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REVIEW

Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea*

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ABSTRACT: Detailed reproductive data are now available for 210 of the ca 600 identified scleractinian reef coral species. The majority (131 species) are hermaphroditic broadcast spawners, although hermaphroditic brooders (11 species), gonochoristic broadcasters (37 species), and gonochoristic brooders (7 species) have also been reported. Characteristics of sexuality and mode of reproduction are generally conservative within species, genera, and even families, although some exceptions occur. Variation in timing or mode of reproduction in allopatric populations may represent adaptations to local environmental conditions or indicate problems in the taxonomy of some groups. Synchronous spawning of numerous species occurs on the Great Barrier Reef, while asynchrony among and within species has been observed in the Red Sea, Caribbean, Central Pacific, Hawaii, and southern Japan. Sexual reproduction is the primary means for successful recruitment for some coral populations, while asexual processes may be the dominant or sole means of recruitment for these same species at the limits of their ranges. Recruitment success of different reproductive strategies may vary within and between localities, and is mediated by both biotic (predation, competition) and abiotic (environmental variability, disturbance) factors. Data on reproductive patterns and recruitment success may be applied to coral reef management practices.

INTRODUCTION

Until the last decade, the majority of data on coral reproduction were anecdotal and incomplete observations based on short-term and sporadic studies (see review by Fadlallah 1983). This situation is not surprising, in light of the remoteness of tropical coral reefs from most universities and research facilities, and the logistical difficulties of studying corals in situ. However, a number of recent investigations have been published based on continuous monitoring of field populations, as well as histological and laboratory examination of individuals. Previous generalizations and perceived trends may now be re-examined, as data for a greater number of species over a wide geographic range have become available.

Detailed reproductive data have been reported for ca 40 % of the known species from the tropical Pacific (studies from the Great Barrier Reef, Guam, Palau, Enewetak, Hawaii, Okinawa, and Panama), 30 % of Caribbean coral species, and 6 % of Red Sea species. These studies provide information on coral sex (hermaphroditism vs gonochorism), mode of reproduction (brooding vs broadcast spawning), and timing of reproduction (seasonality, periodicity, and synchrony). Certain patterns of reproduction and recruitment are now discernible from these data. In this paper, we review data for 210 scleractinian species, and compare reproductive processes observed in the Caribbean, eastern Pacific, Hawaii, Central Pacific, southern Japan, Great Barrier Reef, and Red Sea. As data for more taxa and

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regions become available, additional (or different) patterns and trends may emerge.

The study of coral reproduction has advanced through numerous theses and dissertations over the last 10 yr, as well as from concerted group efforts, most notably on the Great Barrier Reef of Australia. The major pattern that has developed from the Great Barrier Reef studies is one of remarkable similarity and synchrony of reproductive activity among coral species. The majority (90 %) of species studied there broadcast spawn gametes annually, during the week following the full moon in the austral spring (Harrison et al. 1984, Willis et al. 1985, Babcock et al. 1986). Data from other regions (the Caribbean, Red Sea, Central Pacific, Hawaii, and southern Japan) show different patterns, with considerable variation in mode, timing, and synchrony among species. In addition, populations of the same species reported from 2 or more regions may display different reproductive traits. Globally, corals display great plasticity in their life history characteristics. These data are summarized for each region in Table 1, and across regions in Tables 2, 3 and 4.

REPRODUCTION IN GENERAL

Corals reproduce both sexually and asexually. Sexual reproduction involves the process of gametogenesis, which may require from a few weeks for sperm, to over 10 mo for eggs. Spawning and subsequent fertilization of eggs by sperm results in small, presumably genetically unique, dispersive propagules (planula larvae) which may settle, metamorphose and develop into primary polyps. Asexual reproduction is also common in many scleractinian species, and may occur through fragmentation (see review by Highsmith 1982), polyp bail-out (Goreau & Goreau 1959, Sammarco 1982), or asexual production of planulae (Stoddart 1983). Asexual processes result in clonal propagules (genetic replicates of adult colonies) which, if derived from fragments, have the apparent advantages of large size and locally adapted genotypes.

Sexual reproduction in corals

Hermaphroditism vs gonochorism

In hermaphroditic species, ovaries and spermaries may develop on the same mesentery (most favids and mussids), on different mesenteries within the same polyp (most pocilloporids and acroporids; see Fig. 1), in different polyps within the same colony (e. g. *Cladopsammia rolandi;* de Lacaze-Duthiers 1897 in Fadlallah 1983), or at different times within the same colony (e. g. *Stylophora pistillata;* Loya 1976, Rinkevich & Loya 1979a).

Corals can be simultaneous or sequential hermaphrodites (see discussion in Fadlallah 1983). Two species, *Stylophora pistillata* and *Goniastrea favulus,* exhibit protandrous development (Rinkevich & Loya 1979b, Kojis & Quinn 1981a). The only report (Duerden 1902) of true protogyny, in which the colony functions first as a female and becomes hermaphroditic in subsequent years, has been questioned (Szmant 1986). Most hermaphroditic corals exhibit annual protogyny, where eggs develop prior to spermary formation during a reproductive season.

Mixed breeding systems have been described for a brooding species, *Porites astreoides,* in which 26 % of colonies examined were hermaphroditic, 28 % had only female gonads, and 46 % were sterile (Chornesky & Peters 1987). In *Galaxea fascicularis,* some colonies are female and some are hermaphroditic, but eggs in the latter apparently serve only to provide buoyancy for the sperm packets (Heyward et al. 1987, Harrison 1989).

Hermaphroditism is advantageous when the probability of finding (or, in the case of sedentary corals, proximity to) members of the opposite sex is low, and self-fertilization is possible. Heyward & Babcock (1986) found varying levels of success in self-crosses in 4 coral species (0 % in *Montipora digitata,* 1.5 to 16 % in *Acropora tenuis* and *Goniastrea aspera*, and 26 to 89 % in *Goniastrea favulus*). In experiments performed during spawning events on Guam during the summers of 1987 and 1988, no viable planulae developed from mixing gametes from the same individuals in *Acropora irregularis* or *A. humilis,* while nearly 100 % of the embryos resulting from self-fertilized eggs of *Acropora tenuis* developed successfully (Richmond 1989, unpubl.). Barriers to self-fertilization apparently break down with time after spawning for some species, but not for others (Heyward & Babcock 1986, Richmond unpubl.)

Numbers of gonochoristic and hermaphroditic species within each region are summarized in Table 2. Within regions, hermaphrodites range from 60 to 100 % of reported species. Globally, the majority (68 %) of coral species studied are hermaphroditic (Table 3).

Brooding vs spawning

Fertilization may take place within the maternal polyp (brooding), or externally in the water column after gametes are shed (broadcast spawning). Species which broadcast spawn outnumber brooders in the Pacific regions and the Red Sea (Table 2). However, brooding may be the predominant mode of reproduction in the Caribbean. Overall, for the present data

Table 1. Reproductive characteristics of corals from the Caribbean Sea, Great Barrier Reef, Central Pacific, Hawaii, Okinawa, eastern Pacific, and Red Sea. Symbols – Sex: H, hermaphroditic; G, gonochoric; x, unknown. Mode: S, spawner; B, brooder; * possibly sterile. Timing: month and lunar day of gamete release (spawners) or planulation (brooders) [month is divided into phases: 1, new moon, 3, first quarter, 5, full moon, 7, last quarter; 2, 4, 6 and 8 indicate intermediate lunar phases (after Shlesinger & Loya 1985)]; w, winter; sp, spring; sr, summer; f, fall; yr, year-round; x, unknown

