Marine Biology 109, 355–368 (1991)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Reef coral reproduction in the eastern Pacific: Costa Rica, Panama, and Galapagos Islands (Ecuador)

I. Pocilloporidae

P.W. Glynn[1], **N.J. Gassman**[1], **C.M. Eakin**[1], **J. Cortes**[1,2], **D.B. Smith**[1] **and H.M. Guzman**[3]

[1] Division of Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149, USA
[2] Centro de Investigacion en Ciencias del Mar y Limnologia, Universidad de Costa Rica, San Pedro, Costa Rica
[3] Smithsonian Tropical Research Institute, APO Miami 34002-0011, USA

Date of final manuscript acceptance: March 14, 1991. Communicated by O. Kinne, Oldendorf/Luhe

Abstract. Reproductive ecology of two major reef-building corals in the eastern Pacific [*Pocillopora damicornis* (Linnaeus) and *Pocillopora elegans* Dana] was investigated between 1984 and 1990 in Costa Rica, Panama (Gulf of Chiriqui and Gulf of Panama), and the Galapagos Islands (Ecuador) following the 1982–83 El Niño disturbance. Mature spermatocytes and oocytes were found in both species and were usually present in the same polyp in nearly equal ratios. Numerous zooxanthellae were observed in mature, unfertilized oocytes. Although spawning in field populations was not observed, it is likely that both pocilloporids are simultaneous hermaphroditic spawners, as evidenced by the disappearance of mature gametes after full moon. This is in contrast with most known pocilloporid corals that brood and release planula larvae. Corals were reproductively most active in the thermally stable environments of Costa Rica and the Gulf of Chiriqui (Panama) where 32 to 90% of all colonies contained gametes. In the moderately varying thermal conditions in the Galapagos Islands, 16 to 40% of colonies contained gametes, and in the pronounced seasonal upwelling environment of the Pearl Islands (Panama) only 6 to 18% of colonies contained gametes. Year-round reproduction occurred in Costa Rica and the Gulf of Chiriqui, whereas reproduction was confined to warm periods in the seasonally varying environments of the Galapagos Islands and the Gulf of Panama. Pocilloporid corals in Costa Rica and the Gulf of Chiriqui demonstrated lunar spawning activity, with mature gametes present a few days before and after full moon. Some limited spawning may have occurred also at new moon. While frequent gamete maturation has been demonstrated in this study, the relatively low rates of larval recruitment occurring on eastern Pacific coral reefs disturbed by the 1982–83 El Niño suggest that the recovery of important frame-building corals could be greatly prolonged.

Introduction

The mode and timing of coral reproduction can have an important influence on recovery of disturbed coral reefs. Newly opened patches of reef framework, for example, could be colonized rapidly if nearby coral survivors reproduce frequently, producing larvae that settle near the parent colonies (Connell and Keough 1985, Szmant 1986, Sammarco and Andrews 1988). Reef patches far from such source populations could be colonized by distant corals with more dispersive larvae or by other benthic taxa such as coralline algae, fleshy algae, sponges, zoanthids, molluscs or tunicates. Numerous patches of varying size and distance from surviving corals were created on eastern Pacific coral reefs as a result of the severe 1982–83 El Niño event (Cortes et al. 1984, Glynn 1984, 1988, 1990, Prahl 1985, Robinson 1985, Guzman et al. 1987). This study attempts to characterize the reproductive biology of surviving eastern Pacific reef corals to help elucidate the potential for recruitment success of species populations following the El Niño disturbance. A total of ten scleractinian corals and one hydrocoral were studied in reef areas in Costa Rica, Panama and the Galapagos Islands (Fig. 1). In this first paper, we consider the mode and timing of sexual reproduction in *Pocillopora damicornis* and *P. elegans* (order Scleractinia, family Pocilloporidae), which are among the most abundant and important reef-building taxa in the eastern Pacific (Glynn et al. 1972, Porter 1972, 1974, Glynn and Wellington 1983).

While several studies have reported that *Pocillopora* spp. are hermaphroditic brooders releasing sexually derived planula larvae, this pattern is by no means invariant. Corals identified as *Pocillopora verrucosa* (Ellis and Solander) are brooders at Enewetak Atoll (Stimson 1978), but are broadcast spawners in the Red Sea (Fadlallah 1985, Shlesinger and Loya 1985). *P. damicornis* over most of its range in the Indo-Pacific region broods planulae (Stoddart and Black 1985, Richmond and Hunter 1990). However, planula larvae have not been found in Pacific Panamanian populations and it has been sug-

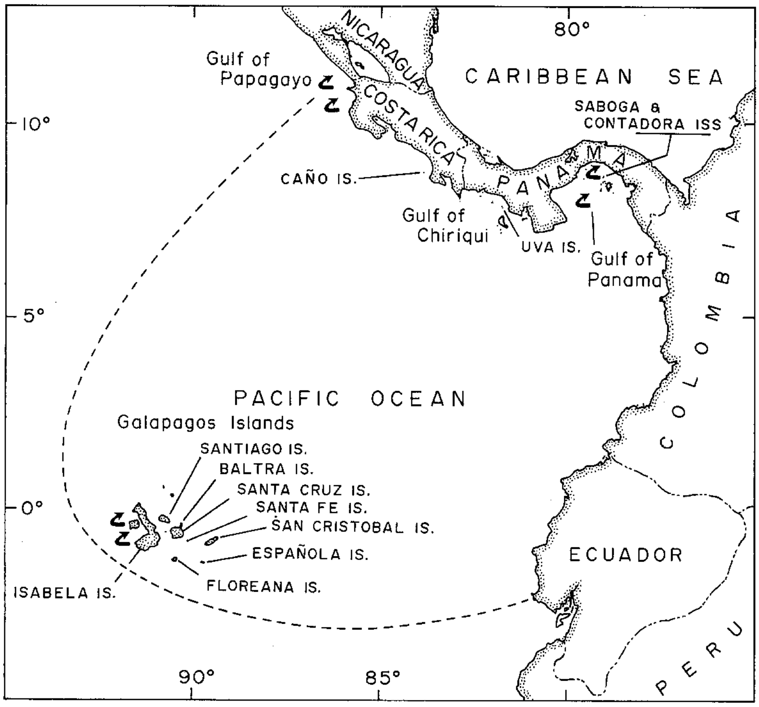


Fig. 1. Equatorial eastern Pacific region of coral reef development. The known bounds of severely disturbed areas during the 1982–83 El Niño warming event are denoted by the dashed line (after Glynn 1990). Arrows denote centers of upwelling in the Gulf of Papagayo, Gulf of Panama, and western Galapagos Islands

gested that *P. damicornis* may be sexually sterile in the eastern Pacific region (Richmond 1985, 1987a). *Pocillopora meandrina* Dana is suspected to be a broadcast spawner in Hawaii (Stimson 1978), and *P. elegans* is a brooder at Enewetak. J. Veron (in Stimson 1978: p. 176) considers *P. meandrina* and *P. elegans* to be taxonomically equivalent. Finally, an electrophoretic study has offered evidence that *P. damicornis* is capable of producing planulae asexually as well as sexually (Stoddart 1983).

Of the 13 to 14 scleractinian corals present on eastern Pacific reefs, only three have received intensive study: the non-zooxanthellate *Tubastraea coccinea* Lesson, and the zooxanthellate species *Pocillopora damicornis* and *Pavona gigantea* Verrill. Reproductive products were commonly present in *T. coccinea* and *P. gigantea*, but no colonies of *Pocillopora damicornis* were found with planulae or mature gonads (Wellington and Glynn 1983, Richmond 1985). Since pocilloporid corals were the predominant frame-building species on most eastern Pacific reefs before 1983 (Glynn 1976, Glynn and Macintyre 1977, Glynn et al. 1982, Glynn and Wellington 1983), it is critical to determine the potential for sexual reproduction in this taxon. Pocilloporid coral mortality on eastern Pacific reefs was high, ranging from ca. 51% at Caño Island to 76–85% in Panama and 97–100% in the Galapagos Islands (Glynn et al. 1988). In order to understand the temporal and spatial scales of reef recovery, it is necessary to know the origin and rates of recruitment of the dominant reef-building species. If the recruitment of pocilloporid corals in the eastern Pacific were dependent upon long-distance dispersal across large expanses of the Pacific Ocean (Richmond 1990), then reef recovery might be greatly prolonged. If coral survivors are locally abundant and asexual fragmentation is effective (Highsmith 1982), then reef recovery could be rapid without significant sexual reproduction. We present evidence that supports frequent sexual reproduction in *P. damicornis* and *P. elegans*, within surviving eastern Pacific populations in Costa Rica, Panama, and the Galapagos Islands.

Materials and methods

Species identifications follow those proposed by J. W. Wells (in Glynn and Wellington 1983). Morphologically, the eastern Pacific *Pocillopora damicornis* resembles most closely the Australian series of ecomorphs from semi-protected biotopes described by Veron and Pichon (1976). Wells (in Glynn and Wellington 1983) considers *P. elegans* to be distinct from *P. verrucosa*, contrary to the synonymy proposed for these two sepcies by Veron and Pichon (1976).

These two pocilloporid species were sufficiently abundant in most areas to allow frequent, long-term sampling. A total of 320 colonies of *Pocillopora damicornis* and 377 of *P. elegans* were collected in Costa Rica, Panama and in the Galapagos Islands (Table 1, Fig. 2). In Costa Rica, corals were collected from the two fringing reefs at the northeast end of Caño Island (see Guzman and Cortes 1989). In Panama, the collections were made primarily in the Gulf of Chiriqui at a rocky point ca. 100 m north of the Uva Island patch reef, with some collections at the main Uva Island reef. Some collections also were made in Panama at Saboga Island and Contadora Island (Pearl Islands) in the Gulf of Panama, a seasonally upwelling environment. Collections in the Galapagos Islands were made primarily at the Itabaca Canal and Point Estrada sites. Additional samples were taken from elsewhere off Santa Cruz Island and other islands in the archipelago. The low number of samples in 1985 resulted from an almost total absence of pocilloporids following the severe 1982–83 El Niño. All corals were sampled at 3 to 8 m depth.

The primary sampling effort entailed obtaining one branch, 5 to 8 cm in length, from three to five different pocilloporid colonies at the various study sites. Nearly monthly sampling was performed in 1986 at the three principal study sites in Costa Rica, Panama and the Galapagos Islands (Table 1). In addition, sequential sampling of *Pocillopora damicornis* and *P. elegans* was performed at 3- to 5-d intervals at four sites, to follow lunar patterns of gametogenesis (Table 2). One half of the February 1989 Uva Island series were sampled from known (tagged) colonies, and half from arbitrarily selected colonies. The October–November 1989 Panama series was begun at Uva Island and continued in the Pearl Islands.

