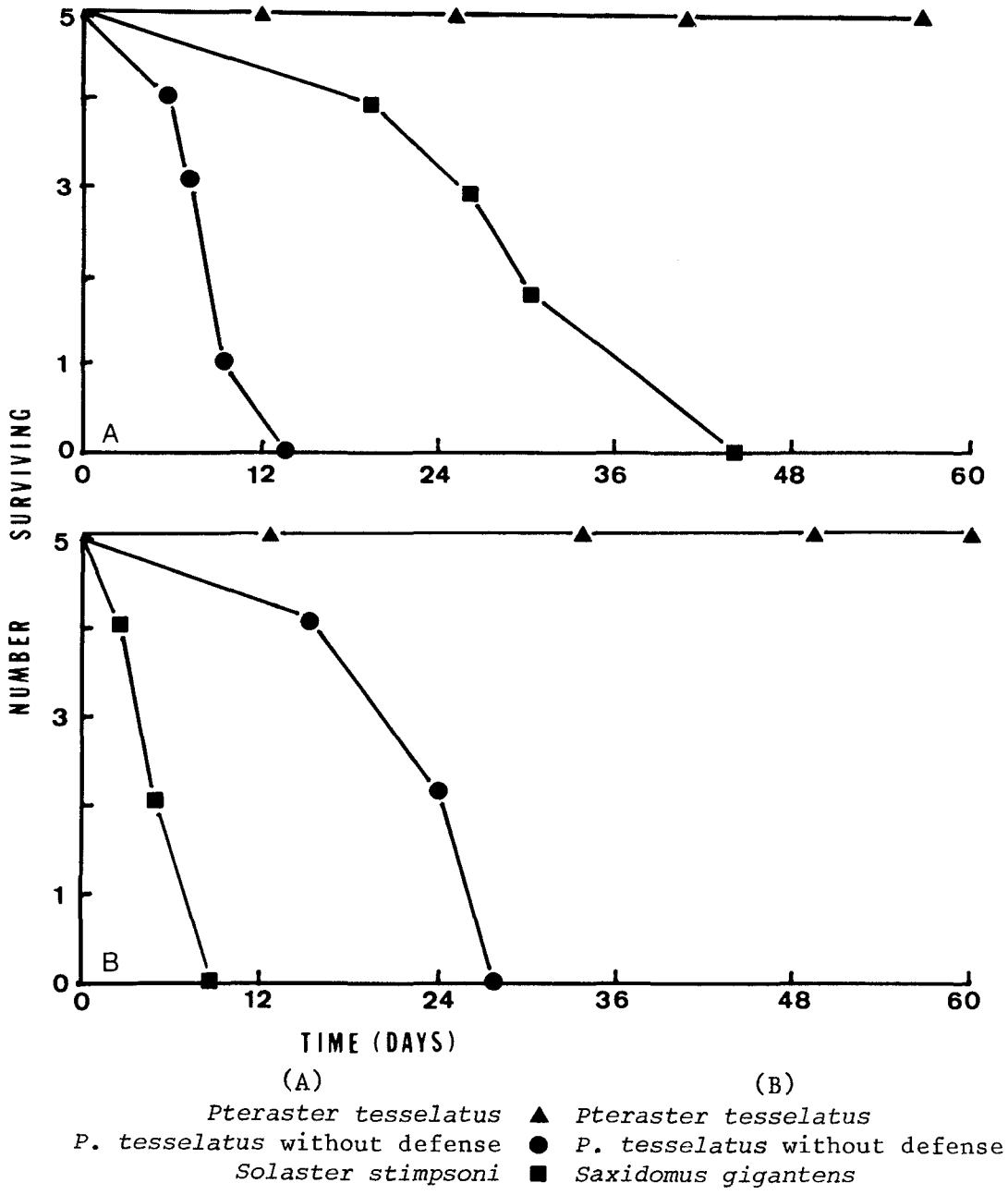


Fig. 5. Feeding rates for *Solaster dawsoni* (A), and *Pycnopodia helianthoides* (B), on *Pteraster tesselatus* and their natural prey.

retreating *P. tesselatus*. In this position *Pteraster* was unable to move and the *S. dawsoni* everted its large cardiac stomach out over the aboral surface of the prey. As feeding continued the prey was taken inside the predator. It took four days for a large *S. dawsoni* to swallow and digest a moderate sized *P. tesselatus*.

