serums of these fishes may have glycoproteins similar to those present in the blood of the Antarctic fishes.

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- 23 February 1971; revised 8 April 1971

Coral-Eating Sea Stars Acanthaster planci in Hawaii

Abstract. An aggregation of 2×10^4 Acanthaster planci was observed from September 1969 to November 1970. The sea stars within the aggregation were very uniform in size, and their reproduction was seasonal. Their average diameter and weight also varied seasonally in a manner that suggests a correlation between average size and breeding condition. The aggregation remained compactly situated in a band a few to tens of meters wide and about 2 kilometers long, parallel to the shore. The band did not move appreciably during the observation period. The sea stars were feeding selectively on a coral which was a minor component of the total coral cover. The coral in the area was predominantly alive, and the proportion of dead coral did not increase appreciably during our period of observation.

12 to 30 m.

Since 1963 large aggregations of Acanthaster planci, the crown-ofthorns starfish, have been observed grazing on reef corals in the Pacific (1, 2). They were observed to be killing most of the hermatypic corals in several places along Australia's Great Barrier Reef and on the lee coast of Guam. In other places "dead" reefs are believed to have resulted from the feeding of A. planci.

In August 1969 a dense aggregation of A. planci was reported in the Kalohi Channel [8 miles (12.8 km) wide] off the south (lee) coast of the island of Molokai, Hawaii. This aggregation was featured in a documentary produced by a Honolulu TV station and has subsequently been investigated by the State Fish and Game Division and by a group of biologists from the University of Hawaii and the Bernice P. Bishop Museum. In April 1970, the State Fish and Game Division, in response to publicity about A. planci, attempted to eradicate the aggregation. Some pertinent observations were made during several months prior to and just after the attempted eradication. Approximately 20,000 A. planci were aggregated in a band varying from a few to tens of meters wide and about 2 km long. The axis of the aggregation was oriented east and west, almost parallel to the coast and about 3 km offshore at depths varying from

The bottom in the vicinity of the aggregation is covered with a dense uniform growth of coral, with occasional narrow sand channels running diagonally out from shore in a northeast-southwest direction. The coral cover is predominantly (about 90 percent) Porites compressa, a finger coral, extending about 1 m above the substrate. The second most abundant species (about 5 percent of the corals) is Montipora verrucosa, a sheetlike encrusting coral which usually occurs at the base of the P. compressa but occasionally grows over it to form larger colonies. This area of uniform coral cover is about 1 km wide and extends from near the 6-m contour to depths of about 30 m where the

bottom becomes a sandy slope. It continues to the west of the aggregation for at least several kilometers. To the east of the aggregation, the coral cover is interrupted by a canyon 30 m deep. East of the canyon the uniform area of coral resumes and extends toward the end of the island. The head of the canyon is a steep slope. At depths of less than 20 m this slope is predominantly covered with M. verrucosa. At greater depths there is no coral cover.

In October 1969 a mile-long transect line approximately parallel to the aggregation was laid on the bottom by the State Fish and Game Division. This main east-west line was crossed every 250 yards (228 m) by lines extending north and south 250 yards on either side of it. The junctions and inshore ends of the lines were marked, both on the bottom with concrete blocks and on the surface with buoys. Five censuses of the sea stars were taken by the State Fish and Game Division at approximately 2-month intervals. Divers swam along these bottom lines, recording the numbers of A. planci within 10 yards on either side of 25-yard line segments. In April 1970 approximately 10,000 individuals were injected, each with 10 ml of household ammonia by means of hypodermic syringes, in an attempt to eradicate the aggregation. During the survey, from October 1969 to May 1970, the aggregation remained in the vicinity of the transects but moved up 55 m or less toward shore at the western end of the aggregation.

The aggregation was also sampled at about the same times by biologists from the University of Hawaii. Acanthaster planci were collected from the aggregation and examined aboard ship. Each animal was measured, weighed wet, and examined for sex and gonad state. Teams of divers also made estimates of species composition and the amount of dead coral along the transect lines. A few tagging experiments were also conducted.

The density of animals within the Molokai aggregation was variable. In one location 158 animals were collected from a circle of radius 10 m. The density was therefore one animal per 2 m². In other locations the animals were crowded together so that they often overlapped each other. Densely aggregated patches did not correspond with particular substrates. Some sea stars occurred on sand or coral rubble whereas others were found on live coral. The majority of the sea stars were conspicuous and actively feeding during the day, predominantly (80 to 90 percent) on M. verrucosa.

Tagging experiments were conducted to determine rates and patterns of movements of the starfish. Animals in an area of starfish concentration were tagged with plastic, numbered dart tags, and their position was recorded. Twenty-four hours later their new location was determined. These tagged but otherwise undisturbed animals exhibited randomness in both direction and distance of movement. Movement distances of these animals ranged from 0 to 18 m.

