Distribution Patterns of Sea Anemones as a Function of Competitive Interactions, Substrate Preferences, and Morphology Types, on a Coral Reef.

Elizabeth Franck and Jonathan Vaccaro

6 March, 1984

Tropical Biology Foreign Study Program

Dartmouth College, Hanover, N.H.

ABSTRACT

The following study investigates possible limiting resources of sea anemones on a coral reef, with respect to a variety of parameters. Spacial limitations are suspected to be a major limiting reef resource. If this is the case, we hypothesize that anemones would develop niche separation and substratum preferences to minimize competition. Aggressive interactions might occur and a competative network would develop based on these interactions. Once an anemone settles on a preferred substrate, it will defend this space from encroaching coral and other anemones.

Six anemone species were examined over a 60 foot gradient, observing substratum preference, species interactions, depth preference, and anemone ablility to damage live coral tissue.

The results suggest that because of the unique successional stage of the Discovery Bay reef, where unlimited substrate is available to anemones, space is not the major limiting resource. Instead a variety of factors, including anemone morphology type, light requirements, reproductive rates and predation are probably responsible for anemone distribution and abundance on the reef.

INTRODUCTION

The coral reef is a dynamic community, built upon the living and dead coral tissue comprising the reef matrix. Areas of cleared substratum constantly appear due to storms, natural disturbance, predation and erosion. This continual turnover allows a constant successional process, colonization of newly cleared areas, and high reef diversity.

High importance has been placed on the occupation of space and the distribution of organisms in benthic coral reef communities (Smith, 1978, through Reichelt). The concept of space limitation has been proposed as an important factor influencing the organization of coral reef communities; and several studies support this idea (Loya 1972, Porter 1972, Connell 1973).

If space is indeed a limiting reef resource, intra- and interspecific competitions will be expected among organisms requiring the same microhabitat. In addition, niche separation and substratum preferences will develop to maximize all available resources. This partitioning may contribute to the high diversity of sessile forms characteristic of coral reefs (Sebens,1976).

Sea anemones (Phylum; Cnidarian, Class; Anthozoa, Order; Actinaria) are sessile benthic organisms closely associated with coral reefs, and frequently found anchored to coral tissue. If spacial limitations are causing interspecific competition among these organisms, we hypothesize differential substratum use will occur between anemone species to minimize competition by separation of niches.

Aggressive behavior has been reported for some temperate anemone species (Bonnen 1964, Francis 1973, through Sebens), although the extent of competition why a network?

for tropical anemones is unknown. We hypothesize that a competitive network will exist between co-occuring anemone species as a result of aggressive encounters at the same attachment sites. This will result in the exclusion of some individuals to less desirable, more stressed substrates.

Corals and sea anemones have similar microhabitat requirements which overlap with respect to two areas. Both groups require a continuous supply of zooplankton in the water flow surrounding them, and well lighted areas to support their zooxanthellae symbiots. Anemone presence on corals suggests that anemones must compete with coral for the same substrate. It is hypothesized that once an anemone settles on a substrate it will defend its position from encroaching coral by killing tissue within its reach.

Sea anemone species exhibit three distinct morphologies, one best suited for flat substrates, the other two being tubular or stalk forms to utilize pockets, holes and crevices of varying sizes. These morphological adaptations allow anemones to exploit the differing substratum types on the reef structure. At the same time however, the body shapes place inherent limitations on the anemone with regard to light requirements, ability to withstand water turbulence, and the need for a bottom surface or crevice microhabitat. A final hypothesis is the expectation that differential species abundance will occur at different depths. This zonation may result from either morphological limitations or competitive pressure or both.

Major natural disturbances drastically alter a coral reef. Hurricane Allen devastated the coral reefs of North Jamaica in 1980 (Woodley et al,1981). Virtually all live branching coral above 40 feet was smashed and reduced to rubble. Large amounts of substratum were exposed and greatly increased the surface available for sessile organism growth and recruitment (Woodley et al, 1981). Thus the hurricane set the stage for a major secondary successional sequence.

This unique reef situation allows a look at the anemone recovery processes leading to climax reef anemone populations, such as those studied by Sebens (1976). In this case the presence of particular microhabitats, an important requirement for anemones, may not be the limiting force in the distribution and abundance of these organisms. The destruction of the hurricane was so great that the substratum slate was wiped clean. If the density of anemones in the area is below saturation levels with regard to this microhabitat it is probable that some density-independant factor controls the number of anemones.

