PETER W. GLYNN

On the Ecology
of the Caribbean Chitons
Acanthopleura granulata
Gmelin and *Chiton*
tuberculatus Linné:
Density, Mortality, Feeding,
Reproduction, and Growth

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ABSTRACT

Glynn, Peter W., On the Ecology of the Caribbean Chitons *Acanthopleura granulata* Gmelin and *Chiton tuberculatus* Linné: Density, Mortality, Feeding, Reproduction, and growth. *Smithsonian Contributions to Zoology,* 66: 1–21, 1970.—Ecological studies on two tropical chiton species (*Acanthopleura granulata, Chiton tuberculatus*), including density, mortality, feeding, reproduction, and growth, were carried out along the shore on coral reefs in Puerto Rico and Panama. Spatial segregation is often complete in the vertical distributions of these chitons on the shore, *Acanthopleura* occurs at a high level and *Chiton* below mean sea level. *Acanthopleura* is usually less numerous, 1–8 individ./m², but present at a higher biomass density, 17–21 gm/m², than *Chiton,* 1–22 individ./m² and 8–13 gm/m². A 40 percent reduction in suitable habitat by hurricanes between 1962 and 1968 was probably the cause of a nearly equal decrease in the numerical density of the chitons. Biomass density per unit area remained essentially constant. Mortality results from low water exposure, dislodgment and abrasion, and probably from predation by shore birds and fishes. Feeding is primarily nocturnal, *Acanthopleura* feeds eight hours a day, and *Chiton* six to seven hours daily. Several species of blue-green, green and red algae, and a relatively large quantity of inorganic material, are browsed from the rock substratum. Breeding in both species is seasonal, principally confined to the late summer and autumn when sea-water temperatures are at a maximum. A nearly 2:1 sex ratio in favor of males was found in sexually mature individuals, and larger chitons seemed to produce a proportionately greater amount of spawn. Spawning in *Acanthopleura* occurs in phase with the new and full moon; no marked rhythm was observed in *Chiton.* Multiple spawning of individuals probably occurs throughout the breeding season and the release of gametes is estimated to equal 5–10 percent of the dry weight standing crop in *Acanthopleura* and around 34 percent in *Chiton.* The rate of growth in both species is similar, equal to about 30–40 mm/yr. Sexual maturity is attained in one year. The bulk of the populations is composed of relatively young animals ($\leq$2 yrs.), indicating a rapid turnover.

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Introduction

Acanthopleura granulata Gmelin and *Chiton tuberculatus* Linné contribute significantly to the numerical and biomass densities of the littoral fauna in the tropical western Atlantic region. *Chiton* ranges as far north as Bermuda, whereas the northernmost range of *Acanthopleura* is in south Florida (Warmke and Abbott, 1961). The two species are members of the family Chitonidae in the Order Chitonina, and commonly cohabit the zone of emergent rubble on the seaward edge of coral reefs. Despite their abundance and apparent dominance in this biotope, little attention has been directed toward a quantitative assessment of these chitons as a functional component of the shore assemblage. The contributions of Crozier and Arey on the general ecology and ethology of *C. tuberculatus* at Bermuda (Crozier, 1918a, 1918b, 1920, 1921; Crozier and Arey, 1918; Arey and Crozier, 1919), and of Lewis (1960) on the reproductive biology of the two species at Barbados, comprise all previous efforts of direct ecological bearing. Analysis of various aspects of the ecology of these species is enhanced by a number of features which simplify field and laboratory measurements—for example, accessibility, limited movements, rapid adjustment to new surroundings, and hardiness. Additionally, marked seasonal breeding in some regions allows recognition of year classes, and thus provides a means for determining the rate of growth.

This paper summarizes the results obtained on studies of reproduction and growth, including seasonal

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activity, spawning, recruitment, rate of growth and age at sexual maturity. Data on numerical and biomass densities, as well as movements and feeding are also included to provide a base for continuing studies of rates of erosion and the energetics of the two species. Most of the work was carried out in the vicinity of La Parguera, Puerto Rico, except where specifically stated otherwise. Data from the Atlantic and Pacific sides of the Isthmus of Panama were obtained in the Canal Zone or immediately adjacent to this area in the Republic of Panama.

Some marked discrepancies with earlier findings became apparent in the course of this study. The most important of these concern a relatively slow rate of growth and prolonged development to sexual maturity reported for *C. tuberculatus* in Bermuda (Crozier, 1918a, 1918b, 1920). Evidence from several sources in the present study indicates that growth and attainment of sexual maturity occur rapidly in the two chiton species. Examination of *C. tuberculatus* from Bermuda, to help clarify the indirect methods of measurement employed by Crozier, indicates that this species develops rapidly and at a similar rate in the northernmost part of its range. Because the earlier data were the only available for a warm-water species, it has been cited repeatedly as a basis for comparison between tropical and temperate regions (e.g., Hyman, 1967). In order to provide a clearer perspective for the assessment of these parameters, a portion of the paper is devoted to a critical discussion of all data now available on growth and reproduction in chitons.

Specimens of the two chiton species forming the basis of this study, and of four other chitons providing

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data on reproductive seasonality, have been deposited in the collections of the United States National Museum, Division of Mollusks. A list of these species, including collecting localities and reference numbers, follows:

Acanthopleura granulata Gmelin, 1791	Puerto Rico	679966
	Panama	679959
Chiton tuberculatus Linné, 1758	Puerto Rico	679961
	Panama	679962
Chiton marmoratus Gmelin, 1791	Puerto Rico	679963
	Panama	679960
Chiton squamosus Linné, 1764	Puerto Rico	679964
Acanthochitona pygmaea Pilsbry, 1893	Puerto Rico	679958
Tonicia schrammi Shuttleworth, 1856	Puerto Rico	679965

The two collections of *C. tuberculatus* examined from Bermuda are cataloged under USNM numbers 621566 and 680745.

Distribution and Numerical Density

In Puerto Rico *Acanthopleura* and *C. tuberculatus* frequently cohabit wave-swept shores composed of boulder-sized rocks. *Acanthopleura* occupies the highest level on the shore, with adults and sometimes the young on the upper surfaces of the substratum. *Chiton* is located at a lower level, usually beneath boulders during the daylight hours. Individuals of all sizes in *Chiton* tended to be photonegative, not just the younger stages (≤ 2 cm) as found by Crozier and Arey (1918). *Chiton tuberculatus* is absent from certain coastal areas in Puerto Rico which lack loose rocks; for example, cemented dune formations and intrusive headlands. On such shores this same level is often occupied by *C. marmoratus*. *Chiton marmoratus* occurs only sporadically on the rubble shores of coral reefs. High population densities of *Acanthopleura* and *C. tuberculatus* are present on most of the emergent, outer coral reefs in southwestern Puerto Rico off La Parguera, and also along much of the rocky coastline subject to adequate circulation and exposure.

The vertical heights occupied by resting chitons indicate the extent of spatial segregation of the two species populations (Table 1). Of 31 *Acanthopleura*, about 77 percent occurred between the +10 to +19 cm level. All the other individuals were at higher levels, up to between +20 and +59 cm. All of the 51 *Chiton* were found below MSL (mean sea level), some occurring as deep as −39 cm. The entire population of *Chiton* was submerged most of the time. No tendency was noted of larger individuals of *Chiton* to occur in

the open and higher up on the shore as at Bermuda (Crozier and Arey, 1918). Although no overlap in vertical zonation is shown here, overlap does occur occasionally, especially on the rubble shore of coral reefs (Glynn, 1968a). The horizontal component of overlapping distributions is usually no greater than 1 m.

TABLE 1.—*Vertical distribution (relative to MSL) of chitons at rest on the shore. Measurements obtained on 24 October 1968 during a calm morning at Papayo, La Parguera (17°58′25″N; 67°01′17″W). Elevations were reckoned by comparing the stand of sea at Papayo with tidal records over the same period at United States Coast and Geodetic Survey tide station, Magueyes Island.*

Acanthopleura				Chiton			
Height(cm)		Number	Per-centage	Height(cm)		Number	Per-centage
From	To			From	To		
+40	+59	1	3.2	0	−9	4	7.8
+30	+39	1	3.2	−10	−19	18	35.3
+20	+29	5	16.1	−20	−29	23	45.1
+10	+19	24	77.5	−30	−39	6	11.8

Chiton populations were first censused at Turrumote Reef in 1962, again in 1968 and at this time on three other reefs. Transect sampling plots 0.5 m wide, extending over the distributional limits of both species, were used. These usually varied in length from 1 m to 5 m, depending on the slope and degree of exposure. The total sampling area therefore included from 0.5 m² to 2.5 m². Spacing between transects ranged between 10 m and 50 m; these distances were established according to the physical homogeneity of the habitat and degree of exposure to the sea. Sampling was carried out during the day at low water. The entire sampling area was thoroughly excavated. Estimates of total densities were extrapolated from the counts obtained in the sample plots combined with field maps of the habitable areas available.

Acanthopleura showed maximum densities of 16 and 17 individ./m² (Tables 2 and 3). *Chiton* exceeded a density of 30 individ./m² in six samples. Variations in abundance in an eastwest direction varied markedly, showing no obvious trend along the length of the reef. Total counts indicated that *Chiton* outnumbered *Acanthopleura* on the mid-islet of Laurel Reef, at Media Luna Reef, and on Turrumote Reef. *Acantho-*

pleura was more abundant at San Cristóbal Reef and on the eastern limb of Laurel Reef. Considering total chiton densities on the various reefs sampled, from August through October, it is seen that *Acanthopleura* was present to the extent of 1 to 8 individ./m² whereas *Chiton* ranged from 1 to 22 individ./m².

As noted above, *C. marmoratus* is comparatively rare in the study area. Two were found on the mid-islet of Laurel Reef and one at Media Luna Reef. The highest overall density of this species, 1.4 individ./m² or a total of 1,150 for the entire reef, was observed on Turrumote Reef in 1968.

