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Population Structure, Spawning, and Growth of the Coral Reef Asteroid *Linckia laevigata* (Linnaeus)[1]

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ABSTRACT: The blue coral reef asteroid *Linckia laevigata* (Linnaeus) makes up conspicuous adult-only populations on shallow reef flat habitats in the tropical Indo-West-Pacific. Monthly year-round census showed a consistent unimodal size-frequency distribution, with mean arm radius for the population fluctuating from 93.8 to 99.4 mm, at Asan reef flat, Guam, Mariana Islands. This census failed to detect a significant influx of smaller individuals within the population. Searching efforts for this and other asteroids yielded only three pretransformation-stage juveniles and less than 10 transforming young (with arm radius of approximately 50 mm) during a 3-year period (1972 through 1974), in spite of the omnipresence of adults. The *L. laevigata* population at Asan showed a peak breeding period during the summer months (May to August), as indicated by the spawning activities of sampled adults after they had been injected with 1-methyladenine. Laboratory-grown juveniles attained a mean arm radius of 13.9 mm, 14 months after metamorphosis (15 months after spawning). The juvenile-to-adult transformation is estimated to take place in average *L. laevigata* at about 2 years of age. Individually marked adults in the field increased 1.1 mm (approximately 1 percent) in arm radius and 0.9 g (approximately 7 percent) in underwater weight (means for 32 individuals) during 5.5 months. The growth rate and population structure indicate that this population of *L. laevigata* has a low turnover rate with a low level of recruitment.

THE BLUE STARFISH *Linckia laevigata* (Linnaeus) is one of the most conspicuous benthic animals associated with coral reefs in the Indo-West-Pacific faunal region. This species is not found in Hawaii where two other species of *Linckia* (*L. multifora* and *L. guildingi*) occur (Ely 1942, Fisher 1906). However, *L. laevigata* is widely distributed from the western Indian Ocean to southeastern Polynesia (Clark and Rowe 1971, Marsh 1974).

Linckia laevigata is seldom found on the seaward reef terrace around the fringing reefs of Guam, but it is common or abundant on the reef flat or on lagoon patch reefs along the lee coasts. A curious form of *Linckia*, which closely resembles *L. laevigata* in morphology but which differs in coloration and proportions (brown, more slender arms), occurs mostly on reef terraces (Yamaguchi 1975, Strong 1975). This may be a sibling species; it is referred to in this paper as *Linckia* sp.

The only author who has described juvenile *Linckia laevigata* is H. L. Clark (1921), from the Torres Straits, northern Australia. Clark (1921: 66) stated: "At Mer [*L.*] *laevigata* is the most abundant and naturally the most conspicuous of the sea-stars. . . . Young specimens were decidedly rare and it seems probable that the early development, after metamorphosis, takes place near the edge of the reef in its inaccessible nooks and crannies."

Juveniles of *Linckia laevigata* have rarely been found in Guam and elsewhere. Indeed, they are so rare and also so different from the adults in appearance that Livingstone (1932) and A. H. Clark (1954) each described new species of *Ophidiaster*, their description being based on juvenile specimens of *Linckia* (most likely

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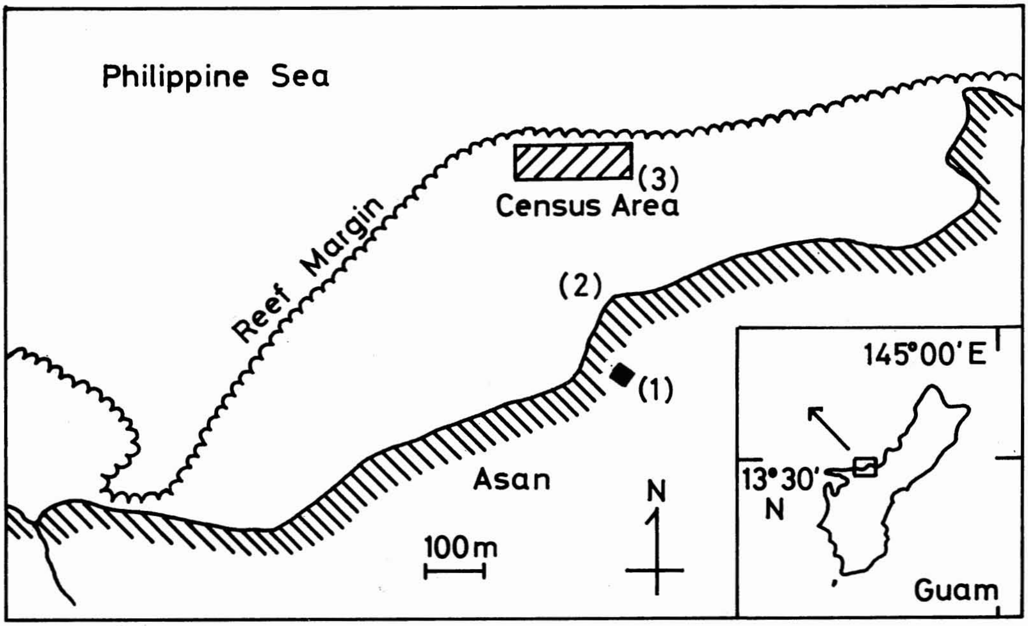

FIGURE 1. Asan reef, Guam, and the census area. The Coral Reef Marine Center Dive Shop (1) is located directly across from the rocky point (2) on the shore. There are three prominent rocks (3), which uncover during low tides, situated in a right-angle triangle at the southeastern edge of the census area.

L. laevigata) from the Great Barrier Reef (*O. propinquus*) and the Marshalls (*O. perplexus*). Clark and Rowe (1971) suspected these two nominal species to be *Linckia multifora*. These forms, however, are distinctly autotomous (asexually reproducing) and do not transform into uniformly colored adults. The pretransformation stage of juvenile *Linckia laevigata* closely resembles species of the genus *Ophidiaster*, but the former is readily distinguishable from the latter by the absence of papular pores along the oral surface. Examination of the specimens on loan revealed the above two *Ophidiaster* species to be juveniles of *Linckia*.

The apparent paucity of juveniles within the adult populations characterizes many larger benthic animals in coral reef habitats. This phenomenon raises the question of how these populations are maintained in view of the evidently very low recruitment. It also implies that the population might be endangered by unnatural destructive forces such as intensive cropping by man if recruitment and population turnover rates are as low as indicated by the paucity of juveniles. For example, giant clams (*Tridacna* spp. show the trend of adult dominance in their populations (Asano 1937, Motoda 1938, Hester and Jones 1974, McMichael 1974). These clams are under increasing pressure by exploitation in certain areas.

Frank (1968) found a parallel between marine macrobenthic animals and terrestrial perennial plants with regard to their long lives and broadcasting reproductive strategies. From his study of coral reef mollusks, he presented some evidence (1969) to support his tentative generalization that these life history characteristics are associated with stable communities, and he called attention to the general lack of data on this subject for marine communities. The present report provides information for one of the most conspicuous benthic animals on the coral reefs.

MATERIALS AND METHODS

Population Census

A population of *Linckia laevigata* on a reef flat at Asan on the west coast of Guam was chosen for year-round census because of the animals' abundance and the accessibility of the area. A section approximately 50 × 100 meters in the middle of the outer reef flat (Figure 1) was visited at monthly intervals from November 1973 to November 1974. Research workers either waded or snorkeled across the section. All arm radii of every individual encountered were measured to the nearest mm *in situ*. Each arm was coded according to the Carpenter system; i.e., the arm opposite the madreporite is arm *A* and one counts clockwise in alphabetical order, viewing the animal on the oral surface. Approximately 160 to 190 individuals were measured during a 3-hour period in each monthly census. Damaged and regenerating arms and numbers of madreporites and anuses were also recorded.

Marking Experiments

Our initial attempts to attach numbered tags to individual *Linckia laevigata* by drilling through the arm (with 1-mm drill bit) failed because the nylon monofilament securing the tags was ejected through the body wall within a month. However, the wounds on the arm where the tags had been ejected remained as conspicuous marks, because the surface granulation there became coarse and less pigmented. Therefore, a scheme of marking circular scars with an electric engraver was devised.

Combinations of two different arms with five different marking patterns produced 250 individual codes. A total of 214 individuals were actually marked and measured for arm radii (from the center of the mouth to the arm tip) and underwater weight (a specific gravity balance was used). They were released to their original habitat (population census section) in November 1974. Approximately 3.5 and 5.5 months after the release, all *L. laevigata* specimens found around the release point were collected and the marked individuals were remeasured. Irregular individuals—those having other than five arms and a single madreporite—were not used in the marking experiments.

At the 3.5-month recapture, the individuals without marks were removed from the area and only the marked individuals were released again. Furthermore, at the 5.5-month recapture, all marked and unmarked individuals were removed from the area and transplanted to other reefs in order that a possible recolonization by new recruits at the experimental site at a later date might be detected and in order that the hypothesis of low recruitment of this population might be tested. Because the Asan reef is isolated, there is little chance for adult and juvenile *L. laevigata* to migrate in from other reefs.