In another experiment 40 animals were tagged and transplanted either 25 m to the west (23 individuals) or 25 m to the east (17 individuals) of their original location. Thirteen of the group transplanted to the west were relocated the next morning and had moved east-southeast (into a compass quadrant from east-northeast to southsoutheast) an average of 7 m. Eight other individuals of the group transplanted to the west were also relocated and had moved east-northeast an average of 3 m. No individual from either group moved west of the release point. Both the east and west release points

were ecologically similar to the original collection area in terms of depth and the composition of the coral substrate. The eastward movement was roughly parallel to both the shoreline and the depth contours at this point. No clear interpretation of this eastward movement of transplanted individuals is evident, but the quite consistent movement response is the only direct observation we have which supports the suggestion that the aggregation of the study population is active.

The persistence of the geographic location and shape of the aggregation is noteworthy. The observed movements of the animals, if random, were great enough to completely disperse the aggregation in a few days. Active aggregation, therefore, is indicated. The lenticular shape did not follow depth contours in spite of its longshore orientation. The food substrate in nearly all contiguous areas was quite comparable with that within the aggregation. The current in this area is dominated by the semidiurnal tides and moves strongly in both directions parallel to the shore. This rectilinear current pattern would enhance one axis at the expense of its orthogonal directions if a cue used in active aggregation were a waterborne component.

| Date | Ν | Total dian | neter (cm)* | | Disk diame | ter (cm)† | | M | eight (g) ‡ | |
|-----------------|-----|--------------------------|-------------|------|-----------------|-----------|------|--------------------------|-------------|-------|
| | | Mean \pm S.E. | Range | S.D. | Mean ± S.E. | Range | S.D. | Mean + S E | Range | L. |
| 3 November 1969 | 486 | 23.0 ± 0.1 | 11-13 | 2.5 | 13.0 + 0.1 | 10 | t t | | Aungo | |
| anuary 1970 | 144 | 23.8 ± 0.2 § | 16-31 | 9.6 | 12.0 - 0.1 | 0 10 | 0.1 | 478 ± 6 | 92- 891 | 121 |
| April 1970 | 266 | 25.0 ± 0.2 | 16-33 | 8 6 | 12.6 ± 0.1 | 01-0 | 0.1 | 498 ± 12 | 161-1034 | 140 |
| June 1970 | 523 | 23.3 ± 0.1 | 8_30 | | | /1-0 | C.I | 537 ± 8 [| 184-965 | 126 |
| August 1970 | 217 | | 10.01 | | 1.0 ± 8.21 | 81-1 | 1.9 | 467 ± 6 | 115- 896 | 138 |
| womber 1070 | 012 | 2.0.4 ± 0.2 | 15-61 | 2.8 | 13.0 ± 0.01 | 8-20 | 1.9 | 422 ± 8 | 92- 942 | 174 |
| sptember and | 617 | 22.1 ± 0.2 § | 11-30 | 2.7 | 12.6 ± 0.1 | 6-19 | 1.8 | 396 ± 8 | 69- 781 | 125 |
| 10 October 1969 | 24 | $31.5 \pm 1.3 \parallel$ | 16-42 | 6.3 | 18.9 ± 0.7 | 11-24 | 3.6 | 5 8 + C 76 | 753 1600 | V I V |

The average linear dimensions (disk diameter and total diameter) and the weight of animals from the aggregation increased between November 1969 and April 1970 and then decreased between June and November 1970 to about the initial values (Table 1). The mean total diameter increased significantly (P < .005) between November 1969 and January 1970 and again significantly (P < .001) between January and April 1970. The disk diameter and weight increased significantly (P <.001) between January and April 1970. The increase in total diameter was greater than the increase in disk diameter, an indication that the arms had elongated. Between April and June 1970, however, all dimensions decreased and were not significantly different from those of the initial sample in November 1969. These dimensions remained the same between June and August 1970 except that the average weight was significantly less in August. The number of rays (mean \pm standard error, 15.6 ± 0.1 ; range, 8 to 23) and the number of rays judged to be regenerating (mean \pm standard error, 1.6 ± 0.1 ; maximum number, 10) did not vary significantly between samples. Animals within the aggregation at each sampling period were quite uniform in size and weight. The smallest animal found, after considerable searching, was 8 cm in total diameter. The average dimensions (weight, disk, and total diameter) of aggregated animals were significantly less (P < .001)

than those of the nonaggregated animals collected on the same type of substrate just east of the aggregation. The largest animals found in the aggregation were about half the maximum size reported for the species [see (2)]. The average size of individuals within the aggregation was the same as that reported by Chesher for aggregated animals on Guam. One of us (J.M.B.) who has seen the aggregation at Guam estimates that the Guam and Molokai aggregations consisted of about the same number of animals and were otherwise comparable.

Our evidence did not permit us to conclude that the aggregation represented the same individuals throughout the study. If there was continual recruitment and loss from the aggregation, this did not alter the size distribution. Several explanations can be offered to account for the narrow range of sizes in the group relative to the known size range for this organism: (i) the group could be strongly domi-

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nated by a single (or very few) year class (or classes); (ii) only animals in this size range show active aggregation behavior; (iii) effects of age-specific mortality, fecundity, and growth rate could produce a population of this size composition.

