

A PREDATOR-PREY RELATIONSHIP
BETWEEN THE LEATHER STAR, *Dermasterias imbricata*,
AND THE PURPLE URCHIN, *Strongylocentrotus purpuratus*

RICHARD J. ROSENTHAL¹ AND JAMES R. CHESS²

ABSTRACT

During 1969 and 1970, we spent more than 150 hr underwater observing interaction between the leather star, *D. imbricata* and the purple sea urchin, *S. purpuratus*. The majority of the observations were made in shallow (13-15 m) nearshore waters off Pt. Loma, Calif.

The defensive responses exhibited by the purple sea urchin when contacted by the leather star indicated the presence of a well-developed predator-prey relationship. The responses included retraction of sea urchin podia, depression of spines, gaping and erection of globiferous pedicellariae, and usually movement away from the asteroid.

Within the study area off Pt. Loma, 437 feeding leather stars were encountered underwater, and of these, 204 or 47% were eating *S. purpuratus*. In contrast, previously published observations by Mauzey, Birkeland, and Dayton (1968) on the feeding behavior of asteroids off the state of Washington indicated that echinoids were excluded from the diet of *D. imbricata*. We suggest that (1) prey density and availability, (2) search time, (3) taste or gustatory preferences of the sea star, and (4) some form of associative learning by the leather star may be responsible for the variation in the feeding behavior of *D. imbricata* in different areas.

Early laboratory studies by Prouho (1890) and Jennings (1907) described the behavioral responses of sea urchins when encountered by predatory sea stars. More recently, Jensen (1966) recorded the responses of two sea urchin species, *Strongylocentrotus dröbachiensis* and *Psammechinus miliaris*, in the presence of the sea star *Marthasterias glacialis*. Since field observations on the feeding behavior of sublittoral sea stars were rarely made, the laboratory studies only provided the basis for speculation about natural predator-prey interactions between asteroids and echinoids.

Sea urchins might appear to be somewhat immune from predatory attacks by other invertebrate species because they possess such formidable looking armature. However, Mauzey, Birkeland, and Dayton (1968) observed the sea star

Pycnopodia helianthoides feeding on sea urchins both intertidally and subtidally along the shores of Washington state. Leighton (1971) reported that two species of sea stars, *P. helianthoides* and *Astrometis sertulifera*, feed heavily on juvenile sea urchins. Also, Rosenthal and Chess (1970) identified the leather star, *Dermasterias imbricata* (Grube) as a predator of the purple urchin, *Strongylocentrotus purpuratus* (Stimpson) off San Diego, California.

This paper examines in detail the predator-prey interactions observed between the leather star *D. imbricata* and the purple urchin *S. purpuratus* in both laboratory and field situations. *Dermasterias imbricata* is reported from Prince William Sound, Alaska, to Baja California (Fisher, 1930; Feder, personal communication), while *S. purpuratus* ranges along the Pacific coast of North America from Alaska to Cedros Island, Baja California (Ricketts and Calvin, 1962). Both species occur in intertidal and subtidal situations in cooler temperate climates of the Eastern Pacific; however, south of Santa Barbara, California, the leather star is common only in the sublittoral zone.

¹ Westinghouse Ocean Research Laboratory, San Diego, CA; present address, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92037.

² Westinghouse Ocean Research Laboratory, San Diego, CA; present address, National Marine Fisheries Service, Tiburon Fisheries Laboratory, Tiburon, CA 94920.

DESCRIPTION OF THE STUDY AREA

The main study site was located approximately 1.5 km offshore from Pt. Loma, California (lat 32°42'N; long 117°16'W). The area is within a stand of giant kelp, *Macrocystis pyrifera*, and the bottom in this vicinity is from 13 m to 15 m deep. The primary observation site encompassed an area about 300 m by 150 m. The sea floor within this area is relatively heterogeneous and is composed primarily of siltstone pavement rocks, rocky outcrops, ledges, and intermittent patches of coarse sand. Vertical relief is generally less than about 2 m. Much of the hard substratum was occupied either by the holdfasts of *M. pyrifera* or by low standing, brown algae such as *Pterygophora californica*, *Cystoseira osmundacea*, and *Laminaria farlowii*.

METHODS

Emphasis was directed towards observing the organisms under natural conditions in the sublittoral zone; however, laboratory observations were used in addition to those made in the field. Experiments in the laboratory were designed to supplement our field observations, since it allowed us to observe behavioral interactions between *D. imbricata* and *S. purpuratus* over a more continuous period of time. The laboratory portion of the study was conducted at the NMFS Fishery-Oceanography Center, La Jolla, California. Experimental animals were maintained from February through April 1970, in fiber glass water tables which contained circulating seawater. Water temperatures in the aquaria varied from 12° to 17°C during the period of observation.

The field studies are the result of approximately 150 hours of underwater observations made while scuba diving from November 1969 through November 1970. All of the leather stars encountered underwater within the perimeter of the study area were included in the feeding behavior observations. In each case we recorded the size (center of the aboral area to the tip of the longest arm) of the leather star, and noted whether or not it was feeding. It was usually necessary to turn the leather star over in order

to make the feeding observation and identify the prey. In situations where the prey was ingested whole by the leather star, we forced the food item out of the sea star's mouth by applying pressure to the aboral and oral surfaces as described in Mauzey et al. (1968). Measurements were made with plastic calipers or rules, and the data were recorded underwater on plastic slates.

