

## A COMPARATIVE STUDY OF SEXUAL REPRODUCTION IN THREE SPECIES OF PANAMANIAN ZOANTHIDS (COELENTERATA: ANTHOZOA)

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### ABSTRACT

Colonies of *Zoanthus sociatus*, *Z. solanderi*, and *Palythoa caribaeorum* were sampled at 1-2 month intervals between December 1974 and April 1976 to determine their reproductive condition. *Z. sociatus* and *P. caribaeorum* exhibited seasonal patterns. *Z. sociatus* underwent gametogenesis from December 1974 through June 1975, and December 1975 through March 1976; *P. caribaeorum* underwent gametogenesis from December 1974 through June 1975.

All three species appear to be broadcast spawners with external fertilization. Maximum oocyte sizes varied between 250 and 450  $\mu\text{m}$ . Comparisons of fecundity and reproductive effort indicate that *Z. sociatus* had the highest number of oocytes per unit dry weight and per unit substrate area. *P. caribaeorum* had the highest reproductive effort in terms of oocyte volume per unit dry weight and per unit substrate area; this zoanthid produced the largest oocytes. *Z. solanderi* had the lowest fecundity and reproductive effort.

All three species are hermaphroditic: *Z. solanderi* (10 of 15 fertile colonies), *Z. sociatus* (4 of 24), and *P. caribaeorum* (4 of 23). We could not distinguish between zoanthids having independent male, female, and hermaphroditic colonies or sequential hermaphroditic patterns.

Zoanthid spawning may have been correlated with seasonal variation in environmental parameters. Near the end of the dry season a combination of long aerial exposures and high reef flat temperatures may have synchronized zoanthid spawning in April 1976. Partial mortality of *Z. sociatus* on the reef flat was also correlated with extreme exposures.

Zoanthids form distinctive, nearly monospecific assemblages in certain shallow reef habitats throughout the Caribbean Sea (Goreau, 1959; Kinzie, 1973; Sebens, 1977; 1982; Karlson, 1980; 1983; Suchanek and Green, 1981). Like scleractinians, zoanthids are colonial anthozoans capable of asexual budding and the formation of dense aggregations of polyps. Zoanthids lack hard skeletal structures and are therefore restricted to lateral growth over the substratum. Anthozoans, like *Zoanthus sociatus* and many branching scleractinians, are capable of relatively high rates of growth and regeneration as well as being capable of asexual dispersal by fragmentation (Highsmith et al., 1981; Tunnicliffe, 1981; Sebens, 1982; Karlson, 1983). These asexual processes appear to be favored by recurrent physical disturbances (storms and hurricanes) (Highsmith et al., 1981; Tunnicliffe, 1981; Karlson, 1983). In some cases, however, catastrophic disturbances are far too destructive, exceeding asexual capabilities for local population recruitment (Stoddart, 1974; Woodley et al., 1981).

The importance of the sexual part of the life cycle (gametogenesis, larval development, dispersal, and settlement) has not been fully documented for a single reef anthozoan. In fact, for quite some time it appeared that sexual reproduction in many species was infrequent (Marshall and Stephenson, 1933; Stimson, 1978; Kojis and Quinn, 1981). This has given rise to hypotheses on the adaptive value of the absence of sexuality in colonial corals (Marshall and Stephenson, 1933; Connell, 1978). Williams (1975), in his strawberry-coral model, predicted that sexual reproduction becomes rare in benign habitats where asexual reproduction is favored. Chia (1976), on the other hand, noted (in the case of clonal sea anemones) that asexual reproduction is often associated with stressful environments.

Table 1. Mean polyp height (mm), proportion of colonies and polyps which were fertile, fecundity (oocytes/gonad) and oocyte size for *Zoanthus sociatus*

