Sexual Reproduction in Solitary Corals: Synchronous Gametogenesis and Broadcast Spawning in *Paracyathus stearnsii*

Y. H. Fadlallah and J. S. Pearse

Center for Coastal Marine Studies, University of California; Santa Cruz, California 95064, USA

Abstract

Samples of the temperate solitary coral *Paracyathus stearnsii* Verrill, 1869 were collected monthly or bimonthly from January 1977 to September 1978 off the Californian coast. This species is gonochoric and reproduces only sexually. Females produce a large number of small eggs (ca. 10^5 per polyp) in gametogenic synchrony and both sexes spawn between February and May. A small planktonic planula (ca. 160 μm long) develops following external fertilization. Broadcast spawning with planktonic development may be more common than previously assumed in scleractinians, and includes both lecithotrophic and planktotrophic larvae.

Introduction

Sexual reproduction in scleractinian corals remains poorly known despite being first studied by Lacaze-Duthiers (1873) in the brooding species *Astroides calycularis,* more than a century ago. Many coral workers focused their attention on ontogenesis (Wilson, 1888; Duerden, 1902, 1904; Mavor, 1915; Boschma, 1929; Abe, 1937; Durham, 1949). Others studied the timing of planulation and planula behavior before settlement and metamorphosis (Marshall and Stephenson, 1933; Atoda, 1953; Harrigan, 1972; Stimson, 1978; Rinkevich and Loya, 1979 b). Very little attention, however, has been given to most aspects of gametogenesis in corals.

Most early workers dealt with corals that brooded their embryos within the coelenteron, and it has been widely assumed that most or all scleractinian corals brood their embryos (e.g. Hyman, 1940; Vaughan and Wells, 1943; Wells, 1956). Heck and McCoy (1978), following this assumption, concluded that the biogeographical distribution of corals and coral reefs, and the recolonization of areas by corals could not be accounted for adequately by larval dispersal. However, several of the earlier studies also noted large numbers of eggs per polyp, spawning of eggs in the laboratory, and lack of evidence of planulation in the field for some species of corals (e.g. Wilson, 1888; Lacaze-Duthiers, 1897; Hargitt, 1914; Marshall and Stephenson, 1933); these observations suggest the presence of non-planulating species of corals. Moreover, contemporary ecological studies of reef corals have considered the possibility of patterns of reproduction other than those involving brooding the embryos. In particular, Stimson (1978) and Rinkevich and Loya (1979 b) predicted that some reef-building corals must broadcast gametes and have external fertilization with planktonic development. Recently, in fact, broadcast spawning with external development has been described for solitary, social, and reef-building species, including *Caryophyllia smithi* by Tranter *et al.* (in press), *Astrangia danae* by Szmant-Froelich *et al.* (1980), *A. lajollaensis* by Fadlallah (in press), and *Goniastrea* cf. *favulus* (as *G. australensis*), *Favites abdita*, *Leptoria phrygia* and *Porites andrewsi* by Kojis and Quinn (1981, 1982, and in press).

Most coral reef ecologists have stressed the asexual capabilities of reef-building corals and largely ignored the role of sexual reproduction. Solitary corals, however, reproduce only by sexual means, and in such species the mode and timing of larval production are particularly important life-history characteristics (Fadlallah, 1981). In this paper we document synchronous gametogenesis, timing of broadcast spawning, and external planktonic development for the solitary coral *Paracyathus stearnsii* Verrill, 1869 on the central California coast.

Materials and Methods

The study was conducted in the Hopkins Marine Life Refuge off Point Cabrillo, Pacific Grove, California (36°37.4'N; 121°54'W) at a depth of 7 to 13 m. Large granite outcrops in the study area were covered luxuriantly with sessile invertebrates and algae throughout the year

(Pearse and Lowry, 1974). Individuals of *Paracyathus stearnsii* Verrill, 1869 were found near the bottom of these outcrops as well as on the undersides of ledges, often within colonies of the social coral *Astrangia lajollaensis* Durham, 1947, with a mean density of 24.5 m^{-2} (standard error: 8.6, based on 49 randomly located 0.0625 m^{-2} quadrats taken in March 1978).

