

Acanthaster Aggregations: Interpreted as Primarily Responses to Natural Phenomena¹

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THE CROWN-OF-THORNS STARFISH *Acanthaster planci* (Linnaeus) has been reported to be undergoing population increases or explosions on reefs scattered throughout the tropical Indo-West-Pacific Ocean (Barnes, 1966; Weber, 1969; Chesher, 1969, 1970; Endean, 1969; Pearson and Endean, 1969; Australian Academy of Science, 1970; Campbell and Ormond, 1970; Antonius, 1971; Walsh, 1971). Because *Acanthaster* may remove the living tissue from large portions (up to 90 percent) of the hard corals comprising these reefs, it has been labeled a serious threat to coral reefs in general. Predicted consequences have ranged from loss of valuable tourist trade, severe land erosion by storm waves, the extinction of madreporarian corals in the Pacific, to economic disaster through loss of fisheries (Chesher, 1969). Goreau (1964) even suggested that under certain conditions *Acanthaster* may be an important factor in limiting the growth and development of coral reefs by keeping the rate of framework deposition to such a low level that no net reef accretion can occur.³ Barnes (1966), Endean (1969, 1971),

Antonius (1971), and especially Chesher (1969, 1970) have contended that large aggregations of *Acanthaster* are unprecedented and are most likely the result of man-induced environmental disturbances. Others (Newman, 1970; Weber and Woodhead, 1970; Dana, 1970, also unpublished abstract, Western Society of Naturalists, 51st annual meeting, 1970; Vine, 1972) have suggested that these aggregations might be the result of natural causes and have cited several instances of past abundances.

Because of the severity of the suggested consequences and a lack of knowledge on the extent of *A. planci* depredations, the Westinghouse Ocean Research Laboratory under contract to the U.S. Department of the Interior carried out a survey of 19 islands and atolls within the Trust Territory of the Pacific Islands during the summer of 1969. At the same time, and in conjunction with the survey, several of the Hawaiian Islands and Johnston Island were examined. Field observations and "debriefing" sessions resulted in a massive accumulation of data (Westinghouse, unpublished). The findings of the survey were for the most part qualitative and have been summarized in a report to the Department of the Interior (Chesher, 1970). We felt that subjecting the data to quantitative and statistical analyses would be useful in defining more clearly the status of *A. planci* populations and in establishing a firmer basis for generating testable hypotheses to explain the so-called "infestations." Permission

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³ Although we would agree with Goreau that *Acanthaster* can influence the composition of reef coral assemblages, our conclusion is based on different data. Goreau considered that the coral-depauperate situation at the islands of Entedebir and Um Aubak in the Dahlak Archipelago, some 50 km south-southeast of Massawa, Ethiopia, was possibly due to *Acanthaster*. However, in actuality this appears not to be the case. Professor L. Fishelson, of Tel-Aviv University, Tel-Aviv, Israel (personal communication, 1969) informed us that the situation was observed by Goreau and other members of the Israeli South Red Sea Expedition during calm weather. Seasonally, monsoon winds blow steadily against these islands, generating waves which scour their gently shelving shores. When the monsoon dies down, the scoured areas are quickly

repopulated by sponges and other encrusting reef organisms, newly recruited corals being among the slowest growing. We observed a comparable situation on the seaward reef of the San Blas Archipelago off the Caribbean coast of Panama when prevailing trades were quiet. Fishelson pointed out that, during subsequent investigations of the Israeli Red Sea Expedition, it was discovered that on the other side of Entedebir, in the lee of the monsoon, coral growth was luxuriant and otherwise flourishing. We observed the same thing in San Blas.

was granted by both Westinghouse and the Department of the Interior to utilize the data collected during the survey.

DATA CLASSIFICATION

Inasmuch as numerous survey teams, each composed of individuals of differing backgrounds and experience, were involved in the data collection, the data are naturally variable in both quantity and quality. However, before teams were sent into the field, training sessions were held at Guam to assure that uniform survey methods would be used throughout (Chesher, 1970). From the standardized field data sheets used during the survey the following information was generally extractable: position of the sampling transects on the island or atoll being surveyed, bottom type, depth interval, number of *A. planci* observed, time spent surveying, and survey techniques employed. As all atolls and islands surveyed were within the belt of prevailing northeasterly trade winds, windward and leeward sides are readily determinable. Eight positions can then be designated relative to wind direction and amount of exposure to waves: (1) leeward lagoon (exposed), (2) windward lagoon (protected), (3) pass, (4) windward seaward reefs (northeast), (5) windward seaward reefs (southeast), (6) leeward seaward reefs (northwest), (7) leeward seaward reefs (southwest), and (8) reef flat.

Categorizing bottom types presented considerable difficulty. Entries on the field data sheets were often incomplete and individual observers differed in their criteria for characterization of the bottom. From our personal field experience, eight categories are recognizable: (1) sand, (2) coral patches and knolls interspersed with sand channels and patches, (3) relative topographic uniformity, nearly rubble-free, abundant living coral present, (4) consolidated, mostly coralline algae with scattered heads and patches of living coral, or rock largely encrusted with coralline algae and scattered heads and patches of coral, (5) broken rubble, (6) rubble with scattered coral heads, (7) large heads and knolls of living coral forming mounds, buttresses, and valleys with small sand patches interspersed, and (8) areas of siltation with only scattered clumps of coral. The distribution of these categories is

dependent on complex interactions among physical, biological, and historical parameters, with perhaps the strongest influence being exerted by the nature, intensity, and temporal distribution of water movements. The data were fitted to these categories as well as possible.

Because survey transects covered wide depth ranges at nearly all stations and the number of observations giving exact depths where *A. planci* was found was exceedingly small, the data were divided into three rather broad depth intervals: (1) 0.0–10.0 m, (2) 10.1–18.3 m, and (3) 18.4–60.8 m (lower depth limit of the survey). These depth intervals were chosen because they roughly correspond to the terrace topography widely observed on seaward reefs of Pacific atolls. Also, the lower limit of the shallowest interval is close to normal wave base for trade-wind-generated swell. Quite frequently a single transect overlapped two or more of these depth intervals. Where this occurred, the time spent surveying and numbers of *A. planci* recorded were divided among the depth intervals in proportion to the fraction of the total depth range of that particular survey included in each of the established depth intervals.

Survey observations were made either by towing or swimming. Towing operations were conducted either behind or beside a boat. Swimming involved either snorkeling or SCUBA diving. The number of *A. planci* seen and the time spent searching were recorded. Counts of *Acanthaster* from towing surveys (but not diving surveys) in which estimates of deepest depths surveyed exceeded 18.3 m were included in the depth interval ending at 18.3 m, as the likelihood of spotting sparsely distributed and normally cryptic starfish at depths greater than this was considered to be very low. H. L. Clark's statement (1921), "The entire coloration harmonizes so well with the general coloring of the reef that, in spite of its large size and remarkable spines, this sea-star is very inconspicuous and I doubt not is often overlooked," conversations with survey participants, and personal experience support this decision. Further, the data showed only one instance where a towing survey overlapping into the 18.4–60.8-m-depth interval determined the number of *Acanthaster* to exceed normal densities.

