

DISTURBANCE AND MONOPOLIZATION OF A SPATIAL RESOURCE BY *ZOANTHUS SOCIATUS* (COELENTERATA, ANTHOZOA)

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ABSTRACT

Zoanthus sociatus is a dominant member of the subtidal *Zoanthus* zone assemblage at Discovery Bay, Jamaica. The benthic biota at four of five study sites include this zoanthid and several algal genera. *Z. sociatus* is present but much less abundant than are *Z. solanderi* and several other cnidarians at a fifth site on the east back reef (Karlson, 1980). Sedimentation data and changes in the percentage of bare substratum suggest that this EBR site is relatively protected from physical disruption caused by storms. Intermediate levels of storm disruption characterize the west back reef; shallow fore reef zones have the highest levels (Woodley et al., 1981).

I have conducted a series of substratum disruption experiments at the WBR and at nearby one palm island (1PI) to document the response of this assemblage to disturbance. Recolonization experiments resulted in growth by *Z. sociatus* at 0.41–1.28 cm/mo in both control and enclosure cages. Lower zoanthid growth rates were typical of clearings in which the sea urchin *Diadema antillarum* was present, algae absent, and *Z. sociatus* the only recolonizing species. These zoanthids tended to be well attached to the substratum and not very susceptible to storm damage. Other experiments demonstrate the high regenerative capability of *Z. sociatus* in response to substratum overturning, shading, transplantation, and predation. *Z. sociatus* exhibited changes in polyp size (possibly altering susceptibility to storm damage and mode of nutrition), phototropic growth responses, and slow colony degeneration in unfavorable microhabitats.

The plasticity of polyps and the regenerative characteristics of zoanthid colonies suggest that disturbance has been an important selective agent over the evolutionary history of *Z. sociatus*. Its successful exploitation and eventual monopolization of disturbed substrata may result from intermediate levels of disturbance. This is suggested as an alternative to the traditional explanation of competitive dominance at low disturbance levels.

Much of our present day understanding of the dynamics of benthic, hard-substratum assemblages can be attributed to the extensive work conducted on rocky intertidal shores along the Pacific coast of North America. Here the dynamics of mid-intertidal mussel beds are greatly influenced by disturbances due to wave stress (Paine and Levin, 1981), log battering (Dayton, 1971), and predators (Dayton, 1971; Paine, 1974), and the eventual reinvasion of disturbed substrata by *Mytilus californianus*. At one intertidal level this competitively dominant mussel will monopolize the substratum in the absence of disturbance (Paine, 1966; 1974; Paine and Levin, 1981).

Subtidal benthic assemblages in which large areas of hard-substrata are dominated by one or a few species have been reported in the literature, but for these, the relative importance of disturbance and competition has not been well documented or is subject to debate. Porter (1974) and Glynn (1976) describe eastern Pacific coral reefs dominated by *Pocillopora* spp. Both authors attribute some of the pocilloporid success to rapid growth and an overtopping morphology but disagree as to the effect of disturbance (particularly predation by the crown-of-thorns starfish *Acanthaster planci*) and digestive dominance (a presumed competitive mechanism) on coral community structure. Some of their differences have recently been resolved by Wellington's (1980) report of reversals in digestive

dominance interactions by the development of sweeper tentacles in *Pocillopora* spp. In another example, Porter (1974) reports "extensive shallow-water reef flats composed almost exclusively of *Porites furcata*" on the Caribbean coast of Panama. He postulates that this coral's tolerance of low salinity and desiccation allows it to occupy a spatial refuge from subtidal competitive interactions (Porter, 1974), but supportive evidence is lacking.

Additional examples occur along the north coast of Jamaica where distinctive reef zones are dominated by corals (*Acropora palmata*, *A. cervicornis*, *Montastrea annularis*, or *Agaricia* spp.) or zoanthids (*Zoanthus sociatus* or *Z. solanderi*) (Goreau, 1959; Kinzie, 1973; Karlson, 1980). As a group these relatively narrow zones span a large range in depth and exposure to disturbances. On coral reefs disturbances include storms (Stoddart, 1974; Connell, 1976; 1978; Highsmith et al., 1980; Woodley et al., 1981), earthquakes (Stoddart, 1972), predation (Stephenson and Searles, 1960; Porter, 1974; Pearson, 1974; Glynn, 1976; Sebens, 1982) and herbivory (Dart, 1972; Sammarco et al., 1974; Sammarco, 1980). Intermediate levels of disturbance generally reduce dominance and increase species diversity (Connell, 1978). It is usually assumed that low levels of disturbance result in low species diversity and dominance by a competitively superior species. This assumption may not always be supportable, however, depending on the basis for determining competitive relationships.

Competition among reef cnidarians may be based on overtopping morphology (Porter, 1974; Connell, 1976; 1978; Glynn, 1976; Maguire and Porter, 1977), digestive dominance (Lang, 1973; Porter, 1974; Connell, 1976), the use of sweeper tentacles (Richardson et al., 1979; Wellington, 1980), or the ability to inhibit overgrowth (Connell, 1976; Karlson, 1980). It has not been determined how these traits affect relative abundance changes, but it is known that digestive dominance ranking is not a good predictor of relative abundance, especially for *A. palmata* and *A. cervicornis* (Lang, 1973). *Z. solanderi* has also been shown not to be a competitive dominant in terms of overgrowth ability (Karlson, 1980).