Samples of *Paracyathus stearnsii* were taken monthly or bimonthly from January 1977 to September 1978. Individuals were knocked off rocks located with randomly determined coordinates, relaxed in the laboratory in a 1:1 solution of 7% MgSO$_4$:seawater, preserved in 5 to 7% formalin in seawater for at least 3 d, then decalcified in a 10% solution of 12N HCl in distilled water. The decalcified polyps were washed in distilled water and stored in 70% ethanol. Parts of the decalcified polyps, each containing several septa, were dehydrated in an ethanol series, cleared in xylene, and embedded in Paraplast. Serial longitudinal sections, 4 to 10 μm thick, were prepared and stained with Harris' hematoxylin and eosin. Other septa were examined in wet preparations for oocyte counts and measurements.

For each sampling period, 5 to 10 female polyps were used to analyse oogenesis. Wet preparations of whole ovaries from 3 to 5 septa from each female were examined under a compound microscope. From each gonad 30 to 50 oocytes were measured with a calibrated ocular microm-eter; the oocytes usually were oval or rectangular in shape and the longest axis was measured. To evaluate the initial stages of oogenesis, small oocytes in histological sections were measured separately.

Within histological sections of testes, clusters of sperms (bouquets) could be distinguished from spermaries filled with earlier stages of spermatogenesis. To analyse male reproductive activity, the relative abundance of sperm clusters to earlier spermaries was determined for sections of 5 to 15 testes from males in each sample.

We produced externally fertilized embryos from eggs spawned by a female isolated in a finger bowl for 48 h and mixed with sperms from a dissected male. Other attempts to induce spawning by exposing corals to different temper-ature regimes, seawater dilutions, pH changes, and anoxic conditions all failed. Moreover, fertilization was not suc-cessful with eggs obtained by dissection.

Results

Reproductive System and Fecundity

The gonads of *Paracyathus stearnsii* are carried on all septa, 1 gonad per septum. Two septa, belonging to different septal cycles (determined by their order of ap-pearance), are sandwiched between each pair of sclero-septa (Fig. 1), and these septa are fused in many areas. The gonads occupy different radial and axial positions on different septa so that there is no overlap of gonadal tissues. Gonads of lower order (older) septa are longer and wider than those of higher order septa. The gonad of a
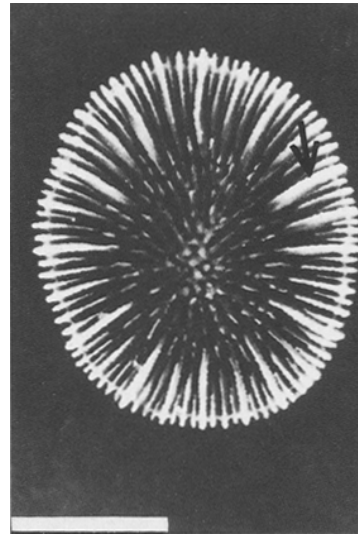

Fig. 1. *Paracyathus stearnsii*. Corallum showing arrangement of the sclerosepta. Sclerosepta of first-order primary cycle (arrow) project farthest into the center of the calice. The septa of the polyps (soft tissue which does not appear here) are usually inserted in pairs between 2 consecutive sclerosepta, and bear the gonads. Scale bar = 5 mm

lower order septum occupies a more central and basal position while that of the adjacent higher order septum usually occupies a higher and more peripheral position within the polyp.

The sex ratio among individuals of *Paracyathus stearnsii* did not appear to deviate from 1:1. For example, among 46 individuals collected on 4 March 1978 and dissected, 26 were females and 20 were males ($X^2 = 0.78$).

We counted all the oocytes in a pair of ovaries taken from a coral collected on 25 September 1978. The ovaries were dehydrated in an ethanol series and cleared in xylene, and the oocytes within each ovary were counted under a dissecting microscope. The lower order ovary (8.5 mm long) had 1 260 oocytes and the higher order ovary (4.5 mm) had 731 oocytes. Ten pairs of septa from the same specimen were inspected, and all had ovaries with similar size ranges (7 to 8 mm and 4 to 6 mm for lower and higher order ovaries, respectively) and similar sized oocytes (50 to 125 μm). The specimen, with a volume of 1 150 mm^3 and 50 pairs of septa, all reproductive, con-tained an estimated 100 000 oocytes.

