

Reproduction and Recruitment in Corals: Critical Links in the Persistence of Reefs

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Each chapter in this book deals with factors that can shift the balance from processes supporting coral-reef growth and development to those that result in reef degradation. Reproduction and recruitment are among the critical processes upon which the persistence of coral reefs depends. Reproduction is the process by which new individuals are formed. Recruitment is the process by which newly formed individuals become a part of the reef community. This distinction is important, as it is possible to have successful reproduction, with healthy larvae, tissue fragments, or other types of seed material being produced, but eventual death of a coral-reef community if these new individuals are unable to find appropriate substrata for settlement, or if conditions prevent growth, maturation, and survival.

This chapter will describe the methods by which corals reproduce, how coral larvae are formed and develop, the factors that affect site selection, settlement, and metamorphosis in coral larvae, and how particular problems can affect the success of both reproduction and recruitment. By studying the biology of coral reproduction and recruitment, we gain an understanding of how it is possible to slowly degrade a reef, through the interruption of the critical processes that replenish populations of these important organisms. This understanding is of central importance to coral-reef management and preservation. Whether a reef is killed quickly by sedimentation or slowly through reproductive or recruitment failure, the result is the same: the loss of the beauty, economic and cultural value, and benefits that coral reefs provide.

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8.1. Coral Reproduction

Corals reproduce both asexually and sexually. Asexual reproduction in corals includes several processes by which one coral colony forms additional colonies through the separation of tissue-covered fragments, or through the shedding of tissue alone. Sexual reproduction is more complex, and requires the fusion of two gametes, egg and sperm, to form embryos that develop into free-swimming planula larvae. Asexual and sexual processes are not mutually exclusive; species and/or individuals may produce "offspring" both ways within the same time period. The products of the two types of reproduction can differ both physically and ecologically.

8.1.1. Asexual Reproduction

In discussing asexual reproduction in corals, it is helpful to separate colony growth from the formation of new colonies. Most reef-building stony corals are true colonies, made up of hundreds to thousands of interconnected polyps. Colonies grow through the asexual process of budding, during which new polyps form. Additional polyps can form when one polyp divides into two (intratentacular budding), or sometimes a new mouth with tentacles can simply form in the space between two adjacent polyps (extratentacular budding). If the polyps and tissue formed by these asexual processes remain attached to the parent colony, the result is considered growth and is seen as an increase in colony size. If polyps or buds become detached from the parent colony and give rise to new colonies, we consider this to be asexual reproduction, that is, the direct formation of new individuals from prior stock.

New coral colonies can be formed asexually in several ways. Fragmentation is common among finely branched or relatively thin plating corals (Highsmith, 1982). Coral fragments, including the underlying skeleton, may become detached from parent colonies as a result of wave action, storm surge, fish predation on associated animals, or other sources of physical impact. If a fragment lands on a solid bottom, it may fuse to the surface and continue to grow through budding. Many fragments generated by storms roll around, eventually losing their thin covering of coral tissue, and do not succeed in becoming new colonies, that is, they do not recruit (Knowlton et al., 1981).

Pieces of living tissue may leave the underlying coral skeleton, and through the use of cilia that cover the outer surface, swim and drift in the water column until coming into contact with an appropriate surface for settlement and attachment. This process has been referred to as polyp bailout (Sammarco, 1982b), as polyps appear to actively leave their skeletons. In a similar process, balls of coral tissue may remain on an otherwise dead skeleton, or may ooze out of the coral calices and later differentiate into coral polyps and begin secreting a calcareous skeleton (Rosen and Taylor, 1969; Highsmith, 1982; Krupp et al., 1993). Sections

taken through coral colonies, particularly massive forms, often reveal periods of growth, diebacks, and regrowth over a previous skeletal base. For this reason, colony diameter may not always be a reliable measure of age (Hughes and Jackson, 1980).

It is also possible that coral larvae may arise from unfertilized eggs, through a process known as parthenogenesis (Stoddart, 1983). While eggs are produced, they are not fertilized by sperm, but develop directly. This asexual mechanism for production of embryos has been observed in plants and many clonal organisms.

Asexual reproduction results in the production of offspring that are genetically identical to the parent. As long as conditions remain the same, the offspring will enjoy the same level of success that the parent colonies had. In reality, the physical and biological aspects of coral-reef communities vary. Seawater temperatures may change because of El Niño events, predators may evolve new feeding habits, a new disease may appear, or a new competitor may immigrate to the reef. A population with no genetic variability is vulnerable to changes in the physical or biological components of the environment. Another disadvantage of asexual reproduction in corals is that fragments, residual tissues, and some shedded tissues have limited dispersal abilities. The distribution of offspring is important to the success of coral populations and coral reefs.

8.1.2. Sexual Reproduction

Unlike asexual reproduction, which produces exact copies of the parent, sexual reproduction offers two opportunities for new genetic combinations to occur: (1) crossing over during meiosis in the formation of eggs and sperm, and (2) the genetic contribution of two different parents when an egg is fertilized by a sperm. These serve to add genetic variation to populations, which may lead to enhanced survival of a species. In corals, the resulting embryo develops into a ciliated planula larva. Planulae are particularly well adapted for dispersal and can seed the reef of origin, nearby reefs, or reefs hundreds of kilometers away (Richmond, 1987, 1990).

8.1.3. Gonochorism Versus Hermaphroditism

If a species has separate males producing sperm and females producing eggs, it is said to be gonochoric. The term *dioecious* is also used, but it is more appropriate for plants. If, however, a single individual of a species is capable of producing both eggs and sperm, it is said to be hermaphroditic. This term originates from Greek mythology, in which Hermes was the male messenger god, and Aphrodite was the goddess of beauty. The joining of these two names is used to describe organisms that have both male and female function within the same individual.

Approximately 25% of the coral species studied to date (e.g., species of *Porites* and *Galaxea*) are gonochoric (Harrison and Wallace, 1990). The identification

of separate sexes in corals is sometimes confused by the fact that it takes eggs longer to develop than sperm; hence a study early in the gametogenic cycle may lead to the conclusion that a coral is female, since no sperm would be seen until later in the year. Additionally, individual colonies of some species are distinctly male or female, while other colonies of the same species may be hermaphroditic (Chornesky and Peters, 1987; Harrison and Wallace, 1990). These cases may represent reproductive plasticity, or in some cases, differences at the species level.

If an organism has both ovaries for producing eggs and testes for producing sperm at the same time, it is called a simultaneous hermaphrodite. If, on the other hand, an individual is a functional male first, then develops into a female later (protandry), or is initially female, eventually changing into a male (protogyny), it is a sequential hermaphrodite. Corals display the full range of sexual characteristics, with the majority of species studied so far identified as simultaneous hermaphrodites (e.g., most acroporids, faviids, and some pocilloporids). A few species have been found to be sequential hermaphrodites (e.g. *Stylophora pistillata* and *Goniastrea favulus*; Rinkevich and Loya, 1979b; Kojis and Quinn, 1981), while others are gonochoric.

Hermaphroditism is particularly favorable in small populations, as it ensures sexual partners will be present if there are more than two individuals. If self-fertilization is possible, a single simultaneous hermaphrodite is capable of sexual reproduction and at least taking advantage of the genetic variation introduced during the crossing-over phase of meiosis.

8.1.4. Brooding Versus Spawning

Corals display two distinct modes of reproduction that differ in the way the gametes come into contact with each other. In brooding species, eggs are fertilized internally, with the embryo developing to the planula stage inside the coral polyp. Alternatively, spawning species release eggs and sperm into the water column, where subsequent external fertilization and development take place. The differences between the two modes of reproduction influence many aspects of coral ecology, including the transfer of symbiotic algae to the larvae, larval competency (the period during which larvae possess the ability to successfully settle and metamorphose), dispersal of larvae, biogeographic distribution patterns, genetic variability, and even rates of speciation and evolution (Richmond, 1990). Also, spawned gametes that float to the surface may be more vulnerable to the effects of pollutants often found in the surface layer in coastal waters.

