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# Growth of Juvenile *Acanthaster planci* (L.) in the Laboratory[1]

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ABSTRACT: Seven juvenile *Acanthaster planci* were reared from fertilized eggs to sexual maturity in 18 to 21 months in the laboratory. Four-month-old juveniles, about 8 mm in total diameter, began to transform into coral predators from the prior herbivore stage that fed on encrusting coralline algae. The transition period lasted for about 1 month. Many juveniles were injured by coral polyps, which had been offered as food, shortly after the transitional period. Except for severely injured ones, all the coral-feeding juveniles grew steadily after recovering from the injuries and, when the animals were well fed, their growth curve was sigmoid. Mean growth coefficient for the early coral-feeding juveniles, growing exponentially, was nearly half that of the previous algae-feeding stage, and the coefficient value reduced rapidly as the juvenile grew near to maturity. *Acropora nasuta* and *Pocillopora damicornis* both sustained full growth of juveniles. However, the juvenile *Acanthaster* killed about twice as much coral mass of *Acropora nasuta* as of *Pocillopora damicornis* to gain the same amount of weight.

DESPITE THE CONTROVERSY concerning the causes of infestations of Indo-Pacific coral reefs by the starfish *Acanthaster planci* (L.), it has been clearly recognized that this animal is one of the most important predators of reef-building corals and is influencing the growth and development of coral reefs (see review by Branham 1973).

Growth of *Acanthaster* was measured for animals collected from the field and maintained in cages or aquaria in Australia (Pearson and Endean 1969). These workers indicated a mean growth rate for the juveniles of 1.1 cm/month and speculated on the correlation between the ages of starfish and their sizes. Their estimate was based on an assumption of linear growth. However, laboratory rearing of postmetamorphosis juveniles up to the stage of transition from herbivore to coral-feeding demonstrated much slower initial growth rates; i.e., the animals reached a mean diameter of ca. 8 mm 4 months after metamorphosis (Yamaguchi 1973). The growth curve obtained in this juvenile culture was nearly exponential. The present paper further describes the growth of laboratory-reared *Acanthaster* to sexual maturity for the same brood of juveniles described in Yamaguchi (1973).

## MATERIALS AND METHODS

Measurements of the size of a living and growing starfish, not only in *Acanthaster* but any species, are hardly reproducible for arm-radius, diameter, or body weight. Touching and handling an animal result in quick contraction of its body to various extents, and measurement of size by any method conducted in the air is not reliable for a growth study. Relaxed animals may be up to 20 percent larger in total diameter than those taken out of water. The diameter of juvenile *Acanthaster* was obtained by measuring sizes from photographs of relaxed animals at smaller stages or by applying dividers against larger animals kept undisturbed in containers. Although the measurements of diameter were kept as a reference record, the main emphasis in the study was placed on a method to measure weight of animals in seawater.

There are some disadvantages in the weigh-

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ing of aquatic organisms in water because of buoyancy and the variable density of the medium. Fortunately, asteroids' bodies consist largely of skeletal ossicles and spines which are dense enough to be weighed in water. This method of determining underwater weight of the animals does not indicate the development of soft tissues such as gonads, because the specific gravity of such tissues may be close to that of seawater. However, the method is satisfactory for indicating the skeletal development of juvenile asteroids, since gonad development occurs only at a later stage when the animals reach maturity. The specific gravity of seawater varies according to its temperature and salinity, and the buoyancy of substances in the medium subsequently changes if such factors vary. However, oceanic seawater has a fairly constant density in the tropics, and the variation in temperature and salinity has little effect on the measurement of underwater weight under normal conditions. Variation in specific gravity of seawater at the 0.001 level caused a relative experimental error of about 1.0 percent in the underwater weight of starfish. This same variation may be caused by a salinity change of ca. 1.3 ‰ or by a temperature change of ca. 3.5° C if the alternative factor is constant in each case. The weighing of juvenile *Acanthaster* was carried out in the laboratory with seawater of $1.024 \pm 0.001$ specific gravity.

Two balances with different sensitivities were used for weighing the animals at the different size ranges. A specific gravity chain balance (Troemner, model S-100) was used for smaller juveniles from 0.07 to about 4 grams underwater weight and another balance (Ohaus, model 310 specific gravity type balance) was used for those larger than 4 grams. Both balances were calibrated prior to use.

Juvenile *Acanthaster* were kept in aquaria or tanks of various sizes in proportion to the size of the animals and the holding capacity of the tanks. They were occasionally kept individually (for experimental observations) but mostly they were raised in groups of several individuals in each holding tank. The holding systems consisted of aquaria or tanks with individual filter beds and circulating pumps. The closed circulating system worked very efficiently as long as the animals were not overcrowded. Occasionally the water in the tanks was replaced by fresh seawater when signs of excessive buildup of animals' waste products were noticed.

After the transitional period of feeding behavior, from algae-feeding to coral-feeding, several species of different coral genera—*Acropora*, *Pocillopora*, and *Pavona*—were regularly fed to the juveniles. The food was kept in surplus most of the time to allow the maximum feeding and growth of the animals. Because the starfish always left a considerable mass of undigested but decomposing coral tissue after feeding, several small scavengers such as harpacticoid copepods and money cowries (*Cypraea moneta*) were kept with the juvenile *Acanthaster* in the same aquaria. These animals cleaned the decaying coral tissues and prevented overgrowth of bacteria in the holding systems.

Growth of seven individuals out of the 14 that are described elsewhere (Yamaguchi 1973) was measured bimonthly from April 1972 to May 1973. Individual identification was based on variations in the number of rays and in the number and positions of madreporites. The number and positions of madreporites in *Acanthaster* did not change after the juveniles transformed into the adult form.

An attempt to observe the effects of temperature on the growth of juveniles was carried out for about 6 weeks in July and August 1972 with some of the above animals and with spare animals from the same brood (V-batch) and another brood (VII-batch). Unfortunately, frequent power-outages and malfunctions of temperature-control units in the experimental aquaria obstructed a thorough study. Simultaneously, some experiments to observe the feeding rate of juveniles were carried out under ambient temperature (25° to 31° C). Underwater weight of the grazed coral tissue without skeleton (by comparing the weight decrease before and after grazing) was not determinable. Moreover, the soft tissues are not completely digested in any case by *Acanthaster* and there always remain considerable but variable (estimated to be up to 50 percent of total soft tissues) amounts of undigested tissues. Since the tissue weight prior to grazing is not determinable, the amount of coral soft tissue digested by *Acanthaster* could not be determined. Therefore, the rate of coral destruction was determined by

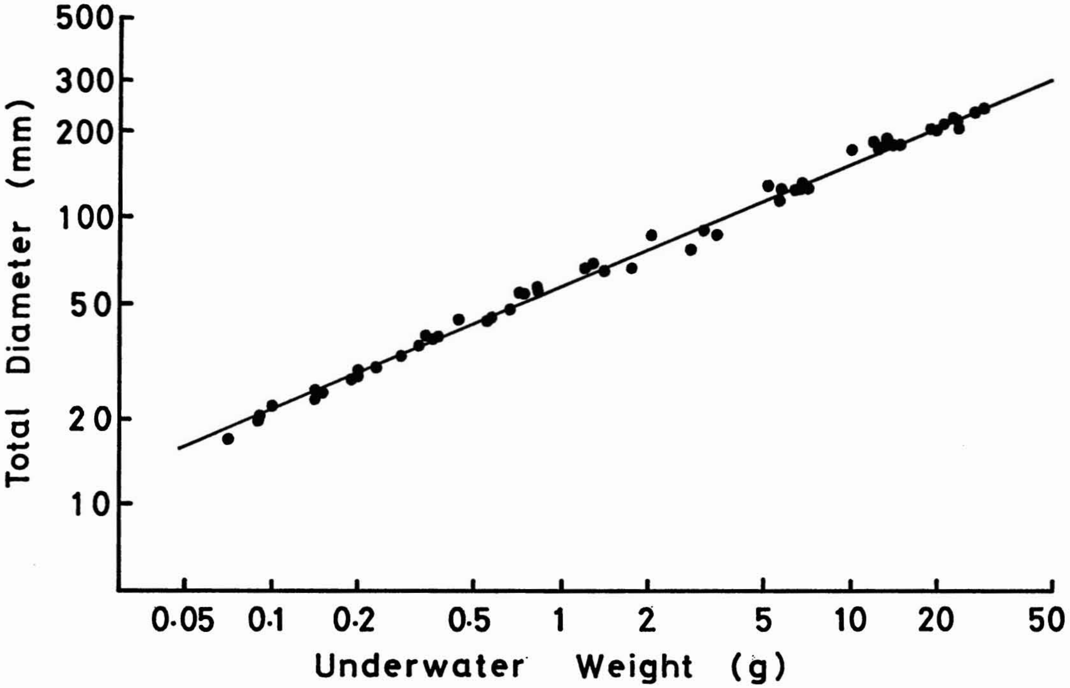

FIG. 1. *Acanthaster planci*: relationships between diameter and underwater weight of laboratory-reared juveniles, logarithmic plot. Regression line: $L = 2.94 \times W^{0.431}$ where $W$ = underwater weight (mg) and $L$ = total diameter (mm).

