REPRODUCTIVE PATTERNS IN *ZOANTHUS* SPP. FROM DISCOVERY BAY, JAMAICA

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ABSTRACT

Sexual reproductive patterns in *Zoanthus sociatus, Z. solanderi*, and *Z. pulchellus* have been examined from May through July, 1977 and January and July, 1980 for three Discovery Bay populations. *Z. pulchellus* exhibited the highest frequency of fertile polyps and the longest period of sexual reproduction. In spite of its small polyp size, it produced large numbers of ova and larger ova and spermaria than *Z. sociatus* or *Z. solanderi*. Fertilization in these zoanthids appears to be external. All three species are hermaphroditic. "Female" polyps produced more ova than "hermaphroditic" polyps. *Z. sociatus* exhibited high intracolonial variability in sexual condition whereas *Z. solanderi* did not. Fecundity and intracolonial sexual reproductive patterns are briefly discussed in terms of polyp size, habitat depth (environmental variability), energetic constraints, and polyp turnover rates.

INTRODUCTION

Colonial zoanthids are extremely abundant in shallow reef habitats along the north coast of Jamaica (Duerden 1898, Goreau 1959, Kinzie 1973, Karlson 1980). Local populations of *Zoanthus sociatus* and *Z. solanderi* can reach mean densities of 671 and 302 polyps per 0.01 m² respectively (Karlson 1981) and can cover extensive areas of the reef flat. Within the *Zoanthus* zone (Goreau 1959) these cnidarians grow on unconsolidated coral rubble and utilize a variety of asexual capabilities which allow them to locally monopolize this spatial resource. In addition to their normal stoloniferous growth form, they exhibit a high degree of plasticity in responding to physical and biological disturbances (Karlson 1981).

Like many colonial organisms, zoanthids are able to regenerate portions of their colonies lost to predators or fragmented during storms (Karlson 1981). The importance of rapid asexual recovery following fragmentation has been stressed previously as a general advantage among colonial organisms (Jackson 1977) and as a specific mechanism favoring the formation of monospecific stands of such corals as *Acropora cervicornis* (Tunnicliffe 1980). Spatial monopolies formed by *Z. sociatus* and *Z. solanderi* are also believed to result primarily from asexual processes (Karlson 1980, 1981).

Very little is known regarding sexual reproduction among zoanthids and its importance for the development of a larval dispersal stage or for local population maintenance. E. Graham (unpublished data) has observed the presettlement behaviour of zoanthina larvae probably of *Z. sociatus*. These metamorphosed into a crawling stage which, after inspecting the coral substratum for some time, permanently attached themselves near the edges of shaded undersurfaces. This is somewhat confirmed by a settlement study I have conducted in the *Zoanthus* zone on the west back reef of Discovery Bay. Only two zoanthid larvae settled near the edges of undersurfaces of 20 substrata (≥232 cm² each) over an eleven month period (Karlson 1981). This low settlement rate suggests that local population maintenance is not heavily dependent on sexual reproduction.

The study reported herein represents a first attempt to determine when and how much sexual reproduction occurs in three zoanthid congeners which live in Discovery Bay. I will describe some short-term temporal and spatial differences among *Z. sociatus, Z. solanderi* and *Z. pulchellus*. These species appear to be much more prolific than previously expected.

METHODS

The reproductive condition of zoanthid polyps was examined at three sites within Discovery Bay. High zoanthid density (Table 1) and low physical disruption during storms (Karlson 1981) were criteria used to select these sites. *Z. sociatus* has dominated the *Zoanthus* zone along the west back reef (Kinzie 1973) and at buoy lagoon (Karlson 1981) for some time (Fig. 1). *Z. solanderi* has been very abundant at an east back reef site where it has occupied up to 66.5% of the substratum (Karlson 1980). *Z. pulchellus*, on the other hand, has been the least abundant of these three zoanthids. It is found on a few, very shallow rocks in the vicinity of the docking area for the Discovery Bay Marine Laboratory (Fig. 1). *Z. pulchellus* has been exposed to air

during extreme low tides and to low salinities due to freshwater seepage at this site. From September, 1976 through August, 1977, temperature and salinity data were collected from the two subtidal sites dominated by Z. sociatus and Z. solanderi. Over 150 daily measurements from surface and bottom water were taken between 1000 and 1400 h. In terms of extremes in temperature, salinity and air exposure, Z. pulchellus experienced the greatest extremes at the shallowest site while Z. solanderi experienced the least (Table 1).