This study will examine the aforementioned hypotheses with regard to the recent, drastic upheaval of the reef. Habitat resource use by anemones will be examined. A comparison to previous studies from climax reef communities may indicate changing patterns of substratum occupation on a maturing coral reef.

STUDY SITE

This study was conducted at Discovery Bay Marine Laboratory, Discovery Bay, Jamaica, West Indies, between 25 February and 4 March, 1984. Transect data was collected on the West Fore Reef below Mooring #1, between 10 and 60 feet. This area consists of buttressed coral reefs, divided by sand channels running north-south, which gradually slope down past 100 feet. The substrate was mainly coral rubble deposited by Hurricane Allen in 1980, most of the coral fauna being obliterated by this storm.

Two transects were taken in the West Back Reef, a relatively protected lagoon area with low water turbulence. The substratum consists of Thalassia beds, soft sand and coral rubble, with anemones, urchins and algal growth present.

On the fore reef, local substrate differences were evident between the transect areas which could influence sea anemone abundances regardless of depth. Brief descriptions of the transect areas follow:

10 feet - Most highly disturbed reef area, massive coral rock debris, interspersed with cleared sand patches, turbulent water, absence of all benthic organisms except algal fuzz.

20 feet - Massive overturned coral boulders with some rubble present between the boulders, less turbulent water than 10' though still strong currents, few sponges and anemones present, scattered sand patches.

30 feet - Substrate leveling out, <u>A. cervicornis</u> rubble fills gaps between boulders, no open sand patches, diversity of fish, anemones, sponges and algae increasing, mild turbulence.

40 feet and 50 feet - Large boulders absent, substrate of tangled, dead coral branches with many pockets and gaps between them, anemones, live branch coral, sponges and algal growth present.

60 feet - Transect located on steep coral wall sloping to sand channel, cover composition similar to 50 feet, with larger gaps and spaces due to the vertical tilt, organism diversity and abundance slightly less than at 50 feet.

METHODS

This report required in situ surveys of sea anemone densities as well as laboratory competitive interaction studies.

Field observations were collected at Mooring #1 on the West Fore Reef of Discovery Bay. Transects were taken at intervals from 10 to 60 feet deep. (The English Measuring system is used for depths only since all guages are calibrated in feet.) Using SCUBA technique, two divers surveyed belt transects 3m. wide by 10 m. long. Each sea anemone in the transect was observed for species type, substratum, diameter of tentacle span and depth below surface. In addition, surrounding corals were examined for any damage due to the anemone. Coral damage was recorded as the percent of dead coral tissue within reach of the anemones tentacles if the coral tissue outside the tentacles reach was still living.

To determine species composition in calm, shallow water, two 3m. by 10m. transects were made in the back reef: the first along a rocky ridge near the boat dock at a depth of 5 feet (" 5 feet inner"), the second transect on the back side of the reef crest in 5 feet of water ("5 feet outer"). These results are included with our graphs and tables for comparison between calm and disturbed reef areas.

In order to gather anemones for laboratory manipulation experiments, SCUBA divers collected samples from the West Back Reef (5 - 10 ft. depth) and from the West Fore Reef (40 ft. depth). Several individuals of each anemone species examined were collected manually by using hammer and chisel. Samples were removed from lose substrates of sand or coral fragments. (Sampling was biased in this respect since anemones on larger substrates could not be removed without organism damage.) The anemones were transported in mesh dive bags back to the boat where they were placed in buckets filled with sea water. All samples were placed with their substrate on wet tables at the Discovery Bay Marine Laboratory. Intraspecific and interspecific competition experiments were conducted among _Condylactis gigantea_, _Heteractis lucida_, _Lebrunia danae_, _Stoichactis helianthus_ and _Bartholomea annulata_. Each pair of anemones was placed within tentacle reach of the other. Relocation movements and tentacle retraction of one species as a result of the others' tentacle touch were considered indicative of aggressive interference. The withdrawing anemone was considered submissive to the undisturbed anemone. Three pairs of each competitive interaction were tested in one twelve hour interval. Using the same anemone pairs, these tests were then replicated once.

RESULTS

The six sea anemones showed distinct vertical zonation patterns (Figure 1A-F). On the West Fore Reef, no anemones were found in the shallow waters. Overall, sea anemone density increased with depth, peaking at 40 feet, then tapering down in deeper water (Table 1). Lebrunia danae was the most abundant species found in all the transects. Although the graph (Fig. 1D) indicated two peaks, at 30 and 50 feet, they were most common in medium depths, below the surf zone yet shallow enough to allow sufficient light to reach the symbiotic zooxanthellae in their tissues. The gap at 40 feet was replaced by the coralliomorph R. sanctithomae (Fig.1-C). This species had the greatest density compared to all anemones on the fore reef, ($\sigma = 0.13/\ m^2$, Table 1). The percentage of H. lucida in each transect remained fairly uniform with depth (Fig. 1-E). In addition, B. annulata were found uniformly across the transects, however, in very low abundance. The slight peak in percentage values in Figure 1-F is due to a small total sample size (n=3).