weighing the dry coral skeletons whose soft tissue was consumed by the juveniles. *Acanthaster* everts its stomach from its mouth and digests the corals *in situ*. An area similar in size to the disc of the starfish is covered by the stomach. The coral species used in the feeding experiments were restricted to small tips of branching forms such as *Acropora nasuta* and *Pocillopora damicornis*. The mean combustible dry tissue weight of both *Acropora nasuta* and *Pocillopora damicornis* is 4.06 percent (S.D., 0.73; *N*, 15) and 4.21 percent (S.D., 0.40; *N*, 16), respectively, of total dry weight of the coral tips, in the size range 1 to 10 grams. The size of coral pieces used for the diet of juveniles in the experiment was kept smaller than that ordinarily covered by the stomach. Therefore, in most cases starfish killed a whole piece of coral and moved to another piece. When some pieces of coral had portions of ungrazed tissues, the percentage of the ungrazed part was visually estimated, and its estimated proportional weight was subtracted from that of the total attributed to the particular starfish. Besides the laboratory-grown animals, three juveniles of 60 to 100 mm in total diameter, collected from the field, were kept in aquaria and their food consumption as coral skeleton weight was recorded for 2 to 5 months.

The weight of the coral skeleton is not an applicable measure for estimating food value or conversion rate of food in relation to feeding activity of the starfish. However, it does give a crude idea how much coral mass will be killed by a starfish during its life cycle and how the feeding rate will vary according to the growth of the animals in a given time scale.

## RESULTS AND DISCUSSIONS

### *Underwater Weight of* Acanthaster *Juveniles in Relation to Dry Weight, Ash-Free Dry Weight, and Total Diameter*

Seven juvenile *Acanthaster* have been repeatedly measured for underwater weight in seawater and for total diameter (maximum diameter exclusive of spines). Fig. 1 indicates

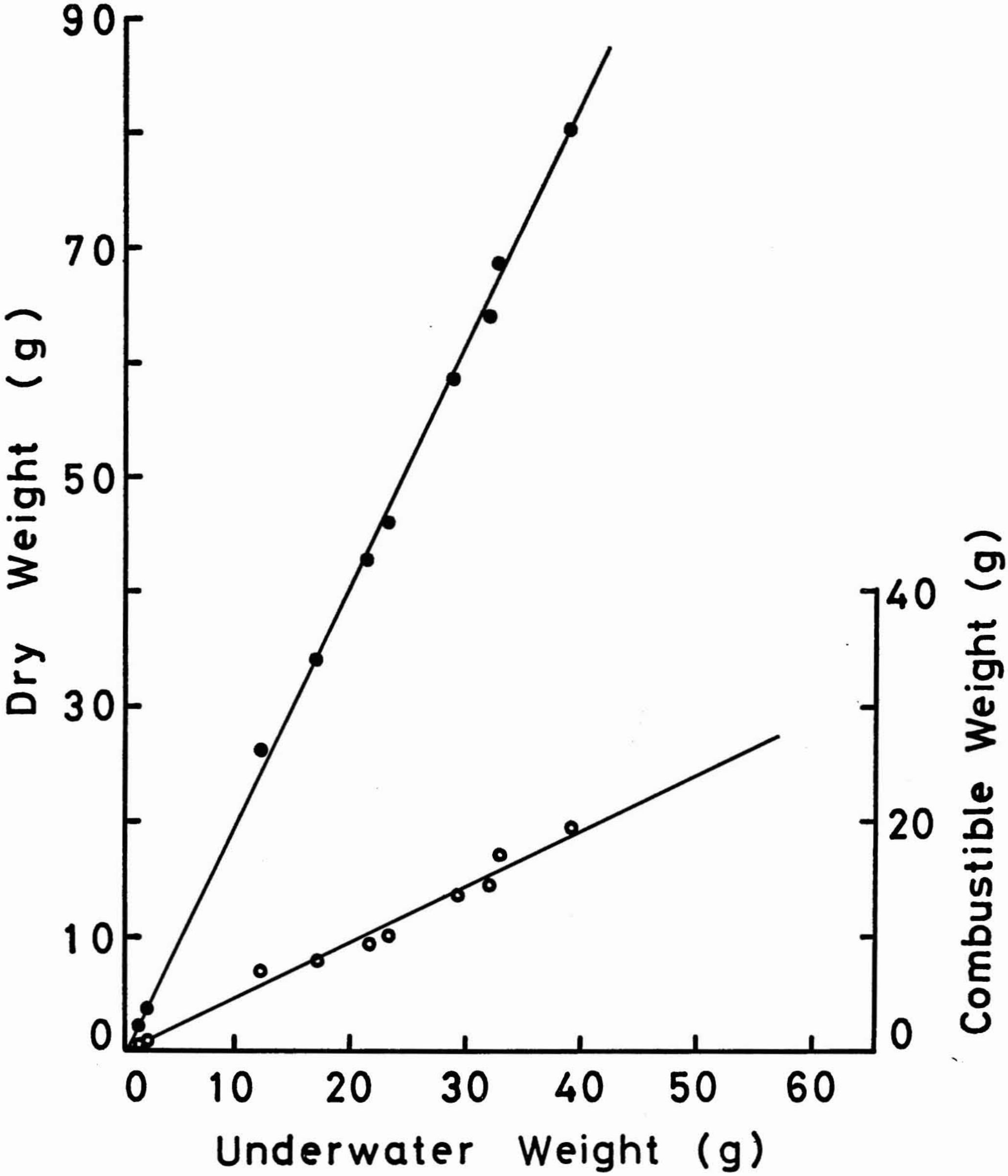

FIG. 2. *Acanthaster planci*: relationships between underwater weight and dry weight and those between underwater weight and combustible (ash-free) weight. Three additional small juveniles of similar size to the two shown were used for calculations of the regression lines. Open circles: (combustible weight) = 0.486 × (underwater weight). Solid circles: (dry weight) = 2.07 × (underwater weight).

the correlation between the weight and the diameter on a logarithmic plot. The diameter ($L$, mm) and the underwater weight ($W$, mg) is expressed as $L = 2.94 \times W^{0.431}$ from the regression line drawn by the least square method. If this were extrapolated to the smallest juvenile size of 0.5 mm in diameter, the estimated weight would be of the order of 0.01 mg in seawater. A large field specimen of about 450 mm in total diameter may have increased its weight up to $10^7$ times in the course of its development. The wet weight, or live weight, of the starfish is not

TABLE 1

CALCULATED PROPORTIONS OF UNDERWATER WEIGHT ATTRIBUTABLE TO ASH AND COMBUSTIBLE FRACTIONS IN *Acanthaster planci*

| | DRY WEIGHT (%) | SPECIFIC GRAVITY | VOLUME (%) | UNDERWATER† WEIGHT (%) |
|---|---|---|---|---|
| Ash Fraction | 76.5* | 2.68* | 56.5 | 97.9 |
| Ash-Free Fraction (Combustible) | 23.5* | 1.07 | 43.5 | 2.1 |
| Total | 100 | 1.98 | 100 | 100 |

NOTE: Seawater trapped inside the starfish body is neglected in this calculation, because its specific gravity is similar to that of the medium and does not contribute to the underwater weight.