Estimates of leather star density were determined by swimming belt transects 4 m wide and 25 m long. Initially, these transect lines were placed haphazardly along the bottom, running either perpendicular or parallel to the shoreline. However, we also placed lines in predetermined locations where leather stars were believed to be more abundant. Size distributions and density estimates of the *S. purpuratus*, which inhabited the study area, were determined by removing all of the visible purple urchins from 16 randomly selected m² quadrats. The quadrats were chosen randomly along two 50-m transect lines. One of the transect lines followed a siltstone ledge, and the other was placed perpendicular to the shoreline through a dense stand of giant kelp, *M. pyrifera*. After removal from the quadrats the *S. purpuratus* were placed into plastic bags and carried to the surface for measurement and enumeration.

Three methods were used in an attempt to determine the rate of feeding and the time necessary for a leather star to digest a purple urchin:

(1) A wire mesh cage which covered an area of 4 m² was placed over a natural population of at least 50 purple urchins, and four leather stars were introduced as predators into the cage.

(2) Leather stars were marked with numbered disc tags which enabled us to identify and observe individuals over extended periods of time. The tags were attached to the aboral surface of the leather star with a loop of monofilament line. The line was passed through the leather star's epidermis and under the calcareous ossicles using a heavy duty needle. All leather stars were tagged at the sea surface and immediately returned to the bottom.

(3) In the laboratory we placed seven leather stars and 76 purple urchins into a 0.915 × 4.27 m (3 ft × 14 ft) fiber glass water table. The water

table contained circulating seawater approximately 0.3 m in depth. Bricks were scattered around the bottom of the tank to provide the urchins additional substratum and cover. The concentration of leather stars to purple urchins was considerably higher than normally found in the field; however, we felt that the increased number of leather stars might increase our chances to observe predation in the laboratory.

FEEDING BEHAVIOR OF *Dermasterias imbricata*

The widespread distribution of *D. imbricata* along the Pacific coast of North America is partially reflected in its feeding behavior. *Dermasterias imbricata* is an active predator that feeds primarily on benthic invertebrates, although it has been observed feeding on algal and detrital material. In areas containing abundant prey, both motile and sessile in habit, the leather star seems to exhibit a "preference" for the sessile forms, in that sessile species are eaten more often than the motile forms. Asteroid feeding behavior experiments by Landenberger (1968) and Mauzey et al. (1968), showed that the sea star *Pisaster ochraceus* exhibited preferences for sedentary mussels to alternative food items offered them. Paine (1969) suggested that few additional prey species are consumed as long as mussels are available to *P. ochraceus*. Landenberger (1968) also found that *Pisaster giganteus* preferred mussels to four gastropod species which were offered to the asteroids as alternative prey. Additional observations by Rosenthal (1971) indicated that, in nature, *P. giganteus* displayed a preference for prey which was either immobilized or sedentary in habit.

Feder (1959) felt that differences in the diet of *P. ochraceus* were largely dependent on changes in prey availability within each intertidal location. A similar situation appears to exist with *D. imbricata*, at least in those regions where feeding observations have been made. Mauzey et al. (1968) found *D. imbricata* to be a major predator of actinians along the rocky outer coast of Washington; yet, in the protected San Juan Islands, its diet was composed primarily of holothurians. At Waddah and Tatoosh Islands off

Washington, they observed *D. imbricata* feeding on encrusting sponges, colonial tunicates, hydroids, and calcareous ectoprocts. Other localities indicate still additional diets. Feder (personal communication) observed leather stars with stomachs everted on eel grass, *Zostera marina*, in the intertidal regions of Prince William Sound, Alaska.

Off Pt. Loma, California we have observed *D. imbricata* feeding on *Strongylocentrotus purpuratus* (sea urchin), *Strongylocentrotus franciscanus* (sea urchin), *Astrometis sertulifera* (sea star), *Pisaster giganteus* (sea star), *Tethya aurantia* (sponge), *Leucilla nuttingi* (sponge), *Membranipora membranacea* (bryozoan), *Epiactis prolifera* (sea anemone), *Corynactis californica* (sea anemone), *Astrangia lajollaensis* (coral), *Muricea californica* (gorgonian), *Kelletia kelletii* (gastropod) egg capsules, unidentified sponges, holothurians, and detritus. *Strongylocentrotus purpuratus* made up 47% of the feeding observations; *L. nuttingi*, 13%; *A. sertulifera*, 4%; detritus, 27%; and all other items combined, 9%, out of a total of 437 feeding leather stars (Figure 1). Over a one-year period, 927 *D. imbricata* were examined for food items; however, some of these observations were repetitive in that the same leather star was re-examined on a different day of observation.

Feeding was accomplished by either ingesting the prey whole or by everting the stomach and

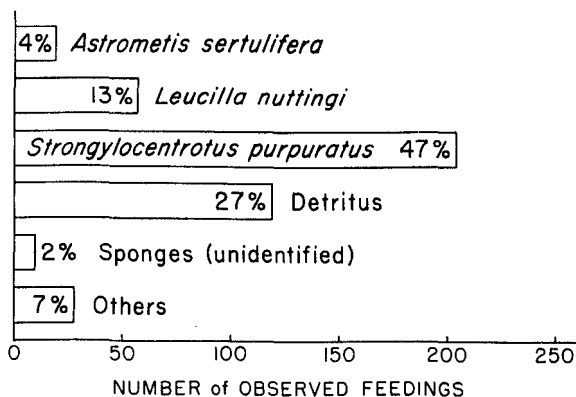


FIGURE 1.—Leather star feeding observations ($N = 437$) off Pt. Loma, California from November, 1969 through November, 1970.

digesting the prey outside of the mouth. Most of the feeding we observed was extraoral in that the leather star's stomach was partially everted out of the mouth (Figure 2). However, the distinction between the two types of asteroid digestion cannot always be determined, since "some species may digest prey partly inside and partly outside the mouth opening at the same time," (Feder and Christensen, 1966, p. 96). In contrast to our observations off Pt. Loma, Mauzey et al. (1968) found that *D. imbricata* usually ingested its prey whole. Again, digestion and method of feeding appears to be dependent on the size and form of the prey species. Often leather stars were observed with their stomachs extended into depressions or everted onto the substrata. In this situation we usually could not identify the food item; however, if the leather star's stomach was everted and there was no prey visible, we assumed that it was feeding on detritus. When feeding observations from the various regions are examined in total, the leather star appears to have a highly variable diet; however, when each location is considered separately the diet becomes much more specialized or restricted.