During a twelve week period beginning in May, 1977, a sample of ≥ 75 polyps was collected biweekly from each species at new and full moon. A winter sample was collected in January, 1980. Sampling at each site involved collection of contiguous polyps from approximately the same location (±0.5 m) at each sampling time. Each sample was collected from a central position within the extensive, zoanthid-dominated areas in order to increase the likelihood of finding reproductively mature polyps. Due to the thin coenenchymal attachment of Z. solanderi and Z.

sociatus, stolonal connections between polyps were difficult to verify. In addition, colony boundaries were not distinct (i.e., polyps intermingle with no sign of aggression or obvious lines of demarcation). These two species also undergo colony fragmentation during storms which further obscures clonal relationships among polyps. In contrast, Z. pulchellus has a thick coenenchymal layer and forms quite distinct boundaries between colonies.

Another set of samples was collected on July 23, 1980 from populations of Z. sociatus at buoy lagoon and Z. solanderi at the east back reef. These were designed to yield additional information on the spatial variability in reproductive condition within the large zoanthid-dominated areas. Greater care in handling these polyps permitted assurance of sampling ≥ 75 polyps within single colonies. At buoy lagoon, three samples were collected several meters apart at 0.5 m and 1.5 m (n = 6). At the east back reef, samples were collected in the same manner at 1.0 m, 2.0 m, and 3.0 m (n = 9).
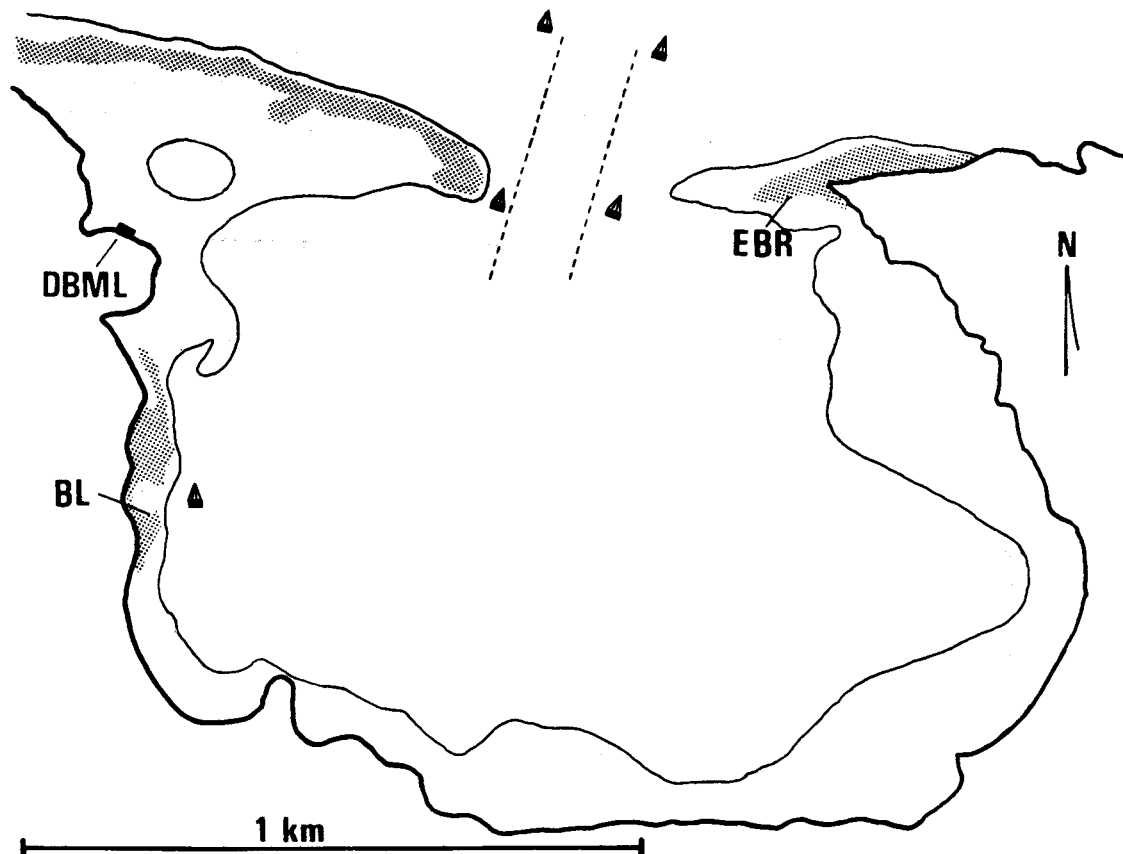

Figure 1. Map of Discovery Bay. DBML, Discovery Bay Marine Laboratory; EBR, east back reef; BL, buoy lagoon. Shading indicates shallow reef (1 m). Contour line is 5 m.