Planula larvae released from brooding corals are immediately competent, that is, capable of settlement and metamorphosis. Brooded larvae are generally larger than spawned larvae, and in hermatypic (reef-building) corals, contain a full complement of symbiotic zooxanthellae from the parent colony (Fig. 8-1). It has been demonstrated that zooxanthellae contribute metabolites to the larvae, giving them additional energy sources to promote long-distance dispersal



Figure 8-1. Planula larva of *Pocillopora damicornis* with bands of symbiotic zooxanthellae.

(Richmond, 1987, 1988). Nevertheless, the ability to immediately settle results in some brooded planulae attaching to the substrata within centimeters of the parent colony.

Brooders, sometimes referred to as planulators, represent only a small portion of the corals studied, perhaps 15%. The pan-Pacific coral *Pocillopora damicornis* releases brooded planulae on a lunar cycle monthly, throughout the year, on the reefs of Micronesia and Hawaii (Richmond and Jokiel, 1984; Jokiel, 1985). This same species releases larvae only a few months per year in Okinawa and in western Australia (Stoddart and Black, 1985; Richmond and Hunter, 1990). *Pocillopora damicornis* has also been reported to spawn in the eastern Pacific and western Australia, raising questions about the taxonomy of corals that look alike but demonstrate differences in reproductive characteristics (Glynn et al., 1991; Ward, 1992).

For over 250 species of corals already studied, the majority (perhaps 85%) are spawners (Table 8-1), many of which participate in multispecies mass-spawning events during limited periods each year (Fadlallah, 1983; Harrison et al., 1984; Harrison and Wallace, 1990; Richmond and Hunter, 1990). In Okinawa, most spawning species release their gametes over a 5-8-day period commencing

Table 8-1. Reproductive Characteristics of Corals from the Caribbean Sea, Hawaii, Central Pacific, Eastern Pacific, Indo-West Pacific, Great Barrier Reef, and Red Sea

Caribbean				
Coral	Sex	Mode	Season	Source
<i>Acropora cervicornis</i>	H(pg)	S	sr	1,6,29
<i>Acropora palmata</i>	H(pg)	S	sr	6,29
<i>Agaricia agaricites</i>	H	B	sp-yr	1,10
<i>Agaricia fragilis</i>	x	B	sr	13
<i>Agaricia crassa</i>	x	B	sp	13
<i>Dendrogyra cylindris</i>	G(pg)	S	sr	6,29
<i>Diploria strigosa</i>	H(pg)	S	sr	6,7
<i>Favia fragum</i>	H	B	sp-yr	1,6,10
<i>Isophyllia</i> sp.	G?	B	sp	1
<i>Manicina areolata</i>	H	B	sp	1
<i>Meandrina</i> sp.	x	B	sp	1
<i>Montastrea annularis</i>	H(pg)	S	sr	6,29
<i>Montastrea cavernosa</i>	G(pg)	S	sr	6,29
<i>Mycetophyllia ferox</i>	H(pg)	B	w-sp	6,29
<i>Porites astreoides</i>	H(s)	B	sp-yr	1,6,10
<i>Porites porites</i>	G?	B	w-sp	1
<i>Siderastrea radians</i>	G	B	yr	1,6,10
<i>Siderastrea siderea</i>	G	S	sr	6
6G:9H:3? 11B:7S				
Pacific Corals				
Hawaii				
<i>Acropora cytherea</i>	H	*	*	12
<i>Acropora humilis</i>	H	*	*	12
<i>Acropora valida</i>	H	*	*	12
<i>Cyphastrea ocellina</i>	x	B	yr	13
<i>Dendrophyllia manni</i>	x	B	sr-f	1
<i>Fungia scutaria</i>	G	S	sr	15
<i>Montipora verrucosa</i>	H	S	sr	10
<i>Pocillopora damicornis</i>	H	B	yr	16,17
<i>Porites lutea</i>	G	S	sr	10
<i>Tubastrea aurea</i>	x	B	sr-f	1,10
2G:5H:3? 4B:3S				
Central Pacific (Guam, Marshall Islands, Palau)				
<i>Acrhelia horrescens</i>	x	B	yr	20
<i>Acropora bruggemanni</i>	x	B	x	18
<i>Acropora cerealis</i>	H	x	sr	14
<i>Acropora corymbosa</i>	x	B	sr	13
<i>Acropora humilis</i>	x	B	sr	13
<i>Acropora hystrix</i>	H	x	sr	14
<i>Acropora irregularis</i>	H	S	sr	10
<i>Acropora nasuta</i>	H	S	sr	10
<i>Acropora palawensis</i>	x	B	x	19
<i>Acropora smithi</i>	H	x	sr	14
<i>Acropora</i> sp.	H	S	sr	10
<i>Acropora striata</i>	x	B	w	13
<i>Acropora tenuis</i>	H	S	sr	10
<i>Acropora valida</i>	H	x	sr	14

Continued

Table 8-1. Continued

	Sex	Mode	Season	Source
Central Pacific (Guam, Marshall Islands, Palau) Continued				
<i>Euphyllia glabrescens</i>	x	B	x	20
<i>Favia mathaii</i>	H	x	sr	14
<i>Favites abdita</i>	H	x	sr	14
<i>Favites flexuosa</i>	H	x	sr	14
<i>Fungia actiniformis</i>	H?	B	yr	21
<i>Fungia fungites</i>	G	x	sr	14
<i>Galaxea apera</i>	x	B	yr	23
<i>Goniastrea aspera</i>	x	B	f	21
<i>Goniastrea edwardsi</i>	H	x	sr	14
<i>Goniopora queenslandiae</i>	G	B	sr	1
<i>Leptoria phrygia</i>	H	x	sr	14
<i>Platygyra pini</i>	H	x	sr	14
<i>Pocillopora damicornis</i>	H	B	yr	13,17
<i>Pocilloporaelegans</i>	x	B	sr	13
<i>Pocillopora verrucosa</i>	x	B	yr	13
<i>Porites lutea</i>	G	x	sr	14
<i>Seriatopora hystrix</i>	x	B	yr	13
<i>Strylaphora pistillata</i>	x	B	yr	13,22
16H:3G:13?	16B :4S:12?			
Philippines				
<i>Acanthastrea hillae</i>	x	x	sp	30
<i>Acropora austera</i>	x	x	sp	30
<i>Acropora cytherea</i>	x	x	sp-sr	30
<i>Acropora florida</i>	x	x	sp	30
<i>Acropora humilis</i>	x	x	sp	30
<i>Acropora hyacinthus</i>	x	x	sp	30
<i>Acropora loripes</i>	x	x	sp	30
<i>Acropora pulchra</i>	x	x	sp	30
<i>Acropora selago</i>	x	x	sp	30
<i>Acropora tenuis</i>	x	x	sp	30
<i>Acropora valida</i>	x	x	sp	30
<i>Astreopora myriophthalma</i>	x	x	sp	30
<i>Echinophyllia aspera</i>	x	x	sp	30
<i>Echinopora gemmacea</i>	x	x	sr	30
<i>Favia pallida</i>	x	x	sp	30
<i>Favia helianthoides</i>	x	x	sp	30
<i>Galaxea fascicularis</i>	x	x	sp	30
<i>Goniastrea edwardsi</i>	x	x	sp	30
<i>Goniastrea favulus</i>	x	x	sp	30
<i>Montipora</i> sp.	x	x	sp	30
<i>Oulophyllia bennettiae</i>	x	x	sp	30
<i>Pectinia lactuca</i>	x	x	sp	30
<i>Platygyra daedalea</i>	x	x	sp	30
<i>Platygyra sinensis</i>	x	x	sp	30

Note: While it may be assumed that coral species identified as spawners elsewhere also spawn in the Philippines, this table lists sex and mode as unknown unless an actual observation was recorded. The corals listed as tentatively spawning in the spring were observed to contain ripe gonads in April and May. The data summarized here are based on preliminary observations reported in Bermas et al. 1993.