PREDATION ON

Strongylocentrotus purpuratus

Our data indicate that the leather star is a major predator of *S. purpuratus* off Pt. Loma. Of the 437 *D. imbricata* observed feeding, 204 or 47% were preying on *S. purpuratus* (Figure 1). However, this feeding behavior may be an areal phenomenon or even specific to Pt. Loma, since purple urchin predation by leather stars has not been reported from other regions along the Pacific Coast. Mauzey et al. (1968) did not find urchins included in the diets of *D. imbricata* off the coast of Washington, despite the presence of *S. purpuratus*, *S. franciscanus*, and *S. dröbachiensis*. All three of these echinoid species appeared to be available to the *D. imbricata* that inhabited these subtidal areas (Dayton, personal communication). One explanation for the exclusion of urchins in the diets of leather stars off Washington might be the availability of alternate or "preferred" prey species. The seden-

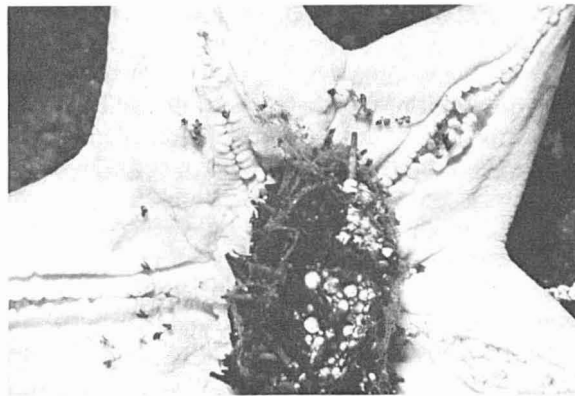


FIGURE 2.—*Dermasterias imbricata* feeding on a purple urchin 15 m underwater off Pt. Loma. Note the *S. purpuratus* pedicellariae attached to the leather star's epidermis.

tary or sessile invertebrates which Mauzey et al. (1968) found in the diets of *D. imbricata* off Washington did not appear to be important numerical constituents of the epibenthic community off the Pt. Loma study site. However, the sea urchin population had increased to a point where Leighton, Jones, and North (1966) suggested that perhaps an ecological imbalance had developed within these stands of giant kelp. Further, North and Pearse (1970) reported that an apparent population "explosion" of herbivorous sea urchins had occurred along the coast of Southern California.

In addition to the high percentage of leather stars observed eating purple urchins, we found that 51% of all *D. imbricata* examined off Pt. Loma had *S. purpuratus* globiferous pedicellariae attached to their epidermis (Figures 2 and 3). A laboratory experiment was performed to determine the maximum length of time that globiferous pedicellariae remain attached to the leather star following contact with a purple urchin. We found that following attachment, 3 to 4 days elapsed before the pedicellariae detached from the leather stars. A *D. imbricata* with purple urchin pedicellariae attached to it provided us with indirect evidence that the leather star had either eaten, or had contact with, one or more purple urchins within the last 3 to 4 days. In either case, the number of

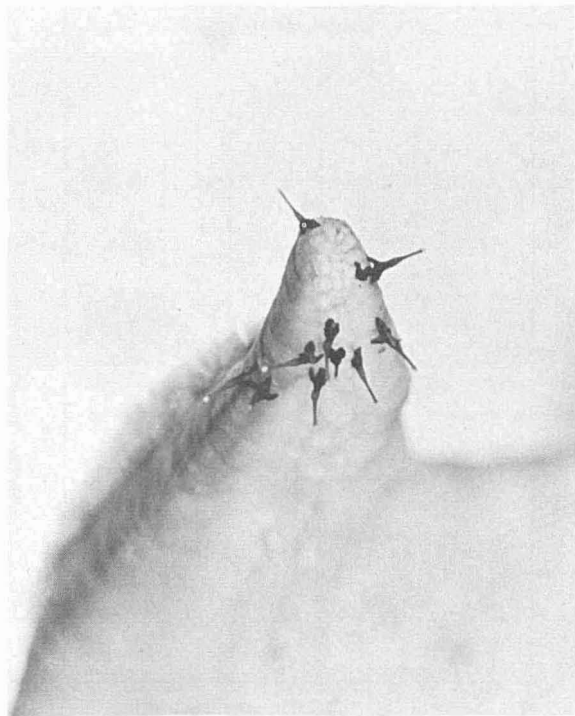


FIGURE 3.—Globiferous pedicellariae from *S. purpuratus* attached to the arm of a leather star following contact between the two species in the laboratory.

contacts between the two species off Pt. Loma appears to be quite frequent.

Both species are conspicuous and abundant members of the benthic community within the study area. *Strongylocentrotus purpuratus* was found in densities between 0 and 100 individuals per m^2 , with $30.2/m^2$ as the mean value within the 16 randomly placed m^2 quadrats. Purple urchin density appeared to vary with the type of substratum. The greatest concentrations of purple urchins were found along or within the siltstone ledges.

We found *D. imbricata* in densities between 0 and 7 individuals per 100 m^2 in the 2,400 sq m of sea floor that was examined quantitatively. Leather stars were most abundant near siltstone ledges and rocky outcrops, where the highest concentrations of purple urchins were also found.