Date	Polyp Height $\bar{x} \pm SE$ (N)	Proportion of Colonies Fertile	Proportion of Polyps Fertile	No. Oocytes per Gonad $\bar{x} \pm SE$ (N)	Oocyte Size ( $\mu\text{m}$ ) $\bar{x} \pm SE$ (N)
28 Dec. 74	13.2 $\pm$ 1.9 (23)	1/5	2/23	14.3 $\pm$ 2.7 (3)	64.4 $\pm$ 5.0 (26)
10 Feb. 75	9.2 $\pm$ 1.1 (17)	2/4	4/17	9.2 $\pm$ 1.2 (11)	102.3 $\pm$ 5.0 (68)
3 Mar. 75	9.2 $\pm$ 1.2 (12)	2/2	4/12	16.0 $\pm$ 4.2 (13)	161.1 $\pm$ 8.8 (109)
10 Apr. 75	8.5 $\pm$ 0.4 (31)	3/5	8/31	13.2 $\pm$ 1.3 (12)	254.7 $\pm$ 6.2 (112)
12 May 75	8.3 $\pm$ 0.5 (31)	3/5	12/31	—	213.4 $\pm$ 11.4 (18)
30 June 75	6.3 $\pm$ 0.5 (34)	4/4	24/34	24.5 $\pm$ 2.2 (39)	176.8 $\pm$ 3.4 (417)
1 Sept. 75	8.6 $\pm$ 0.6 (32)	1/5	2/32	0	0
13 Oct. 75	8.1 $\pm$ 0.4 (54)	0/5	0/54	0	0
5 Dec. 75	10.3 $\pm$ 0.5 (28)	1/5	2/28	3.2 $\pm$ 0.4 (11)	94.6 $\pm$ 6.1 (35)
16 Jan. 76	8.6 $\pm$ 0.4 (39)	1/6	2/40	14.0 $\pm$ 1.5 (3)	216.0 $\pm$ 14.5 (37)
Mar. 76	9.7 $\pm$ 1.0 (42)	5/5	24/42	18.0 $\pm$ 1.4 (24)	201.0 $\pm$ 6.5 (281)
Apr. 76	7.4 $\pm$ 0.5 (39)	1/5	1/39	0	0

Connell (1973), in an effort to explain the absence of sexuality in some long-lived large colonies, suggested that some colonial corals may delay sexual reproduction until a certain size is achieved. Recent work indicates that sexuality in reef and nonreef corals is more prevalent than previously expected, and that corals exhibit more varied modes of larval development and types than previously known (Szmant-Froelich et al., 1980; Bothwell, 1981; Kojis and Quinn, 1981; Fadlallah and Pearse, 1982a; b).

As with other reef cnidarians, there has been very little work on the sexual phase of the zoanthid life cycle. To date, the few species studied all appear to be broadcast spawners with external development (Kimura et al., 1972; Yamazato et al., 1973; Cooke, 1976; Karlson, 1981). The fate of reproductive products and the importance of sexual reproduction to local population regulation and regional dispersal are entirely unknown. Two post-planula larval types (given the generic names *Zoanthea* and *Zoanthina*) have been taken in plankton samples (Menon, 1926; Hyman, 1940; Scheltema, 1971; Rutzler et al., 1980), but only indirect evidence has linked these larvae with the adult species (Scheltema, 1971).

Table 2. Mean polyp oral diameter (mm), proportion of colonies and polyps which were fertile, fecundity (oocytes/gonad) and oocyte size for *Palythoa caribaeorum*

Date	Polyp Oral Diameter $\bar{x} \pm SE$ (N)	Proportion of Colonies Fertile	Proportion of Polyps Fertile	No. Oocytes per Gonad $\bar{x} \pm SE$ (N)	Oocyte Size ( $\mu\text{m}$ ) $\bar{x} \pm SE$ (N)
24 Dec. 74	4.1 $\pm$ 0.2 (53)	1/6	1/62	0	0
10 Feb. 75	4.2 $\pm$ 0.1 (54)	1/5	9/54	24.7 $\pm$ 2.0 (15)	134.0 $\pm$ 6.2 (94)
3 Mar. 75	4.9 $\pm$ 0.2 (46)	3/3	39/46	45.2 $\pm$ 7.6 (11)	354.6 $\pm$ 6.0 (98)
10 Apr. 75	5.3 $\pm$ 0.2 (55)	5/5	40/55	23.7 $\pm$ 1.3 (36)	223.5 $\pm$ 5.2 (425)
12 May 75	4.7 $\pm$ 0.2 (59)	3/5	13/59	0	0
30 June 75	4.0 $\pm$ 0.1 (37)	3/5	15/37	0	0
1 Sept. 75	3.2 $\pm$ 0.2 (54)	0/5	0/54	0	0
13 Oct. 75	3.4 $\pm$ 0.1 (48)	0/6	0/48	0	0
5 Dec. 75	3.3 $\pm$ 0.2 (44)	1/5	1/44	0	0
16 Jan. 76	4.2 $\pm$ 0.2 (48)	0/5	0/48	0	0
Mar. 76	3.9 $\pm$ 0.2 (55)	5/5	32/55	4.7 $\pm$ 0.8 (6)	429.5 $\pm$ 8.7 (29)
Apr. 76	4.1 $\pm$ 0.1 (76)	1/7	8/76	0	0