Table 1. Zoanthid collection site characteristics.

	Z. sociatus	Z. solanderi	Z. pulchellus
Site (see Fig. 1)	BL	EBR	DBML
Zoanthid density (#/0.01 m^2)	397 (N = 5)	302 (N = 5)	—
Zoanthid depth range (m)	0.5 — 2.5	1.0 — 3.5	0.0 — 0.5
Sample depth (m)	0.5	3.0	0.0
Annual temperature range (°C)			
surface	26.3 — 30.7	26.2 — 30.3	*
bottom	26.4 — 30.3	26.4 — 29.7	
Annual salinity range (o/oo)			
surface	20.3 — 34.3	33.0 — 34.7	*
bottom	26.1 — 34.5	33.9 — 34.9	

*comparable to BL except during extreme low tides.

After collection, all zoanthid polyps were anesthetized in standard magnesium salt solutions for 20-30 min and then fixed in Bouin's (1977) or 10% formalin (1980). 75 polyps from each sample were individually dissected and visually inspected under magnification for the presence of fertile mesenteries bearing the spherical-to-ovoid ova and/or spermaria. A subsample of 24 fertile polyps was embedded in paraffin, sectioned, mounted and stained with hematoxylin and eosin to verify the identity of ova and spermaria and to validate visual criteria. Spermaria were generally translucent and possessed a clear central lumen. A lateral germinal vesicle was a conspicuous feature of the opaque ova.

Another subsample of fertile polyps was used to determine the number of ova per polyp and the size of ova and spermaria in polyps collected during 1977 and January, 1980. Up to ten randomly selected fertile polyps of each species at each of eight sampling dates were censused; the total subsample included 36 *Z. sociatus*, 21 *Z. solanderi* and 80 *Z. pulchellus*. Since the number of ova (and spermaria) in many fertile polyps was very high, it was considered impractical to determine mean sizes of ova and spermaria. Instead, the maximum diameter of ova and spermaria in each fertile mesentery was measured with an ocular micrometer. Most fertile polyps had 20-30 fertile mesenteries although some had as few as only three.

RESULTS

There were dramatic differences in sexual reproductive activity among *Zoanthus* spp. in the 1977 and January, 1980 samples. Among 1800 polyps, a total of 99, 31 and 487 fertile polyps were sampled from *Z. sociatus, Z. solanderi* and *Z. pulchellus* respectively (Table 2). The small, lower intertidal population of *Z. pulchellus* was sexually reproductive at all sampling dates reaching 100% fertility in mid-June and early July (Fig. 2). *Z. solanderi*, on the other hand, exhibited the lowest level of fertility reaching a maximum of only 27% in mid-July (Fig. 2). Maximum values for *Z. sociatus* occurred in mid-June (49%) and late July (48%). Polyps from the winter collections of *Z. solanderi* and *Z. sociatus* were non-fertile (Fig. 2). July, 1980 samples further confirm that *Z. sociatus* (38.4%) exceeds *Z. solanderi* (11.2%) in frequency of fertile polyps (Table 3).

Table 2. Numbers of polyps with ova and/or spermaria in 1977 and January, 1980 samples.

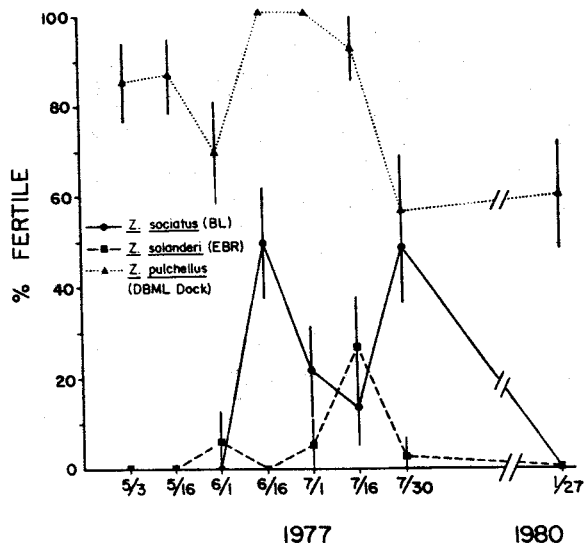|	Z. sociatus	Z. solanderi	Z. pulchellus
Polyps with only ova	1	6	9
Polyps with only spermaria	46	0	8
Polyps with ova and spermaria	0	19	71
Total fertile polyps examined	47	25	88
Total fertile polyps	99	31	487
Total polyps	600	600	600