Table 8-1. Continued

Taiwan	Sex	Mode	N	Season S	Source
<i>Acanthastrea echinata</i>	x	x		May	31
<i>Acropora austera</i>	x	x		May	31
<i>Acropora cerealis</i>	x	x	Jun	Apr, May	31
<i>Acropora cytherea</i>	x	x		May	31
<i>Acropora danai</i>	x	x		May	31
<i>Acropora digitifera</i>	x	S		Apr, May	31
<i>Acropora divaricata</i>	x	x		Jun	31
<i>Acropora formosa</i>	x	S		Jun	31
<i>Acropora humilis</i>	x	S		Apr, May	31
<i>Acropora hyacinthus</i>	x	x		May	31
<i>Acropora monticulosa</i>	x	S		May	31
<i>Acropora nana</i>	x	x		Apr, Jun	31
<i>Acropora nasuta</i>	x	x		Jun	31
<i>Acropora nobilis</i>	x	S		May	31
<i>Acropora palmerae</i>	x	S		May	31
<i>Acropora spicifera</i>	x	S		Jun	31
<i>Acropora valida</i>	x	x	Jun		31
<i>Acropora spp.</i>	x	x		Apr, May	31
<i>Astreopora gracilis</i>	x	x		May	31
<i>Astreopora listeri</i>	x	S		May	31
<i>Cyphastrea chalcidicum</i>	x	x	Jul	Apr, May	31
<i>Cyphastrea microphthalma</i>	x	x		May	31
<i>Cyphastrea serailia</i>	x	x	Jul	May	31
<i>Echinophyllia aspera</i>	x	x	Jul	May	31
<i>Echinopora lamellosa</i>	x	x	Jul	Sep	31
<i>Euphyllia ancora</i>	x	S		Apr, May	31
<i>Favia laxa</i>	x	x	Jul	May	31
<i>Favia pallida</i>	x	x	Jul	May	31
<i>Favia sp.</i>	x	S		Apr	31
<i>Favia speciosa</i>	x	S	Jun	Apr, May	31
<i>Favites abdita</i>	x	x		Apr, May	31
<i>Favites chinensis</i>	x	x	Jul	Apr	31
<i>Favites complanata</i>	x	x	Jun	May	31
<i>Favites russelli</i>	x	x	Jul		31
<i>Galaxea astreata</i>	x	S		Apr, May	31
<i>Galaxea fascicularis</i>	x	S		Apr, May, Jun	31
<i>Goniastrea aspera</i>	x	S		Apr, May	31
<i>Goniastrea edwardsi</i>	x	S	Jul	May	31
<i>Goniastrea retiformis</i>	x	S	Jul	Apr, May	31
<i>Leptoria phrygia</i>	x	x		Apr, May	31
<i>Merulina ampliata</i>	x	x		Sep	31
<i>Montastrea curta</i>	x	x	Jul		31
<i>Montastrea valenciennesi</i>	x	x	Jun	Jun	31
<i>Montipora aequituberculata</i>	x	S		Jun	31
<i>Montipora digitata</i>	x	S		Apr, May	31
<i>Montipora efflorescens</i>	x	S		Apr, May	31
<i>Montipora foliosa</i>	x	S		Jun	31

Continued

Table 8-1. Continued

Taiwan-Continued	Sex	Mode	N	Season S	Source
<i>Montipora informis</i>	x	S		Apr. May	31
<i>Montipora spp.</i>	x	S		Apr. May	31
<i>Montipora tuberculosa</i>	x	S		Apr. May	31
<i>Montipora venosa</i>	x	S		Apr. May	31
<i>Mycedium elephantotus</i>	x	x	Jul	May	31
<i>Pachyseris rugosa</i>	x	x		May	31
<i>Pachyseris speciosa</i>	x	x		May	31
<i>Platygyra daedalea</i>	x	x		Apr. May	31
<i>Platygyra lamellina</i>	x	S		Apr. May	31
<i>Platygyra pini</i>	x	x	Jul	Apr. May	31
<i>Platygyra sinensis</i>	x	S	Jul	Apr. May	31
<i>Plesiastrea versipora</i>	x	S		Apr	31
<i>Pocillopora damicornis</i>	x	B		Nov-Mar	31
<i>Porites annae</i>	x	x		May	31
<i>Porites lobata</i>	x	x	Jul		31
<i>Seriatopora hystrix</i>	x	B		yr	31
<i>Strylaphora pistillata</i>	x	B		yr	31

N = North Taiwan, S = South Taiwan

Eastern Pacific	Sex	Mode	Season	Source
<i>Pocillopora damicornis</i>	H(s)	S(?)	sr	32
<i>Pocillopora elegans</i>	H(s)	S(?)	sr	32
<i>Tubastrea aurea</i>	x	B	Jun-Nov	33

Great Barrier Reef

<i>Acropora aspera</i>	H(s)	S	seasonal	4
<i>Acropora cuneata</i>	H(s)	B	x	4
<i>Acropora digitifera</i>	H(s)	S	sp-sr	4
<i>Acropora formosa</i>	H	S	sp-sr	5
<i>Acropora humilis</i>	H(s)	S	sp-sr	4
<i>Acropora hyacinthus</i>	H(s)	S	sp-sr	4
<i>Acropora millepora</i>	H(s)	S	sp-sr	4
<i>Acropora palifera</i>	H(s)	B	x	4
<i>Acropora pulchra</i>	H(s)	S	sp-sr	4
<i>Acropora robusta</i>	H(s)	S	sp-sr	4
<i>Acropora variabilis</i>	H(s)	S	sp-sr	4
<i>Favia abdita</i>	H(s)	S	sp-sr	3
<i>Favia fava</i>	H(s)	S	sr	5
<i>Favia pallida</i>	H(s)	S	sp-sr	1
<i>Goniastrea aspera</i>	H(pg)	S	x	9,11
<i>Goniastrea australensis</i>	H(pa)	S	sp-sr	2,9
<i>Leptoria phrygia</i>	H(s)	S	sp-sr	3
<i>Lobophyllia corymbosa</i>	H(s)	S	sr	1,5
<i>Montipora ramosa</i>	H	S	x	5
<i>Pavona cactus</i>	G	S	x	25
<i>Platygyra sinensis</i>	x	S	x	9

Continued

Table 8-1. Continued

	Sex	Mode	Season	Source
Great Barrier Reef—Continued				
<i>Pocillopora damicornis</i>	H	B	yr	1,25
<i>Porites andrewsi</i>	G	S	sp-sr	24
<i>Porites australiensis</i>	G	S	sp-sr-f	5
<i>Porites haddoni</i>	x	B	sr-f	25
<i>Porites lobata</i>	G	S	sp-sr	24
<i>Porites lutea</i>	G	S	sp-sr	5,24
<i>Porites murrayensis</i>	G	B	sp-sr-f	24
<i>Seriatopora hystrix</i>	x	B	sp-sr	26
<i>Symphylia recta</i>	H	S	sp-sr	25
	6G:21H:3?	6B:24S		
Note: A total of 133 species out of 356 have been observed to mass spawn during the week following the full moon in October (see Willis et al., 1985, for details).				
Red Sea				
<i>Acropora eurytoma</i>	H(pg)	S	sp	27
<i>Acropora hemprichii</i>	H	x	x	28
<i>Acropora humilis</i>	H(pg)	S	sp	27
<i>Acropora hyacinthus</i>	H(pg)	S	sr	27
<i>Acropora scandens</i>	H(pg)	S	sr	27
<i>Alveopora daedalea</i>	H(pg)	B	f-w	27
<i>Astreopora myriophthalma</i>	H(pg)	S	sr	27
<i>Favia fava</i>	H(pg)	S	sr	27
<i>Galaxea fascicularis</i>	H(pg)	S	sr	27
<i>Goniastrea retiformis</i>	H(pg)	S	sr	27
<i>Platgyra lamellina</i>	H(pg)	S	sr	27,28
<i>Pocillopora verrucosa</i>	H(pg)	S	sr	27
<i>Seriatopora caliendrum</i>	H(pg)	B	sp-sr-f	27,28
<i>Stylophora pistillata</i>	H(pg)	B	w-sp-wr	27,28
	OG:14H	3B:10S:1?		