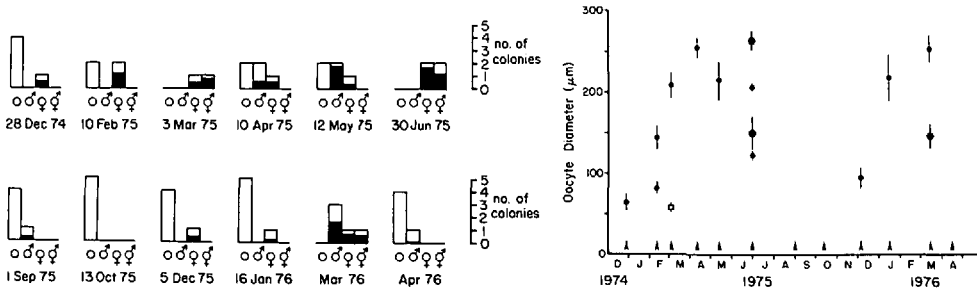


Figure 1. (Left) Number of infertile, male, female and hermaphroditic colonies of *Z. sociatus*. Dark areas represent the proportion of fertile polyps within each type.

Figure 2. (Right) Temporal distribution of mean oocyte diameters ( $\mu\text{m}$ ) per colony of *Zoanthus sociatus*. Arrows indicate dates of sample collections. Colonies with oocytes were entirely female (circles), hermaphroditic with female polyps (stars) or hermaphroditic with polyps bearing both oocytes and spermata (squares). 95% confidence intervals are indicated.

In this study, we examine sexual reproduction in three Caribbean zoanths collected along the coast of Panama. Our objectives were to examine the temporal patterns of sexual reproductive activity and to determine whether these patterns correlated with changes in environmental parameters. We compare these three species on the basis of reproductive mode, timing, fecundity and effort.

## MATERIALS AND METHODS

Specimens were collected from the intertidal *Zoanthus* and low coralline zones off the Smithsonian Tropical Research Institute Marine Laboratory at Galeta Island, Panama ( $9^{\circ}34'47''\text{N}$ ,  $78^{\circ}43'11''\text{W}$ ); a detailed site description appears in Sebens (1982). Collections were made every 1–2 months from December 1974 through April 1976 in conjunction with the long-term Environmental Monitoring Program (see below). During each sampling period five clusters of polyps were collected from colonies of *Zoanthus sociatus*, *Z. solanderi* and *Palythoa caribaeorum* which were found on solid coral rock or cemented rubble. These samples were at least 1 m apart and were taken without regard to their position within a colony. Colonies were not repeatedly sampled during successive sampling periods. In the zones with high densities of *Zoanthus* spp., colony boundaries were indistinct; intermingling of polyps from different colonies was common (Sebens, personal observations).

All specimens were taken to the laboratory, preserved in Bouin's fixative, and later transferred to 70% ethanol. Typically, 5–10 polyps from each cluster were dissected and examined for reproductive condition and sex. At least 2–5 gonads from each fertile polyp bearing ova were examined to determine the number of oocytes per gonad. Approximately 5–15 representative oocytes in each of these gonads were measured using a Wild M8 dissecting microscope equipped with an ocular micrometer in order to determine average oocyte size to the nearest  $20\ \mu\text{m}$  increment. In some cases wet preparations of gonad tissue were viewed under a compound microscope to ascertain the sex of the gonad. This was particularly necessary for early stages of gametogenesis.

Estimates of reproductive effort and related parameters were made for each of the three species. Gonad volume was calculated using the maximum number of gonads per polyp, the mean number of oocytes per gonad, and the mean oocyte diameter at their peak values. Oocyte volume was estimated as the volume of a sphere and was then multiplied by the number of oocytes per gonad and the maximum number of gonads per polyp to give total oocyte volume per polyp. This procedure yielded an estimate of the maximum reproductive material produced by a single polyp at this Panamanian site. We have assumed that all polyps in a colony reproduced at the maximum rate in order to convert our data to reproductive effort per unit weight and area. Ash-free dry weight per polyp was taken from Sebens (1977) for zoanths collected on the Galeta reef flat. Reproductive effort was then expressed as volume of oocytes per mg ash-free dry weight and per  $100\ \text{cm}^2$  substrate. The former measure was used because the zoanths differed greatly in polyp size and in percent inorganic content (ash). *Palythoa* had much more inorganic material (e.g., sand, sponge spicules) in the polyp walls than did the *Zoanthus* species (Sebens, 1977).