Gametogenesis

Individuals of *Paracyathus stearnsii* had an annual cycle of oogenesis (Figs. 2 and 3). Synchrony among ovaries both within and among females was very close. Small oocytes (5 to 20 μm diam) appeared in January and February, and predominated in March, just before or just after most ovaries were spent. Oocyte growth and increase in ovarian thickness proceeded through spring, summer and fall. Ovaries were filled with large oocytes (100 to 175 μm) by
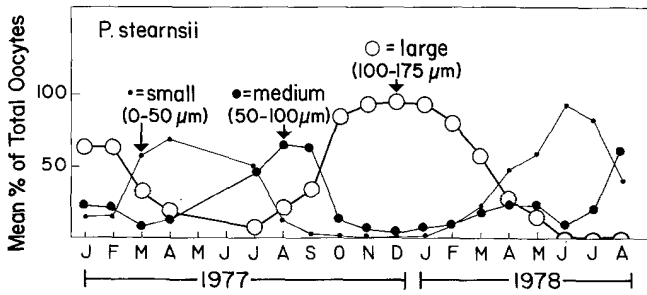
Fig. 2. *Paracyathus stearnsii.* Seasonal changes in proportions of 3 size classes of oocytes. An average of 8 (range 5 to 20) individuals were dissected and 310 (range 36 to 741) oocytes were measured for each sample

October. The large oocytes remained in the ovaries for 2 to 3 mo, and spent ovaries did not appear until February. All ovaries were spent by May; spawning therefore occurred from February to May.

The spermatogenic cycle closely paralleled the oogenic cycle (Figs. 4 and 5). Spawned testes were first seen in

March and spawning was completed by May. New spermatogonial clusters appeared in June. Gonadal build-up continued from June to December with spermaries filled with spermatocytes appearing first, followed by spermaries filled with spermatids. Spermaries filled with sperms (bouquets) first appeared in a few clusters in July and they increased in number until December when nearly all the clusters were filled with sperms. The clusters continued to increase in size, many fusing together, until March, just before spawning.

Spawning and Development

Individuals of *Paracyathus stearnsii* were never found with embryos within their bodies. Moreover, released planulas were not seen at any time of the year. Spawning of gametes was observed only twice: (1) when a female released eggs in the laboratory in March 1979 after being
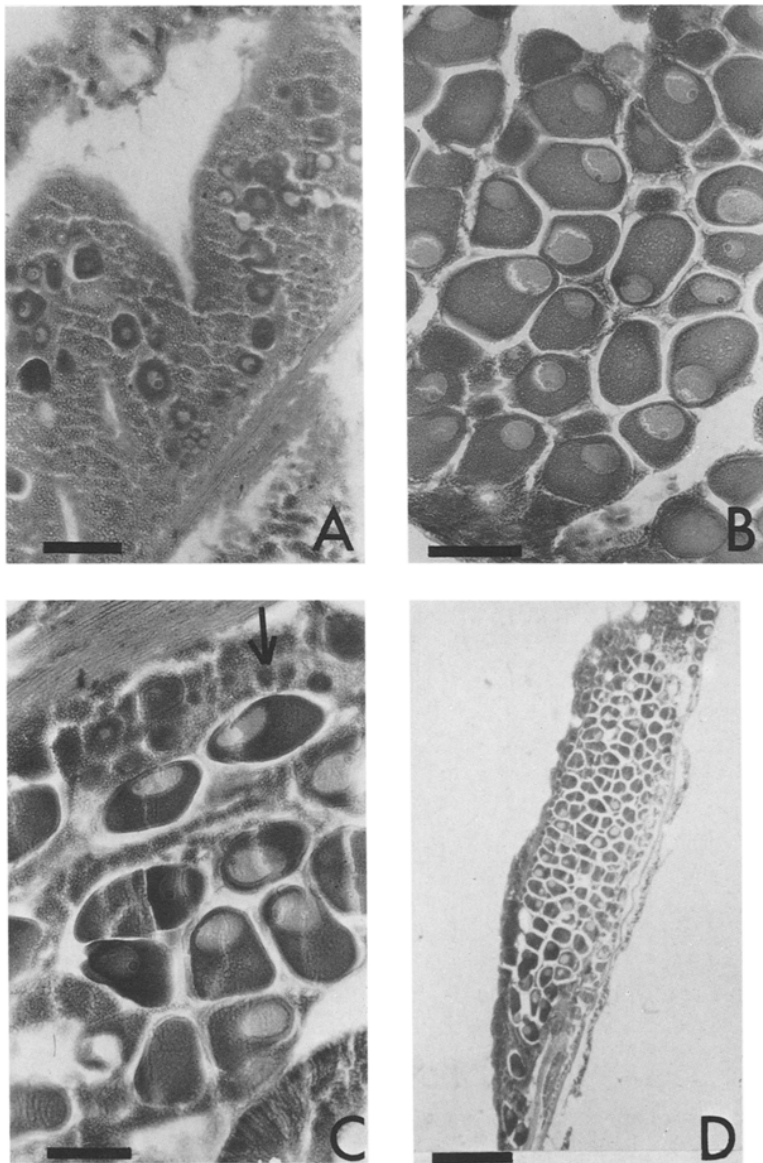