Sources: 1. Fadlallah, 1983; 2. Kojis and Quinn, 1981a; 3. Kojis and Quinn, 1982; 4. Bothwell, 1982; 5. Harriot, 1983a; 6. Szmant-Froelich, 1984; 7. Wyers, 1985; 8. Van Moorsel, 1983; 9. Babcock, 1984; 10. Richmond, pers. obs.; 11. Babcock, 1984; 12. Grigg et al., 1981; 13. Stimson, 1978; 14. Heyward, 1989; 15. Krupp, 1983; 16. Harrigan, 1972; 17. Richmond and Jokiel, 1984; 18. Atoda, 1951a; 19. Kawaguti, 1940; 20. Kawaguti, 1941; 21. Abe, 1937; 22. Atoda, 1947b; 23. Atoda, 1951b; 24. Kojis and Quinn, 1982a; 25. Marshall and Stephenson, 1933; 26. Sammarco, 1982b; 27. Shlesinger and Loya, 1985; 28. Rinkevich and Loya, 1979b; 29. Szmant, 1986; 30. Bermas et al., 1993; 31. Dai et al., 1993; 32. Glynn et al., 1991; 33. Richmond, pers. obs. Sex: H = hermaphroditic; G = gonochoric; pg = protogynous; pa = protandrous; s = simultaneous; x = unknown. Mode: S = spawner; B = brooder. Season: w = winter; sp = spring; sr = summer; f = fall; yr = year-round; x = unknown. Abbreviations for months are used when available and appropriate. (Updated from Richmond and Hunter, 1990.)

around the night of the May and June full moons each summer (Hayashibara et al., 1993). In Guam, Micronesia, peak spawning occurs 7–10 days after the July full moon (Richmond and Hunter, 1990). In the nearby islands of Palau, coral spawning appears to occur several months per year, including March, April, and May (Kenyon, 1995). In Australia, mass spawning events occur during November (Harrison et al., 1984).

Why are there differences in timing of coral spawning among sites, and yet so many species have a high degree of synchronization at a particular location? A critical aspect of spawning is synchronization among members of a species in the production and release of sperm and eggs. If eggs are ripe while the sperm are not, reproduction will be unsuccessful.

Corals have the ability to respond to several environmental factors. Water temperature is one signal that determines the time of year when spawning will occur (Shlesinger and Loya, 1985; Oliver et al., 1988). Many invertebrates in polar, temperate, subtropical, and tropical habitats reproduce during the times of maximum water temperatures. The “fine-tuning” seems to be in response to lunar phase. Since tides are affected by the moon, these may also affect timing, but studies have shown that nocturnal illumination plays a key role in reproductive timing in corals (Jokiel, 1985; Jokiel et al., 1985).

Corals are sensitive to chemical compounds that may also facilitate synchronized reproduction on a particular reef (Coll et al., 1989, 1990; Atkinson and Atkinson, 1992). In simultaneous comparisons among reefs in Japan separated by distances of over 50 km, different species were found to spawn on different nights during the period following the June full moon; but by the end of the week, all of the same species had released their gametes. Contagious spawning events occur as the gametes from one coral colony stimulate other colonies of the same species downcurrent to release their eggs and sperm upon contact with the gamete cloud. These observations support the notion that chemical signals are a likely cause of synchronized spawning within a reef.

Spawning species that are simultaneous hermaphrodites typically release combined egg-sperm packets (Fig. 8–2), with egg size and number of eggs per cluster varying among species. Gamete bundles may consist of between 9 and 180 eggs surrounding or embedded within a mass of sperm. Sections taken through a coral polyp prior to gamete release reveal the eggs lined up vertically or in clusters along mesenteries (Fig. 8–3). Sperm-filled packets have also been observed within the same polyp, but attached to different mesenteries (Harrison and Wallace, 1990). On the night of spawning, sperm packages are moved up from within the colony to a position near the mouth of the polyp and are rotated as eggs are either attached to the outer surface (many acroporids) or embedded within the sperm packet (e.g., *Favites*). The exact sequence of events may differ among species. In some, the transparent expanded polyps appear white as the sperm packets are moved up toward the mouth, but later become orange, pink, or red, as the colored eggs are attached (Fig. 8–4). Eventually the mouth of the polyp

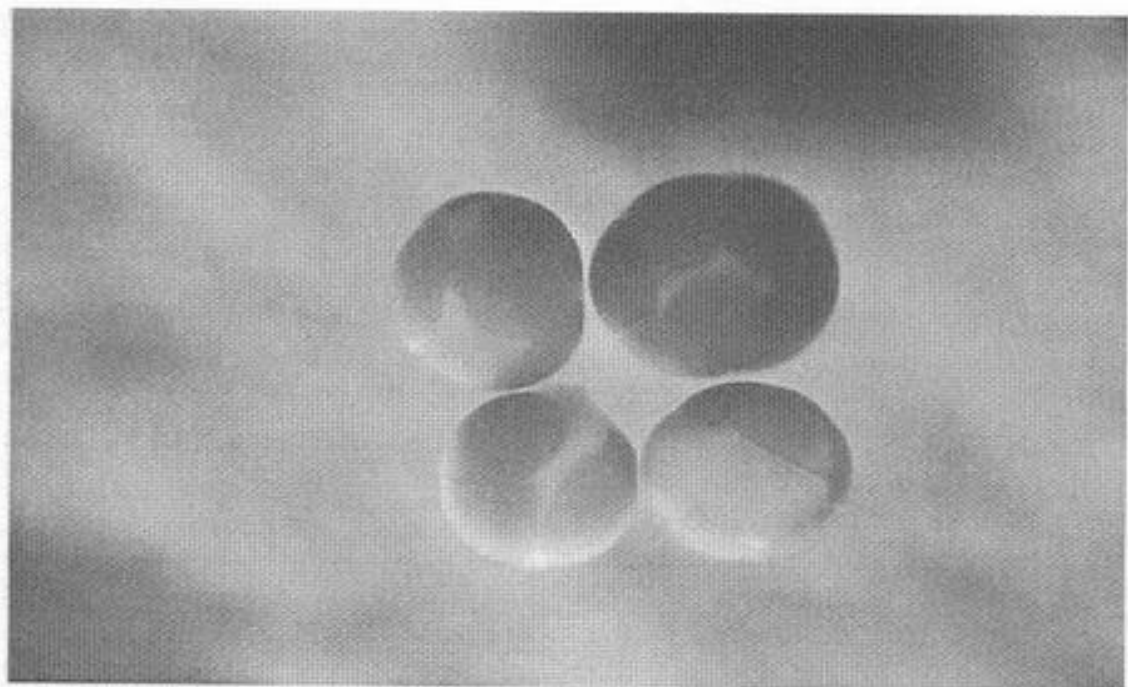


Figure 8-2. Egg-sperm clusters of *Acropora* sp. Each cluster contains 9-16 eggs surrounding a central sperm packet. Each cluster is approximately 1 mm in diameter.



Figure 8-3. A cross-section of a branch of an *Acropora* containing pigmented eggs and white sperm packets.