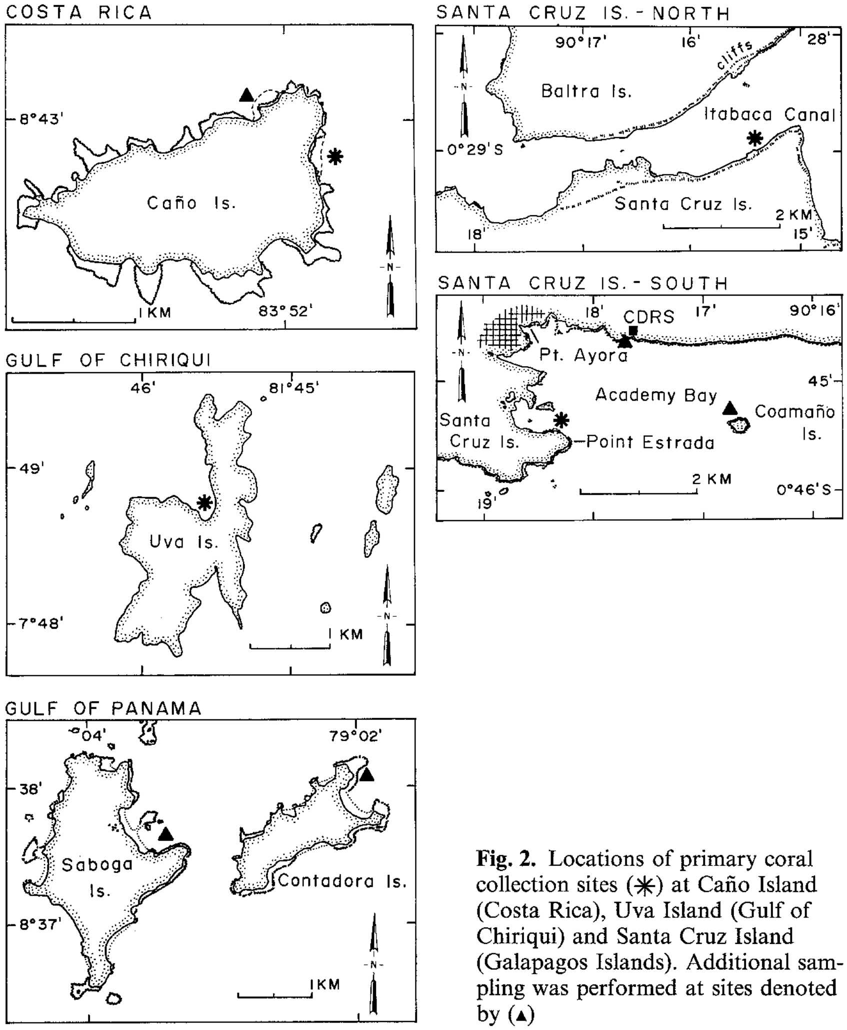


Fig. 2. Locations of primary coral collection sites (✱) at Caño Island (Costa Rica), Uva Island (Gulf of Chiriqui) and Santa Cruz Island (Galapagos Islands). Additional sampling was performed at sites denoted by (▲)

Within 1 h after collection, corals were fixed in a seawater Zenker's solution with 5% formaldehyde for 18 to 24 h. They were rinsed by suspension in seawater or occasionally by immersion in running freshwater for 18 to 24 h and then preserved in 70% ethanol, with renewal of the alcohol when necessary to remove dissolved pigments and precipitates from the fixative. Fixed corals were decalcified for 4 to 6 h or more in 10% HCl with 0.7 g EDTA, 0.008 g sodium potassium tartrate and 0.14 g of sodium tartrate per liter of solution. Tissues used were from distances at least 2 to 3 cm below the branch tips. After decalcification, acid was removed from tissues by rinsing for 24 h in running tap water. Employing a Technicon Tissue Processor, the tissues were dehydrated in a series of alcohols and Tissue Dry dehydrant, cleared with xylenes and then infiltrated with paraffin. The tissues were embedded in Paraplast and oriented so that both cross sections and longitudinal sections were obtained (see Szmant-Froelich et al. 1980, 1985 for further details). Tissues were sectioned, 6 to 8 μm thick, and stained with a slightly modified Heidenhain's aniline-blue method (Luna 1968), using Azocarmine G.

The developmental condition of gonads was determined as follows. A centrally located series of polyps was selected from 2 to 4 equivalent sections present on each slide and outlined with a fine-point pen. Both longitudinal and cross sections of polyps were counted and then scanned slowly at 40 × magnification with an Olympus BH-2 light microscope. Only polyps with at least 50% of their tissues present in the mid-body (mesenterial) region were scored. For *Pocillopora* spp. from Costa Rica and Panama, the number of polyps sampled per slide ranged from 10 to 100, with usually ca. 45 unique polyps sampled for each coral on each date. In the Galapagos Islands, the polyps were generally larger than at the continental sites, resulting in 10 to 40 polyps per slide and usually ca. 25 unique polyps sampled per colony from each collection.

Gonads were located at 100 × and the classification of gametocytes was performed at up to 600 × magnification. Gametocytes stained with Heidenhain's aniline-blue were classified according to the modified criteria of Szmant-Froelich et al. (1985) as follows. Stages I and II oocytes appeared as enlarged interstitial cells, with large nuclei, in the mesenterial mesoglea. Stage I oocytes were relatively small (10 to 20 μm diameter), whereas Stage II oocytes were larger (20 to 40 μm) due to accumulation of cytoplasm. Stage III oocytes stained orange, sometimes light blue, and revealed a clear nucleus. [Stage III oocytes in Szmant-Froelich et al. (1985) were variable in size (40 to 80 μm) and undergoing vitellogenesis.] Stage IV oocytes were full size (ca. 100 μm) and often exhibited an indented nucleus as noted by Szmant-Froelich et al. (1985). Additionally, the nucleus appeared condensed (possibly due to the presence of chromatin), and in some Stage IV oocytes the nuclei became slightly detached from the vitellogenic material. During Stage IV, large lipid vacuoles in the cytoplasm increased in number, staining often changed from red to orange-brown, and zooxanthellae were present in the oocytes at this stage (see Fig. 5). This classification differed from that of Stoddart and Black (1985) only in the presence of zooxanthellae in Stage IV oocytes. Stage IV oocytes never underwent changes indicative of fertilization, and/or development into Stage I embryos. Also, reproductive products were never seen in the gastrovascular cavity.

Spermaries were classified into four instead of the five developmental categories of Szmant-Froelich et al. (1985). Stoddart and Black's (1985) classification is similar to that of Szmant-Froelich

Table 1. *Pocillopora damicornis* and *P. elegans*. Summary information on collection of corals from the major study sites in Costa Rica, Panama, and the Galapagos Islands. Values in parentheses are totals

Study sites and collection period	Years	No. of months collected	No. of collections	No. of colonies (*P. damicornis*/*P. elegans*)
Costa Rica				
Caño Island;	1985	5	6	10/ 32
25 Mar 1985	1986	11	15	45/ 48
to 13 Dec 1989	1987	3	3	10/ 13
	1988	2	2	4/ 3
	1989	3	7	9/ 21
				(78/117)
Panama				
Uva Island;	1984	1	1	1/ 2
21 Jul 1984	1985	4	5	14/ 14
to 14 Mar 1990	1986	11	12	42/ 42
	1987	2	3	9/ 9
	1988	1	3	6/ 10
	1989	2	13	59/ 60
	1990	1	4	0/ 12
				(131/149)
Pearl Islands: Saboga	1984	1	1	2/ 0
Island, Contadora	1985	1	1	5/ 4
Island; 11 Jul 1984	1989	2	8	24/ 24
to 4 Nov 1989				(31/ 28)
Galapagos Islands				
Santa Cruz, Santa	1985	1	1	3/ 0[a]
Fe, Española, San	1986	11	14	14/ 17
Christobal, Floreana,	1987	10	11	24/ 9
Bartolome; Islands;	1988	7	14	15/ 13
4 May 1985 to	1989	6	16	24/ 44
20 Oct 1989				(80/ 83)
			Grand total	320/377

[a] Only three colonies of *P. damicornis* were found at Española and San Cristobal Islands in 1985

Table 2. *Pocillopora damicornis* and *P. elegans*. Locations and timing of coral sampling. T: tagged (known) colonies; A: arbitrarily selected colonies

Study sites	Collection period	No. of collections	No. of samples (*P. damicornis*/*P. elegans*)	Colonies
Costa Rica				
Caño Island	5–16 Sep 1989	5	0/15	A
Panama				
Uva Island	6–24 Feb 1989	7	42/42	T/A[a]
	3–12 Oct 1989	4	12/12	A
Pearl Islands	14 Oct–4 Nov 1989	8	24/24	A
Galapagos Islands	10 Apr–11 May 1989	11	0/30	A

[a] One half of sampled colonies were tagged, the other half arbitrarily selected

et al. (1985) except that the former did not recognize the early migration of interstitial cells (Stage I) in their scheme. Stage I spermaries, characterized by small clusters of interstitial cells located near or entering the mesoglea, were rarely seen. Stage II spermaries contained clusters of spermatocytes with large nuclei and distinct spermary boundaries. Spermaries were sometimes visible on stalk-like extensions of the mesoglea, and the Stage II spermatocytes stained an orange-brown color. Stage III spermatids, more numerous than earlier stage spermatocytes, were relatively small with small nuclei and stained a red to mauve color. Lumina were present in some spermaries before completion of the final reduction division. We considered Stages IV and V (as in Szmant-Froelich et al. 1985) to be equivalent. The Stage IV spermatozoa, approximately half the size of Stage III spermatids, were small and dense and stained dark magenta or red. Tails were usually present and orange-staining sperm bouquets were frequently seen. Sizes of gonads, selected from among the five largest on a slide, were measured with a stage micrometer.

To assess temporal patterns of gametogenesis, all colonies sampled were scored with respect to the presence or absence of gametocytes, and for each date the abundance of colonies with gametocytes present was expressed as a percentage of the total number of colonies examined for that date. The seasonal and lunar occurrence of mature gonads also was expressed as a percentage of all gonads observed on a given Julian or lunar date. To test for significant annual or lunar trends in reproductive condition, chi-square analyses were performed respectively for 12 categories (12 mo) and 4 categories (4 lunar phases, equal intervals beginning with new moon). If an expected value of 0 was encountered, adjacent categories were combined in order to eliminate expected frequencies of <1.

Environmental conditions

The primary study sites in Costa Rica and Panama were located on islands ca. 25 km offshore of mainland Central America (Fig. 1). Both areas are influenced by well-defined wet and dry seasons, a result of the latitudinal migration of the Intertropical Convergence Zone (ITCZ) (Forsbergh 1969). Centered near 9° and 8°N, respectively, the rainy season at Caño Island (Costa Rica) and Uva Island (Panama) begins in both areas in May and ends in December (Fig. 3). The seasonal distribution of rainfall in the Pearl Islands, Gulf of Panama, is similar to that in Costa Rica and western Panama, but with relatively low rainfall over much of the wet season (Glynn 1977).