Table 3. Mean polyp height (mm), proportion of colonies and polyps which were fertile, fecundity (oocytes/gonad) and oocyte size for *Zoanthus solanderi*

Date	Polyp Height $\bar{x} \pm SE$ (N)	Proportion of Colonies Fertile	Proportion of Polyps Fertile	No. Oocytes per gonad $\bar{x} \pm SE$ (N)	Oocyte Size ( $\mu\text{m}$ ) $\bar{x} \pm SE$ (N)
28 Dec. 74	23.2 $\pm$ 2.5 (21)	0/5	0/21	0	0
10 Feb. 75	16.0 $\pm$ 1.3 (23)	0/5	0/23	0	0
3 Mar. 75	10.8 $\pm$ 0.5 (24)	0/5	0/25	0	0
12 May 75	12.6 $\pm$ 0.9 (23)	5/5	22/30	22.8 $\pm$ 3.6 (45)	134.8 $\pm$ 3.9 (109)
30 June 75	11.0 $\pm$ 0.8 (18)	4/4	15/18	21.6 $\pm$ 5.6 (5)	296.8 $\pm$ 14.0 (22)
1 Sept. 75	12.6 $\pm$ 0.7 (58)	0/5	0/58	0	0
13 Oct. 75	14.4 $\pm$ 0.6 (50)	2/5	17/55	17.1 $\pm$ 1.1 (45)	120.6 $\pm$ 3.6 (284)
5 Dec. 75	11.3 $\pm$ 0.6 (25)	0/5	0/25	0	0
16 Jan. 76	15.5 $\pm$ 0.8 (25)	0/5	0/25	0	0
Mar. 76	9.2 $\pm$ 0.5 (47)	4/7	24/57	20.1 $\pm$ 4.5 (24)	239.5 $\pm$ 3.6 (191)
Apr. 76	7.4 $\pm$ 0.3 (46)	0/6	0/46	0	0

## RESULTS

A total of 175 zoanthid samples were analyzed for reproductive condition. The overall frequency of fertile colonies sampled was 42.9%, 37.1%, and 26.3% for *Zoanthus sociatus*, *Palythoa caribaeorum*, and *Z. solanderi*, respectively. Tests of the null hypothesis that fertile colonies occur at the same frequency during the first (January–June) and last (July–December) 6 months of the year indicate that a significantly higher proportion of fertile colonies were sampled during the January through June period for *Z. sociatus* ( $\chi^2_c = 8.26$ ,  $P < 0.005$ , Table 1), and *P. caribaeorum* ( $\chi^2_c = 9.80$ ,  $P < 0.005$ , Table 2); we could not reject the null hypothesis for *Z. solanderi* ( $\chi^2_c = 3.11$ ,  $P > 0.05$ , Table 3).

*Zoanthus sociatus*.—Twenty-four of 56 colonies of *Z. sociatus* contained fertile polyps (Table 1). There were four types of fertile colonies encountered: female colonies (possibly with extremely small developing spermata); male colonies; hermaphroditic colonies with separate male and female (dioecious) polyps; and hermaphroditic colonies with monoecious polyps (Figs. 1 and 2). Much of the variation in oocyte number and size may have been due to differences between these colony types. Hermaphroditic and female colonies were collected at the same sampling date on three occasions: March 1975, June 1975, and March 1976 (Fig. 2). In March 1975, oocytes were significantly larger ( $t = 12.43$ , d.f. = 107,  $P < 0.001$ ) but less numerous ( $t = 11.19$ , d.f. = 11,  $P < 0.001$ ) in female colonies (208.0  $\mu\text{m}$  and 6.8 oocytes per gonad) than in monoecious polyps of hermaphroditic colonies (57.6  $\mu\text{m}$  and 36.8 oocytes per gonad). In June 1975, oocytes were significantly smaller ( $t = 8.50$ , d.f. = 415,  $P < 0.001$ ) but more numerous ( $t = 3.79$ , d.f. = 37,  $P < 0.001$ ) in female colonies (160.5  $\mu\text{m}$  and 27.9 oocytes per gonad) than in dioecious polyps of hermaphroditic colonies (219.4  $\mu\text{m}$  and 9.0 oocytes per gonad). Finally, in March 1976, we found significantly larger ( $t = 9.31$ , d.f. = 279,  $P < 0.001$ ) oocytes in female colonies (251.3  $\mu\text{m}$ ) than in dioecious polyps of hermaphroditic colonies (145.0  $\mu\text{m}$ ). There was no significant difference in oocyte number at this sampling date.