Spawning Activity

From February 1974 to January 1975, 12 (16 in February 1974) individuals of *L. laevigata* were collected monthly from the sector east of the census but on the same reef flat. Approximately 5 ml of 3×10^{-4} *M* 1-methyladenine in seawater was injected in each individual, which was then kept in a separate container on the beach. Reaction time, sex, intensity of spawning activity, and size (arm radius) of each individual were recorded. The test animals were removed from the Asan reef flat after the spawning observation. The activity of spawning was arbitrarily categorized for both sexes by four levels: $-$, no reaction; $+$, trace; $++$, active; and $+++$, vigorous. The chemical 1-methyladenine induces maturation and the subsequent release of gametes in asteroids when they are ripe (Kanatani 1969), so that the above treatment should detect the ripeness of gonads within individual test animals. Animals that did not spawn usually revealed immature or spent gonads upon dissection. Vigorous spawning was characterized by abundant sperm that made the seawater in the container very milky, or for females, approximately a million eggs shed.

Growth of Postmetamorphic Juveniles in the Laboratory

A cohort of postmetamorphic juvenile *L. laevigata* was raised in the laboratory for up to 14 months after the animals had metamorphosed. Eggs were spawned and fertilized on 17 January and brachiolariae settled and metamorphosed 10–14 February 1974. Eighteen juveniles were kept in two groups, 8 in a 15-liter aquarium and 10 in a 50-liter aquarium, both equipped with a subsand filter and an air-lift recirculation system, from September 1974 to February 1975. Four of the 8 and 5 of the 10 juveniles were further reared in a 50-liter

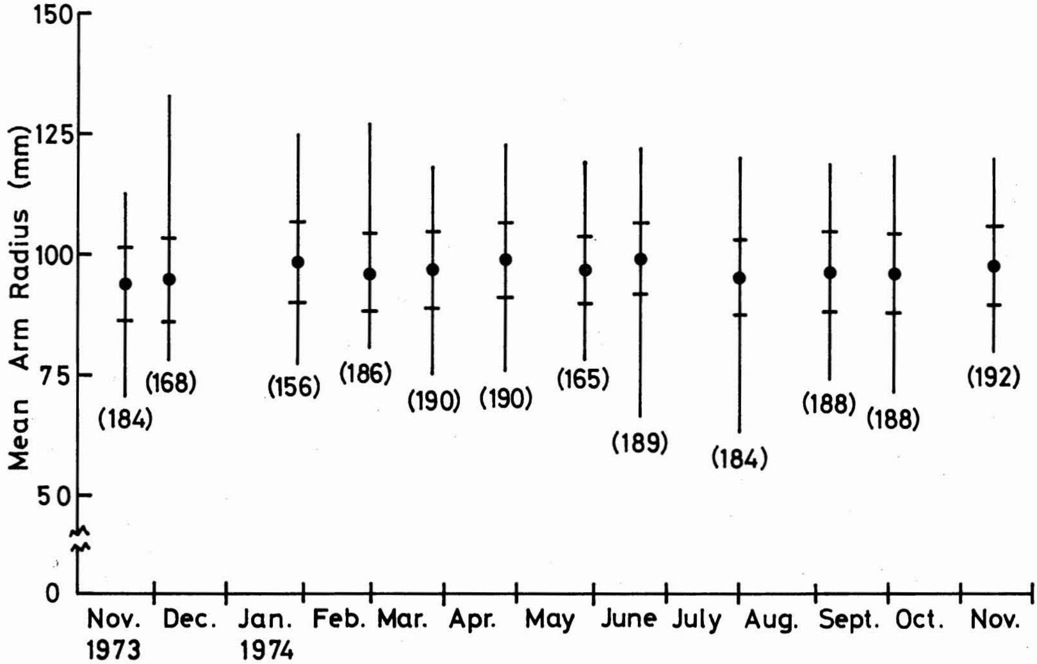

FIGURE 2. *Linckia laevigata*: year-round population structure of Asan reef population. Mean, ± one standard deviation, and range for each census sample are shown with number of individuals in parentheses.

aquarium until April 1975 when the culture experiment was terminated. Each juvenile was measured monthly and recorded by photographs so that, after September 1974, individual identification could be made by the distinctive brown and dark green blotches which had appeared on the juvenile bodies. Juveniles were uniformly opaque white when they were smaller than about 3 mm in arm radius. Juveniles were fed epibenthic microorganisms encrusting dead coral skeletons (*Acropora*).

RESULTS

A total of 2180 (plus 49 not included in the size-distribution because they had more than two damaged arms) *L. laevigata* were measured in 12 censuses from November 1973 to November 1974. Mean arm radii for individuals were calculated from measurements for each arm of the individual, with recently damaged arms being excluded. The mean arm radius fluctuated between 93.8 and 99.4 mm and one standard deviation ranged from 7.1 to 8.6 mm (Figure 2). The largest individual was 133.0 mm and the smallest 63.2 mm in mean arm radius. The size-frequency histogram of all the 2180 animals indicates a unimodal distribution as do those of individual censuses (Figure 3). These distributions are close to the normal distribution as shown by linearity of the cumulative curve on probability paper, and by a normality test (Snedecor 1956: 201–202).

No significant influx of small individuals appeared within the population throughout the 1-year census. Approximately 5 percent only of the individuals with mean arm radius less than 85 mm appeared during the following marking experiments (May 1975 recapture). Animals with mean arm radii as small as 75 mm spawned in the spawning observations, so that almost all animals treated in the census were sexually mature adults.

Two distinctive individuals of *L. laevigata* that possessed an abnormal number of madreporites (three and four) were identified during the monthly censuses. The asteroid with three madreporites appeared in three censuses and the other with four madreporites in two censuses and they were assumed to be the same indi-

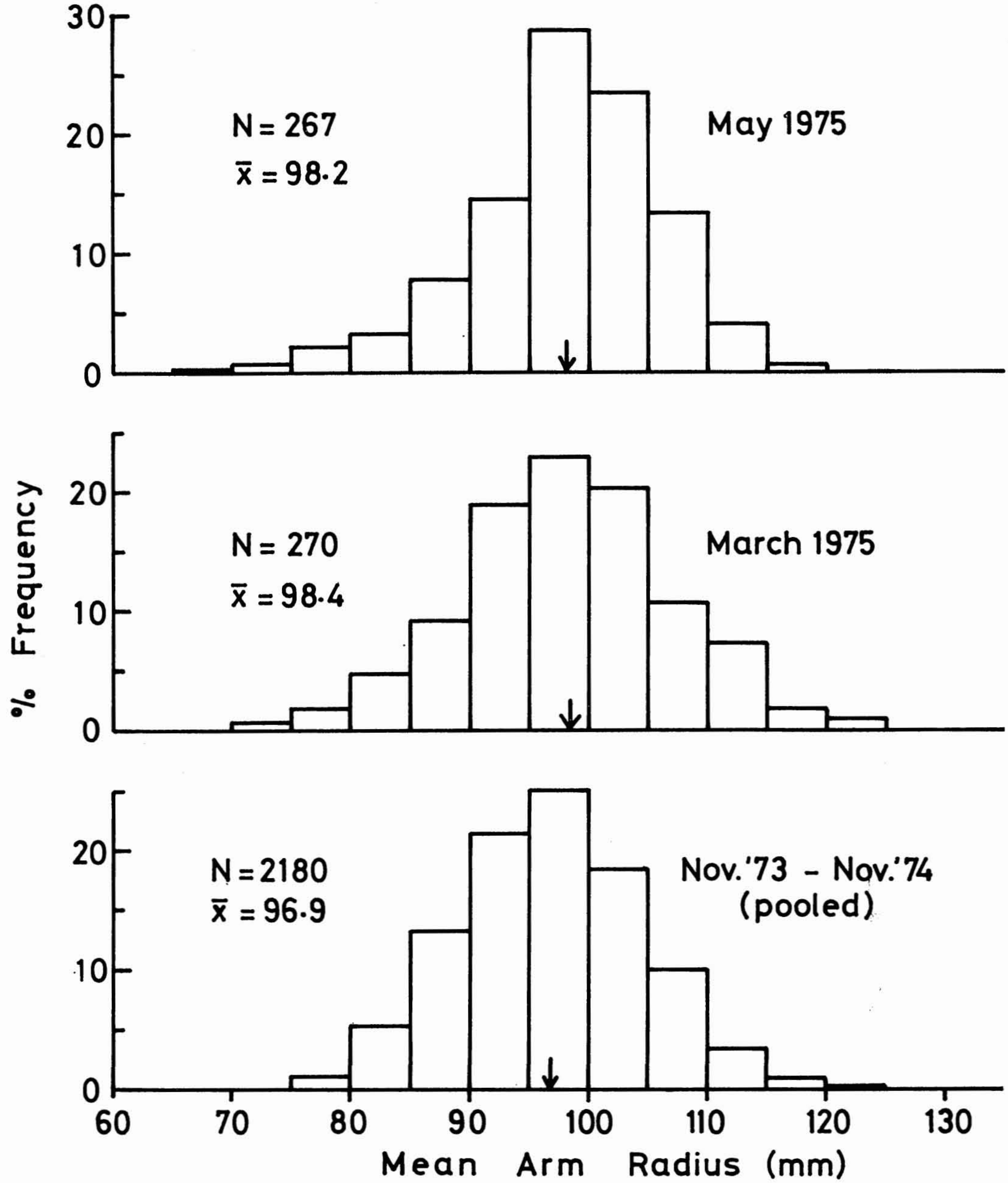

FIGURE 3. *Linckia laevigata*: size-frequency distribution of Asan reef population.

viduals. Mean arm radius of the former fluctuated: 92.4 mm in February, 96.6 mm in June, and 95.0 mm in September 1974. That of the latter increased from 94.0 mm in May to 98.8 mm in November 1974.