* Mean values from direct determinations ($N = 8$); other values calculated from these.

† Measured in seawater of 1.024 in specific gravity.

determinable critically but it is approximately seven times greater than the underwater weight.

Dry weight and ash-free dry (combustible) weight of *Acanthaster* (five laboratory-grown juveniles and eight field specimens) were determined with temperatures of 105° to 110° C and 400° to 450° C in an oven and a furnace, respectively. Correlations between underwater weight and the dry or ash-free dry weight in the animals are shown in Fig. 2. The dry weight is about twice as heavy as the underwater weight, and the combustible (ash-free) weight is about half the underwater weight. The specific gravity of ossicles and spines of *Acanthaster* is approximately 2.68 from the direct determination. If the dry weight of an *Acanthaster* is divided into the ash and combustible (ash-free) fractions, and if the ash is equivalent in density to the skeletal materials, then the estimated underwater weight of the combustible fraction is approximately 1.07. The underwater weight of the ash-free, or combustible, fraction contributes only about 2.1 percent to total underwater weight, although it occupies 43.5 percent of volume and 23.5 percent of dry weight. The overall specific gravity of *Acanthaster* is about 1.98 from the value calculated above. Thus, the underwater weight is primarily a function of the skeletal fraction in *Acanthaster* (Table 1).

### *Growth of Juvenile* Acanthaster

The transition of feeding in some of the juveniles started at about 4 months after metamorphosis and lasted about 1 month. The smallest juveniles which fed on coral polyps were about 8 mm in total diameter. The completion of the transition of feeding coincides well with the completion of morphological transformation of juveniles into adult forms with 16 to 18 rays. Number of rays and number of madreporites stopped increasing at about 5 months after metamorphosis and their positions were fixed thereafter.

Growth in total diameter of juveniles up to sexual maturity is shown in Fig. 3 and in underwater weight in Fig. 4. The growth curve of these well-fed juvenile *Acanthaster* represents a typical exponential growth in the earlier stage and deviates from the exponential as the juveniles advance in age. Individual variations in size become greater as growth rate is accelerated.

The growth rate (increment per unit time) in the herbivore-stage juveniles up to 150 days old was much smaller than that of the subsequent coral-feeding ones (Fig. 3). However, if the growth is compared in terms of daily growth coefficient or doubling time (duration for doubling length or weight), and if we assume that the growth curve is exponential in the earlier stages, then the herbivore juveniles grew more rapidly than did the coral-feeding ones.

The herbivorous juveniles doubled their mean total diameter every 38 days from November 1971 to January 1972, while the subsequent coral-feeding juveniles doubled every 61 to 63 days from January to May 1972. Thereafter, the growth curve started to deviate rapidly from the exponential one as the daily growth coefficient decreased and the doubling time (a reciprocal of the growth coefficient) increased. The growth rate of total diameter increased as the juveniles grew to 150 mm in mean diameter, reaching 25.4 mm per 30 days.

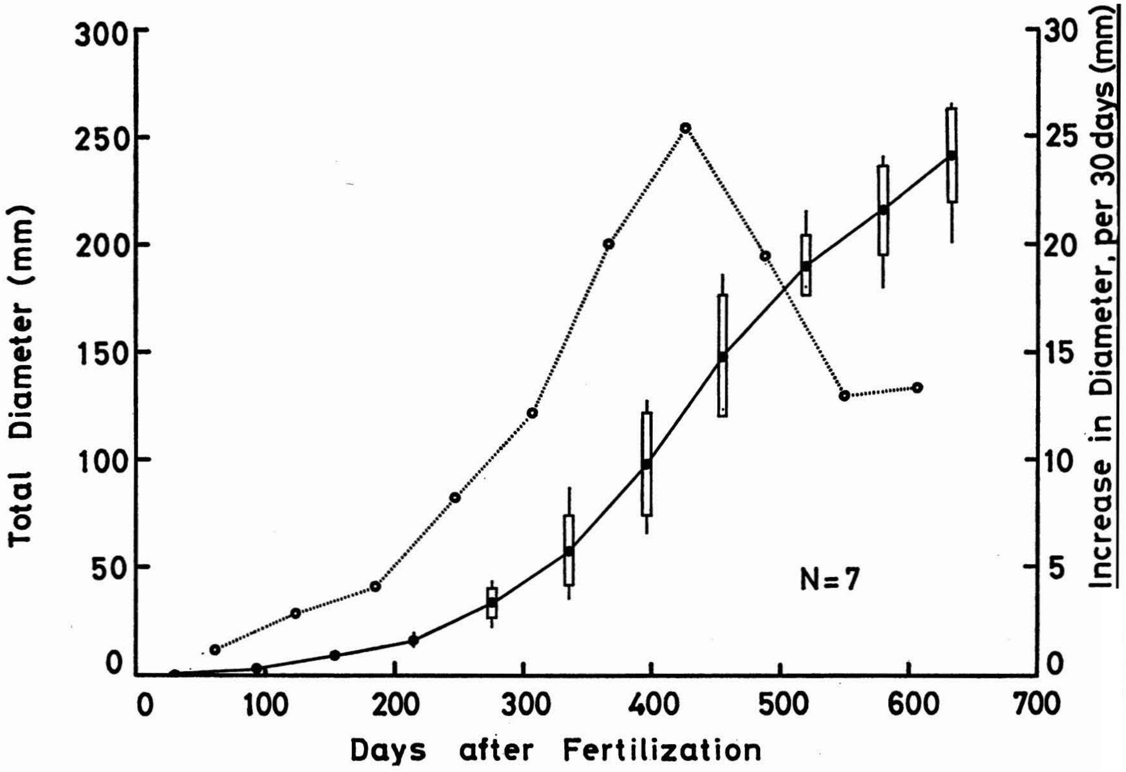

FIG. 3. *Acanthaster planci*: growth in diameter and growth rate of laboratory-reared juveniles. Mean ± one standard deviation and range for seven individuals are shown. Open circles indicate mean growth rates of diameter per 30 days.

This growth rate dropped to about 13 mm per 30 days at sizes about 200 mm in mean diameter. On the other hand, three field specimens of 60 to 90 mm in initial diameter grew at the rate of 30 to 40 mm per 30 days for 2 to 5 months under conditions similar to the present study. This may represent a maximum potential growth rate for individual juvenile *Acanthaster*.

The seven laboratory-reared *Acanthaster* were injected with a spawning agent, 1-methyladenine, in February 1973 when they were 17 months old (after metamorphosis) and at monthly intervals after the first injection. Two males first spawned in February, with no reaction in March. One female reacted in April, when the two males again spawned. In May one additional female and one additional male spawned, together with the ones previously spawning. Two out of seven were still unripe by May 1973. The gametes spawned in April and May were artificially inseminated, and the fertilized embryos were raised to advanced brachiolariae in 3 weeks. I consider that my animals are beginning to mature when they are about 20 grams in underwater weight or 200 mm in total diameter. The smallest field specimens that were induced to spawn were around 150 mm in total diameter (ca. 10 individuals), but they were collected from reef-flat pools and were considered to be dwarf adults, having the papulae area distinctly banded by a colored circle (juvenile ring). The juvenile ring is conspicuous in small (usually up to 150 mm in diameter) *Acanthaster*. This is mainly due to faint colored papulae in the middle zone of the disc; when all papulae withdraw inside the disc, the ring becomes obscure.