Because coral spawning often occurs during seasonal warming periods (e.g. Stimson 1978, Fadlallah 1983, Harrison et al. 1984, Babcock et al. 1986, Richmond and Hunter 1990), annual synoptic variations in sea surface temperature (SST) also are characterized for the four study sites (Fig. 3). Surface sea water temperature is high (27 to 29 °C) and relatively constant at Caño and Uva Islands (Glynn et al. 1972, Dana 1975, Glynn 1977, 1990, Kwiecinski and Chial-Z. 1983, Glynn et al. 1988). Seasonal upwelling occurs in the Gulf of Panama with relatively low and variable mean monthly SST (24 to 26 °C) prevalent from January through April, the height of the dry season (Glynn and Stewart 1973, Kwiecinski et al. 1988, Glynn and D'Croz 1990). In some years, extreme low SSTs of 14 to 18 °C have been observed during 3- to 5-d upwelling pulses (Kwiecinski et al. 1988, Glynn and D'Croz 1990, Richmond 1990). At such times, nutrient concentrations increase in the euphotic zone, with subsequent increases in plankton productivity (Forsbergh 1969).

The Galapagos Islands are centered on the equator, ca. 1 100 km west of mainland Ecuador (Fig. 1). The influence of the ITCZ is diminished at this southerly location. Except during El Niño years, rainfall is relatively low in the wet (warm) season (January to April) and nearly absent over the remainder of the year. Exceptionally heavy rains occurred during the 1982–83 El Niño event, with a daily maximum of 138 mm in December 1982 and an annual total

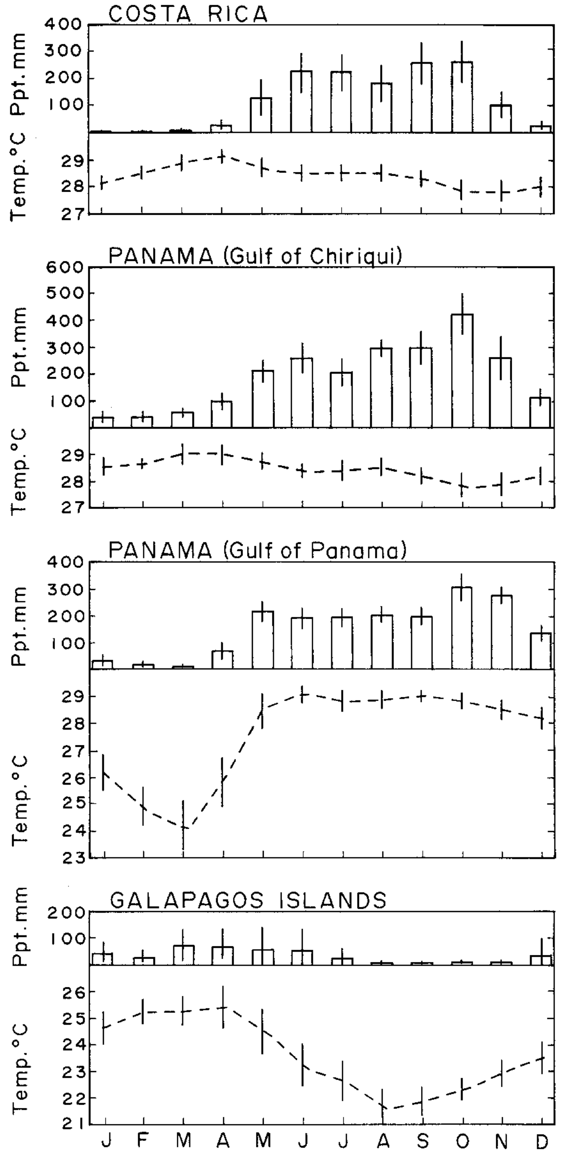


Fig. 3. Synoptic seasonal variations in precipitation (Ppt., in mm) and sea surface temperature (SST) near the three primary collection sites and the Gulf of Panama (see Fig. 2). Monthly means and 95% confidence intervals of means are from data sets of several years, as follows. Rainfall: Costa Rica, Puntarenas, 1961 to 1970, NOAA (1982); Panama, Gulf of Chiriqui, Puerto Armuelles, 1961 to 1970, NOAA (1982); Panama, Gulf of Panama, Balboa, 1951 to 1968, Forsbergh (1969); Galapagos Islands, Santa Cruz Island, Charles Darwin Research Station, 1965 to 1972 and 1977 to 1985. SST: Costa Rica and Gulf of Chiriqui, Panama, 1947 to 1958, Renner (1963), and 1980 to 1985, from F. Miller's (Inter-American Tropical Tuna Commission, La Jolla, California, USA) monthly synoptic charts of ship injection temperatures from 2° latitude/longitude squares; Gulf of Panama, Panama, Balboa, 1971 to 1987, Meteorological and Hydrographic Branch, Panama Canal Commission; Galapagos Islands, Santa Cruz Island, Charles Darwin Research Station, 1965 to 1972 and 1977 to 1985

of 2769 mm in 1983 (Robalino 1985). The dry season (May to December) is relatively cool due to the prevalence of overcast/misty ("garua") conditions. The sea state (i.e., swell size and direction) is commonly unsettled during the cool season. SSTs at all collection sites east of Isabela Island are relatively high in the wet season (January to May) and low in the dry season (June to December) (Glynn and Wellington 1983). Rainfall and SST variability is greater in the Galapagos than at the continental sites largely because of the varying interannual influence of the Panama Current in the Galapagos area and the sporadic occurrence of El Niño events.

Results

Reproductive condition

Gonads were attached to or otherwise closely associated with the 12 primary mesenteries in both *Pocillopora damicornis* and *P. elegans*. Where attachment sizes were visible in histological preparations, the gonads appeared as extensions of the mesenteries. Prominent stalks, reported by Harriott (1983a) and Stoddart and Black (1985) for *P. damicornis* in Australia, were not observed in either species of *Pocillopora* in the eastern Pacific. Oocytes and spermaries occurred separately or together within the same polyp and even shared the same mesentery in some polyps (Fig. 4A, B). Other studies have shown zooxanthellae in the planulae of *P. damicornis* (see Fadlallah 1983); however, zooxanthellae have not been reported in mature oocytes as shown here (Fig. 5). Most colonies contained both spermaries and oocytes, with nearly equal sex ratios (Table 3).

In the thermally stable environments of Caño Island and Uva Island, 32% to nearly 90% of the colonies sampled contained gonads. Percentage of colonies with gonads was highest for *Pocillopora elegans* at Uva Island (89.9%). In the Pearl Islands and Galapagos Islands, with marked seasonal thermal variations, lower proportions of corals were gravid. *P. elegans* revealed 17.9 and 39.2% gravid colonies in the Pearl Islands and Galapagos Islands respectively (Table 3). Relatively few colonies of *P. damicornis* were gravid in the Pearl Islands (6.4%) and Galapagos Islands (16.2%).

No clear pattern was apparent in the disposition of spermaries and oocytes. However, if oocytes and spermaries were present on the same mesentery, the spermaries were always situated basally (Fig. 4B). In polyp cross sections, oocytes and spermaries either were situated alternately between mesenteries, were present in mesenteries on opposite sides or were distributed randomly among mesenteries within the polyp. When oocytes and spermaries were present in the same intraseptal space, the two were separated distally. Typically, between one and three, and up to ten, ripe gonads per mesentery were visible in cross and longitudinal sections of sexually mature polyps. At Uva Island, the mean (SD) number of spermaries in sexually mature *Pocillopora damicornis* ranged between 3.0 (1.8) and 4.5 (2.8) per polyp section ($n = 204$ polyp sections examined), and mean (SD) oocyte number ranged between 2.2 (2.2) and 6.1 (5.0) per polyp section ($n = 138$). Mature oocyte mean diameters were ca. 100 μm (range = 80 to 138 μm, $n = 63$), and mature spermaries were nearly twice the diameter of oocytes ($\bar{x} = 180$ μm, range = 101 to 266 μm, $n = 69$) at all collection sites over the course of the study. The complete absence of mature male or female gonads occurred near new (Lunar Day 15) or full (Lunar Day 29) moon in a few samples, when spawning presumably occurs (see 'Lunar