In the 3.5-month recapture in March, 4 man-hours were spent locating 56 marked and 274 unmarked individuals (the latter were removed from the study area). Only 32 of the original 214 marked individuals were recaptured about 5.5 months after the release, with 11 man-hours being spent (two dates in May 1975; searching

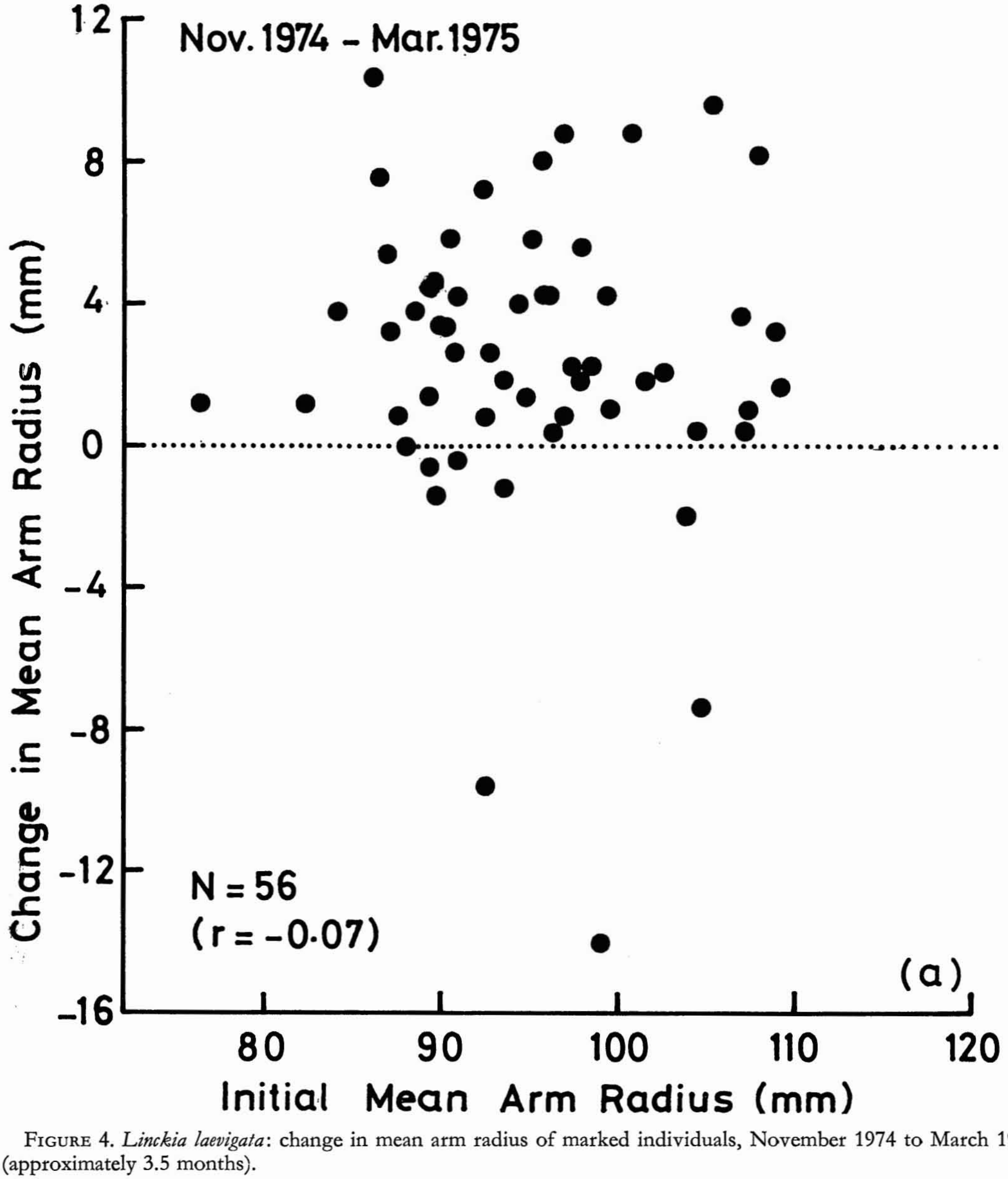

FIGURE 4. *Linckia laevigata*: change in mean arm radius of marked individuals, November 1974 to March 1975 (approximately 3.5 months).

area expanded) and a total of 571 unmarked individuals collected then.

The differences in arm radii of 56 individuals recaptured in March (approximately 3.5 months after release) varied from +10.4 to −14.0 mm, with a mean increase of 2.47 mm (Figures 4–6). The mean arm radius of the 32 recaptured individuals, approximately 5.5 months after release, changed from +8 to −10 mm, with a mean increase of 1.13 mm (Figure 5). As for the 17 individuals recaptured both in March and May 1975, the change in arm radius between the two measurements varied from +1.8 to −5.4 mm, with a mean decrease of 1.17 mm (Figure 6). There is no marked correlation between the change in mean arm radius and the initial size ($r = -0.07$, -0.16, and -0.20, respectively).

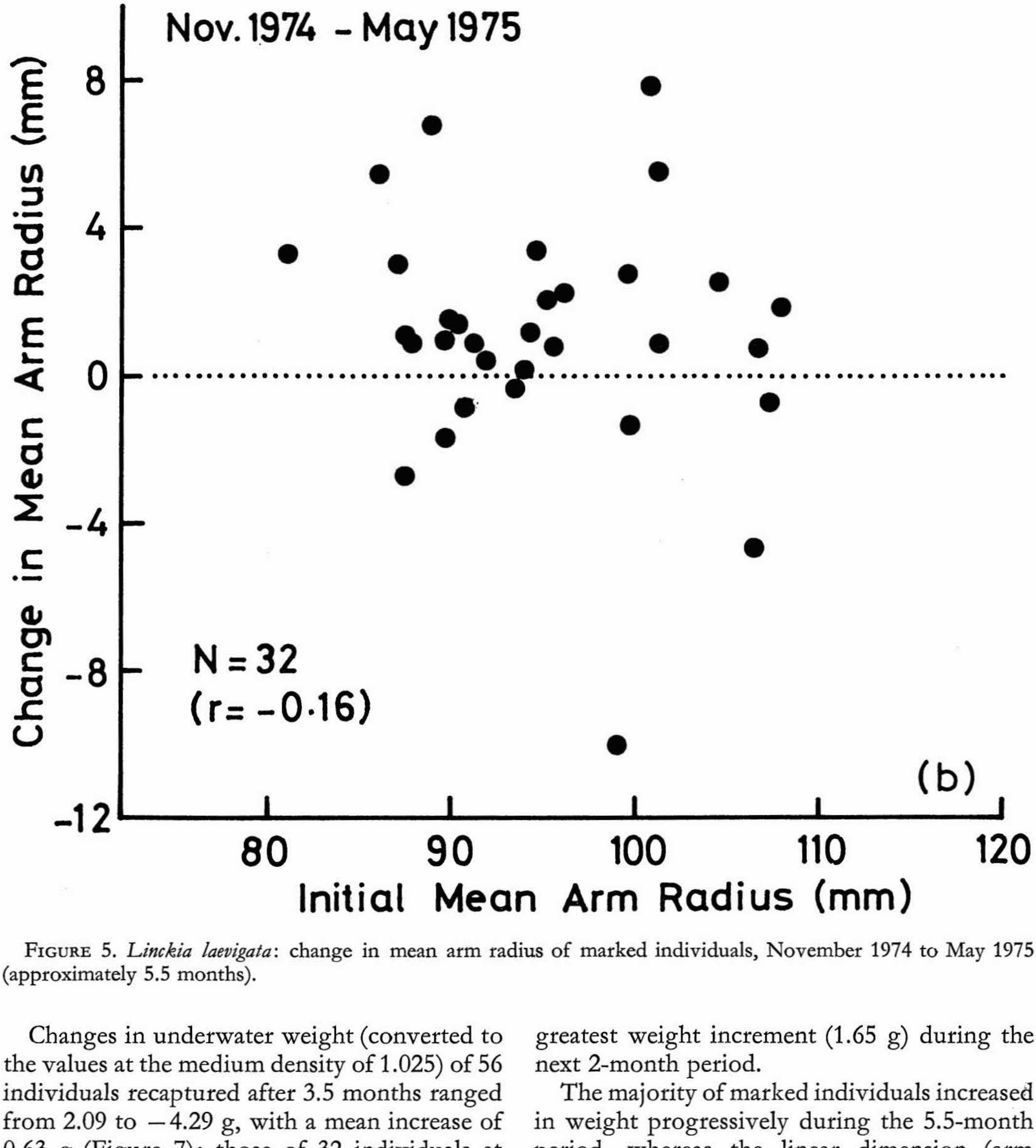

FIGURE 5. *Linckia laevigata*: change in mean arm radius of marked individuals, November 1974 to May 1975 (approximately 5.5 months).