Pycnopodia helianthoides attacked in a similar manner, but when it touched the prey, it just moved rapidly over the aboral surface, never raising its arms off *Pteraster*. The prey was immediately taken inside and, for a moderate sized *Pteraster*, digestion took only 2 days to complete.

Feeding and Prey

Table IV contains the results of my underwater observations concerning the prey of *P. tesselatus*. Though only a little over half of the sea stars were observed to be feeding, a large number of these were feeding on detritus.

This sea star was an active chemoreceptive hunter, but it fed upon detritus a great deal of the time.

The single prey chemoreception experiments (Table V) showed that *P. tesselatus* had a very definite attraction for most sponge tissue. The results also indicated that this sea star was attracted to most of the organisms it fed on in nature and was repelled by the two sea stars that try to feed on *P. tesselatus*.

As shown by the prey preference tests (Table VI), *P. tesselatus* had two prey species which it was strongly attracted to. Both *Myxilla incrustans* and *Mycale adhaerens* were usually found on the valves of *Chlamys* (Bakus, 1966) and therefore provided a great deal of

Table IV

Food of *Pteraster tesselatus* at the Cantilever Pier area

Food	Percentage
NOT FEEDING	44
detritus	33
Balanus nubilus	9
Chlamys with sponge covering valves	5
Didemnum albidum	3
Iophon pattersoni	2
Pododesmus cepio	2
Sigmadocia edaphus	1
Balanophyllia elegans	1

Table V

Responses of *Pteraster tesselatus* to living prey

Prey	+ response	- response	X^2
Balanophyllia elegans	18	22	0.2
Balanus nubilus	28	10	7.6**
Biddulphia laevis	28	9	9.5**
Chlamys hastata (no sponge)	27	13	4.2*
Chlamys rubida (no sponge)	26	12	4.5*
Cliona celata	31	8	12.41***
Corella willmeriana	27	12	5.0*
Didemnum albidum	30	9	10.3***
Halichondria panicea	34	5	20.1***
Haliclona permollis	35	5	21.0***
Mycale adhaerens	35	4	23.1***
Myxilla incrustans	37	3	27.2***
Pododesmus cepio	23	17	0.6
Pycnopodia helianthoides	11	29	7.2**
Solaster dawsoni	3	37	27.2***
Syringella amphispicula	25	15	2.0
Terebratulina unguicula	21	19	0.0

* $<.05$, ** $<.01$, *** $<<.01$

Table VI

Pteraster tesselatus prey preference

Prey A	Prey B	to A	to B	X^2
Cliona celata	*Didemenum albidum*	13	27	4.2*
Halichondria panicea	*Haliclona permollis*	18	22	0.2
Mycale adhaerens	*Myxilla incrustans*	17	23	0.6
Didemnum albidum	*Halichondria panicea*	9	29	9.5**
Didemnum albidum	*Haliclona permollis*	10	28	7.6**
Haliclona permollis	*Myxilla incrustans*	4	35	23.1***
Haliclona permillis	*Mycale adhaerens*	9	30	10.3***
Halichondria panicea	*Myxilla incrustans*	3	37	27.2***
Halichondria panicea	*Mycale adhaerens*	5	35	21.0***

* $<.05$, ** $<.01$, *** $<<.01$

energy, if found and captured. It is interesting to note that this type of prey, though highly sought after chemoreceptively, accounted for only a small percentage of the food used by *Pteraster* in nature. This showed how effective the escape response of scallops was (Moore & Trueman, 1971; Thomas & Gruffydd, 1971). In conclusion, most *P. tesselatus* must settle for nonmotile prey to provide them with their energy requirements.