RELATIONSHIP OF ABUNDANCE TO HABITAT

The data were summarized by totaling the number of hours spent surveying and the number of *A. planci* recorded for each position, bottom type, and depth interval according to each survey technique. Table 1 presents this summary. Positions 2 (protected lagoon) and 6 and 7 (leeward seaward reefs) received the most attention (approximately 66 percent of the survey time) and contained the largest average numbers of starfish. That *A. planci* is generally more abundant in normally protected locations is in agreement with the observations of others (Endean, 1969; Pearson and Endean, 1969; Chesher, 1970; Campbell and Ormond, 1970). The high average number of *Acanthaster* associated with position 4 (windward seaward reefs, northeast) is the result of concentrations of starfish found on the northern reefs of Tinian and Ponape (Westinghouse, unpublished). The significance of the location of these aggregations will be mentioned later. Bottom types 2, 3, and 4, all with moderate to luxuriant coral growth, dominated the kinds of habitats surveyed, and 2 and 4 appeared to support greater-than-average population sizes. The high value of *Acanthaster* per hour in Table 1 for bottom type 8 requires a note of explanation. The habitat categorized as bottom type 8 (areas of siltation with only scattered clumps of coral) is restricted to localized coral reef areas around high islands and along continental margins. Three surveys were conducted over this bottom type: two at Truk for a total of 15 minutes (no starfish) and one at Tinian for 20 minutes (22 starfish). Density figures extrapolated from such a small sample to other areas would be highly tenuous at best. Most observations (approximately 69 percent)

were made in water less than 10 m deep; however, the largest average density of *Acanthaster* was found between 10.1–18.3 m.

To determine which of the parameters considered in the data summary were primarily responsible for the observed differences in population sizes, a four-factor analysis of variance (ANOVA) was carried out. Realizing from the outset that all the variables were not truly independent of each other, we examined interactions of position, bottom type, depth, and survey technique. Position 8, bottom types 1, 5, 7, and 8, and depth interval 3 were not included in the ANOVA as observations were lacking in enough combinations involving these to make fulfillment of balanced design requirements impossible. Values used for the 112 combinations remaining (seven positions \times four bottom types \times two depth intervals \times two survey techniques) were either means based on one to 61 individual observations each, or, for the 19 not available in the data, were estimates.⁴ Only position had a significant effect on population sizes (Table 2). Of the set of environmental factors related to position, incident wave energy is probably the most important.

After ascertaining that the position of an island's reefs relative to trade wind direction was the significant single factor variable affecting the density of *Acanthaster* populations, we employed the Tukey ANOVA procedure, which allows for individual comparisons (Miller, 1966:37–48), to determine which position means were different from each other. An island-versus-position array with cell values being the mean number of *Acanthaster* seen per hour for each position on each island was used, and this test indicated that position 6 (leeward seaward reefs,

⁴ For each combination of position, bottom type, and depth interval, there is a sampling technique pair. Where only one of the pair existed, the "swim" member was constructed by multiplying the "tow" element by 2.20 (the overall swim/tow ratio of the average number of *Acanthaster* seen per hour), or the "swim" value was divided by 2.20 to obtain the "tow" value. Where neither element existed, the following example illustrates the formula used for the calculations: for position 4, bottom type 2, depth interval 1, "swim" survey technique,

$$\frac{\sum A. planci \text{ position 4} + \sum A. planci \text{ bottom type 2}}{\sum \text{hr position 4} + \sum \text{hr bottom type 2}} \times 2 \text{ (avg no. } A. planci/\text{hr for depth interval 1)}$$

avg no. *A. planci*/hr for depth interval 1 + avg no. *A. planci*/hr for depth interval 2.

The paired "tow" value was obtained by dividing by 2.20.

TABLE 1
SUMMARY OF ALL VALUES, BASED ON 549 SURVEY TRANSECTS

ITEM	HOURS		<i>Acanthaster</i> PER HOUR	
	SWIM	TOW	SWIM	TOW
Position				
(1) leeward lagoon (exposed)	22.70	13.08	6.12	5.66
(2) windward lagoon (protected)	46.20	30.22	4.85	20.25*
(3) pass	2.75	5.33	2.91	0.56
(4) windward seaward reefs (northeast)	7.08	20.42	2.40	15.13*
(5) windward seaward reefs (southeast)	5.92	12.92	0.00	1.39
(6) leeward seaward reefs (northwest)	27.75	26.83	114.16*	7.16
(7) leeward seaward reefs (southwest)	23.63	19.58	2.16	22.01*
(8) reef flat	1.50		0.00	
Bottom type				
(2) coral patches and knolls interspersed with sand channels and patches	62.92	51.63	3.42	21.15*
(3) relative topographic uniformity, nearly rubble-free, abundant living coral present	26.67	38.88	8.51	7.84
(4) consolidated, mostly coralline algae with scattered heads and patches of living coral, or rock largely encrusted with coralline algae and scattered heads and patches of coral	35.17	40.87	84.34*	13.16*
(6) rubble with scattered coral heads	11.70	14.42	17.01	7.08
(7) large heads and knolls of living coral forming mounds, buttresses, and valleys with small sand patches interspersed	0.92	2.17	0.00	1.38
(8) areas of siltation with only scattered clumps of coral	0.17	0.42	0.00	52.80*
Depth				
(1) 0.0 to 10.0 m	93.40	89.00	16.62	9.27
(2) 10.1 to 18.3 m	27.85	39.39	72.74*	20.66*
(3) 18.4 to 60.8 m	16.28		1.75	
SURVEY TECHNIQUE	TOTAL HOURS	TOTAL <i>Acanthaster</i>	<i>Acanthaster</i> PER HOUR	
swim	137.53	3,607	26.23	
tow	128.38	1,639	12.77	
	(a) 265.91	(b) 5,246	(b/a) 19.73	

Ratio of Swim Hours:Tow Hours, 1.07; *Acanthaster*, 2.20; *Acanthaster* per Hour, 2.05

* Values greater than the overall average for this survey technique.