Variations in Density and Mortality

Significant seasonal variations in density, due to predation and other forms of mortality, have been detected in *Acanthopleura* over an 11-month period on Turrumote Reef. A maximum numerical density of 6.9 individ./m² was found in November 1967. The density diminished steadily through the remaining ten months, demonstrating approximately bimonthly

values as follows: 5.8, 5.8, 4.3, 3.3 and 3.0 individ./m². Although indicative of the survival rate of older individuals ($\geqq$34 mm), further measurements are considered necessary because adequate sampling of the younger chitons was not realized.

Evident changes in density and patterns of distribution following hurricanes suggest that alterations in the physical structure of reefs can have a marked influence on the overall abundance of chitons. Acting concurrently with these major fluctuations, of a year or more in duration, are short-term effects bringing about mortality through tidal exposure, crushing by movements of the substratum and predation. The importance of these various factors will be considered in this order below.

A marked reduction in the density of chitons at Turrumote Reef occurred over a six-year period, following destruction of the emergent coral-rubble shore by storms (Table 3). Much of the exposed rubble on the midsection of the reef was displaced to a lower level due to the heavy seas generated by hurricanes Inez in 1966 and Beulah in 1967. The principal shore fea-

TABLE 2.—*Numerical density of chitons (no./m²) on four reef islets offshore of La Parguera. Transects were located consecutively from east to west.*

Locality	Geographic position	1968 date	Species	Transect number							Habitat area (m²)	Estimated total number present
				1	*2*	*3*	*4*	*5*	*6*	*7*		
San Cristóbal	17°56'38"N 67°04'40"W	16 September	*Acanthopleura*	3	8	17	2	3	9	–	155	1200
			Chiton	1	1	3	1	0.7	0.3	–		240
Laurel (mid)	17°56'35"N 67°03'37"W	17 September	*Acanthopleura*	0	5	3	5	2	9	1	150	552
			Chiton	7	38	15	8	0	4	0		1820
Laurel (east)	17°56'43"N 67°03'24"W	18 September	*Acanthopleura*	1	8	2	3	16	1	0.5	150	610
			Chiton	0	4	5	2	5	5	0		420
Media Luna (west)	17°56'22"N 67°03'07"W	14 October	*Acanthopleura*	3	2	7	0.7	0	–	–	150	421
			Chiton	0	0.7	10	13	0	–	–		702

TABLE 3.—*Numerical density of chitons (no./m²) on Turrumote Reef. Figure 1 shows the location of transects.*

Species	Date	Transect number											Habitat area (m²)	Estimated total number present
		1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*		
Acanthopleura	8 October 1962	–	5	4	3	4	15	17	5	6	15	0.4	1430	11,010
Chiton		–	19	40	13	9	52	62	0.4	0	5	15		31,800
Acanthopleura	22 November 1968	0	0	0	0	0	2	10	1	0	3	1	850	4,500
Chiton		7	31	26	4	3	1	13	0	0	2	36		14,750

tures were little affected by hurricane Edith in 1963 (Glynn, Almodóvar, and González, 1964). The central area of the reef flat was awash and contained few loose boulders in the fall of 1968 (Figure 1, transects 3–8). Compared with 1962, the more recent census showed a relatively low density of chitons over the submerged midsection of the reef. A few large, emergent coral blocks provided a substratum for *Acanthopleura* across transect 7; however, approximately 40 percent reduction in suitable habitat (coral rubble shore) was evident. The corresponding reduction in chiton densities was 41 percent for *Acanthopleura* and 46 percent for *Chiton*. Sampling pressure during the early phase of the study amounted to removal of less than 10 percent of the population from one area; therefore, the main results are not thought to be seriously affected by this factor.

Estimates of the differences in biomass have been calculated from length-weight relationships (Figure 2) and the size structure of the populations at Turrumote Reef in the fall of 1962 and 1968. Biomass densities in terms of dry weight and organic matter content were derived from the measurements in Table 4. The total organic matter content of *Acanthopleura* on the reef was reduced to about half its original value (Table 5); however, the biomass densities per unit area of habitat (gm/m²) agreed reasonably well over the six-year period, differing by about 18 percent. *Chiton* showed only a slight decline in biomass over the entire reef, and actually gained 36 percent on a unit area basis. This difference is partly attributable to the size structure of the population. The 14 mm class in 1962 made up 33.8 percent of the sample, whereas in 1968 small chitons were relatively rare in the fall, with only 0.8 percent of the sample in this size range.

Several hundred *Chiton tuberculatus* were found dead on the western end of Turrumote Reef on 26 July

FIGURE 1.—Recent changes in the emergent structure of Turrumote Reef. (A) Verified 22 October 1968, from U.S. Coast and Geodetic Survey shoreline *ms*, T–13121, Puerto Rico SW coast, Bahía Fosforescente, scale 1:10,000, datum plane: MHW. Darkened areas are emergent coral rubble, approximately above MHW. Water moves across breaks in midsection of reef except at extreme low tide. (B) Appearance in 8 August 1962. Locations of transects 1—11 are indicated.
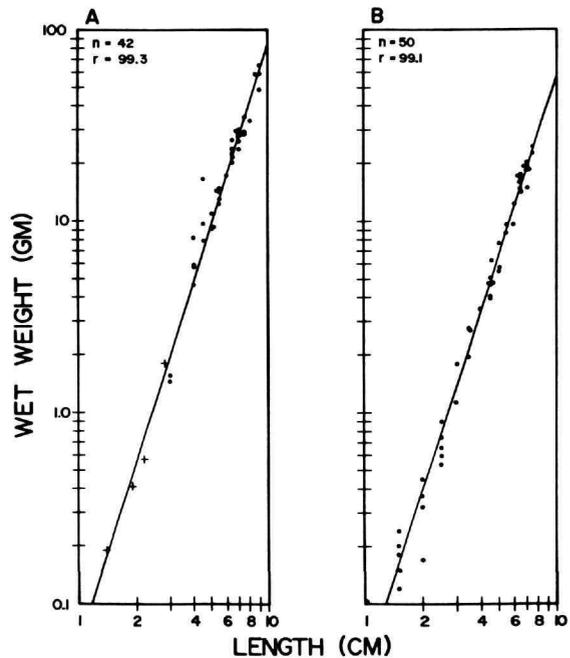

FIGURE 2.—Length-weight relationship in *Acanthopleura* (A) and *C. tuberculatus* (B). The length was obtained from animals in a relaxed condition on a flat surface, and the weight from animals blotted dry with paper towel. The regression equations are log W=−1.198+3.132 log L for (A) and log W=−1.322+3.064 log L for (B). Samples collected at Turrumote Reef, 8 August 1962, except for smallest *Acanthopleura* (+) which were obtained from Enrique Reef, 22 November 1968.

TABLE 4.—*Percent dry weight and ash-free organic matter content of chitons collected from coral reefs at La Parguera (September–November 1968). Ashing was carried out for 24 hours at 530°C. Sample size is noted in parentheses. Dry weight and organic matter content were independent of size (p >> 0.05). Spearman's rank correlation coefficients for the effect of size on these attributes, in the order given, were 0.32 and 0.14 in* Acanthopleura, *and 0.30 and 0.43 in* Chiton.

Species	Statistic	Wet weight (gm)	Dry weight (gm)	Percentage dry weight	Organic matter (percentage of dry weight)
Acanthopleura	Range	1. 80–25. 61	0. 84–15. 20	40. 6–75. 3	27. 5–34. 2
	X̄	12. 96	7. 27	55. 6(18)	30. 6(6)
	S.D.	—	—	9. 0	2. 5
Chiton	Range	1. 71–35. 82	1. 00–18. 94	51. 7–59. 8	17. 4–21. 9
	X̄	9. 83	5. 21	54. 5(5)	19. 8(6)
	S.D.	—	—	3. 4	1. 7

TABLE 5.—*Estimates of the biomass of chiton populations on Turrumote Reef before and after changes in structure of habitat by hurricanes.*

Species	Date		Wet weight (gm/m²)	Dry weight (gm/m²)	Organic matter (ash-free dry weight)	
					gm/m²	kg/reef
Acanthopleura	8 October	1962	123. 7	68. 8	21. 0	30. 0
Chiton			75. 5	41. 2	8. 1	11. 6
Acanthopleura	22 November	1968	101. 2	56. 3	17. 2	14. 6
Chiton			117. 5	64. 0	12. 6	10. 7

1968. This mortality was estimated to represent less than 5 percent of the total number present. It is believed the kill was due to prolonged exposure which accompanied a series of low tides (−4.3 cm below mean low water) during the preceding four days. On the first two days of this low series, the tides were diurnal in character. A few dead *Acanthopleura* were also observed at this time. The potency of the tidal factor has been documented previously (Glynn, 1968b).

Some mortality must also result from dislodgment and abrasion due to the impact of waves and surge on the loose rubble. Crushed individuals of both species were occasionally found. Inspection of the shoreline after storms, however, showed a lower mortality than expected. The ability to cope with such hazards must be enhanced by certain adaptations which seem well suited to the rigors of this environment. Hamilton (1903), for example, observed a rhythmic movement of the girdle of *Acanthopleura* in phase with the wave period. The girdle was brought flush and tight against the substratum with each approaching wave and then was raised during the backwash. It was shown in an earlier study (Glynn, 1968a) that both chiton species can retain a grip on the substratum under artificially induced pressures of 2.4 kg/cm² (directed vertically downward on the animals), equivalent to the force generated by waves 5.5 meters high. *Chiton* is much more active than *Acanthopleura*; it can reposition itself on the undersurface of an overturned rock in less than a minute. The turbulence is often quite high near the center of distribution of *Chiton*.