As Bloom (1975) showed in his research, *Chlamys* in the San Juan Archipelago were in mutualistic relation with both *Mycale adhaerens* and *Myxilla incrustans*. My experiments supported his conclusions. The scallops with their escape response from *Pteraster* provided an escape for the epizoic sponge, and the sponge in turn on the scallop's valves made it more difficult for *P. tesselatus* to capture the *Chlamys*, because the star's tube feet couldn't attach well. Figure 6 shows the rates at which *Pteraster* consumed the variety of *Chlamys* with or without epizoic sponge growths. Sponge found on scallops were eaten very rapidly, as were the scallops, when the bivalves were rendered nonmotile with internal organs exposed by wiring their valves shut onto a short piece of rubber tubing. As for motile *Chlamys*, it was easier for *Pteraster* to capture the scallops with their sponge epizoites removed than with them left on. When the ratio of clean to sponge-covered scallops was 1:3, then the sponge-covered scallops began to be captured at a more rapid rate.

When my data is compared with Bloom's (1975) it can be seen that the graphs for *Pteraster* are very similar to those he obtained for *Orthasterias koehleri*, indicating these two sea stars have similar hunting habits.

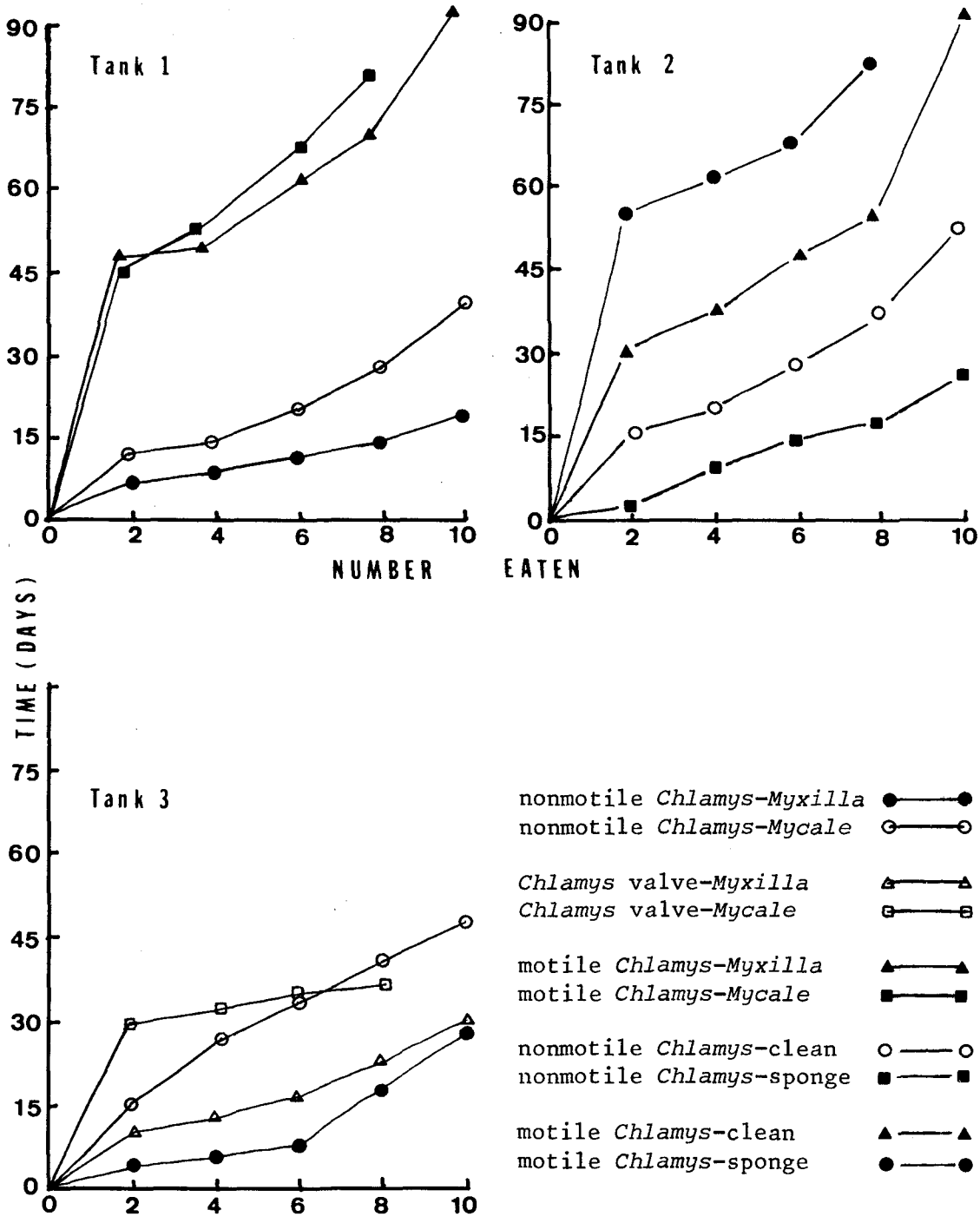


Fig. 6. Feeding rates for *Pteraster tesselatus* on different combinations of scallop-sponge prey.