As indicated previously, a higher proportion of fertile colonies occurred in January through June samples. The smallest mean oocytes were detected in December samples (Fig. 2 and Table 1); the largest oocytes occurred in April and June 1975 and March 1976 (Fig. 2).

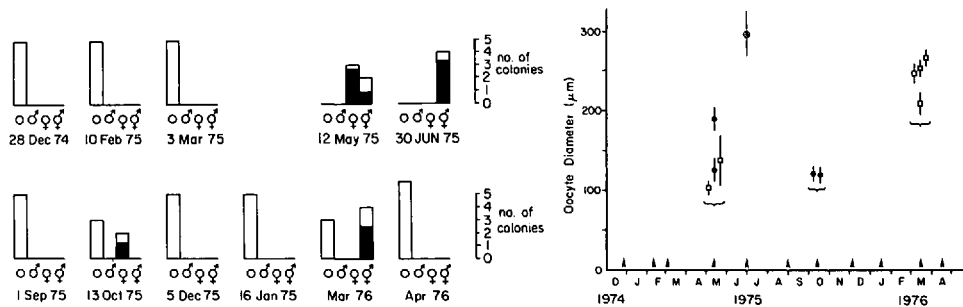


Figure 3. (Left) Number of infertile, male, female and hermaphroditic colonies of *Z. solanderi*. Dark areas represent the proportion of fertile polyps within each type.

Figure 4. (Right) Temporal distribution of mean oocyte diameters ( $\mu\text{m}$ ) per colony of *Zoanthus solanderi*. Arrows indicate dates of sample collections. Colonies with oocytes were entirely female (circles), hermaphroditic with female polyps (stars) or hermaphroditic with polyps bearing both oocytes and spermata (squares). 95% confidence intervals are indicated.

*Zoanthus solanderi*.—Only 15 of 57 colonies of *Z. solanderi* were fertile (Table 3). These occurred in samples taken in May, June, and October 1975, and in March 1976. There were only three types of fertile colonies encountered: female colonies, hermaphroditic colonies with dioecious polyps, and hermaphroditic colonies with hermaphroditic (monoecious) polyps (Figs. 3 and 4). As in Karlson (1981), no male colonies were found. Only once, in May 1975, were colonies of more than one type collected at the same time (Fig. 4). Comparisons between the fertile polyps from female and hermaphroditic colonies (with monoecious polyps) in this sample indicate that oocytes were significantly larger ( $t = 5.84$ , d.f. = 107,  $P < 0.001$ ) and more numerous ( $t = 4.12$ , d.f. = 45,  $P < 0.001$ ) in female colonies ( $157.6 \mu\text{m}$  and 33.2 oocytes per gonad) than in hermaphroditic colonies ( $107.1 \mu\text{m}$  and 7.1 oocytes per gonad). However, the largest mean oocyte sizes were determined for hermaphroditic colonies collected in June 1975 and March 1976 (Fig. 4 and Table 3); no female colonies were available for comparisons at these two dates.

*Palythoa caribaeorum*.—Like *Zoanthus sociatus*, *P. caribaeorum* was reproductively active primarily during the January through June interval (Table 2 and Fig. 5). Twenty-three of 62 colonies of *Palythoa caribaeorum* contained fertile polyps. As with *Z. sociatus*, all four types of colonies were encountered (Figs. 5 and 6). Oocytes from the April 1975 sample were significantly larger ( $t = 7.23$ , d.f. = 423,  $P < 0.001$ ) and more numerous ( $t = 2.64$ , d.f. = 34,  $P < 0.025$ ) in female colonies ( $239.1 \mu\text{m}$  and 25.2 oocytes per gonad) than in monoecious polyps of hermaphroditic colonies ( $135.9 \mu\text{m}$  and 17.1 oocytes per gonad). The largest oocytes ( $429.5 \mu\text{m}$ ) were found in a single hermaphroditic colony with dioecious polyps collected in March 1976 (Fig. 6).