The quick movements performed by *Chiton* may also play a role in limiting predation by fishes. Although several species of subtidal chitons have been shown to comprise a portion of the diet of fishes (Randall, 1967), no predator of *C. tuberculatus* has as yet been positively identified. Only a single chiton actually preyed upon was found in this study. This was a 6 centimeter *Acanthopleura* which was entered dorsally through the broken second valve. Nearly all of the soft parts had been removed; only the mantle and connective tissue

holding the valves together remained. Several Ruddy Turnstones, *Arenaria interpres* Linné, and one Little Blue Heron, *Florida caerulea* Linné, were present in the area. Moribund and recently dead chitons of both species were frequently found being fed on by the columbellid gastropod *Mitrella ocellata* (Gmelin, 1791). This species is most probably a scavenger. Other potential predators of *Chiton* include rats and possibly oyster drills (Arey and Crozier, 1919). Chitons are not generally eaten by man in Puerto Rico. The quantities consumed elsewhere seem limited at present (for example in Bermuda, the Dominican Republic and by the Cuna Indians of San Blas, Panama), but in time a greater utilization is expected.

Feeding

FREQUENCY.—Locomotory movements and feeding appear to be closely associated activities. The radula was nearly always extruded and in motion in actively moving chitons removed suddenly from the substratum. Rasping of the radula, as observed through the

glass walls of an aquarium, was also closely correlated with the animal's motility. In addition, the foregut was empty in chitons at rest, but filled rapidly after they began moving. These related activities are well suited for arriving at estimates of the time spent in feeding.

Each species was observed continuously in the field on two different occasions over periods of 18 to 24 hours. A vigil was kept of the individual movements of at least 25 animals. An indirect, weak light source from a flashlight aided observation at night. Chitons in the immediate vicinity were dissected open every two to three hours (every half hour at twilight) to determine whether or not ingestion was taking place.

Motility and feeding increase markedly at night in both species. The diel feeding activity of *Acanthopleura* is shown in Figure 3, which also includes the light and tidal regimes as well as extent of exposure of the majority of individuals observed. Feeding began before twilight and involved at least 80 percent of the animals between 1730 and 2430, after which time the number feeding decreased steadily until the following
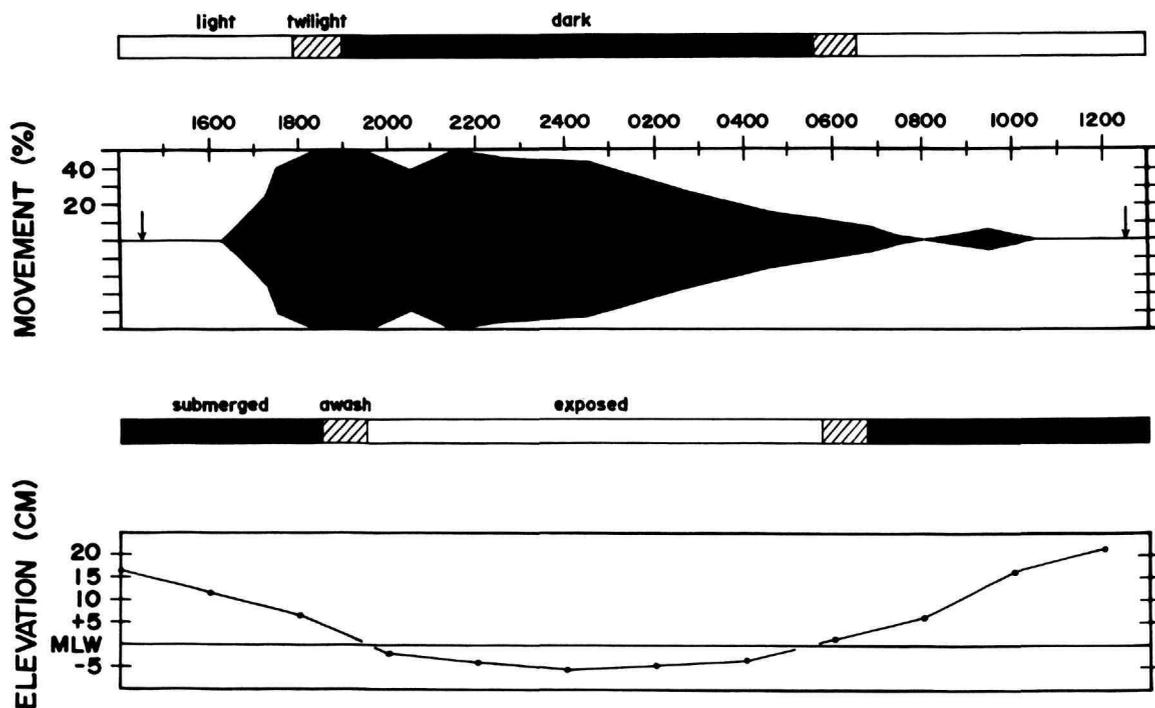

FIGURE 3.—Time spent moving and presumably feeding by *Acanthopleura* (n=28) over a 22-hour period, Laurel Reef, 20–21 November 1968. The diel light regime is noted above, degree of exposure of the chitons in the center, and height of tide below.

morning. The feeding of a second group of *Acantho-pleura* observed 2–3 December 1968, occurred between 1730 to 1000 of the following morning. Day length, sky cover and tidal movement were similar to the conditions shown in Figure 3. Between 56 and 74 percent of the individuals in this group of 27 animals were feeding over a period of 9 hours; however, on several occasions single individuals, as well as groups of two to five, were seen browsing at all hours during the daylight, irrespective of the tidal stand. From these observations, it can be tentatively concluded that feeding in *Acanthopleura* is largely a nocturnal activity which seems to be regulated more by the natural day-night regime than by the tides. It is interesting that Thorne (1968) reported feeding by *Acanthozostera gemmata* on the Great Barrier Reef only at night while uncovered by the tide.

Chiton demonstrated a more rigid feeding schedule which began suddenly just after sunset (Figure 4). This species began moving to the upper surfaces of rocks between 1800–1900; the maximum number feeding was reached by 2030. The numbers feeding diminished through the remainder of the evening until all were concealed by 0800 of the following morning. A similar activity pattern was observed in a group of 30 animals at Turrumote Reef on 24–25 September 1968.

The time involved in individual feeding sorties, even when the majority of animals are active at night, is not constant. For example, in *Acanthopleura* (Figure 3) the mean feeding time was 6.18 ± 1.40 hrs (d.f.$=27$, $p=0.05$). Also, some individuals have been observed at rest over periods of 24 hours. Once an individual starts feeding, this activity usually continues uninterrupted. Seventy-one percent of *Acanthopleura* fed continuously; the remainder fed two to three times
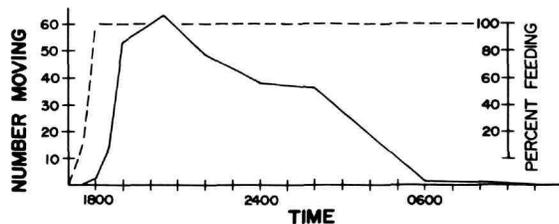

FIGURE 4.—Time spent moving and feeding by *Chiton tuberculatus* (n=62) over a 22.5-hour period, Papayo, 2–3 December 1968. Broken line belongs to right-hand scale. A thorough search of the 15 m² study area afterwards showed that the maximum number visible at 2030 probably included all of the chitons present in this locality.

during the night with resting periods ranging between two and eight hours. The resting periods occurred sporadically in different individuals. Feeding in *Chiton* proceeded continuously in those individuals that were visible. Examination of the undersides of coral blocks during the early evening hours showed that virtually all individuals were out and browsing. All individuals of *Chiton*, however, were below the water level, regardless of the height of the tide. Inspection of the activity curves (e.g., Figure 4) indicates varying times involved in feeding in this species as well. The feeding of *Chiton* may be further restricted on a regular periodic basis due to a photonegative response to moonlight claimed by Crozier (1921).

Despite the high individual variability already noted, and an apparent response to unknown factors, present observations indicate that the mean time engaged in feeding by the two chiton populations may be significantly different. Accounting for diurnal browsing in *Acanthopleura*, it is likely that around eight hours each day are spent in pursuit of food. *Chiton* spent less time feeding, nearer to six to seven hours daily; however, some data obtained on the rate of ingestion indicate that *Chiton* may actually consume greater quantities of food over equal periods of time.

An ability to home, though not pronounced, was observed in both chiton species. Generally, this behavior was best developed in *Acanthopleura*, where it was observed frequently. Homing was not always perfect in *Acanthopleura*, in the sense that some individuals would often come to rest within a few centimeters of their original site of attachment, and with a slightly different orientation. The mean distance over which *Chiton* ranged, including movement onto upper surfaces, was equal to a radius of about 45 centimeters. The feeding sorties in *Acanthopleura* were somewhat less, with a mean radius near 30 centimeters.

FOOD QUALITY.—Gut analyses, coupled with careful observations of the movements executed while browsing, have shown that neither species is selective in its feeding habits, but rather both chitons appear to ingest indiscriminately the numerous algae present within the feeding area. Feeding trails left on the substratum by the abrasive action of the radula often showed an undeviating course through mixed growths of encrusting algae. Moreover, *Acanthopleura* has been seen browsing over surfaces contaminated with oily residues on the shore and in captivity has consumed and expelled large quantities of paper and cork as well as more

nutritious but foreign items of diet (e.g., large, fleshy algae occurring subtidally).

The following algae were frequently found in abundance in the gut of *Acanthopleura:* Cyanophyceae—*Calothrix crustacea* Bornet and Flahault, *Calothrix juliana* (Menegh.), *Microcoleus lyngbyaceus* (Kützing) Crouan; Chlorophyceae—*Cladophoropsis membranacea* (C. Agardh) Børgesen, *Enteromorpha* species (young plants); Rhodophyceae—*Centroceras clavulatum* (C. Agardh) Montagne. The movement of *Chiton* onto the upper surfaces of rocks to feed leads to ingestion of some of the same species of algae consumed by *Acanthopleura.* This is especially true where the two chiton populations overlap in vertical distribution. The same species of blue-green algae previously listed were also recovered from the gut of *Chiton.* Ingested Chlorophyceae included *Enteromorpha flexuosa* (Wulfen) J. Agardh and *Rhizoclonium riparium* (Roth) Harvey. *Herposiphonia* species and *Polysiphonia* species were the only red algae consumed that could be identified. The diet of *Chiton* probably contains a greater proportion of fleshy thalli which are more common at the lower level occupied by this species. A small amount of animal food is probably ingested by both species; a considerable quantity of rock fragments, comprising up to 40 percent (dry weight) of the total material removed, is also ingested.