TABLE 2
ANALYSIS OF VARIANCE RESULTS

ITEM	MEANS
Position	
(1) leeward lagoon (exposed)	8.23
(2) windward lagoon (protected)	12.15
(3) pass	1.19
(4) windward seaward reefs (northeast)	8.22
(5) windward seaward reefs (southeast)	0.58
(6) leeward seaward reefs (northwest)	42.03
(7) leeward seaward reefs (southwest)	9.64
Bottom Type	
(2) coral patches and knolls interspersed with sand channels and patches	8.96
(3) relative topographic uniformity, nearly rubble-free, abundant living coral present	6.51
(4) consolidated, mostly coralline algae and scattered heads and patches of living coral, or rock largely encrusted with coralline algae and scattered heads and patches of coral	23.25
(6) rubble with scattered coral heads	8.16
Depth Interval	
(1) 0.0 to 10.0 m	9.37
(2) 10.1 to 18.3 m	14.06
Survey Technique	
swim	14.57
tow	8.87
Terms	
	<i>p</i>
position	.005 > <i>p</i> > .001*
bottom type	.10 > <i>p</i> > .05
depth interval	.75 > <i>p</i> > .50
survey technique	.25 > <i>p</i> > .10
position × bottom type	.005 > <i>p</i> > .001*
position × depth interval	.90 > <i>p</i> > .75
position × survey technique	.005 > <i>p</i> > .001*
bottom type × depth interval	.75 > <i>p</i> > .50
bottom type × survey technique	.05 > <i>p</i> > .025
depth interval × survey technique	<i>p</i> > .9995
position × bottom type × depth interval	.25 > <i>p</i> > .10
position × bottom type × survey technique	.025 > <i>p</i> > .10
position × depth interval × survey technique	.50 > <i>p</i> > .25
bottom type × depth interval × survey technique	.50 > <i>p</i> > .25

NOTE: All means are *Acanthaster* per hour. Mean values are not the same as shown in Table 1 because of omitted classifications (see text).

* *p* < .005 considered significant.

northwest) had a higher mean *Acanthaster* density than all other positions. None of the other positions were different from each other at the 5-percent level.

The interaction terms for position and bottom

type and position and survey technique were also statistically significant. The interaction between position and bottom type was expected, as the structural characteristics of reefs are strongly influenced by circulation phenomena, particularly

wave action, which vary with position. The interaction of position and survey technique is nonsensical in terms of *Acanthaster*. This interaction perhaps reflects the fact that certain features of the environment, such as waves, large sharks, and scenic beauty, which might differentially affect the efficiency of the two techniques for locating specimens of *A. planci*, are associated with position in a fairly consistent manner.

NORMAL DENSITY

Defining normal populations of *Acanthaster* and their configuration is a prerequisite to determining what constitutes abnormal or infestive aggregations and to explaining circumstances under which they occur. Endean (1969) suggested that about 10–100 min of search on shallow reefs is normal. Pearson and Endean (1969) later gave a more detailed definition based on a hypothetical density necessary to kill an arbitrary percentage of a reef's living coral. A reef is considered uninfested if less than 10 *Acanthaster* are found during 20 min of search. In the report to the Department of the Interior (Chesher, 1970), seven different definitions of a normal population are given: (1) 2 or 3 per 1,000 m², with none in adjacent areas; (2) 4 or 5 per km of reef; (3) on reefs adjacent to infestations, approximately 1 per km; (4) a concentration of *A. planci* whose combined predation pressure is balanced by the regrowth of coral; (5) 20 starfish per 20 min of search but usually no more than eight; (6) a reef inhabited by sparse concentrations of *A. planci* such that large continuous sections of dead coral are not produced; and (7) occasional areas—particularly near passes through the reef and where there is lush coral growth—may have as many as five or six specimens. There is also the statement that the number of specimens constituting a normal population varies. These definitions are neither explicitly clear nor are they all compatible with each other. Their unsatisfactory nature in quantitative terms stems from a multiplicity of sources: (1) prior to the Westinghouse survey and preliminary investigations on the Great Barrier Reef, no special effort had been made to enumerate *A. planci* populations, especially on portions of reefs other than

reef flats; (2) exacting quantitative measurements of populations occupying an entire reef complex have never been made; (3) no knowledge of natural fluctuations in population sizes exists; and (4) beyond the fact that concentrations of thousands of *Acanthaster* appear quite capable of drastically reducing the amount of living coral on extensive portions of a reef, the capacity of any given reef to support an *A. planci* population without serious damage is unknown.

Thirty-four of the 41 samples containing more than 20 starfish per 20 min of search (the most commonly used definition of normal populations in Chesher, 1970) are from protected locations, 27 of these being from leeward seaward reefs. Table 3 gives a summary of survey observations in which the numbers of *Acanthaster* equalled or exceeded the above value.

It has been asserted (Chesher, 1970) that there is an order of magnitude difference between the numbers comprising a normal population and the numbers constituting a so-called "seed population," the first stage leading to an infestation. The latter population "is characterized by large groups of 500 to 1,000 specimens located within a very small area" (Chesher, 1970). The data in Table 3 show, however, that there were at least 40 survey records in which the number of *A. planci* observed was greater than 20 but less than 500 for search periods of 20 minutes or longer. The number of individuals within *Acanthaster* aggregates spans a wide range, from less than 1 per 1,000 m² to several per m², but there appear to be no secondary peaks in abundance. Table 4 presents the sampling distribution. Data collected over a 4-year span on the Great Barrier Reef (Pearson and Endean, 1969) show a similar trend. Such a continuous distribution of population sizes makes the distinction between normal and abnormal arbitrary. Data from both of the above sources indicate that along any one reef the population densities of *Acanthaster* may be highly variable in space. Further, various citations referring to past abundances (Pearson and Endean, 1969; Dana, 1970; Vine, 1970) indicate that fluctuations in numbers in time might also be large. It is worth noting that the data collected by the Westinghouse survey revealed no aggregations of the scale found on Guam's

TABLE 3
LOCATIONS AND SIZES OF ABNORMAL CONCENTRATIONS OF *Acanthaster planci*

ISLAND OR ATOLL	POSITION	BOTTOM TYPE	DEPTH INTERVAL	SEARCH TIME (min)	SURVEY TECHNIQUE	NUMBER OF <i>A. planci</i>
Johnston	6	6	1	20	swim	26
	6	6	1	30	swim	43
	6	6	1	30	swim	32
	6	6	1	30	swim	33
Arno	2	2	1	30?	swim	ca. 100
Kwajalein	2	2	1	ca. 20	swim	26
Majuro	2	2	1,2	10	tow	estimated 390
Pingelap	6	4	1,2	20	tow	21
Ponape	6	4	2	20	swim	30
	2	2	1,2	20	swim	25
	6	3	1	20	swim	49
	4	3	2	50	tow	188
	4	3	?	20	swim	"too numerous to count"
Ant	1	4	1	20	swim	22
Truk	6	3	1,2	20	swim	50
	6	3	1	20	tow	33
	6	4	1,2	20	tow	29
	2	2	1	20	tow	25
	2	2	1	20	tow	53
	1	2	1	10	tow	37
	1?	2?	1	10	swim	40
Saipan	7	4	1	20	tow	58
	7	4	1	20	tow	103
	7	4	1	20	tow	63
	7	4	1,2	20	tow	"too many to count"
	7	2	1,2	60	swim	"thousands"
	2	2	1	20	tow	450
	2	2	1	15	tow	43
Tinian	7	6	1,2	20	tow	30
	7	8	1	20	tow	22
	7	harbor breakwater	1?	20	tow	ca. 50
	6	4	1,2	30	swim	32
	4	4	1,2	20	tow	20
Rota	4	4	1,2,3	20	tow	61
	6	4	1,2	15	swim	40
	6	4	1,2	90	swim	300
	6	3	1,2	20	swim	50
	6	4	1,2	20	swim	360
	6	4	1,2	20	swim	490
	6	4	1,2	70	swim	1,600
	6	4	1,2	180?	tow?	"clusters of 16 to 48"
	7?	4	2	30	swim	ca. 50

NOTE: Twelve of the values in this table could not be completely categorized for the data summary or ANOVA and were not included in them.