Fig. 3. *Paracyathus stearnsii.* Photomicrographs of sections of ovaries in different stages of development. (A) Cohort of small new oocytes in May; (B) part of an ovary filled with similar-sized large oocytes in October; (C) large oocytes immediately before spawning in February, note also numerous small oocytes (arrow); (D) longitudinal section through a ripe ovary filled with full-grown oocytes in February. Scale bars = 100 μm in (A)–(C), 00 μm in (D)
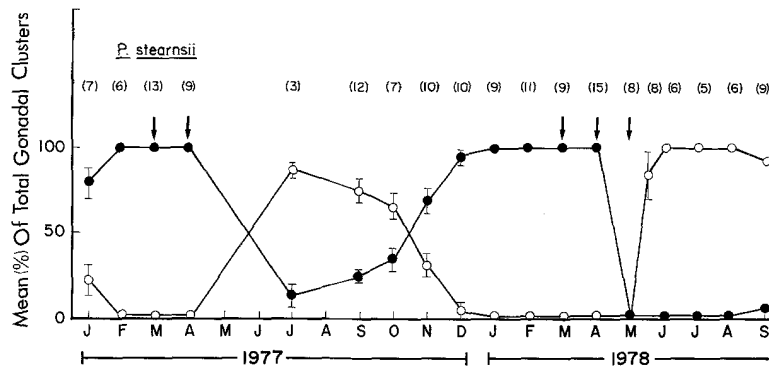
Fig. 4. *Paracyathus stearnsii*. Mean percentages (± SD) of spermaries filled with sperms ("bouquets"-filled circles) and other spermaries with spermatids and spermatocytes (open circles) in testes. Arrows indicate presence of partially or fully spent testes. Number of testes examined in each sample is given in parentheses
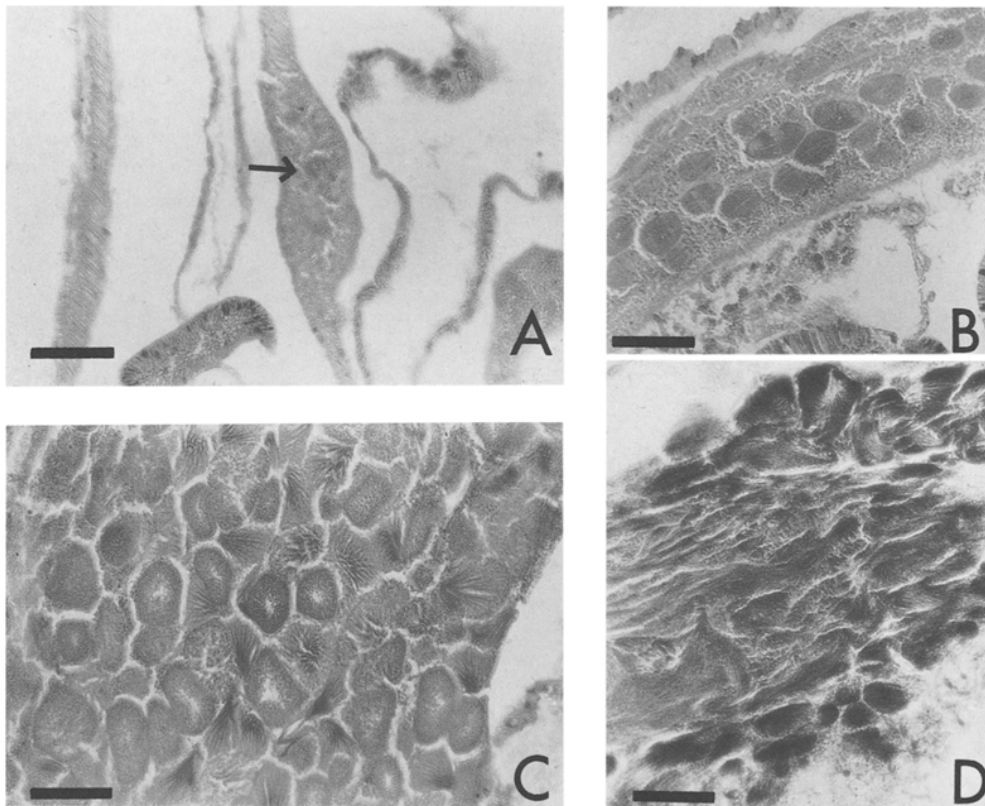