Species	Sex	Mode	Timing	Source
Caribbean				
ACROPORIDAE				
Acropora cervicornis	H	S	Jul/Aug, 6–7	Szmant-Froelich (1984), Szmant (1986)
Acropora palmata	H	S	Aug	Szmant-Froelich (1984), Szmant (1986)
AGARICIDAE				
Agaricia agaricites	H	B	sp	Duerden (1902), Van Moorsel (1983)
Agaricia crassa	x	B	sp	Vaughan (1910)
Agaricia fragilis	x	B	sr	Mavor (1915)
Agaricia humilis	H	B	yr	Van Moorsel (1983)
FAVIIDAE				
Diploria strigosa	H	S	Aug, 7	Szmant-Froelich (1984)
Favia fragum	H	B	yr	Duerden (1902), Vaughan (1910)
			yr, 3–5	Szmant-Froelich (1984), Szmant (1986) Szmant-Froelich et al. (1985)
Manicina areolata	H	B	sp	Wilson (1888) in Fadlallah (1983)
			yr	Duerden (1902)
Montastrea annularis	H	S	Aug, 7/Sep, 7	Szmant-Froelich (1984), Szmant (1986)
Montastrea cavernosa	G	S	Aug	Szmant-Froelich (1984), Szmant (1986)
MEANDRINIDAE				
Meandrina (= *Meandra*) *areolata*	x	B	Jul/Aug, 3–8	Boschma (1929), Yonge (1935) in Fadlallah (1983)
MUSSIDAE				
Isophyllia sp.	G?	B	sp	Duerden (1902)
Mycetophyllia ferox	H	B	Feb–Mar	Szmant-Froelich (1984), Szmant (1986)
PORITIDAE				
Porites astreoides	H	B	May–Jun	Vaughan (1910), Szmant-Froelich (1984)
			Jan–Sep	Szmant (1986)
	(or female only)		yr, 6–8	Chornesky & Peters (1987)
Porites porites	G? (some hermaphroditic)	B	Nov–Feb	Tomascik & Sander (1987)
SIDERASTREIDAE				
Siderastrea radians	H	B	yr	Duerden (1902)
	G	B	yr?	Szmant-Froelich (1984), Szmant (1986)
Siderastrea siderea	G	S	Jul–Sep	Szmant-Froelich (1984), Szmant (1986)
TROCHOSMILIIDAE				
Dendrogyra cylindrus	G	S	Aug	Szmant-Froelich (1984), Szmant (1986)
	6G:10H:3x	12B:7S		
Pacific				
Great Barrier Reef				
ACROPORIDAE				
Acropora aculeus	H	S	Nov, 6	Babcock et al. (1986)
Acropora aspera	H	S	seasonal	Bothwell (1981)
Acropora austera	H	S	Nov, 6	Babcock et al. (1986)
Acropora cerealis	H	S	Nov, 6	Babcock et al. (1986)
Acropora cuneata	H	B	sp–sr	Bothwell (1981)
Acropora cytherea	H	S	Oct/Nov, 6	Willis et al. (1985), Babcock et al. (1986)
Acropora digitifera	H	S	sp–sr	Bothwell (1981)
			Oct, 6	Willis et al. (1985)
Acropora divaricata	H	S	Oct, 6	Willis et al. (1985)
Acropora elseyi	H	S	Nov, 6/Dec, 1	Babcock et al. (1986)
			Oct, 1/Nov, 6	Willis et al. (1985)
Acropora florida	H	S	Nov, 6	Willis et al. (1985), Wallace (1985b), Babcock et al. (1986)
Acropora formosa	H	S	Nov, 5–6	Babcock et al. (1986)
			Oct, 6/Nov, 6	Willis et al. (1985)
Acropora gemmifera	H	S	Nov, 6	Willis et al. (1985), Babcock et al. (1986)
Acropora grandis	H	S	Nov, 6	Willis et al. (1985), Babcock et al. (1986)

Table 1 (continued)

Species	Sex	Mode	Timing	Source
Pacific				
Great Barrier Reef				
ACROPORIDAE				
Acropora granulosa	H	S	Feb/Mar	Wallace (1985b)
Acropora horrida	H	S	sr?	Wallace (1985b)
Acropora humilis	H	S	sp–sr	Bothwell (1981)
			Oct, 6	Willis et al. (1985)
			Nov, 5–7	Babcock et al. (1986)
Acropora hyacinthus	H	S	sp–sr	Bothwell (1981)
			Oct/Nov, 6	Willis et al. (1985), Wallace (1985b)
			Nov, 5–6	Babcock et al. (1986)
Acropora latistella	H	S	Sep, 6/Oct, 6	Willis et al. (1985)
			Nov, 1	Babcock et al. (1986)
Acropora longicyathus	H	S	Nov, 5	Willis et al. (1985), Wallace (1985b)
				Babcock et al. (1986)
Acropora loripes	H	S	Nov/Dec	Wallace (1985b)
			Nov, 6	Babcock et al. (1986)
Acropora lutkeni	H	S	Nov, 6	Babcock at al. (1986)
Acropora micropthalma	H	S	Oct, 6	Willis et al. (1985)
			Nov, 5	Babcock et al. (1986)
Acropora millepora	H	S	sp–sr	Bothwell (1981)
			Oct, 6/Nov, 5–6	Willis et al. (1985)
			Nov, 5–7	Babcock et al. (1986)
Acropora nasuta	H	S	Nov, 6–7	Willis et al.(1985), Babcock et al. (1986)
Acropora nobilis	H	S	Oct, 6	Willis et al. (1985)
			Oct/Nov	Wallace (1985b)
			Nov, 5–6	Babcock et al. (1986)
Acropora palifera	H	B	x	Bothwell (1981)
Acropora pulchra	H	S	sp–sr	Bothwell (1981)
			Oct, 6–7	Willis et al. (1985)
			Nov, 5	Babcock et al. (1986)
Acropora robusta	H	S	sp–sr	Bothwell (1981)
			Nov, 6	Babcock et al. (1986)
Acropora samoensis	H	S	Nov, 6	Willis et al. (1985)
Acropora sarmentosa	H	S	Nov, 6	Willis et al. (1985)
			Feb/Aug/Nov?	Wallace (1985b)
			Nov, 7	Babcock et al. (1986)
Acropora secale	H	S	Nov, 6–7	Babcock et al. (1986)
Acropora selago	H	S	Nov, 6	Willis et al. (1985), Babcock et al. (1986)
Acropora solitariensis	H	S	Oct, 6	Willis et al. (1985)
Acropora tenuis	H	S	Oct, 6–7/Nov, 6	Willis et al. (1985)
			Nov, 5–6	Babcock et al. (1986)
Acropora valenciennesi	H	S	Nov, 6	Willis et al. (1985)
Acropora valida	H	S	Oct, 6–7/Nov, 6	Willis et al. (1985), Wallace (1985b)
			Nov, 5–6	Babcock et al. (1986)
Acropora cf. *variabilis*	H	S	sp–sr	Bothwell (1981)
Acropora cf. *vaughani*	H	S	Nov, 6	Willis et al. (1985)
Acropora yongei	H	S	Nov, 6	Babcock et al. (1986)
Astreopora microphthalma	H	S	Nov, 6	Babcock et al. (1986)
Montipora aequituberculata	H	S	Oct, 6	Willis et al. (1985)
Montipora digitata	H	S	Oct, 5/Nov, 5	Willis et al. (1985)
			Nov, 5	Babcock et al. (1986), Heyward & Collins (1985)
Montipora foliosa	H	S	Nov, 5	Babcock et al. (1986)
Montipora hispida	H	S	Oct/Nov, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Montipora informis	H	S	Oct, 5	Willis et al. (1985)
Montipora monasteriata	H	S	Nov, 5	Babcock et al. (1986)
Montipora spumosa	H	S	Nov, 5	Babcock et al. (1986)
Montipora tuberculosa	H	S	Nov, 6	Babcock et al. (1986)
Montipora turgescens	H	S	Nov, 6	Babcock et al. (1986)
AGARICIIDAE				
Pachyseris rugosa	G	S	Nov, 5–6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)

Table 1 (continued)