SYMBOLS (see also p. 358): *Position*—1, leeward lagoon (exposed); 2, windward lagoon (protected); 4, windward seaward reefs (northeast); 6, leeward seaward reefs (northwest); 7, leeward seaward reefs (southwest). *Bottom type*—2, coral patches and knolls interspersed with sand channels and patches; 3, relative topographic uniformity, nearly rubble-free, abundant living coral present; 6, rubble with scattered coral heads; 8, areas of siltation with only scattered clumps of coral. *Depth interval*—1, 0.0 to 10.0 m; 2, 10.1 to 18.3 m; 3, 18.4 to 60.8 m.

TABLE 4
FREQUENCY DISTRIBUTION OF SAMPLE SIZES

NUMBER OF <i>A. planci</i> OBSERVED	NUMBER OF OBSERVATIONS
0	400
1-20	173
21-100	32
101-500	8
501-1,000+	4 or 5

NOTE: Table includes observations which could not be categorized and hence were not included in the data summary or ANOVA.

leeward reef or the inner patch reefs of the central Great Barrier Reef. Nor did Vine, diving on a number of South Pacific reefs, encounter aggregations which met Pearson's requirements for an "infestation" (Vine, 1970). Reported infestations on other islands and atolls have failed to meet the criteria established in the Westinghouse report. The aggregation of some 20,000 individuals off the southern (leeward) coast of Molokai in the Hawaiian Islands (not included in Table 3) has appropriate dimensions to be classified as an "infestation," yet is reported not to be decimating the coral in its vicinity (Branham et al., 1971).

ALTERED POPULATION DYNAMICS HYPOTHESES

Most hypotheses advanced to account for the occurrence of large concentrations of *Acanthaster* have invoked population explosions or expansions, which are assumed to have resulted from either changes in the general environment or in the biology of the species. Such increases could stem from increased larval survival. Very preliminary experiments with *Acanthaster* larvae by Henderson and Lucas (1971) on the Great Barrier Reef suggest that metamorphosis is completed only at temperatures which normally prevail there during the breeding season. The results of those experiments have been cited in support of the theory that a rise in seawater temperatures would hasten larval development, in turn leading to increased larval survival by lessening the time the larvae are exposed to predation while in the plankton (Vine, 1972). That surface layer temperatures were 1°-2° C higher than normal from 1954 to 1959 in Aus-

tralian waters has been given as evidence that this hypothesis could account for the Great Barrier Reef aggregation (Vine, 1972). We do not feel that the results provided by Henderson and Lucas are adequate to warrant the extensions made from them by others, especially when the responses of other elements of the reef community to elevated temperatures are not considered. We will return to sea surface temperatures later.

On the Great Barrier Reef, juveniles in any abundance were reported from Green Island and Fitzroy Island only after the majority of adult starfish had departed from their reefs (Endean, 1969; Pearson and Endean, 1969). "Numerous" juveniles were reported from Guam in an area outside the existing infestation some 5 months subsequent to the completion of a nearby channel (Chesher, 1970). It was also stated that small specimens of *Acanthaster* "abound" at Guam and Rota and that at least three size classes are present at Guam (Chesher, 1970); however, no data were given. There are no reports of large populations of juveniles observed preceding the appearance of adult aggregations and the suggestion that the latter are the result of abnormal juvenile recruitment remains an unsupported speculation.

Several crustacean larvae, molluscs, and fish fry have been demonstrated to be sensitive to chlorinated hydrocarbons (National Academy of Sciences, 1971). The suggestion has been put forward that populations of known and potential *Acanthaster* predators could be declining as a result of increasing levels of these and other pollutants (Pearson and Endean, 1969; Australian Academy of Sciences, 1970). Blasting and dredging (Chesher, 1970), shell collecting (Endean, 1969), and spearfishing (Vine, 1972) are all human activities which have been suggested as reducing predation pressure on various life stages of *Acanthaster*. Predators on the planktonic larvae and newly metamorphosed juveniles are assumed to be numerous, but remain unidentified. Among predators on juveniles one must at least consider the known adult predators. Known predators of adult *Acanthaster*—the gastropods *Charonia tritonis* (Pearson and Endean, 1969) and *Cymatium lotorium* (Vine, 1972), the crustacean *Hymenocera* (Wickler and Seibt, 1970), and the fishes *Chei-*

linus undulatus (Chesher, 1970; Ormond and Campbell, 1971) and *Pseudobalistes flavimarginatus* (Vine, 1972)—are all thought to be relatively uncommon on most reefs. Demonstration of the act of predation itself has largely been confined to laboratory or controlled field situations. Predation under existing field conditions by any predator on any life stage of *Acanthaster* remains an unknown quantity.

If the rate of juvenile recruitment has been increasing gradually over the last decade, with no accompanying change in adult survivorship, populations should show a preponderance of younger individuals. If adult mortality has been reduced with no accompanying change in juvenile recruitment and survivorship, populations should be characterized by relatively greater proportions of large individuals. Simultaneous changes in the survivorship of both juveniles and adults occurring over periods of several years should result in nearly equal numbers in all size classes and a sharp drop at maximum size. Populations which resulted from abnormal bursts of juvenile recruitment should show marked peaks for those cohorts. The shape of size-frequency curves taken from widely separated populations reputedly in different infestive stages should help elucidate the manner of population growth. Figure 1 gives histograms for *A. planci* populations from the Saipan infestation (Goreau, unpublished), from either the "fizzling out" infestation or "seed" population at Kapingamarangi (Chesher, 1970; Westinghouse, unpublished), and from normal *A. ellisii* (Gray) populations in the lower Gulf of California (Dana and Wolfson, 1970). All three of the curves can be interpreted as unimodal with peaks at intermediate sizes; none appears bimodal or strongly skewed. The mean sizes of individuals collected from infested areas on Guam and from the Molokai aggregation are also intermediate (Guam: 13.8 cm disc diameter, 24.2 cm total diameter [Chesher, 1969]; Molokai: 13.8 cm disc diameter, 24.6 cm total diameter [Branham et al., 1971]). Pearson and Endean (1969) give 30 cm as an average total diameter for the starfish they observed on the Great Barrier Reef. For 1,076 individuals measured in Fiji, Owens (1971) reported a normal distribution of sizes with a mean total diameter of 25 cm. One must bear in mind that sample

sizes, sampling procedures, and methods of measurement were different for each of the above areas. Also the size of adult individuals will be affected by reproductive state (Branham et al., 1971) and population density relative to food supply.