One of the laboratory-reared juveniles matured without the juvenile ring disappearing, while the others all turned into the adult forms without juvenile rings. The adult with the juvenile ring had accidentally been kept in an aquarium with high salinity (about 40‰) for several weeks until I noticed that the animal did

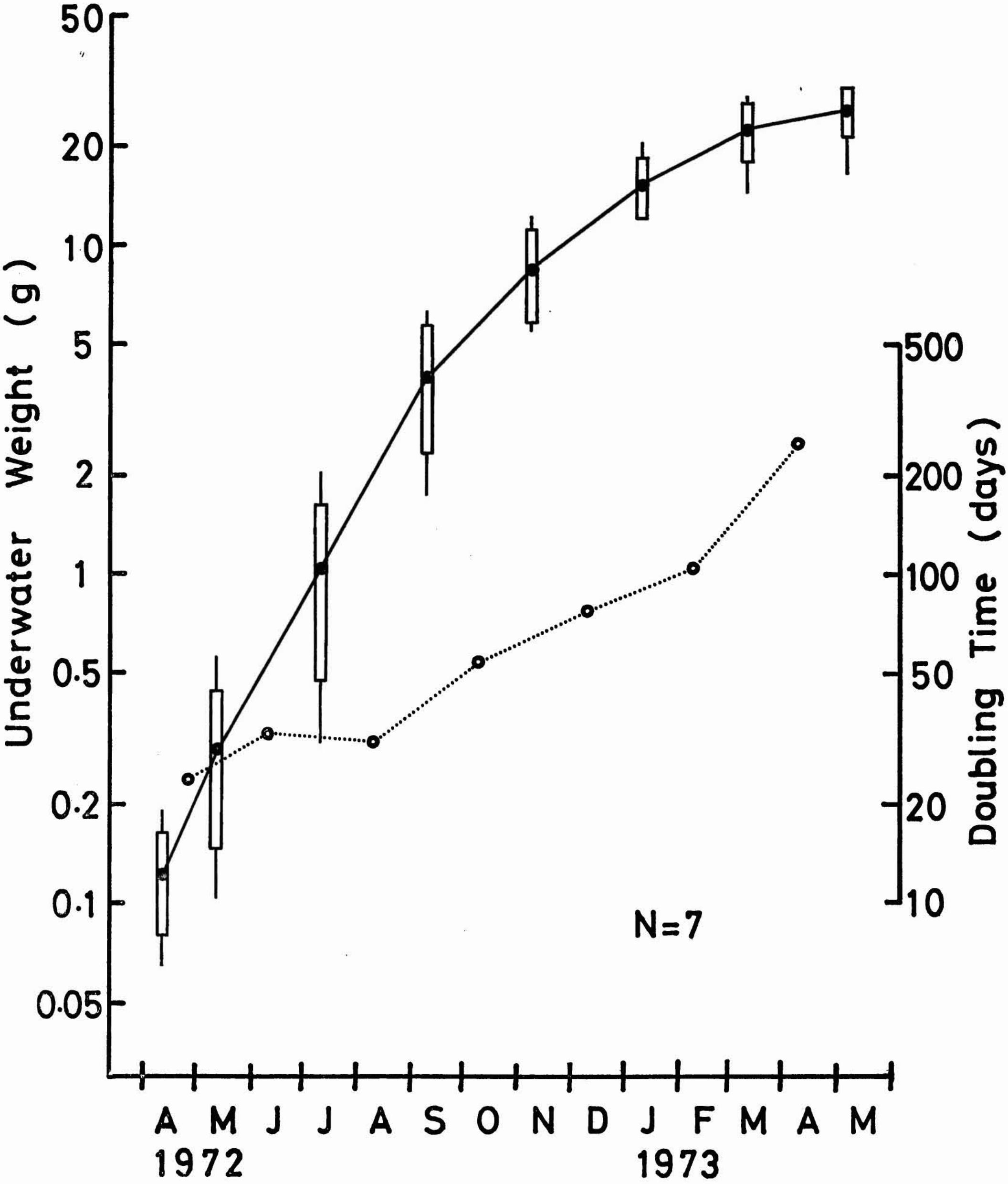

FIG. 4. *Acanthaster planci*: growth in underwater weight and doubling time of laboratory-reared juveniles, semi-logarithmic plot. Mean ± one standard deviation and range for seven individuals. Open circles indicate mean weight doubling time.

not feed on corals and looked unhealthy. It recovered its appetite after being transferred to seawater of normal salinity (about 34‰), but it apparently stopped increasing in size and matured at a relatively small size (ca. 180 mm in total diameter). Starfish may be experimentally induced to mature if they are exposed to a stressed condition. The reef-flat environment is quite variable in temperature and salinity and may be detrimental to this starfish, which has a

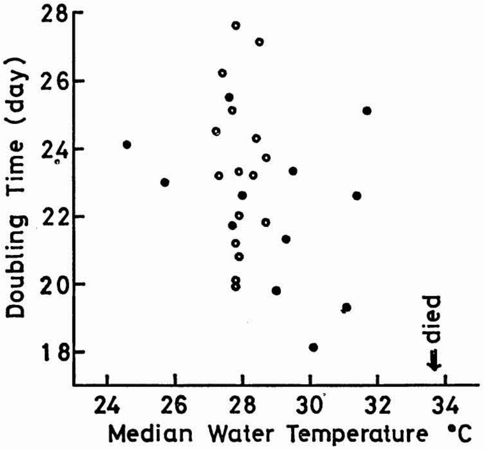

FIG. 5. *Acanthaster planci*: effect of water temperatures on doubling time in laboratory-reared juveniles. Open circles: ambient conditions (controls) with temperature fluctuations of ± 2.5° to 3.0° C around the median points. Solid circles: temperature controlled conditions (experiments) with temperature fluctuations of ± 0.5° to 1.0° C around the median points. Two experimental animals died at 33.6° and 33.7° C median temperatures, respectively.

narrow tolerance limit of upper lethal temperature of ca. 33° to 34° C (Yamaguchi, 1974). The dwarf adults on the reef flats may reflect the effect of this factor.

*Acanthaster* may not increase its size greatly after attaining its individual ultimate size as a matured animal (determinate growth). The data to support this view are still to be collected by monitoring the animals' growth in the laboratory. However, the facts that a field population in Hawaii consists of animals with a unimodal size-frequency distribution and that no increase of size occurs in the animals (Branham 1973) indicate the hypothesis to be correct. If this is so, it is impracticable to estimate the age of starfish from their sizes, except for the small ones which are usually very rare in the field population. The report on a bimodal size distribution of *Acanthaster* in the Red Sea (Ormond and Campbell 1971) may be analyzed as mixing two or more subpopulations with ultimate adult size modes different from each other, rather than the explanation given, that it consisted of two or more age classes. Indeed, the bimodal size distribution was constructed not from a single aggregation but from animals that were widely scattered and living in different depth zones (Ormond and Campbell 1971). The cessation of growth in echinoderms after they attain individual ultimate sizes as adults has been reported for a heart urchin (Moore and Lopez 1966), sand dollars (Birkeland and Chia 1971, Yamaguchi 1970), and a sea urchin (Ebert 1968). *Acanthaster* may follow the same trend of determinate growth.

A series of experimental observations was planned to detect the effect of temperature on the juveniles' growth at the exponential growth stage when the animals were fully fed. I could not detect any gradient of the temperature effect on the growth coefficient of the exponentially growing juveniles in the experiments so far carried out because the coefficient was highly variable among individuals of the same brood under ambient control conditions (Fig. 5). The causes of this fluctuation in the individual growth rate are not clear. Unfavorable chance factors (such as injuries and failures in locating food) may reduce the rate of growth of individual animals to different degrees. Sensitivity or reaction of individuals against stimuli appeared to vary greatly; some were more sensitive to manipulation than others.

The above fluctuation, however, may be responsible for increasing standard deviations in individual sizes during the exponential growth phase of juvenile *Acanthaster* (Fig. 3).

### *Feeding Rate of* Acanthaster *Juveniles*

*Acanthaster* is capable of withstanding starvation for several months (Chesher 1969). One juvenile of ca. 90 mm in diameter survived for 3 months without any food but reduced its size about 10 percent in diameter. Food is apparently the most important factor influencing the growth of *Acanthaster* juveniles.