Reproduction

The breeding condition was determined from a monthly assessment of gonad volumes, examination of fresh smears of gonads, presence of mature gametes, artificial fertilization and occurrence of spontaneous spawning. The period of maximum breeding was further delimited from the time of first appearance of young and by extrapolation of growth curves derived from size-class analyses. Lewis (1960) has shown that the two chitons have a very brief larval life; metamorphosis is complete within a week's time of fertilization. Routine sampling was conducted over a 25-month period, and during this time a marked periodicity in breeding activity was evident, with a regular annual pattern of similar appearance in both species.

GONADS, SEX RATIO, GONAD SIZE AND AGE.—During the breeding season the chitons could be readily sexed by exposing the reproductive organs. The gonads in both species are light salmon pink or orange in males and greenish in females. It was not possible to dis-

tinguish the sexes externally. Females of *Chiton* in the breeding condition failed to show any pinkish tone on the ventrum as reported by Crozier (1920). Hermaphroditism was never detected over a wide range of body sizes. The relatively low gonad index (gonad vol. x 100/wet body wt.) in *Acanthopleura* (see under "Seasonal Changes," page 9 is a true reflection of the small absolute size attained by this organ and not due to a proportionately greater mass of shell or other inorganic materials in this species (Figure 5). Actually, a significantly higher mean ash content was found in *Chiton,* 80.2 percent, than in *Acanthopleura,* 69.4 percent (Table 4). The calculated t-statistic of 9.82 exceeds the tabular value (p<0.001). These data are based on six mature individuals of each species which ranged in size as follows: *Chiton,* 3.24–7.94 gm dry weight; *Acanthopleura,* 3.56–12.10 gm.
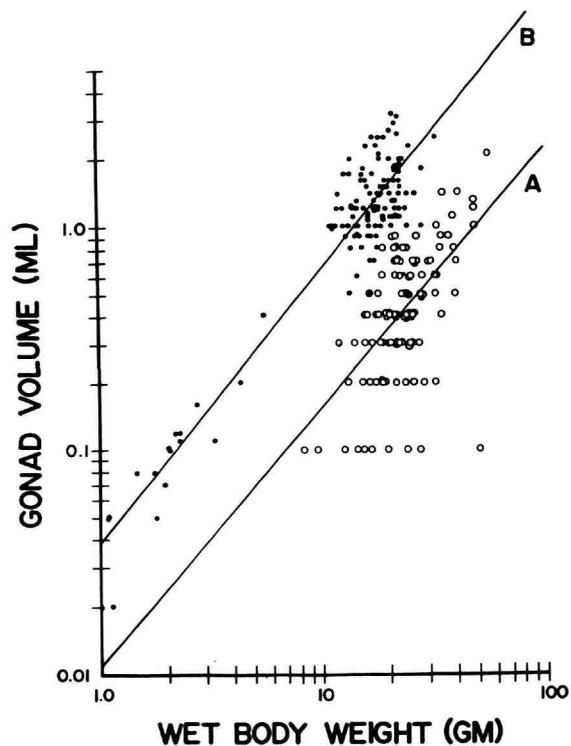

FIGURE 5.—Relationship of body weight to gonad volume in *Acanthopleura* (A) and *Chiton tuberculatus* (B). Data include all animals sampled during height of breeding season (August–December), except for omission of three individuals of *Acanthopleura* with a gonad volume of <0.1 ml. The regression equations are log V=−1.958+1.144 log W for (A) and log V=−1.409+1.218 log W for (B).

A sex ratio in favor of males was noted at a highly significant level (p<0.005) in both species. In *Chiton*, among 255 individuals, this was 1.93♂♂:1.00♀♀, with $X^2 = 25.63$. In *Acanthopleura*, among 160 individuals, the sex ratio was 1.81♂♂:1.00♀♀, $X^2 = 13.22$. Males in *Chiton* were significantly larger than females, the mean wet weight differences were 17.9 gm and 16.2 gm. The t-statistic of 2.21 (d.f.=254) exceeds the tabular value at p=0.05. The mean weight differences between males and females in *Acanthopleura* were 24.8 gm and 22.7 gm, respectively. In this case t=1.41 (d.f.=138), indicating an absence of any size differences in the sexes (p>0.1).

A preponderance of large males in *Chiton* is suggestive of consecutive sexuality. It was already noted above, however, that no hermaphroditic individuals were ever found. Furthermore, Crozier (1918b) emphasized the gonochoristic condition of this species. Also, examination of the gonads in 15 individuals of approximately one year of age (1.00–3.30 gm wet wt.), when sexual maturity is first reached, gave a sex ratio of 4:1 in favor of males. *Chiton* males predominated in all sexually mature populations, regardless of age, and were not a result of sex reversal or differential mortality. Crozier's (1918b) explanation of the condition, the result of a different death rate operative over an age span of 6–12 years, is not in accordance with my findings; however, elimination of females may occur early in development, preceding or following metamorphosis. While examination of a sufficiently large sample of small but sexually mature *Acanthopleura* was not undertaken, casual observation indicated that a similar condition may also exist in this species.

The reproductive organs were large and contained mature gametes in *Chiton* over a considerable range in size (Figure 5). The few year-old individuals of *Acanthopleura* examined also contained large gonads distended with gametes. Three individuals of *Acanthopleura* ranging in wet weight from 2.8 gm to 3.6 gm actually spawned under laboratory conditions. Some of the scatter in Figure 5, particularly as regards *Acanthopleura* (r=55.9) at gonad volumes of 0.1 to 0.2 ml, is due to a marked reduction in the size of gonads of spent individuals. A stronger correlation is evident in *Chiton* with r=93.7. The general trend in both species, however, indicates that the size of the reproductive organs increases in growth at a greater rate than does the body weight. This confirms the suggestion that the largest individuals are endowed with a proportionately higher reproductive potential. Crozier (1918b) implied that the gonad volume is relatively smaller in older individuals of *C. tuberculatus*. He noted further that no gonad could be detected in *Chiton* less than 3.4 cm (Crozier, 1920). Neither of these reports is in accordance with my findings.

SEASONAL CHANGES.—The gonad index was highest during the late summer and fall (Figure 6). Gonadal buildup was not evident in *Acanthopleura* until late summer, but took place in *Chiton* in the spring or early summer. Spawning activity, usually evident in November or December, was generally well reflected by a decrease in the size of the gonads. In the 1961–62 season, the gonads in *Chiton* remained large through January and February with a mean gonad index near seven and nine, respectively. A brief decline in the gonad index in the fall was observed once in *Acanthopleura* and on two occasions in *Chiton*. This may not be significant, especially in view of the expected variations due to size effects.

The appearance of mature eggs followed closely the attainment of maximum gonadal size during the late summer-fall period. Success in effecting artificial fertilization and early development (up to the time of hatching of the larva) was also greatest in this season. In *Acanthopleura*, large quantities of eggs were present and embryogenesis observed in samples with a mean gonad index equal to or exceeding one. A similar trend was found in *Chiton*, with the exception that a few mature eggs were present in May 1961 and 1962 when the mean gonad index was very low. Mature spermatozoa were found in both species the year round. These seasonal trends were fairly well correlated with the annual variations in the sea surface temperatures (Figure 7). Mean winter temperatures of 26–27°C ascended to near 29°C by September or October, and the chitons had large gonads and were fully ripe and breeding at this time. A lag effect was apparent, however, with numerous reproductively mature individuals present a month or two beyond an abrupt decline in the thermal structure in the fall. This was especially evident in *Chiton* in the winter of 1961–62, when the gonads were large and contained copious quantities of mature gametes at the minimum annual mean temperature of 25.5°C. Subsequent studies of the availability of plankton around reefs, have shown that a relatively high density of diatoms and zooplankton tend to occur in the fall (September-October). Thus, the occurrence of chiton larvae
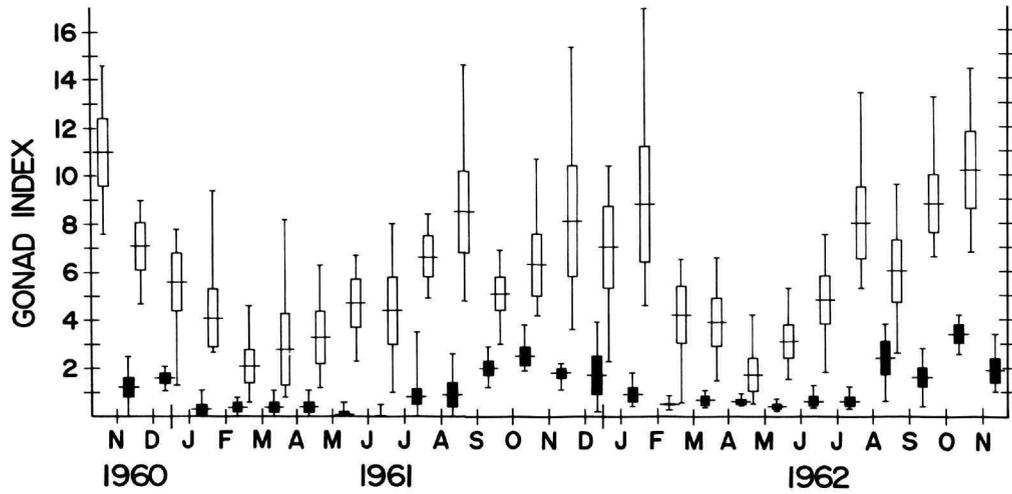
FIGURE 6.—Seasonal pattern of the gonad index in *Acanthopleura* (dark) and *Chiton tubercu-latus* (clear), Turrumote Reef. Collections were made at approximately mid-month. The range, mean, and confidence limits of the mean (p=0.05) are shown for each sample. Samples included 10 to 15 animals with the following ranges in wet weight, 8.30–55.68 gm (*Acanthopleura*) 4.31–32.70 gm (*C. tuberculatus*). Gonad size was determined from the displacement volume; body mass from the living animal blotted dry.
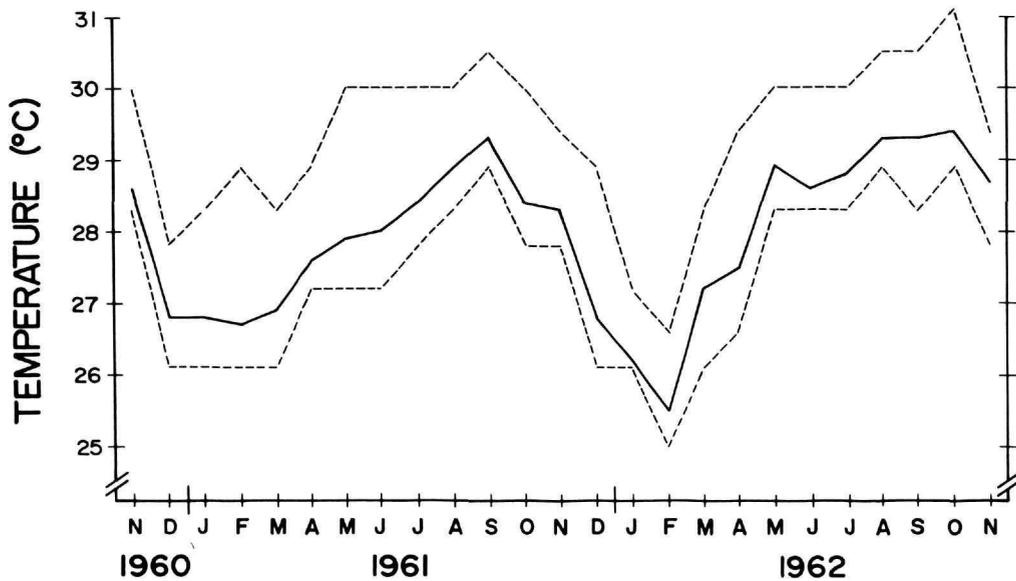