Species	Sex	Mode	Timing	Source
Pacific				
Great Barrier Reef				
AGARICIIDAE				
Pachyseris speciosa	G	S	Oct, 6–7/Nov, 5–6	Willis et al. (1985)
			Nov, 6–7	Babcock et al. (1986)
Pavona cactus	G(?)	S(sperm)	x	Marshall & Stephenson (1933)
CARYOPHYLLIDAE				
Catalaphyllia jardineri	G	S	Oct, 6	Willis et al. (1985)
Euphyllia ancora	G	S	Oct, 6	Willis et al. (1985)
Euphyllia divisa	G	S	Oct, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Physogyra lichtensteini	G	S	Nov, 6	Willis et al. (1985)
				Babcock et al. (1986)
DENDROPHYLLIDAE				
Dendrophyllia sp.	G	B	Dec, 1	Babcock et al. (1986)
Heteropsammia cochlea	G	S	Jan–Jun	Fisk (1981) in Harriott (1983a)
Heteropsammia aequicostatus	G	S	Apr–Jun	Fisk (1981) in Harriott (1983a)
Tubastrea faulkneri	G	B	Nov, 6–7	Babcock et al. (1986)
Turbinaria frondens	G	S	Oct, 6	Willis et al. (1985)
Turbinaria reniformis	G	S	Nov, 7	Willis et al. (1985)
FAVIIDAE				
Australogyra zelli	H	S	Nov, 6	Willis et al. (1985), Babock et al. (1986)
Barbattoia amicorum	H	S	Nov, 5–7	Babcock et al. (1986)
Caulastrea furcata	H	S	Nov, 5	Willis et al. (1985), Babcock et al. (1986)
Cyphastrea chalcidium	H	S	Oct, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Cyphastrea micropthalma	H	S	Oct, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Cyphastrea serailia	H	S	Oct, 6	Willis et al. (1985)
Diploastrea heliopora	G	x	x	Harrison (1985)
Echinopora gemmacea	H	S	Nov, 6	Babcock et al. (1986)
Echinopora horrida	H	S	Nov, 6	Babcock et al. (1986)
Echinopora lamellosa	H	S	Oct, 6/Nov, 5	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Favia favus	H	S	Nov/Dec	Harriott (1983a)
			Nov, 6	Babcock et al. (1986)
Favia lizardensis	H	S	Nov, 6	Babcock et al. (1986)
Favia mathaii	H	S	Nov, 5–6	Willis et al. (1985)
				Babcock et al. (1986)
Favia pallida (as *F. doreyensis*)	H	S	Dec	Marshall & Stephenson (1933)
Favia pallida			Oct/Nov, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Favia rotumana	H	S	Nov, 6	Willis et al. (1985)
Favia stelligera	H	S	Nov, 6	Babcock et al. (1986)
Favia veroni	H	S	Nov, 5–7	Babcock et al. (1986)
Favites abdita	H	S	Nov, 6	Kojis & Quinn (1982), Babcock et al. (1986)
			Nov, 5–6	Willis et al. (1985)
Favites bennettae	H	S	Nov, 5–7	Babcock et al. (1986)
Favites chinensis	H	S	Nov, 6	Willis et al. (1985)
Favites complanata	H	S	Nov, 6	Willis et al. (1985), Babcock et al. (1986)
Favites flexuosa	H	S	Nov, 6	Willis et al. (1985), Babcock et al. (1986)
Favites halicora	H	S	Nov, 6	Willis et al. (1985), Babcock et al. (1986)
Favites pentagona	H	S	Oct, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Favites russelli	H	S	Nov, 6	Babcock et al. (1986)
Goniastrea aspera	H	S	Oct, 5–7	Babcock (1984)
			Oct, 6–7/Nov, 6	Willis et al. (1985)
			Nov, 5–6	Babcock et al. (1986)
Goniastrea edwardsi	H	S	Nov, 6	Babcock et al. (1986)
Goniastrea favulus (as *G. australensis*)	H	S	Oct/Nov, 5–6	Kojis & Quinn (1981a), Kojis & Quinn (1982)
Goniastrea favulus			Oct, 6/Nov, 5–6	Willis et al. (1985)
			Nov, 5–6	Babcock et al. (1986)

Table 1 (continued)

Species	Sex	Mode	Timing	Source
Pacific				
Great Barrier Reef				
FAVIIDAE				
Goniastrea palauensis	H	S	Oct, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Goniastrea pectinata	H	S	Nov, 6	Willis et al. (1985)
				Babcock et al. (1986)
Goniastrea retiformis	H	S	Nov, 6	Willis et al. (1985), Babcock et al. (1986)
Leptoria phrygia	H	S	Dec	Kojis & Quinn (1982)
			Nov, 6	Willis et al. (1985), Babcock et al. (1986)
Montastrea curta	H	S	Nov, 6	Willis et al. (1985), Babcock et al. (1986)
Montastrea magnistellata	H	S	Nov, 6	Willis et al. (1985), Babcock et al. (1986)
Montastrea valenciennesi	H	S	Oct, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Moseleya latistellata	H	S	Oct, 6–8	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Oulophyllia crispa	H	S	Nov, 6	Willis et al. (1985), Babcock et al. (1986)
Platygyra daedalea	H	S	Oct, 6–7	Willis et al. (1985), Babcock et al. (1986)
			Nov, 6–7	
Platygyra lamellina	H	S	Nov, 6–7	Babcock et al. (1986)
Platygyra pini	H	S	Nov, 6	Babcock et al. (1986)
Platygyra sinensis	x	S	x	Babcock (1984)
			Oct, 6/Nov, 6	Willis et al. (1985)
	H		Nov, 6–7	Babcock et al. (1986)
FUNGIIDAE				
Fungia concinna	G	S	Nov, 7–8	Willis et al. (1985)
Fungia fungites	G	S	Oct, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Fungia paumotensis	G	S	Nov, 6	Willis et al. (1985)
Heliofungia actiniformis	G	S	Oct, 5/Nov, 5	Willis et al. (1985)
Polyphyllia talpina	G	S	Oct, 6/Nov, 6	Willis et al. (1985)
Sandolitha robusta	G	S	Nov, 6	Babcock et al. (1986)
MERULINIDAE				
Clavarina triangularis	H	S	Nov, 6	Babcock et al. (1986)
Merulina ampliata	H	S	Nov, 6	Babcock et al. (1986)
Scapophyllia cylindrica	H	S	Nov, 6	Willis et al. (1985)
MUSSIDAE				
Acanthastrea echinata	H	S	Nov, 5–7	Willis et al. (1985), Babcock et al. (1986)
Lobophyllia corymbosa	H	S	Nov/Dec	Harriott (1983a)
			Nov, 6	Willis et al. (1985), Babcock et al. (1986)
Lobophyllia hemprichii	H	S	Oct/Nov, 6–7	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Scolymia vitiensis	H	S	Nov, 6	Willis et al. (1985)
Symphyllia radians	H	S	Nov, 6	Babcock et al. (1986)
Symphyllia recta	H	S	sp–sr	Marshall & Stephenson (1933)
			Nov, 6	Willis et al. (1985)
				Babcock et al. (1986)
OCULINIDAE				
Galaxea astreata	H	S	Oct/Nov, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Galaxea fascicularis	H	S	Oct/Nov, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
PECTINIDAE				
Echinophyllia aspera	H	S	Oct/Nov, 7–8	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Echinophyllia orpheensis	H	S	Nov, 6	Babcock et al. (1986)
Myoedium elephantotus	H	S	Oct, 6–7/Nov. 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Oxypora glabra	H	S	Nov, 5–6	Babcock et al. (1986)
Oxypora lacera	H	S	Oct, 6/Nov, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Pectinia alcicornis	H	S	Nov, 6	Willis et al. (1985), Babcock et al. (1986)

Table 1 (continued)