Fig. 5. *Paracyathus stearnsii*. Photomicrographs of sections of testes at different stages of development. (A) Immature testis in May with barely discernable spermaries (arrow) with spermatocytes; (B) testis with larger spermaries in July containing spermatocytes and spermatids; (C) spermaries in September at different stages of development, including some "bouquets" filled with sperms; (D) spermaries in February filled with sperms, many spermaries completely dispersed. Scale bars = 100 μm

isolated for 48 h in a finger bowl, and (2) when females spawned eggs in a glass jar within an hour of collection on 16 March 1980.

Artificial fertilization was successful only when eggs were spawned freely. The eggs released by the female isolated in the laboratory settled on the bottom of the finger bowl. These were collected in a pipette and mixed with sperms taken from a dissected male. A day later many of the eggs had developed into round ciliated embryos rotating on the bottom of the bowl, and by the second day these were planulas swimming freely through

the water. The planulas were bullet-shaped, 160 μm long, and covered with long flagella (20 to 30 μm) (Fig. 6). The oral end (posterior end during forward motion) had a depression that appeared to be the ectodermal invagination of the future mouth; the coelenteron appeared to be filled with a mass of cells or vacuoles. We could not determine whether the coelenteron opened through the oral depression. Septa were not seen. The planulas swam about rapidly with classical planular patterns of stop-and-go swimming, flagellary reversal and backward swimming, spiral swimming, and stopping on contact with surfaces
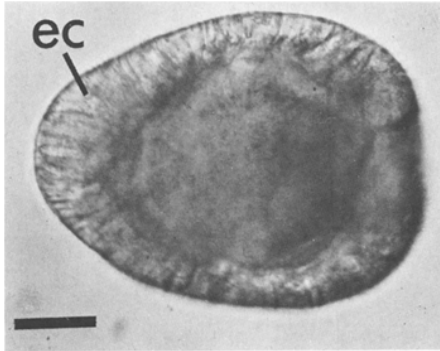
Fig. 6. *Paracyathus stearnsii.* Swimming planula 3 d after fertilization. Probable oral pore and stomodeal invagination are on flattened (posterior) end. Nematocysts are concentrated in the thickened ectoderm (ec) of the anterior end. Scale bar = 40 μm

(see Harrigan, 1972; and Rinkevich and Loya, 1979a). Of the more than 50 planulas obtained, a few persisted for up to 4 wk before perishing. None settled.

Discussion

The highly synchronized gametogenic cycle we found for *Paracyathus stearnsii* in central California leads to spawning in late winter and early spring. The resulting swimming planulas presumably would be swept into the plankton and dispersed widely. Many other species in central California also have restricted winter-spring spawning periods, including those of echinoderms (Giese, 1959), prosobranchs (Webber, 1977), and chitons (Pearse, 1979). The late winter spawning period corresponds with the end of the Davidson Countercurrent (November–February) and the beginning of the upwelling period (February–June) (Broenkow and Smethie, 1978; Garrison, 1979). These oceanographic features may include conditions that favor larval survival in late winter and early spring, such as current regimes favorable for larval retention in nearshore waters or the production of phytoplankton used by larvae as food. It is not known whether the planulas of *P. stearnsii* are planktotrophic, but many other species with late winter spawning in central California do not have feeding larvae (e.g. chitons, limpets). Moreover, the other species of solitary corals common along the shores of central California, *Balanophyllia elegans,* releases large, crawling, non-feeding planulas mainly in the winter, and these seem independent of both phytoplanktonic food and dispersive currents (Fadlallah and Pearse, 1982). That both *P. stearnsii* and *B. elegans* produce such different forms of larvae during the same late winter period indicates that the conditions restricting spawning times act not on larvae, but rather in some way on juvenile recruitment and survival, or the reproductive capacity of the adults.