FIGURE 7.—Annual variation of the surface sea-water temperature at the United States Coast and Geodetic Survey tide station, Magueyes Island, La Parguera. Monthly mean and extremes are shown by solid and broken curves, respectively.

would coincide in part with the presence of a richer plankton community.

SPAWNING.—The incidence and intensity of spawning during the breeding period was investigated in order to determine: (a) its timing in relation to variations of certain environmental factors, and (b) the proportion of tissue mass expended in the release of gametes over the breeding season. Night-long vigilance of chitons in the field failed to reveal any clues of spawning under natural conditions. Observations on the voluntary spawning of chitons in captivity, *Acanthopleura* in Puerto Rico and Panama, and *Chiton* in Puerto Rico, were carried out on a continuous basis for over three months and a month, respectively. Between 25 and 35 individuals of each species were collected approximately every 15 days, on and between periods of new and full moon. The animals were confined separately to half-full, liter capacity bowls with cheesecloth covers, and positioned near windows in order not to interfere completely with the natural lighting. A small amount of algal food was present; this grew on the bowls during a 10-day conditioning period in running water exposed to full sunlight. The water was removed daily and examined for the pres-

ence of gametes. Under these conditions, uninjured chitons survived for as long as two months. As a matter of routine, however, the animals were usually returned to the field after a confinement period of 30 days. Dead and moribund individuals were removed immediately and replaced by the new animals collected every two weeks.

Acanthopleura exhibited a regular, bimonthly rhythm in spawning, correlated with the new and full lunar phases (Figure 8). This pattern was similar in Puerto Rico and Panama in different years. The spawning was not confined solely to the evenings of new and full moon. On two occasions it preceded the new or full moon by four days and continued once for a week beyond full moon. The data in *Chiton* are incomplete, but fail to show the marked regularity evident in *Acanthopleura*.

Evidence that spawning in *Acanthopleura* may follow a bimonthly periodicity in the wild was found in an oscillation of the gonad index, which followed the changing phases of the moon (Table 6). The low gonad volumes observed at new and full moon are suspected to result from the release of gametes over these periods. A gradual diminution in gonad size was
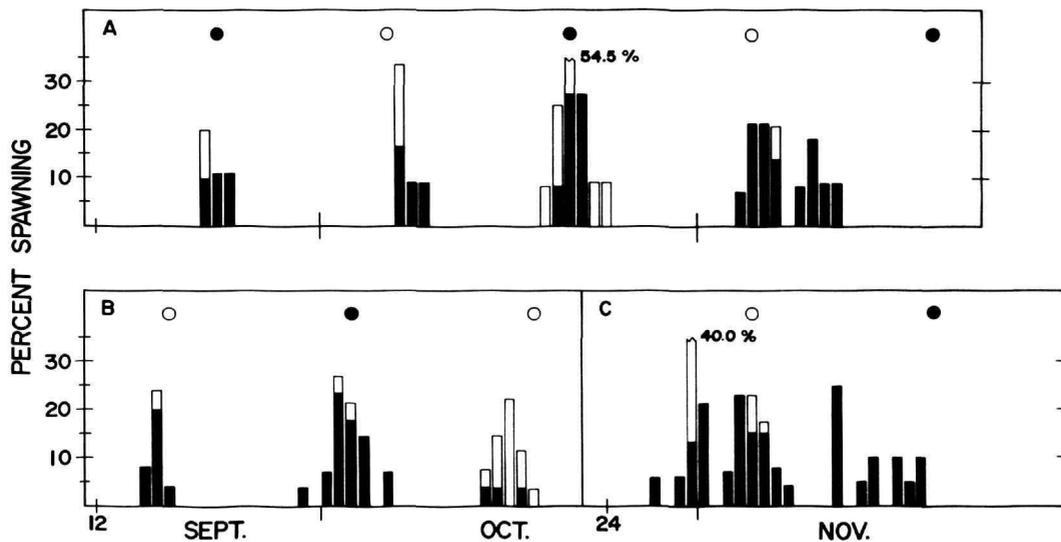

FIGURE 8.—Voluntary spawning in captivity of *Acanthopleura* (A, B) and *Chiton tuberculatus* (C) in relation to the lunar phases. A: La Parguera, Puerto Rico, 12 September to 23 November 1968; B: Galeta Point, Panama, 12 September to 21 October 1967; C: La Parguera, 24 October to 30 November 1968. Proportion of females spawning represented by darkened area of bar. The percent spawning was calculated from the total number of living animals in a given sample, including spent individuals that continued to survive.

TABLE 6.—*Weekly variations of the gonad index in* Acanthopleura *and* Chitcn *in relation to lunar phase and tide range, Turrumote Reef, 10 November 1965 to 5 January 1966. Each sample contained ten individuals.*

Date	Moon phase	Tide range (M)	Acanthopleura			Chiton		
			Mean	Maximum	Minimum	Mean	Maximum	Minimum
10 November	new	−0. 04 0. 39	1. 8	2. 4	1. 1	11. 2	15. 5	7. 0
17	first quarter	0. 06 0. 30	4. 4	6. 7	2. 7	8. 7	11. 4	5. 3
24	full	−0. 06 0. 35	1. 4	2. 1	0. 7	3. 7	5. 7	1. 3
1 December	last quarter	0. 09 0. 26	2. 7	4. 0	1. 8	6. 3	10. 8	3. 0
8	new	−0. 13 0. 35	1. 5	2. 6	0. 6	5. 7	6. 8	3. 9
15	first quarter	0. 02 0. 24	2. 0	4. 1	0. 9	8. 5	11. 6	6. 3
22	full	−0. 13 0. 28	1. 0	1. 4	0. 7	6. 6	8. 5	4. 4
29	last quarter	0. 02 0. 19	1. 1	2. 0	0. 8	8. 2	11. 9	5. 4
5 January	new	−0. 13 0. 18	1. 0	1. 5	0. 6	7. 3	10. 6	4. 7

also evident toward the end of the breeding season. This was accompanied by an abrupt decline in the presence of mature gametes on 22 December 1965. A similar oscillation of the gonad index in *Chiton* was noted, but it lacked the complete regularity observed in *Acanthopleura*. Intrasample variations in gonad size during the breeding season (Figure 6) are in part a result of the sudden shedding of gametes and subsequent gonadal buildup.

Although the data in Table 6 show a consistent, inverse relationship between the occurrence of spring tides and gonad size, additional spawning records show that gametes are shed during neap tides and at other phases of the tidal cycle (over periods of ascending and descending amplitude). While these spawnings appeared unrelated to the tides in their timing, they did show a high correlation with the lunar phases. A possible incitement of spawning by the tides encounters further difficulties in the following observations. Individuals in the laboratory could not have any direct tidal clues, and, in fact, some spawned after they crawled about the water surface. Spawning occurred most frequently at the same time in the early evening, and not according to the tidal cycle, which undergoes a daily progression and change in timing every fortnight.

Similar evidence was used by Brewin (1942), who argued against entrainment of spawning by tides in *Cryptoconchus,* also with a bimonthly spawning rhythm. Tide-induced spawning, however, is known. In the *Sypharochiton* complex this occurs twice monthly during spring tides near high water in the early evening (Johns in Knox, 1963).