I have recently speculated that local dominance by some colonial invertebrates and perennial plants may be achieved at intermediate levels of disturbance through vegetative colonization of disturbed areas and the subsequent defense of these areas (Karlson, 1980). This form of preemptive competition can delay the expression of competitive dominance by other species (Karlson, 1981) and slow the rate of community succession (Connell and Slayter, 1977). The degree of success of such a competitive strategy depends on the relative rates of disturbance and substratum colonization as well as the generation time of these sessile organisms. Generation time among reef cnidarians can be exceedingly long (Hughes and Jackson, 1980).

This study examines substratum disruption and colonization in the *Zoanthus* zone at Discovery Bay, Jamaica between September 1976 and February 1978. Following a brief description of the biota and some of the physical characteristics of this habitat, I will describe a series of simulated disturbance experiments involving substratum clearing, overturning, shading, and transplantation. Emphasis will be placed on the response of *Z. sociatus* to physical disruption and predation and the importance of the regenerative properties of this colonial organism.

HABITAT DESCRIPTION

I have selected five study sites in Discovery Bay which have been characterized by a dense cover of *Z. sociatus* or *Z. solanderi*. These sites are situated in shallow water in the lee of the highly turbulent *A. palmata* zone (Goreau, 1959) on both the east (EBR) and west sides (WBR and 1PI) of the bay

Table 1. Annual ranges in midday temperature and salinity at the WBR, CPC, BL, and EBR sites (n = 151-163 days)

Site	Depth (m)	Temperature (°C)		Salinity (‰)	
		Surface	Bottom	Surface	Bottom
WBR	1.6	26.6-30.7	26.6-30.6	32.3-35.8	32.3-35.8
CPC	1.8	26.1-30.5	26.5-30.5	30.0-34.0	31.3-34.7
BL	2.5	26.3-30.7	26.4-30.3	20.3-34.3	26.1-34.5
EBR	3.9	26.2-30.3	26.4-29.7	33.0-34.7	33.9-34.9

and at comparable protected locations at buoy lagoon (BL) and Columbus Park cove (CPC) on the western side of the back bay. The substratum at these sites is largely unconsolidated coral rubble (mostly dead *Acropora* spp.) which has been transported leeward during storms. Stoloniferous zoanthid growth over this substratum and budding of zoanthid polyps result in high polyp densities. In February 1977, mean polyp densities for *Z. sociatus* at a depth of -1.0 m were 671 (SD = 82), 353 (SD = 61), 397 (SD = 69), and 499 (SD = 47) per 0.01 m² (n = 5) at the WBR, 1PI, BL, and CPC sites, respectively. *Z. sociatus* was present but not very abundant at the EBR site where *Z. solanderi* occupied up to 66.5% of the substratum between -1.5 and -3.5 m (Karlson, 1980).

The sessile biota occurring with *Zoanthus* spp. at these five sites includes algae typical of damselfish territories (especially at BL and CPC), at least 17 genera of macroalgae at the WBR and 1PI (Karlson, unpublished data), and mostly cnidarians at the EBR (Karlson, 1980). These benthic organisms are fed upon by a variety of predators and herbivores. A notable omnivore is the sea urchin *Diadema antillarum* which feeds on algae (Dart, 1972; Sammarco et al., 1974; Sammarco, 1980), small corals (Bak and van Eys, 1975; Sammarco, 1980), hydrocorals (Bak and van Eys, 1975), and the encrusting gorgonian *Erythropodium caribaeorum* (Karlson, personal observations). *Diadema* is common in the *Zoanthus* zone at the WBR, 1PI, and the EBR site. Occasional censuses of *Diadema* over the period of this study (Sept. 1976-Feb. 1978) indicate significantly higher densities ($t = 3.18$, $P < .005$) in the vicinity of 1PI ($\bar{x} = 3.9/m^2$, SD = 7.4, n = 116; maximum = 36/m²) than at the WBR site ($\bar{x} = 1.1/m^2$, SD = 3.8, n = 84; maximum = 22/m²). The effect of *Diadema* on zoanthid populations will be discussed later.

Members of five families of omnivorous, benthic-feeding fish (Chaetodontidae, Ephippidae, Monacanthidae, Ostraciontidae, and Pomacentridae) are known to eat *Zoanthus* spp. in the West Indies (Randall, 1967), the Florida Keys (Emery, 1973), and Panama (Sebens, 1982). Four of these fish (all pomacentrids) are common in Discovery Bay. The sergeant major *Abudefduf saxatilis* is common around 1PI. The night sergeant *A. taurus* is common in shallow, subtidal pools adjacent to the Discovery Bay Marine Laboratory. Throughout the zoanthid study areas, the threespot damselfish *Eupomacentrus planifrons* and the dusky damselfish *E. dorsopunicans* (= *fuscus*) are common.