*Reproductive Effort*.—*Palythoa caribaeorum* had over twice the reproductive effort ( $2.7 \text{ mm}^3$  oocytes/mg) of *Zoanthus sociatus* ( $1.0 \text{ mm}^3$  oocytes/mg); *Z. solanderi* had far less ( $0.6 \text{ mm}^3$  oocytes/mg) (Table 4). *P. caribaeorum* also produced slightly more oocytes per polyp (723) than did *Z. solanderi* (684) or *Z. sociatus* (686) (Table 4). However, *Z. sociatus* had the highest fecundity per unit dry weight (114) and, because of its high density, it also had the highest fecundity per unit

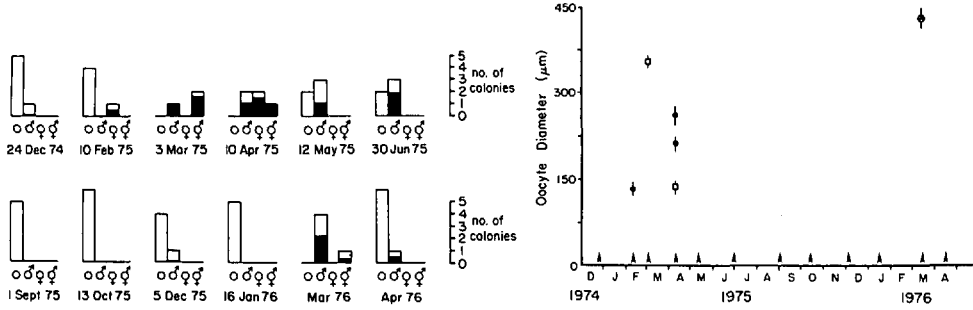


Figure 5. (Left) Number of infertile, male, female and hermaphroditic colonies of *P. caribaeorum*. Dark areas represent the proportion of fertile polyps within each type.

Figure 6. (Right) Temporal distribution of mean oocyte diameters (μm) per colony of *Palythoa caribaeorum*. Arrows indicate dates of sample collections. Colonies with oocytes were entirely female (circles), hermaphroditic with female polyps (stars) or hermaphroditic with polyps bearing both oocytes and spermata (squares). 95% confidence intervals are indicated.

area (274,000 oocytes/100 cm<sup>2</sup>) (Table 4). *P. caribaeorum* had the greatest oocyte production by volume (4,700 mm<sup>3</sup> oocytes/100 cm<sup>2</sup>) (Table 4).

In summary, *Palythoa caribaeorum* produced the largest oocytes and had the highest reproductive effort. *Zoanthus sociatus* produced the smallest oocytes and had the highest fecundity per unit dry weight and substrate area. *Z. solanderi* had the lowest reproductive effort and fecundity. *Z. solanderi*, however, has been shown to produce new polyps in the field at least as rapidly as do *Z. sociatus* and *P. caribaeorum* (Sebens, 1982). Since *Z. solanderi* has the largest polyps (17 mg ash-free dry weight, Table 4), it appears that it devotes more energy to growth and asexual reproduction than do the other two species.

DISCUSSION

In our study we have sampled populations of three zoanthid species at 1–2 month intervals over a 17-month period. *Zoanthus sociatus* and *Palythoa caribaeorum* exhibited a seasonal reproductive pattern; *Z. solanderi* did not. Due to the low fecundity measured for *Z. solanderi*, greater sampling effort would have been necessary in order to establish a temporal reproductive pattern.

Table 4. Reproductive effort per unit weight and per unit substrate area for the three zoanthid species

Species	<i>Z. sociatus</i>	<i>Z. solanderi</i>	<i>P. caribaeorum</i>
Maximum gonad number per polyp	28	30	16
Maximum mean oocyte number per gonad	24.5	22.8	45.2
Maximum mean oocyte diameter (μm)	255	297	430
Oocytes per polyp	686	684	723
Oocyte volume (mm <sup>3</sup> ) per polyp	6.0	9.4	30.1
Ash-free dry weight per polyp (mg)	6*	17*	11*
Oocytes per mg ash-free dry weight	114	40	66
Oocyte volume (mm <sup>3</sup> ) per mg ash-free dry weight	1.0	0.6	2.7
Polyp oral disc diameter (mm)	5*	8*	8*
Polyps per 100 cm <sup>2</sup> substrate	400	156	156
Oocytes per 100 cm <sup>2</sup> substrate (×10 <sup>3</sup> )	274	107	113
Oocyte volume (mm <sup>3</sup> × 10 <sup>3</sup> ) per 100 cm <sup>2</sup> substrate	2.4	1.5	4.7

\* Data from Sebens (1977).