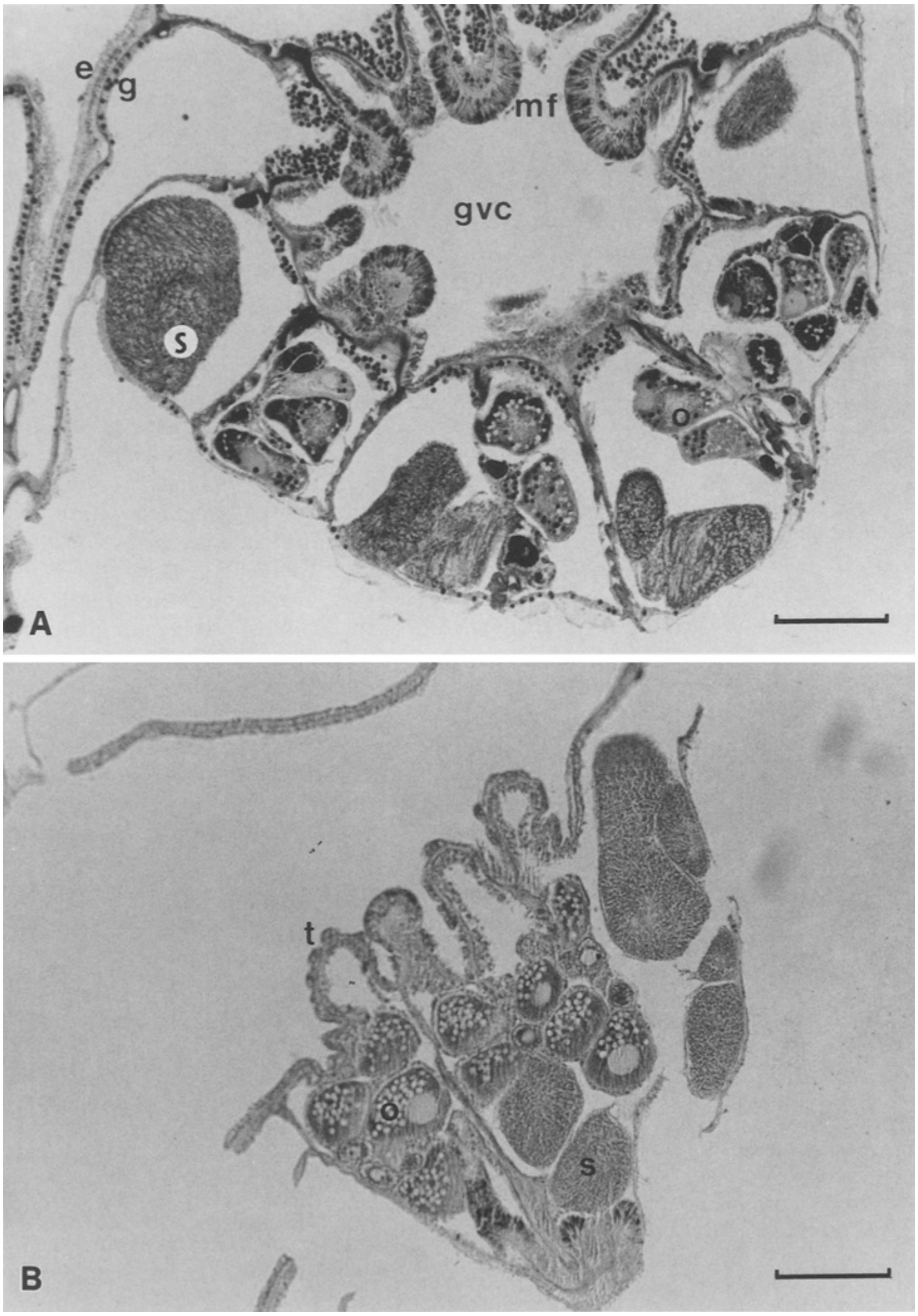


Fig. 4. *Pocillopora damicornis.* (A) Disposition of oocytes and spermaries in a cross section of coral polyp, Uva Island, Panama (14 June 1988). e: epidermis; g: gastrodermis; gvc: gastrovascular cavity; mf: mesenterial filaments; o: Stage IV oocyte; s: Stage III spermatids. (B) Disposition of gonads in a longitudinal section of coral polyp, illustrating the basal location of spermaries, Uva Island, Panama (11 August 1985). o: Stage III oocyte; s: Stage III spermatids; t: tentacle. Scale bars = 100 μm

Table 3. *Pocillopora damicornis* and *P. elegans*. Number of colonies sampled, percentage of colonies with gonads and number of colonies with oocytes and/or spermaries in corals from Costa Rica, Panama and the Galapagos Islands

Species	Location	No. of colonies	% Colonies with gonads	Number of colonies with:		
				Oocytes	Spermaries	Oocytes and spermaries
P. damicornis	Caño Island	78	32.0	23	22	20
	Uva Island	131	59.5	39	43	53
	Pearl Islands	31	6.4	1	2	1
	Galapagos Islands	80	16.2	10	10	8
P. elegans	Caño Island	117	59.5	62	66	59
	Uva Island	149	89.9	67	61	109
	Pearl Islands	28	17.9	5	4	4
	Galapagos Islands	83	39.2	28	17	15

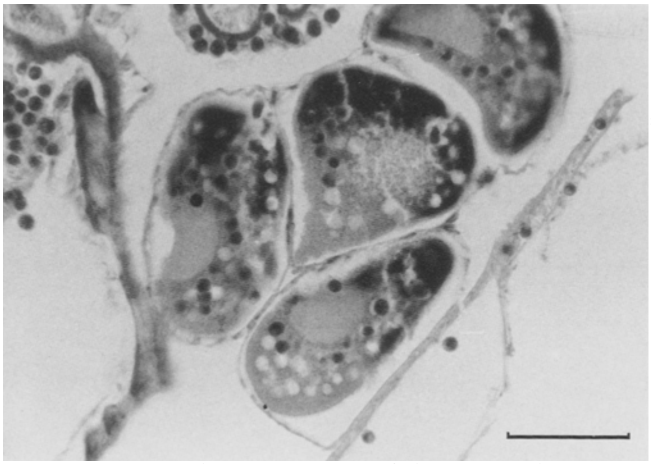


Fig. 5. *Pocillopora damicornis.* Zooxanthellae (dark spheres) present in Stage IV oocytes, Uva Island, Panama (14 June 1988). The clear spheres are lipid vacuoles. Scale bar = 50 μm

activity' below). Finally, polyp diameters and tissue layer thicknesses tended to be greater in pocilloporids from the Galapagos than in those from Costa Rica and Panama. A statistical comparison indicated that polyps of *P. damicornis* from the Galapagos ($\bar{x}=0.72$ mm diameter, $n=47$) were significantly larger than polyps from Panama ($\bar{x}=0.62$ mm, $n=24$) ($p<0.05$, Student's *t*-test).

Mature spermaries were present in polyps with both mature and immature oocytes. The ratio of male to female gonads per polyp appeared to remain constant during reproductive maturation. No early-stage embryos or planulae were found in the histological examination of over 300 colonies of each of the two *Pocillopora* species. Although spawning has not been observed in the field, present evidence strongly suggests that both pocilloporids are simultaneous hermaphroditic broadcast spawners (see 'Lunar activity' below). At full moon, the gonads separated from the mesenteries. Also, structures that looked like spent spermaries and others resembling empty sacs were observed in histological sections of *P. elegans* from Caño and Uva Islands from 1 to 3 d following full moon. Finally, samples from known colonies followed for several days after full moon contained no spermatozoa but early-stage (I and II) oocytes only, suggesting that gametes were released and not resorbed.

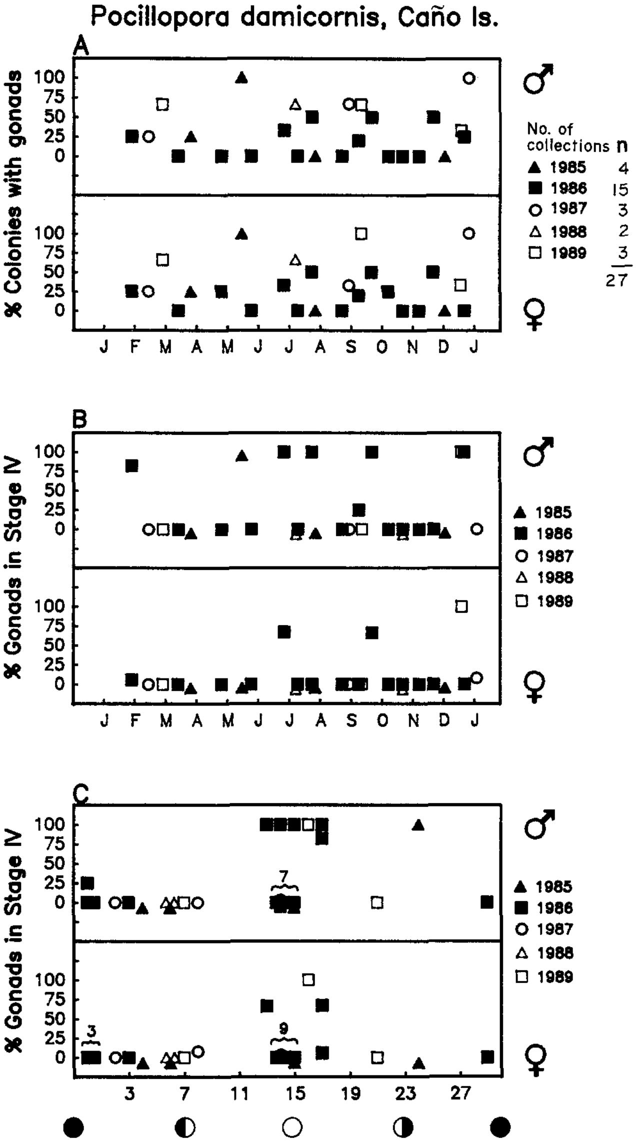


Fig. 6. *Pocillopora damicornis.* Reproductive condition at Caño Island, Costa Rica (1985 to 1989). (A) Annual trend in percentage of colonies with gonads; (B) annual trend in percentage of gonads in Stage IV; (C) lunar trend in percentage of gonads in Stage IV. Spermaries are shown on the upper portion of each panel, oocytes on the lower. Number of collections plotted in each panel is indicated after each year in Panel A. The total record consists of 27 collections with 78 colonies sampled ($\bar{x}=2.9$ colonies collection^{-1}) and 787 unique polyps scored ($\bar{x}=29.2$ polyps collection^{-1})

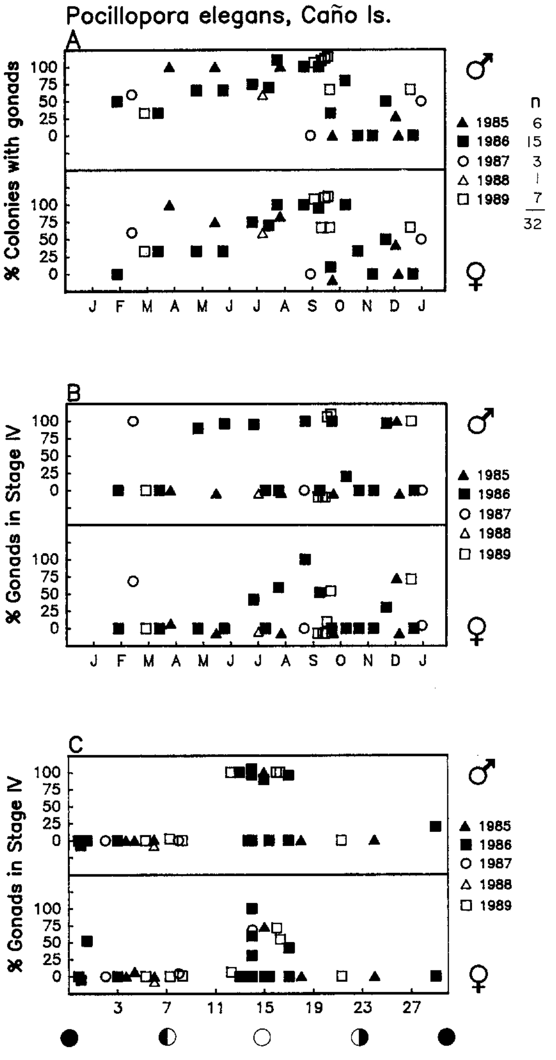
Seasonality

At Caño Island, Costa Rica colonies of *Pocillopora damicornis* with male and female gonads were found in various stages of reproductive development in both the dry and wet seasons (Fig. 6A). *P. elegans*, however, demonstrated a statistically significant seasonal trend, with both sexes showing peak reproductive activity at mid wet season (August and September) and minimal activity in November when mean seawater temperature is lowest (Fig. 7A, Table 4).