For the *Acanthaster* populations observed in the Sudanese Red Sea, Ormond and Campbell (1971) reported a bimodal size distribution with peaks at 22.5 cm and 32.5 cm (total diameter). They suggested that these peaks represent consecutive year groups of animals 2 and 3 years old. However, they provided additional information in their paper which leads to an alternative explanation for the observed bimodality. They stated that the supposed 2-year-old starfish were generally limited to two small areas that had the highest proportions of bare coral limestone and the greatest numbers of *Acanthaster*, i.e., the lowest relative food supply. Although favoring a different idea, they stated further that, on the basis of other evidence presented, starfish in the less favorable areas may feed less often. It appears plausible to us that the two peaks in Ormond's and Campbell's size distribution might well represent the mean size of starfish of several year classes occupying habitats where differences in relative food supply have influenced growth rates. The bimodality they reported could, therefore, be an artifact of their sampling and not in disagreement with observations from other areas.

What is noteworthy is that neither very small nor very large individuals predominated in any of the observed populations, but rather individuals of intermediate sizes. Such a size distribution can arise from combining a non-linear growth-age function⁵ with various sur-

⁵ The only growth rate data available are those of Pearson and Endean (1969) for 28 starfish kept either in aquaria or in cages on the reef. Based on sizes (total diameter) at the start of the experiments, there were three groups: less than 5 cm (14 individuals), between 10 and 20 cm (12 individuals), and close to 30 cm (two individuals). Only the last two individuals approach the average size for starfish in the area. The first group (smallest juveniles) was kept in aquaria for 1 month; the intermediate group in either aquaria or cages for 1 to 6 months; and the two largest individuals in cages for 3 months. Of the two largest individuals, one exhibited positive, the other negative, growth. For the intermediate group, initial growth rate slopes are not readily distinguishable from final ones.

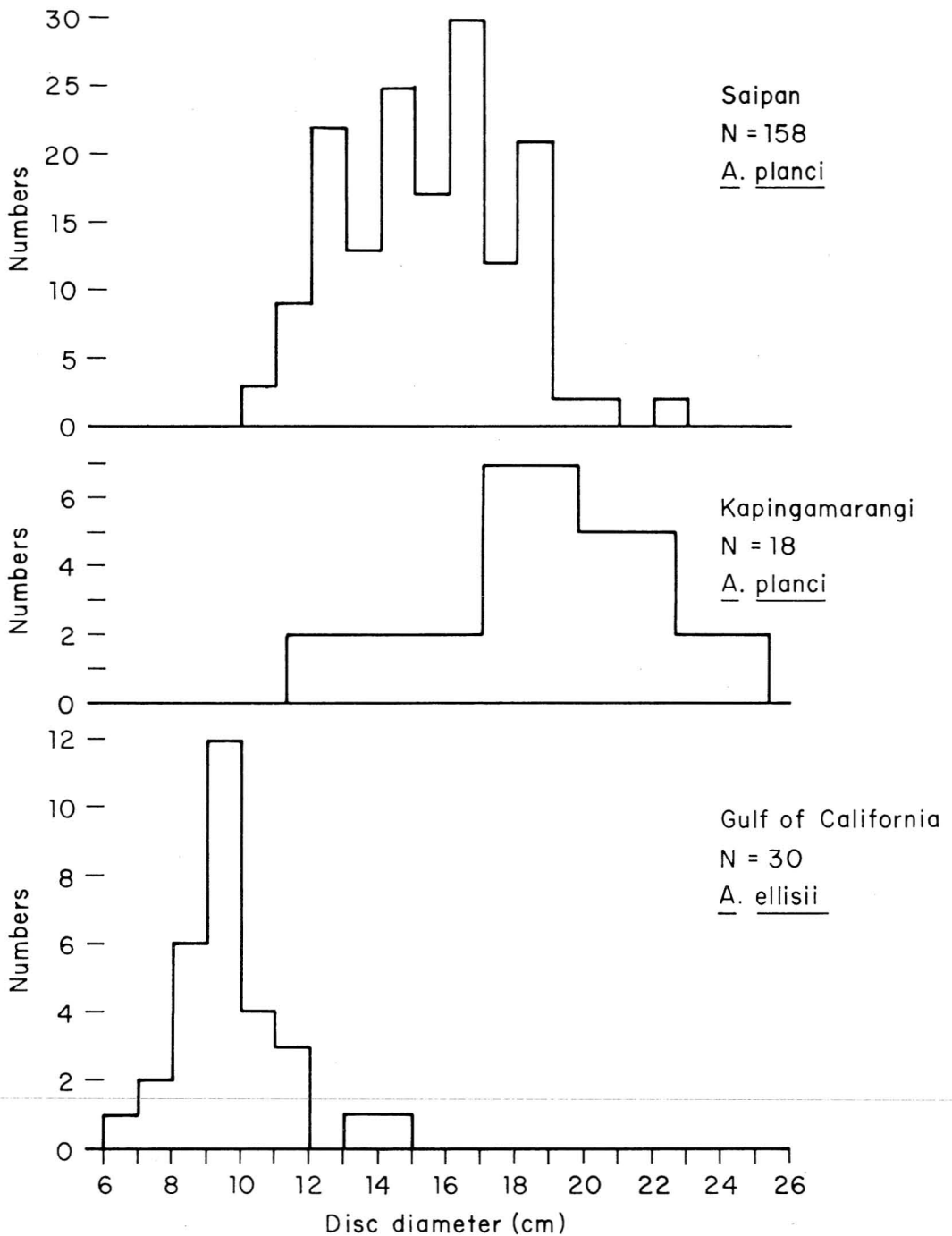


FIG. 1. Size frequency distributions. The Saipan measurements were made to the nearest one-half inch (Goreau, unpublished); the valleys in the diagram reflect bias against half-inch categories. The Kapingamarangi measurements were given as total diameters (Westinghouse, unpublished); the conversion to disc diameters was made using ratios from Guam (Chesher, 1969) and Molokai (Branham et al., 1970).

vivorship curves. No sudden changes in population dynamics are required. Admittedly the amount of data is small, but "infestive" populations do not appear to have grown in a fashion different from that expected for "normal" ones.

AGGREGATIONS AS REDISTRIBUTED POPULATIONS

Since it seems highly unlikely that the presence and persistence of large *Acanthaster* aggregations could be due to chance alone, these aggregations may result from active behavioral phenomena (see Branham et al., 1971). Ormond and Campbell (1971) postulated that chemoattraction between feeding animals may serve to bring them together. Although Goreau (1964) observed that *A. planci* was concentrated in limited patches (no scale given), he did not observe any attraction between feeding individuals, but rather a solitary mode of feeding which led him to suggest territorial behavior. Further, on any undisturbed, flourishing reef, sufficient coral should be present to make homing on a feeding individual unnecessary, if not maladaptive. The time span of persistence—several years for both Guam and the Great Barrier Reef—casts doubt on the idea that these large aggregations, forming bands or herds moving together along the reef and obviously overwhelming its carrying capacity, are for breeding purposes. However it is plausible and even quite probable that during the peak of spawning activity starfish would congregate briefly in modest numbers to shed gametes. Ormond and Campbell (1971) suggested that successful breeding may be limited to such aggregations. A paucity of known predators on adults, a solitary mode of feeding on sessile prey organisms, and the infrequency of the aggregates all rule against *Acanthaster* swarms being the result of social interaction. Within-habitat gradients in the physical and chemical environments of undisturbed reefs seem insufficiently different from atoll to atoll or island to island to lead to large aggregations

Slopes for the juveniles are generally slightly steeper than those for the intermediate group. Limitations on the experimental procedure do not permit the construction of a general growth curve. Pearson and Eudean did state, however, that growth is rapid following metamorphosis.

on some but not on others. One thus arrives at the conclusion that large aggregates of *Acanthaster* may arise as a response to severe disturbances which differentially affect the various reef habitats.