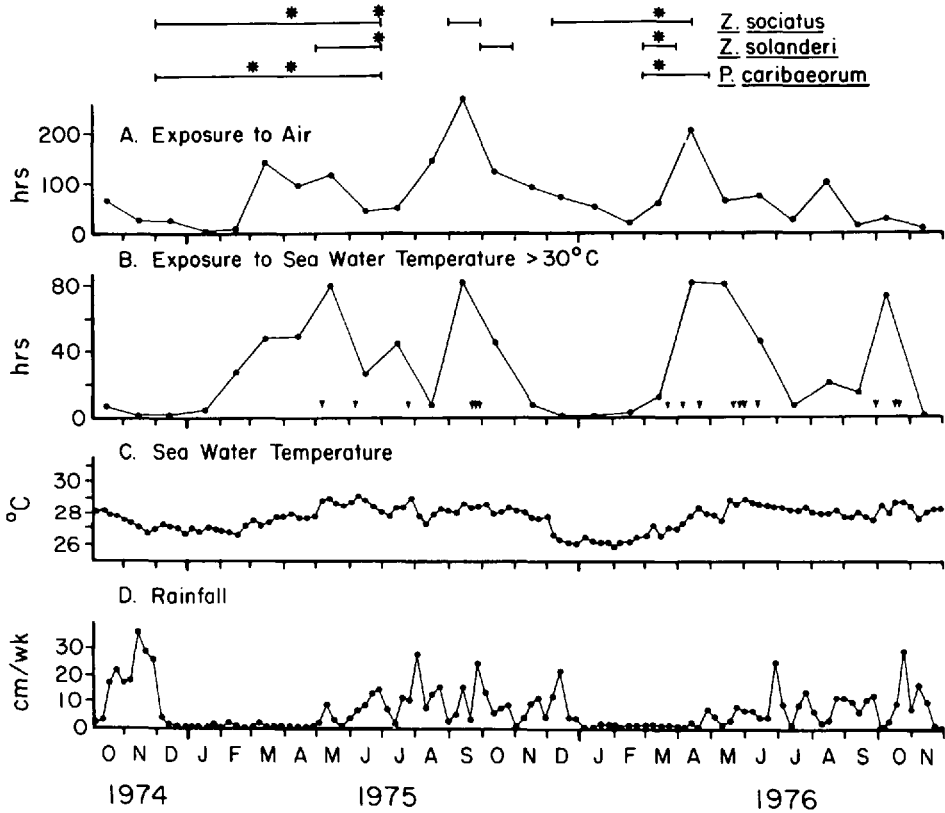


Figure 7. Environmental characteristics of the Galeta reef flat from October 1974 through November 1976. Data are from Hendler (1976; 1977a). A. Total hours per month of reef flat, aerial exposure (at the reef crest in the *Laurencia* zone). Horizontal bars above graph indicate months when each zoanthid species had fertile gonads. Asterisks indicate times when mean ovum size per colony exceeded 250  $\mu\text{m}$ . B. Total hours per month during which the reef flat sea water temperature was above 30°C. Most such periods were a few hours before and after midday. Arrows indicate days which had 8 or more hours of temperatures above 30°C. Peak temperatures during such periods were usually 33–36°C. C. Mean weekly sea water temperatures on the Galeta reef flat. D. Total weekly rainfall on the Galeta reef flat.

Maximum sizes of oocytes in the three species varied between 250 and 450  $\mu\text{m}$  and are well within the range expected for lecithotrophically developing embryos. We found no evidence of internal fertilization or brooding. Spawning has never been reported in the zoanthid literature and we have no direct evidence for it here.

All three species are hermaphroditic. In the absence of repeatedly sampled colonies, we cannot determine the sequence of sexual events. In a study of the zoanthid *Palythoa tuberculosa*, Yamazato et al. (1973) repeatedly sampled several colonies over an entire year. They found both strictly male and protogynous hermaphroditic colonies. Both types of colonies may be present in our populations of *Zoanthus sociatus* and *P. caribaeorum*. No strictly male colonies have yet been sampled from *Z. solanderi* populations (Fig. 3 and Karlson, 1981).