In most instances leather stars were observed feeding on purple urchins which were located in

holes or depressions (Figure 4), under ledges, or in the holdfasts of giant kelp. Rarely was urchin predation observed on uniform substratum devoid of irregularities or discontinuities in the bottom. In the field we have observed *S. purpuratus* reacting to the presence of *D. imbricata*. When an approaching leather star disturbed an urchin tactually, it usually evoked a running or escape response. The *S. purpuratus* that inhabited substrata where avoidance maneuvers were possible usually escaped from pursuing leather stars. However, when purple urchins occupied depressions or irregularities along the sea floor, they became more vulnerable to asteroid entrapment and predation.



FIGURE 4.—Leather star feeding on a purple urchin. The sea star has pressed its oral surface into a depression to reach the prey.

In the laboratory most of the purple urchins that were preyed upon were captured on the sides of the water table at the water-air interface. Predation, in this case, appeared to be an artifact of the aquarium, since the two species do not experience this water-air barrier in the sublittoral zone. However, this interface was one of the few physical obstacles besides the corners of the water table that hampered the escape of the purple urchin, and thus allowed a pursuing leather star to capture it. In a similar observation, Mauzey et al. (1968) found that *S.*

purpuratus tended to move to the top of a tank and stop when pursued by *P. helianthoides* in the laboratory.

The 162 *D. imbricata* which were found feeding on whole purple urchins ranged in size (radius) from 79 mm to 166 mm, with 118 mm as the mean value. In comparison, a sample ($N = 344$) of the leather star population within the perimeter of the study area contained individuals from 50 mm to 202 mm and had a mean size value of 108 mm. The purple urchins that were preyed upon ranged from 12 mm to 52 mm in test diameter, with a mean value of 34 mm and a standard deviation of 8.5 mm. For comparative purposes we removed 494 *S. purpuratus* from 16 randomly selected m^2 quadrats. These urchins ranged from 7 mm to 60 mm in diameter and had a mean value of 39 mm and a standard deviation of 8.8 mm. Using these data we compared the mean of the *S. purpuratus* prey and the mean of the urchin population using a *t*-test. We found that at the 5% level there was a significant difference between the two means. It appeared as though the *D. imbricata* were feeding on a smaller size class of *S. purpuratus* than was available to them from the urchin population (Figure 5).

Landenberger (1968) found that in the laboratory large *Pisaster* spp. tended to eat large mussels. To determine if an optimal predator-prey size relationship existed between *D. imbricata* and *S. purpuratus*, the size of each predator and its prey was recorded as a point on a scatter diagram (Figure 6). A non-parametric corner test of association or independence was then applied to these data. We found that the two variables (predator size and prey size) were independent at the 95% level of significance. Therefore, no association between the size of a leather star predator and the size of a purple urchin prey is believed to exist. There was, however, an upper limit to prey size in that we observed no predation on purple urchins greater than 52 mm in test diameter.

FEEDING AND DIGESTION RATES

Most of the purple urchins we observed were killed and digested extraorally by leather stars

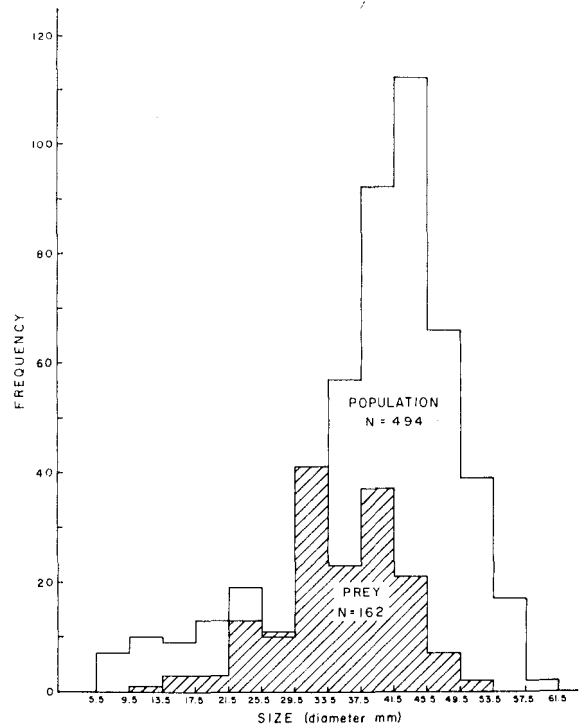


FIGURE 5.—A size frequency histogram comparing the 162 *S. purpuratus* prey with a sample ($N = 494$) from the urchin population within the Pt. Loma study area.

following capture. However, purple urchins smaller than about 22 mm in test diameter were usually ingested whole. Kjerskog-Agersborg (1918) found that the sea star, *Pycnopodia helianthoides*, digested large prey extraorally, whereas smaller prey were regularly ingested whole.

