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Deep Sea Corals Collected by the Lamont Geological Observatory. 3 Larvae of the Argentine Scleractinian Coral *Flabellum curvatum* Moseley[1]

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INTRODUCTION

Direct observations of the reproductive behavior of corals, other than reef corals, are quite rare. Evidence relating to the time, duration, and nature of reproduction of the deeper water corals is largely circumstantial or conjectural. Histological studies of gonads, analysis of population structures, and other approaches have been utilized in attempts to appreciate the breeding periodicity of these corals.

Recently, I was able to observe planulation in a single individual of the solitary coral *Flabellum curvatum* Moseley, a common constituent of the shelf and upper-slope faunas of the Patagonian Continental Shelf (Squires, 1961). During studies carried out in cooperation with the Lamont Geological Observatory, Columbia University, on the seventeenth cruise of the R/V "Vema," the species was taken in considerable numbers in biological trawls on the continental shelf off Bahia Blanca, Argentina, in depths of from 80 to 160 meters. In the first of several trawls in which they were encountered, large numbers of adult coralla of *F. curvatum* of approximately the same size range (30 to 40 mm. high) were obtained,

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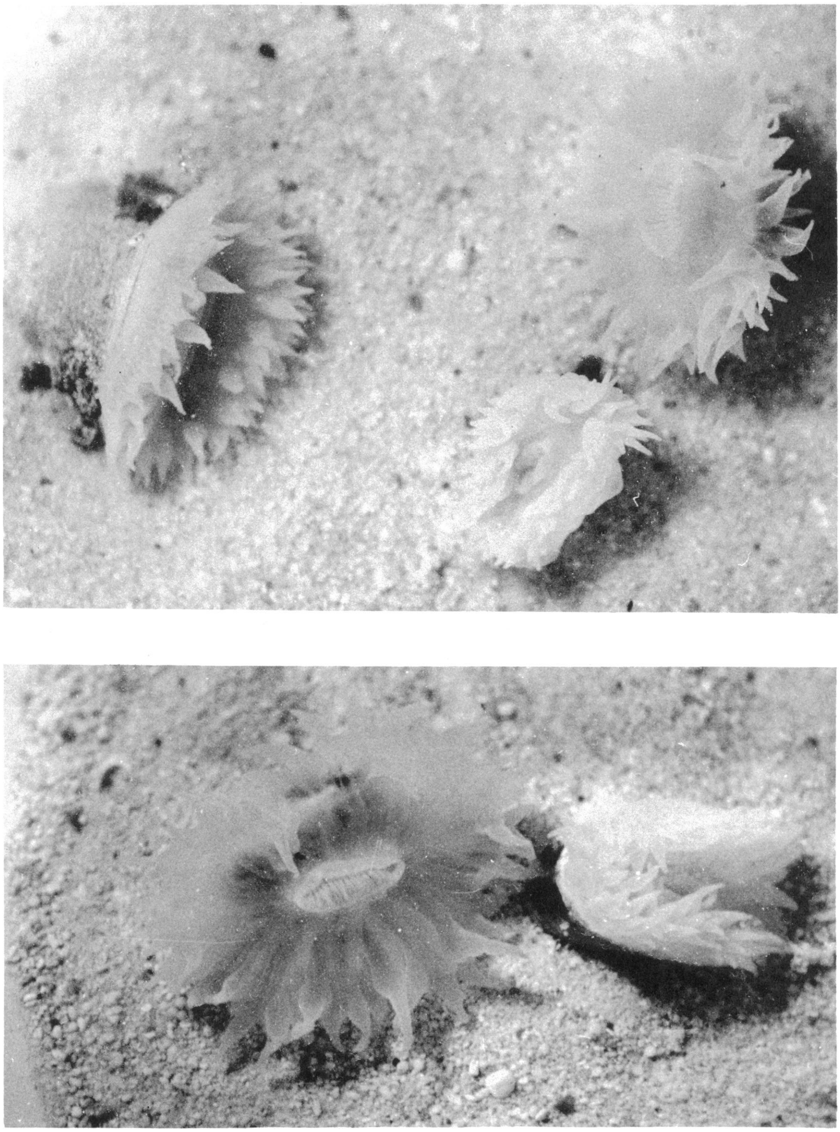