The benthic polychaete *Hermodice carunculata* is also known to prey on zoanthids and numerous other cnidarians including corals, hydrocorals, the corallimorpharian *Recordia florida*, the actinian *Stoichactis helianthus*, and the gorgonians *Erythropodium caribaeorum* and *Briareum asbestinum* (Marsden, 1962; Ott and Lewis, 1972; Sebens, 1982; personal observations). *Hermodice* may be important in affecting zoanthid distribution patterns in Discovery Bay as it is in Panama (Sebens, 1982), but data on its density, dispersion, and feeding preferences are not adequate at this time for comparing these two reefs.

The Discovery Bay study sites can also be characterized by physical parameters, such as temperature, salinity, sedimentation rates, and the availability of bare substratum. From September 1976 through August 1977, midday (1000-1400) measurements of surface and bottom water temperature and salinity were taken at the WBR, CPC, BL, and EBR sites (n = 151-163 days). The annual ranges in these parameters (Table 1) indicate that: (1) temperature varied less than 5°C between summer and winter extremes; the mean monthly range was only 1.9°C, and (2) salinity varied up to 14‰ especially at BL where fresh water seepage substantially reduced surface salinity; the mean BL monthly minimum for surface water was 23.4‰ and the mean BL monthly range was 10.9‰ (Table 1). These low salinities may cause physiological stress in some reef organisms and may be partially responsible for the prevalence of zoanthid species; *Palythoa variabilis* and *Zoanthus pulchellus* are also present in this region of the bay. *Zoanthus sociatus* is common here but is also very common at other sites where salinity was not as variable (Table 1). [*Z. sociatus* occurs intertidally in Panama (Sebens, 1982).]

The most extreme physical factor affecting subtidal zoanthid-dominated assemblages is water turbulence associated with major storms. One of several effects of this turbulence is the resuspension and deposition of bottom sediments. Wind speed data collected at the Discovery Bay Marine Laboratory

Table 2. Sediment analysis. Inverted control traps (after White and Wetzel, 1973) collected negligible sediment

Site	Sediment Depth (m)	Trap Depth (m)	Sieve Size (μ)	g dry-wt m^{-2} day $^{-1}$			
				Jan. 12-25	Mar. 8-Apr. 8	Apr. 8-May 11	May 12-June 14
EBR	3.90	2.70	1,000	35.0	0.5	0.5	0.5
			500	612.5	4.0	7.3	4.9
			250	12,880.0	125.0	22.6	6.9
			125	3,797.5	292.0	126.8	11.3
			44	122.5	44.5	53.1	8.8
			PAN	52.5	34.0	23.6	2.9
TOTAL	17,500.0	500.0	233.9	35.3			
WBR	1.60	0.65	1,000	5.2	0.4	0.3	
			500	9.0	2.9	1.5	
			250	11.8	6.3	2.1	*
			125	32.4	8.2	2.7	
			44	86.4	13.0	6.5	
			PAN	56.2	9.3	6.7	
TOTAL	201.0	40.1	19.8				
CPC	1.80	0.85	1,000	0.4	0.1		
			500	5.4	8.6		
			250	7.2	10.9	*	*
			125	10.0	7.8		
			44	9.4	13.9		
			PAN	18.1	27.1		
TOTAL	50.5	68.4					

* Total sample dry weight < 16.5 g m^{-2} day $^{-1}$.

indicates that from November 1976 through August 1977, there were four days on which the average wind speed exceeded 25 kmph (December 9 = 38 kmph, January 19 = 28 kmph, March 27 = 26 kmph, and April 20 = 27 kmph). Cylindrical PVC sediment traps (diameter = 5 cm, length = 38 cm) at the EBR, WBR, and CPC sites were used to estimate sedimentation rates from January through June. These traps were tied to stakes with the top opening of each being 0.55–0.65 cm above the coral rubble and 0.95–1.20 cm above the nearby sedimentary bottom. These samples were treated with dilute sodium hypochlorite, oven dried, and then sorted using mechanical and sonic sifting. The highest rate of sedimentation was 1.75×10^4 g dry-wt m^{-2} day $^{-1}$ at the EBR following the January 19 storm (Table 2). Over 73% of this sediment was retained on a 250- μ m sieve.

Finer particles and lower sedimentation rates were measured at the WBR and CPC locations and for the later sampling periods at the EBR site (Table 2) than were collected at the EBR site in January. A range in sedimentation rates previously measured for Discovery Bay patch reefs and sites near Columbus Park (15 m) is 24–66 g m^{-2} day $^{-1}$ (Brakel, 1976; Foster, 1978); these are over two orders of magnitude lower than the EBR measurements for January 1977 (Table 2). S. Ohlhorst (personal communication) has also measured lower sedimentation rates for ten other Jamaican reef sites from August 1976 through August 1977. The EBR site would appear to be a somewhat protected location given the large amount of deposited sediment during or immediately following storm turbulence; suspended sediment is deposited in relatively low energy environments. The dominant sessile organisms at this site (Karlson, 1980) exhibited no apparent ill effects due to this high sedimentation rate.