In advancing a hypothesis to account for *Acanthaster* aggregations, one must bear in mind that they are observed to be relatively more abundant in protected locations, especially on leeward reefs. Wells (1957) has noted certain distinguishing characteristics of such reefs; particularly, a richer, more profuse growth of reef corals on margins and upper seaward slopes with the less surge-resistant branching species of *Acropora* and ramose and foliate species of *Montipora* and *Porites* being abundant. Species of *Acropora* and *Montipora* are all asserted to be *Acanthaster's* most common food items (Chesher, 1970; Weber and Woodhead, 1970; Branham et al., 1971) and species of both *Acropora* and *Porites* elicited positive feeding responses in the experiments of Brauer, Jordan and Barnes (1970). Thus, such protected habitats should be capable of supporting higher normal population levels than could exposed reefs.

One possible means of making *Acanthaster* populations conspicuous without significantly altering their population dynamics would be to reduce their food supply drastically, and thereby increase their active searching for suitable items (see Weber and Woodhead, 1970). Freshwater flooding, heavy sedimentation, and mechanical damage by wave action are all means of reducing the amount of living coral on a reef. Typhoons affect tropical reefs in all three of these ways, with abrasion and physical breakage of corals by wave action being the predominant mode of destruction for most storms (Stoddart, 1969). Also, the effects of large-scale dredging and blasting, as originally suggested by Chesher (1969), could result in extensive coral kills through breakage and smothering by sediment.

The widespread, devastating effects of typhoons and hurricanes on coral reefs are well documented (Stoddart, 1969). However, even areas of fragile corals may survive severe storms as a result of variations in local exposure (Stoddart, 1969). The degree and location of damage are governed by the intensity, track, and proximity of the storm. In the western tropical Pacific

north of the equator, leeward seaward reefs should be most heavily affected because of the fact that leeward reefs are characterized by assemblages of more delicate coral growths unaccustomed to strong surge and breaking waves and the physical characteristics of tropical cyclones in this region⁶ should result in the highest waves being directed at leeward reefs. Such a conclusion is supported by the field observations of others (Tracey, Ladd, and Hoffmeister, 1948; Wells, 1951).

Acanthaster populations might survive such episodes because the animal is reported to seek out crevices, caves, and the undersides of overhangs when not feeding (Chesher, 1969; Goreau, 1964). If the residual populations are great enough in relation to the degree and extent of reduction in food supply (corals), one would expect their presence to be conspicuous as they actively search for suitable colonies of living coral (see Weber and Woodhead, 1970). Inasmuch as events, such as typhoons, which occasionally strip large portions of the living coral from reefs are not new, it is not unreasonable to suggest that *Acanthaster* would have evolved a behavioral mechanism to maximize survival under conditions of food limitation. The experiments of Brauer, Jordon, and Barnes (1970) suggest that *Acanthaster* might be able to locate other individuals feeding nearby. Such an ability would be of great advantage to individuals in a situation of reduced food supply and could result in an actively coherent aggregation. Such populations might in their search for food move into adjacent, less disturbed areas. If the immigrants combined with the resident populations exceed the carrying capacity of a reef area, the compounded aggregation, avoiding shallow, surgy areas and deep water where corals are sparse or absent, might advance laterally as a "front" along a reef, accumulating resident populations and leaving mostly dead coral in its wake. Pearson and Endean (1969) have suggested that infestations on some reefs along the Great Barrier Reef are adults which have migrated from previously devastated reefs.

⁶In the westward drift zone the highest waves would come from the southern component of the storm whirl, the wind rotation is counterclockwise, and usual storm tracks are westerly, curving north. For a discussion see Wiens, 1962: 163-184, 203-204.

Entries taken from the Westinghouse study (unpublished) indicate that the groups of starfish located at the northern tips of Tinian and Ponape may be migratory aggregations which originated on more southerly, leeward reefs. The only natural means of cessation for such an advance would be either starvation following exhaustion of the food supply or movement into an area where the amount of living coral would be sufficient to support the aggregation's feeding pressure. The latter may apply to the observed Molokai aggregation (Branham et al., 1971).

We do not mean to imply that every disturbing episode (typhoon, long period large swells, heavy rainfall, etc.) would serve to aggregate large numbers of *Acanthaster*. Reefs in various successional stages, capable of supporting different population densities of *Acanthaster*, would be more or less prone to the formation of starfish aggregations following perturbation. Reefs characterized by luxuriant growths of delicate branching and foliate corals and having a high *Acanthaster* standing stock should be the most susceptible. However, the coincidence of a severe disturbance striking a reef in this stage of development must be a relatively rare event. The various ramifications of this hypothesis could be experimentally tested by removing the favored corals from selected stretches of appropriate reefs and following the responses of the resident *Acanthaster* populations.

In an attempt to support the above hypothesis, we made density estimates from the Westinghouse data. Estimates of area searched per hour by the two techniques were obtained by field trials and discussions with some of the participants in the Westinghouse survey. Table 5 gives these estimates. The values are averages for all habitat types. That obtained by the "swim" technique is considered to be the more reliable. It is slightly less than the value given by Pearson and Endean (1969) as the maximum density for normal reefs (1 per 100 m²). On the basis of the density value obtained from the "swim" technique, estimates of 500 to 1,000 *Acanthaster* per kilometer of reef, 100 m wide, seem realistic. If only observations from leeward reefs are used, the estimates are approximately 2.5 times as large. Approximately 1,700 individuals of *Acanthaster* per km were collected along

TABLE 5
DENSITY DETERMINATIONS

SURVEY TECHNIQUE	ESTIMATED AREA SEARCHED PER HOUR	RATIO OF AREAS	MEAN NO. <i>A. planci</i> OBSERVED PER HOUR	DENSITY	RATIO OF DENSITIES
Swim	3,000 m ²	1:6.67	26.23	$8.74 \times 10^{-3}/\text{m}^2$	13.7:1
Tow	20,000 m ²		12.77	$0.64 \times 10^{-3}/\text{m}^2$	

NOTE: Assume *A. planci* is evenly distributed in the areas surveyed by diving, and all present were located. Then $8.74 \times 10^{-3} A. planci/\text{m}^2 \times 2 \times 10^4 \text{ m}^2 = 175 A. planci$ were theoretically present, on the average, in an area surveyed in 1 hour of towing. The number of *A. planci* actually seen while towing represents about 7.3 percent of this. (Endean [1971] has estimated that starfish readily visible represent less than a fifth of those actually present in an area.)

some 8 km of the southwestern coast of Upolu Island, Western Samoa, after a bounty had been placed on the species; however, no mention was made of extensive damage to the corals on these reefs (Garlovsky and Bergquist, 1970). Assuming an average width of 100 m of suitable reef along Guam's western coast, we find that *A. planci*, distributed at a density of 0.5–1 per 100 m² over the 38 km of reef reported to have been devastated, could furnish without additional juvenile recruitment nearly all the starfish estimated to have constituted the plague there.⁷ If density estimates obtained from surveys of leeward seaward reefs alone are used, a surfeit of starfish results.