At Uva Island, Panama, relatively few gonads were present in *Pocillopora damicornis* from the end of the wet season (November to mid-December) to the beginning of the dry season (mid-December to January) (Fig. 8A). This trend was highly significant in both sexes (Table 4). The occurrence of Stage IV gametes (Fig. 8B) was confined largely to mid wet season, suggesting that gonadal maturation and spawning did not take place until after cooler dry-season seawater temperatures had passed (Fig. 3). In *P. elegans*, a significant decline in oocyte abundance was evident during January–February, with an increase in March (Fig. 9A, Table 4). No seasonal trends were apparent in the occurrence of spermaries (Fig. 9A, Table 4). Stage IV spermatozoa were found most frequently in the dry season, but this trend was non-significant (Fig. 9B, Table 4). All colonies of

Table 4. *Pocillopora damicornis* and *P. elegans*. Chi-square analyses of temporal patterns of gametogenesis in both pocilloporid species at the three primary collection sites. Observed annual frequencies were compared with expected frequencies for each of 12 mo, and lunar frequencies for each of 4 equal periods within the cycle. Chi-square analyses were not performed when data were insufficient (ns, $p > 0.05$). Freq. col.: frequency of colonies with gonads; Freq. SIV: frequency of Stage IV gonads; Ann.: annual; Lun.: lunar

Location	Test	Period	*P. damicornis*						*P. elegans*					
			Spermaries			Oocytes			Spermaries			Oocytes		
			χ^2	p	n	χ^2	p	n	χ^2	p	n	χ^2	p	n
Caño Is.	Freq. col.	Ann.	1.9	ns	26	5.6	ns	51	8.1	<0.05	76	8.0	<0.05	138
		Lun.	13.1	ns	26	20.5	<0.05	51	23.6	<0.05	76	26.2	<0.01	138
	Freq. SIV	Ann.		–			–			–			–	
		Lun.		–			–		12.8	<0.01	23	11.9	<0.01	27
Uva Is.	Freq. col.	Ann.	33.1	<0.005	129	15.8	<0.005	132	0.5	ns	130	7.3	ns	302
		Lun.	305.4	<0.005	129	61.1	<0.005	132	4.8	ns	30	24.1	<0.05	302
	Freq. SIV	Ann.		–			–		19.2	ns	49	8.8	ns	69
		Lun.	26.2	<0.005	11	13.9	<0.005	15	21.1	<0.005	49	2.5	ns	69
Galapagos Iss.	Freq. col.	Ann.	3.2	ns	14	18.0	<0.005	24	8.3	<0.05	24	3.6	ns	66
		Lun.		–			–		14.4	ns	24	26.4	<0.01	66
	Freq. SIV	Ann.		–			–			–			–	
		Lun.		–			–			–			–	



P. damicornis ($n=1$) and *P. elegans* ($n=2$) sampled at Uva Island in August 1984 contained gonads, indicating a return to normal reproductive activity within 1 yr after the El Niño disturbance (Glynn 1988, 1990). Overall, a higher proportion of colonies of *P. elegans* than *P. damicornis* were reproductively active (Table 3).

At the Pearl Islands (Gulf of Panama), gonads were present in *Pocillopora damicornis* and *P. elegans* only during the nonupwelling wet season (June to December). *P. damicornis* possessed Stage III and IV oocytes and spermaries in July and November only. From the ten collections and 31 colonies analyzed, only two colonies (6.4%) contained gonads (Table 3). Stage IV oocytes and spermaries were present in *P. elegans* in October and November. From nine collections and 28 colonies, five colonies (17.9%) contained Stage II and IV gonads (Table 3).

In the Galapagos Islands, the only significant seasonal trend in *Pocillopora damicornis* was a high incidence of Stage II oocytes in early July 1987 (Fig. 10A, Table 4). Stage IV spermatozoa were present in November 1986 and in January, May and June 1987, and a few Stage IV oocytes were present in May 1987. The unusually high reproductive activity in 1987 occurred during an El Niño event of moderate strength (Quinn et al. 1987). *P. elegans* had significantly more gonads in the normally cool water season and limited sexual activity at the beginning of the warm season (Fig. 11A, Table 4). Stage IV gametes were present only in the 1987 collections.

Fig. 7. *Pocillopora elegans*. Reproductive condition at Caño Island, Costa Rica (1985 to 1989). Panels (A) to (C) as in Fig. 6. The total record consists of 32 collections with 116 colonies sampled ($\bar{x}=3.6$ colonies collection^{-1}) and 1239 unique polyps scored ($\bar{x}=38.7$ polyps collection^{-1})

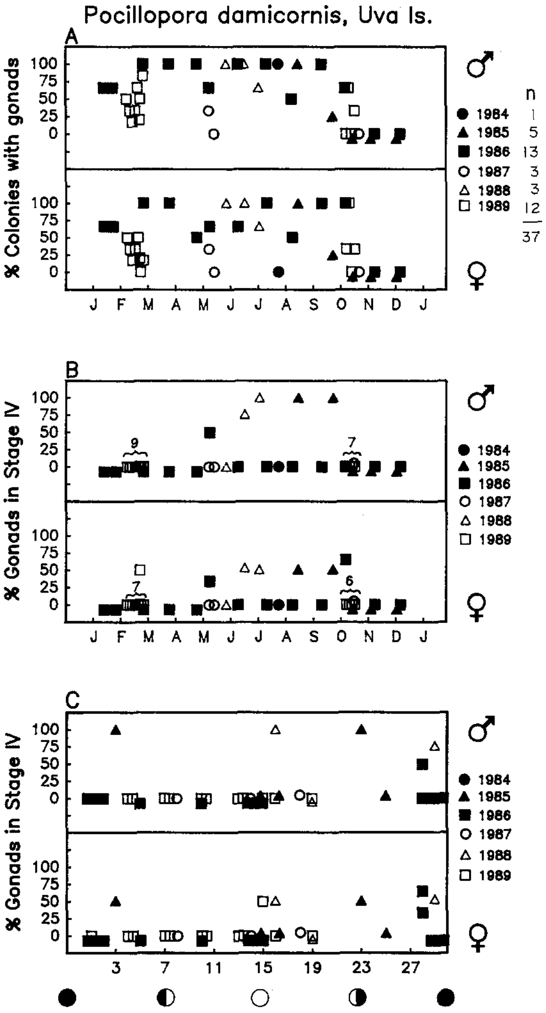


Fig. 8. *Pocillopora damicornis*. Reproductive condition at Uva Island, Panama (1984 to 1989). Panels (A) to (C) as in Fig. 6. The total record consists of 37 collections with 74 colonies sampled ($\bar{x}=2.0$ colonies collection^{-1}) and 1031 unique polyps scored ($\bar{x}=27.9$ polyps collection^{-1})

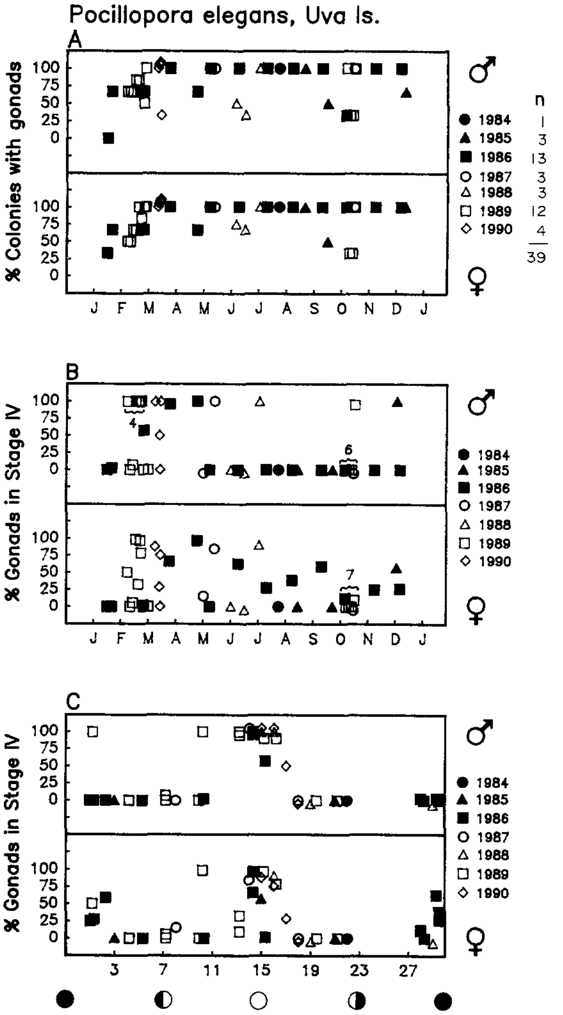


Fig. 9. *Pocillopora elegans*. Reproductive condition at Uva Island, Panama (1984 to 1990). Panels (A) to (C) as in Fig. 6. The total record consists of 39 collections with totals of 89 colonies sampled ($\bar{x}=2.3$ colonies collection^{-1}) and 1339 unique polyps scored ($\bar{x}=34.3$ polyps collection^{-1})

Lunar activity

There was a tendency for mature gametes to occur more frequently around new and full lunar phases than at other times. This was especially evident in *Pocillopora damicornis* and *P. elegans* at Caño Island (Figs. 6 and 7) and Uva Island (Figs. 8 and 9). From collections with sufficient data, chi-square tests were performed on the occurrence of Stage IV gametes at the four lunar phases. For *P. elegans* at Caño Island, males ($p<0.001$) and females ($p=0.01$) contained the highest frequency of mature gametes around the full moon (Fig. 7, Table 4). The significant ($p<0.001$) lunar trends in both sexes of *P. damicornis* at Uva Island indicated increased maturity at and around the new moon (Fig. 8, Table 4). Mature spermaries in *P. elegans* at Uva Island were significantly ($p<0.001$) clustered around full moon (Fig. 9, Table 4). Ripe oocytes also occurred more frequently around full and new moon, but this trend was non-significant ($p>0.05$). The low reproductive activity of Galapagos pocilloporids precludes any assessment of lunar periodicity in that area.

Sequential sampling of the gonadal condition in *Pocillopora elegans* also revealed a high incidence of mature gametes in both sexes on and around full moon (Fig. 12). Stage IV gametes were present in corals over 5- to 7-d periods spanning the full moon phase at Caño Island (Fig. 12A) and Uva Island (Fig. 12B). The disappearance of Stage IV gametes occurred within 3 d after the full moon at Uva Island in March 1990 (Fig. 12C). These patterns indicate that spawning probably occurred 1 to 2 nights after the full moon. At Uva Island, Stage IV gametes were present 1 night after new moon and were absent 3 nights later (Fig. 12B). This indicates that some spawning activity may occur around the new moon as well (see Figs. 8C and 9C). Since early embryos and planula larvae were never observed during these peak reproductive periods, it is highly probable that *P. elegans* is a broadcast spawner.

Pocillopora damicornis was sampled repeatedly in 1989 during two periods at Uva Island (in February and October) and during one period in the Pearl Islands (October–November), but mature gonads were sufficiently rare to negate any analysis of lunar synchrony.