FIG. 1. Adult *Flabellum curvatum* Moseley. The three specimens maintained alive aboard R/V "Vema." *Upper:* The specimens on the right are upright, with the corallum partially immersed in the substrate; the specimen on the left is lying on the side of its corallum. *Lower:* Another view of the two specimens on the right, above. The specimen on the left is the one from which larvae were obtained. Approximately × 1.

together with numbers of immature coralla up to several millimeters in height. Three individuals from another trawl (V. 17-74) were segregated from the collection and were maintained in aquaria for several days on the vessel until foul weather forced the termination of the experiment. This trawl was taken at a depth of 74 meters approximately 200 miles southeast of Bahia Blanca, Argentina (latitude 41° 27′ S., longitude 59° 33′ W.), 1 P.M., local time, May 23, 1961. The substrate was mud and sand. A small fauna consisting mainly of infaunal types, ophiuroids,

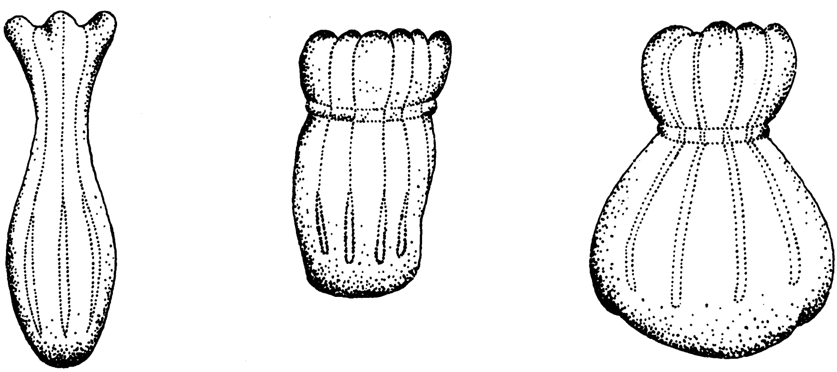

FIG. 2. Larvae of *Flabellum curvatum* Moseley after extrusion. The larva on the left is most similar in form to the larvae of reef corals. Dotted areas appeared translucent on the original specimens. Not to scale.

small Mollusca, and numerous worms was associated with the corals. The surface temperature of the water at the time of collection was 11.4° C.

The three corals selected for maintenance in aquaria were placed so that the side of the corallum rested on some of the substrate obtained in the trawl. Most of the time the corals were kept in darkness, but they were brought out into the light for short periods of observation. Exposure to light in this fashion did not seem to affect the polyps; no contractile responses were observed. At 10 P.M., May 23, nine hours after the collection of the corals, three larvae were observed on the substrate immediately in front of the tentacular ring of one of the larger and more expanded polyps. These larvae were removed and kept in a separate container under conditions of light, temperature, and substrate similar to those of the adults. Measurements and drawings of the larvae were made during subsequent short periods of examination. Complete changes of water in both aquaria were made at approximately hourly intervals to maintain a low temperature; the added water had a temperature of 10.6° C.

During this period, polyps of all three corals were in an expanded state, and the larvae were very motile but sluggish.

At 10.30 P.M., May 23, nine and one-half hours after collection of the adults, a fourth larva was observed on the substrate but was not directly associated with any single polyp. This larva was left in the aquarium with the adult corals but could not be found the next day; its fate is unknown. At 11.15 P.M., May 23, a fifth larva was observed in the stomadeum of the largest polyp (the coral with which the original three larvae were associated). Five minutes later, this larva was extruded and was then removed from the aquarium and kept separate.