Changes in underwater weight (converted to the values at the medium density of 1.025) of 56 individuals recaptured after 3.5 months ranged from 2.09 to −4.29 g, with a mean increase of 0.63 g (Figure 7); those of 32 individuals at 5.5-month recapture ranged from 3.44 to −2.64 g (Figure 8). Those of 17 individuals recaptured in March and May ranged from 0.05 to 1.65 g, with a mean increase of 0.54 g during the 2-month period (Figure 9). One individual drastically increased its weight (and arm radius) (−4.29 g from 15.64 g initial weight) after it had received a severe injury to one arm during the first 3.5-month period, but it regenerated the lost arm tip and gained the greatest weight increment (1.65 g) during the next 2-month period.

The majority of marked individuals increased in weight progressively during the 5.5-month period, whereas the linear dimension (arm radius) fluctuated. However, there is a trend of progressive reduction in the rate of weight increment with increase of initial weights, particularly for the heavier weight range (Figures 7–9).

Spawning responses of the *L. laevigata* population at Asan reef flat were strongest from May to August (Figure 10). Most individuals injected with 1-methyladenine showed only a weak spawning reaction in the winter months,

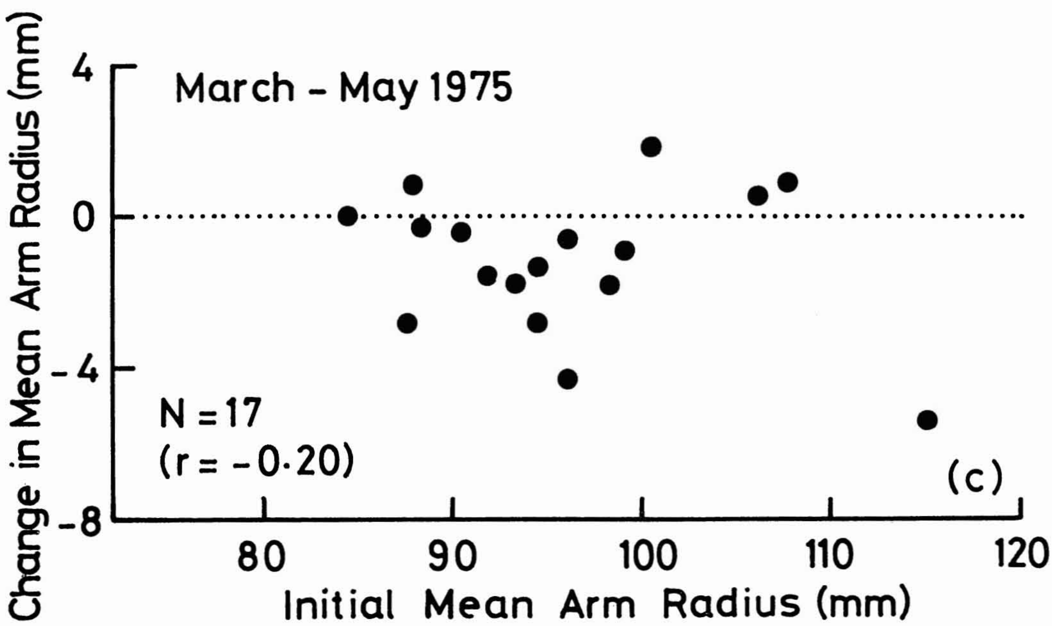

FIGURE 6. *Linckia laevigata*: change in mean arm radius of marked individuals, March to May 1975 (2 months).

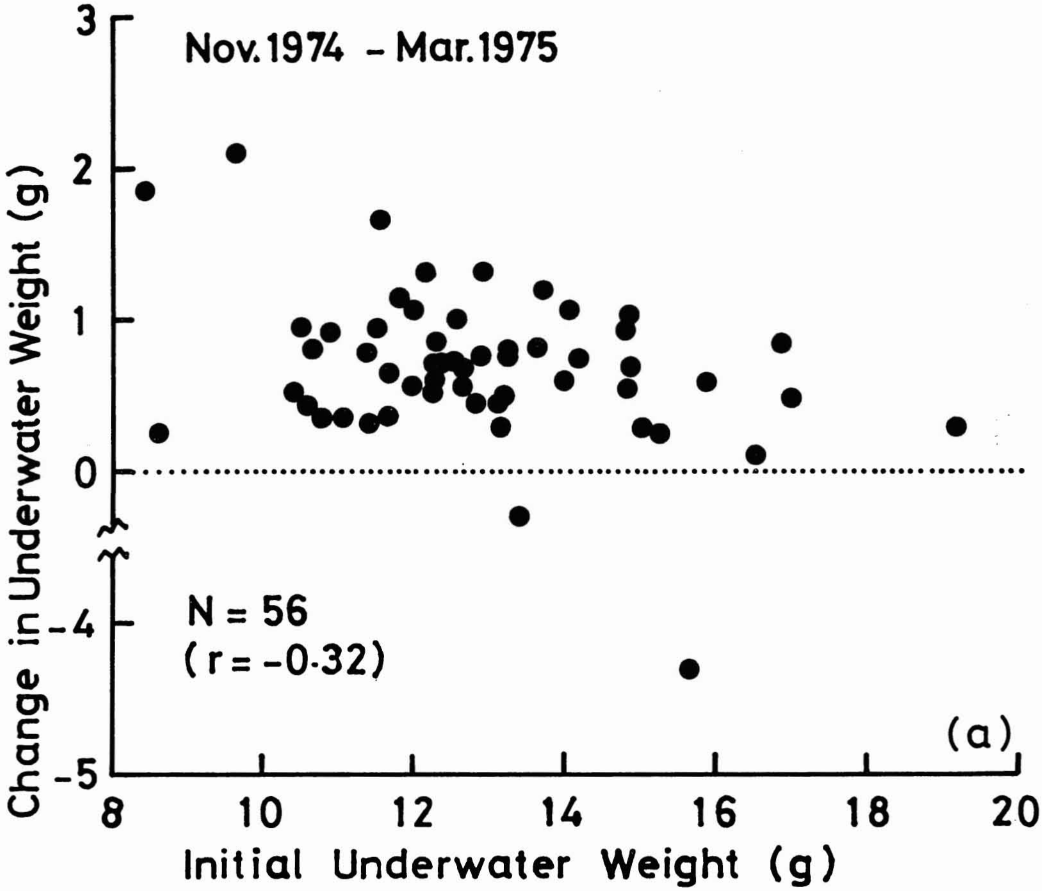

FIGURE 7. *Linckia laevigata*: change in underwater weight of marked individuals, November 1974 to March 1975 (approximately 3.5 months).

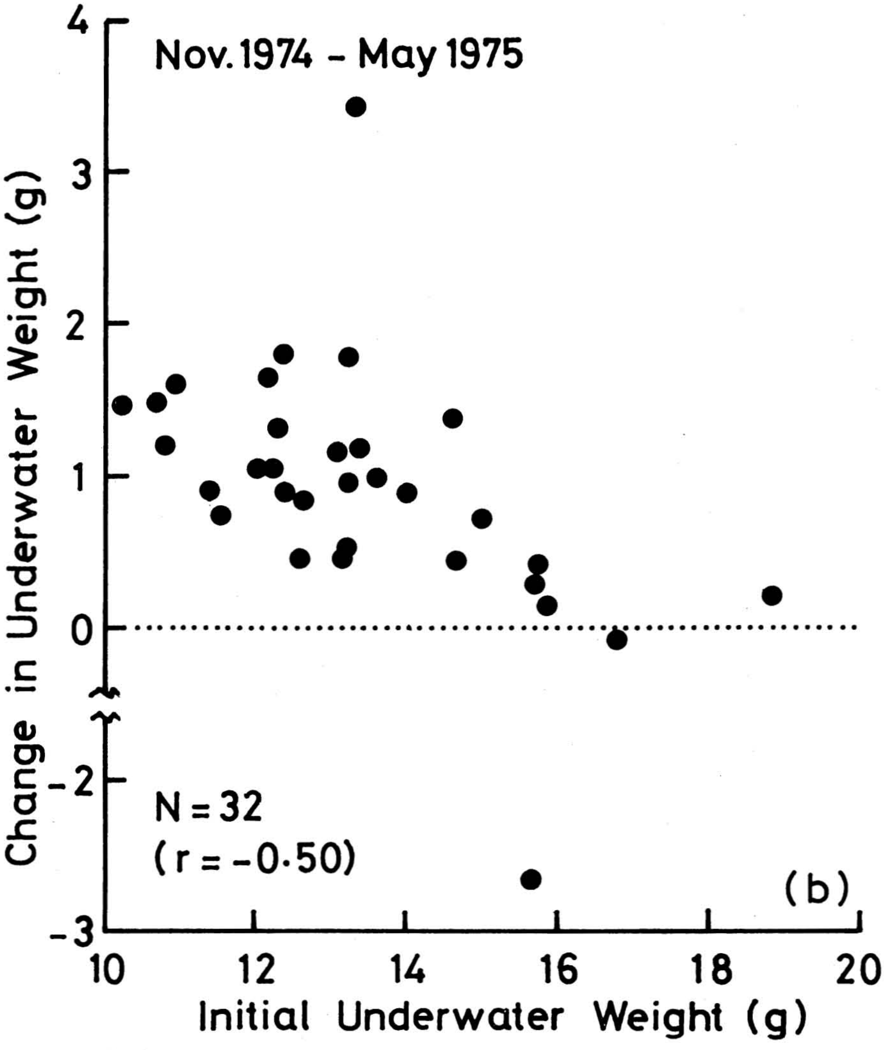

FIGURE 8. *Linckia laevigata*: change in underwater weight of marked individuals, November 1974 to May 1975 (approximately 5.5 months).