By contrast, there was a complementary group of sea anemones in the back reef. While L. danae, H. lucida, B. annulata were common on the fore reef, they were absent on the back reef. They were replaced by C. gigantea and S. helianthus. In addition, a few C. gigantea were present on the fore reef. C. gigantea were most common along the reef crest (5 ft. outer) whereas S. helianthus was found more frequently in the inner back reef. S. helianthus had the greatest density of anemones in the inner back reef ($\sigma = .157/m^2$,Table 1). This fact may be due to its clumped distribution on shallow rocks. One rock supported 15 individuals, almost one third of the total number of S. helianthus.

The substratum preference for the sea anemones was related to the distinct morphology of each species. The following is a brief description of species morphology and substratum preference.

Condylactis gigantea: This species lived on large rocks and dead corals. The pedal disk of the wide, short body was usually attached to a shallow crevice, and the tentacles were exposed to passing water currents.

Stoichactis helianthus: Usually clumped, these were found on the upper surfaces of large rocks, only in shallow water. Having dense stubby tentacles across the entire oral disk, it lay flat against the substrate. It had the greatest mean tentacular span, 10.6cm, of all anemones tested.

Rhodactis sanctithomae: Like S. helianthus, this species was highly clumped and lay flat on the substrate. However, it was most commonly found on dead corals and coral rock at depths greater than 30ft.

Lebrunia danae: Another clumped species, these prefer crevices in loose substrate such as entwined dead Acropora cervicornis branches or coral rock debris. The long pseudotentacles extended through the dead coral branches with the long tubular body protected in the crevice.

Heteractis lucida: These anemones required a hole in which to place their tubular body. They are found in crevices in living or dead corals. They have long delicate tentacles.

Bartholomea annulata: These also have long bodies tucked into crevices. Often a sand layer covers the hard substrate upon which they attach.

Coral tissue damage resulting from sea anemones was observed in field sites. However, there were few large living coral heads present at the time of the study, most likey as a result of the destruction of Hurrican Allen in 1980. Only _H. lucida_ was found on living coral with dead tissue within reach of the tentacles. Of the 68 _H. lucida_ located within the fore reef transects, 12 were near live coral and all caused damage to the live tissue. All tissue within the radius of the expanded tentacles was dead. The coral species attacked were _Agaracia agaracites_, _Montastrea annularis_, _Madracis mirabolis_ and _Mycetophyllia lamarckana_.

Lab interactions?

TABLE 1 - Total number, density and mean size of tentacular crown for each sea anemone species found in 300 m^2 transects at the depth indicated

	Depth in Feet	Total # Anemones at depth	*Condylactis gigantea*		*Stoichactis helianthus*		*Rodactis sactithomae*		*Lebrunia danae*		*Heteractis lucida*		*Bartholomea annulata*	
		n_T	n	σ	n	σ	n	σ	n	σ	n	σ	n	σ
Inner Back Reef	5	69	22	.073	47	.157	–		–		–		–	
Outer Back Reef	5	21	20	.067	1	.003	–		–		–		–	
Fore Reef Transects	10	0	–		–		–		–		–		–	
	20	3	1	.003	–		–		–		1	.003	1	.003
	30	68	–		–		9	.03	42	.14	15	.05	2	.007
	40	71	1	.003	–		40	.13	6	.02	22	.073	2	.007
	50	44	3	.010	–		5	.017	24	.080	10	.033	2	.007
	60	38	–		–		7	.023	10	.033	20	.067	1	.003

Mean Anemone Size (diameter) cm	*Condylactis gigantea*	*Stoichactis helianthus*	*Rodactis sactithomae*	*Lebrunia danae*	*Heteractis lucida*	*Bartholomea annulata*
	10.0 ± 2.55	10.6 ± 0.44	4.7 ± 0.14	6.3 ± 0.23	6.9 ± .30	4.5 ± .42