Determining the feeding rate or number of purple urchins which can be eaten by a leather star over a given period of time was perhaps the most inconclusive aspect of the study. The experiment where leather stars and purple urchins were confined within a 4 m^2 area provided little information on feeding rates in nature. Although three urchins were eaten during the first seven days of observation, we observed no further predation after this initial period. We concluded that the enclosure interfered with the normal movements of the experimental animals, since the four leather stars were fre-

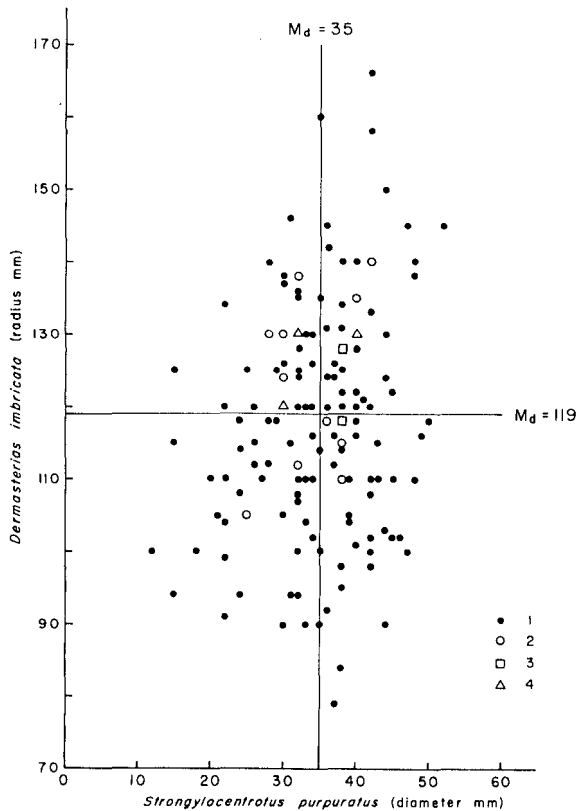


FIGURE 6.—Size of the leather star predator vs the size of the purple urchin prey. Open symbols indicate two or more identical data points.

quently observed crawling on the frame or the wire mesh of the cage.

Our tagging efforts in the field proved to be somewhat more valuable. The disc tags remained attached to the leather stars for at least eight months. During this period we were able to study the feeding behavior of tagged *D. imbricata* on an individual basis. The tagging procedure might have inhibited normal feeding behavior in *D. imbricata*; however, we observed leather stars actively feeding within three days after being marked. Out of 69 marked individuals, the maximum rate of urchin predation occurred with a 151-mm leather star. This individual was observed feeding on three purple urchins (32-36 mm) during seven consecutive days of underwater observations.

Laboratory feeding observations were carried

out for 20 days. During this period every one of the seven *D. imbricata* in the water table preyed on at least one *S. purpuratus*. One leather star (140 mm) fed on three purple urchins (16-38 mm) during a five-day period. Sixteen of the 76 *S. purpuratus* present were eaten by the leather stars. The prey ranged from 15 mm to 42 mm in diameter.

From these observations it was learned that the digestion of a purple urchin's soft tissues usually took between 20 and 48 hours. However, on one occasion a 138-mm *D. imbricata* completely digested a 22-mm purple urchin in seven hours. Fisher (1928) reported that *P. helianthoides* digested the soft parts of *Strongylocentrotus* spp. in 24 to 36 hours. The digestion rate varied with the size of the leather star and the size of the prey, as well as the method of digestion. Large purple urchins (≥ 22 mm), which were usually digested extraorally, were not digested as rapidly as smaller urchins. As an example, 19 hours were required for a 140-mm leather star to digest a 16-mm purple urchin, whereas 28 hours were required for this same leather star to digest a 38-mm purple urchin.

As pointed out in the section on methodology, it was usually necessary to lift up or turn the leather star over to determine whether or not it was feeding on an urchin. In the laboratory, when we disturbed a leather star that had captured or was in the process of digesting a purple urchin, it retracted its stomach, released hold of the urchin, and moved away from the prey. A similar disruption in feeding behavior was also noticed in the field. By marking the *D. imbricata* we had a method which we thought would allow us to study the feeding behavior of individual leather stars in nature. However, the tactile sensitivity that most members of this species displayed negated most of the benefit attained from individual recognition.

One physical factor in nature which appeared to influence predation on *S. purpuratus* by *D. imbricata* was water turbulence. The incidence of urchin predation decreased when a long-period swell generated a strong surge along the bottom off Pt. Loma. For example, on 9 January 1970, we recorded 48% of the *D. imbricata* ob-

served ($N = 60$) to be feeding on *S. purpuratus*; in contrast in this same area on 3 June 1970, only 13% of the leather stars observed ($N = 58$) were eating urchins. On the former day we noted that it was extremely calm underwater, while on the latter a very strong surge prevailed along the bottom at a depth of 15 m. We felt that there was a correlation between water movement and urchin predation by *D. imbricata*, although we had no quantitative measurement of this parameter. Feder (1956 and 1970) found that populations of *P. ochraceus* ate much less in relatively unprotected intertidal areas than in areas which provided the sea stars better protection from wave action.

SPECIES-SPECIFIC REACTIONS

Strongylocentrotus purpuratus reacted to the presence of *D. imbricata* by exhibiting defensive, as well as escape or avoidance, responses. No visible responses were exhibited by *S. purpuratus* which could be considered predator-induced until it was actually touched by a leather star. The podia or tube feet of the purple urchin appeared to be active sites for the reception of chemical and tactile stimuli (Figure 7). In regular urchins, such as *S. purpuratus*, the podia are symmetrically spaced and arranged in five double rows along the sea urchin's test. These

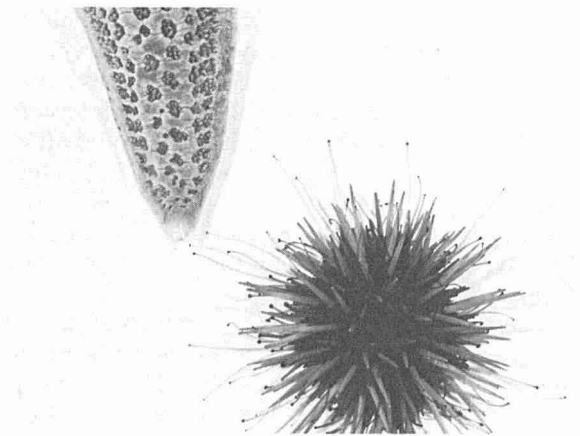


FIGURE 7.—*S. purpuratus* with extended podia just prior to initial contact with the arm of a leather star.

podia are capable of extending nearly twice the length of the primary spines and function somewhat like the tentacles or antennae of other marine invertebrates. If viewed from the aboral surface, the area of sensory reception surrounding *S. purpuratus* can best be illustrated by drawing a circle around the urchin, with the locus of the points touching the tips of the fully extended podia.