although a few individuals spawned at significant intensity. If we assume that the spawning reaction indicates relative ripeness of individuals, then we can calculate a ripeness index for the population (100 as maximum score) from the spawning reaction data (Figure 11). This index changed seasonally in phase with seasonal variations of low tide sea levels occurring in daytime but not with those of surface water temperatures (Figure 11). The outer reef flat becomes partially exposed during spring low tide during the midafternoon from May to August. Some individuals of *Linckia laevigata* were exposed to the air and others remained in isolated shallow pools during the extreme low tides. The animals probably were stressed by this condition and a few individuals were killed by total exposure to the air. This seasonal sea level change of low tides caused marked destruction of macroscopic algae such as *Turbinaria* and *Sargassum*, which had formed a dense cover on the outer reef flat during the winter months, and the habitat became nearly barren with regard to macroscopic algae in the summer months (cf. Tsuda 1974).

The laboratory-grown juveniles showed a

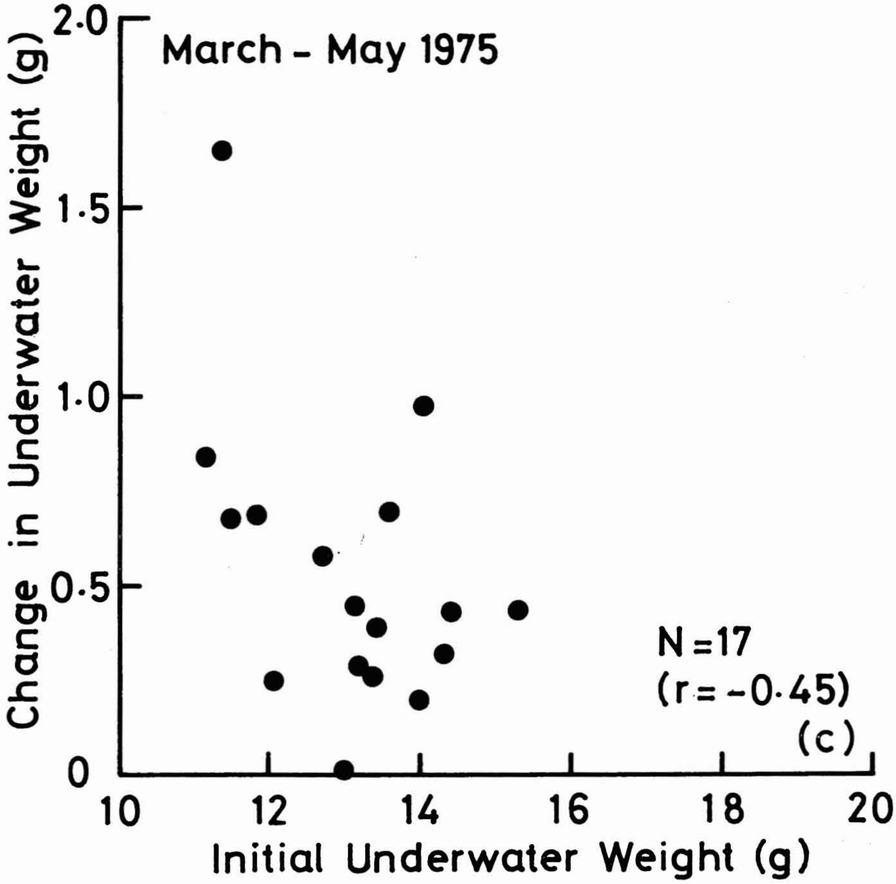

FIGURE 9. *Linckia laevigata*: change in underwater weight of marked individuals, March to May 1975 (2 months).

trend of exponential growth. The size increments per 2 months increased linearly with increase of initial size (arm radius), although there were great individual variations. The variation was more pronounced in the smaller culture aquarium (Figure 12). Mean arm radius for 8 individuals in the 15-liter aquarium and 10 individuals in the 50-liter aquarium increased from 1.94 to 8.61 mm and from 3.71 to 9.26 mm, respectively, during the 5-month period from September 1974 to February 1975. Nine individuals (4 from the 15-liter aquarium and 5 from the 50-liter aquarium) grew from 9.24 to 13.90 mm in mean arm radius from February to April 1975 (14 months after metamorphosis) in the 50-liter aquarium. Two weeks after metamorphosis the juvenile is about 0.5 mm in arm radius. The mean growth curves for the above are shown in Figure 13.

Young juveniles of *L. laevigata* were sought on reefs where large adult populations were found. However, a total of only three pretransformation stage juveniles (mean arm radii of 22.0, 23.0, and 28.0 mm) and less than 10 transforming stage (dark green and brown mottled coloration changing into uniform blue at about 50 mm in arm radius) juveniles were found around Guam during a 3-year period (1972 to 1974). These juveniles were all cryptic in habit and were found mostly under large pieces of coral rubble on the outer reef flat. It was difficult to be confident in identification of the pretransformation stage juveniles from the field before I had raised the laboratory-grown *L. laevigata* to equivalent size (the largest one was 21.4 mm in arm radius 14 months after metamorphosis).

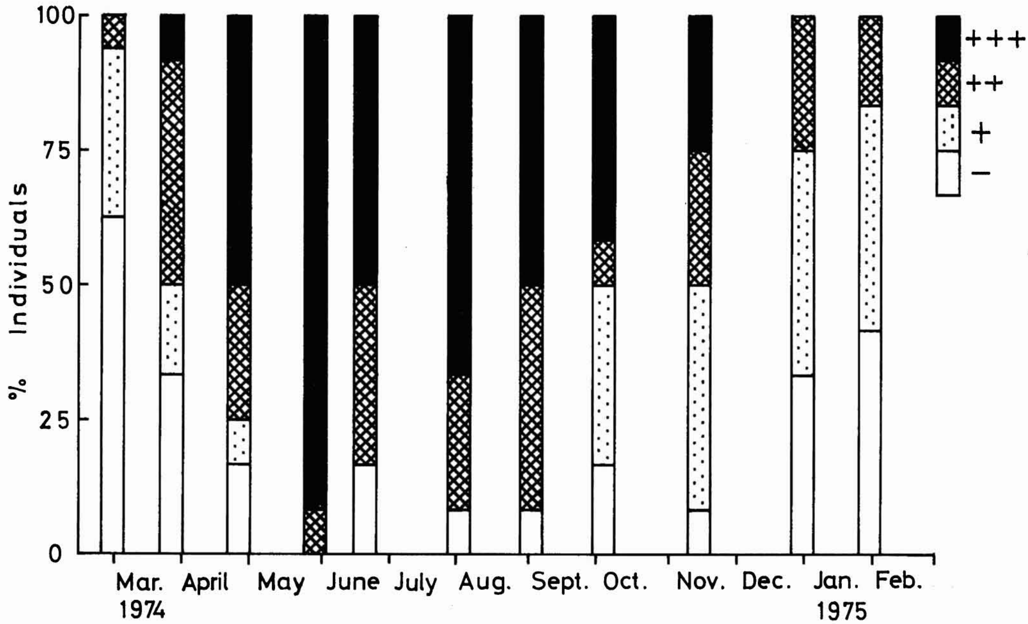

FIGURE 10. *Linckia laevigata*: year-round spawning activity of individuals sampled from the Asan reef population. Figures for males and females have been pooled. + + +, vigorous spawning; + +, active spawning; +, trace; −, negative spawning.

DISCUSSION

Pearse (1968) discussed reproductive patterns of *L. laevigata* from specimens that had been collected at many localities in the Indo-Pacific. He noted that gametogenesis is rather asynchronous in individual *L. laevigata* within the same population as well as in oocytes within the same gonads. However, he noted in the same paper that populations from Honiara, Guadalcanal Island, and Fiji were all "unripe" in austral winter samplings. These cases are in accord with the *L. laevigata* population at Asan, Guam, which were "unripe" during the winter months (Figures 10–11). Laxton (1974) reported a case of spontaneous spawning in *L. laevigata* held in an aquarium in October (austral early summer) at Heron Island, southern Great Barrier Reef. Pearse's sample from One Tree Island, near Heron Island, collected in April (austral fall) appear to be "nearly ripe" (my interpretation) in one-half of the population. These reports and my observations suggest that *L. laevigata* populations tend to have peak breeding activity in summer. This trend is similar to the spawning activity of *Acanthaster planci* reported for populations in Australia (Pearson and Endean 1969, Lucas 1973), Hawaii (Branham et al. 1971), and Guam (Cheney 1974).