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF LARVAE OF *Flabellum curvatum* MOSELEY AT AGE OF FIVE HOURS

Specimen	Length	Diameter
A	3.7	2.4
B	4.5	2.1
C	2.8	2.6

The escape of the larva from the coelenteron and stomadeum of the adult polyp was accomplished without visible muscular contractions on the part of the polyp. The mouth of the polyp was relaxed, slightly everted, and somewhat open. When first observed, the last larva was about 5 mm. inside the mouth, on the lower surface of the longer side of the stomadeum. The larva progressed slowly up the stomadeum, then down the oral disc through the tentacular ring to the substrate. No mucous streams were observed in association with the larva. In the absence of visible muscular contractions, it is assumed that the movement of the larva was by ciliary action of the stomadeum of the parent polyp.

The larvae of *Flabellum curvatum* were large and obviously in an advanced stage of morphological development (figs. 1–3). Measurements made on those first observed are given in table 1.

Twelve small lumps on the outer periphery of the oral surface represented preliminary outgrowths of the tentacles. Twelve mesenterial pairs could be observed through the outer surface of the larvae as alternating longitudinal bands of opaque, pearly white, and clear, nearly transparent tissue. No oral pore or mouth was observed, and no preliminary permanent flattening of the oral disc could be observed. Shape changes in all three larvae could be seen, but they were usually induced by mechanical stimulation and then occurred only very slowly. A general tendency for all to assume a tympanoid form was noted, that is, the vertical or oral axis of the larvae tended to become shorter with both the oral and aboral ends flattening. At no time during the period of observation did the larvae make any attempt to move except for the slow changes of shape mentioned. No swimming or floating of the larvae occurred.

No change in the behavior of the larvae was observed through the period of May 23 to 25, and there was no indication of attachment to the substrate or of skeletal secretion, although the larvae had assumed an upright position on the substrate. At 7.30 P.M. on May 25, the experiment was terminated because of high seas which made stabilization of

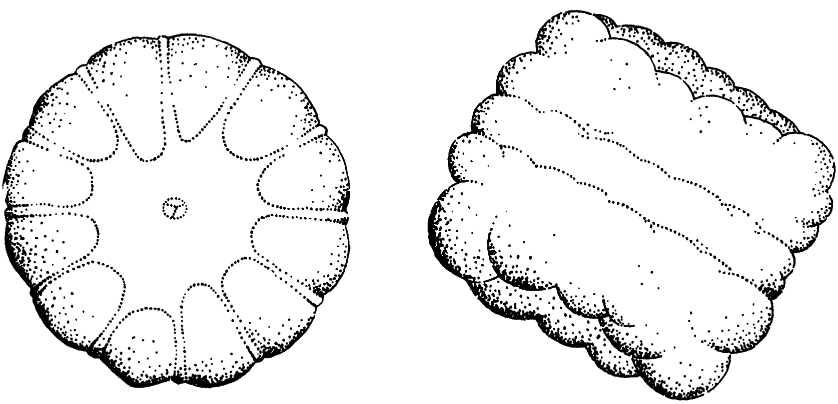

FIG. 3. Two views of larvae of *Flabellum curvatum* Moseley at an age of two days. The figure on the left shows the oral surface with the mouth opening and 12 bulbous projections representing the first two cycles of tentacles. The right-hand figure is a side view. Notice the indentations at both the oral and the aboral surfaces. Not to scale.

the aquaria impossible. At this time, the health of the larvae could not be determined satisfactorily. There seemed to be no perceptible motion in response to mechanical stimulation, although microscopic examination of the specimens was difficult and unreliable. Adult corals maintained under the same conditions were, however, in good condition and, only shortly before the end of observations, had responded vigorously to infusion of beef broth into the water.