There was a slight feeding preference, though not statistically significant, for *Myxilla incrustans* over *Mycale adhaerens* on both the nonmotile and motile *Chlamys*.

When a *Pteraster* attacked a *Chlamys* the leading ray of the sea star flexed upward when contact was made. The mantle tentacles of the scallop extended and pointed in the direction of contact. *Pteraster* then extended its leading ray onto the upper valve of the prey. At this point the scallop began its swimming defense response. If *Pteraster* maintained its hold and climbed up onto *Chlamys*, it could capture the prey.

Once centered over the prey, *Pteraster* everted its stomach over the sponge tissue. For a small *Pteraster*, feeding ended after the sponge was consumed. This was because its stomach folds were not large enough for complete envelopment of *Chlamys*.

For a large *P. tesselatus*, after the sponge was eaten (12 hours), the stomach began to extend down over the gape between the valves and continued its migration along the lower valve towards its center point. In this manner, most of the *Chlamys* was covered by the stomach lobes of *Pteraster*; the only portion of the scallop not being covered was a thin circle around the center of the bottom valve.

In this feeding position no force could be exerted by the tube feet in order to pull the valves apart. Most sea stars require force (Burnett, 1955; Feder, 1955; Christensen, 1957) to allow stomach lobes to gain contact with the prey's flesh. Yet, once the valves were covered by the stomach of *P. tesselatus*, feeding was completed in about 24 hours.

In my experiments on scallops, I found that it took on the average 30 hours for a *Chlamys* specimen to die from lack of oxygen. This time was far too long to allow *Pteraster* to gain entry into the valves. I found, however, that *Chlamys* became anesthetized causing a relaxation of the adductor muscle in 2 hours, when placed in the "stomach juice" of *Pteraster*. These anesthetized scallops were unresponsive to touch, and would not close their valves when their mantle tissues were pinched by forceps. If these scallops were placed in fresh sea water they would respond normally in 24 hours, showing that the bivalves were in some way drugged and not dead. This state, caused by the stomach juices of *Pteraster*, allowed the lobes of the star's stomach to be inserted between the *Chlamys* valves without the scallop responding, so that predator feeding took place with ease.

It was next observed that *Pteraster* fed on diatoms introduced into their tank. *Biddulphia laevis* was introduced into a test tank and within one hour most of the *Pteraster* individuals migrated to that side of the tank and many began to feed on the diatoms. The only other sea stars that are known to feed on diatoms are *Patiria miniata* and *Odontaster validus*, which are described as omnivorous scavengers (Feder & Christensen, 1966).

P. tesselatus was able to detect large deposits of diatom material in the substratum by chemoreception (Table V), and could therefore move to areas rich in nutrient supplies.

DISCUSSION AND CONCLUSIONS

In order for an aquatic organism to use a toxic liquid for defense, it must either be immune to the toxins in the material or have some means of keeping the material away from its own tissues. *Pteraster tesselatus* uses copious amounts of mucus for defense without being harmed itself. It is able to do so because its supradorsal membrane provides a gap between the secreted mucous and the sea star's own respiratory surfaces. If the supradorsal membrane is experimentally removed and *Pteraster* mucus applied, it is detrimental.

The mucus, a mucopolysaccharide, is not toxic to organisms, but owes its repelling powers to the fact that it is very adhesive. Its liquid and adhesive nature allows the mucus to surround and stick to the respiratory surfaces of an organism, thus disrupting normal gas exchange. This disrupts respiration, repels the organisms, and allows *Pteraster* to defensively escape.