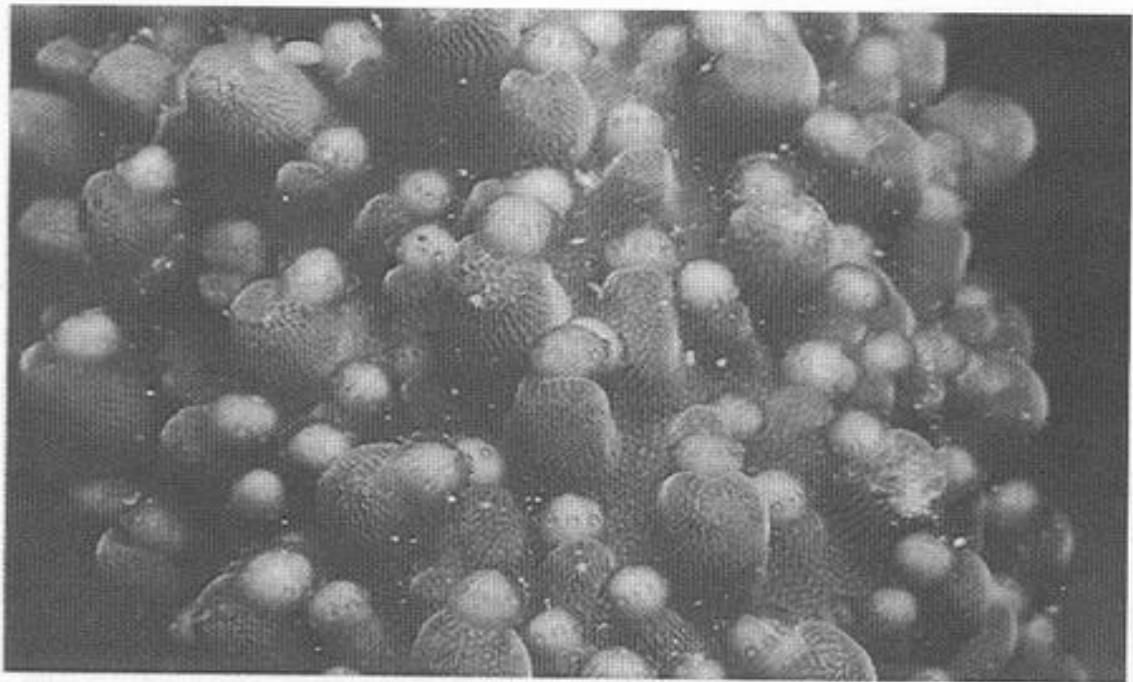


Figure 8-4. *Acropora* colony ready to release egg-sperm clusters.

expands and the gamete clusters are released (Fig. 8-5). In the field, these events are visible to the naked eye as the outer surface of the coral colony takes on color and as the colored gamete clusters are released.

The high lipid content of eggs makes the clusters positively buoyant. Sperm are neutrally buoyant and would otherwise have to swim to the surface in order to fertilize the eggs. Combining the eggs and sperm as a cohesive unit guarantees the sperm will reach the ocean's surface within moments of their release at no energetic cost, and will be in the proximity of appropriate eggs if conspecifics are nearby.

Once the combined egg-sperm packets reach the surface, there is a delay of approximately 10–40 minutes before they break apart and fertilization can take place (Fig. 8-6). Experiments have shown that eggs will not become fertilized until after this breakup occurs. Whatever the mechanism, the time delay reduces the chance of self-fertilization among eggs and sperm from the same colony, and increases the chances of fertilization among gametes from different individuals (outcrossing). However, this observed characteristic also increases the period during which gametes will be exposed to pollutants, like oil and contaminants carried in freshwater runoff, that are found at highest concentrations at the ocean surface.

8.1.5. *Self-Fertilization Versus Outcrossing*

A number of interesting questions arise from the observations of multispecies mass-spawning events. Does self-fertilization occur, and if so, at what frequency

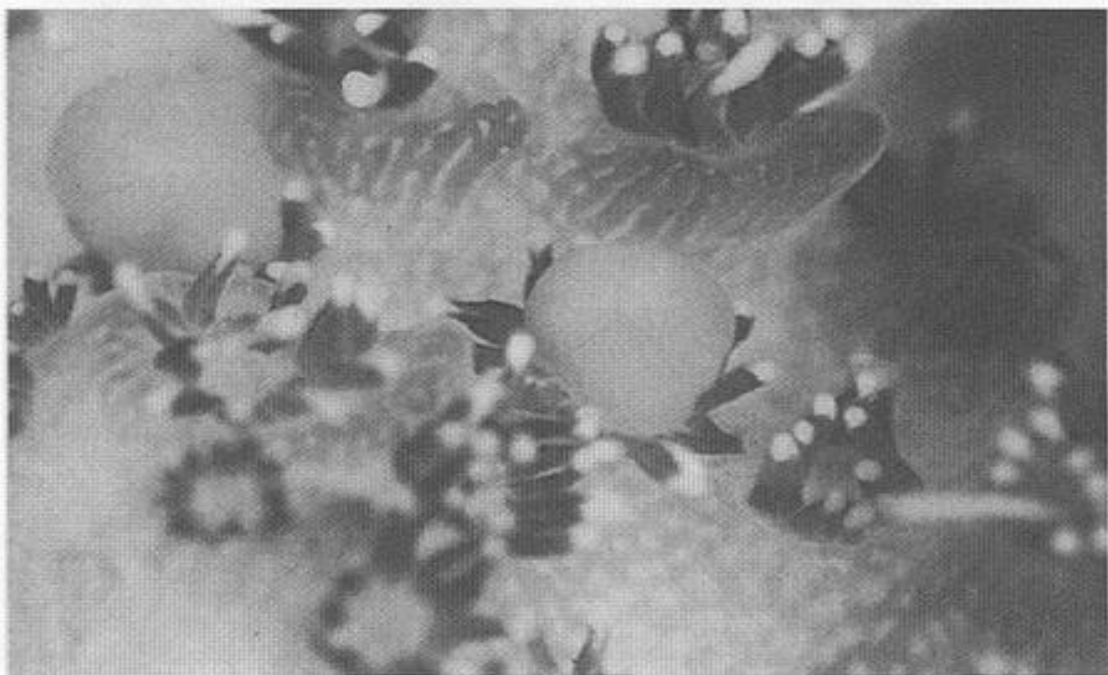


Figure 8-5. *Acropora* polyps releasing egg-sperm clusters.

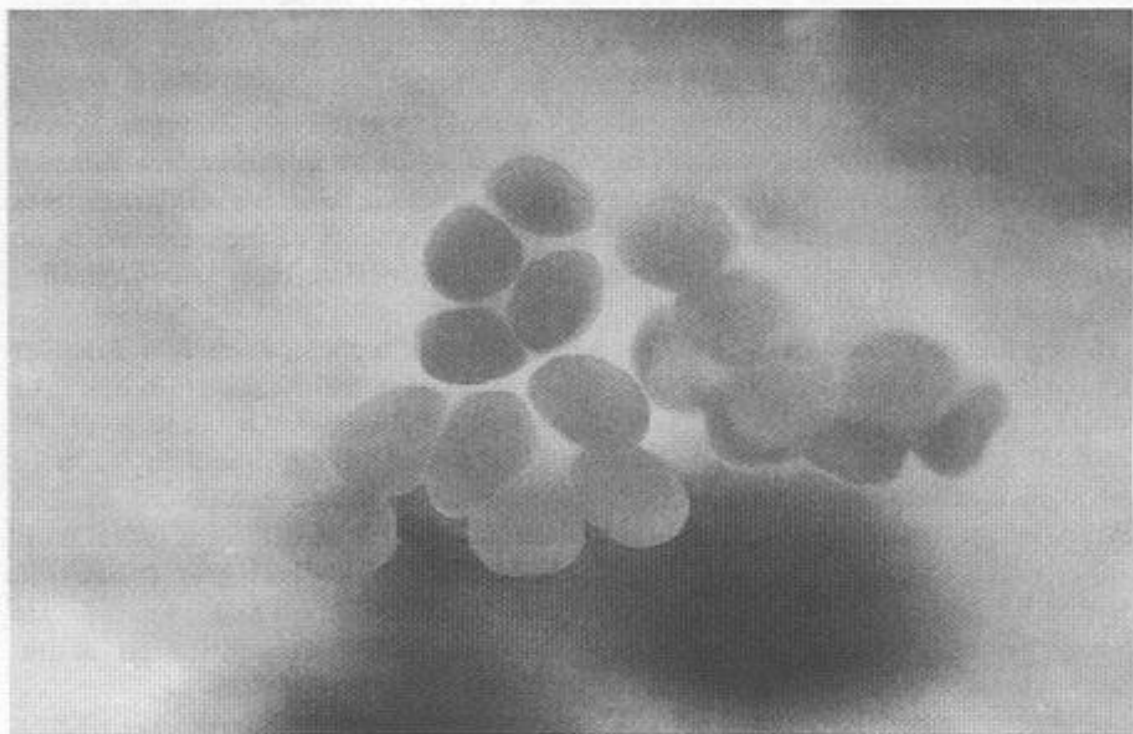


Figure 8-6. Egg-sperm clusters breaking apart approximately 20 minutes after release. The eggs are now ready to be fertilized by sperm from different colonies.

compared to outcrossing? Does hybridization occur among closely related species? Why does multispecies synchronization occur?