In the laboratory sea urchin podia were touched with various biotic and abiotic objects to determine which ones elicited avoidance or defensive responses. When touched with human skin, a glass rod, or a "non-predatory" invertebrate, the podia in contact usually retracted and then were extended again. However, if the podia of a purple urchin touched a leather star, the urchin displayed definite signs of predator awareness: in the region of the tactile stimulus, the podia retracted rapidly, spines were depressed, and the poisonous globiferous pedicellariae gaped and became erect (Figure 8). In most instances the urchins moved in the opposite direction of the leather star stimulus.

In another experiment we tested the response of *S. purpuratus* to additional stimuli, using the gaping of the globiferous pedicellariae as an overt sign of predator recognition. The test animals were taken from two populations of *S. purpuratus*. One group was from the jetty in-

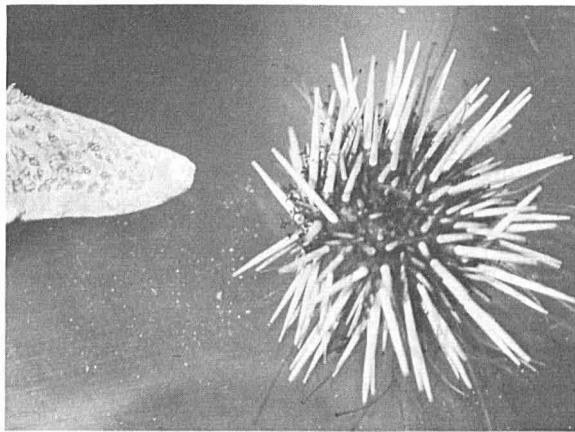


FIGURE 8.—The defensive behavior of *S. purpuratus* immediately after being touched by *D. imbricata*.

side Mission Bay, San Diego County (lat 32° 45'30" N; long 117°14'30" W), and the other was from the study site off Pt. Loma. Asteroid tube feet were selected as the biotic stimuli because of the known effectiveness of this tissue in eliciting avoidance reactions in other invertebrate species (Bullock, 1953). Coarse, washed sand grains were used as the abiotic control. Purple urchins were placed individually into glass bowls which contained seawater, and then an asteroid tube foot, or sand grain, was dropped onto the urchin's test. Each urchin was tested for a 2-min period using a different stimulus on each run. Fresh seawater was placed into the bowls prior to each test. The tube feet of *D. imbricata* elicited gaping and erection of purple urchin globiferous pedicellariae in 28 out of 30 test animals. These 28 individuals had an average reaction time of 8 sec, with a range between 2 and 20 sec. None of the *S. purpuratus* displayed gaped globiferous pedicellariae when either *Pisaster giganteus* tube feet or sand grains were presented to them.

Additional asteroids that were found in the sublittoral zone off Pt. Loma were also tested. The tube feet from *Astrometis sertulifera*, *Patiria miniata*, and *Pycnopodia helianthoides* evoked the pedicellariae response in *S. purpuratus*; however, no response was elicited when eight other asteroid species were tested (Table 1). It is interesting to note that the former three species were the only other sea stars, besides *D. imbricata*, that have been observed feeding on live *S. purpuratus* off Pt. Loma.

TABLE 1.—A list of sea stars found off Pt. Loma, California. All 12 species were individually used to test the globiferous pedicellariae response in *S. purpuratus*.

Species	Reaction
<i>Astrometis sertulifera</i>	+
<i>Astropecten armatus</i>	—
<i>Dermasterias imbricata</i>	+
<i>Henricia leviuscula</i>	—
<i>Linckia columbiana</i>	—
<i>Mediaster aequalis</i>	—
<i>Patiria miniata</i>	+
<i>Pisaster brevispinus</i>	—
<i>Pisaster giganteus</i>	—
<i>Pisaster ochraceus</i>	—
<i>Orthasterias koehleri</i>	—
<i>Pycnopodia helianthoides</i>	+

+ = pedicellariae response
 — = no pedicellariae response

The erection and gaping of the globiferous pedicellariae initially occurred only on the area of the urchins' test which was directly stimulated by the sea star's tube foot. Jensen (1966) found that a single tube foot from the sea star, *Marthasterias glacialis*, activated the globiferous pedicellariae only in a restricted area on the test of the sea urchin, *Psammechinus miliaris*, whereas the sea star arm tip caused a response from all globiferous pedicellariae. In contrast, we found that the arm tip of *D. imbricata* activated the pedicellariae of *S. purpuratus* only in the region of the stimulus. The defensive response and recognition of predatory stimuli was so acute in *S. purpuratus* that an arm of a *P. giganteus* placed on one side of a purple urchin's test, and a *D. imbricata* arm positioned on the opposite side elicited a response from the globiferous pedicellariae only in the area of leather star contact.

Defensive use of globiferous pedicellariae by sea urchins when disturbed by predatory asteroids has been described by Prouho (1890), Jennings (1907), Jensen (1966), Mauzey et al. (1968), and Rosenthal and Chess (1970). Jensen (1966) reported that the poison contained in globiferous pedicellariae of *Psammechinus miliaris* was not strong enough to paralyze a *M. glacialis*; however, it did have an irritating effect on the sea star which caused it to retreat from the urchin. We found that in some laboratory situations, globiferous pedicellariae bites on the arms of *D. imbricata* caused localized withdrawal of gills or papulae, and a shortening or retraction of the affected arm. Despite this irritation, 90% of all the leather stars we found feeding on purple urchins had from one to over 300 sea urchin pedicellariae attached to their epidermis.