Both adult and juvenile *L. laevigata* evert their stomachs over hard substrates that are usually encrusted with fine detritus and microscopic organisms. Laxton (1974) reported that *L. laevigata* grazed encrusting coral line algae on the Great Barrier Reef. However, my observations do not support this type of "grazing" by this species, although *L. laevigata* in Guam often everts its stomach on coralline algae encrustation and appears to digest microorganisms covering the algae. *Acanthaster planci* juveniles digest encrusting coralline algae and produce feeding marks (Yamaguchi 1973*a*), but *Linckia* and other ophidiasterids do not produce such marks after everting their stomachs over coralline algae. Laxton (1974) further postulated that the grazing activity of *L. laevigata* might destroy small coral colonies and newly settled planulae and retard coral recolonization at the area where *Acanthaster planci* had grazed live corals. However, his own data on population density, sizes of animals, and

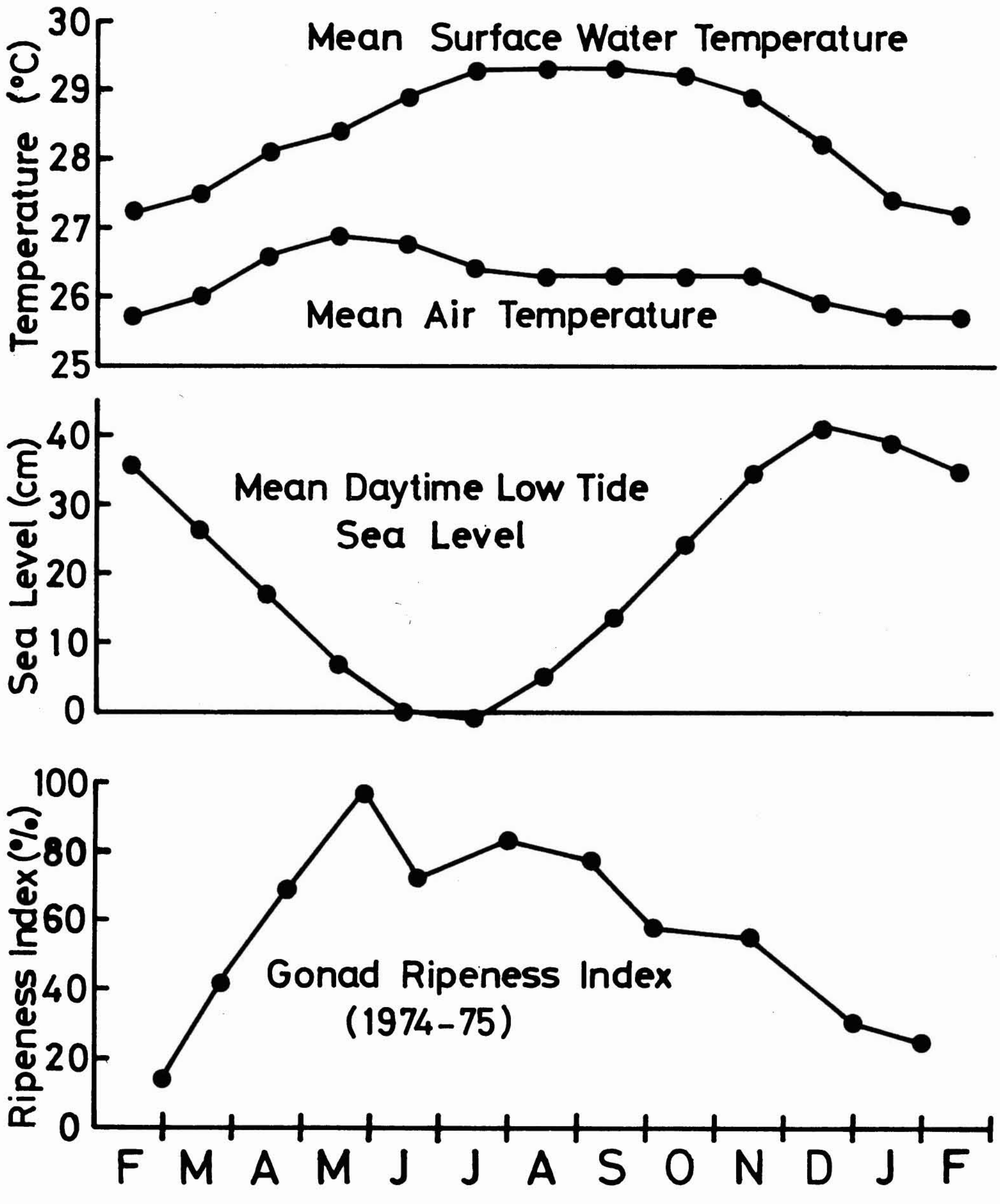

FIGURE 11. Seasonal fluctuation in gonad ripeness index of *Linckia laevigata* at Asan reef, 1974–1975, and environmental parameters. I calculated the index from the results in Figure 11 by scoring 3, 2, 1, and 0 for each category and setting the maximum score as 100 (percent). Mean surface water temperature is given for Apra Harbor, as recorded by the Environmental Science Service Administration, Coast and Geodetic Survey (C & GS Publication 31-3, 1967), and the mean air temperature was recorded by the National Climatic Center (local climatological data, Guam, Pacific). The latter data were converted from degrees Fahrenheit to degrees centigrade. I calculated mean daytime low tide sea level from the predictions (tide tables: high and low water predictions), taking means of all low tide sea levels (converted from feet to centimeters) occurring from 0600 to 1800 hours.

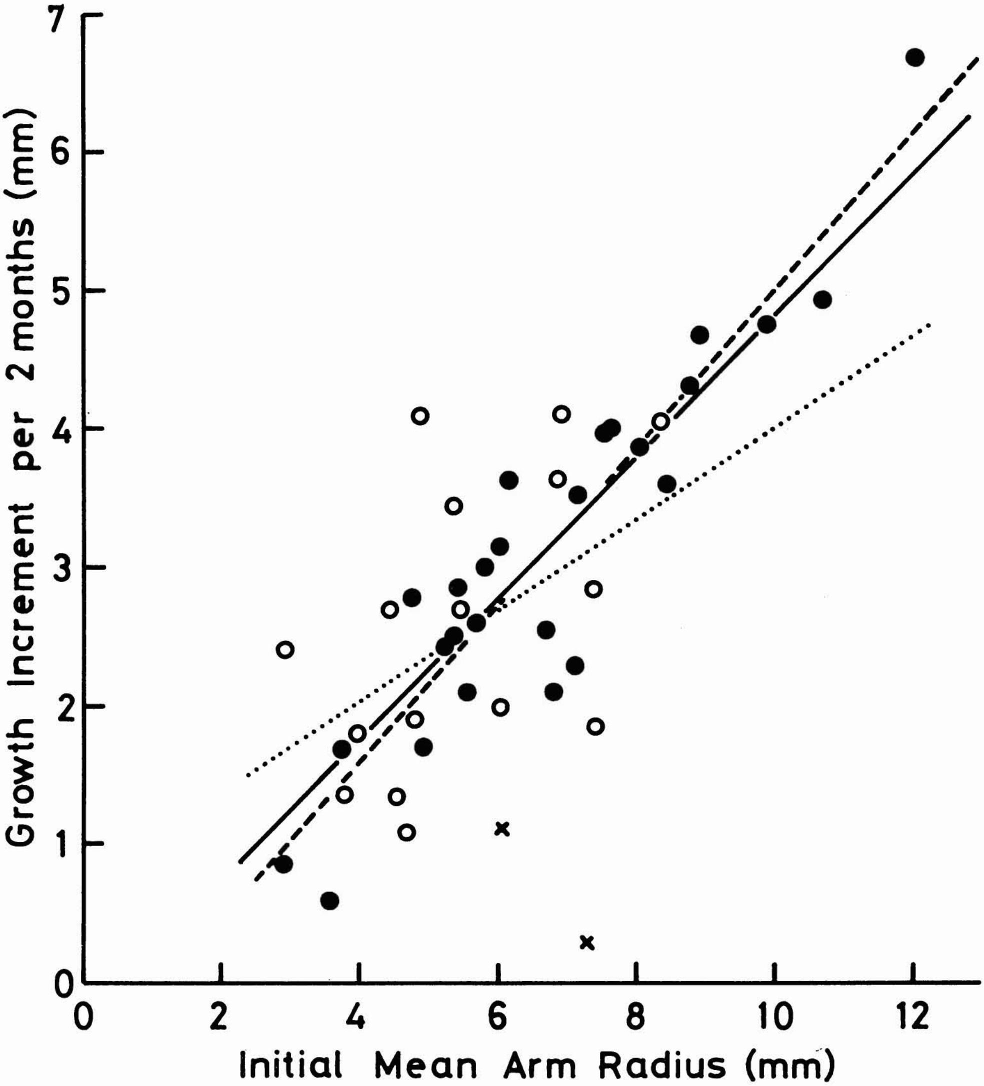

FIGURE 12. *Linckia laevigata*: growth of juveniles in the laboratory. Growth increments per 2 months for individuals have been plotted against the initial arm radius (mm). Open circles, animals reared in a 15-liter aquarium; solid circles, animals reared in a 50-liter aquarium. Two points (X) represent an individual in a 50-liter aquarium which decreased in rate of growth as it grew and was excluded from the regression analysis. Solid line, regression line ($Y = 0.509X - 0.262$) for the data combined; dotted line, growth data for 15-liter aquarium; broken line, growth data for 50-liter aquarium.

feeding and locomotive activities do not support his speculation. At the highest density reported (1.48 per 10 m^2), this asteroid may "graze" only about 0.20 percent of the area in one feeding cycle because its stomach covers the area of a disc 4 cm in diameter. Since *L. laevigata* does not specifically attack corals, random "grazing" at this magnitude must have insignificant impact on colonization of coral, in comparison to other more aggressive grazers such as fishes (Randall 1974).