Paracyathus stearnsii is one of two strictly solitary corals known to have broadcast spawning and external fertilization. The other species, *Caryophyllia smithi,* was found by Tranter *et al.* (in press) to have planktotrophic

planulas that swim and grow for 8 to 10 wk before settling. Szmant-Froelich *et al.* (1980) also reported spawning and successful laboratory fertilization in the asexually reproducing temperate coral *Astrangia danae. A. lajollaensis* at our study site similarly produces numerous small eggs and almost certainly is a broadcast spawner (Fadlallah, in press).

The planulas produced by *Astrangia danae* and *Paracyathus stearnsii* are among the smallest known among scleractinians (75×45 μm and 160×95 μm, respectively), apparently even smaller than those produced by *Caryophyllia smithi,* and seem closest to Chia's (1976) oviparous-pelagic-planktotrophic category for actinian planulas. Unlike all other coral planulas that have been described, they failed to settle in the laboratory. Among other coral planulas, only those of *C. smithi* were fed (ground pieces of prawn). It seems certain that the planulas of *A. danae* and *P. stearnsii* require food as well.

Reports of probable broadcast spawning in scleractinian corals date from the 19th century. Wilson (1888) and Duerden (1902) found that *Manicina areolata* extruded eggs and sperms in the laboratory. Wilson noted, however, that the eggs underwent irregular cleavages and eventually broke apart, and Duerden discounted the phenomenon as an aberration. Hargitt (1914) obtained eggs spawned by *Astrangia danae* in midsummer, but was unable to promote development. Seasonal, synchronous production of eggs and sperms was described for *Favia pallida* (= *doreyensis*) by Marshall and Stephenson (1933). Egg size (305 to 374 μm greatest diam), egg number per gonad, gametogenic synchrony, sudden disappearance of the gametes, and lack of embryos in the coelenteron all strongly suggested broadcast spawning and external development. Although their data for other large-polyp corals were less informative about mode of reproduction, *Symphyllia recta* and *Lobophyllia* sp. also seem to be broadcast spawners.

Authors who have examined numerous species of corals report the absence of planulation in many. Marshall and Stephenson (1933), for example, monitored planulation in 10 species of corals on the Great Barrier Reef, but only two species produced planulas. Atoda (1974) noted that over a period of 4 yr he could obtain planulas from only 10 of over 100 species of corals in Iwayama Bay, Palao (Belau). Stimson (1978) also reported an absence of planulation in many corals he examined in Hawaii and Enewetak; only 2 of 7 Hawaiian and 7 of 12 Enewetak species planulated.

Connell (1973) noted that high fecundity probably indicates external development, as seemed to be the case for *Favia pallida* described by Marshall and Stephenson (1933). Rinkevich and Loya (1979a) further proposed that reef corals with massive colonies, large polyps, and numerous eggs developing within the septa would have high fecundities and be broadcast spawners with external development. In contrast, branching, small-polyp corals with lower fecundities might increase the survival rate of their offspring by brooding embryos to relatively late

stages of development. In support of this proposal, they reported that the branching coral *Stylophora pistillata* broods embryos and releases swimming planulas while the massive coral *Favia favus* was seen to release large numbers of pinkish-red eggs into the water. Moreover, Shlesinger (cited by Rinkevich and Loya, 1979 a) did not find planulas within the polyps of *F. favus* during a 2 yr study, and plankton nets placed over colonies every month for 1 yr failed to trap planulas. In a more extended survey, Rinkevich and Loya (personal communication) found that the majority of the hermatypic corals in the Gulf of Aqaba probably do not brood their embryos but freely spawn both eggs and sperms. Similarly, Kojis and Quinn (1982) reported that several species of the massive faviids on the Great Barrier Reef broadcast eggs and sperms in "gonad spheres", and they suggested that external development may be the dominant mode of sexual reproduction in hermatypic corals.