Species	Sex	Mode	Timing	Source
Pacific				
Great Barrier Reef				
PECTINIDAE				
Pectinia lactuca	H	S	Oct, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Pectinia paeonia	H	S	Oct, 6–7/Nov, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
POCILLOPORIDAE				
Pocillopora damicornis (as *P. bulbosa*)	H	B	yr, 1–5	Marshall & Stephenson (1933)
Pocillopora damicornis			w, 5/sr, 1	Harriott (1983b)
Seriatopora hystrix	x	B	sp–sr	Sammarco (1982)
PORITIDAE				
Goniopora columna	G	S	Oct/Nov, 6	Willis et al. (1985)
Goniopora dijboutiensis	G	S	Nov, 6	Willis et al. (1985)
Goniopora lobata	G	S	Oct, 6	Willis et al. (1985)
			Nov, 6	Babcock et al. (1986)
Goniopora minor	G	S	Nov, 5–6	Babcock et al. (1986)
Goniopora norfolkensis	G	S	Oct, 6	Willis et al. (1985)
Goniopora tenuidens	G	S	Nov, 6	Willis et al. (1985)
Gonipora sp. 1	G	S	Nov, 5–7	Babcock et al. (1986)
Gonipora sp.	G	S	Nov, 6	Babcock et al. (1986)
Porites australiensis	G	S	Oct–Jan	Harriott (1983a)
Porites cylindrica (as *P. andrewsi*)	G	S	Dec, 5–7	Kojis & Quinn (1981 b)
	(2–4 % hermaphroditic)			
Porites cylindrica			Nov, 6	Willis et al. (1985), Babcock et al. (1986)
Porites lobata	G	S	Dec, 1, 4–7, 8	Kojis & Quinn (1981b)
			Nov, 6	Babcock et al. (1986)
Porites lutea	G	S	Jan, 4–8	Kojis & Quinn (1981b)
			Nov–Jan	Harriott (1983a)
			Nov, 5–7	Babcock et al. (1986)
Porites murrayensis	G	B	sp–sr–f	Kojis & Quinn (1981b)
Porites solida	G	S	Nov, 5–7	Babcock et al. (1986)
Porites stephensoni (as *P. haddoni*)	x	B	sr–f	Marshall & Stephenson (1933)
	34G:109H:2x	8B:136S:1x		
Central Pacific (Guam, Marshall, Islands, Palau)				
ACROPORIDAE				
Acropora bruggemanni	x	B	yr	Atoda (1951a)
Acropora cerealis	H	x	sr	Heyward (1989)
		S	Jul, 4–5	this study
Acropora corymbosa[a]	x	B	Jun/Jul, 1–4	Stimson (1978)
Acropora delicatula[b]	•	•	•	this study
Acropora humilis	x	B	Jun/Jul, 1–3	Stimson (1978)
	H	S	Aug, 7	this study
Acropora hystrix[c]	H	S	sr	Heyward (1989)
Acropora irregularis[d]	H	x	sr	Heyward (1989)
		S	Aug, 4–7	this study
Acropora nasuta	H	S	Jul, 7	this study
Acropora ocellata	H	S	Jul, 5–6	this study
Acropora palawensis	x	B	x	Kawaguti (1940) in Fadlallah (1983)
Acropora smithi[e]	H	x	sr	Heyward (1989)
		S	Jul/Aug, 6–7	this study

Note: all taxonomic assignations for Central Pacific are according to Randall (1983, pers. comm.) and samples of each species are deposited in the University of Guam Marine Laboratory reference collection

[a] Synonymized with *A. cytherea* by Veron & Wallace (1984)

[b] Synonymized with *A. selago* by Veron & Wallace (1984)

[c] Synonymized with *A. cerealis* by Veron & Wallace (1984)

[d] Synonymized with *A. danae* by Veron & Wallace (1984)

[e] Synonymized with *A. robusta* by Veron & Wallace (1984)

Table 1 (continued)

Species	Sex	Mode	Timing	Source
Pacific				
Central Pacific (Guam, Marshall, Islands, Palau)				
ACROPORIDAE				
Acropora squarrosa[f]	H	S	Jul, 2–3	this study
Acropora striata	x	B	Jun/Jul, 3–4 Jan, 1–8	Stimson (1978)
Acropora surculosa[g]	H	S	Jul, 7–8	this study
Acropora tenuis	H	S	Jul, 7–8	this study
Acropora valida	H	x	sr	Heyward (1989)
		S	Jul, 6–7	this study
Acropora variabilis[h]	H	S	sr	Heyward (1989)
Astreopora randalli	H	S	Jul, 8/Aug, 1	this study
Montipora foveolata	H	S	Jul, 2–3	this study
Montipora verrucosa	H	S	Jun, 7–8 Sep, 2–3	this study
CARYOPHYLLIDAE				
Euphyllia glabrescens	x	B	x	Kawaguti (1941)
DENDROPHYLLIDAE				
Balanophyllia sp.	x	B	yr	Abe (1937)
FAVIIDAE				
Favia mathaii	H	x	sr	Heyward (1989)
		S	Jun/Jul, 6–8	this study
Favia stelligera	H	S	Jun/Jul, 5–7	this study
Favites abdita	H	S	sr	Heyward (1989)
Favites flexuosa	H	S	sr	Heyward (1989)
Goniastrea aspera	x	B	Oct/Nov, 1	Abe (1937)
Goniastrea edwardsi	H	S	sr	Heyward (1989)
			Jun/Jul, 7–8	this study
Goniastrea retiformis	H	S	Jul, 1–2/7–8	this study
Leptoria phrygia	H	x	sr	Heyward (1989)
		S	Jul, 7–8	this study
Montastrea curta	H	S	Aug, 6–7	this study
Platygyra daedalea	H	S	Jul, 7–8	this study
Platygyra pini	H	S	sr	Heyward (1989)
FUNGIIDAE				
Fungia fungites	G	S	sr	Heyward (1989)
Heliofungia actiniformis	H?	B	Sep–Apr, 1	Abe (1937)
OCULINIDAE				
Acrhelia horrescens	x	B	yr	Kawaguti (1941)
Galaxea fascicularis	H	S	Jul/Aug, 1–3	this study
(as *G. aspera*)	x	B	yr	Atoda (1951b)
POCILLOPORIDAE				
Pocillopora damicornis	H	B	yr	Hada (1932), Kawaguti (1941)
(as *P. caespitosa*)			yr, 1–3	Atoda (1947a)
			Jun/Jul/Jan, 7–3	Stimson (1978)
			yr, 2–3	Richmond & Jokiel (1984)
Pocillopora elegans (*P. meandrina?*)	x	B	Jan, 3–4	Stimson (1978)
Pocillopora verrucosa	x	B	Jun/Jul, 1–3 Jan, 1–4	Stimson (1978)
Stylophora pistillata	x	B	yr, 5–7	Atoda (1947b)
Seriatopora hystrix	x	B	sr/w, 1–5	Kawaguti (1941), Atoda (1951c), Stimson (1978)
PORITIDAE				
Goniopora fruticosa	•	•	•	this study
Porites cylindrica	•	•	•	this study

Note: all taxonomic assignations for Central Pacific are according to Randall (1983, pers. comm.) and samples of each species are deposited in the University of Guam Marine Laboratory reference collection

[f] Synonymized with *A. loripes* by Veron & Wallace (1984)

[g] Synonymized with *A. hyacinthus* by Veron & Wallace (1984)

[h] Synonymized with *A. valida* by Veron & Wallace (1984)

Table 1 (continued)

Species	Sex	Mode	Timing	Source
Pacific				
Central Pacific (Guam, Marshall, Islands, Palau)				
PORITIDAE				
Porites lobata	G	S	Jul, 7–8	this study
Porites lutea	G	x	sr	Heyward (1989)
Porites (Synarea) rus	G	x	x	this study
	4G:28H:3*:12x	14B:28S:3*:2x		
Hawaii				
ACROPORIDAE				
Acropora cytherea	*	*	*	Grigg et al. (1981)
Acropora humilis	*	*	*	Grigg et al. (1981)
Acropora valida	*	*	*	Grigg et al. (1981)
Montipora dilatata	H	S	Jul, 5–6	Heyward (1985)
			Jun/Jul/Aug	Heyward (1985)
			Jul/Aug, 5–7	Hunter (1989)
			Jul, 1	
Montipora flabellata	H	S	sr–f	Heyward (1985)
Montipora studeryi	H	S	Jul, 5–6	Heyward (1985)
Montipora verrucosa	H	S	Jul, 1	Heyward (1985)
(sensu Vaughan 1907)			Jun/Jul, 1	Hunter (1989)
Montipora verrilli	H	S	Jul, 5–6	Heyward (1985)
DENDROPHYLLIDAE				
Dendrophyllia manni	x	B	sr–f	Edmondson (1929), Edmondson (1946)
Tubastrea coccinea	x	B	sr–w	Edmondson (1929), Edmondson (1946)
(as *T aurea*)				
FAVIIDAE				
Cyphastrea ocellina	x	B	yr	Edmondson (1929), Edmondson (1946), Stimson (1978)
FUNGIIDAE				
Fungia scutaria	G	S	Jul–Sep, 5	Krupp (1983)
POCILLOPORIDAE				
Pocillopora damicornis	H	B	yr, 5–1	Edmondson (1946), Harrigan (1972)
			Jun/Jul/Aug, 1	Reed (1971)
			yr, 5	Stimson (1978)
'Type Y'			yr, 6–8	Richmond & Jokiel (1984)
'Type B'			yr, 3–5	
PORITIDAE				
Porites compressa	G	S	Jun–Aug, 5	Hunter (1988), Hunter & Hodgson unpubl.
Porites evermanni	G	S	Aug–Sep, 5–6	Hunter & Hodgson unpubl.
Porites lobata	G	S	Aug, 7–8	Hunter & Hodgson unpubl.
Porites brighami	x	B	sr	Hunter & Hodgson unpubl.
	4G:6H:3*:4x	5B:9S:3*		
Okinawa				
ACROPORIDAE				
Acropora anthocercis	H	S	Jun, 5	Richmond pers. obs.
Acropora cytherea	H	S	Jun, 5	Heyward et al. (1987), Richmond pers. obs.
Acropora digitifera	H	S	Jun, 5	Richmond pers. obs.
Acropora florida	H	S	Jun, 5–8	Heyward et al. (1987), Richmond pers. obs.
Acropora formosa	H	S	Jun, 5–8	Heyward et al. (1987)
Acropora grandis	H	S	Jun, 5	Heyward et al. (1987)
Acropora hyacynthus	H	S	Jun, 5	Richmond pers. obs.
Acropra latistella	H	S	Jun, 7	Heyward et al. (1987)
Acropora micropthalma	H	S	Jun, 7	Heyward et al. (1987)
			Jun, 5	Richmond pers. obs.
Acropora nobilis	H	S	Jun, 5	Richmond pers. obs.
Acropora tenuis	H	S	Jun, 5	K. Sakai pers. comm.
Acropora valida	H	S	Jun, 5	K. Sakai pers. comm.
Montipora aequituberculata	H	S	Jun, 5–6	Heyward et al. (1987)
Montipora digitata	H	S	Jun, 5–6	Heyward et al. (1987)
Montipora effusa	H	S	Jul, 6/Aug, 6–7	Heyward et al. (1987)