Reef flat *L. laevigata* populations contain only adult or posttransformation stage individuals and the juveniles are cryptic in habit, occupying different microhabitats. Thus, a superficial population census may not reveal any juvenile

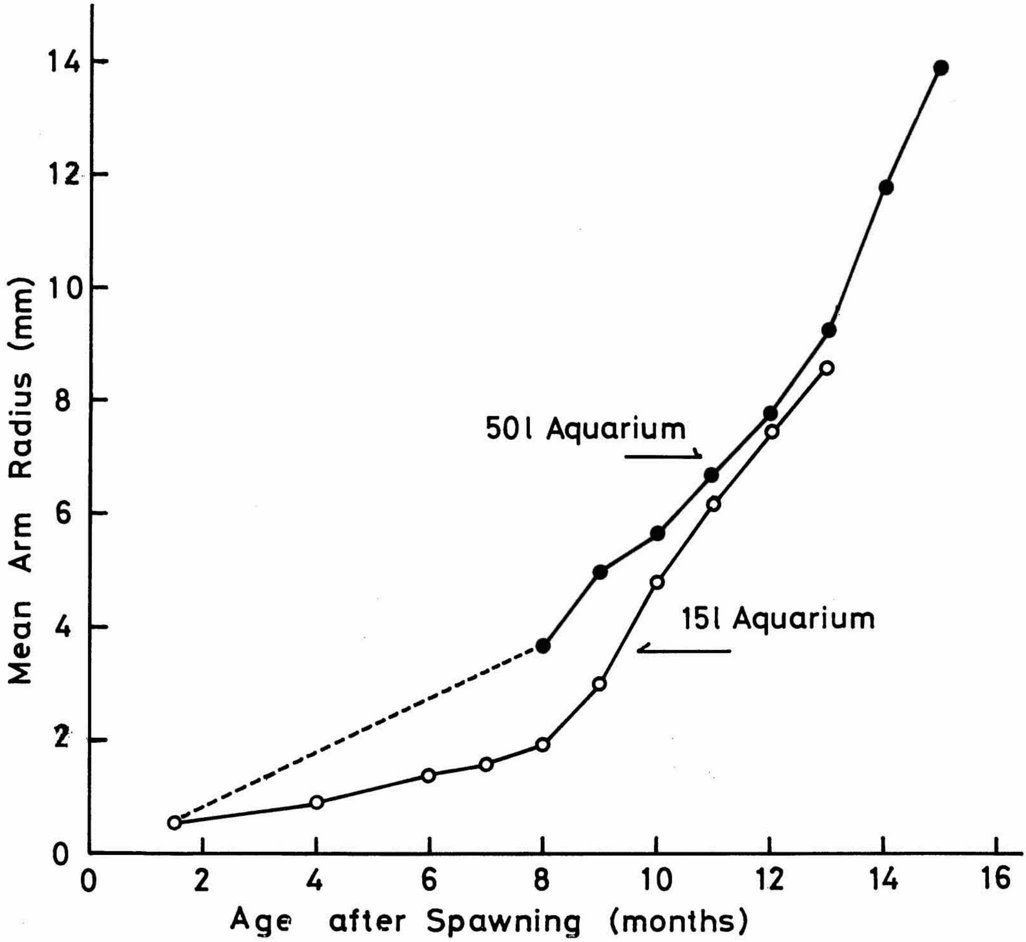

FIGURE 13. *Linckia laevigata*: mean growth curves of laboratory-grown juveniles. Open circles, juveniles reared in a 15-liter aquarium (8 individuals); solid circles, juveniles reared in a 50-liter aquarium (10 individuals). The latter can be approximated by an exponential growth function ($L_t = 0.463e^{0.225t} + 1.201$) for the period from 8 to 16 months after spawning.

individuals within the conspicuous adults-only populations. Laxton (1974) noted the lack of juveniles within the *L. laevigata* populations throughout the reefs surveyed along the Great Barrier Reef, Australia. However, Marsh (personal communication) found a number of juveniles hidden under large boulders on an outer reef flat in Fiji. The specimens (examined on loan from Western Australian Museum) contained a juvenile as small as 11 mm in arm radius. She noted that the number of juveniles was very small compared to the abundance of adults in the field.

It is likely that the actual juvenile population was small around Guam and particularly at Asan reef flat during this study period. For example, no juvenile *L. laevigata* was found in a 22-man-hour search among the dead coral thickets (*Acropora*) at the midsector of Asan reef flat adjacent to the present study area, whereas more than 800 individuals of *Linckia multifora* and a few other species of asteroids that are comparable in size to juvenile *L. laevigata* were found (Rideout 1975). Another population census series that comprised about 40 man-hours was made for *Ophidiaster granifer*, a cryptic species similar in size to *L. laevigata* juveniles, at the reef flat of Cocos Lagoon, Guam (Yamaguchi, unpublished). Here, only one pretransformation stage juvenile *L. laevitaga* was found,

TABLE 1

FLUCTUATIONS OF ARM RADII AND UNDERWATER WEIGHTS OF 14 INDIVIDUALS OF *Linckia laevigata* IN FIVE CONSECUTIVE DETERMINATIONS

	MEAN ARM RADII*			UNDERWATER WEIGHTS†		
INDIVIDUALS	MEANS (mm)	S.D.	C.V.‡	MEANS (g)	S.D.	C.V.‡
Ar-Cl	84.36	0.68	0.81	11.326	0.036	0.32
Dl-Ep	84.80	0.98	1.16	12.306	0.049	0.40
Bd-Dl	90.40	1.00	1.11	11.132	0.055	0.50
Bl-Cd	90.76	0.43	0.48	10.914	0.013	0.12
Bu-Cp	91.68	1.12	1.22	13.680	0.061	0.44
Cr-Dl	94.44	2.11	2.24	12.696	0.060	0.47
Al-Ep	96.08	1.35	1.41	13.150	0.052	0.40
Bd-Ed	98.76	1.54	1.56	15.522	0.062	0.40
Bu-Cd	99.08	1.54	1.55	14.022	0.055	0.39
Ar-Eu	99.44	0.62	0.63	15.436	0.075	0.48
Cu-Dr	101.20	1.96	1.94	13.200	0.059	0.45
Cd-Dl	105.24	2.59	2.46	16.586	0.074	0.44
Bl-Ep	106.32	2.37	2.23	14.892	0.070	0.47
Ad-Bl	112.24	2.45	2.18	16.454	0.086	0.52
Means	96.77	1.48	1.50	13.665	0.058	0.41

* Mean arm radius is given for the five arms of each individual; five determinations were made to obtain the listed mean values for each individual.

† Underwater weight has been adjusted to that in the medium density of 1.025.

‡ Coefficient of variation (C.V.) is the standard deviation (S.D.) divided by the mean and multiplied by 100.

along with a few transforming individuals; adults, however, were abundant. Seaward reefs (reef terraces and reef slopes) were searched only occasionally but no adult individuals of *L. laevigata* were found in such habitats, which are separated from the reef flat by oceanic surf breaking along the reef front (Strong 1975). Juveniles found so far occurred only near the adult populations. Because they are very sluggish, it is hard to imagine that juveniles would migrate from the seaward reef to the reef flats through the physical barrier of the breaker zone.

The unimodal size-frequency distribution of *L. laevigata* persisted throughout the monthly censuses in the Asan population from November 1973 to November 1974. The smallest individual found during the series of censuses was 63.2 mm in mean arm radius. Individuals smaller than 80 mm in arm radius totaled only 34 (1.6 percent) out of 2180 from the 12 censuses combined (Figure 3). Thus, the lack of smaller adults within the population suggests that recruitment to the population was low throughout the 1-year period. Even though the young (posttransformation stage) *L. laevigata* would grow faster than juveniles or adults, the monthly census should have revealed an influx of young animals if significant recruitment to the adult population had taken place during the observation period.