Defensive mucus comes from numerous Type II gland cells and is discharged as fresh sea water is pumped into the nidamental cavity through the ambulacral pores and out the spiracula to cover the vulnerable aboral area. It is only in the region of the spiracula where the Type II gland cells secrete this mucus. Because of this the dermal branchiae are never allowed to come into contact with the mucus which is being used for defense.

Chia (1976) believes that the supradorsal membrane was phylogenetically developed for defensive purposes first, and then the interior nidamental cavity was secondarily used as a brood chamber

in some species. Martin (1974) also supports this hypothesis, indicating both males and females are endowed with this membrane.

The functions of the three types of gland cells found in *P. tesselatus* can only be speculated upon. It seems probable that small Type I gland cells act as cleaners for the supradorsal membrane, possibly compensating for lack of cleaning pedicellariae. Since they are not as the other gland cells, it seems unlikely that the Type I gland cells are used for defense, but possibly provide only a cleansing service for the sea star.

The Type II gland cells, as stated, are the glands which most likely contribute the copious amounts of mucus used in defense. They are very abundant, the largest, and are contained in the tissues which make up most of the surface area of *Pteraster*.

The function of the Type III gland cells is even less clear as for the other two. Based on only a histochemical analysis, these gland cells would also have been placed under the category of providing mucus for defense. But, when the behavioral analysis was made and the supradorsal membrane was removed no mucus for defense was secreted, showing that this is not the function of these gland cells. Clearly more investigation is needed to determine the function of the Type III gland cell.

The defense mechanism of *Pteraster* is essentially 100 percent effective in preventing it from becoming the prey of other asteroids in the San Juan Archipelago. With the supradorsal membrane and its gland cells removed by dissection *Pteraster* was found to be the most preferred prey for *S. dawsoni*, and will be eaten by *Pycnopodia helianthoides*, if other prey are not available. Even with its defense

system intact there are still possible predators for *Pteraster* which were not checked in this research. Very large *Pteraster* individuals ($R \geq 13cm$), which Chia (1976) believe to be near 50 years of age, are common below 60 m around the San Juan Archipelago and throughout Puget Sound, and can be collected only by dredging. Moderate sized individuals ($5cm < R > 13cm$) are common at around 15 to 60 m and can be collected with SCUBA. Very young specimens ($R \leq 5cm$) are not common anywhere and are probably the age group which is being heavily preyed upon by predators such as large fish and crustaceans. Fernald (1976) observed that the large box crab *(Chionoecetes bairdi)* will pick up small *P. tesselatus* contained in the same aquarium. Though, he never observed the crab to feed on these sea stars, they did seem undisturbed by the mucus secreted by *Pteraster*. However, even with heavy predation on the young stars, the population size remains at a near constant level, because the life span of this asteroid is long, and predation is only limited to the small size class.

Though the supradorsal membrane provides *Pteraster* with an effective means of defense, energy is required continuously to provide the dermal branchiae with oxygenated sea water. A massive amount of energy is also required in mucus production, even though the defensive secretion is about 97% water, with only 3% being mucoid material. But, even with these added energy drains, the gonadal index for *Pteraster* is similar to that of other sea stars which also produce pelagic lecithotrophic larvae (Chia, 1976).

In order for *Pteraster* to produce as much energy for reproduction as most sea stars and still maintain its defense mechanism, it must either take in more potential energy per unit of time in food than

the others, or use less energy in other aspects of its behavior. The manner in which *Pteraster* feeds accounts for conservation of energy loss to maintain a powerful defense system as well as a good gonadal index. *Pteraster* is an active benthic hunter and relies on its very competent chemoreceptive ability to locate prey. Its sessile prey are found only sparsely on the substratum, but when encountered, most can readily be consumed, since they have no obvious protection. The conducted field survey which by no means was exhaustive, showed that 32% of the *Pteraster* individuals, that were feeding, were doing so on sessile prey. Most of the prey were *Balanus nubilus* which was more abundant than other sessile prey in the area checked, so its higher percentage in the diet would be expected.