Table 1 (continued)

Species	Sex	Mode	Timing	Source
Pacific				
Okinawa				
ACROPORIDAE				
Montipora turgescens	H	S	Jun, 5	Heyward et al. (1987)
FAVIIDAE				
Favia pallida	H	S	Jun, 5	Heyward et al. (1987)
Favites chinensis	H	S	Jun, 6–7/Jul, 7	Heyward et al. (1987)
			Aug, 7	Heyward et al. (1987)
Goniastrea aspera	H	S	Jun/Jul, 5–6	Heyward et al. (1987)
Platygyra pini	H	S	Jun, 2	Heyward et al. (1987)
Platygyra ryukuensis	H	S	Jul, 7/Aug, 6–7	Heyward et al. (1987)
FUNGIIDAE				
Fungia sp.	G	S	Jul, 7	Heyward et al. (1987)
MUSSIDAE				
Lobophyllia corymbosa	H	S	Jun, 6	Heyward et al. (1987)
Symphyllia recta	H	S	Jun, 5	Richmond pers. obs.
OCULINIDAE				
Galaxea fascicularis	H	S	Jun/Jul/Aug, 6–7	Heyward et al. (1987)
PORITIDAE				
Gonipora queenslandiae	G	B	Jul/Aug	Yamazato et al. (1975)
	2G:24H	1B:25S		
Eastern Pacific – work in progress				
Pocillopora damicornis	After 2 yr, only immature ovaries observed (spring). No complete gametogenesis, spawning or planulation observed (Richmond 1985)			
Pocillopora elegans	Spermaries and ovaries observed near maturity during summer (A. Yedid pers. comm.)			
Tubastrea aurea	Planulated Jun through Nov during both 1984 and 1985 (Richmond unpubl.)			
Red Sea				
ACROPORIDAE				
Acropora eurystoma	H	S	May/Jun, 5	Shlesinger & Loya (1985)
Acropora hemprichii	H	x	x	Rinkevich & Loya (1979a)
Acropora humilis	H	S	May/Jun, 7	Shlesinger & Loya (1985)
Acropora hyacinthus	H	S	Jul, 3	Shlesinger & Loya (1985)
Acropora scandens	H	S	Jun/Jul, 5	Shlesinger & Loya (1985)
Astreopora myriophthalma	H	S	Jul/Aug/Sep, 5	Shlesinger & Loya (1985)
FAVIIDAE				
Favia favus	H	S	Jun/Jul, 6–7	Shlesinger & Loya (1985)
			Aug, 6	
Favites abdita	H	S	x	Rinkevich & Loya (1979a)
Goniastrea retiformis	H	S	Jul/Aug, 7	Shlesinger & Loya (1985)
Platygyra lamellina	H	S	Jun/Jul, 1–2	Rinkevich & Loya (1979a)
			Aug, 1	Shlesinger & Loya (1985)
OCULINIDAE				
Galaxea fascicularis	H	S	Jul/Aug/Sep, 6–7	Shlesinger & Loya (1985)
POCILLOPORIDAE				
Pocillopora verrucosa	H	S	May, 1	Fadlallah (1985)
			Jul/Aug, 1	Shlesinger & Loya (1985)
Seriatopora caliendrum	H	B	May–Dec, 8–1	Rinkevich & Loya (1979a), Shlesinger & Loya (1985)
Stylophora pistillata	H	B	Dec–Jul, 1–8	Loya (1976), Rinkevich & Loya (1979a, b), Shlesinger & Loya (1985)
PORITIDAE				
Alveopora daedalea	H	B	f–w	Shlesinger & Loya (1985)
	0G:15H	3B:11S:1x		

base, spawners outnumber brooders 168:37 (Table 3). Spawning is usually associated with higher fecundity, while brooding produces fewer, larger larvae (Fadlallah 1983).

Szmant-Froelich (1984) proposed that brooders experience the greatest recruitment success in the Caribbean, while spawners (particularly acroporids and poritids) are the more successful recruiters in the Pacific.

Table 2. Global comparisons of reproductive characteristics in scleractinian corals from the Caribbean, Red Sea, and Pacific regions. See individual entries under regional headings for literature citations

	Caribbean			Pacific		
		Hawaii	Central	GBR	Okinawa	Red Sea
No. of species for which reproductive data are recorded	19	17	47	145	26	15
Gonochoric	6	4	4	34	2	0
Hermaphroditic	10	6	28	109	24	15
Not reported	3	7	15	2	0	0
Brood	12	5	14	8	1	3
Spawn	7	9	28	136	25	11
Not reported	0	3	5	1	0	1
No. of species in region	62[1]	45[2]	353[3]	356[4]	242[5]	244[6]

Sources: (1) Goreau & Wells (1967), (2) Jokiel (1987), (3) R. Randall, pers. comm., (4) Willis et al. (1985), (5) Veron (1985), (6) Sheppard (1987)

Table 3. Summary of reproductive mode for 210 species of scleractinian corals for which data are available. Entries reflect cumulative counts, omitting repeats for species found in 2 or more regions

	Hermaphroditic	Gonochoric	Unknown
Spawn	131	37	0
Brood	11	7	19
Unknown	1	2	390+

She also noted that Caribbean *Porites*, which are brooders, have small adult colony size, while the spawning gonochoric Pacific *Porites* are large and long-lived. Pacific *Porites* species which brood form small, encrusting colonies (*P. stephensoni* [as *P. haddoni*], Marshall & Stephenson 1933; *P. murrayensis*, Kojis & Quinn 1981 b; *P. brighami*, Hunter & Hodgson unpubl.).

Timing, seasonality, synchrony, and periodicity

Sexual reproduction in corals may occur yearly (Willis et al. 1985, Babcock et al. 1986), seasonally (Rinkevich & Loya 1979a, b, Szmant 1986, Tomascik & Sander 1987), monthly (Marshall & Stephenson 1933, Kawaguti 1941, Atoda 1947a, Richmond & Jokiel 1984), or not at all (Grigg et al. 1981, Richmond 1985, Richmond & Hunter unpubl.). Annual multispecies synchronous spawning has been observed for over 140 species on the Great Barrier Reef (Harrison et al. 1984, Willis et al. 1985, Babcock et al. 1986, Harrison pers. comm.), while asynchrony is exhibited among coral species in the Central Pacific, Hawaii, Okinawa, and the Red Sea (Table 1). Synchronous development and release of gametes among individuals in a population are important to maximize the probability of successful cross (and/or self) fertilization. Conversely, a presumed advantage to multiple spawnings or planulations is to minimize the effects of a single catastrophic event on an individual's or population's reproductive success.