The fluctuation of adult size in linear dimension (arm radius) observed in *L. laevigata* is similar to that observed in adults-only populations of *Acanthaster planci* in Hawaii (Branham et al. 1971); and Western Australia (Wilson and Marsh 1974). Skeletal matrices of these asteroids are loose, making the linear dimensions of animals difficult to measure precisely. I have made five consecutive determinations of arm radii and underwater weights in 14 marked *L. laevigata*, during a 2-day period. Underwater weights varied very little (mean coefficient of variation for 14 was 0.41) compared with the more variable arm radii (1.50) (Table 1). This variation (erratic and spontaneous fluctuation) in linear dimensions makes it difficult to detect real size changes in the growth analyses (Figures 4–6). Nevertheless, the underwater weight determination revealed progressive net size increases in the marked *L. laevigata* individuals during the 5.5-month period (Figures

7–9). These increases, however, were small (mean, 7.0-percent weight increase in 5.5 months), and this magnitude of weight increase did not contribute to a significant increase in the linear dimension of adult animals; e.g., for an average individual of 13.0 g in underwater weight and 93.7 mm in arm radius, a 0.9 g (9.7 percent) increase resulted in a 2.4 mm (2.6 percent) increase. This calculation is based on the arm radius–underwater weight relationships determined for the 214 marked individuals, prior to release, as $\log R = 0.383 \log W + 1.545$, where R is arm radius in mm and W is underwater weight in g. Actual (measured) mean arm radius increase was approximately 1.1 mm per 5.5 months in the 32 marked individuals. In short, *L. laevigata* changed only little in linear dimension during the census and mark-recapture experiments, although it did fluctuate within about 6 percent in mean arm radius for the sampled population.

There is a gap in size range, where growth rate is unknown between the juvenile stage and adult stage, i.e., the stage just before and after the transformation from cryptic-habit juvenile to exposed-habit adult. If the laboratory-grown juveniles represented growth capacity of *L. laevigata* and if the exponential growth trend is persistent up to the transformation stage (50 mm in arm radius), then the life span of an average juvenile prior to the transformation stage may be estimated as about 21 months after spawning (from the fitted exponential growth curve equation $L_t = 0.463 e^{0.225t} + 1.201$). The method of fitting the exponential growth curve is discussed elsewhere (Yamaguchi, unpublished). On the other hand, the period is about 27 months on the assumption that the exponential growth changed to a linear growth (3 mm per month) at a size of 12 mm in arm radius when the average animal was 14 months old. The two figures (21 and 27 months) may represent the lower and upper life span estimates of juvenile stage in *L. laevitaga*. In other words, around 2 years may be required for an average juvenile to reach the transformation stage after having been spawned as an egg.

The disappearance of marked individuals after 3.5-month recapture and rerelease is difficult to explain but I suspect that they were collected by reef-gleaners. The 5.5-month recapture search covered about three times the area of the original census but failed to find a significant number of marked individuals, so that migration did not appear to be the reason for the disappearance. In fact, a few days after rereleasing the marked individuals at the 3.5-month recapture, I checked the study area and found that almost all the released ones had disappeared, unlike the case with the initial release after marking. *Linckia laevigata* is a sluggish asteroid and migrates only short distances during such a period (Laxton 1974, Clark 1921).

Although the mortality rate of *L. laevigata* could not be assessed, the slow growth of adults and juveniles indicates that populations of this asteroid have a low turnover rate. Apparently the adult populations are releasing gametes every year, possibly with a peak period in the summer months, as indicated by Asan reef population. Not only the chemically-induced spawning but spontaneous spawning of *L. laevigata*, when handled or disturbed, was common during the supposed peak breeding period. However, there is a poor synchronization of the gametes within the same gonad and among different individuals (Pearse 1968). Amount of eggs shed at individual spawning was very variable (Figure 6). Perhaps, this asteroid sheds gametes repeatedly within a season. On the order of one million eggs were shed by a single female in vigorous spawning, so that many billions of eggs are being released in the sea around Guam without any evident sign of recruitment success. The adults-only populations of *L. laevigata* may be maintained by gradually building up the individuals over a long time period or by occasional high recruitment success (Yamaguchi 1973*b*).

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LITERATURE CITED

ASANO, N. 1937. On the shell and the habitat of the giant clam of Palau [in Japanese]. Bot. Zool. Theor. Appl. (Tokyo) 5: 711–713.

BRANHAM, J. M., S. A. REED, J. H. BAILEY, and J. CAPERON. 1971. Coral-eating sea stars *Acanthaster planci* in Hawaii. Science 172: 1155–1157.

CHENEY, D. P. 1974. Spawning and aggregation of *Acanthaster planci* in Micronesia. Proc. Second Int. Coral Reef Symp., Brisbane 1: 591–594.

CLARK, A. H. 1954. Records of Indo-Pacific echinoderms. Pac. Sci. 8: 243–263.

CLARK, A. M., and F. W. E. ROWE. 1971. Shallow-water Indo-West-Pacific echinoderms. 238 pp. Trustees of the British Museum (Natural History), London.

CLARK, H. L. 1921. The echinoderm fauna of Torres Strait. Pap. Dep. Mar. Biol. Carnegie Inst. Washington 10: 1–223.

ELY, C. A. 1942. Shallow water Asteroidea and Ophiuroidea of Hawaii. Bull. Bernice P. Bishop Mus. 176: 1-63.

FISHER, W. K. 1906. The starfishes of the Hawaiian Islands. Bull. U.S. Fish. Comm. 23: 987–1130.

FRANK, P. W. 1968. Life histories and community stability. Ecology 49: 355–357.

———. 1969. Growth rates and longevity of some gastropod mollusks on the coral reef at Heron Island. Oecologia (Berlin) 2: 232–250.

HESTER, F. J., and E. C. JONES. 1974. A survey of giant clams, Tridacnidae, on Helen Reef, a western Pacific atoll. NOAA, Mar. Fish. Rev. 36: 17–22.

KANATANI, H. 1969. Induction of spawning and oocyte maturation by 1-methyladenine in starfishes. Exp. Cell Res. 57: 333–337.

LAXTON, J. H. 1974. A preliminary study of the biology and ecology of the blue starfish *Linckia laevigata* (L.) on the Australian Great Barrier Reef and an interpretation of its role in the coral reef ecosystem. Biol. J. Linn. Soc. 6: 47–64.

LIVINGSTONE, A. A. 1932. Asteroidea. Sci. Rep. Great Barrier Reef Exped. 4: 241–265.

LUCAS, J. S. 1973. Reproductive and larval biology of *Acanthaster planci* in Great Barrier Reef waters. Micronesica 9: 197–203.

MARSH, L. M. 1974. Shallow-water asterozoans of southeastern Polynesia. I. Asteroidea. Micronesica 10: 65–104.

MCMICHAEL, D. F. 1974. Growth rate, population size and mantle coloration in the small giant clam *Tridacna maxima* (Röding) at One Tree Island, Capricorn Group, Queensland. Proc. Second Int. Coral Reef Symp., Brisbane, 1: 241–254.

MOTODA, S. 1938. On the ecology, shell form, etc., of the Tridacnidae of the South Seas [in Japanese]. J. Sapporo Soc. Agr. For. 29: 375–401.

PEARSE, J. S. 1968. Patterns of reproductive periodicities in four species of Indo-Pacific echinoderms. Proc. Indian Acad. Sci. 68: 247–279.

PEARSON, R. G., and R. ENDEAN. 1969. A preliminary study of the coral predator *Acanthaster planci* (L.) (Asteroidea) on the Great Barrier Reef. Fish. Notes, Queensl. Dep. Harbours Mar. 3: 27–55.

RANDALL, J. E. 1974. The effect of fishes on coral reefs. Proc. Second Int. Coral Reef Symp., Brisbane 1: 159–166.

RIDEOUT, R. S. 1975. Asexual reproduction as a means of population maintenance of the coral reef asteroid *Linckia multifora* (Lamarck). M.S. Thesis. University of Guam, Agana. 27 pp.

SNEDECOR, G. W. 1956. Statistical methods. Iowa State University Press. 5th ed. Ames, Iowa. 534 pp.

STRONG, R. D. 1975. Distribution, morphometry, and thermal stress studies on two forms of *Linckia* (Asteroidea) on Guam. Micronesica 11: 167–183.

TSUDA, R. T. 1974. Seasonal aspects of the Guam Phaeophyta (brown algae). Proc. Second Int. Coral Reef Symp., Brisbane 1: 43–47.

WILSON, B. R., and L. M. MARSH. 1974. Pages 167–179 *in* Seasonal behavior of a 'normal' population of *Acanthaster planci* in western Australia. Crown-of-thorns starfish seminar proceedings, Brisbane, 1974.

YAMAGUCHI, M. 1973*a*. Early life histories of coral reef asteroids, with special reference to *Acanthaster planci* (L.). Pages 369–387 *in* O. A. Jones and R. Endean, eds. Biology and geology of coral reefs. Vol. 2, biol. 1. Academic Press, New York.

———. 1973*b*. Recruitment of coral reef asteroids, with emphasis on *Acanthaster planci* (L.). Micronesica 9: 207–212.

———. 1975. Coral reef asteroids of Guam. Biotropica 7: 12–23.