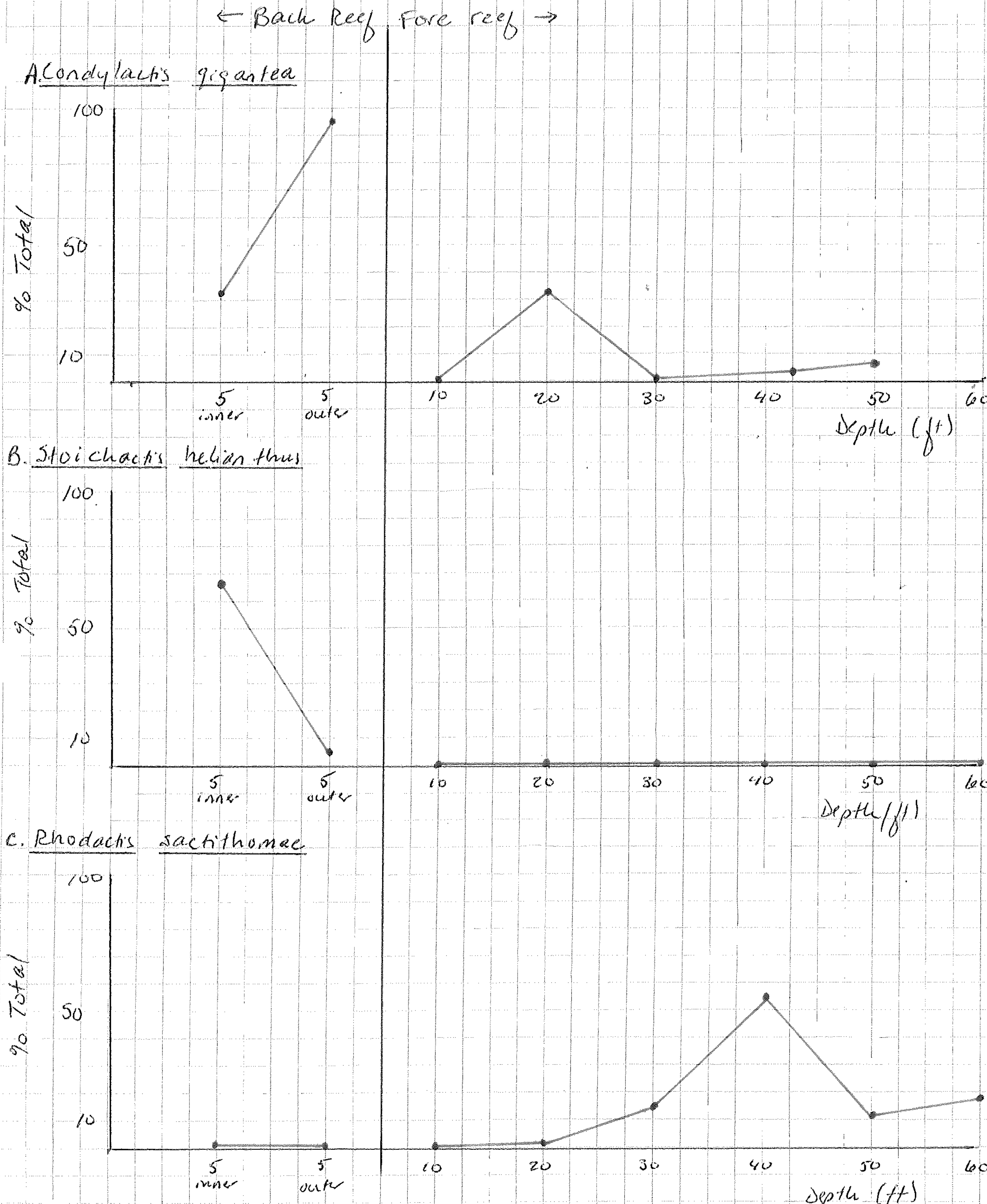

Figure 1A-C. The percentage of the sea anemones Condylactis gigantea (A), Stoichactis helianthus (B), and Rhodactis sanctithomae (C) found in each transect at the indicated depth.