SEA SURFACE TEMPERATURES

Sea surface temperatures taken by the U.S. Coast and Geodetic Survey at 12 island stations in the western tropical North Pacific from the late 1940s to the present were used to compute annual anomalies for each station from its long-term median temperature. The anomalies were summed by sign only for all stations for each year. The entire area from Midway to the Philippines displayed a positive anomaly from 1947 through 1954, a negative one from 1955 to 1965, and a positive one again from 1966 to the present. Annual temperature means were averaged for a more limited set of stations in the Philippine, Mariana, Caroline, and Marshall islands and plotted against annual western tropical North Pacific typhoon frequencies (Fig.

2). From the figure it can be seen that, as typhoon frequency rose in this region during the early 1960s, sea surface temperature declined; and as typhoon frequency decreased toward the end of the decade, sea surface temperature began to rise. Concurrently, Namias (1970) has furnished evidence for unusually warm sea surface temperatures in the North Pacific above lat 20° N. He suggests that regional phenomena, interacting through atmospheric dynamics, could cause hemispheric and even global climatic fluctuations. We propose the possibility that the unusually high frequency of typhoons during the 1960s could have produced the observed western tropical North Pacific cooling and extratropical North Pacific warming by serving as a vehicle for rapid heat transport between the two regions (see Erickson and Winston, 1972, for supporting evidence).

Sea surface temperatures presented in the Australian Academy of Science report on *Acanthaster* (1970) show a warm period through most of the 1950s and early 1960s, and have been cited as evidence of a general warming in Australian waters (Vine, 1972). However, these data were obtained at approximately lat 34° S, not from tropical waters near the Great Barrier Reef. This spell of unusually warm extratropical sea surface temperatures corresponds closely with the period of maximum tropical cyclone frequency for the northeastern Australian region (Coleman, 1971). Consequently, if our analysis of the relationship between tropical and extratropical sea surface temperatures and typhoon frequency in the North Pacific (for which we have considerable data) is correct, waters off the Great Barrier Reef should have been cooler than average at the time the first observations of large numbers of *Acanthaster* were made there. (The hypothesis men-

⁷ According to Chesher (1970), 12,000 starfish had been removed from the reefs of Guam by the summer of 1969. Using the density in Chesher (1969) for Double Reef, Guam, as an average for the entire 38 km, we estimate that approximately 38,000 starfish would have been present.

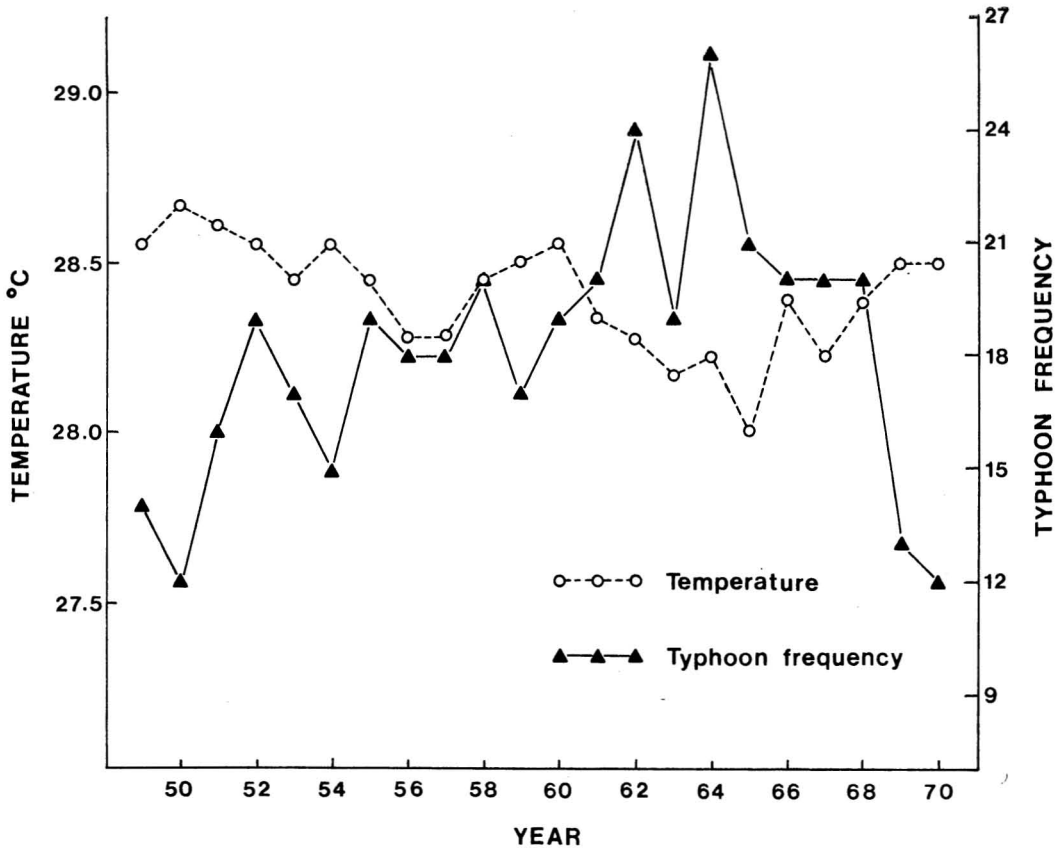


FIG. 2. Sea surface temperature vs. typhoon frequency. Sea surface temperatures are annual temperature means obtained from the U.S. Coast and Geodetic Survey, averaged together for stations in the Philippine, Mariana, Caroline, and Marshall islands. Typhoon frequencies are from the U.S. Naval Oceanographic Office, Pilot Charts for the North Pacific, 1947-1971.

tioned earlier of population increases stemming from greater success in larval metamorphosis at elevated temperatures would not now seem to hold.)

That the timing of these large-scale climatic events was not simultaneous in both hemispheres is not surprising. Namias (1963) has demonstrated for two occasions latitudinal bands of opposing temperature and precipitation anomalies extending through North, Central, and South America. Thus we would expect peak typhoon activity in one hemisphere to occur more or less at the same time that relative quietude prevailed in the other—the observed condition for the Pacific from the 1940s to the present.