During the controlled temperature experiments, the amount of coral skeleton killed by the juvenile starfish at ambient temperatures was determined. Two different coral species, *Pocillopora damicornis* and *Acropora nasuta* were selected for food and were fed separately to individual juveniles for given periods (8 to 11 days). Both coral species sustained exponential growth, and the growth rates between the two

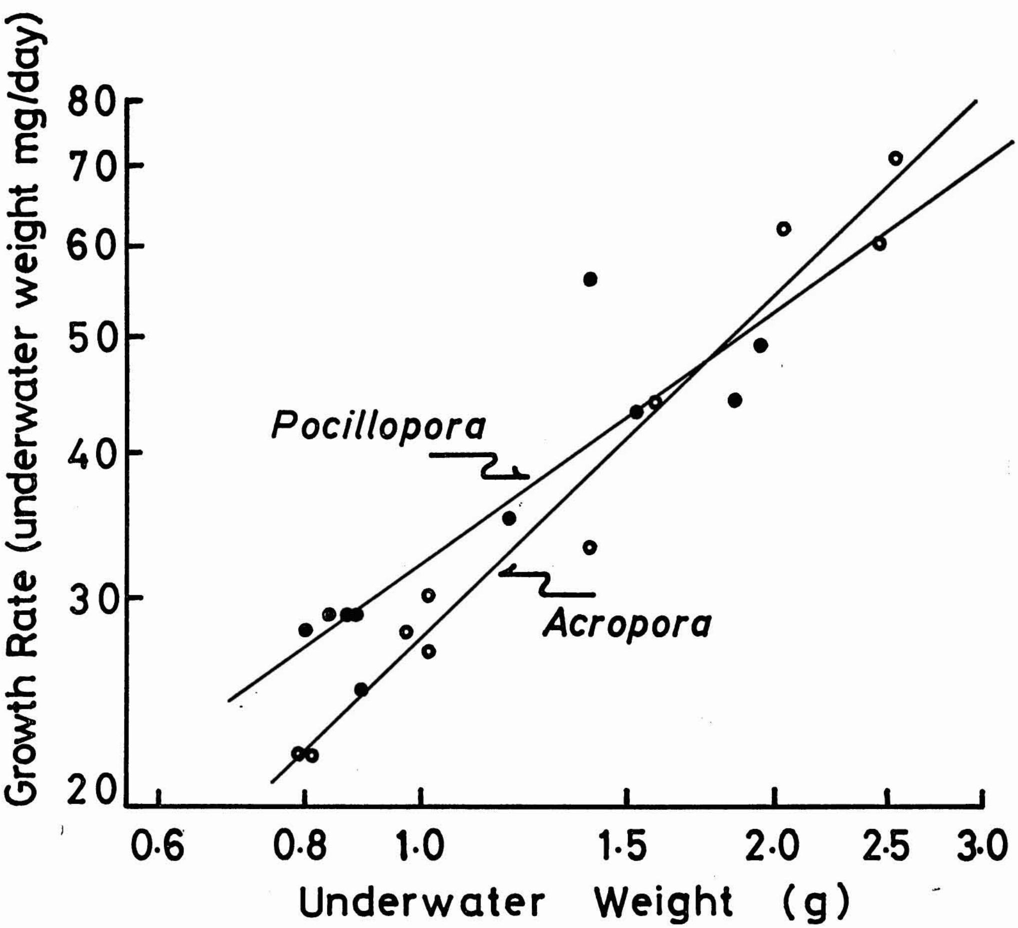

FIG. 6. *Acanthaster planci*: effect of food coral species on growth and feeding of laboratory-reared juveniles. Relationship between growth rate and weight when the animal is well fed, logarithmic plot. Open circles: juveniles fed *Acropora nasuta*; solid circles: juveniles fed *Pocillopora damicornis*.

groups of juveniles fed different corals were not markedly different (Fig. 6 and Table 2). However, the feeding rates of the two groups were clearly different. At a given growth rate, the juveniles killed almost twice as much mass of *Acropora* as they did of *Pocillopora* (Fig. 7).

The data collected from the *Acanthaster* population in Panama to estimate the carrying capacity of the *Pocillopora* reef for the asteroid (Glynn 1973) may not be applicable directly to the *Acropora*-dominated coral reefs in the western Pacific in light of the difference in grazing of the asteroid on different coral genera. *Acropora* reefs may be more vulnerable than are *Pocillopora* reefs against *Acanthaster* predation pressure if densities of coral mass are

TABLE 2

DOUBLING TIME OF UNDERWATER WEIGHT FOR *Acanthaster planci* ON TWO DIFFERENT CORAL DIETS

| | DOUBLING TIME (DAYS) | |
|---|---|---|
| INDIVIDUAL STARFISH NO. | *Acropora nasuta* | *Pocillopora damicornis* |
| V-2 | 26.0 | 24.0 |
| V-3 | 23.5 | 22.2 |
| V-4 | 22.9 | 23.2 |
| VII-2 | 25.5 | 21.9 |
| VII-3 | 23.3 | 23.3 |
| Mean | 24.24 | 22.92 |

NOTE: Determinations made at ambient temperature.
$s = 1.584$
$t = 1.67$ with $P > 0.1$ ($\nu = 4$, $t_{0.1} = 2.13$).

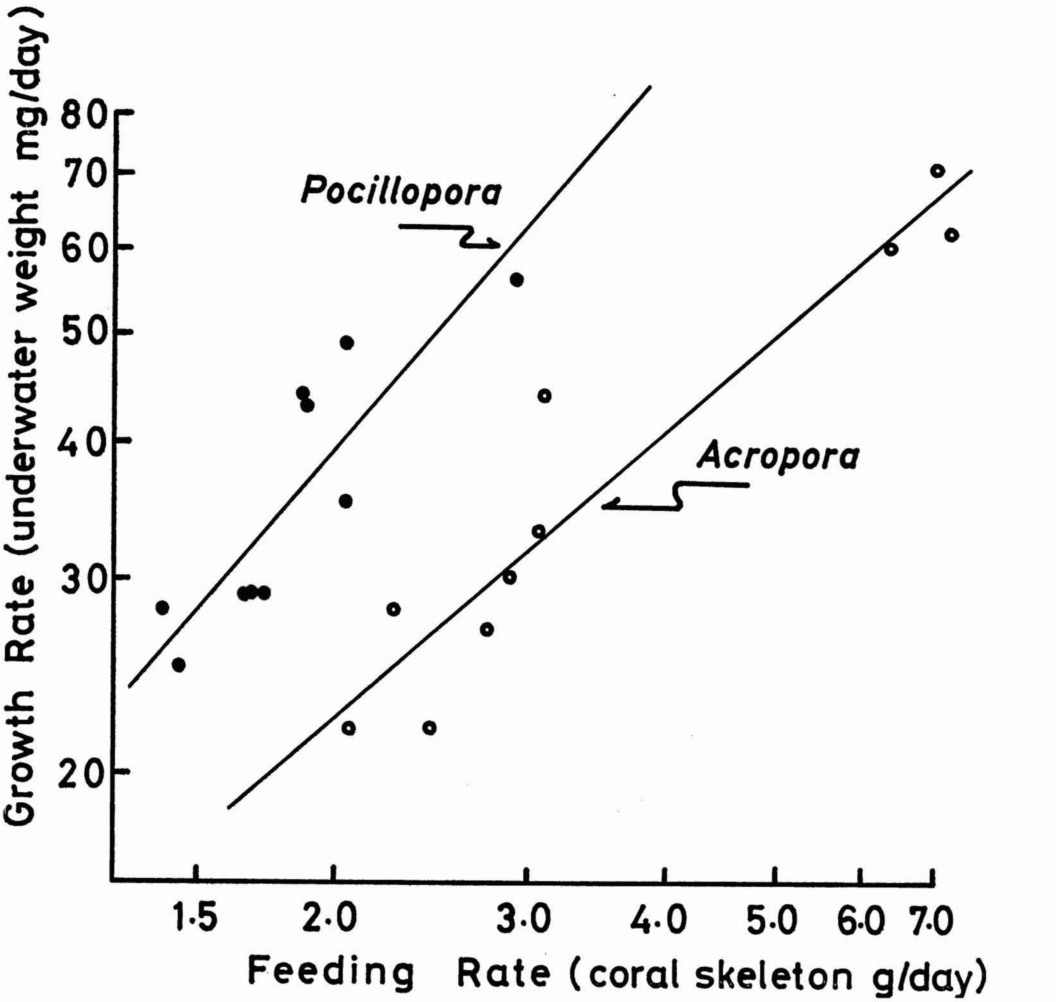

FIG. 7. *Acanthaster planci*: effect of food coral species on growth and feeding of laboratory-reared juveniles. Relationship shown is that between growth rate and feeding rate (dry coral skeleton weight per day), logarithmic plot. Open circles: juveniles fed *Acropora nasuta*; solid circles: juveniles fed *Pocillopora damicornis*.

similar. Growth rates are not markedly different between the two genera of corals (Vaughan and Wells 1943).