Figure 2. Percentage of fertile polyps in samples of 75 polyps each for three species and eight sampling dates. Intervals are 95% confidence limits (2 $\sqrt{(pq/75)}$, see Snedecor and Cochran 1967).

Examination of fertile polyps for the presence of ova, spermaria, or both revealed the following patterns. In the 1977 samples, most fertile polyps of *Z. solanderi* and *Z. pulchellus* contained both ova and spermaria (usually in the same mesenteries) thus indicating simultaneous hermaphroditism (Table 2). Polyps of *Z. sociatus*, on the other hand, contained either ova or spermaria (Table 2). Simultaneous hermaphroditism in this third species is clearly indicated, however, in the July, 1980 replicate

samples (Table 3). *Z. sociatus* polyps containing only ova, only spermaria, or both within replicates is also indicative of a high level of intracolonial variability in reproductive condition of fertile polyps. *Z. solanderi* polyps contained only ova or both ova and spermaria (Tables 2 and 3). The absence of "male" polyps bearing only spermaria may represent a sampling bias (i.e., colony size classes were not considered) or a protogynous developmental sequence. Fertile polyps within each of nine replicate samples were either all "female" bearing only ova or all "hermaphroditic" (Table 3).

Within the subsample of 137 fertile polyps which were analyzed for the total number of ova per polyp and maximum ova and spermaria sizes, it was determined that there was no interspecific difference in number of ova per polyp between *Z. solanderi* and *Z. pulchellus* (Table 4). However, *Z. pulchellus* had more ova per unit volume than did *Z. solanderi* (Mann-Whitney U-test, $p < 0.001$). There were also significantly more ova per polyp in "female" than in "hermaphroditic" polyps of both *Z. solanderi* and *Z. pulchellus* (Mann-Whitney U-tests, $p < 0.01$).

Comparisons of the maximum sizes of ova and spermaria were made using the maximum sizes per polyp. This parameter was highly correlated with the mean maximum sizes per mesentery ($r \geq 0.84$ for all three species). There were significant interspecific differences in the maximum ovum size per polyp (Mann-Whitney U-test, $p < 0.001$, Table 4) and in the maximum spermarium size per polyp (Kruscal-Wallis test, $p < 0.005$, Table 4). Although *Z. solanderi* polyps were the largest of the three species, *Z. solanderi* had the smallest ova and spermaria; *Z. pulchellus* had the largest (Table 4). Intraspecific comparisons between "hermaphroditic"

Table 3. Numbers of polyps with ova and/or spermaria in replicate samples taken July 23, 1980.

	Sample Replicate								
	1	2	3	4	5	6	7	8	9
Z. sociatus (BL)									
Polyps with only ova	21	42	7	15	9	0	—	—	—
Polyps with only spermaria	15	10	6	0	1	12	—	—	—
Polyps with ova and spermaria	16	5	1	1	12	0	—	—	—
Non-fertile polyps	23	18	61	59	53	63	—	—	—
Sample depth (m)	0.5	0.5	0.5	1.5	1.5	1.5	—	—	—
Z. solanderi (EBR)				*					
Polyps with only ova	24	8	0	19	0	0	0	0	0
Polyps with only spermaria	0	0	0	0	0	0	0	0	0
Polyps with ova and spermaria	0	0	4	0	4	3	9	1	4
Non-fertile polyps	51	67	71	56	71	72	66	74	71
Sample depth (m)	1.0	1.0	1.0	2.0	2.0	2.0	3.0	3.0	3.0

*Sample retaken August 1, 1980

Table 4. Mean polyp size (± s.e.), number of ova per polyp, and maximum size of ova and spermaria in female, male and hermaphroditic polyps.