CORRELATION WITH TYPHOONS

According to Wiens (1962), most North Pacific typhoons are spawned in the vicinity of the southern Marshalls and Eastern Carolines but infrequently attain typhoon-intensity wind speeds until much farther west. The predominantly westerly path of North Pacific tropical cyclones divides into two channels near Truk. Storms in the southern channel travel through much of the Western Carolines with Yap being more or less in the center of the channel. The northern channel originates near Ponape and runs northwestward with most typhoons passing within 200 miles south of Guam. Storms in the northern channel tend to reach typhoon intensity some 500 miles farther east than those in the

southern channel. However, as Wiens points out, individual atolls, even within the storm channels, may experience destructive storms only at long intervals.

Data on both typhoon frequencies and total tropical cyclonic activity in the western tropical North Pacific collected from 1945 to 1970 (U.S. Naval Oceanographic Office, 1947–1971) show a definite increase for the years 1961 through 1968. In 1965 a new record was set for both the number of warning days and the number of supertyphoons (wind speeds in excess of 130 knots) recorded in the Pacific. Guam was struck by a severe typhoon in 1962 and was affected by the close passage of three in 1963 and one in 1964. Both 1967 and 1968 were years of unusually high frequency for typhoon strikes in the Marianas (seven within 100 miles of Saipan in 1968 alone) (U.S. Naval Oceanographic Office, 1947–1971; U.S. Weather Bureau, 1956–1970). In fact, Guam, Rota, Saipan, and Tinian were all declared major disaster areas in 1968 (U.S. Naval Oceanographic Office, 1947–1971) and were all reported later as being “infested” with *Acanthaster* (Chesher, 1969).

The relationship between storm activity and *Acanthaster* aggregations reported from other islands and atolls is more difficult to assess. In January 1969, the Marshall Islands, among which Arno and Majuro were reported to have minor concentrations of *Acanthaster* (Chesher, 1970), were subjected to a newly developing, but rare, typhoon (U.S. Naval Oceanographic Office, 1947–1971). Both Ponape and Truk lie in a region of frequent tropical storm development (Wiens, 1962) and both are occasionally mentioned in typhoon accounts (U.S. Naval Oceanographic Office, 1947–1971). Palau, also reported to have large concentrations of *Acanthaster* (Chesher, 1970) but not included in our data summary or analysis, lies south of the principal typhoon tracks, but was struck at least glancing blows in both 1967 and 1969 (U.S. Naval Oceanographic Office, 1947–1971).

Patterns of typhoon development and tracks are more complicated in the South Pacific. However, as pointed out by Newman (1970) and thoroughly documented by Coleman (1971), that portion of the Great Barrier Reef reported

as having abnormal aggregations of *Acanthaster* (centered around Cairns between Cooktown and Townsville, Queensland [Pearson and Endean, 1969]) is the coastal region of northeastern Australia most frequently struck by tropical cyclones. Additional data in Coleman (1971) indicate that in the Cooktown to Townsville area an extended period of high tropical cyclone activity began in the 1940s and lasted throughout the 1950s. The 1960s show a dramatic decrease. Most important is an apparent flurry of cyclonic activity in this region from 1958 to 1961 (Coleman, 1971). In both 1958 and 1959 rather severe typhoons crossed the Queensland coast between Townsville and Bowen, with the 1959 storm being the third most intense on record (Newman and Bath, 1959; Forecasting Section, Divisional Office, Brisbane, 1959). Concomitant with heavy rainfall (Maxwell, 1968:89), winds and waves from the west and northwest would have lashed the normally protected sides of reefs to the north of Townsville. Extensive damage to the corals of those reefs would have been the expected result (see Stephenson, Endean, and Bennett, 1958). It is in this region, north of Townsville, that, as early as 1959, the first reports of large numbers of *A. planci* originated (Pearson and Endean, 1969).

Prolonged periods of unusual typhoon activity—of a decade or so—could be expected to influence the composition of reef-coral assemblages over the entire area of typhoon occurrence. If rapidly growing acroporids were favored during these epochs, one might expect a more favorable environment for recruitment and survival of *Acanthaster* (Newman, 1970). The resulting relatively high standing crops of *Acanthaster* and predominance of delicate branching corals should make such reefs more susceptible to the formation of *Acanthaster* aggregations should a typhoon make a direct hit. The western tropical Pacific in both hemispheres was subjected to decade-long periods of high typhoon activity at the end of which severe typhoon strikes occurred at both locations where *Acanthaster* was subsequently observed overwhelming the carrying capacity of individual reefs.

It is worth repeating here that the aggrega-

tions reported from Ponape, Truk, Palau, Majuro, Arno, Rota, Saipan, Tinian (Chesher, 1970), and elsewhere do not begin to approach in magnitude those of Guam or the Great Barrier Reef. Therefore, although *Acanthaster* aggregations have been widely noted, situations where they are overwhelming the carrying capacity of reefs are extremely rare. If the environmental disturbance hypothesis is correct, then large *Acanthaster* aggregations have occurred sporadically in the past. With the unusual frequency of typhoons in the 1950s and 1960s, the increasing number of divers investigating coral reefs, and a rising concern over man's impact on the environment, it is not surprising that such rare events were more frequently observed during the last decade.

SUMMARY

Information from the 1969 Westinghouse *Acanthaster* survey provided a basis for examining the problem of large aggregations of *A. planci* on coral reefs in the Pacific. The data were categorized by habitat type and summarized to indicate the relation of abundances to habitat. Although abundances were highly variable, large numbers of *A. planci* were most frequently associated with leeward seaward reefs, areas of moderate to luxuriant coral growth, and water less than 18.3 m deep. An analysis of variance procedure indicates that position relative to trade wind direction on any given island or atoll is the most significant environmental factor associated with *Acanthaster* abundance.

Definitions in the literature of what constitutes normal and infestive population sizes are judged inadequate. There are no sharp breaks in the distribution of numbers of samples versus population density. Few of the reported infestations meet the published criteria.

Field evidence is lacking to support the idea of increased larval settlement or increased survivorship at any life stage. Size-frequency distributions from normal and infestive populations can all be interpreted as unimodal with peaks at intermediate sizes. This shape does not require abrupt changes in population dynamics, indicating that populations comprising large aggre-

gations of *Acanthaster* have grown in a manner little, if any, different from those considered normal.

The hypothesis is presented that large aggregations of *A. planci* represent active behavioral phenomena; that is, they are redistributions of existing populations which at some point in their recent history have been brought under conditions of food limitation. Typhoons are the proposed principle causative agents. Average *A. planci* density estimates and recorded recent typhoon frequencies are cited in support of the hypothesis. An experimental test is suggested.

APOLOGIA

"False facts are highly injurious to the progress of science, for they often endure long; but false views, if supported by some evidence, do little harm, for everyone takes salutary pleasure in proving their falseness: and when this is done, one path towards error is closed and the road to truth is often at the same time opened" (Darwin, 1871:385).

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