The above observations and the other observation on the feeding of larger juveniles on mixed coral species (mostly *Pocillopora* and *Acropora*) provided the data that allowed the correlation between size of the starfish (underwater weight) and its feeding rate (dry coral skeleton mass) to be made (Fig. 8). Fig. 8 gives a crude idea of how much coral mass would be killed by a given sized starfish in a given period. Fig. 9 was drawn from the mean size of laboratory-reared juveniles given in Fig. 4 and the feeding rate obtained from the regression line in Fig. 8 for the feeding rate and the size. Fig. 9 further indicates the graphically integrated mass of coral killed by a single *Acanthaster* if the starfish consumes at the feeding rate shown in the same figure. The estimated accumulative consumption in Fig. 9 shows that the total coral mass killed by a juvenile *Acanthaster* increases nearly exponentially until the starfish reaches maturity. An average-sized juvenile may consume about 200 grams of coral skeleton (which is about a fist-sized piece of *Pocillopora damicornis*) in the first year and about 50 kg in the second. If the feeding rate stabilizes after the

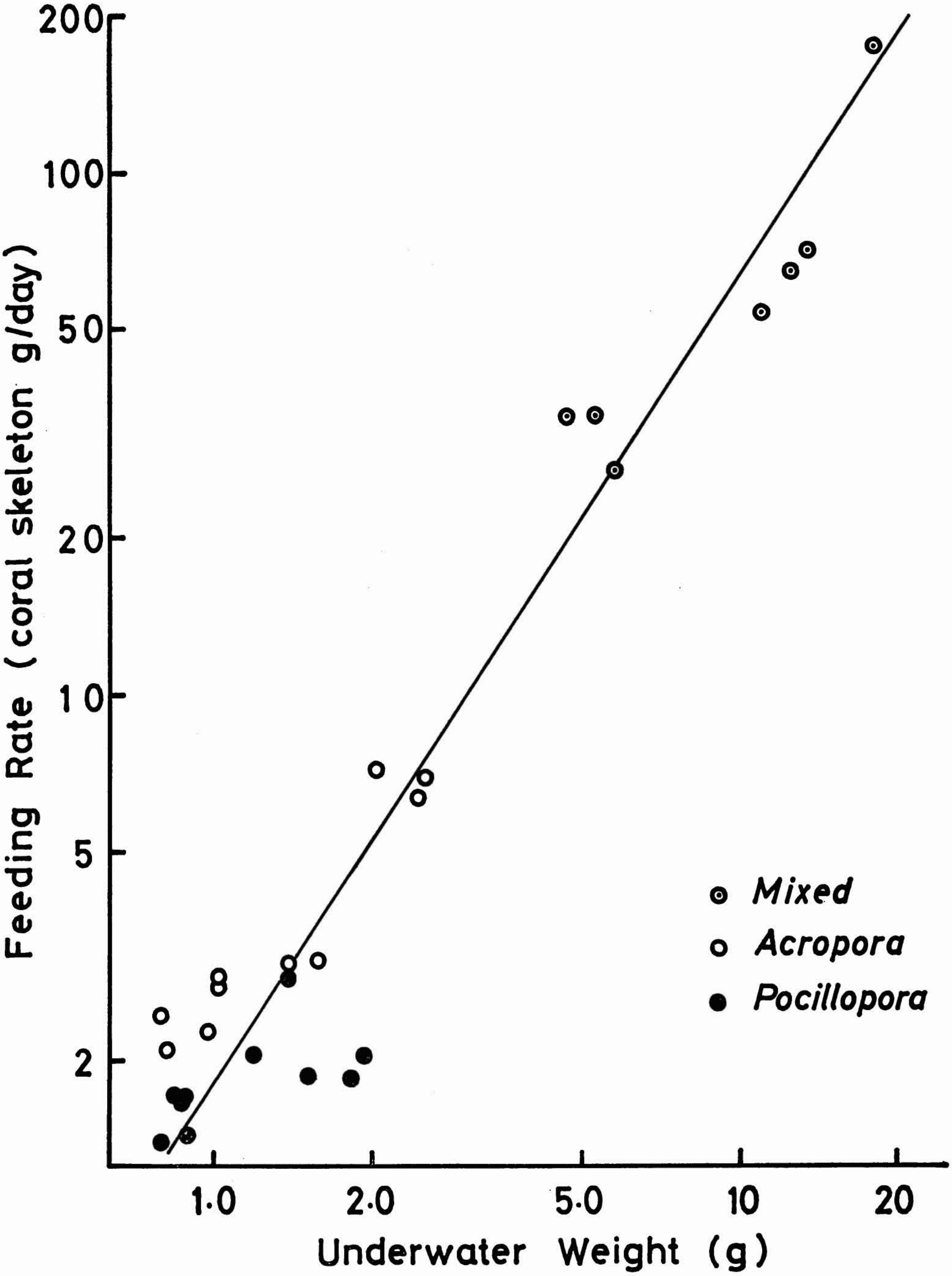

FIG. 8. *Acanthaster planci*: relationships between feeding rate and underwater weight of juveniles, logarithmic plot. The regression line was drawn from all available data, regardless of the food coral species, by the least-squares method.