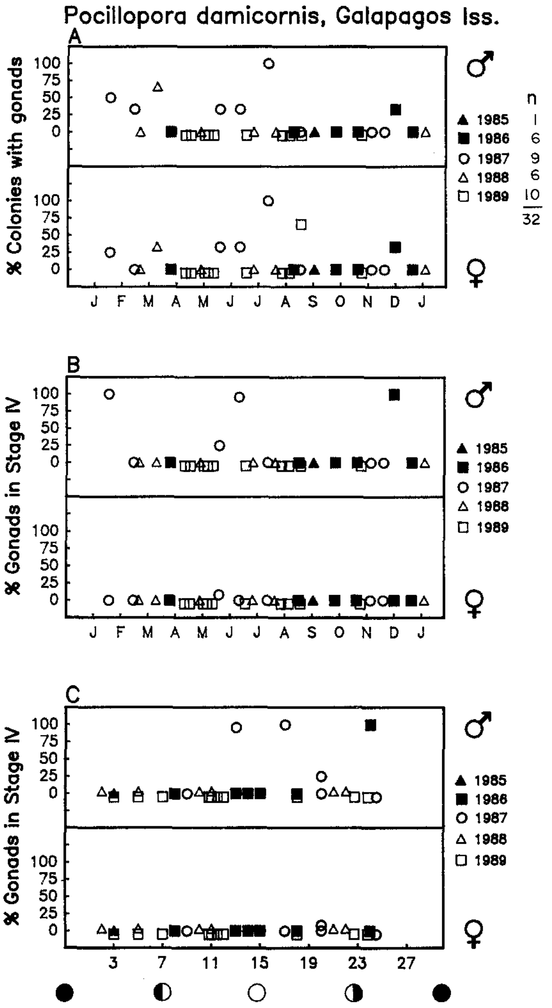


Fig. 10. *Pocillopora damicornis*. Reproductive condition in the Galapagos Islands, Ecuador (1985 to 1989). Panels (A) to (C) as in Fig. 6. The total record consists of 32 collections with totals of 80 colonies sampled ($\bar{x}=2.5$ colonies collection^{-1}) and 915 unique polyps scored ($\bar{x}=28.6$ polyps collection^{-1})

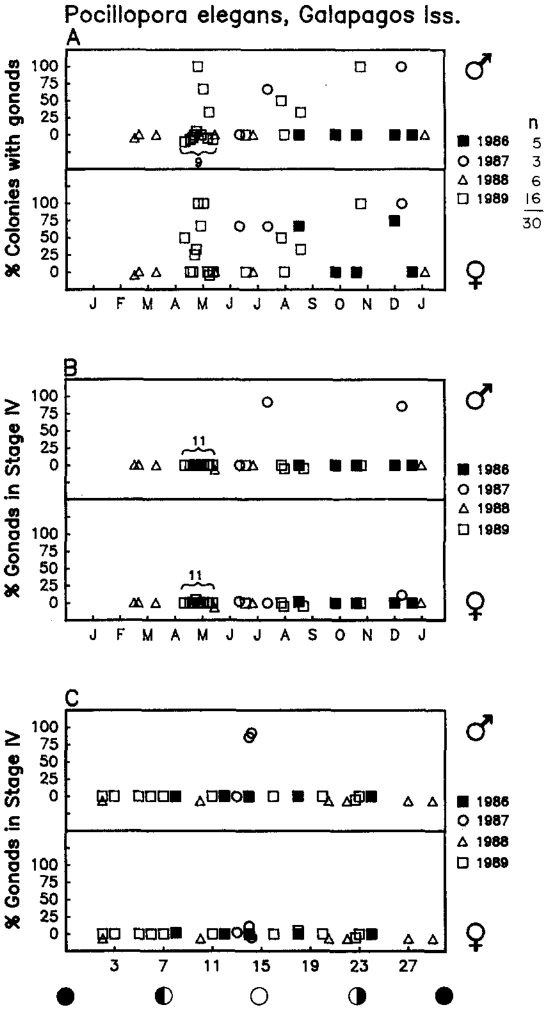


Fig. 11. *Pocillopora elegans*. Reproductive condition in the Galapagos Islands, Ecuador (1986 to 1989). Panels (A) to (C) as in Fig. 6. The total record consists of 30 collections with 74 colonies sampled ($\bar{x}=2.5$ colonies collection^{-1}) and 1000 unique polyps scored ($\bar{x}=33.3$ polyps collection^{-1})

Discussion

Reproductive condition

In agreement with previous studies, we did not observe the release of planula larvae from pocilloporid corals in Panama (Birkeland 1977, Wellington 1982a, Richmond 1985, 1987a), Costa Rica or the Galapagos Islands. Moreover, no embryos or planulae were found in the histological examination of nearly 700 colonies combined of *Pocillopora damicornis* and *P. elegans*. By contrast, however, we found that a relatively high proportion of corals, ca. 49% overall (both species, all sites) and as high as 90% (*P. elegans*, Uva Island), contained gonads in advanced stages of development over the 5- to 7-yr sampling period at the three principal study sites. Most gravid colonies contained both oocytes and spermaries in similar stages of development, indicating a capacity to function as simultaneous hermaphrodites. Richmond (1985) found no mature gonads in the histological examination of over 900 branches of *P. damicornis* sampled in Panama from upwelling and nonupwelling areas over a ca. 2-yr period (February 1984 to September 1985). Since some of our sampling of *P. damicornis* was performed during the same time interval and at the same localities in Panama as Richmond's (1985) study, we can only surmise that apparently contradictory findings resulted from differences between the sample sizes and the histological procedures used. For example, many of Richmond's (1985) collections were made in the upwelling environment of the Gulf of Panama where we found gonads in only ca. 6% of all colonies sampled. Further, Richmond (1985) examined 10 to 15 polyps colony^{-1}, whereas we examined 20 to 100 polyps colony^{-1}. Finally, Richmond's (1985) samples were fixed in 10% formalin (instead of Zenker's fixative), which may have interfered with staining of the reproductive tissues. In any case, neither study found any indications of planular development. Thus, like *P. verrucosa* in the Red Sea (Fadlallah 1985, Shlesinger and Loya 1985) and *P. meandrina* at

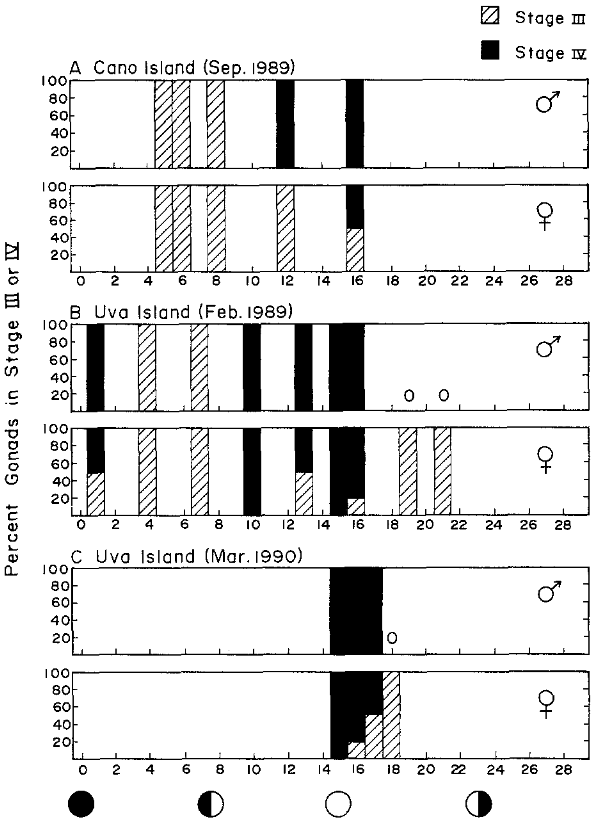


Fig. 12. *Pocillopora elegans*. Frequency of Stage III and Stage IV gametes occurring in coral sampled sequentially at (A) Caño Island and (B and C) Uva Island. "0" values indicate absence of gonads in the samples collected

Hawaii (Stimson 1978), *P. damicornis* and *P. elegans* in the eastern Pacific are probably broadcast spawners that produce externally fertilized, free-swimming planulae.

Seasonality

The majority of studies conclude that gametogenesis is most common in reef-building corals during seasonal warming periods or at mid-summer when sea temperatures are high (Fadlallah 1983, Harriott 1983 b, Harrison et al. 1984, Shlesinger and Loya 1985, Babcock et al. 1986, Szmant 1986, Heyward et al. 1987, Richmond and Hunter 1990). However, a few species, including *Pocillopora damicornis*, breed during the cooler winter months in some areas (Harriott 1983 a, Shlesinger and Loya 1985, Szmant 1986). Also, the reproductive seasonality of corals (Oliver et al. 1988, Richmond and Hunter 1990) and many other tropical-subtropical invertebrate taxa (Giese and Pearse 1974) is less marked at lower latitudes, with more frequent gametogenesis in areas where annual sea temperature ranges are slight. Although in the present study all sampling was performed between ca. 8°N and 1°S, seasonal upwelling and changing current paths cause marked annual variations in sea temperature in the Gulf of Panama and Galapagos Islands.

Reproductive activity in the eastern Pacific was related to local thermal regimes, with generally higher incidences of gravid corals at sites with stable, warm water conditions or during warming periods in areas that experience significant seasonal variations. At Caño Island (Costa Rica) and Uva Island (Panama), where thermal conditions are relatively high and stable, 60 to 90%, respectively, of all *Pocillopora elegans* sampled contained gonads throughout the year, and 32 and 60%, respectively, of *P. damicornis* were gravid. This year-long gametogenesis at Caño and Uva Islands differs from all known broadcast-spawning pocilloporids, which are characterized by a highly seasonal breeding period (Stimson 1978, Fadlallah 1985, Shlesinger and Loya 1985). No gonads were found in pocilloporid corals in one collection from the Pearl Islands (Gulf of Panama) during the upwelling season (March 1985, $n=4$ colonies for *P. damicornis* and $n=3$ for *P. elegans*). Annual variation in mean monthly seawater temperature in the Gulf of Panama is 5 C° and overall only 6 to 18% of the coral samples contained gonads. By contrast, annual variation in mean monthly seawater temperature in the central Galapagos Islands is 3 C°, and overall 16 to 40% of the corals in this area were gravid. Relatively few gonads were present in Galapagos corals during the dry season, when the relatively cool South Equatorial Current is dominant. However, Stage IV spermaries were present in both pocilloporid species throughout the year from December 1986 to December 1987, which spanned a moderate El Niño event (Quinn et al. 1987). During this period, SST anomalies ranged between 1 and 2 C° above average (Lander 1989).