If the same individuals composed the aggregation during the course of our study, then the growth rate was too low to be detected with our techniques. Thus, either the aggregation was representative of the size distribution of the total population, or the aggregation behavior was selectively exhibited by a narrow size range.

The average size of aggregated animals was apparently correlated with breeding cycles, as can be seen from the following analysis. The gonadal condition of individuals was scored subjectively after several arms and part of the disk had been slit open. Animals with large whitish gonads were considered to be ripe and ready to spawn; those with no gonads or small whitish ones were considered to be unripe; and those with small orange gonads were considered to be spent. Testes were distinctively less yellow than ovaries and were composed of smaller, more numerous lobules. The proportion of animals in each condition is depicted in Fig. 1. Ripe animals were most abundant in April. Several animals were reported to be spawning in their natural habitat during the attempted eradication (23-24 April 1970). The relationship between the attempted eradication and spawning is unknown, but other A. planci in holding tanks at the Hawaii Institute of Marine Biology, Oahu, spawned spontaneously on 23 April and again on 7 May (full moon, 25 April; new moon, 5 May). Prior to these dates the average dimensions and the percentage of ripe animals were maximum values. Subsequently both of these characteristics decreased, whereas the percentage of spent animals increased (Table 1 and Fig. 1). On the basis of this evidence it seemed likely that individuals increased in size as their gonads engorged and decreased again after spawning. These data suggest that, in Hawaii, A. planci are reproductively quiescent during the winter but enter into an extended breeding season in the spring.

Fertile gametes could be obtained from ripe animals at any time of the year by mincing bits of gonad. Eggs were in various stages of maturity, and only some were fertile. Similar results



Fig. 1. Seasonal variation in reproductive state of aggregated A. planci. The percentage of ripe (\bigcirc), spent(\bigcirc), and unripe (\Box) individuals was determined at each collection period. The arrow indicates the time of the attempted eradication of the aggregation and observations of natural spawning.

were reported by Mortenson [see (3)]. Typically, about 90 percent were oocytes and the rest were mature eggs which developed into bipinnaria after fertilization.

In three ripe females the wet weight of the ovaries was about 4 percent of the total weight. Approximately 10⁶ oocytes and eggs were obtained from each of these females after the ovaries had been torn apart.

The reason for the presence of the aggregation off Molokai is not clear. The species is not new to the Pacific nor is it new to Hawaii (3, 4). Edmondson (4) reported in 1933 that it could be found, although not commonly, in "from one to several fathoms." That is still the case, but deeper searching almost anywhere in the major Hawaiian Islands commonly reveals occasional specimens. The state of aggregation did not change noticeably throughout the year and therefore seemed to be unrelated to breeding cycles. The substrate and other environmental conditions were not obviously different from those in adjacent areas where few or no A. planci were found. The coral species being selectively eaten was a minor component of the coral cover in the vicinity of the aggregation, although the coral species was more abundant in some adjacent areas.

The densely aggregated sea stars did not decimate the coral in their vicinity. About 85 percent of all corals in the area were alive, as was the case in adjacent areas. Most of the M. verrucosa, the coral being selectively eaten, was alive even near the dense aggregation of A. planci. [Montipora verrucosa is the only member of the family Acroporidae presently found in Hawaiian waters. In other places where Acropora is abundant it is the primary prey (3, 4)]. Montipora verrucosa apparently grows more rapidly than the predominant species, P. compressa, for in some places it had overgrown and smothered areas of the finger coral (see cover). Montipora verrucosa apparently grew fast enough to replace the coral eaten by the sea stars, but such selective feeding could account for the relative sparsity of this more rapidly growing species.

These observations suggest that coral growth can, in some places, support dense aggregations of A. planci. In other places, as on Guam and the Great Barrier Reef, grazing exceeded coral growth and a large proportion of the coral was killed. Such imbalance could have resulted from either increased grazing pressure [as previously hypothesized (1, 2)] or decreased coral growth, or a combination of both.

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 Rep. No. 2 (1964), p. 23] described feeding territoriality and suggested that A. planci limited coral growth in the Red Sea.
 C. H. Edmondson [Bishop Mus. Spec. Publ.
 22, 67 (1933)] discussed A. planci distribution in Howeii and considered A. planci to have
- in Hawaii and considered A. planci to have been "common" at Christmas Island in the Line Islands.
- Supported in part by NSF Sea Grant funds. This research would not have been possible without assistance by the Oceanic Foundawithout assistance by the Oceanic Founda-tion, which donated the use of their R.V. *Westward*. The research was conducted en-tirely by volunteers who worked under extremely hazardous conditions. We thank Dr. A. H. Banner who arranged for funds to cover most of the expenses and for the use of the R.V. Westward, and Dr. D. Devaney of the Bishop Museum who contributed to most of the expeditions and who read the manuscript. The computations were facilitated by a grantin-aid from the University of Hawaii Computing Center.
- 7 January 1971; revised 26 February 1971