The disruptive water turbulence associated with storms can also cause scouring, substratum displacement, and fragmentation of epifaunal colonies. These processes generate bare substratum which is then available for recolonization. The relative availability of bare substratum at each of the five sites was measured bimonthly along fixed transects of 15–22, $\frac{1}{4}$ - m^2 quadrats. These quadrats were sampled photographically; area determinations were made using a planimeter. Differences in the percentage of bare substratum between samples at each site were used to characterize the susceptibility of the benthic biota to disturbance. The largest increases in bare substratum occurred at the WBR site presumably due to December 1976 (+6.5%) and winter 1978 (+19.0%) storms (Fig. 1). Bare substratum became less abundant at the EBR during these two periods (Fig. 1) which again may be indicative of a higher degree of protection from storm damage at this site. Bare substratum was always less than 4% of the substratum area at IPI, CPC, and BL. As will be mentioned below, IPI is near

the channel opening to Discovery Bay. Storm disruption to the biota at this site appears to have been minimal probably because these organisms have been subjected to daily wave action and turbulence. Less predictable turbulence would appear to characterize the nearby WBR site where erect macroalgae and elongated zoanthid polyps are more commonly encountered and are apparently more susceptible to damage during storms than those at IPI (see below).

SUBSTRATUM RECOLONIZATION

Estimates of percent cover for *Z. sociatus* along the fixed transects at the WBR and IPI exceeded 79% over the entire study period. This high zoanthid cover was typical of this part of the reef and was the basis for its selection as a site for a substratum recolonization experiment. Artificial clearings of the zoanthid-dominated substrata were created in both control and enclosure cages to evaluate the relative impact of storm disruption and large predators or herbivores (e.g., *Dia-dema* and damselfish) on the benthic assemblage. Sixteen cage sites were located at a depth of 0.9–1.3 m along the west back reef. There were four sets of replicates in a randomized block design, two blocks being located at IPI (adjacent to the channel opening) and the remaining two further west (WBR) approximately 0.1–0.4 km from IPI. At monthly intervals beginning in November 1976, an approximately 15 × 15 cm area was picked, scraped, and brushed clear of all biota (mostly *Z. sociatus*) at each site. Another site (#17) was located just southwest of IPI at a depth of –2.2 m where a single large area (approximately 50 × 50 cm) was cleared each month. Each of the first 16 sites were enclosed by a large tubular steel frame 1 m wide × 2 m long × 0.7 m high which supported either a complete cage of 2.54 cm wire mesh, a topless cage, a sideless cage, or a control cage with no wire mesh. The monthly clearings at each site were located within a randomly selected, ¼-m² quadrat enclosed in the 2-m² caged area. The cages were checked for damage several times each week and were brushed clean every 5–7 days.

The cages experienced varying degrees of physical disruption by wave action. Due to the proximity of IPI to the channel opening, cages there were exposed daily to the effects of waves generated by the prevailing northeasterly (Goreau, 1959) winds. On December 9–11, 1976, a storm totally destroyed the enclosed sample area within two complete cages and a topless cage at IPI. Two additional complete cages were constructed and located at IPI and WBR. The former cage was badly damaged by another storm on March 26–30. Repairs were made immediately after the storm. All cages were maintained until late June or early July when the caging treatments were terminated and all wire mesh was removed from the frames.

Each cage site was sampled photographically using standardized ¼-m² quadrats. Samples were taken at approximately monthly intervals from November through July and again in February 1978. Initial clearing size (A_0) was determined using a planimeter on photographs taken a few days following the clearing treatment. At subsequent sampling times (t), the area which remained free of *Z. sociatus* (A_t) was measured. This area was either bare substratum or occupied by one of several algae; invertebrate recruitment here was very rarely encountered.

Since A_0 varied somewhat with each treatment, I have analyzed the proportional response A_t/A_0 in order to make comparisons between clearings. If zoanthid growth into each clearing were to have proceeded at a constant rate from all sides, a linear relationship between $\sqrt{A_t/A_0}$ versus time would result. I have compared my actual data with this idealized model and determined average growth rates for *Z. sociatus* at each site.

Linear regression analysis of $\sqrt{A_t/A_0}$ against time resulted in negative slopes (i.e., zoanthid growth) at all experimental sites during the first seven months of this study (prior to mesh removal) (Table 3). In all but three cases, a significant