Long-term coral growth records in the Galapagos indicate periods of accelerated linear skeletal growth during moderate El Niño years (Glynn and Wellington 1983). Jokiel and Guinther (1978) also found that optimal temperatures (26 to 27 °C) are the same for both growth and reproduction in *Pocillopora damicornis*, thus supporting the possibility that moderate El Niño warming can stimulate gametogenesis in Galapagos pocilloporid corals. Correlation between gametogenesis and skeletal growth rate would indicate that corals are showing an overall positive response to favorable environmental conditions. Since light-enhanced calcification is dependent upon endosymbiotic zooxanthellae productivity, and large amounts of photosynthate are translocated from zooxanthellae to coral host tissues (Muscatine and Porter 1977, Falkowski et al. 1984), it is reasonable to assume that surplus energy would be available for other needs (e.g. reproduction) during periods of rapid colony growth. It should be noted, however, that pavonid corals, whose skeletal growth is dependent on zooplankton abundance, undergo maximum growth during periods of low water temperature and high productivity, and reproduce during warm periods (Wellington 1982 b, Wellington and Glynn 1983). Shlesinger and Loya (1985) speculated that Red Sea corals reproduce during the warm summer months when algal cover is low. At such times, the settlement of larvae and juvenile coral growth would be favored by the increased availability of space and reduced competition with benthic algae. Selection also might be acting on eastern-Pacific pocilloporid corals to favor reproduction during warm, non-upwelling periods when growth rates are high and competition with algae and suspension-feeding animal populations would be minimal (Birkeland 1977).

Lunar activity

Lunar periodicity of planula release in *Pocillopora* spp. has been observed in many studies (Fadlallah 1983, Harriott 1983a, Jokiel 1985, Richmond and Hunter 1990), but the synchrony of planulation has been found to vary both among species and among locations within species (Stimson 1978, Richmond and Jokiel 1984). *P. verrucosa* was observed to broadcast gametes at Eilat, Red Sea, during the new moon (Shlesinger and Loya 1985). Fadlallah (1985) failed to detect lunar spawning in *P. verrucosa* farther south in the Red Sea, but this may have been due to his infrequent sampling schedule. Our sequential sampling and histological evidence from longer-term collections indicate that most spawning in *P. damicornis* and *P. elegans* occurred during a few days around full moon, with some spawning also occurring around new moon. Since spawning has not been observed in the field, the extent of synchrony in eastern Pacific pocilloporids is still unknown.

Reproduction and recovery

The recruitment of *Pocillopora* spp. by settling planulae has been less frequent in Panama (Birkeland 1977, Highsmith 1982, Wellington 1982a, Richmond 1985, 1987a) than in the central and western Pacific (Birkeland et al. 1982, Harriott 1983a, Richmond 1985, 1987a). Only two larval recruits of *Pocillopora* spp. were found on settling plates by Birkeland (1977) in a 5-yr study in Panama, whereas larval settlement was commonplace over a 180-d period at Guam (Birkeland et al. 1982). From the shapes of colonies (branch growth orientation) and the appearance of their attachment sites, Highsmith (1982) and Richmond (1985, 1987a) concluded that asexual fragmentation accounted for 100 and 97%, respectively, of *P. damicornis* recruitment onto seaward reef slopes in Panama. In Highsmith's (1982) study, 1.2 *Pocillopora* spp. colonies m^{-2} were replaced every 3 yr by fragmentation. Seven minute colonies (with 1 to 12 polyps each) of *P. damicornis* were found attached to the underside of a brick in the Gulf of Panama, but Richmond (1985) surmised that these originated from polyps that separated from a nearby, stressed colony ('polyp bail-out'; see Sammarco 1982). The comparatively low rates of larval recruitment in eastern Pacific pocilloporids is in agreement with the low rates generally reported for broadcast spawners (Szmant 1986). Although similar morphologically, the fundamental life-history differences between eastern Pacific and central-western Pacific *P. damicornis* raise doubts of their genetic similarity (Richmond 1985, 1987a).

Some workers have related the reproductive mode of corals to the levels of habitat disturbance they experience. Stimson (1978) found that shallow-living Pacific corals that were frequently disturbed and experienced high mortality reproduced by releasing planulae year-round. Szmant (1986) has also argued that some Caribbean corals inhabiting unstable habitats and suffering high adult mortality rates may have evolved a year-round, brooding mode to enhance local recruitment. Moreover, Richmond's (1985) failure to find evidence for sexual reproduction in *Pocillopora damicornis* in Panama led him to conclude that selection for an asexual, fragmentative mode of reproduction has been predominant in the eastern Pacific. Present results do not fit these models. Firstly, the broadcast spawning found in these corals occurred more frequently in physically stable environments (nonupwelling Costa Rica and Gulf of Chiriqui) and less frequently in unstable environments (upwelling Gulf of Panama and cool/warm currents in the Galapagos). Secondly, eastern Pacific *Pocillopora* spp. are broadcast spawners with low rates of recruitment, but they appear to suffer physical and biotic disturbances (e.g. extreme tidal exposures, intense upwelling, El Niño warming events, dinoflagellate blooms, competition with benthic algae and predation) more frequently (Glynn et al. 1972, Glynn 1974, 1976, 1982, 1990, Glynn and Wellington 1983, Glynn and D'Croz 1990, Guzman et al. 1990) than implied by Richmond (1985).

Following the high coral mortality (50 to 97%) that accompanied the 1982–83 El Niño disturbance (Glynn et al. 1988), numerous pocilloporid recruits have been observed at some sites in Costa Rica, Panama and the Galapagos Islands (P. W. Glynn unpublished data). Many of the recruits were small (1 to 2 cm maximum diameter) when first observed, and most were attached to vertical, non-carbonate rock surfaces or to the summits of boulders, indicating that recruitment by fragmentation was unlikely. Their form and type of colony attachment also conform to Richmond's (1985) criteria for recognizing the larval origin of corals. In the Galapagos Islands, larval settlement presumably has been the predominant mode of recruitment, and the only observed form of recruitment in areas that experienced high mortality (97 to 100%) in 1983. Only on coral reefs in Panama, where some large pocilloporid patches survived the 1983 disturbance, has fragmentation been important in reef recovery.

The occurrence of larval recruitment in eastern Pacific *Pocillopora* spp., although low compared with other Pacific areas, suggests that local populations have the capacity to recover from disturbances. For *P. verrucosa*, a broadcast spawner like the eastern Pacific pocilloporids, planulae settle 3 to 5 d after spawning (Shlesinger and Loya 1985). From several lines of evidence, including energetic needs, larval life, competency, and current transport, Richmond (1982, 1985, 1987b, 1990) has argued that planulae from brooding pocilloporid corals can cross the eastern Pacific barrier. Such long-distance dispersal may be important over geologic time as an occasional means serving to re-introduce populations that suffer extinctions at the limits of their distribution or to maintain gene flow among relatively isolated subpopulations. However, it does not seem necessary to invoke long-distance dispersal in the present case, where relatively large numbers of pocilloporid corals survived the 1982–83 disturbance event.

Acknowledgements. We thank the following for help in obtaining the coral collections: L. D'Croz, J. Eakin, R. Espinosa, J. Feingold, P. Martinez, R. H. Richmond, F. Rivera, J. Rosario B., A. Velarde and A. Yedid. We also gratefully acknowledge the assistance of M. Basile, J. Feingold and J. H. Stout in the histological preparations. A. Szmant offered valuable advice on coral histology and reproductive biology. Collecting permission and logistical support were facilitated through M. M. Murillo (Centro de Investigacion en Ciencias del Mar y Limnologia, Costa Rica), L. D'Croz (Centro de Ciencias del Mar y Limnologia, Panama), J. B. C. Jackson (Smithsonian Tropical Research Institute), G. Reck and D. Evans (Charles Darwin Research Station), and M. Cifuentes, H. Ochoa and F. Cepeda (Galapagos National Park Service, Ecuador). Permission to work in Panamanian waters was granted by the Direccion de Recursos Marinos, Ministerio de Comercio e Industrias, Republic of Panama. This study was supported by U.S. National Science Foundation Grants OCE-8415615 and 8716726. Contribution from the University of Miami, Rosenstiel School of Marine and Atmospheric Science.

Literature cited

Babcock, R. C., Bull, G. D., Harrison, P. L., Heyward, A. J., Oliver, J. K., Wallace, C. C., Willis, B. L. (1986). Synchronous spawning of 105 scleractinian coral species on the Great Barrier Reef. Mar. Biol. 90: 379–394

Birkeland, C. (1977). The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proc. 3rd int. Symp. coral Reefs 1: 15–21 [Taylor, D. L. et al. (eds.) Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida]

Birkeland, C., Rowley, D., Randall, R. H. (1982). Coral recruitment patterns at Guam. Proc. 4th int. Symp. coral Reefs 2: 339–344 [Gomez, E. D. et al. (eds.) Marine Sciences Center, University of the Philippines, Quezon City]

Connell, J. H., Keough, M. J. (1985). Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: Pickett, S. T. A., White, P. S. (eds.) The ecology of natural disturbance and patch dynamics. Academic Press, New York, p. 125–151

Cortes, J., Murillo, M. M., Guzman, H. M., Acuña, J. (1984). Perdida de zooxantelas y muerte de corales y otros organismos arrecifales en el Caribe y Pacifico de Costa Rica. Revta Biol. trop. 32: 227–231

Dana, T. F. (1975). Development of contemporary eastern Pacific coral reefs. Mar. Biol. 33: 355–374

Fadlallah, Y. H. (1983). Sexual reproduction, development and larval biology in scleractinian corals. A review. Coral Reefs 2: 129–150

Fadlallah, Y. H. (1985). Reproduction in the coral *Pocillopora verrucosa* on the reefs adjacent to the industrial city of Yanbu (Red Sea, Saudi Arabia). Proc. 5th int. coral Reef Congr. 4: 313–318. [Gabrié, C. et al. (eds.) Antenne Museum-EPHE, Moorea, French Polynesia]

Falkowski, P. G., Dubinsky, Z., Muscatine, L., Porter, J. W. (1984). Light and the bioenergetics of a symbiotic coral. BioSci. 34: 705–709

Forsbergh, E. D. (1969). On the climatology, oceanography and fisheries of the Panama Bight. Bull. inter-Am. trop. Tuna Commn 14: 49–385

Giese, A. C., Pearse, J. S. (eds.) (1974). Introduction. In: Reproduction of marine invertebrates, Vol. I, Acoelomate and pseudocoelomate metazoans. Academic Press, New York, p. 1–49

Glynn, P. W. (1974). The impact of *Acanthaster* on corals and coral reefs in the eastern Pacific. Envir. Conserv. 1: 295–304

Glynn, P. W. (1976). Some physical and biological determinants of coral community structure in the eastern Pacific. Ecol. Monogr. 46: 431–456

Glynn, P. W. (1977). Coral growth in upwelling and nonupwelling areas off the Pacific coast of Panama. J. mar. Res. 35: 567–585