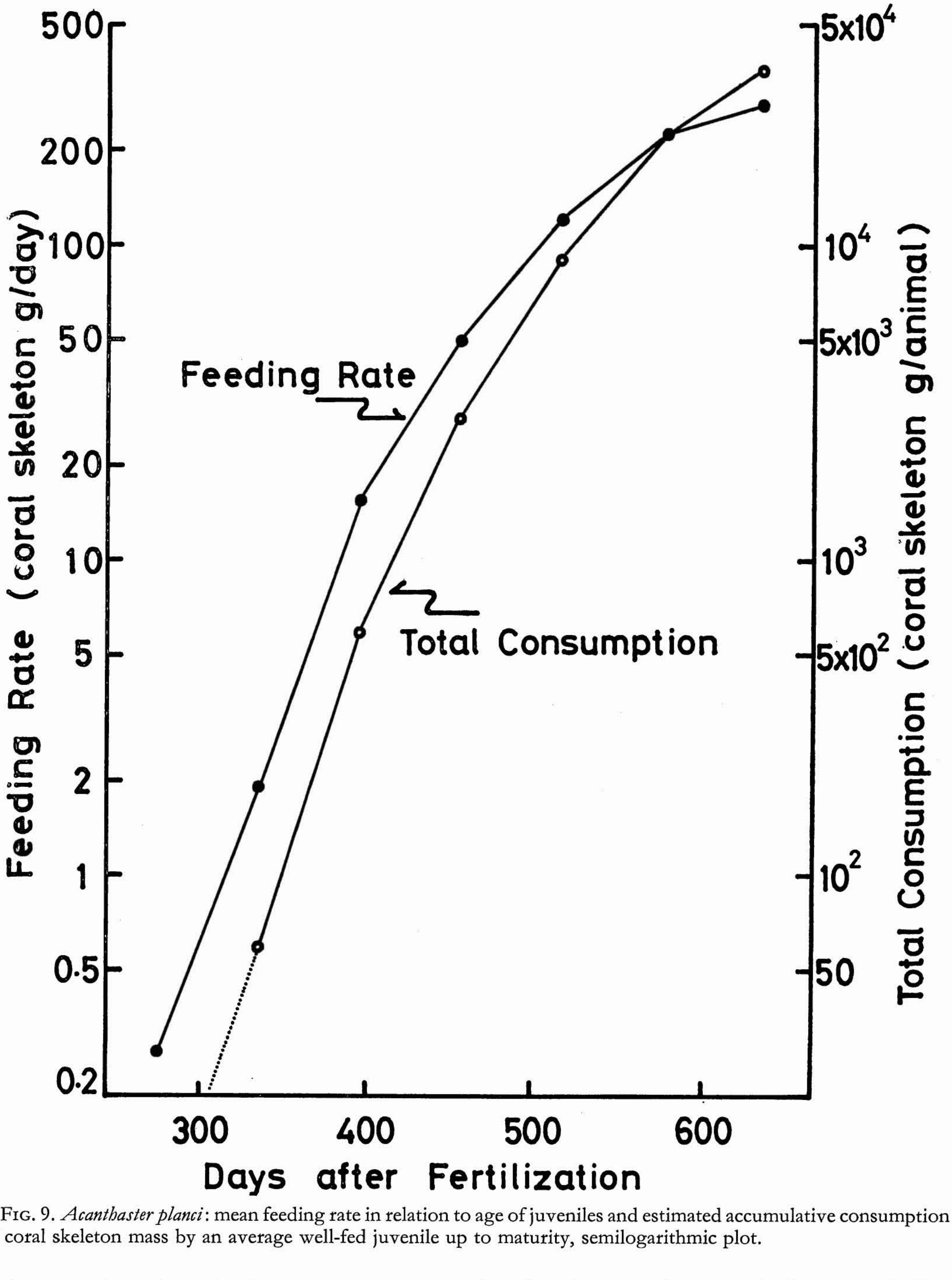

FIG. 9. *Acanthaster planci*: mean feeding rate in relation to age of juveniles and estimated accumulative consumption of coral skeleton mass by an average well-fed juvenile up to maturity, semilogarithmic plot.

3rd year, when the animals mature, at about 300 g coral skeleton per day, then the annual consumption of the adult starfish is of the order of 100 kg. Thus, the influence of feeding by *Acanthaster* on the corals is almost negligible during the period when juveniles are developing in the 1st year, and it increases rapidly as they grow. Significant damage to coral reefs

TABLE 3

COMPARISON OF GROWTH COEFFICIENTS BETWEEN *Acanthaster* AND *Pisaster*

| STARFISH NO. | DURATION (DAYS) | WEIGHT INCREASE (GRAMS) | GROWTH COEFFICIENT (PER DAY) | DOUBLING TIME (DAYS) |
|---|---|---|---|---|
| *Pisaster* | | Live Weight | | |
| No. 8 | 192 | 35.8–150.6 | $3.25 \times 10^{-3}$ | 92.6 |
| No. 9 | 192 | 25.2–128.7 | $3.69 \times 10^{-3}$ | 81.6 |
| No. 10 | 193 | 30.1–113.9 | $2.99 \times 10^{-3}$ | 100.5 |
| No. 11 | 185 | 29.3–195.5 | $4.46 \times 10^{-3}$ | 67.6 |
| No. 12 | 270 | 7.9–106.5 | $4.18 \times 10^{-3}$ | 71.9 |
| *Acanthaster* | | Underwater Weight | | |
| V- 2 | 184 | 3.10–13.71 | $3.51 \times 10^{-3}$ | 85.8 |
| V- 3 | 184 | 3.41–13.00 | $3.16 \times 10^{-3}$ | 95.3 |
| V- 4 | 184 | 2.80–14.36 | $3.86 \times 10^{-3}$ | 78.0 |
| V- 9 | 184 | 1.75–12.64 | $4.67 \times 10^{-3}$ | 64.5 |
| V-10 | 149 | 1.28–12.19 | $6.57 \times 10^{-3}$ | 45.8 |
| V-11 | 149 | 1.39–11.74 | $6.22 \times 10^{-3}$ | 48.4 |
| V-12 | 182 | 1.19–12.61 | $5.63 \times 10^{-3}$ | 53.4 |

NOTE: Data on *Pisaster* were calculated from the figures given by Feder (1956), with his kind permission to use.

is likely to be caused only by an aggregation of fully grown *Acanthaster*.

### *Comparison of Growth with Other Asteroid Species*

The time scale used in the above speculations may represent rapidly growing animals, because the data were based on well-fed starfish. Field animals would consume less per unit time than the laboratory animals, because the former have to expend much time locating food and also because they are under various stresses such as predation. Feder (1956, 1970) found that *Pisaster ochraceus* grows at a much higher rate in the laboratory where it is well fed than it does in the field. His data on the live-weight increment in laboratory-reared *Pisaster* are compared with those of *Acanthaster* in Table 3. If the live weights of the two asteroid species are about 10 times their underwater weights, then their daily growth coefficient or doubling time in weight is very close, in spite of the wide difference in water temperature (9.5° to 16.8° C for *Pisaster* and 25° to 31° C for *Acanthaster*).

Halpern (1970) reported on the growth of *Luidia senegalensis* near Florida. He found that juvenile *Luidia* grew at the rate of 11.6 mm in arm-radius per month. This figure is comparable with the maximum mean growth rate of juvenile *Acanthaster*, 25.4 mm in diameter per 30 days, since the arm-radius is about half the total diameter.

### *Damage of* Acanthaster *Juveniles by Coral Polyps Shortly after the Feeding Transition Period*

The juveniles completed the transition from feeding on algae to feeding on coral polyps, as well as the transformation to the adult structure, by February 1972, 5 months after metamorphosis. In February and March many of the early coral-feeding juveniles were seen to be injured by the coral polyps on which they were feeding. When a juvenile fed on some polyps of part of a branching coral colony, the polyps in contact with the dorsal surface of the juvenile *Acanthaster* attacked the predator. The free coral polyps near the ones covered by the stomach of the juvenile also attacked the starfish. The starfish did not show any escape responses to such attacks when they were feeding. Thus, the juveniles were injured on various parts of their bodies, mostly on the dorsal surfaces and rays, from the attacks by coral polyps. The injured part turned fresh pink and keloid-looking. Some juveniles were so severely injured that they lost arm tips or several complete arms, including small parts of the disc. The most heavily damaged juvenile received a large hole through the disc. Fig. 10 illustrates the damages and