	Z. sociatus	Z. solanderi	Z. pulchellus
Polyp height (mm), n = 100	19.6 ± 0.44	18.7 ± 0.69	9.5 ± 0.34
Polyp diameter (mm), n = 100	4.7 ± 0.06	5.2 ± 0.08	4.3 ± 0.06
Polyp volume (mm³)	340	397	138
Ova per polyp			
Females: Mean	274 (n = 1)	1885 (n = 6)	719 (n = 9)
Range		268-3218	315-1034
Hermaphrodites: Mean	—	193 (n = 15)	454 (n = 63)
Range		8-1013	55-1484
Max. ovum size per polyp (μ)			
Females: Mean	296 (n = 1)	220 (n = 6)	383 (n = 9)
Range		138-296	296-473
Hermaphrodites: Mean	—	196 (n = 15)	348 (n = 63)
Range		138- 296	256- 433
Max. spermarium size per polyp (μ)			
Males: Mean	187 (n = 35)	—	246 (n = 8)
Range	98-374		138-414
Hermaphrodites: Mean	—	96 (n = 15)	192 (n = 63)
Range		39- 236	98-296

polyps and those bearing only ova or spermaria resulted in no significant differences in maximum ovum or spermarium size per polyp (Table 4).

DISCUSSION

Although zoanthid settlement rates are apparently low (Karlson 1981), they produce large numbers of ova. These develop in the mesenteries and are presumably fertilized externally. No fertilized zygotes or planulae were collected from zoanthid polyps in this study. This developmental pattern conforms with that described by Rinkevich and Loya (1979a) for large-polyped corals. These corals develop many large ova which are externally fertilized. Mortality rates of zoanthid zygotes and/or planulae in the plankton must be quite high.

Small-polyped corals generally produce few ova and often brood their embryos (Rinkevich and Loya 1979a). It has been hypothesized that brooding can be a consequence of small size and low fecundity in alcyonaceans (Hartnoll 1977) and asteroids (Menge 1975). Although there is almost a threefold difference in polyp size among *Zoanthus* spp. (Table 4), small polyp size does not appear to constrain fecundity in *Z. pulchellus*. On the contrary, fecundity appears to be highest in this species based on its high frequency of fertile polyps and the extended period of sexual reproduction.

This same pattern of higher fertility and longer sexual reproductive period in an intertidal zoanthid species has been described for *Palythoa vestitus* in the Pacific (Cooke 1976). In Jamaica, reduced reproductive activity with increasing depth appears among *Zoanthus* spp. (Fig. 2) and within replicate samples of both *Z. sociatus* (54.7% → 22.2%) and *Z. solanderi* (16.0% → 11.6% → 6.2%) (Table 3). Although this latter trend is not statistically significant, it is consistent between species. Additional sampling is obviously necessary to confirm this relationship.

There are a number of potentially important factors which may affect fecundity over a depth gradient. A higher frequency of catastrophic events in shallower habitats has been argued to favor eurytopic species with efficient dispersal stages (Jackson 1974). Higher fecundity may also be selectively advantageous in such habitats. In deeper water, reduced nutritional resources or higher energetic expenditures for competition or colony regeneration may be involved. Zoanthids primarily rely on autotrophic (Trench 1974) and heterotrophic (Sebens 1977) nutritional resources. It is not likely that there is a significant reduction in available light over so narrow a depth range (Tables 1 and 3), but planktonic food resources may vary significantly. Spatial competition involving *Z. solanderi* and other cnidarians (Karlson 1980) and *Z. sociatus* and algae (Karlson 1981) have been described elsewhere.

Z. pulchellus engages few, if any other spatial competitors in Discovery Bay. Fecundity may be affected by differences in the energetic costs of competition. The same reasoning applies to energetic costs of colony regeneration following partial mortality (sensu Hughes and Jackson 1980) due to predation or physical disturbance.

Polyp mortality and colony regeneration may also result in a high degree of variability in the sexual condition of polyps within colonies. *Z. sociatus* exhibited such variability whereas *Z. solanderi* did not (Table 3). Fertile polyps from within colonies of *Z. solanderi* were either all "female" or all "hermaphroditic". This zoanthid appears to be similar to *Stylophora pistillata* in having synchronized sexual reproduction within colonies, but not among different colonies (Rinkevich and Loya 1979b). The asynchronized reproductive pattern within colonies of *Z. sociatus* suggests the possibility of high polyp turnover rates in this species. Comparison of actual rates of polyp turnover (due to budding, fragmentation, predation, etc.) in *Z. sociatus* and *Z. solanderi* should help resolve how colony regeneration affects zoanthid fecundity and intracolonial variability in sexual reproductive condition.

ACKNOWLEDGMENTS

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