Rinkevich and Loya (1979 a) proposed that massive, large polyp, colonial, broadcasting corals, such as *Favia favus* might be expected to produce relatively large eggs and have lecithotrophic development. Other massive, large polyp, colonial faviids, including *Goniastrea* cf. *favulus*, *Favites abdita* and *Leptoria phrygia*, were recently observed spawning large (about 400 to 500 μm diameter) eggs that clumped together and adhered to substrates where at least those of *G.* cf. *favulus* developed into planulas (Kojis and Quinn, 1981, 1982). In contrast, the solitary corals *Caryophyllia smithi* and *Paracyathus stearnsii*, and the small, social corals *Astrangia danae* and *A. lajollaensis* produce numerous, small eggs (100 to 200 μm diam) that almost certainly develop into planktotrophic planulas. Among other solitary corals, *Balanophyllia elegans* and *Astroides calycularis* produce relatively few eggs that are brooded to be released as very large crawling planulas (Fadlallah and Pearse, 1982). Relative to colonial corals, solitary and social corals will always have low fecundities. Consequently, they may be selected to reproduce at opposite extremes of the various modes of sexual reproduction and either (1) produce relatively few large embryos that are nourished and protected by the parent until they are released as planulas ready to settle, thereby minimizing both larval mortality and larval dispersion, or (2) produce relatively large numbers of small planulas that are neither nourished nor protected by the parent, and are dispersed widely but suffer high mortalities. Individuals of *B. elegans*, of the first category, are short-lived (6 to 11 yr: Fadlallah, 1981) and can be locally very abundant. In contrast, individuals of *P. stearnsii*, of the second category, are usually rather scarce and may be extremely long-lived, with estimated ages in excess of 40 yr (Gerrodette, 1979), further increasing their life-time fecundity.

Literature Cited

Abe, N.: Postlarval development of the coral *Fungia actiniformis* var. *palawensis* Doderlein. Palao trop. biol. Stn Stud. *1,* 73–93 (1937)

Atoda, K.: The larva and postlarval development of some reef-building corals. I. *Pocillopora damicornis* (Dana). Sci. Rep. Tôhoku Univ. (Ser. 4) *18,* 24–47 (1947)

Atoda, K.: The larva and postlarval development of the reef-building corals. Sci. Rep. Tôhoku Univ. (Ser. 4) *20,* 105–121 (1953)

Boschma, H.: On the postlarval development of the coral *Maeandra areolata* (L.). Pap Tortugas Lab. *26,* 128–147 (1929)

Broenkow, W. W. and W. M. Smethie, Jr.: Surface circulation and replacement of water in Monterey Bay. Estuar. cstl mar. Sci. *6,* 583–603 (1978)

Chia, F.-S.: Sea anemone reproduction: patterns and adaptive radiations. *In:* Coelenterate ecology and behavior, pp 261–270. Ed. by G. O. Mackie. New York: Plenum Press 1976

Connell, J. H.: Population ecology of reef corals. *In:* Biology and geology of coral reefs, Vol 2, Biol. 1, pp 205–245. Ed. by O. A. Jones and R. Endean. New York: Academic Press 1973

Duerden, J. E.: West Indian madreporarian polyps. Mem. natn. Acad. Sci. *8,* 401–597 (1902)

Duerden, J. E.: The coral *Siderastrea radians* and its postlarval development. Publs Carnegie Instn *20,* 1–129 (1904)

Durham, J. W.: Ontogenetic stages of some simple corals. Univ. Calif. Publs Bull. Dep. Geol. *28,* 137–172 (1949)

Fadlallah, Y. H.: The reproductive biology of three species of corals from central California, 193 pp. Ph.D. thesis, University of California, Santa Cruz 1981

Fadlallah, Y. H.: Reproductive ecology of the coral *Astrangia lajollaensis:* sexual and asexual patterns in a kelp forest habitat. Oecologia (In press)

Fadlallah, Y. H. and J. S. Pearse: Sexual reproduction in solitary corals: overlapping oogenic and brooding cycles, and benthic planulas in *Balanophyllia elegans.* Mar. Biol. *71,* 223–231 (1982)

Garrison, D. L.: Monterey Bay phytoplankton. I. Seasonal cycles of phytoplankton assemblages. J. Plankton Res. *1,* 241–265 (1979)

Gerrodette, T.: Ecological studies of two temperate solitary corals, 112 pp. Ph.D. thesis. University of California, San Diego 1979

Giese, A. C.: Reproductive cycles of some west coast invertebrates. *In:* Photoperiodism and related phenomena in plants and animals, pp 625–638. Ed. by R. B. Withrow. Washington D.C.: American Association for the Advancement of Science 1959. (Publs Am. Ass. Advmt Sci. No. 55)

Hargitt, C.: The Anthozoa of the Woods Hole Region. Bull. Bur. Fish., Wash. *32* (788), 225–253 (1914)

Harrigan, J. F.: The planula larva of *Pocillopora damicornis.* Lunar periodicity of swarming and substratum selection behavior, 319 pp. Ph.D. thesis, University of Hawaii, Honolulu 1972

Heck, K. L., Jr. and E. D. McCoy: Long-distance dispersal and the reef-building corals of the eastern Pacific. Mar. Biol. *48,* 349–356 (1978)

Hyman, L. H.: The invertebrates. Vol. I. Protozoa through Ctenophora, 726 pp. New York: McGraw-Hill 1940

Kojis, B. L. and N. J. Quinn: Aspects of sexual reproduction and larval development in the shallow water hermatypic coral *Goniastrea australensis* (Edwards and Haime, 1857). Bull. mar. Sci. *31,* 558–573 (1981)

Kojis, B. L. and N. J. Quinn: Reproductive ecology of two faviid corals (Coelenterata: Scleractinia). Mar. Ecol. Prog. Ser. *8*, 251–255 (1982)

Kojis, B. L. and N. J. Quinn: Reproductive strategies in four species of *Porites* (Scleractinia). Proc. 4th int. Symp. coral Reefs (Ed. by E. Gomez. Manila, Philippines, May 1981). (In press)

Lacaze-Duthiers, H. de: Développement des coralliaires. actiniaires à polypiers. Archs Zool exp. gén. *2*, 269–348 (1873)

Lacaze-Duthiers, H. de: Faune du Golfe du Lion. Coralliaires zoanthaires sclerodermes. Archs Zool. exp. gén. (sér 3) *5*, 1–249 (1879)

Marshall, S. M. and T. A. Stephenson: The breeding of reef animals. Part I. The corals. Scient. Rep. Gt Barrier Reef Exped. *3*, 219–245 (1933)

Mavor, J. W.: On the development of the coral *Agaricia fragilis* Dana. Proc. Am. Acad. Arts Sci. *51*, 485–511 (1915)

Pearse, J. S.: Polyplacophora. *In:* Reproduction of marine invertebrates, Vol. V. pp 27–85. Ed. by A. C. Giese and J. S. Pearse. New York: Academic Press 1979

Pearse, J. S. and L. F. Lowry (Eds.): An annotated species list of the benthic algae and invertebrates in the kelp forest community at Point Cabrillo, Pacific Grove, California. Tech. Rep. Cent. cstl mar. Stud. Univ. Calif. S Cruz *1*, 1–73 (1974)

Rinkevich, B. and Y. Loya: The reproduction of the Red Sea coral *Stylophora pistillata.* I. Gonads and planulae. Mar. Ecol. Prog. Ser. *1*, 133–144 (1979 a)

Rinkevich, B. and Y. Loya: The reproduction of the Red Sea coral *Stylophora pistillata.* II. Synchronization in breeding and seasonality of planula shedding. Mar. Ecol. Prog. Ser. *1*, 145–152 (1979 b)

Stimson, J. S.: Mode and timing of reproduction in some common hermatypic corals from Hawaii and Enewetak. 'Mar. Biol. *48*, 173–184 (1978)

Szmant-Froelich, A., P. Yevich and M. E. Q. Pilson: Gametogenesis and early development of the temperate coral *Astrangia danae* (Anthozoa: Scleractinia). Biol. Bull. mar. biol. Lab., Woods Hole *158*, 257–269 (1980)

Tranter, P. R. G., D. N. Nicholson and D. Kinchington: A description of the spawning and post-gastrula development of the cool temperate coral *Caryophyllia smithi* (Stokes & Broderip). J. mar. biol. Ass., U.K. (In press)

Vaughan, T. W. and J. W. Wells: Revision of the suborders, families and genera of the Scleractinia. Spec. Pap. geol. Soc. Am. *44*, 1–336 (1943)

Webber, H. H.: Gastropoda: Prosobranchia. *In:* Reproduction of marine invertebrates, Vol. IV. pp. 1–97. Ed. by A. C. Giese and J. S. Pearse. New York: Academic Press 1977

Wells, J. W.: Scleractinia. *In:* Treatise on invertebrate paleontology, pp 328–444. Ed. by R. C. Moore. New York: Geological Society of America and University of Kansas Press 1956

Wilson, H. V.: On the development of *Manicina areolata.* J. Morph. *2*, 191–253 (1888)