Certain groups of aquatic organisms have been observed to respond to chemical signals or alarm substances emitted by injured conspecifics (von Frisch, 1941; Pfeiffer, 1963; Snyder and Snyder, 1970). Recently, Snyder and Snyder (1970) found that the tropical sea urchin, *Diadema antillarum*, exhibited an alarm or escape response when stimulated with the juices of injured members of its own species. Laboratory and field

tests were conducted to determine if a similar alarm response existed in *S. purpuratus*. A purple urchin within a group of urchins was crushed underwater, and the reactions of neighboring conspecifics noted for 5 min. In both situations we observed no change in movement or alteration in behavior which could be considered alarm oriented following injury to a conspecific. In place of an alarm response we occasionally noted an entirely different reaction from *S. purpuratus* in the laboratory. If a leather star was disturbed while feeding on a purple urchin or moved away from an urchin test following predation, occasionally other *S. purpuratus* in the aquaria approached the conspecific and scavenged the remains.

DISCUSSION

The behavioral responses exhibited by *S. purpuratus* when it is disturbed by *D. imbricata* suggest a well-developed predator-prey relationship. In most instances purple urchins erected globiferous pedicellariae when touched by the four sea stars (*D. imbricata*, *P. helianthoides*, *A. sertulifera*, and *P. miniata*) which are known to prey upon them. In contrast, no evasive or defensive responses were noted in the same purple urchins when they were touched by eight additional asteroid species. It appears as though *S. purpuratus* either responds to sea stars that are biochemically similar, or through selection the urchin has acquired the ability to recognize particular asteroid species as potential predators.

The predator-prey association which exists between these two species off Pt. Loma, California may be a regional phenomenon, since the relationship has not been reported from other localities along the Pacific Coast. However, from the responses in both laboratory and field situations we believe that the occurrence is probably more widespread than indicated in the literature. The large number (47%) of *S. purpuratus* we found included in the overall diets of leather stars off Pt. Loma, as opposed to the total exclusion of this species in the diets of leather stars off Washington state as reported by Mauzey et al. (1968) is extremely puzzling to us. We can only spec-

ulate at this time on what could account for this variation in feeding behavior. Selection of potential prey by *D. imbricata* may be determined by the following conditions: (1) Prey density and availability, (2) search time or the time required by the sea star to find and capture suitable prey, (3) taste or gustatory preferences of the sea star, and (4) some form of associative learning by *D. imbricata*.

Strongylocentrotus purpuratus appeared to be available to *D. imbricata* on almost a continuous basis within the study area, since the population of purple urchins was estimated to have a mean density value of 30.2/m². Predator search and capture time also seems to be related to the density and distribution patterns of the prey, as well as to the avoidance tactics employed by these potential prey. Encounters between the two species on uniform substratum usually resulted in the escape of *S. purpuratus*; however, when the purple urchins occupied depressions, holes, or crevices along the sea floor, they became more vulnerable to asteroid predation. In response to asteroid predation *S. purpuratus* has apparently evolved countermeasures such as evasive movement, and defensive utilization of spines and poisonous globiferous pedicellariae. The large number (90%) of feeding leather stars with purple urchin pedicellariae attached to their epidermis might lead one to suspect that these appendages are ineffective as a defensive mechanism. The pedicellariae, however, appear to act as an irritant that in certain situations halts the pursuit of a leather star and thus allows the urchin to escape. Marler and Hamilton (1966, p. 142) stated that "there is evidently a subtle and dynamic balance between these different evasive characteristics of the prey species on the one hand and the abilities of the predators to overcome them on the other". The taste or gustatory preferences of individual *D. imbricata* as compared to a leather star population has not been explored.

From our observations off Pt. Loma we would expect that at least a few purple urchins would show up in the diets of *D. imbricata* off Washington, even if other species were "preferred" above *S. purpuratus*. Possibly before leather stars prey on live urchins there is a learning

process involved before the sea star recognizes or associates specific stimuli with food. Tinbergen (1960) proposed that learning was involved in the feeding behavior of insect-eating birds, and that initial non-acceptance of specific insects by these birds was due to an unfamiliarity with these forms as prey. He further related initiation of feeding on a new food item with chance experience and prey density. Tinbergen (1960) suggested that the predator acquires a "specific search image" for the prey after being sufficiently impressed with it from frequent chance encounters. Holling (1958 and 1965) studied predation on the cocooned pupae of sawflies by shrews and mice, and suggested that associative learning was an important component in the feeding behavior of these small mammals.

Unfortunately, associative learning has been studied in only a relatively small number of lower animal (invertebrate) groups. Evans (1968) discussed this form of learning in cephalopods, insects, annelids, and flatworms. There is some evidence to suggest that associative learning exists in echinoderms. Landenberger (1966) found that the sea star *P. giganteus* learned to associate a light stimulus with food. The association apparently disappeared when the response to the light stimulus was no longer rewarded with food. If associative learning, with food as a reinforcement or reward, is a component in the feeding behavior of *D. imbricata*, then it might account for the presence of purple urchins in the diets of leather stars off Pt. Loma. This area contained a large number of highly accessible *S. purpuratus*, and yet at the same time appeared to be practically devoid of many of the sessile or sedentary invertebrates that these sea stars are reported to feed on. *Derma-sterias imbricata* probably responds to a small class of chemical and/or tactile stimuli; however, only through associative learning and experience can it exploit an evasive prey species such as *S. purpuratus*. The leather star may not acquire the experience necessary to capture live *S. purpuratus* in other subtidal areas that contain alternate prey in greater abundance, since these forms are more accessible and possibly can account for the total nutrient requirements of *D. imbricata*.