Intraspecific variation in colony reproductive state was quite high in all three species studied here. A significant proportion of the polyps within most fertile colonies were infertile throughout the reproductive season. This may be indicative

Table 5. Periods during which *Zoanthus sociatus* mortality occurred on the reef flat at Galeta, Panama (Neither *Palythoa caribaeorum* nor *Zoanthus solanderi* showed obvious damage during these periods)

Month	Year	<i>Z. sociatus</i>		
		Percent Damaged Colonies (black)	Percent Cover Before	Percent Cover After
September	1971	65	75	52
May, June	1973	1	60	49
September	1973	31	49	54
May	1974	69	72	48
October	1974	1	64	51
April	1976	53	50	23

Source: Meyer and Birkeland, 1974, 1975; Hendler, 1976, 1977a.

of the importance of asexual budding in these colonial organisms. Vegetative regeneration of polyps lost due to predators or to physical disruption (Sebens, 1982; Karlson, 1983) and vegetative overgrowth interactions (Karlson, 1980; Suchanek and Green, 1981) have all been stressed previously as important aspects of zoanthid biology. Local variation in biological interactions are likely to contribute to greater asynchrony in the sexual phase of the zoanthid life cycle. As will be discussed below, larger scale environmental factors may have the opposite effect.

#### Effects of Environmental Factors on Sexual Reproduction

The Environmental Monitoring Program of the Smithsonian Tropical Research Institute in Panama has been collecting data on physical environmental factors (climatological and oceanographic) on the Galeta reef flat daily since 1972 (Meyer and Birkeland, 1974; 1975; Hendler, 1976; 1977a). We examined this data to find out which events might correlate with zoanthid reproductive patterns. The Galeta reef flat environment is highly seasonal. Meteorological and oceanographic conditions are radically different between the wet season (late April or May to December) and the dry season (January to April) (Fig. 7). During the dry season, wind and wave action increase markedly, water clarity is severely reduced, rainfall is negligible, and sea water temperature slowly increases with the increasing solar radiation. Reef flat aerial exposure is rare except at the very end of this season (March, April) when a combination of long exposures and high reef flat temperatures cause severe desiccation and death of reef flat organisms (e.g., echinoids [Hendler, 1977a; b]). During the wet season, rainfall occurs almost daily, salinity is lower (Lessios, 1981), temperatures are slightly higher, wind and wave action are decreased, water is very clear, and reef flat exposures are common. Such exposures are most common during the months of March, April, and May and then again in August, September and October (Fig. 7). During the latter 3 months, exposure can be combined with heavy rainfall potentially resulting in severe osmotic shock.

The seasonal reproductive patterns exhibited by *Zoanthus sociatus* and *Palythoa caribaeorum* include sampling intervals which began with the presence of large oocytes and ended with the absence of oocytes. Such intervals began in June 1975 and March 1976 for *Z. sociatus* and in April 1975 and March 1976 for *P. caribaeorum*. If we assume that spawning occurred during these intervals and again examine the environmental data, we find that in 1975 *Z. sociatus* probably spawned toward the middle of the wet season and *P. caribaeorum* at the beginning of the wet season. In 1976 both species probably spawned at the beginning of the



wet season. There were no obvious differences in rainfall or in average sea water temperatures between the 2 years (Fig. 7). However, there were differences in the frequency and severity of aerial exposures. The April exposures were longer in 1976 than in 1975 while March exposures were greater in 1975.

During severe exposures, water sits in pools on the reef flat and heats up to 30–36°C. Exposed zoanthid colonies probably reach even higher temperatures. From hourly records of reef flat sea water temperature, we calculated the number of hours each day when water temperature exceeded 30°C; the most severe of these exposures exceeded 8 hours. In 1975 the first such severe exposures occurred in early May, early June, and in mid-July (Fig. 7). In 1976 there was an early series of such exposures in late March and early April (Fig. 7). During this period approximately half of the *Zoanthus sociatus* died and turned black (Table 5). This was the earliest significant death of *Z. sociatus* on the reef flat recorded between 1972 and 1976. Previous deaths have been recorded in May, June, September, and October (Table 5). Thus 1976 seems to have been an atypical year and 1975 more typical based on timing of the first serious exposures. Several sea urchin species suffered heavy mortality during April 1976 as well (Hendler, 1977a; b). The apparent synchrony in spawning between zoanthid species suggests that this early series of exposures acted as a stimulus for spawning. *P. caribaeorum* may have responded to the May exposures in 1975 while *Z. sociatus* apparently did not. Extreme exposures in July 1975 may have been a stimulus for spawning in *Z. sociatus*.

#### ACKNOWLEDGMENTS

We thank C. Birkeland, G. Hendler, and D. Meyer for collecting most of the zoanthid samples and the Smithsonian Tropical Research Institute (E.S.P. program) for the provision of facilities and environmental data. Funds have been provided by the School of Life and Health Sciences, University of Delaware, and the Museum of Comparative Zoology, Harvard University.

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DATE ACCEPTED: June 15, 1983.

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