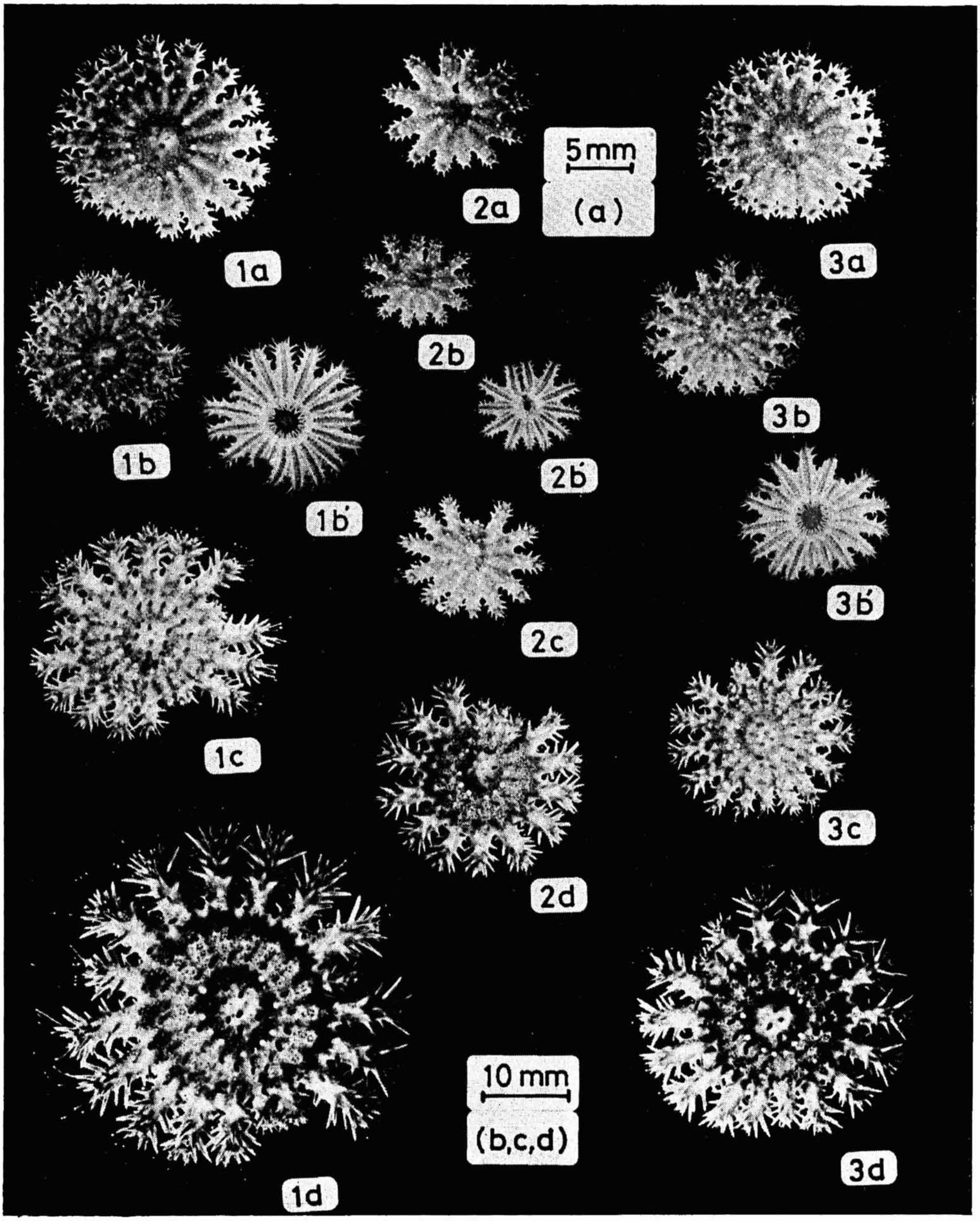

FIG. 10. *Acanthaster planci*: growth and regeneration of juveniles after they have received injuries. All starfish pictures are placed so as to show vertical anterior-posterior axis. Three individuals are shown—V-11, V-16, and V-4. Starfish no. V-11: 1a, 1b, 1b′, 1c, and 1d; starfish no. V-16: 2a, 2b, 2b′, 2c, and 2d; and starfish no. V-4: 3a, 3b, 3b′, 3c, and 3d. Photographs were taken 1 March 1972 (about 6 months after the animals had metamorphosed) for 1a, 2a, and 3a; 21 March 1972 for 1b, 1b′, 2b, 2b′, 3b, and 3b′; 11 April 1972 for 1c, 2c, and 3c; and 11 May 1972 for 1d, 2d, and 3d. 1b′, 2b′, and 3b′ show oral surface and the others show the aboral surface.

The short rays of 1a, 2a, and 3a indicate the latest-formed rays, while the rays on the top are old ones,i ncluding the original five (V-16 lost these).

subsequent regeneration in several juvenile *Acanthaster*. Starfish V-4 and V-11 lost tips of several rays during 1 to 21 March, and regenerated the lost parts. Starfish V-16 lost five complete rays as well as a part of its disc before 1 March. It regenerated three new rays subsequently, making a 15-rayed asteroid from an original 17-rayed one. The severely injured juveniles slowly regenerated the lost parts, but others rapidly recovered from the injuries as they grew. No further damage was observed once the juveniles grew to a large enough size, with lengthened spines, to avoid attacks by coral polyps.

I have observed several juveniles attached to immersion heaters held inside the aquaria; they showed no avoidance response to the hot heater and died after receiving severe injuries. *Acantheraster*'s lack of an escape reaction against adverse stimuli is interesting in light of its feeding on corals.

Two series of madreporites distribute almost in parallel with a vertical anterior-posterior axis of *Acanthaster* although there is marked irregularity in the distribution patterns (Fig. 10). The interradii of newer rays are crowded with the madreporites but those of the original five rays usually keep only a single (presumably the original) madreporite. The interradius between ray C and ray D (located upper right in the figures) keeps the original madreporite (see Yamaguchi, 1973, concerning the ray-formation of juvenile *Acanthaster* and the naming of rays).

## CONCLUSIONS

The postmetamorphosis *Acanthaster* juvenile completed transformation into the adult structure and transition from algae-feeding to coral-eating within 5 months after metamorphosis. Juveniles received damage and injuries to various extents from coral polyps on which they fed when they were too small to avoid attacks by the polyps. However, *Acanthaster* juveniles, except for those that were severely injured, grew steadily after recovering from the injuries. The growth curve for the juveniles was a sigmoid one, and growth rate in terms of increments of diameter or weight varied greatly during the juvenile development. Earlier juveniles grew almost exponentially. Daily growth coefficients or doubling times gave good indices for the growth of the exponential growth stage. The growth curve deviated from the exponential one as juveniles grew to maturity.

Measurements of weight of the starfish in the normal seawater proved to be precise and reproducible. The increase in underwater weight of the starfish expressed the skeletal development as a whole. The correlation between the underwater weight and dry weight or combustible weight was determined, and the latter two could be estimated from the measurement of the underwater weight of the animals. This method would be useful for the study of metabolic activity such as oxygen uptake, since the combustible weight of intact animals can be estimated from the underwater weight without the animals' having to be killed.

The feeding rate of juvenile *Acanthaster* on corals increased exponentially up to near sexual maturity. The estimated coral mass killed by an average, but well-fed, juvenile during its development to maturity also increased exponentially. The starfish does not begin its extensive grazing on corals until it has nearly reached its ultimate size, which may be variable according to the environmental conditions. Most of the well-fed *Acanthaster* reared in the laboratory grew to sexual maturity in 17 to 20 months after metamorphosis (18 to 21 months after spawning).

## LITERATURE CITED

BIRKELAND, C., and F. S. CHIA. 1971. Recruitment risk, growth, age and predation in two populations of sand dollars, *Dendraster excentricus* (Eschscholtz). J. Exp. Mar. Biol. Ecol. 6: 265–278.

BRANHAM, J. M. 1973. The crown of thorns on coral reefs. Bioscience 23: 219–226.

CHESHER, R. H. 1969. Destruction of Pacific corals by the sea star *Acanthaster planci*. Science 165: 280–283.

EBERT, T. A. 1968. Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. Ecology 49: 1075–1091.

FEDER, H. M. 1956. Natural history studies on the starfish *Pisaster ochraceus* (Brandt, 1835) in the Monterey Bay area. Ph.D Dissertation. Stanford University, Stanford, California. 294 pp.

———. 1970. Growth and predation by the ochre sea star, *Pisaster ochraceus* (Brandt), in Monterey Bay, California. Ophelia 8: 161–185.

GLYNN, P. W. 1973. *Acanthaster*: effect on coral reef growth in Panama. Science 180: 504–506.

HALPERN, J. A. 1970. Growth rate of the tropical sea star *Luidia senegalensis* (Lamarck). Bull. Mar. Sci. 20: 626–633.

MOORE, H. B. and N. N. LOPEZ. 1966. The ecology and productivity of *Moira atropos* (Lamarck). Bull. Mar. Sci. 16: 648–667.

ORMOND, R. F. G., and A. C. CAMPBELL. 1971. Observations on *Acanthaster planci* and other coral reef echinoderms in the Sudanese Red Sea. Symp. zool. Soc. Lond. 28: 433–454.

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, Dep. Harbours Marine 3: 27–55.

VAUGHAN, T. W., and J. W. WELLS. 1943. Revision of the suborders, families, and genera of the Scleractinia. Spec. Pap. geol. Soc. Amer. 44. 363 pp.

YAMAGUCHI, M. 1970. Ecological observations of the population of a sand-dollar, *Clypeaster japonicus* at Tenjin-jima Marine Biological Garden [in Japanese, English abstract]. Sci. Rep. Yokosuka City Mus. 16: 74–82.

———. 1973. 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, Biology 1. Academic Press, New York. xxii + 480 pp.

———. 1974. Effect of elevated temperature on the metabolic activity of the coral reef asteroid *Acanthaster planci* (L.). Pacif. Sci. 28: 139–146.