As noted above, all spawning occurred in individuals isolated in separate containers. Several replicates of large and small groups of chitons containing both sexes (determined subsequently by dissection), failed to show any greater frequency or intensity of spawning than that illustrated in Figure 8. An assessement of this activity in groups was facilitated by the tendency of individuals to spawn in restricted areas and by the adhesive properties of the mass of gametes. Viable gametes innoculated into the water of isolated individuals of the opposite sex also failed to incite a spawning reaction. These results suggest that spawning may not be triggered by the release of gametes from one sex, thus leading to mass reciprocal stimulation. Similar findings have been reported for at least three other chiton species (Grave, 1922; Brewin, 1942; Christiansen, 1954). It must be pointed out, however, that spawning in several species is dependent on the associa-

tion of both sexes, often with males initiating this activity (Heath, 1905; Murti and Nagabhushanam, 1968). The greater frequency of female spawners (Figure 8), especially in view of the skewed sex ratio, is not readily explained. The degree of synchrony realized among different individuals of *Acanthopleura*, in the early evening during the new or full lunar phases, may be sufficient to insure a high success in fertilization.

The incidence of spawning in both chiton species indicates that some individuals shed gametes at least twice within a single lunar month. From the group spawning activities illustrated in Figure 8, it can be seen that *Chiton*, on an individual basis, spawned 2.2 times per lunar month. For *Acanthopleura* (in Puerto Rico), the individual spawning frequency at new moon in October was 1.3 and at full moon in November 1.2.

A greater frequency of spawning in *Chiton*, and also its pronounced irregularity, were evident in the individual spawning records. For example, 47 percent of *Chiton* that spawned did so on two or more occasions. One individual spawned six times over a 17-day period. In addition, spawning in this species usually occurred on nonconsecutive days (in 82 percent of the sample). In *Acanthopleura*, 48 percent spawned twice, all on consecutive days. Only one individual spawned on three nights in succession. If spawning were to occur this frequently during the breeding season, individuals of *Acanthopleura* would release gametes bimonthly over a duration of about three months. Supporting this assumption are a few records for both species, of individuals that spawned on two consecutive lunar phases.

In order to estimate the magnitude of biomass being diverted to reproduction, gametes were collected quantitatively from laboratory spawnings and their mass (dry weight, including the ash content) determined according to the following procedure. Eggs were collected from the water with a pipette, passed through bolting silk of 0.076 mm aperture size to remove feces and extraneous debris, then transferred to a preweighed glass fiber filter (Number 934–AH, Hurlbut Paper Company). A correction was made for adsorption of salts to the filter; this amounted to 21.3±0.5%, determined for four blank filters. The quantity of salts adhering to gametes, resulting in a higher apparent mass, was not determined. Neither was a method de-

veloped for concentrating sperm; only three samples were obtained when spawning occurred out of water on the sides of the bowls.

Tables 7 and 8 summarize the dry-weight values of gametes spawned and provide estimates of the proportion of biomass released by individuals. Mature eggs in both species had a mean diameter close to 0.19 mm, indicating that the number of gametes per unit mass of spawn is probably nearly equal. It is seen that larger individuals of *Acanthopleura* shed the greatest quantity of spawn, thus indicating that large gonads in older animals are functional and contribute toward the production of a proportionately higher number of gametes. The three largest females (6.5—7.4 cm) spawned a mass of gametes ranging between 4.8 and 9.4 percent of the ash-free dry body weight,

TABLE 7.—*Mass of gametes spawned by* Acanthopleura *in captivity, October–November 1968 (La Parguera, Puerto Rico). The proportion of the body mass released in spawning (expressed on the basis of ash-free dry weight) was calculated from data in Figure 2 and Table 4.*

Individual number	1968 date	Body length (cm)	Sex	Dry weight gametes (mg)	Percent body mass spawned
1	7 Oct.	–	♀	23. 8	–
2	7	–	♀	4. 6	–
	8			42. 5	
3	8	–	♀	56. 2	–
4	10	–	♀	24. 4	–
5	20	6. 5	♀	196. 7	5. 3
6	20	6. 4	♂	7. 3	0. 9
	21			25. 4	
7	21	5. 3	♀	15. 1	0. 8
8	21	7. 2	♀	291. 5	9. 4
	22			190. 9	
9	22	7. 4	♀	258. 6	4. 8
10	4 Nov.	5. 9	♀	3. 0	0. 8
	5			18. 0	
11	6	–	♀	15. 3	–
12	5	5. 4	♀	14. 3	0. 8
	6			<0. 1	
	7			1. 9	
13	5	5. 7	♀	17. 9	1. 3
	6			<0. 1	
	7			11. 7	
14	7	5. 4	♂	<0. 1	<0. 1
15	9	5. 4	♀	<0. 1	
	10			<0. 1	<0. 1
16	10	5. 3	♀	13. 5	0. 8
17	11	5. 3	♀	2. 7	0. 2

while all seven females below six centimeters spawned less than 1.3 percent. *Chiton* did not follow this trend, but two-thirds of the animals listed spawned at least 4.8 percent of their tissue weight; and the proportion of tissue weight in gametes released by four individuals exceeded 10 percent. Light spawning by some individuals may be due to an earlier shedding of greater intensity.

Another indication that *Chiton* expends more energy in spawning is evident in the variations of the gonad index (Figure 5). The gonadal size in *Chiton* fluctuated by about 6 percent of the animal's wet weight, whereas in *Acanthopleura* this amounted to between 2 and 3 percent.

Growth

Measurements of the growth rate were based primarily on interpretation of size-class frequency distri-

butions. In *Acanthopleura,* growth data for individuals were used to verify the growth curve derived from the analysis of modal classes. The younger stages of *Acanthopleura* were not sampled adequately due to their inaccessibility in the spaces penetrating the coral substratum. Only later (September–November 1968) was it learned that the young live in deep recesses of large coral boulders. These were obtained by breaking open the coral with a sledge hammer. Representative sampling of *Chiton* was achieved, since all growth stages were included in the collections.

A monthly growth increment of 2 mm in *Acanthopleura* of 30 mm length is indicated in Figure 9A. If growth occurred at this rate over the first 12 to 14 months, a size of 28–32 mm would be attained in this period. Extrapolation of the growth curve to the point of intersection with the time axis, indicates settlement of young in September, at the beginning of the breeding season. It is more likely that major recruitment would occur somewhat later (cf., Figure 5).

Individual growth measurements obtained in Panama are also indicative of relatively rapid growth during the first year (Table 9). The monthly growth increment of individuals between 20–28 mm ranged between 1.0 and 4.8 mm. The smallest chiton observed, initially 8.0 mm, demonstrated a very high rate of growth, an increase of 68.8 percent during the first month and 65.2 percent in the second month. The mean growth rate in Panama, for 8–28 mm chitons, was 3.8 mm/mo. These data indicate more accelerated growth in smaller individuals. Therefore, the slope of

TABLE 8.—*Mass of eggs spawned by females of* Chiton *in captivity, October–November 1968 (La Parguera, Puerto Rico). Percent body mass spawned in units of ash-free dry weight.*

Individual number	1968 date	Body length (cm)	Dry weight gametes (mg)	Percent body mass spawned
1	30 Oct.	4.4	<0.1	<0.1
	1 Nov.		<0.1	
	5		<0.1	
	6		<0.1	
	7		<0.1	
2	1	3.6	11.2	4.9
	4		<0.1	
	6		<0.1	
3	1	3.4	30.8	16.0
	6		<0.1	
	7		<0.1	
4	4	3.5	8.0	3.7
5	4	3.5	<0.1	<0.1
6	4	4.3	<0.1	8.1
	5		<0.1	
	6		35.1	
7	6	3.2	25.4	15.4
8	12	3.5	15.1	7.0
9	12	4.3	20.9	4.9
10	12	4.1	18.2	4.8
11	14	4.1	8.9	2.4
12	15	3.5	32.3	14.8
13	15	4.2	6.7	1.7
14	19	3.3	19.8	11.6
15	19	3.8	28.6	10.0

TABLE 9.—*Growth rate of young individuals of* Acanthopleura *on reef flat at Galeta Island, Panama. Individual identity was attained by isolating animals on marked coral boulders.*

Observation period	Individual number	Body length (mm) initial	Body length (mm) final	Growth per month	Percentage growth
16 January to 19 February 1969	1	21.2	22.2	1.0	4.7
	2	27.5	28.5	1.0	3.6
	3	20.3	23.3	3.0	14.8
	4	8.0	13.5	5.5	68.8
	5	21.2	22.5	1.3	6.1
19 February to 18 March 1969	1	22.2	27.0	4.8	21.6
	2	28.5	32.7	4.2	14.8
	4	13.5	22.3	8.8	65.2
	5	22.5	25.5	3.0	13.3

the hypothetical curve in Figure 9A would probably be greater if it had been possible to include the growth of smaller forms. The origin of the curve would shift to November or January, a more likely time of recruitment. Accordingly, an adjustment of the growth curve on the basis of the component rate differences in size, would result in a mean growth of about 34–38 mm/yr.