Approximately 48 hours after extrusion, the larvae possessed well-defined, short tentacles, an oral disc, and a mouth. Mesenterial development has not been studied. There is no apparent skeletal material, and none was noted while the larvae were alive. The basal region of all specimens is highly concave, one specimen having a nearly conical, deep

TABLE 2

BREEDING ACTIVITY IN *Flabellum curvatum* MOSELEY, AS SHOWN BY THE PRESENCE OF YOUNG, LIVE CORALS ATTACHED TO OTHER SPECIMENS

(No data are available for the months of July, August, November, and December.)

Month of Collection	1925	1926	1927	1929	1932	1934	1938	1941	1955	1957	1958	1959	1961
January	—	—	0[a]	—	—	—	—	0	—	—	—	—	—
February	—	—	—	0	—	+	—	—	+	—	+	—	—
March	0	—	—	—	—	—	—	—	—	—	0	0	—
April	—	+	—	—	—	—	—	—	—	—	—	—	—
May	0	0	—	—	—	—	—	+	—	—	—	—	+
June	—	—	—	—	—	—	—	+	—	—	—	—	—
September	—	—	—	—	—	—	+	—	—	—	—	—	—
October	—	+	—	—	—	—	—	—	—	—	—	—	—

[a]*Symbols:* 0, immature corals absent; +, immature corals present.

TABLE 3

A COMPILATION OF DATA ON BREEDING PERIODICITY FOR SCLERACTINIAN CORALS (OBSERVATIONS OF SINGLE SPAWNING PERIODS NOT INCLUDED)

Species	Periodicity	Duration of Planulation	Free Life of Larvae	Source
Acropora bruggermanni	Through year, no periodicity	More or less continuously	A few days	Atoda, 1951a
Agaricia fragilis	Summer?	Late June and early July	1 day	Mayor, 1916
Balanophyllia sp.	(Several observations)	New moon	—	Abe, 1937
Cyphastrea ocellina	Probably through year	At 5–10-day intervals	2–10 days	Edmondson, 1946
Dendrophyllia manni	Late summer–early winter	Liberation continuous	1–21 days	Edmondson, 1946

TABLE 3—(*Continued*)

Species	Periodicity	Duration of Planulation	Free Life of Larvae	Source
Favia doryensis [a]	December and June?	—	—	Marshall and Stephenson, 1933
Fungia actiniformis var. *palawensis*	Monthly through year	Before and after new moon	2–3 days	Abe, 1937
Galaxea aspera	Through year, lunar?	Continuously, most active at last quarter	To 60 days, usually about 3 weeks	Atoda, 1951b
Goniastrea aspera	(Several observations)	New moon	16–23 days	Abe, 1937
Manicina areolata	(Single observation)	March through May	4 days (late spawned), 4–6 weeks	Wilson, 1888
Manicina areolata	Twice yearly, July and August	Two weeks, ending at new moon	Few days	Yonge, 1935
Pocillopora bulbosa	Yearly?, lunar?	Summer and early winter, new moons Winter, full moons	—	Marshall and Stephenson, 1933
Pocillopora damicornis	All year	—	1–18 days	Edmondson, 1946
Pocillopora damicornis caespitosa	Through year, lunar	1 week following new moon	2–3 days, up to 8	Atoda, 1947a
Porites haddoni	Through year	Continuous	—	Marshall and Stephenson, 1933
Seriatopora hystrix	Through year, lunar	15 days following new moon most active	1–4 days	Atoda, 1951c
Siderastrea radians	Summer?	Throughout July	1 week	Duerdan, 1904
Stylophora pistillata	Through year, lunar	Two weeks following full moon	Usually 1 day, up to 6 days	Atoda, 1947b

[a] Based on examination of the gonads.

depression in the basal disc. This condition is accentuated in the preserved larvae, but was also present in the living forms. Neither included bodies such as zooxanthellae nor pigmentation of the larvae was observed.