ACKNOWLEDGMENTS

We especially wish to thank W. D. Clarke, P. K. Dayton, T. A. Ebert, H. M. Feder, and H. R. Melchior for stimulating discussions and critical evaluation of this manuscript. We also wish to thank Virginia Moore who prepared Figures 1, 5, and 6. Westinghouse Ocean Research Laboratory assisted in financial support of this study and the National Marine Fisheries Service generously provided laboratory facilities at the Southwest Fisheries Center, La Jolla, California.

LITERATURE CITED

- BULLOCK, T. H.
1953. Predator recognition and escape responses of some intertidal gastropods in presence of starfish. *Behav.* 5: 130-140.
- EVANS, S. M.
1968. *Studies in invertebrate behavior.* Heinemann Educational Books Ltd. London. 110 p.
- FEDER, H. M.
1956. Natural history studies on the starfish, *Pisaster ochraceus* (Brandt, 1835) in the Monterey Bay area. Doctoral dissertation, Stanford University. 294 p.
1959. The food of the starfish, *Pisaster ochraceus*, along the California Coast. *Ecol.* 40: 721-724.
1970. Growth and predation by the ochre sea star, *Pisaster ochraceus* (Brandt), in Monterey Bay, California. *Ophelia.* 8: 161-185.
- FEDER, H. M., AND A. M. CHRISTENSEN.
1966. Aspects of asteroid biology. In R. A. Boo-lottian (editor), *Physiology of Echinodermata.* p. 87-127. Interscience Publishers, New York.
- FISHER, W. K.
1928. Asteroidea of the North Pacific and adjacent waters. Part II, *Bull. U.S. Nat. Mus.*, 76: 245 p.
1930. Asteroidea of the North Pacific and adjacent waters. Part III, *Bull. U.S. Nat. Mus.*, 76: 356 p.
- FRISCH, K. VON.
1941. Über einen Schreckstoff der Fischhaut und seine biologische Bedeutung. *Z. Vergl. Physiol.* 29: 46-145.
- HOLLING, C. S.
1958. Sensory stimuli involved in the location and selection of sawfly cocoons by small mammals. *Can. J. Zool.* 36: 633-635.
1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45:1-60.
- JENNINGS, H. S.
1907. Behavior of the starfish *Asterias forreri* De Loriol. *Univ. Calif. Publ. Zool.* 4(2):53-185.

- JENSEN, M.
1966. The response of two sea urchins to the sea star *Marthasterias glacialis* (L.) and other stimuli. *Ophelia*. 3:209-219.
- KJERSKOG-AGERSBORG, H. P.
1918. Bilateral tendencies and habits in the twenty-rayed starfish *Pycnopodia helianthoides* (Stimpson). *Biol. Bull. Mar. Biol. Lab., Woods Hole*. 35: 232-254.
- LANDENBERGER, D. E.
1966. Learning in the pacific starfish *Pisaster giganteus*. *Anim. Behav.* 14:414-418.
1968. Studies on selective feeding in the Pacific starfish *Pisaster* in Southern California. *Ecol.* 49:1062-1075.
- LEIGHTON, D. L., L. G. JONES, AND W. J. NORTH.
1966. Ecological relationships between giant kelp and sea urchins in Southern California. *Proc. 5th Intl. Seaweed Symp.*, p. 141-153. Pergamon Press, Oxford.
- LEIGHTON, D. L.
1971. Grazing activities of benthic invertebrates in Southern California kelp beds. *In* W. J. North (editor), *The Biology of Giant Kelp Beds (Macrocystis)* in California, p. 421-453. Verlag von J. Cramer, Germany.
- MARLER, P., AND W. J. HAMILTON, III.
1966. *Mechanisms of animal behavior*. J. Wiley and Sons, New York. 771 p.
- MAUZEY, K. P., C. BIRKELAND, AND P. K. DAYTON.
1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. *Ecol.* 49:603-619.
- NORTH, W. J., AND J. S. PEARSE.
1970. Sea urchin population explosion in Southern California coastal waters. *Science* 167(3915):209.
- PAINE, ROBERT T.
1969. The *Pisaster-Tegula* interaction: prey patches, predator food preference and intertidal community structure. *Ecol.* 50:950-961.
- PFEIFFER, W.
1963. The fright reaction in North American fish. *Can. J. Zool.*, 41:69-77.
- PROUHO, H.
1890. Du role des pedicellaires gemmiformes des oursins. *C. r. hebd. Seanc. Acad. Sci., Paris III*: 62-64.
- RICKETTS, EDWARD F., AND JACK CALVIN.
1962. *Between Pacific Tides*. Stanford Univ. Press, Stanford, 516 p.
- ROSENTHAL, R. J., AND J. R. CHESSE.
1970. Predation on the purple urchin by the leather star. *Calif. Fish and Game*, 56:203-204.
- ROSENTHAL, RICHARD J.
1971. Trophic interaction between the sea star *Pisaster giganteus* and the gastropod *Kelletia kelletii*. *Fish. Bull. U.S.* 69:669-679.
- SNYDER, N., AND H. SNYDER.
1970. Alarm response of *Diadema antillarum*. *Science*. 168(3928):276-278.
- TINBERGEN, L.
1960. The natural control of insects in pine woods. *Arch. Neerl. Zool.* 13:265-343.
- WOOD, L.
1968. Physiological and ecological aspects of prey selection by the marine gastropod *Urosalpinx cinerea* (Prosobranchia: Muricidae). *Malacol.* 6: 267-320.