Numerous young of *Chiton* were first noted in January 1968, most probably a result of autumn breeding (Figure 9B). A gradual increase in size of this cohort (curve I) was evident through September; by this time a mean length of 32 mm had been attained. An earlier year class was recognizable in July 1967 (curve II). As in the following year, the 24 mm size group was the most prominent with the mean lengths differing by only 0.5 mm in succeeding generations. Growth of the earlier cohort (curve II) proceeded rapidly through January, resulting in a slightly steeper aspect of this portion of the growth curve. The slope of curve I is 0.08 and of curve II 0.12, equal to an annual growth of 32 mm and 41 mm, respectively. Ex-

trapolation of the growth curves to their point of origin agrees reasonably well with the seasonal breeding period. Thus, in the 1967 year class, heavy settlement presumably occurred in early winter; in 1968, in the fall. A separate curve (III), with slope=0.05, was constructed for the 44-mm and 54-mm size classes. Deceleration of growth appeared evident in these larger animals, but this may not be valid considering the high frequency of the 64-mm class in July and September of the preceding year. Although an overlap in size with older generations is expected with increasing age, the nearly continuous progression of the 1967 cohort indicates that a high proportion of individuals in the 54-mm and 64-mm size classes were 20 to 24 months old. A general retardation of growth during the breeding season was not apparent in *Chiton* one year of age. The likelihood of a storage function of the digestive gland (Lawrence, Lawrence, and Giese, 1965) or of the gonad itself (Giese and Araki, 1962) would serve to alleviate the energy requirements during reproduction and perhaps allow continuous growth.
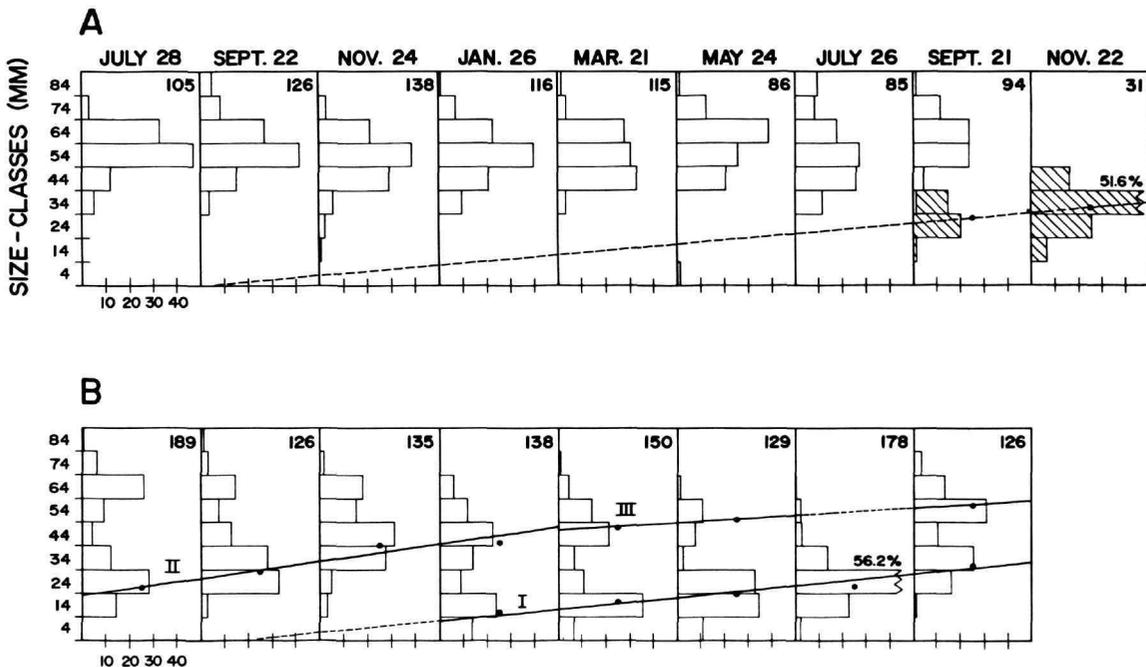
FIGURE 9.—Growth curves constructed from size-class frequency distributions in *Acanthopleura* (A) and *Chiton* (B), July 1967–November 1968, Turrumote Reef. Sample size and date are noted for each collection. The last two samples of *Acanthopleura* were purposely biased in favor of small individuals (cross hatching). Regression curves were calculated from the weighted mean values of the two most frequent classes in a given cohort.

A mean annual growth in *Chiton* of 32 mm to 41 mm is of the same magnitude as that observed in *Acanthopleura* (34 mm—38 mm/yr), indicating that the two species may not differ significantly in this attribute.

While Crozier's (1918a) technique for determining the growth rate and longevity of *Chiton tuberculatus* seems logically sound, a number of serious difficulties were met in an attempt to adopt it for use in this study. The method is based on the number of "growth lines" present on the valves and the underlying assumption that each "growth line" is formed at the rate of one per year. The following is the clearest description of the "growth lines" given by Crozier. "The central area of the tegmentum of each plate is marked by a series of more or less distinct transverse grooves, or 'growth-lines'." Evidently he was referring to the curved ridges and grooves on the median triangle of the valves (see Figures 30 C and D, Hyman, 1967). This sculpturing, oriented longitudinally along the anteroposterior axis of the body, is clearly evident in a slightly lateral position to the smooth jugal tract. In some noneroded specimens, however, the sculpturing is visible near the midline on the apex or mucro. The lateral triangles are also provided with a sculpturing of ridges and grooves, but they are fewer in number and oriented perpendicular to those of the median triangle. It is doubtful that these could be accurately enumerated since the linearity of the ridges is usually indistinct, and they are often broken into a series of elongate tubercles.

The relationship between the number of grooves on the median triangle and body length revealed an ill-defined curvilinear trend among animals examined in Puerto Rico (Figure 10). Considerable scatter is also evident in log-normal and log-log transformations of the data. The number of grooves in some individuals of equal size (35 mm and 57 mm) differed by as much as 30 percent. Sculpturing was absent from two chitons less than 10 mm in length. Numerous grooves were present on individuals above 19 mm, indicating that sculpturing develops rapidly, probably within a few months' time. It also appears that the number of grooves approaches a limit with advancing age. This is probably a result of effacement of the sculpturing due to erosion, which is often pronounced toward the midline in larger chitons. The valves were very often worn—showing radular marks—by the feeding activities of other chitons.

An attempt to improve Crozier's technique was un-
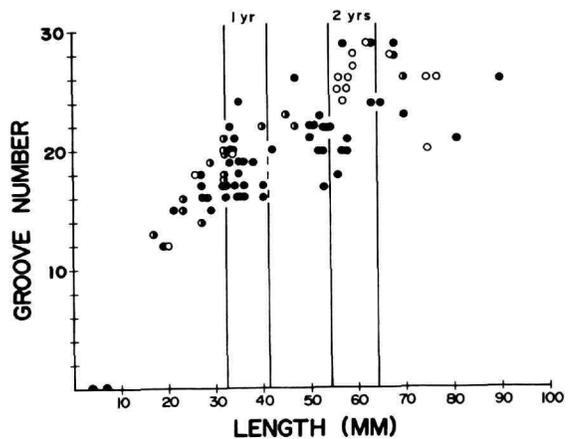
FIGURE 10.—Relationship between body length and number of grooves on the median triangle in *Chiton tuberculatus*. The 53 dark circles represent chitons collected from La Parguera, Puerto Rico, 2–14 October 1968. Bermudian samples include 15 individuals each from St. George's Island, open circles, 7 July 1956, and Sue Wood Bay, partly occluded circles, 19 September 1969. Specimens with badly eroded valves were not used in this analysis. The range in body length of one- and two-year-old chitons in Puerto Rico is also shown.

successful. *Chiton* attained a size of 32–41 mm in the first year in Puerto Rico. The number of grooves at this age was 16–24, with a mean of 20 grooves. Chitons two years of age (54–64 mm), with 18 to 29 grooves, illustrate the extent of overlap of the sculpturing between year classes.

A direct comparison with Crozier's (1918a) results is not possible since he failed to state explicitly the method of calibration. Presumably some kind of adjustment was made because the number of grooves would exceed 20 in individuals estimated by Crozier to be five or six years of age (about 6 cm). The length-groove relationship was examined in the present study in two different samples of *C. tuberculatus* from Bermuda. All points appear to follow the same, highly dispersed trend observed in Puerto Rico (Figure 10). Therefore, the number of grooves and the time of their appearance in development may be assumed to be similar at the two localities; i.e., their growth rates are probably similar. Lewis et al. (1969) found the growth rates of some West Indian littoral gastropod species to also be similar in tropical and subtropical regions. If the growth rates and the rate of groove development are similar in Puerto Rico and Bermuda chitons, then individuals 3 cm and 6 cm in body length would be

one and two years old at both localities, rather than two and six years old as Crozier estimated. In addition, a mean life span of eight years determined by Crozier is probably closer to two years. Consequently, Crozier's (1918a, 1918b) estimates of growth, longevity and age at sexual maturity are considered questionable if not entirely in error.

Discussion

So few quantitative data are available on the structure of littoral assemblages that a comparison of the standing crop of ecological analogs on a geographic basis cannot always be made with adequate precision. Some results reported from temperate and boreal seas, however, indicate that motile browsers and grazers often range in dry-weight biomass between 5 and 184 gm/m² on consolidated surfaces (Mokyevsky, 1960; Glynn, 1965). The density of chitons, approaching a sustained level of 70 gm/m² for each species, suggests an equivalent carrying capacity on some tropical shores. Greater trophic-level densities for primary consumers have been reported in the higher latitudes. But the standing crop would also have been greater in the areas investigated in this study if gastropods, decapods, and other herbivorous species were included. Estimates of the biomass (ash-free dry weight) of an entire coral-reef community at Eniwetok Atoll resulted in a mean value of 132 gm/m² for all herbivores, including the Scleractinia (Odum and Odum, 1955). In the present study, the standing crop densities of Chiton and Acanthopleura were equal to about 8 percent and 15 percent, respectively, of the herbivore trophic level of Eniwetok Reef, indicating that chitons can constitute an important element on certain tropical shores.

Present knowledge of the reproductive activities of shallow-living Caribbean chiton species reveals a seasonal aspect in breeding which is most pronounced in the late summer-fall period. This pattern has been well documented in the present study for *Acanthopleura granulata* and *Chiton tuberculatus*. Monthly assessment of gonads in *Chiton squamosus* and *Chiton marmoratus* in Puerto Rico has shown maximum reproductive activity in September through November and November through February, respectively (Glynn, unpublished). Yet occurrence in these two species of some ripe individuals of both sexes throughout the year probably results in sporadic breeding at other times. Metcalf (1892) obtained embryos artificially from

these species in June and July at Jamaica, and Lewis (1960) has reported October through November as the breeding period for *C. marmoratus*. Bimonthly analysis of gonads in *Tonicia schrammi* over a three-year period revealed a pronounced seasonal pattern with greatest activity in August through October. Winter and spring breeding may also occur since young chitons were plentiful in the field in the spring and summer. The first appearance of the young of *Acanthochitona pygmaea* indicates summer to fall recruitment with limited breeding in the spring as well (Glynn, unpublished).