Temperature, photoperiod, and nocturnal illumination all appear to be important in providing temporal cues which may allow synchrony within populations (Kojis & Quinn 1981a, Jokiel et al. 1985, Willis et al. 1985, Hunter 1989). The expanding database suggests that the degree of multispecies synchrony may be correlated with the annual temperature range experienced by the corals (Shlesinger & Loya 1985, Babcock et al. 1986). Annual variation in seawater temperature is 2.2 °C in the Central Pacific (Guam; Emery 1962), 3.2 °C in the Caribbean (Barbados; Tomascik & Sander 1987), 4.0 °C in Hawaii (Oahu; Jokiel 1985), 6.0 °C in the Red Sea (Eilat; Rinkevich & Loya 1979 b), 9.8 °C in Okinawa (Nakamura 1984), and 12.0 °C on the Great Barrier Reef (Magnetic Island; Babcock et al. 1986). The percentage of reported coral species spawning within the same month and lunar phase for each of these regions is 18, 26, 29, 20, 65, and 88 %, respectively. Oliver et al. (1989) reported that reproductive seasonality and synchrony among and within coral species distributed from the southern Great Barrier Reef to Papua New Guinea diminishes at lower latitudes. The trend appears to be one of tighter interspecific synchrony with increased temperature range. A similar pattern of less restricted spawning patterns with increasing proximity to the equator was reported for echinoderm species by Pearse (1968).

Differences in reproductive seasonality can occur within a species over its distributional range (Table 4). Most Great Barrier reef species spawn in the austral spring, while spawnings in the Central Pacific, Hawaii,

Table 4. Global comparisons of reproductive periodicity in coral species which have been reported from 2 or more regions. Abbreviations are for month and lunar day. Month is divided into 8 phases: 1, new moon, 3, first quarter, 5, full moon, 7, last quarter; 2, 4, 6 and 8 indicate intermediate lunar phases (after Shlesinger & Loya 1985); w: winter, sp: spring, sr: summer, f: fall, yr: year-round; • possibly sterile

	GBR	Central Pacific	Okinawa	Hawaii	Red Sea
ACROPORIDAE					
Acropora cerealis	Nov, 6	Jul, 4–5	–	–	–
(as *A. hystrix*)[a]		sr			
Acropora cytherea	Oct/Nov, 6	–	Jun, 5	•	–
(as *A. corymbosa*)[b]		Jun/Jul, 1–4			
Acropora digitifera	Oct, 6	Jun, 5			
Acropora florida	Nov, 6	–	Jun, 5?8	–	–
Acropora formosa	Oct, 6/Nov, 5–6	–	Jun, 5?8	–	–
Acropora grandis	Nov, 6	–	Jun, 5	–	–
Acropora humilis	Oct, 6/Nov, 5–7 (spawn)	Jun/Jul, 1–3 (brood) Aug, 7 (spawn)	–	•	May/Jun, 7 (spawn)
Acropora hyacinthus	Oct/Nov, 5–6	–	Jun, 5	–	Jul, 3
(as *A. surculosa*)[c]		Jul, 7–8			
Acropora latistella	Sep/Oct, 6	–	Jun, 7	–	–
Acropora loripes	Nov/Dec, 6				
(as *A. squarrosa*)[d]		Jul, 2–3			
Acropora micropthalma	Oct/Nov, 6	–	Jun, 5/7	–	–
Acropora nasuta	Nov, 6–7	Jul, 7–8 Aug, 6–7	–	–	–
Acropora nobilis	Oct/Nov, 6		Jun, 5		
Acropora robusta	Nov, 6				
(as *A. smithi*)[e]		Jul, 4–5			
Acropora selago	Nov, 6				
(as *A. delicatula*)[f]		•			
Acropora tenuis	Oct, 6 Nov, 5–6	Jul, 6	Jun, 5	–	–
Acropora valida	Oct, 6–7 Nov, 5–6	Jul, 7–8	Jun, 5	•	–
(as *A. variabilis*)[g]	sp–sr	sr			
Montipora aequituberculata	Oct, 6	–	Jun, 5–6	–	–
Montipora digitata	Oct/Nov, 5	–	Jun, 5–6	–	–
Montipora turgescens	Nov, 6	–	Jun, 5	–	–
FAVIIDAE					
Favia favus	Nov, 6	–	–	–	Jun/Jul, 6–7 Aug, 6
Favia mathaii	Nov, 5–6	Jul, 7–8	–	–	–
Favia pallida	Oct/Nov, 6	–	Jun, 5	–	–
Favia stelligera	Nov, 6	Jul, 7–8	–	–	–
Favites abdita	Nov, 5–6	sr	–	–	–
Favites chinensis	Nov, 6	–	Jun, 6–7/Jul, 7 Aug, 7	–	–
Favites flexuosa	Nov, 6	sr	–	–	–
Goniastrea aspera	Oct, 5–7 Nov, 5–6 (spawns)	Oct/Nov, 1 (broods?)	Jun/Jul, 5–6	–	–
Goniastrea edwardsi	Nov, 6	sr	–	–	–
Goniastrea retiformis	Nov, 6	Jul, 1–2	–	–	Jul/Aug, 7
Leptoria phrygia	Nov, 6	Jul, 7–8	–	–	–

[a] Synonymized with *A. cerealis* by Veron & Wallace (1984)
[b] Synonymized with *A. cytherea* by Veron & Wallace (1984)
[c] Synonymized with *A. hyacinthus* by Veron & Wallace (1984)
[d] Synonymized with *A. loripes* by Veron & Wallace (1984)
[e] Synonymized with *A. robusta* by Veron & Wallace (1984)
[f] Synonymized with *A. selago* by Veron & Wallace (1984)
[g] Synonymized with *A. valida* by Veron & Wallace (1984)

Table 4 (continued)

	GBR	Central Pacific	Okinawa	Hawaii	Red Sea
FAVIIDAE					
Montastrea curta	Nov, 6	Aug, 6–7	–	–	–
Platygyra daedalea	Oct/Nov, 6–7	Jul, 6–7	–	–	–
Platygyra lamellina	Nov, 6–7	–	–	–	Jun/Jul, 1–2 Aug, 1
Platygyra pini	Nov, 6	sr	Jun, 2	–	–
FUNGIIDAE					
Fungia fungites	Oct/Nov, 6	sr	–	–	–
Heliofungia actiniformis	Oct/Nov, 5	Sep–Apr, 1	–	–	–
MUSSIDAE					
Lobophyllia corymbosa	Nov, 6	–	Jun, 6	–	–
Symphyllia recta	Nov, 6		Jun, 5		
OCULINIDAE					
Galaxea fascicularis	Oct/Nov, 6 (spawns)	Jul, 2–3 (spawns) yr (broods)	Jun/Jul/Aug, 6–7 (spawns)	–	Jul/Aug/Sep, 6–7 (spawns)
POCILLOPORIDAE					
Pocillopora damicornis	yr, 1–5	yr, 1 yr, 3–8	–	yr, 5–3	–
Pocillopora verrucosa	–	Jun/Jul, 1–4 Jan, 1–4 (broods)	–	–	Jul/Aug, 1 (spawns)
Seriatopora hystrix	sp–sr	sr/w, 1–8	–	–	–
Stylophora pistillata	–	yr, 5–7	–	–	Dec–Jul, 1–8
PORITIDAE					
Porites cylindrica	Nov, 6	•	–	–	–
Porites lobata	Nov, 6 Dec, 1, 4–7, 8	Jul, 7–8	–	Aug, 7–8	–
Porites lutea	Jan, 4–8 Nov–Jan Nov, 5–7	sr	–	–	–

Okinawa, and the Red Sea occur mostly during summer. For many species, variations in timing and synchrony of spawning have been observed within as well as between the regions summarized in this paper (Table 1). Seasonal (latitudinal) variability within regions (e. g. between Palau, Enewetak and Guam) may be of sufficient magnitude to cause differences in reproductive timing. In addition, spawning may occur at different times for different sections of a single colony, or for different colonies within a population (Willis et al. 1985, Babcock et al. 1986, Hunter & Richmond unpubl.).

While temperature may be the seasonal cue, nocturnal illumination (lunar phase) may provide the 'fine tuning' for the particular night or nights of gamete or planula release. Both brooding and broadcasting species have been shown to cue on night-time illumination (Jokiel et al. 1985, Hunter 1989). It has also been suggested that tidal regime and onset to darkness may play roles as 'forcing functions', determining the actual time of day when spawning will occur (Harriott 1983 a, Babcock et al. 1986, Hunter 1989).