COMPARATIVE NOTES

In the following discussion, the larvae of *F. curvatum* are compared with other described scleractinian larvae. For this information, I have drawn upon the studies of Duerden, Edmondson, and particularly the Japanese workers Abe, Atoda, Kawaguti, Hada, and others. As the data given are generalized, specific references are not made, but the pertinent works of these authors are given in the bibliography and are cited in table 3.

Larvae of *F. curvatum* observed are strikingly different in behavior, morphology, and mode of extrusion from those of the reef corals. Each of these differences is considered, but, as most are dependent in some way on the age of the larvae under consideration, the reproductive periodicity of the species is considered first. One direct observation of planulation does not establish a pattern of periodicity. The advanced morphological development of the larvae suggests that they were spawned late in the planulation period. Many larvae are presumed to have been released prior to May 23, and, indeed, such activity is indicated by the large number of young coralla 1 or 2 mm. in height that were observed growing on other adults.

If small coralla of this sort are indicative of breeding activity within a period of approximately a month preceding the date of collection, it becomes possible to utilize collections in which adult coralla bear young, live coralla of a few millimeters in height as evidence of reproductive activity. The identification of these young corals poses no particular problem on the Argentine Shelf, for in most occurrences of the species, no other Scleractinia are present. An examination of the collections of *F. curvatum* in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires showed that some collections of adult *F. curvatum* had small coralla attached to their sides, and from these records the data presented in table 2 have been assembled. No clear pattern emerges, so that it is probable that breeding in *Flabellum curvatum* occurs throughout the year and that planulation may occur during any month.

Lunar periodicity of planulation has been shown for many species of reef corals, but it is not invariable, and, further, the maximum activity of planulation may be related to new moon, full moon, or the quarters, according to the species. (See table 3.) It would be premature to attempt an analysis of the periodicity in *F. curvatum* on such scanty information as is presented here. However, as a matter of information, it is here recorded that the phases of the moon during May, 1961, were: new moon, May 14, the full moon occurring May 1. Planulation was observed following the first quarter of the moon.

The advanced state of morphological development of the larvae suggests that they were among the last extruded by the polyps during that planulation cycle. Observations on the hermatypic coral *Manicina areolata* (Linnaeus) (Wilson, 1888; Squires, 1958) have shown that the larvae extruded early during the planulation cycle are in a less advanced stage of development than those extruded from the same parent polyp at a later time. The earliest extruded larvae are the longest lived, completing much of their development during a free swimming stage, while those liberated later, being older and more advanced, settle rapidly to the substrate and begin the secretion of a skeleton. Such a mechanism is efficient in the dispersal of a species, as it simultaneously provides for both distant and local colonization.

In general, most planulae are club-shaped, fusiform, or pyriform and may assume a wide variety of shapes in the course of their initial motion. Even advanced forms of the larvae of *Manicina areolata* (Linnaeus), liberated late in the planulation period, were of typical form (Wilson, 1888). Although there is considerable range in size, the larvae of most species are within a range of 1 to 3 mm. in length, the majority being small.

Larvae of *F. curvatum* are in contrast to the generalized type, apparently larger, at least in the late extruded forms, and lack the ciliated fusiform stage so characteristic of planulae. It can only be assumed, on the basis of this observation, that the discrepancies arise from the age of the larvae observed.

It has often been noted that larvae are extruded in large numbers, often accompanied by streams of mucous secretions, following a convulsive contraction of the polyp. The larvae then commonly float to the surface, or, should they sink, swim to the surface shortly thereafter. After this initial period, the larvae then sink or swim to the bottom, exhibiting a number of tropisms. In contrast, the larvae of *F. curvatum* were liberated with no conspicuous muscular activity on the part of the parent polyp, and the larvae remained dormant (and presumably were unable to swim), without showing any initial negative geotropism. Again, this latter behavioral aspect may result from the morphological character of the larvae. But the mode of extrusion is not so easily explained. A factor that has not been assessed is the shock of the dredging operation on the animal, which might have induced abnormal procedures during planulation.

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