Thus far, it has been found that the breeding activities of chitons inhabiting warm-water regions display an annual, periodic rhythm more or less in phase with the highest yearly sea-water temperatures. This has also been demonstrated for *Acanthozostera gemmata* (Blainville) on the Great Barrier Reef (Stephenson, 1934) and for *Acanthopleura haddoni* Winckworth and *Onithochiton erythraeus* Thiele in the Gulf of Suez (Pearse, 1968a). In addition, as contrasted with the majority of temperate species, the reproductive period is often prolonged and limited breeding is evident outside the main breeding season.

It should be emphasized that all of these species were studied in low-latitude localities which experience rather marked seasonal variations in temperature. This is evident in the annual range of the sea surface temperatures (based on monthly maximum and minimum readings) recorded at La Parguera, Puerto Rico, 8°C; Low Isles, Great Barrier Reef, 12°C; Wadi el Dom, Gulf of Suez, 14°C. Several markedly different thermal regimes characteristic of various tropical areas within the Indo-Pacific Province have been summarized by Pearse (1968b). Pearse provided data indicating that breeding in echinoderms tends to occur seasonally in tropical areas subject to marked seasonal variations in temperature, but nearly continuously in the lower latitudes where annual variations in temperature are not so pronounced.

Preliminary information on the breeding patterns of chiton and echinoid species obtained on either side of the Isthmus of Panama tend to support the above relations. The annual thermal regimen in Panama is decidedly different on Atlantic and Pacific shores of equal latitude (Hubbs and Roden, 1964; Collier, 1964); periodic upwelling leads to an abrupt decline in sea temperatures in the Bay of Panama. The observed annual ranges in maximum and minimum tem-

peratures on Pacific and Atlantic shores are 18°C and only 6°C, respectively (Rubinoff, 1968). *Chiton stokesii* Broderip, 1832, and *Echinometra vanbrunti* (Agassiz, 1863), both Pacific species, indicate an adjustment of breeding to periods of high temperature. Reproduction in *Chiton* usually occurs before the onset of upwelling, and sometimes following this period. *Echinometra vanbrunti* breeds after the upwelling season (May–July). At the Atlantic sampling station *Acanthopleura granulata* and *Acanthochitona hemphilli* Pilsbry, 1893, lack a well-defined seasonal cycle in gonad size, contain mature eggs the year round, and the population structure is not made up of distinct size groups, all evidence of continuous breeding. *Echinometra lucunter* (Linnaeus, 1758), the Atlantic analog of *E. vanbrunti,* shows no regular variations in gonad size through the seasons. The gonad index in *E. lucunter* was relatively high in March, May, June, August, and September, whereas in *E. vanbrunti* gonad size increased abruptly and the maximum gonad index was observed in May and July on different years. Also, discrete size classes are not observed in Atlantic populations, but are usually present in populations of the Pacific echinoid.

Comparing these observations with Puerto Rico, it is seen that a more pronounced seasonal aspect in breeding is evident at the higher latitude. This condition was observed in *Echinometra lucunter* in Puerto Rico as well, where breeding and recruitment of young are seasonal, occurring in the summer or early fall (Glynn, unpublished). A similar breeding pattern was described for *E. lucunter* in the Florida Keys (McPherson, 1969).

Orton (1920) and Thorson (1946) pointed out how annual variations in temperature may regulate breeding, and Yonge (1940) suggested that temperature might be important for tropical animals. Presently much of the data on the reproductive patterns of shallow-living tropical species are accommodated by Pearse's (1968b) model and emphasize the sensitivity of breeding to the different temperature regimes characteristic of the low latitudes. New evidence indicates that the accumulation of nutrient reserves, possibly indirectly related to temperature effects, may also be important in the regulation of reproductive periodicities (Pearse, 1969a, 1969b).

A divergent sex ratio favoring males in chitons is unusual in view of the great body of evidence that the majority of gonochoristic mollusk species tend to show a greater frequency of females (Fretter and Graham, 1964). This disparity was highly significant, however, over a wide size range in *Acanthopleura* and *Chiton tuberculatus. Acanthochitona hemphilli* Pilsbry, 1893, and *Chiton stokesii* Broderip, 1832, in Panama also show this trend. In the former species males predominated, 1.59 ♂ ♂ : 1.00 ♀ ♀, in a sample of 241 individuals, $X^2 = 12.62$ (p < 0.001). The sex ratio in 258 individuals of *C. stokesii* was 1.46 ♂ ♂ : 1.00 ♀ ♀, $X^2 = 8.92$ (p < 0.01). Stephenson's (1934) data for *Acanthozostera gemmata* indicate this species, too, has a proportionately greater number of males among the breeding adults. The sex ratio was 1.52 ♂ ♂ : 1.00 ♀ ♀ in 335 individuals, $X^2 = 14.19$ (p < 0.001). *Chiton squamosus* and *C. marmoratus* examined in Puerto Rico did not show a skewed sex ratio. A sample of 130 individuals of the former species contained 52.4 percent males, and 48.0 percent males were present among 129 individuals of the latter. An equal sex ratio was also evident in *Acanthopleura haddoni* (Pearse, 1968a), indicating that the skewed condition occurs in only certain tropical species.

Ward (1966) has shown that males predominate in the limpet *Fissurella barbadensis* Gmelin, also a member of the shore fauna. Evidently this condition is common to many intertidal species which broadcast their gametes. The difficulty of explaining differences in the sex ratio on the basis of adaptation was first pointed out by Fisher (1930) and subsequently supported by Williams (1966) and Leigh (1970), in latter showing that the neonate sex-ratio can probably not be affected by differential mortality between the sexes. Still, it is conceivable that spermatozoa may become limiting under certain conditions, perhaps from rarefaction due to high turbulence, in which case a superabundance of males to help counteract this effect would be advantageous. The chorion membrane of chiton eggs is provided with elongate projections that may allow them to adhere to the substratum and thus increase their chances of survival. Fertilized eggs undergoing development do adhere tenaciously to the substratum.

Some of the differences in the reproductive biology of *Acanthopleura* and *Chiton tuberculatus* are possibly related to the different conditions of exposure experienced by these chitons. *Acanthopleura* is usually uncovered and subject to atmospheric drying at low water, whereas *Chiton is* rarely exposed for any length of time. Spawning in *Acanthopleura,* in phase with

the new and full moon, shows a degree of synchrony not evident in *Chiton*. Lunar spawning is apparently common among species of the Polyplacophora inhabiting the intertidal zone, and therefore under the influence of alternating periods of exposure and submergence. It occurs fortnightly in *Cryptoconchus* (Brewin, 1942) and in *Sypharochiton* (Johns in Knox, 1963), and around full moon in *Chaetopleura* (Grave, 1922) and in *Acanthozostera* (Stephenson, 1934). It could be reasoned that a finer regulation in the timing of spawning would reduce wastage of gametes, perhaps a crucial adjustment necessary for continued reproductive success at higher levels in the littoral zone.

The quantity of spawn released by *Acanthopleura* was much less than in *Chiton*. Over the entire breeding season, *Acanthopleura* with a biomass density (ash-free dry weight) of 19 gm/m² shed between 1.0 gm and 2.0 gm of spawn. This is equivalent to 5–10 percent of the dry-tissue weight of the species. In contrast, *Chiton* at a population density of 10 gm/m² released an amount of spawn equal to 31–37 percent of the dry-tissue biomass. These calculations are based on the mean percentage mass recovered from 3 cm and 4 cm individuals. Comparing the output of gametes, it appears that *Acanthopleura* is more efficient, requiring a lower expenditure of energy in reproduction, than is *Chiton*. A high production of gametes in *Chiton* may be necessary because of its apparent asynchronous spawning behavior or as a compensatory adjustment to ensure adequate recruitment and survival in the face of a presumed higher rate of mortality at the relatively low level occupied. Additionally, asynchronous spawning may serve to reduce predation. While data are scarce on this subject, high gamete production apparently occurs in *Cryptochiton,* also an essentially subtidal species which spawns asynchronously (Okuda, 1947; Tucker and Giese, 1962).

It is also possible that the homing behavior in *Acanthopleura* evolved as an adaptation to help relocate suitable resting sites in order to avoid excessive drying. Homing is exercised in the *Sypharochiton* group in only those populations living highest on the shore (Johns in Knox, 1963).

Crozier's (1918a, 1918b) greatly underestimated growth-rate determinations have led to the tentative conclusion that chitons in colder seas reach maturity at essentially the same rate or even sooner than those inhabiting the lower latitudes. Present evidence shows a very rapid rate of growth for tropical chitons; *Acan-*

thopleura and *Chiton tuberculatus* both grow to approximately 36 mm in a year. This rate of growth is significantly higher than the data now available for temperate species. The mean adult size of seven chiton species on the California coast was attained in three years (Heath, 1905). One of these, *Katharina tunicata* (Wood), reached a length of 55 mm in this period. Two small chiton species, *Cyanoplax dentiens* (Gould), 8 to 10 mm in body length, and *Nuttallina thomasi* Pilsbry, 12 mm, were not fully grown until one and two years, respectively. *Cryptochiton stelleri* (Middendorff), the largest chiton known, grows to about 85 mm in the first year and 148 mm in the second. Based on a fully grown animal of 300 mm, the relative growth would equal 28 percent and 21 percent in the first and second years, respectively. Estimates of the relative growth in *Acanthopleura* and *C. tuberculatus* over the first and second years, are near 43 percent and 29 percent, respectively. The growth rate of *Chaetopleura apiculata* (Say), present along the northeastern coast of the United States, was 10 to 12 mm per year, or fully grown (25–29 mm) in three years (Grave, 1932).

Considering the age at sexual maturity, *Acanthopleura* and *Chiton* reach the breeding condition (gonads distended with mature gametes, voluntary spawning) by the end of the first year, and not in three years as previously reported for *Chiton* (Crozier, 1918a). Although several temperate species also attain reproductive maturity in one year (Heath, 1905; Grave, 1932; Christiansen, 1954), most require two years to reach this condition.

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