Barriers to self-fertilization do exist in corals that promote outcrossing, but these barriers may be time dependent and break down after several hours (Heyward and Babcock, 1986; Richmond, 1993a). In some experiments, it has been shown that sperm do not fertilize eggs from the same colony until 6 hours after release, and even then, observed rates of self-fertilization are less than 10%. The same eggs treated with sperm from another colony of the same species demonstrated fertilization rates of 70–100% within 2 hours of gamete release. This warns us that fertilization rates and reproductive success of corals may be reduced by pollution with chemical contaminants that can interfere with chemical recognition between gametes.

8.1.6. Hybridization

During a multispecies mass-spawning event, sizable slicks of coral eggs and sperm can be observed above reefs, extending hundreds to thousands of meters in some cases (Oliver and Willis, 1987). With so many eggs and sperm from a wide variety of species intermingling, the question arises, Can eggs of one species become fertilized by sperm from another?

Laboratory experiments have demonstrated that hybridization does occur among corals. This has been observed not only among closely related species within the same genus, but across genera (Richmond, 1993a, 1995; Willis et al., 1993; Kenyon, 1993). In one case, crosses of *Acropora digitifera* and *Acropora gemmifera* were unidirectional, meaning eggs of *A. digitifera* were fertilized by sperm from *A. gemmifera*, but eggs of *A. gemmifera* were not fertilized by *A. digitifera* sperm (Richmond, 1995). This type of unidirectional hybridization has been observed in echinoderms and fruit flies (Kaneshiro, 1987; Uehara et al., 1990).

Hybridization among species spawning on the same evening may be deterred by differences in the timing of gamete release. Some species usually release their eggs and sperm around 8 P.M. (e.g., *Acropora tenuis* on Guam), whereas others consistently release gametes at 10 P.M. (*Acropora humilis* on Guam), 11 P.M. (*Acropora valida* on Guam), and 11:45 P.M. (*Acropora irregularis* on Guam). Corals may also spawn during the day, as demonstrated by certain pocilloporids (Kinzie, 1993).

8.1.7. Larval Development

The planula larvae that develop from brooding and spawning corals are similar in some aspects. Both are ciliated, rich in lipid, and have chemoreceptors used for detecting the appropriate substrata for settlement and metamorphosis. But brooded larvae tend to be larger than larvae that develop from spawned gametes,

possess zooxanthellae, and are capable of settling immediately upon release from the parent colony. The smaller larvae that develop from spawning corals require time to reach a stage capable of settlement and metamorphosis. Smaller eggs of the spawning coral genera *Leptoria*, *Goniastrea*, and *Montastrea*, averaging 350–400 μm in diameter, require 18 hours before they become ciliated and capable of settlement, whereas the larger eggs of many spawning *Acropora* species take nearly 72 hours to reach the same stage of development.

Most planula larvae that develop from spawned gametes do not contain symbiotic zooxanthellae, and do not appear to obtain them until after settlement and metamorphosis. Calculated competency periods indicate such larvae retain their ability to recruit for only 3–4 weeks (Richmond, 1988). After that, they may remain alive but lack the energy reserves needed to make the transformation to a benthic calcified coral. Corals in the genus *Montipora* are an exception, as the spawned eggs contain zooxanthellae. All brooded planulae studied to date possess zooxanthellae, and in the case of *Pocillopora damicornis*, the competency period has been found to exceed 100 days, attributable in part to the contribution of the symbiotic algae to the nutritional needs of the larva (Richmond, 1987a, 1988).

The biogeographic distribution patterns of specific groups of corals suggest that possession of zooxanthellae during the larval stage enhances dispersal ability. Widely distributed species have a decreased risk of extinction from local events. Some corals endemic to Japan may be threatened with extinction due to anthropogenic (human-induced) disturbance (Chapter 14; Veron, 1992).

8.2. Larval Recruitment

Successful reproduction is only the first step in the replenishment of corals on the reef. In order for coral populations to be maintained, dead corals must be replaced, either from larvae or asexually produced products. Recruitment depends on the ability of larvae to identify an appropriate site for settlement and metamorphosis. These two distinct and critical processes are often dependent on specific chemical signals for marine invertebrates (Pawlik and Hadfield, 1990).

8.2.1. Settlement

Settlement of coral larvae is a change from a planktonic existence to a benthic lifestyle, and usually includes attachment to the reef. In order for settled larvae to survive and develop into young corals, they must settle on an appropriate site. The criteria for appropriate sites include substratum type, water motion, salinity (generally above 32‰), adequate sunlight for zooxanthellae, limited sediment deposition, and sometimes specific algal species or biological films of diatoms and bacteria.

Site selection by coral planulae may be made on the basis of chemical signals that are affecting receptors located on the outer surface of the larvae. Coral

planulae react to biological films, and in the case of species of *Agaricia*, species-specific chemical signals from particular types of crustose coralline algae (Morse and Morse, 1993).

In the laboratory, competent planula larvae can be observed to swim downward until they contact a surface. If the substratum has the proper texture and biochemical coating, the planula forms an attachment with the aboral surface, begins to contract, and lays down an organic matrix layer, followed by the deposition of the stony carbonate skeleton (Vandermuelen, 1974).

Substratum type as well as orientation can affect recruitment, growth, and survival rates. In most laboratory settlement experiments, planulae would not settle on loose sediment, especially if solid substrata were available. When settlement did occur on sediment, coral planulae had poor survival rates. In field experiments, Birkeland (1977) found recruits had faster growth rates on upper surfaces of artificial substrata, but survivorship was greater for those larvae settling on vertical surfaces. The same study reported faster growth rates of recruits at shallower depths, but higher survivorship with intermediate depth and at lower nutrient levels. Survival of young corals depends not only on the attributes of the settlement surface, but on competition with other organisms including algae and encrusting invertebrates such as sponges.

8.2.2. *Metamorphosis*

Metamorphosis is a developmental process during which a larva undergoes a series of morphological and biochemical changes while completing the transformation to the benthic juvenile stage. A planula larva is quite different from a coral polyp in that it does not have tentacles for feeding, the mouth has not yet opened to the gastrovascular cavity, digestive enzymes have not yet been produced for heterotrophic feeding, and no calcification has taken place.

During metamorphosis, a commitment is made to the settlement site. A calcified basal plate is secreted along with the first skeletal cup, and tentacles complete with stinging cells known as nematocysts form surrounding the mouth. A new coral colony will develop from this first or primary polyp through growth, budding, and continued calcification. Larvae that develop from spawned eggs, and that did not acquire zooxanthellae from the parent colony, will incorporate these algal symbionts from external sources. Observations made on a variety of *Acropora* species found that these corals obtain their zooxanthellae only after settlement and metamorphosis, and that recruits that did not pick up their algal symbionts within 2 weeks were often overgrown by crustose coralline or other red algae.

Larvae that settle in unfavorable sites may get a second chance. If a newly metamorphosed coral is stressed within days of settlement and development, it may be able to retract its tissue from the freshly secreted skeleton and return to the plankton until another suitable site is encountered (Richmond, 1985). This

has been observed in *Pocillopora damicornis*, but only from the single-polyp stage and within 3 days of initial settlement and metamorphosis.

The process of settlement does not guarantee metamorphosis will follow. For many types of invertebrate larvae, metamorphosis is a complex chain of reactions that commences only in the presence of a chemical inducer (Hadfield and Pennington, 1990). The inducer of metamorphosis can be highly specific as seen in coral planulae that will only settle on a single species of coralline algae, or more general in nature, as with short-chain peptides or general biological/diatomaceous films (Pawlik and Hadfield, 1990; Morse and Morse, 1991). Observed differences in species distribution patterns are more likely the result of larval selection than colony survivorship (Morse and Morse, 1991; Morse et al., 1994).

An important consideration in studies of recruitment is that coral larvae may be sensitive to chemical signals at levels below the detectable limits of human technology. Bioassays, biological tests using sensitive organisms, are the appropriate tools to determine if environmental contamination is at levels that can interfere with critical biological processes like reproduction and recruitment (Connell and Miller, 1984).

However, the choice of bioassays is also important (Cairns et al., 1978). Accepted standardized protocols, such as a 96-hour LC_{50} (the concentration at which 50% of the test organisms die within 96 hours of exposure), are not useful to the reef manager, as sublethal effects to organisms can be as damaging to a reef over time as lethal effects. For example, an environmental toxin at a level that allows 100% survival of larvae over 96 hours, but prevents them from detecting the appropriate settlement cue and hence prevents recruitment, has the same overall effect on the reef as causing 100% mortality of the larvae. Recent experiments demonstrated that the pesticide Chlorpyrifos, a chemical often used on golf courses, can be taken up by crustose coralline algae and that coral larvae had statistically lower recruitment rates on substrata exposed to the chemical (5 parts per billion) than on untreated controls.

By understanding the biology of coral reproduction and recruitment, it is easy to see how environmental quality can affect these two processes that are responsible for the persistence of reefs. While corals may not represent the greatest biomass on the reef, they do serve as primary framework builders and as an initial link in reef food chains as the host for symbiotic zooxanthellae.

8.3. Reproductive and Recruitment Failure of Corals

Coral reefs are diverse and productive ecosystems with complex interactions at the cellular, organismal, and community levels. Many interactions, including those between adjacent corals, between their gametes, and between larvae and their settlement substrata, are chemically mediated (Coll et al., 1990; Atkinson and Atkinson, 1992; Richmond, 1993a, b; Morse et al., 1994). Changes in water

quality that affect transmission of these chemical signals can have negative effects on reproductive timing, synchronization, egg-sperm interactions, settlement, metamorphosis, and the incorporation of zooxanthellae. Jokiel (1985) observed that changes in salinity, water temperature, and light availability affected planula production in the coral *Pocillopora damicornis*. Kojis and Quinn (1984) found a negative correlation between fecundity and depth, turbidity, and sedimentation for the coral *Acropora palifera*. They also found that allocation of energy to tissue repair in *Goniastrea favulus* resulted in a decrease in reproductive ability (Kojis and Quinn, 1985).

Colony size has been found to be a determinant of fecundity. Among small-polyped coral colonies of the same size, age can also affect overall reproductive output, with older corals being more fecund (Kojis and Quinn, 1985). For large-polyped forms, such as *Lobophyllia corymbosa*, polyp size was found to be more important than colony size for both maturity and fecundity (Harriott, 1983). For branching corals, including representatives from the genera *Pocillopora* and *Acropora*, it appears to take at least 2–3 years to attain reproductive maturity and produce the first gametes and/or larvae. Massive corals (e.g., species of *Porites*) may require a longer period of growth and development, ranging from 4 to 7 years (Rinkevich and Loya, 1979a; Szmant-Froelich, 1985; Szmant, 1986; Babcock, 1988a). For species that exhibit a direct relationship between colony size and reproduction (both onset of sexual maturity and reproductive output), reduced growth from "stress" (Brown and Howard, 1985) will also lead to a depression of reproductive potential.

Normal seawater salinity for thriving coral reefs is near 35‰. Coral colonies can survive higher and lower salinities for periods of time, and if exposed by an extremely low tide, can secrete a layer of mucus to act as a barrier against desiccation. Coral gametes, however, are more sensitive to conditions of altered salinity than adult colonies. Since peak coral spawning occurs during the rainy season in Micronesia and Okinawa, gametes released may end up in a surface layer of reduced salinity. Field samples have found surface salinities over reefs adjacent to streams and storm drains may be decreased by more than 25% to 26‰ or lower. Bioassays designed to test the effects of salinity on fertilization and larval development in corals found a 20% drop in salinity from 35‰ to 28‰ caused a corresponding 86% decrease in fertilization rate (Richmond, 1993b, 1994; Fig. 8–7). If red clay soil is included in the runoff, the same drop in fertilization was observed to accompany a smaller decrease in salinity (to 33‰), demonstrating synergistic effects. Additionally, larvae formed in uncontaminated waters showed decreased settlement rates in areas of lowered salinity.

8.3.1. Terrestrial Runoff and Water Clarity

Water clarity is an important factor affecting coral growth, and has also been observed to affect reproduction and recruitment (Jokiel, 1985; Tomascik and

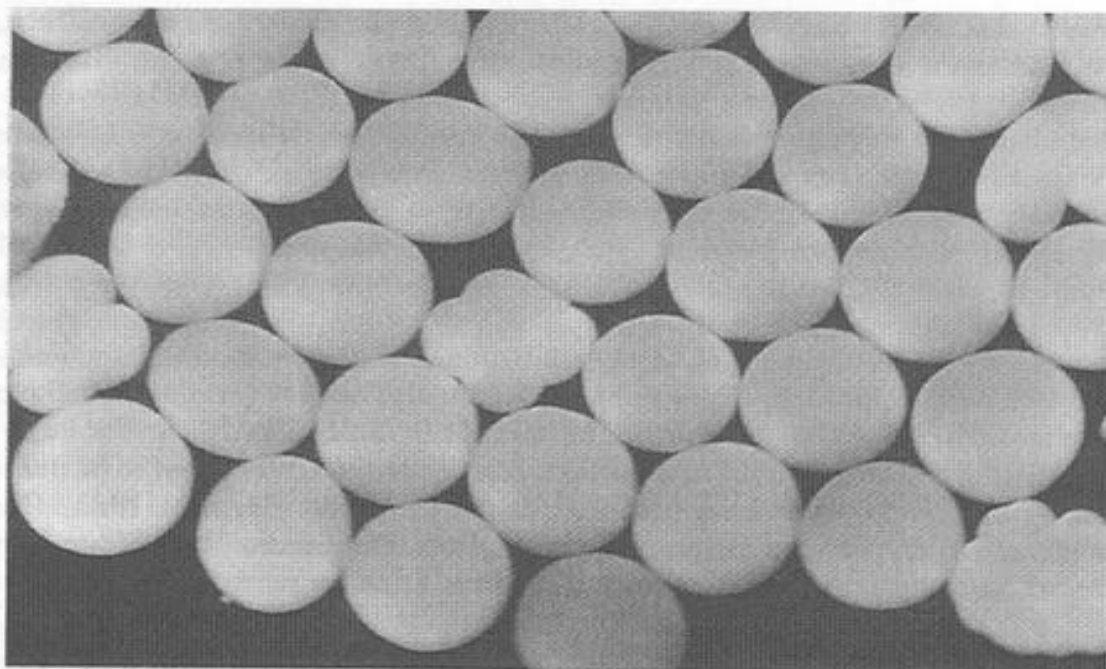


Figure 8-7. Coral eggs from a reduced salinity (28‰) fertilization bioassay showing only 4 of 35 eggs fertilized. The control (34‰) displayed an 88% fertilization rate versus 25% for the experimental treatment.

Sander, 1987b). The symbiotic association between corals and zooxanthellae (Chapter 5) allows reefs to flourish in nutrient-poor waters and also helps fulfill the energetic demands of coral reproduction. Photosynthetic products of zooxanthellae contribute to the production of eggs and larvae (Rinkevich, 1989). Since coral reefs are predominantly coastal, shallow-water features, they are vulnerable to the influence of land-based activities that result in runoff and increased turbidity (Chapter 15).

Sedimentation continues to be the most persistent problem affecting coastal reefs and those surrounding high islands (Johannes, 1975; Rogers, 1990; Richmond, 1993b). Sediments may exact an energetic cost to the coral that must cleanse its surface. The results are lower growth rates and less energy available for reproduction (Tomascik and Sander, 1987b). Sediment can also be a barrier preventing coral larvae from detecting the chemical signals from preferred settlement substrata like coralline algae.

Nutrient enrichment or eutrophication can be a problem affecting reproduction and recruitment of corals (Tomascik, 1991) and can originate from several sources including agricultural runoff and sewage outfalls. Eutrophication can lead to reduced light levels by increasing turbidity. Furthermore, elevated nutrient levels give fast-growing organisms like algae, sponges, tunicates, and bryozoans a competitive advantage over slower-growing corals (Birkeland, 1977, 1988a).

Such competitors can overgrow corals and dominate available substrata, preventing coral larvae from settling, and may lead to alternate stable states (Hatcher, 1984; Tomascik, 1991; Done, 1992; Hughes, 1994).

8.3.2. Water Pollution

A general consideration for islands and coastal communities is that substances used on land today often end up in the coastal zone tomorrow. The distance between sources of chemical contamination and coral reefs may be small. Common toxins in street runoff, including oil and petroleum products, cadmium from automobile tire wear, and miscellaneous heavy metals, enter the coastal zone every time it rains. If industrial wastes and toxins are released into residential drainage and sewer systems, they too can reach the reef. These problems all point to the need for sound watershed management and serve as examples of how land-based activities must be regulated to protect the marine environment.

Substances adhering to soil particles and contained in runoff water can be toxic and/or interfere with chemical signals (Ingersoll, 1995). Pesticides and other chemicals may bind to soil particles on land, but due to the difference in the pH of seawater, they can be released when these particles reach the ocean (Connell and Miller, 1984). The pesticide Chlorpyrifos was found to decrease levels of larval settlement and metamorphosis on settlement substrata that had been incubated in the presence of the chemical at the level of 5 parts per billion. The behavior of pesticides and toxic substances can change over time and space. Breakdown products may be more toxic to cells than the original chemical form, and processes including photoisomerization and methylation may increase stability, toxicity, and biological activity (Connell and Miller, 1984).

Corals in an area affected by an oil spill showed decreased gonad size compared to colonies from unaffected reefs years after the spill occurred (Guzman and Holst, 1993). Oil pollution was found to abort the formation of viable larvae in a brooding species of coral (Loya and Rinkevich, 1979). The presence of contaminants in coral-reef waters can also interfere with chemical signals that allow reproductive synchrony among coral colonies as well as interactions between egg and sperm (Richmond, 1994).

8.3.3. Population Depletion

Coral planula competency and recruitment patterns suggest some reefs may depend on distant coral communities for their supply of planulae larvae (Richmond, 1987; Babcock, 1988). If source reefs are disturbed, the effects may also be felt on downcurrent reefs. This issue is important, as it points to the need for interisland and regional cooperation if reefs are to be protected. This also has implications for planning coral-reef reserves, which should include consideration of dispersal patterns (Williams, et al., 1984).

Even if reproduction is successful, replenishment of reef populations is not guaranteed until larvae and asexual products successfully recruit. Planulae produced from corals living on healthy reefs will not recruit onto reefs where substrata or water quality are unacceptable. For example sedimentation and runoff may be sublethal to adult corals, yet can prevent larvae from settling (Richmond, 1993b). Living coral cover alone (abundance and diversity) does not reliably reflect the health of a reef. Such values only describe the state of the reef at that moment in time. Recruitment patterns are important in predicting what the future of a reef may be. Adult corals can survive in areas where reproduction is failing and larvae are unable to settle.

Commercially valuable sea cucumbers in Micronesia have provided an example of how populations of reef organisms may be affected by reproductive and recruitment failure. In the late 1930s, prior to World War II, large numbers of edible sea cucumbers were exported from Chuuk (Truk) to Japan, with records reflecting quantities in the hundreds to thousands of tons. Surveys performed in 1988 found only two individuals of the valuable species *Holothuria nobilis* from over eight sites in Chuuk Lagoon. Based on interviews with local residents and fishermen, it appears that populations of several species of sea cucumbers have not recovered from the severe exploitation levels prior to and during the Second World War. It is reasonable that for spawning species, once populations are reduced below a certain level, chances of successful reproductive events are low because of gamete dilution (Allee effect; Levitan et al., 1992). If an island is beyond the dispersal range of larvae from other source areas, immigration is not going to occur, and populations will not rebound. The effect of population reductions on future numbers is clear when considering the decrease in reproductive success.

8.3.4. Prevention and Mitigation

Corals can die as a result of both natural occurrences and human activities. If these corals are not replaced through the processes of reproduction and recruitment, the reef will eventually degenerate. Corals provide a primary link in the food chain as the sites of photosynthetic fixation of light energy through their zooxanthellae. They also provide a habitat for numerous associated fish and invertebrates. If the coral populations on the reef go into decline, so will the rest of the community. Whether a reef is killed quickly by catastrophe or slowly by attrition (no population replenishment), the result is the same: the loss of the reef and all it has to offer.

Our present knowledge of factors affecting reproduction and recruitment enables us to better understand how to manage activities that affect reefs, and also allows us to examine methods for applying this knowledge to reseeded and rehabilitating damaged reefs once suitable conditions return. Experiments on the cultivation of coral larvae for reseeded have proven successful. Larvae raised from mass-spawning events have been introduced onto suitable substrata in three

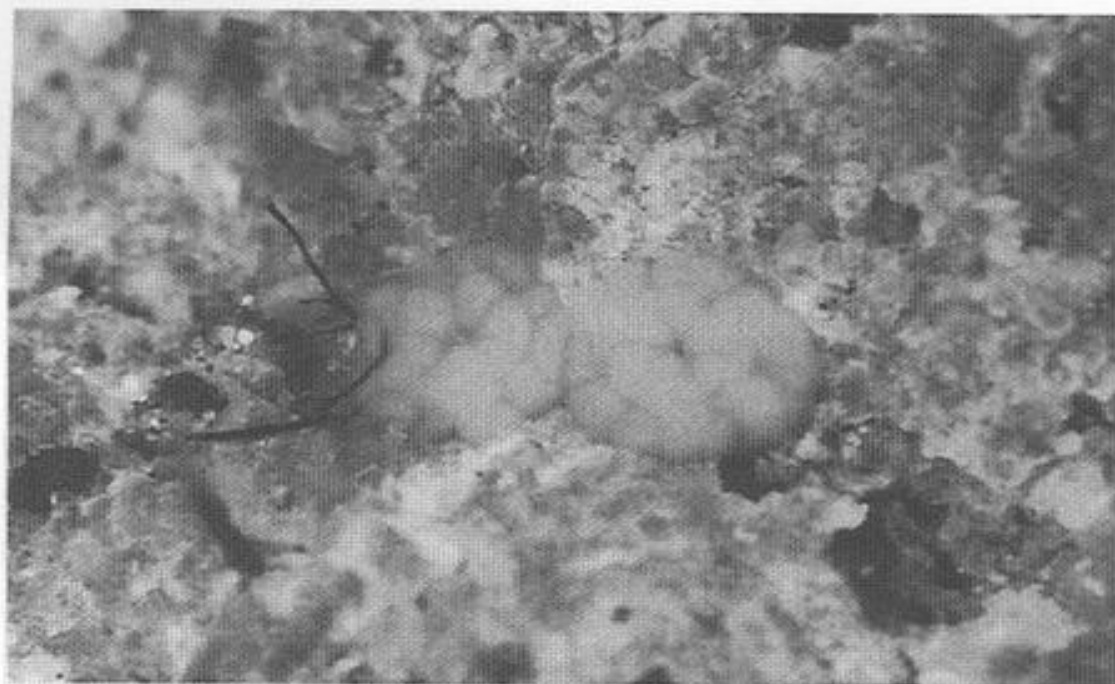


Figure 8-8. *Acropora* recruits, approximately 24 hours after settlement and metamorphosis.

areas damaged by crown-of-thorns starfish predation and by sediment. Numerous recruits were found in the seeded areas (Fig. 8-8), while no recruits of the species used were found in adjacent reference sites. These results indicate that if the environment is appropriate for recovery, reseeded can enhance recruitment rates above natural levels. Unfortunately, a 50-year-old coral cannot be replaced by reseeded in less than the 50 years it took to grow to a particular size. Prevention of human-induced damage and protection of water and substratum quality are the most effective means of supporting successful reproduction and recruitment of corals, and hence, the persistence of coral reefs.