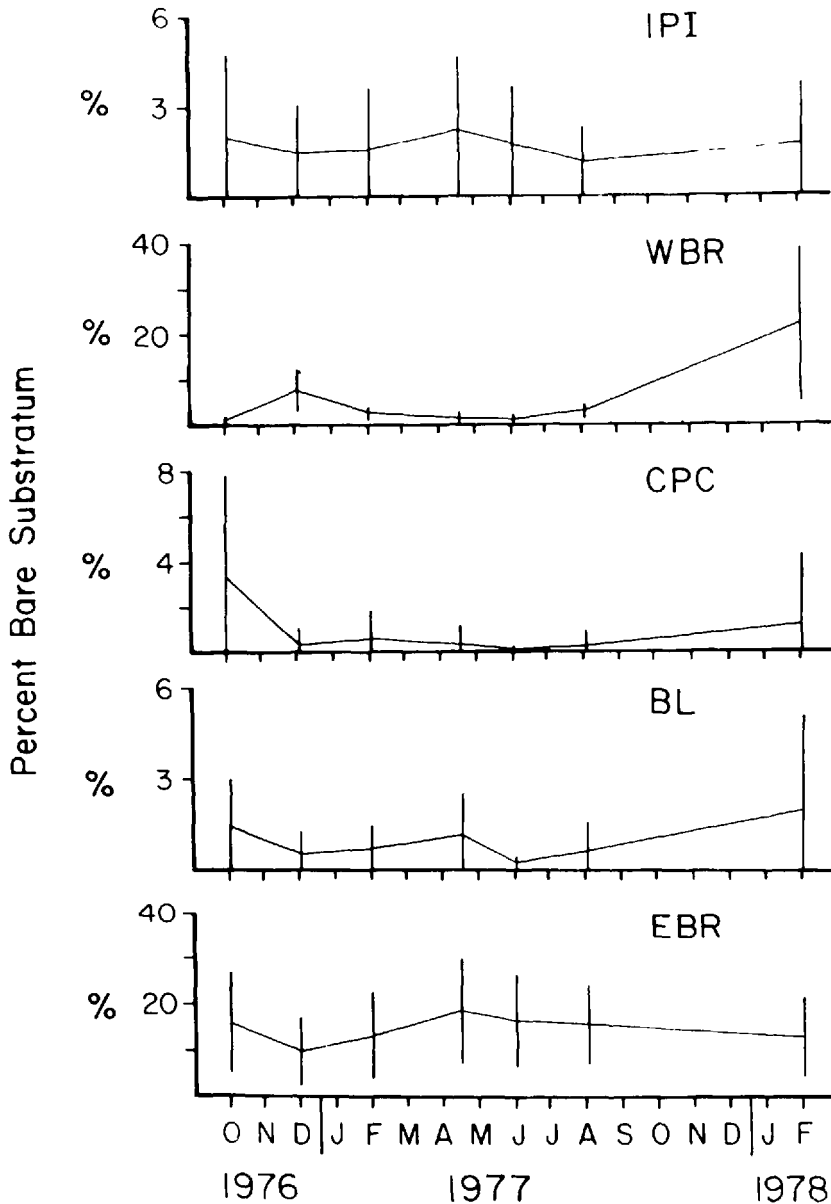


Figure 1. Mean percentage of bare substratum per quadrat vs. time along fixed transects of $\frac{1}{4}$ -m² quadrats ($n = 15-22$) at each of five study sites between October 1976 and February 1978. Ranges indicate standard deviations. Note scaling differences along the percentage axes.

nonzero growth rate was determined. The range in these growth rates across all treatments was 0.41–1.28 cm/mo (Table 3). There were no significant differences in growth rates due to caging treatments ($F_{3,9} = 2.18, P > .05$) or due to block effects ($F_{3,9} = 3.43, P > .05$). However, the mean growth rate for the IPI sites (0.41 cm/mo) was significantly different ($t = 2.16, P = .05$) from that calculated for the WBR blocks (0.71 cm/mo).

Other differences between IPI and the WBR sites include greater storm damage

Table 3. Linear regression analysis of growth by *Z. sociatus* into experimental clearings at cage sites along the west back reef

Cage Type	Cage Site (block) #	N	Area (cm ²)	Slope (b) ×10 ⁻³	Standard Error of Slope ×10 ⁻³	R ²	Growth Rate (cm/mo)
	17	22	2,500	-1.02	0.224	.51	.77**
Control	1 (1-1PI)	20	225	-1.85	0.204	.82	.42**
	6 (2-1PI)	20	225	-1.82	0.217	.80	.41**
	10 (3-WBR)	20	225	-3.29	0.590	.63	.74**
	13 (4-WBR)	20	225	-3.46	0.812	.50	.78**
Topless	5 (2-1PI)	20	225	-1.07	0.513	.19	.24n.s.
	12 (3-WBR)	20	225	-0.76	0.588	.08	.17n.s.
	15 (4-WBR)	20	225	-3.74	0.485	.77	.84**
Sideless	4 (1-1PI)	16	225	-1.88	0.647	.38	.42*
	7 (2-1PI)	20	225	-2.03	0.553	.43	.46*
	11 (3-WBR)	17	225	-5.70	0.913	.72	1.28**
	16 (4-WBR)	20	225	-4.27	0.963	.52	.96**
Complete cages	9 (3-WBR)	20	225	-3.50	0.612	.64	.79**
	14 (4-WBR)	20	225	-1.92	0.706	.29	.43*
	18 (1-1PI)	9	225	-2.33	0.893	.49	.52*
	19 (4-WBR)	6	225	-1.92	2.428	.14	.43n.s.

* $P < .05$ (*t*-test, $H_0: b = 0$).** $P < .001$.

n.s. = not significantly different from zero.

to cages, higher *Diadema* densities, yet lower estimates of the percent bare substratum at 1PI (Fig. 1). The low 1PI growth rates for *Z. sociatus* were measured from clearings which were generally kept free of other biota by foraging *Diadema*. In many of these cases *Z. sociatus* was the only recolonizing species. These zoanths tended to be very well attached to the coral substratum and not very susceptible to wave stress during storms. Increased susceptibility to this form of disruption was evident at several caged sites (but not at control sites) following the removal of the wire mesh. Cage effects on water flow and/or light were probably responsible for some changes in zoanthid growth form, substratum attachments, and susceptibility to storm disruption, but additional supportive data were not collected at the cage sites.

More Substratum Disruption Experiments

I have simulated the disruptive effects of storms on *Z. sociatus* by a variety of substratum manipulations including overturning, shading, or transplanting zoanthid-covered substratum and the placement of bare substratum into zoanthid-covered areas. These experiments demonstrate the response of this zoanthid to perturbations typical of the *Zoanthus* zone.

In March 1977 five, ~250-cm² substrata covered with *Z. sociatus* were overturned onto coral rubble at a depth of 1 m in the vicinity of 1PI. The bottom central 100-cm² of these substrata were censused after five and eleven months. Zoanthid polyps exhibited a remarkable ability to persist in this suboptimal situation although their condition did deteriorate. Over the eleven month period the polyps significantly decreased in both size and density (Table 4). They had also lost most of their green coloration and appeared incapable of extending their tentacles in a typical feeding posture.

Another result of substratum disruption is the shading of previously exposed zoanthid polyps. In April 1977 I simulated this type of disturbance near 1PI by

Table 4. The effects of overturning zoanthid-covered substrata on polyp size and density after 5 and 11 months (95% confidence limits are given). See Table 5 for control values. A fifth replicate was damaged in an early spring storm

	5 Months (Aug. 1977)	11 Months (Feb. 1978)
Maximum height (mm)	10.6 ± 2.0 (n = 4)	5.4 ± 2.1 (n = 4)
Maximum diameter (mm)	2.9 ± 0.6 (n = 4)	2.5 ± 0.6 (n = 4)
Mean density (#/0.01 m ²)	175 ± 163 (n = 4)	139 ± 132 (n = 4)

constructing four, 12-cm-high concrete block tunnels onto substrate covered by *Z. sociatus*. Each tunnel shaded approximately 10 × 30 cm. As in the previous experiment, polyp density significantly decreased in response to shading (Table 5). However, polyps initially increased in height and diameter of the oral surface. This was especially true at the tunnel openings where large, dark green polyps extended towards the light. Such large polyps are typical of naturally shaded conditions on the reef as in crevices or under algal mats where polyp attachments may be up to 80 mm (largest observed polyp) from full light exposure. After four months, mean polyp sizes began to decrease (Table 5). There were still some large polyps at the tunnel openings but smaller polyps (similar to those observed in the previous experiment) were prevalent in the central, shaded areas.

A third substratum disruption experiment simulated the movement of *Z. sociatus* attached to coral rubble into areas outside the *Zoanthus* zone. Such dispersal was evident in the lee of IPI where the depth range of *Z. sociatus* extended at least to 8 m. In July 1977, two *Z. sociatus* colonies were transplanted onto the silty bottom south of IPI at depths of 10 m and 20 m. These colonies were undamaged and apparently quite healthy after 30 days. This was not true for transplants at WBR which had been placed 20 m and 40 m south of the *Zoanthus* zone at depths of 1.0 and 1.5 m, respectively. After 30 days, the first transplant appeared to have been damaged by predators such as damselfish and the polychaete *Hermodice carunculata* (as in Sebens, 1982). *Hermodice* had, in fact, been observed feeding on this transplant once during the 30 days. The second transplant showed signs of sediment accumulation after 17 days and was mostly buried in sand after 30 days.

Table 5. The effects of shading on the mean size of randomly selected zoanthid polyps and their density (95% confidence limits are given). Replicates for shaded treatments were taken from the four, block tunnels

	April 1977		May 1977	August 1977
	Unshaded Controls	Naturally Shaded Controls	Unshaded Controls	Unshaded Controls
Height (mm)	20.9 ± 2.3 (n = 10)	28.9 ± 4.6 (n = 10)	18.9 ± 4.0 (n = 20)	20.4 ± 9.5 (n = 40)
Diameter of oral surface (mm)	5.0 ± 0.0 (n = 10)	13.7 ± 1.2 (n = 10)	5.0 ± 1.2 (n = 20)	4.9 ± 1.3 (n = 41)
Density (#/0.01 m ²)	—	—	—	513 ± 94 (n = 5)
	Shaded Treatment			
Height (mm)		21.8 ± 4.1 (n = 20)	39.5 ± 4.0 (n = 20)	26.4 ± 5.0 (n = 39)
Diameter of oral surface (mm)		4.3 ± 0.3 (n = 20)	9.6 ± 1.0 (n = 20)	8.5 ± 1.3 (n = 42)
Density (#/0.01 m ²)		—	—	170 ± 49 (n = 12)

Two more sets of transplants were placed 1–2 m from substrata covered by *Z. sociatus* in seaward locations (at the same depth) characterized by bare substratum at WBR and at CPC. Within 5 days, minimal zoanthid damage had been observed in five transplants at WBR. At censuses 2, 4, and 10 months after transplantation, these zoanthid colonies appeared to be healthy and had grown onto the underlying bare substratum. Three CPC transplants, on the other hand, exhibited several headless polyps indicative of damselfish damage (Sebens, 1982) within 3 days of transplantation. The absence of naturally occurring *Z. sociatus* at the seaward WBR location may be due to the unlikelihood of zoanthid dispersal in this seaward direction. At CPC several yellowtail damselfish *Microspathodon chrysurus* resided at this site and may have caused the zoanthid damage. I have not, however, directly observed *M. chrysurus* preying on *Z. sociatus* nor do Randall (1967) and Emery (1973) indicate that this benthic omnivore actually feeds on zoanthids.

A last set of substratum disruption experiments involved the placement of bare substrata in contact with *Z. sociatus* at IPI. These simulated the transport of new substrata into and the reorientation of old substrata within the *Zoanthus* zone. Sixteen substrata (dead *A. cervicornis* 7–26 cm long) were strewn about a 1-m² area covered by *Z. sociatus*. Zoanthid polyps were not damaged by this treatment. Instead, they exhibited an elongation response as in the previously described shading experiment. At approximately 3-day intervals, two substrata were carefully examined for zoanthid attachment and removed from the area. No attachment was observed until the seventeenth day when zoanthid polyps had attached to 7 of the remaining 10 substrata. A similar experiment conducted concurrently in the laboratory sea water system resulted in some polyp attachment after 13 days. Undisturbed conditions following disruptive manipulations were necessary for successful attachment to these substrata.

In a longer term experiment I used ten, ~250-cm² *A. palmata* substrata and ten, 232-cm² ceramic tile plates (as in Sutherland and Karlson, 1977) to examine postattachment events. Half of the *A. palmata* substrata had been previously covered with *Z. sociatus*. These were cleared of all biota as in the previously described clearing experiments. The remaining five, *A. palmata* substrata had not been covered with *Z. sociatus*; these were cleaned, treated with dilute sodium hypochlorite overnight, and sun-dried before reintroduction to the experimental site at IPI.

Both sides of these 20 substrata were examined after 5 and 11 months. Most upper surfaces developed an algal mat or were colonized by macroalgae, such as *Padina*, *Dictyota*, or *Halimeda*. Zoanthid polyps invaded the periphery of the upper surfaces of these substrata by exhibiting one or several of the following: (1) elongation of shaded polyps and stolons, (2) attachment of polyps and stolons to coral substrata, tile plates, or *Halimeda*, (3) transformation of attached polyps into stolons, (4) budding from both polyps and stolons, and (5) polyp extension through the algae to exposed, full light conditions. The undersurfaces of these substrata were heavily colonized by ascidian, bryozoan, and serpulid larvae. There was no zoanthid larval recruitment after 5 months and only two such recruits after 11 months; these settled on a single tile plate. These two recruits had settled near the edge of the plate and had just begun growing stolons towards the edge.

Although some fecundity data is available for *Z. sociatus* (Karlson, In Press), the importance of sexual reproduction and larval recruitment for the maintenance of benthic zoanthid populations remains unknown at this time. As with *A. cervicornis* (Gilmore and Hall, 1976; Tunnicliffe, 1980; 1981) and *A. palmata* (Highsmith et al., 1980), the vegetative aspects of the zoanthid life cycle appear to be

primarily responsible for the successful persistence and monopolization of the spatial resource within the *Zoanthus* zone.

Predation

Most of the disruption to the benthic assemblage in the *Zoanthus* zone at Discovery Bay was due to storms or grazing by *Diadema*. Predatory damselfish and *Hermodice*, however, have been implicated as important determinants of zoanthid distribution in Panama where *Z. sociatus* is abundant in an intertidal refuge from predators (Sebens, 1982). *Z. sociatus* and these predators coexist in the subtidal *Zoanthus* zone in Jamaica.

From September 1976 through April 1977, no signs of predator damage to *Z. sociatus* had been observed at any of the Discovery Bay study sites. During the late spring and summer, however, occasional zoanthid damage or polyp removal was evident at the WBR, CPC, and BL. This may have been due to seasonal variation in damselfish aggressiveness associated with their reproductive activities and/or the creation of new territories by maturing juveniles (L. Kaufmann, *personal communication*). *E. planifrons* and *E. dorsopunicans* can remove an entire polyp or just the polyp's oral end (Sebens, 1982; *personal observation*). In the latter case, stolon attachments are maintained. The following two experimental manipulations suggest that the regenerative capabilities of *Z. sociatus* are sufficient to minimize the impact of eupomacentrids on zoanthid spatial utilization patterns.

Prior to July 1977, *Z. sociatus* exhibited no sign of predator damage at 1PI. Zoanthid cover along the fixed transect was 91% at this time and the complete cage at this site enclosed approximately 68,000 zoanthid polyps. In three days following the removal of the wire mesh from this cage, ~80% of the previously enclosed zoanthid polyps had been bitten in two by a single *E. planifrons*. One might speculate that this damselfish was opening a new territory, but why it had not attacked polyps outside the cage remains unclear. Examination of the photographs of zoanthid recolonization into clearings at this site indicate no significant effect of this biological disturbance to zoanthid stolon attachments (i.e., percent cover).

The regenerative potential of *Z. sociatus* was also tested at another 1PI location near a small population of *A. saxatilis* (sergeant majors). I simulated damselfish predation by cutting off the top half of all the zoanthid polyps in a 225-cm² area. Here again no bare substratum was generated by this process. Instead, each polyp regenerated its oral end after several weeks.

In the laboratory I determined that *Hermodice* could potentially cause a great deal of zoanthid mortality. Four large *Hermodice* were collected from the WBR and placed into a running sea water table with *Z. sociatus*. Each polychaete ate an average of seven polyps per day for 12 days until all the polyps were removed from 95 cm² of coral substratum. This localized, rapid denuding of the substratum has not been observed (by the author) at Discovery Bay suggesting that alternative prey are eaten and/or that field densities of *Hermodice* are relatively low and the regenerative capabilities of *Z. sociatus* sufficient to compensate mortality due to predation.

DISCUSSION

Z. sociatus clearly dominates the subtidal, algal-zoanthid assemblage at the WBR, 1PI, CPC, and BL sites. It successfully colonizes substratum in the presence of *Diadema* and can regenerate following predator-induced mortality and sub-

stratum disruption caused by storms. The effects of substratum colonization and disturbance on the *Zoanthus* zone assemblage may be analogous to that described for *Mytilus*-dominated intertidal shores (Paine, 1974; Paine and Levin, 1981). However, at this time the relative competitive status of *Z. sociatus* and other sessile organisms is still in question and it is not entirely clear how this assemblage will respond to an extended period without disturbance.

An alternative to the above scenario is that intermediate levels of disturbance may be necessary for the persistence of *Z. sociatus* as the numerically dominant sessile organism. Disturbance in this case would create bare substratum and significantly reduce the abundance of competitively superior species [e.g., *Erythropodium* (Karlson, 1980)]. This scenario would favor relatively rapid substratum colonization by *Z. sociatus* between disturbances. In this study, low levels of physical disturbance have characterized the EBR site. Here, *Z. sociatus* is present but less abundant than *Z. solanderi* and six other cnidarian species (Karlson, 1980). Intermediate levels of disturbance along the WBR appear to favor the algal assemblage and *Z. sociatus* as the dominant species. High levels of disturbance would be overly disruptive exceeding zoanthid regenerative capabilities (e.g., in the breaker zone with *A. palmata*, few other cnidarians, and much bare substratum). The WBR is more protected from storm damage than are shallow fore reef sites [as noted by Woodley et al. (1981) following Hurricane Allen, 6 August 1980].

I have described several aspects of zoanthid colony regeneration. Most of these are consequences of asexual reproduction among colonial organisms (Jackson, 1977). Some may represent particularly advantageous adaptations to the disruptive effects of storms. Even the slow colony degeneration exhibited by *Z. sociatus* in unfavorable microhabitats indicates the potential for a regenerative role for these polyps. Degenerating polyps generally retained their stolonal connections which may have favored more rapid substratum recolonization in the event of another disruption. These connections may also have served an active transport function involving the intracolony redistribution of matter in response to altered microhabitat conditions. Changes in the relative positions of zoanthid polyps and coral substrata increase the importance of new substratum attachments, polyp-to-stolon transformations, and the phototropic behavioral and growth responses exhibited by shaded polyps and stolons. Such a wide range in polyp responses is not typical of all colonial organisms, especially among those whose morphology is restricted by hard skeletal structures.

The increase in polyp size exhibited by *Z. sociatus* in response to shading can be interpreted in terms of increasing the likelihood of polyp-substratum contact, attachment, and growth. The cost of this extension may include increased zoanthid susceptibility to storm disruption which was observed following the removal of wire mesh from some cages. It may also be relevant to consider the relationship between the polytrophic mode of nutrition of this species (von Holt, 1968; von Holt and von Holt, 1968; Trench, 1974; Sebens, 1977) and polyp size. The elongated polyps typical of my shading experiments and naturally shaded situations had a greatly expanded oral disk (Table 5). This response to shading greatly increased the surface area exposed to the light source and presumably the light capturing ability of these polyps (via their autotrophic zooxanthellae). Many of these polyps also exhibited tentacle protrusion (a predatory posture) as described by Reimer (1971). This suggests that large polyp size can favor both autotrophy and heterotrophy in these suboptimal microhabitats. This polytrophy may represent another mechanism which enhances the rate at which zoanthids respond to habitat disruption. Porter (1976) has presented the argument that Caribbean,

reef-building corals partition their nutritional resources along heterotrophic and autotrophic axes and that they are limited to some degree as polytrophs by constructional and/or energetic constraints. The absence of a hard skeleton in *Z. sociatus* allows greater plasticity in polyp response to shading and other effects of disruption and may generally enhance polytrophy in this species.

The absence of a hard skeleton is also an obvious structural disadvantage constraining zoanthid growth and microhabitat utilization patterns. *Z. sociatus* grows within the two-dimensional constraints of the substratum surface which limits its distribution to the reef understory or to disturbed habitats in which erect, canopy forming species are absent. *Z. sociatus* has a stoloniferous growth form exhibiting both runner and sheet morphologies described by Jackson (1979) and Buss (1979). Such a morphological strategy has been predicted to be most successful in disturbed environments characterized by strong water movement, low sedimentation, high substratum instability, and abundant predators (Jackson, 1979—Table 13). These predictions appear to be supported here. In addition, I suggest that intermediate rather than high levels of disturbance favor *Z. sociatus* in the *Zoanthus* zone.

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