A distinct lunar planulation cycle was reported for *Stylophora pistillata* in Palau (Atoda 1947 b), while Red Sea populations of this species show no lunar synchrony (Rinkevich & Loya 1979 b). Lunar periodicity of planulation was found to differ between populations of *Pocillopora damicornis* at Enewetak and Hawaii, and within populations in Hawaii (Richmond & Jokiel 1984). The 'Type B' morph of *P. damicornis* planulated consistently at first quarter moon, while 'Type Y' planulated at last quarter. Van Moorsel (1983) proposed identification of a new species of *Agaricia* based partly on its distinct planulation schedule.

Differences in timing among allopatric populations of a species may represent adaptations to local environmental parameters and cues. Richmond & Jokiel (1984) suggested that asynchrony among sympatric populations of an identified 'species' may be the result of the immigration of planulae from one region into another. Reproductive isolation, in this case via temporal mechanisms, allows for divergence and eventual speciation. Such reproductive differences within nominal

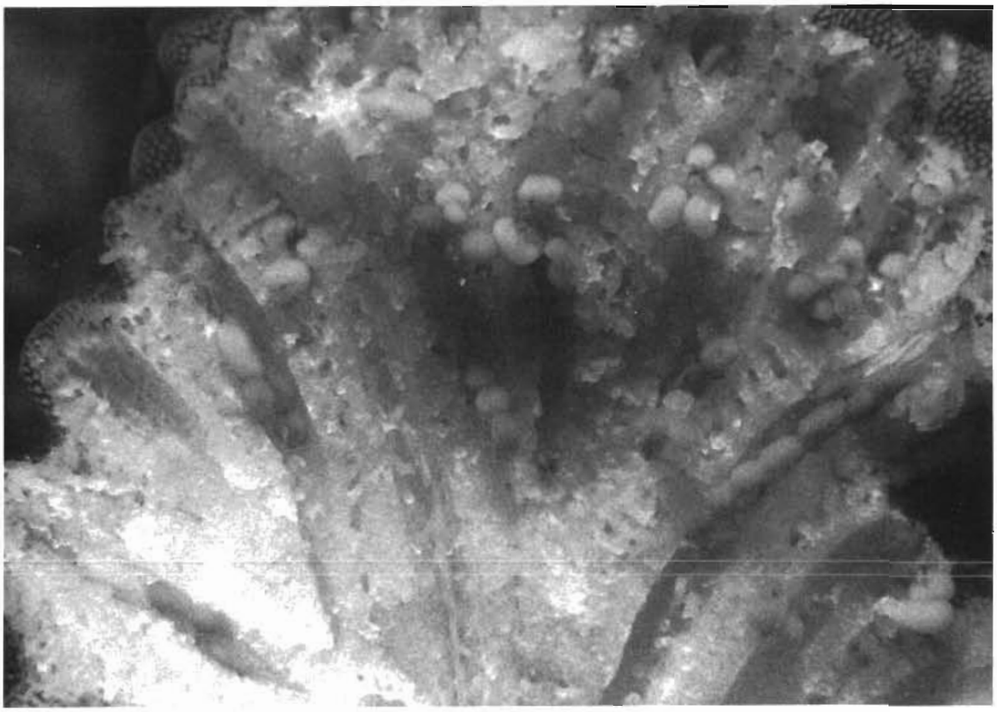

Fig. 1 *Acropora tenuis*. Section through a ripe colony of a simultaneous hermaphrodite, 1 wk prior to spawning. Egg and sperm are found within the same polyp. Egg diameter is ca 0.5 mm

species raise questions concerning taxonomy based on morphological characteristics alone.

Asexual reproduction in corals

Corals possess the ability to reproduce asexually, which is displayed by a variety of mechanisms. Asexual reproductive processes include formation of 'polyp-balls' (Rosen & Taylor 1969), polyp bail-out (Goreau & Goreau 1959, Sammarco 1982, Richmond 1985), asexual production of planulae (Stoddart 1983), and fragmentation (Highsmith 1982).

Asexual reproduction via fragmentation appears to be important for many coral species, and especially for populations living at the extremes of their physiological limits. Grigg et al. (1981) reported lack of mature gonads in populations of 3 species of *Acropora* from the Northwest Hawaiian Islands. Reproduction via fragmentation appeared to be the major means of population growth. Likewise, *Pocillopora damicornis* populations in the eastern Pacific had not produced mature gonads nor planulae during a 2 yr study, yet were the dominant reef species off the coast of Panama (Richmond 1985). Eastern Pacific *P. damicornis* exhibit higher colony growth rates than Central Pacific populations, which enhances population growth via fragmentation (Richmond 1985). High bioerosion rates on corals in the eastern Pacific are proposed as making fragmentation important for massive species such as *Pavona cactus* (Highsmith 1982).

Asexual reproduction of corals is found in all regions covered in this review, but appears to dominate in areas which are marginal for coral growth, including the eastern Pacific (Richmond 1985), the northwest Hawaiian Islands (Grigg et al. 1981), southwestern Australia (Stoddart 1984), and possibly Bermuda (Wyers 1985). Within regions with optimal conditions for coral growth, asexual processes may dominate specific habitats including areas of high wave energy (Tunnicliffe 1981), soft or unconsolidated substrata (Gilmore & Hall 1976), and stable, undisturbed sites (Hunter 1988, unpubl.). In areas where sexual reproductive processes are prevalent, asexual reproduction may augment recruitment at any time, especially during periods of environmental stress or disturbance (Highsmith et al. 1980).

Enhanced colony growth rate and subsequent fragmentation may result from allocation of energy away from production of sexual products, notably in environments where sexual processes may be physiologically constrained (Richmond 1987a). The occurrence of sterile populations has been described for other invertebrate taxa as well (Mileikovsky 1971). Asexual reproduction has the advantages of not requiring a partner, propagating locally adapted genotypes, and providing a refuge-in-size from predation and burial by sediments.

PLANULA LARVAE

Coral planulae can result from either internal fertilization and brooding, or external fertilization of spawned gametes and subsequent development outside the parent colony (Harrigan 1972, Babcock & Heyward 1986). Stoddart (1983) suggested that planulae of *Pocillopora damicornis* may also be produced asexually, based on similarities of parental and planular multilocus genotypes and adult population structure. Two other species, *Tubastrea coccinea* and *T. diaphana*, were also found to have planulae with isozyme patterns identical to their broodparents, while planulae of *Acropora palifera* and *Seriatopora hystrix* had genotypes consistent with sexual origin (Ayre & Resing 1986).

The brooded planulae of *Pocillopora damicornis* contain symbiotic zooxanthellae upon release from the parent, as well as a large quantity of lipid (Fig. 2). With the additional ability to feed while planktonic, these planulae remain competent for over 100 d, a period sufficient to allow dispersal over large distances (Richmond 1981, 1987 a). Planulae resulting from spawned gametes (Fig. 3) may lack zooxanthellae upon fertilization (known exceptions being poritids and *Montipora* spp., whose eggs contain maternal zooxanthellae), but eventually acquire the algal cells from the environment, usually after settlement and metamorphosis (Babcock 1989). Planulae of *Fungia scutaria* acquire zooxanthellae after release from the parent colony but before metamorphosis (Krupp 1983).

The spawned larvae of *Acropora tenuis* do not contain zooxanthellae, and have a shorter competency period (ca 20 d) than the brooded larvae of *Pocillopora damicornis* (Richmond 1989). Larval competency (the ability of larvae to successfully settle and metamorphose) is a major factor affecting the distribution of coral species, particularly for reefs in the eastern Pacific. It has been proposed that the present coral fauna of the eastern Pacific is the result of long-distance dispersal of planulae from Central Pacific stock (Dana 1975, Richmond 1987 b). Some instances of limited distribution patterns and endemism may be the result of abbreviated larval competency periods.