The only motile prey that *Pteraster* feeds on in the San Juan Archipelago are *Chlamys hastata* and *C. rubida*. They are very abundant over the area surveyed, and most are covered with epizoic sponges. Of the feeding stars checked, only 9% were feeding on *Chlamys* prey. This is because *Chlamys* has an excellent escape response, and the stout rays of *Pteraster* are not well adapted for capturing motile prey. The body plan of *Pteraster* is built around defense and not hunting. Its short, broad rays are located close to the central disk to allow the mucus covering to be in a large centralized ball around the entire animal. This would not be possible if the mucus were spread out over long slender rays.

Though the agility of *Pteraster* is handicapped by its rather rigid rays and only two rows of tube feet on each, it still hunts *Chlamys* with occasional success before *Chlamys* can detach its byssal threads and flee.

When *Pteraster* captures *Chlamys*, it does so by entirely enveloping the scallop with its large cardiac stomach. The cardiac stomach is then pressed against the substratum so that the *Chlamys* is contained in a tightly sealed area. Burnett (1960) showed that asteroids are capable of secreting stomach substances, even though the stomach is not in direct contact with prey flesh. After the seal is made, *Pteraster* secretes a toxin into the interior of the sealed "bag" it has created. In this way *Chlamys* is overcome in a short period of time, and the stomach lobes of *Pteraster* are sent between the valves to the prey's tissues. Digestion is completed in the normal asteroid manner with the sea star's stomach and the prey's tissues touching. *Crossaster papposus* feeds in a very similar manner to *Pteraster* (Hancock, 1974), and many other sea stars also use toxins to gain entry into the interior of bivalve prey (Sawano & Mitsugi, 1932; Hashimoto & Yasumoto, 1960; Fange, 1963). Between prey captures, *P. tesselatus* maintains a high level of energy intake by supplementing its diet with detritus from the substratum.

Intake of detritus makes up a large percentage of the food consumed by *Pteraster*, because 59% of those checked were feeding on it. Since the detritus material is made up largely of diatoms, which I showed *Pteraster* could detect and feed upon in the laboratory, the sea star must be classified as an omnivorous scavenger, like *Patiria miniata* and *Odontaster validus*.

MacGinitie & MacGinitie (1949) and Anderson (1959) believe *Patiria miniata* uses its remarkably large cardiac stomach as a ciliary mucous feeding organ. Pearse (1965) found this to be true for *Odontaster validus*. More research is needed to determine if *P. tesselatus*

is also feeding by this method. It is suspected to do so because it does have an extremely large cardiac stomach, and the stomach lining is largely made up of ciliated cells (Rodenhouse & Guberlet, 1946).