Glynn, P. W. (1982). Coral communities and their modifications relative to past and prospective Central American seaways. Adv. mar. Biol. 19: 91–132

Glynn, P. W. (1984). Widespread coral mortality and the 1982/83 El Niño warming event. Envir. Conserv. 11: 133–146

Glynn, P. W. (1988). El Niño-Southern Oscillation 1982–1983: nearshore population, community, and ecosystem responses. A. Rev. Ecol. Syst. 19: 309–345

Glynn, P. W. (ed.) (1990). Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. In: Global ecological consequences of the 1982–1983 El Niño-Southern Oscillation. Elsevier Oceanography Series, Amsterdam, p. 55–126

Glynn, P. W., Cortes, J., Guzman, H. M., Richmond, R. H. (1988). El Niño (1982–83) associated coral mortality and relationship to sea surface temperature deviations in the tropical eastern Pacific. Proc. 6th int. coral Reef Symp. 3: 237–243 [Choat, J. H. et al. (eds.) Sixth International Coral Reef Symposium Executive Committee, Townsville, Australia]

Glynn, P. W., D'Croz, L. (1990). Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. Coral Reefs 8: 181–191

Glynn, P. W., Macintyre, I. G. (1977). Growth rate and age of coral reefs on the Pacific coast of Panama. Proc. 3rd int. Symp. coral Reefs 2: 251–259 [Taylor, D. L. et al. (eds.) Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida]

Glynn, P. W., Prahl, H. von, Guhl, F. (1982). Coral reefs of Gorgona Island, Colombia, with special reference to corallivores and their influence on community structure and reef development. An. Inst. Invest. mar. Punta de Betín 12: 185–214

Glynn, P. W., Stewart, R. H. (1973). Distribution of coral reefs in the Pearl Islands (Gulf of Panama) in relation to thermal conditions. Limnol. Oceanogr. 18: 367–379

Glynn, P. W., Stewart, R. H., McCosker, J. E. (1972). Pacific coral reefs of Panama: structure, distribution and predators. Geol. Rdsch. 61: 483–519

Glynn, P. W., Wellington, G. M. (1983). Corals and coral reefs of the Galapagos Islands. University of California Press, Berkeley

Guzman, H. M., Cortes, J. (1989). Coral reef community structure at Caño Island, Pacific Costa Rica. Pubbl. Staz. zool. Napoli (I: Mar. Ecol.) 10: 23–41

Guzman, H. M., Cortes, J., Glynn, P. W., Richmond, R. H. (1990). Coral mortality associated with dinoflagellate blooms in the eastern Pacific (Costa Rica and Panama). Mar. Ecol. Prog. Ser. 60: 299–303

Guzman, H. M., Cortes, J., Richmond, R. H., Glynn, P. W. (1987). Efectos del fenomeno de El Niño-Oscilacion Sureña 1982–83 en los arrecifes coralinos de la Isla del Caño, Costa Rica. Revta Biol. trop. 35: 325–332

Harriott, V. J. (1983a). Reproductive seasonality, settlement, and post-settlement mortality of *Pocillopora damicornis* (Linnaeus), at Lizard Island, Great Barrier Reef. Coral Reefs 2: 151–157

Harriott, V. J. (1983b). Reproductive ecology of four scleractinian species at Lizard Island, Great Barrier Reef. Coral Reefs 2: 9–18

Harrison, P. L., Babcock, R. C., Bull, G. D., Oliver, J. K., Wallace, C. C., Willis, B. L. (1984). Mass spawning in tropical reef corals. Science, Wash., D.C. 223: 1,186–1,189

Heyward, A. J., Yamazato, K., Yemin, T., Minei, M. (1987). Sexual reproduction of corals in Okinawa. Galaxea 6: 331–343

Highsmith, R. C. (1982). Reproduction by fragmentation in corals. Mar. Ecol. Prog. Ser. 7: 207–226

Jokiel, P. L. (1985). Lunar periodicity of planula release in the reef coral *Pocillopora damicornis* in relation to various environmental factors. Proc. 5th int. coral Reef Congr. 4: 307–312. [Gabrié, C. et al. (eds.) Antenne Museum-EPHE, Moorea, French Polynesia]

Jokiel, P. L., Guinther, E. B. (1978). Effects of temperature on reproduction in the hermatypic coral *Pocillopora damicornis*. Bull. mar. Sci. 33: 181–187

Kwiecinski, B., Chial, B., Torres, A. (1988). El Niño and post El Niño (1982–1986) in the Gulf of Panama. Trop. Ocean-Atmos. Newsl. 44: 7–8

Kwiecinski, B., Chial-Z., B. (1983). Algunos aspectos de la oceanografia del Golfo de Chiriqui, su comparacion con el Golfo de Panama. Revta Biol. trop. 31: 323–325

Lander, M. A. (1989). A comparative analysis of the 1987 ENSO event. Trop. Ocean-Atmos. Newsl. 49: 3–6

Luna, J. G. (1968). Manual of histologic staining methods of the armed forces institute of pathology, 3rd edn. McGraw-Hill Book Company, New York

Muscatine, L., Porter, J. W. (1977). Reef corals: mutualistic symbioses adapted to nutrient-poor environments. BioSci. 27: 454–460

NOAA (National Oceanic and Atmospheric Administration) (1982). World weather records, 1961–1970. Environmental Data Information Service, Vol. 3. National Oceanic and Atmospheric Administration, National Climatic Center, Asheville, North Carolina

Oliver, J. K., Babcock, R. C., Harrison, P. L., Willis, B. L. (1988). Geographic extent of mass coral spawning: clues to ultimate causal factors. Proc. 6th int. coral Reef Symp. 2: 803–810 [Choat, J. H. et al. (eds.) Sixth International Coral Reef Symposium Executive Committee, Townsville, Australia]

Porter, J. W. (1972). Ecology and species diversity of coral reefs on opposite sides of the Isthmus of Panama. Bull. biol. Soc. Wash. 2: 89–116

Porter, J. W. (1974). Community structure of coral reefs on opposite sides of the Isthmus of Panama. Science, Wash., D.C. 186: 543–545

Prahl, H. von (1985). Blanqueo masivo y muerte de corales hermatipicos en el Pacifico Colombiano atribuidos al fenomeno de El Niño 1982–83. Boln ERFEN (CPPS, Bogota) 12: 22–24

Quinn, W. H., Neal, V. T., Antunez de Mayolo, S. E. (1987). El Niño occurrences over the past four and a half centuries. J. geophys. Res. 92: 14,449–14,461

Renner, J. A. (1963). Sea surface temperature monthly average and anomaly charts. Eastern tropical Pacific Ocean, 1947–58. U.S. Department of the Interior, U.S. Fish and Wildlife Service Special Scientific Report – Fisheries No. 442. U.S. Fish and Wildlife Service, Washington, D.C., p. 1–57

Richmond, R. H. (1982). Energetic considerations in the dispersal of *Pocillopora damicornis* (Linnaeus) planulae. Proc. 4th int. Symp. coral Reefs 2: 153–156 [Gomez, E. D. et al. (eds.) Marine Sciences Center, University of the Philippines, Quezon City]

Richmond, R. H. (1985). Variations in the population biology of *Pocillopora damicornis* across the Pacific. Proc. 5th int. coral Reef Congr. 6: 101–106. [Gabrié, C. et al. (eds.) Antenne Museum-EPHE, Moorea, French Polynesia]

Richmond, R. H. (1987a). Energetic relationships and biogeographical differences among fecundity, growth, and reproduction in the reef coral, *Pocillopora damicornis*. Bull. mar. Sci. 41: 595–604

Richmond, R. H. (1987b). Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. Mar. Biol. 93: 527–533

Richmond, R. H. (1990). The effects of the El Niño/Southern Oscillation on the dispersal of corals and other marine organisms. In: Glynn, P. W. (ed.) Global ecological consequences of the 1982–83 El Niño-Southern Oscillation. Elsevier Oceanography Series, Amsterdam, p. 127–140

Richmond, R. H., Hunter, C. L. (1990). Reproduction and recruitment of corals: comparisons among the Caribbean, the tropical Pacific, and the Red Sea. Mar. Ecol. Prog. Ser. 60: 185–203

Richmond, R. H., Jokiel, P. L. (1984). Lunar periodicity in larva release in the reef coral *Pocillopora damicornis* at Enewetak and Hawaii. Bull. mar. Sci. 34: 280–287

Robalino, M. (1985). Registros meterologicos de la estacion cientifica Charles Darwin para 1982–1983. In: Robinson, G., del Pino, E. M. (eds.) El Niño in the Galapagos Islands: the 1982–1983 event. Charles Darwin Foundation for the Galapagos Islands, Quito, Ecuador, p. 83–90

Robinson, G. (1985). The influence of the 1982–83 El Niño on Galapagos marine life. In: Robinson, G., del Pino, E. M. (eds.) El Niño in the Galapagos Islands: the 1982–1983 event. Charles Darwin Foundation for the Galapagos Islands, Quito, Ecuador, p. 153–190

Sammarco, P. W. (1982). Polyp bail-out: an escape response to environmental stress and a new means of reproduction in corals. Mar. Ecol. Prog. Ser. 10: 57–65

Sammarco, P. W., Andrews, J. C. (1988). Localized dispersal and recruitment in Great Barrier Reef corals: the Helix experiment. Science, Wash., D.C. 239: 1,422–1,424

Shlesinger, Y., Loya, Y. (1985). Coral community reproductive patterns. Red Sea versus the Great Barrier Reef. Science, Wash., D.C. 228: 1,333–1,335

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

Stoddart, J. A. (1983). Asexual production of planulae in the coral *Pocillopora damicornis*. Mar. Biol. 76: 279–284

Stoddart, J. A., Black, R. (1985). Cycles of gametogenesis and planulation in the coral *Pocillopora damicornis*. Mar. Ecol. Prog. Ser. 23: 153–164

Szmant, A. M. (1986). Reproductive ecology of Caribbean reef corals. Coral Reefs 5: 43–53

Szmant-Froelich, A., Reutter, M., Riggs, L. (1985). Sexual reproduction of *Favia fragum* (Esper): lunar patterns of gametogenesis, embryogenesis and planulation in Puerto Rico. Bull. mar. Sci. 37: 880–892

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

Veron, J. E. N., Pichon, M. (1976). Scleractinia of eastern Australia, part I. Families Thamnasteriidae, Astrocoeniidae, Pocilloporidae. Monogr. Ser. Aust. Inst. mar. Sci. 1: 1–86

Wellington, G. M. (1982a). Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. Ecol. Monogr. 52: 223–241

Wellington, G. M. (1982b). An experimental analysis of the effects of light and zooplankton on coral zonation. Oecologia 52: 311–320

Wellington, G. M., Glynn, P. W. (1983). Environmental influences on skeletal banding in eastern Pacific (Panama) corals. Coral Reefs 1: 215–222