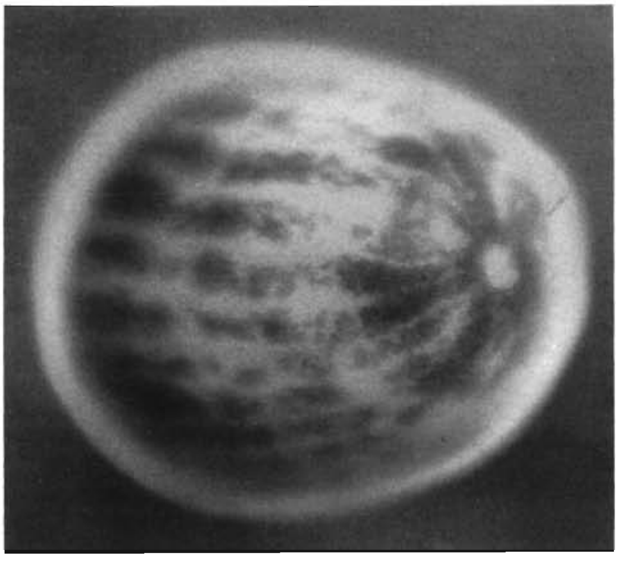

Fig. 2. *Pocillopora damicornis*. Brooded planula of a coral. Note the bands of zooxanthellae, and the oral opening. The larva is ca 1 mm in length

RECRUITMENT

Reproductive success may best be measured by recruitment. Recruitment of both sexual and asexual propagules is mediated by biotic factors, such as predation and competition, and by abiotic factors such as environmental variability and disturbance. Sexual recruitment of corals is a function of several parameters including the timing of reproduction, competency periods of planula larvae, current regimes, availability of substrata, and densities of predators and competitors (Birkeland et al. 1981, Fitzhardinge 1985, Babcock 1989). Several studies have found evidence for 'open populations' with non-localized sources of coral planulae (Wallace 1985 a, Babcock 1989), but others have suggested that reefs can be self-seeded (Baggett & Bright 1985, Sammarco & Andrews 1988, 1989, Andrews et al. 1989). In some areas, juvenile abundance is directly related to adult cover (Bak & Engel 1979,

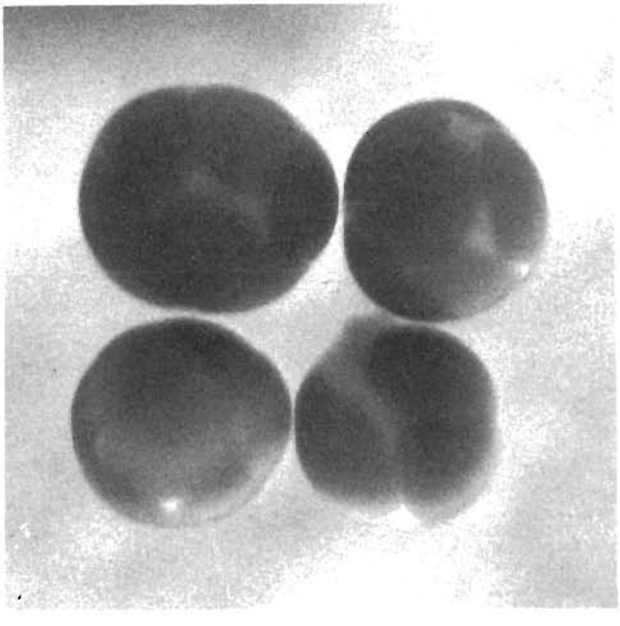

Fig. 3. *Acropora tenuis*. Spawned clusters of eggs surrounding sperm from a coral. Each cluster contains between 9 and 16 eggs around a single sperm packet Cluster diameters range between 1.3 and 1.6 mm

Rylaarsdam 1983), although this is not always the case (Fitzhardinge 1985, Harriott 1985). Relative recruitment rates have been shown to vary from year to year, and among sites on the Great Barrier Reef (Wallace 1985 a).

There appears to be an inverse correlation between success of larval recruitment and propagation by fragmentation in some coral species (Kojis & Quinn 1981 b, Highsmith 1982, Wallace 1985 b). Sammarco (1985, 1987) reported that, while planular recruitment of *Acropora* spp. on the Great Barrier Reef is high, juvenile recruits are rare in the Caribbean and populations there are structured primarily by asexual processes. Temporal and regional variations in biotic and environmental factors can cause differences in reproductive and recruitment patterns of coral communities.

The pan-Pacific coral *Pocillopora damicornis* provides an example of how life history characteristics may vary with respect to local conditions (Richmond 1985, 1987 a). Enewetak Atoll and Hawaii are characterized as having low rates of predation on *P. damicornis,* relatively low seasonal variability, yet relatively high frequencies of mortality-causing disturbances (typhoons and winter storms). *P. damicornis* colonies planulate monthly throughout the year in Hawaii and the Central Pacific, and the oldest colonies observed are estimated to be less than 10 yr old (branch lengths < 20 cm). The eastern Pacific of Panama is characterized as having high rates of predation on *P. damicornis,* high levels of seasonal variability, and low frequencies of mortality-causing events. In this area, *P. damicornis* has never been found to release planulae, has a higher colony growth rate, and is the dominant coral in terms of competitive interactions with other corals, with some colonies estimated as over 70 yr old (branch lengths > 240 cm).

Theories on the evolution of life history characteristics have been proposed which suggest that under conditions of environmental instability, where lethal disturbances occur at a relatively high rate, formation of large numbers of motile propagules should occur, while under stable conditions, selection will favor clonal (asexual) growth (Williams 1975, Maynard-Smith 1978). Likewise, under conditions of low juvenile versus high adult mortality, and relatively low competitive ability versus competitive dominance, selection will favor the sexual mode (Abrahamson 1980, Douglas 1981). *Pocillopora damicornis* fits these predicted patterns over its distributional range.

RESOURCE MANAGEMENT IMPLICATIONS

As coral reefs throughout the world are showing signs of degradation, management of reef resources is becoming a growing concern. In the case of corals which spawn during a very brief period each year, the presence of contaminants such as petroleum products, pesticides, herbicides and heavy metals from soils may prevent successful fertilization of eggs by sperm, and hence, severely limit coral recruitment (Richmond unpubl.). It is suggested that pollution levels which may not affect adult coral colonies could still be responsible for the eventual loss of reefs if reproductive processes are disturbed. In Guam and in Okinawa (southern Japan), the peak coral spawning occurs during the rainy season, when levels of coastal contamination via runoff are at their highest (pers. obs.).

With reef degradation and destruction occurring on a global scale, an application of the reproductive data is in the area of reef recovery. Areas of reef which have been destroyed may be re-seeded, and the most efficient means will depend on local conditions. In areas where sedimentation is high, corallivores are present in large numbers, and/or disturbance rate is low, cementing larger numbers of smaller fragments may be more effective based on reproduction and recruitment data. In areas where environmental conditions support sexual reproduction of corals, juvenile mortality is expected to be relatively low, and suitable substratum is available, transplantation of gravid adult colonies into an area may result in highest return of effort. Reef re-seeding is an expensive process (Harriott & Fisk 1989) and management efforts might best be expended in coral reef protection and conservation.

SUMMARY

Data on the reproductive biology of 200+ scleractinian corals indicate several apparent trends. Species which broadcast spawn outnumber those which brood planula larvae. Broadcast spawners typically have limited, annual spawning periods, while most brooders are iteroparous, releasing larvae over a large part of the year. Most corals reported to date are hermaphroditic, some of which have been found to self-fertilize readily in the laboratory; the capacity for selfing is low to non-existent in other hermaphroditic species. There are reports of coral populations which are apparently sterile, particularly those at the extreme limits of their distributions.

There appear to be several geographical trends in coral reproduction. The majority of species on the Great Barrier Reef participate in an annual synchronous spawning event following full moon in the austral spring. In other areas of the Pacific, the Caribbean, and the Red Sea, there is a greater partitioning of spawning periods over more months, days, and lunar phases. Degree of synchrony among species may be related to seawater temperature ranges in each region.

Mode of reproduction within a given taxa is generally conservative, while timing may be variable within and among species. Differences in reproductive patterns may represent adaptations to local environmental conditions or may represent groups which have not been sufficiently taxonomically differentiated. A point which clearly emerges from the data reviewed in this paper is the need for examination of reproductive characteristics in conjunction with skeletal characters to elucidate what may be real problems in coral taxonomy. Do observed reproductive differences indicate that speciation has occurred among populations? If we accept the biological species definition, it is evident that morphological characters alone may fail to detect valid biological differences. As more studies of reproduction are pursued, resulting information will enable development of a more accurate understanding of the ecology and evolutionary biology of the Scleractinia.

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