APPENDIX

PLATE I

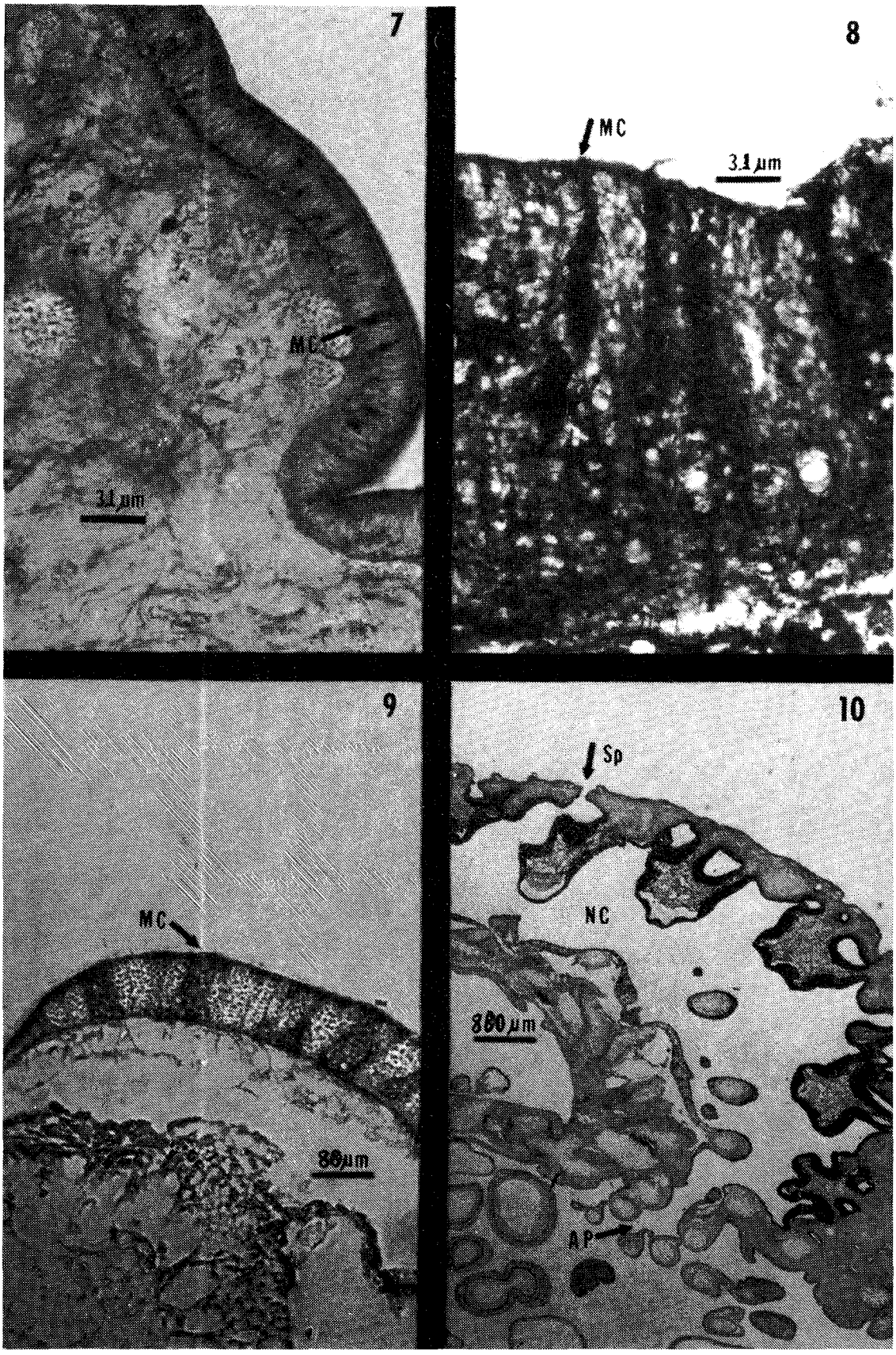
PHOTOGRAPHS OF PREPARED TISSUE SECTIONS FROM *PTERASTER TESSELATUS*

Fig. 7. Section of supradorsal membrane showing the Type I mucous gland cells (MC). Stained with PAS. Taken at 400x with Bright-Field.

Fig. 8. Section of supradorsal membrane showing the Type II mucous gland cells (MC). Stained with PAS. Taken at 400x with Phase-Contrast.

Fig. 9. Section of the body wall showing the Type III mucous gland cells (MC). Stained with PAS. Taken at 160x with Phase-Contrast.

Fig. 10. Section of ray showing spiraculum (Sp) and ambulacral pore (AP). Stained with PAS. Taken at 10x with Bright-Field.


7
MC
1.1 µm
8
MC
3.1 µm
9
MC
86µm
10
Sp
NC
880 µm
AP

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DEFENSE MECHANISM AND FEEDING BEHAVIOR OF *PTERASTER TESSELATUS* IVES (ECHINODERMATA, ASTEROIDEA)

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ABSTRACT

Pteraster tesselatus is noted for its external secretion of massive amounts of mucus. The mucus repels most animals, and fouls their respiratory physiology, if contact is maintained for any length of time. It provides protection essentially 100% of the time from *Solaster dawsoni* and *Pycnopodia helianthoides*, the only local stars that attempt to feed on *Pteraster*.

The mucus, which is a simple mucopolysaccride, is produced in three different types of unicellular glands located in the epidermal tissues along the supradorsal membrane. Pores along the lateral walls of the ambulacral grooves provide fresh sea water for the dermal branchiae contained in the nidamental cavity located between the supradorsal membrane and the body wall.

P. tesselatus has a very strong chemoreceptive ability to locate prey. It prefers sponges, but feeds on a great variety of sessile organisms, as well as detritus. It also feeds on *Chlamys hastata* and *C. rubida*, which have their valves epizoically overgrown with either *Myxilla incrustans* or *Mycale adhaerens*.

COMMITTEE APPROVAL: