A CONTRIBUTION TO THE BIOLOGY OF A DEEP SEA ECHINOID, ALLOCENTROTUS FRAGILIS (JACKSON)[1]

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In February, 1957, a hydrographic team[3] from the Hopkins Marine Station accidentally discovered a bed of *Allocentrotus fragilis* (Swann, 1953) at a depth of 68 to 98 fathoms in Monterey Bay, California. This discovery was made during a routine hydrographic run. At the time a mid-water plankton haul with a standard one-meter net was in progress. The Hopkins Marine Station research vessel, the "Tage," had apparently drifted with the onshore current. When the net was surfaced, to their surprise and delight, the team found approximately two dozen specimens of the deep sea urchin, *Allocentrotus.* This was the first time that the animal had been obtained alive and intact in large numbers. At this spot the fathometer indicated 80 fathoms and a radio "fix" recorded the position of the boat to be 36°37′54″ N and 122°01′12″ W. All subsequent hauls were started from this station.

Since a project on the biology of the shore sea urchins, *Strongylocentrotus purpuratus* and *S. franciscanus,* was in progress at the Hopkins Marine Station, the chance finding of a bed of the deep sea urchins was of immediate comparative interest. Consequently, whenever possible, studies were made on the biology of *Allocentrotus* for comparison with *Strongylocentrotus.*

The oceanographic vessel, "Tage," was used for all work reported here. For dredging a four-meter beam trawl was employed. The average dredging time was twenty minutes. The entire sample, consisting of a variety of organisms, was brought into the laboratory in live condition in a tub of sea water. The animals were sorted and placed in separate tanks of running sea water. The species were identified and at times the number of individuals counted.

The gonad index of the sea urchins, indicating the reproductive condition of the urchins, was determined as in previous studies, as were also the biochemical constituents of body fluid and tissues (Lasker and Giese, 1954; Bennett and Giese, 1955).

Habitat of Allocentrotus

Some of the physical features of the habitat of *Allocentrotus* should be considered in order to gain an understanding of the conditions under which this species

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lives in this area in Monterey Bay. By systematic grid dredging, the area of the sea urchin bed was estimated to be about one square mile. The depth of the area in which the urchins were taken varies between 55 to 90 fathoms, the shallow part of the bed lying on the continental shelf, the deeper part bordering the Monterey Canyon.

Dredges at various depths indicate that the larger animals tend to inhabit the deeper regions near the Canyon, whereas the smaller animals are more frequently found in shallower areas. These results are summarized in Table I.

The area nearest the Canyon is relatively flat and is composed of gravel and sand overlying gray silt (Galliher, 1932a, 1932b). From time to time, however, large boulders mainly of granite and shale, the largest of which weighed approximately 15 kilograms, were brought up in the dredge. In the shale young urchins were frequently observed in their burrows, as illustrated in Figure 1E. As the shoreline is approached the configuration of the bottom is somewhat changed, consisting mainly of granitic rock and coarse sand.

TABLE I

Sizes of Allocentrotus taken at various depths

Bathymetrical range in fathoms	Range in size of test diameter* in mm.
55–65	11.2– 21.3
60–65	11.2– 18.0
68	13.3– 29.4
65–90	55.0–103.3

* The measurement was made across the widest part of the test (the ambitus).

Olga Hartman (1955) has published a photograph of *Allocentrotus* taken at 350 to 400 fathoms in the San Pedro Basin 11 miles northeast of Avalon, Catalina Island, California. It was found in a sandy mud which appears to be relatively flat except for small mounds.

As this species has been taken from 48 to 417 fathoms (Clark, 1912), the data considered in this paper represent only a limited aspect of the habitat of *Allocentrotus*. It is possible that for the larger range over which it occurs, physical conditions other than those described above may obtain.

Animals associated with Allocentrotus

Since the organisms found in the same habitat as *Allocentrotus* may play a role in the ecology of the species, all of the organisms which came up in the beam trawl were identified when possible and counts of their numbers were made to ascertain their relative abundance. These organisms are listed in Table II. It is observed that protozoans, coelenterates, annelids, nematodes, mollusks, arthropods, echinoderms and fishes are found in the association. The interrelationships between the various forms have not been studied.

Because of the random nature of the sampling it is difficult to say much about the relative abundance of the various species in the natural habitat. However, the crab, *Mursia,* is usually obtained, sometimes in large numbers as is the holothuroid, *Stichopus* and an unknown tectibranch. The starfishes *Mediaster, Pycnopodia,*

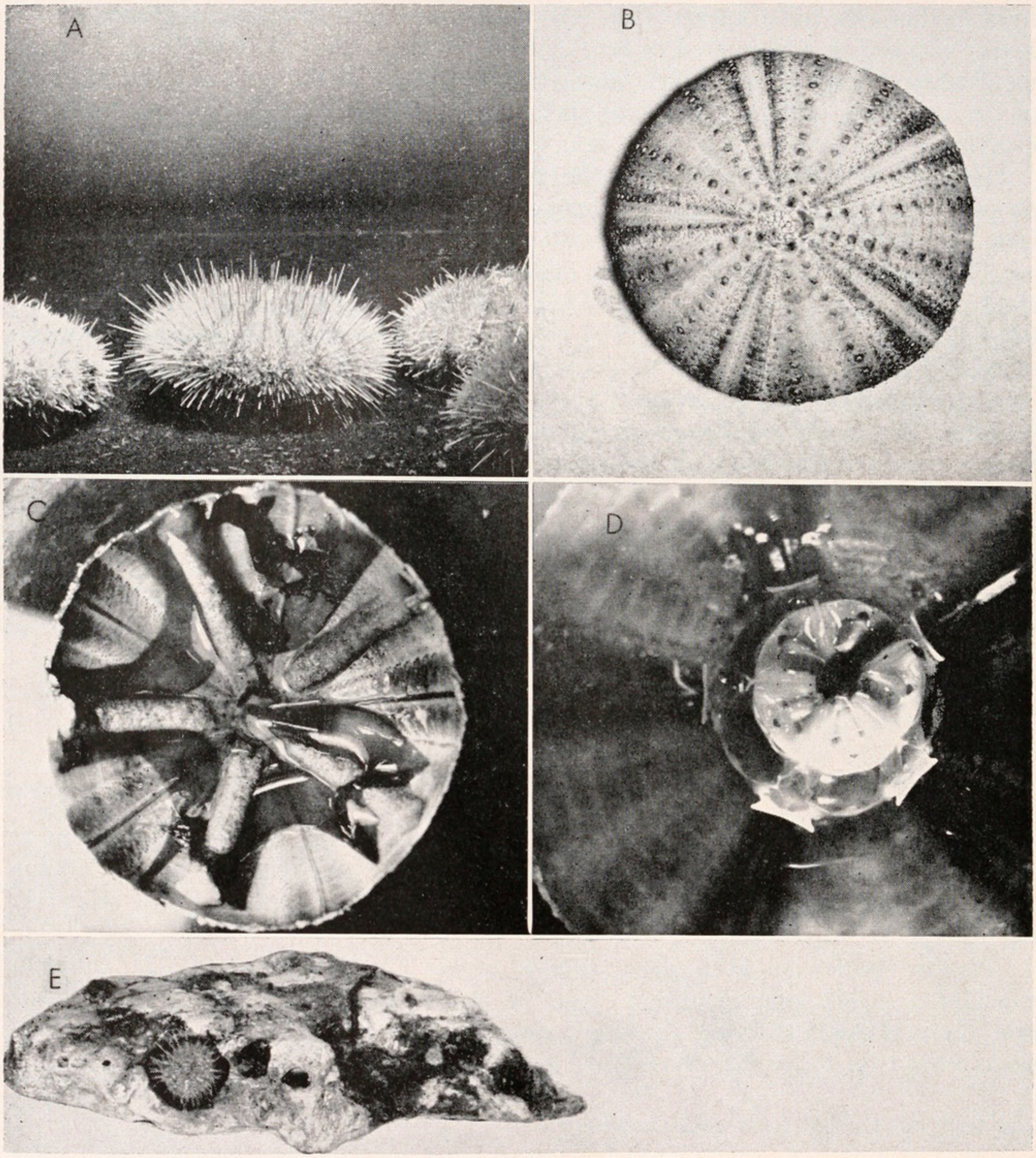

FIGURE 1. A, An adult *Allocentrotus fragilis* 67 mm. in diameter. B, A test of *Allocentrotus fragilis* 73 mm. in diameter. C, A photograph of the aboral half of the shell of *Allocentrotus* showing the gonads. D, The Aristotle's lantern and the peripharyngeal coelom of *Allocentrotus*. E, A specimen of *Allocentrotus fragilis* (15 mm. in diameter) imbedded in its shale burrow.

Henricia, Pteraster and *Astropecten* are also rather likely to be among the specimens brought up in the trawl. From the numerous species and their relative abundance it seems likely that the habitat of *Allocentrotus* is one with relative abundance of food.

Olga Hartman (1955) found *Allocentrotus* in deep waters (350–400 fathoms) in association with a variety of animals (legend to plate 2A): "A two-foot square sample from the bottom yielded glass sponge, many foraminiferans, 20 or more species of annelids, many ophiuroids, and a large percentage of new or little known animals." In her photograph of the benthos a crinoid and a sea star are seen among the numerous *Allocentrotus* which appear to be spaced about a meter from one another.

It is of interest to note that a rhabdocoel parasite similar to *Syndesmus franciscanus* commonly found in the shore urchin (Lehman, 1946) was observed in the gut of several specimens of *Allocentrotus*, and the specimens are of the same size as those found in *Strongylocentrotus*. One, two or three at most, were found in the gut and the incidence of infection was low.

TABLE II

Animals taken in association with Allocentrotus fragilis

Protozoans
- Foraminiferans

Coelenterates
- *Psammogorgus*
- *Metridium senile*

Annelids
- Three different species of polychaetes

Nematodes
- A variety of specimens

Mollusca
- *Rosea pacifica* (octopus)
- Numerous unidentified small gastropods

Arthropods
- Crustaceans
- *Munidopsis* sp.
- *Spirontocaris* sp.
- *Mursia quadichaudii*
- *Paguristes* sp.

Echinoderms
- Asteroids
- *Mediaster aequalis*
- *Pycnopodia helianthoides*
- *Pteraster tessalatus*
- *Henricia aspera*
- *Orthasterias koehleri*

Echinoderms
- *Stylasterias* sp.
- *Astropecten californicus*
- *Luidia foliolata*

Ophiuroids
- *Gorgonocephalus eucnemis*
- Two other species of brittle stars

Holothuroids
- *Stichopus californicus*

Vertebrates
- Fishes representing the following families:
  - Liparidae
  - Agonidae
  - Zoarcidae
  - Ophidiidae
  - Cottidae
  - Batrachoididae
  - Scorpaenidae
  - Bothidae
  - Pleuronectidae
  - Petromyzontidae
    - *Entophenus tridentatus*
  - Rajidae
    - *Raja* sp.
  - Chimaeridae
    - *Hydrolagus colliei*

Nutrition of Allocentrotus

Although the *Allocentrotus* bed occurs in the euphotic zone (down to 200 meters according to Sverdrup *et al.*, 1942), no conspicuous algae have ever come up in our numerous dredgings. The large algae serve as the main food of the shore urchins of the genus *Strongylocentrotus* (Lasker and Giese, 1954; Bennett and Giese, 1955). The sediments collected along with *Allocentrotus* in the dredge hauls consist of a variety of decomposing organic materials in which strands of algae, diatoms, sponge spicules, nematodes, foraminiferan and other shells, as well as other protozoans are found among numerous bacteria. Sometimes live nematodes and protozoans were observed in the mud.

The gut usually contains numerous olive-green pellets measuring 1.2 to 2.8 mm. in diameter, relatively compact but soft in texture. When these pellets are crushed and examined microscopically they are found to contain many small glassy rings (desmids?), foraminiferans, sponge spicules, a variety of diatoms, sand particles and unidentifiable organic particles. Acidification with HCl indicates that most of the skeletal particles are silicious since they do not dissolve. Treatment with concentrated HNO_3 oxidized all the fluffy organic material leaving the silicious diatom skeletons, sponge spicules and glassy rings. In the collection of July 25, 1958 the intestines of all the animals sampled were more completely filled with pellets than in the other collections. The pellets were, in addition, a more vivid green than in all the other cases. Extracts indicated the presence of a brown pigment, fucoxanthin, plus a large amount of chlorophyll. The feeding was correlated with a rich plankton bloom in the surface waters nearby. In the collection made on August 14, 1958, some reddish pellets consisting entirely of organic debris and bacteria were found among the green ones. The constituents of the gut pellets are shown in Figure 2.

Specimens of *Allocentrotus* which survive the hazards of the trip to the surface and arrive at the laboratory in good condition remain alive for many days. When the animals are kept out of water for even a brief time they lose body fluid and air is trapped inside the test, after which they float and die. Normal animals move about the aquaria like *Strongylocentrotus purpuratus,* though less actively, and they adhere less firmly so that they are more readily knocked off by even a small push. They right themselves much more slowly than the purple sea urchin. Attempts were made to feed *Allocentrotus* with boiled potatos, *Phyllospadix* (eel grass) and the algae, *Ulva, Iridaea,* and *Gigartina,* as well as with animal matter such as crushed mussel (*Mytilus*) and crushed deep sea crab (*Mursia*) after several days of fasting. The animals nibbled at some of the algae and at *Mytilus* and *Mursia,* dropping the material after a while, then going down to the bottom of the aquaria to nibble again. It would appear, therefore, that *Allocentrotus* is more selective than *S. purpuratus,* which eats almost any organic material when hungry and shows sustained intake for hours. However, it must be remembered that the specimens are being tested at sea level and at about 15–16° C. whereas they come from a deep sea environment where they are subjected to about 15 atmospheres of pressure and temperatures of about 9° C. It is difficult to say what their behavior might be in their natural environment.

It has been shown that the gonads of a purple sea urchin are probably the main storage organs of the animal, the gonads in a gravid animal increasing to a size which all but obliterates the body cavity left unoccupied by the gut and its contents. The relative mass of the gonads in gravid *Allocentrotus* is much less than that of a gravid *Strongylocentrotus.* At its peak the gonad of *Allocentrotus* is still a delicate structure, both in size and in color (pale creamy-white in the male and yellowish in the female). The gut of an *Allocentrotus* is generally well filled with pellets, but it does not appear to be as full as the gut of the two species of *Strongylocentrotus* studied. It appears, then, that food is generally less available in deeper waters

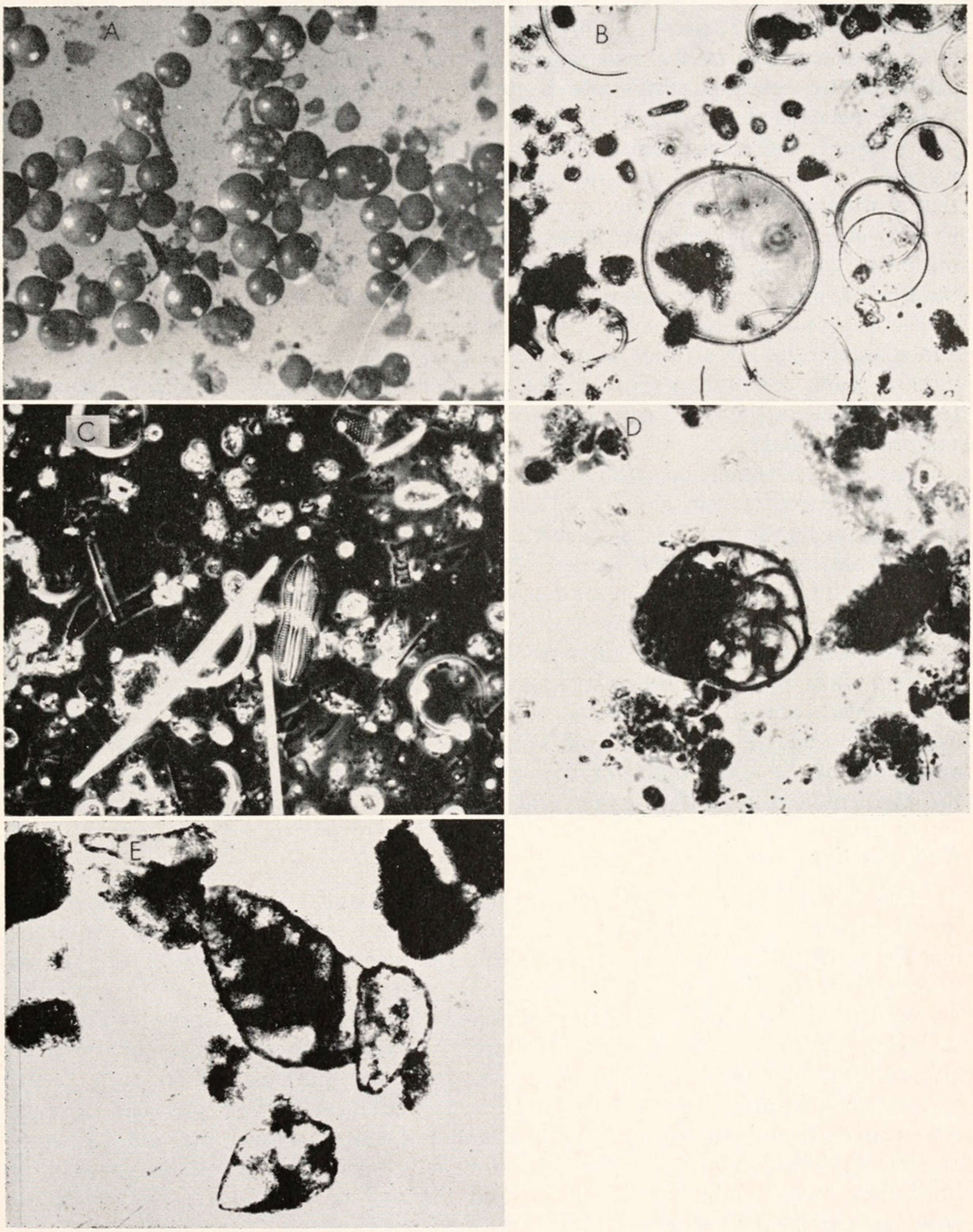

FIGURE 2. Food pellets of *Allocentrotus* as seen under low and high powers. A, Food pellets as removed from the intestine (× 6). B, Crushed food pellets showing desmids (× 60). C, Diatoms and sponge spicules in crushed food pellets (× 60). D and E, Foraminiferans in crushed food pellets (× 60).

than on the shore, except after an unusually rich bloom of plankton as in the collection of July 25, 1958.

Like the gonad of the two species of *Strongylocentrotus* tested, the gonad of *Allocentrotus* contains a little stored glycogen (0.36 to 0.83 per cent or an average of 0.57 per cent of the dry weight), considerable protein (about 30 per cent of the dry weight), and a large store of lipid (an average of about 28 per cent of the dry weight). The chemical constitution of the gonad of *Allocentrotus* is much like that of the gonads of other species of sea urchins although it is smaller in proportion to body size. The perivisceral fluid, which is possibly one of the channels for distribution of the food from the gut, contains nutrients in solution much like the same fluid in the other species of sea urchins tested. Total nitrogen amounted to 3.78 to 4.98 milligrams per cent, non-protein nitrogen to 1.28 to 1.34 milligrams per cent, and a small amount of lipid is present. A variety of cells is present in the perivisceral fluid, resembling those of the other species of sea urchin (Boolootian and Giese, 1958) and a clot forms much as in the other species of sea urchins tested (unpublished data).

Healthy specimens of *Allocentrotus* kept in aquaria at about 15° C. in the laboratory defecate very slowly. This may be an indication of a rather slow rate of digestion but it may be the result of the abnormal conditions in the laboratory. When animals with the gut loaded with food were brought in on July 25, 1958, they defecated copiously. Defecation may therefore depend upon how full the gut is at the time of collection.

All specimens collected sooner or later fall prey to a peculiar disorder. Small spots of dark red color begin to appear on the surface of the test. These spots then spread, covering the animal with large blotches of color. The tube feet degenerate and the spines fall off after which the animal dies. Microscopic examination of the spots indicates that they are composed mainly of dead eleocytes, the pigmented cells of the perivisceral fluid.

Reproduction

The first collection of *Allocentrotus* in February of 1957 contained individuals in full reproductive condition, the gonads of many males and females containing mature gametes in large numbers. The eggs were readily fertilized and normal development to the pluteus followed. Development was best at temperatures between 9°–14° C., cleavage being inhibited by higher temperatures.[4] The same was true for the second collection in March of 1957. However, the gonads of the animals collected in April no longer contained ripe gametes. Thereafter storms and other difficulties prevented collecting the urchins until September of 1957. The gonads of animals sampled in September, October, November and December of 1957 and in January of 1958 were well developed and of relatively large size until they spawned between January and the end of February, 1958, when the next collection was made. The gonads during the second breeding season were never as well developed as those of the first season, nor was as good a development of the embryonic stages observed.[4]

[4] The results on development of *Allocentrotus* are being published by Dr. A. R. Moore in a separate report. We are indebted to Dr. Moore for permitting us to quote here and in footnote 6 from his unpublished data.

The reproductive state of an animal can be ascertained by measuring the ratio of the volume of the gonad to the wet weight of the animal (Lasker and Giese, 1954). This ratio times 100 has been called the gonad index. The average gonad indices determined in this manner are plotted in Figure 3. The course of the

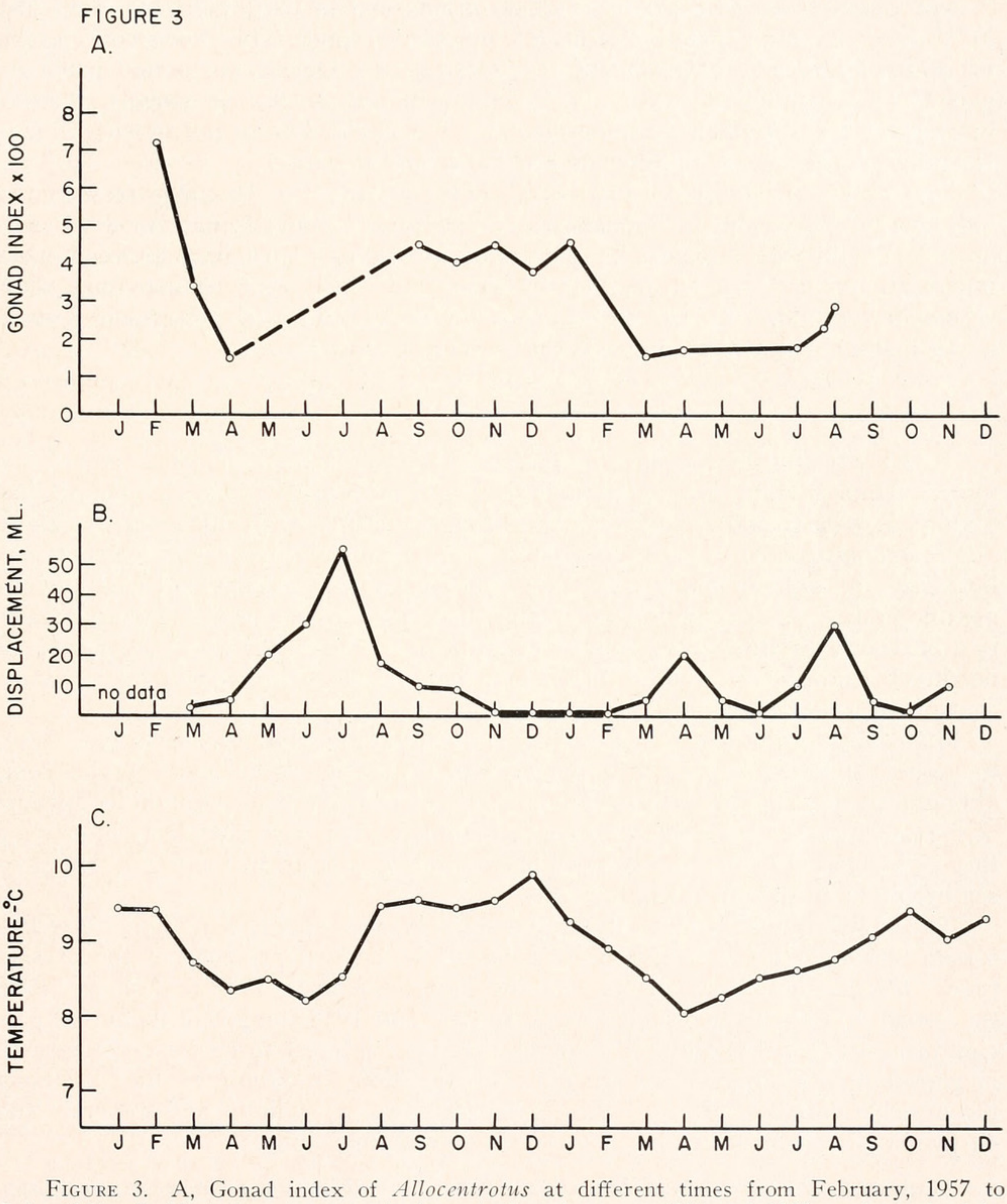

FIGURE 3. A, Gonad index of *Allocentrotus* at different times from February, 1957 to July, 1958. B, Variations in phytoplankton during the years 1954 and 1955 as determined by Barham (1957). C, Variations of thermal monthly averages between 100–200 m. as reported by Skogsberg and Phelps (1946) for the years 1936 and 1937. Same locality as that used in the present study.

curve (dashed line) from April to September, 1957 is not known but since in 1958 the gonads of animals obtained in July were just beginning to enlarge, a period of reproductive quiescence may have occurred from April to the end of June, 1957 as happened in 1958.[5]

All of the urchins used in determining the gonad index were mature, varying in wet weight from 45.5 grams to 264.0 grams and in test diameter[6] from 55.0 to 96 mm. Even a population of mature animals of similar size shows considerable variability in gonadal development at a given time. During the period when the gonads of some individuals are well developed and large, the gonads of other individuals are shrunken or undeveloped. The variability of gonad size is considerably smaller when the gonads are immature or spent.

The great variability in the gonad index during the breeding season may indicate: 1) that some individuals do not have access to adequate food to ripen or to maintain their gonads, 2) that some individuals have just spawned while others are ready to do so, or 3) that some individuals may be immature when others are gravid. A histological study of the gravid and non-gravid gonads might make it possible to decide between these alternatives.

Discussion

It is interesting to compare the biology of *Allocentrotus fragilis* to that of the intertidal sea urchin, *Strongylocentrotus purpuratus* and to that of the subtidal urchin, *S. franciscanus*. Whereas the inshore urchins generally graze on algae, *Allocentrotus* appears to graze on whatever organic material occurs in the substrate, but chiefly on organic detritus, bacteria, and microscopic animals and plants of the organic "rain." *S. purpuratus* is, on the other hand, omnivorous. When trapped in a burrow with an opening smaller than the test diameter it feeds largely on the detritus brought by sea water. In a sense, then, *Allocentrotus* represents an extension of this special feeding habit of *S. purpuratus*.

Allocentrotus lives in a community of invertebrates and fishes perhaps fewer in species and in numbers than the urchins of the intertidal and subtidal zone, although no decisive comparison can be made between the two communities because of the paucity of data for the deep sea community. It is also singularly interesting that a rhabdocoel containing hemoglobin should be present in the gut of the deep sea urchin as in the gut of shore forms.

The data gathered in 1957–58 suggest that *Allocentrotus* has an annual breeding season although the span of the cycle cannot be defined precisely at the present time. During the fall and winter months from September, 1957 to January, 1958 the gonad index remained high. In both 1957 and 1958 the gonad index fell precipitously between February and March. It is of interest to correlate 1) growth of gonads, and 2) spawning with physical conditions in Monterey Bay. Among the possible variables are 1) light, 2) temperature, 3) salinity and minerals and 4) planktonic bloom which may be correlated with upwelling.

[5] Only one *Allocentrotus* was obtained on August 14, 1957 but this male had a gonad index of 6.72 per cent, suggesting that the gonads were probably increasing in volume. Because of the general variability of size of gonads in any sample, the measurement is only indicative.

[6] The largest test diameter observed in specimens from Monterey Bay is 103.3 mm. according to Dr. A. R. Moore.

Although day-length has been correlated with breeding cycles of some invertebrates and vertebrates (Borthwick *et al.*, 1956), it does not seem likely that it is a controlling factor for *Allocentrotus* because of the low intensity of light at the depths in which this animal lives. However, some photoperiodic animals are affected by very low light intensities and to them the span of illumination is of greater importance than the intensity of the light. The possible action of light in timing the reproductive cycle of *Allocentrotus* is not excluded.

Cyclic variations in temperature of the habitat of *Allocentrotus* have been observed (Skogsberg, 1936; Skogsberg and Phelps, 1946). The data for the years 1936 and 1937 are given in Figure 3C at a depth between 100 and 200 meters. A seasonal rhythm is seen with low and fairly constant temperatures in spring and early summer. In May the temperature range at 150 meters was 8.2 to 8.5° C. in 1936, and 7.9 to 8.4° C. in 1937. In July the temperature at 150 meters began to rise, reaching a maximum by December at which time it ranged from 9.6 to 10.1° C. in 1936, and was 9.3° C. in 1937. The difference between highest and lowest temperatures is greater during upwelling of cold waters than during the period of warmer waters. The temperature variations may be correlated with three major water movements: the Oceanic period lasting from September to October, the Davidson current period lasting from November through February, and the Upwelling period occurring from late February through August. The Oceanic period and the Davidson Current generally coincide with the high thermal phase and the somewhat lower chlorinity, although chlorinity variation is never large (Skogsberg, 1936). The onset of upwelling in late February coincides with the spawning of *Allocentrotus* and may act as the trigger for initiation of the spawning. The subsequent warmer phase coincides with the period of growth of the gonads. As is to be expected, surface temperatures were found to be more variable than deep water temperatures according to Skogsberg and Phelps (1946) and the more recent CCOFI report of 1958.

The upwelling in Monterey Bay is followed by a phytoplankton bloom (Barham, 1956), as seen in Figure 3B. It is possible that the phytoplankton is used by the planktonic larvae of *Allocentrotus* and by the metamorphosed young urchins themselves when they reach the sea bottom. In this way the timing of events in the breeding cycle may ultimately depend upon the food supply, the larvae appearing at the most favorable time for their growth, namely, when phytoplankton is most abundant. All of these attempts to explain the breeding cycle of *Allocentrotus* must be considered as tentative hypotheses for which substantiating data are still needed.

Summary

1. Following a chance collection of a deep sea urchin, *Allocentrotus fragilis*, from a depth of 80 fathoms, it subsequently became possible to collect the urchins on numerous occasions from the same area.

2. The area of the bed was determined by grid dredging and the nature of the habitat determined to be relatively flat, gravel and sand underlaid with gray silt containing organic detritus and microscopic organisms.

3. The deep sea urchin appears to graze on the bottom since the organisms and organic debris of the bottom sediment appear in little pellets in its gut.

4. Many types of invertebrates are associated with *Allocentrotus,* including various other echinoderms. A variety of fishes is found as well.

5. Individuals with mature gametes were obtained in February and March of 1957 and during the period of September, 1957 to January, 1958. Spawn-out appeared to occur between February and March during both years.

6. Attempts to correlate the life cycle of *Allocentrotus* with various environmental factors led to the suggestion that upwelling may trigger spawning. The planktonic larvae then presumably develop during the most effective time when the planktonic blooms occur.

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