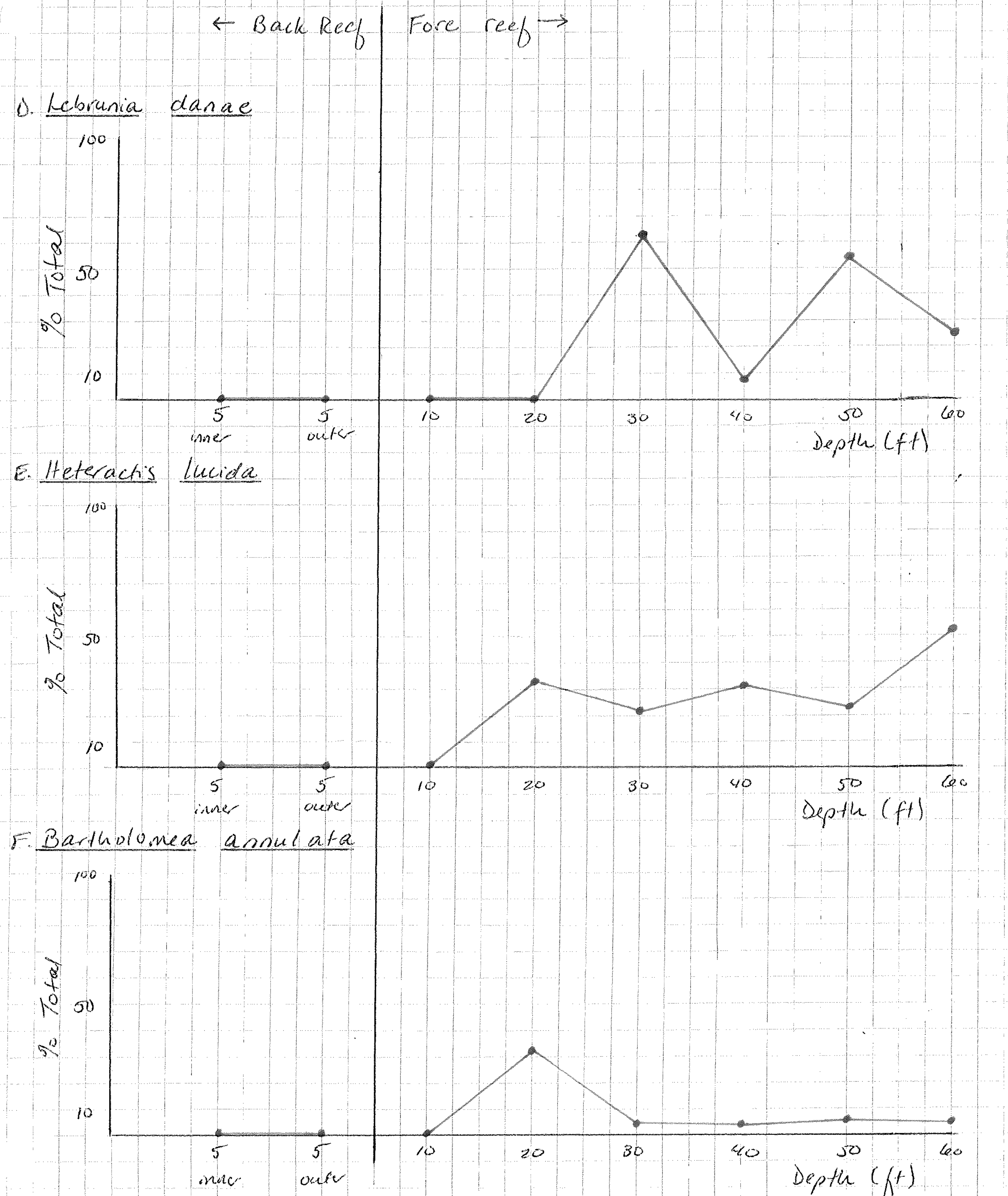

Figure 10-F. The percentage of the sea anemones Lebrunia danae (D), Heteractis lucida (E), and Bartholomea annulata (F) found in each transect at the indicated depth.

DISCUSSION

Substrate partitioning and vertical zonation among the different anemone species results in varied distribution patterns. Although a competitive hierarchy existed in laboratory manipulations, competition for space was not seen in the field; different species of anemones rarely occupied the same substratum. In fact, since S. helianthus and H. lucida never co-occured on the same substratum, their competitive interaction can be negated to yield the following hierarchy, shown in Figure 2.

Hierarchy:	S.helianthus > C.gigantea >	H. lucida >	B. annulata >	L. danae
Substratum Preference:	large rocks and dead coral heads	dead coral and coral rock	sand over rock	broken coral mesh
	Exposed → →	→	→	Crevice
Morphology:	Flat with short tentacles →	Tentacles with tubular body →	Long pseudotentacles and long tubular body	

Figure 2. Diagram of Competitive hierarchy among five sea anemone species. Trends in substrate preference and morphology characteristics are indicated by arrows.

The hierarchy presented here agrees with Sebens' competitive interactions (1976). The network design suggested by Norris and Whittington (1981) can be rejected since they do not account for substrate preferences or vertical zonation partitioning.

Differing substrate preferences may not be a result of interspecific competition; instead they may depend on anemone morphology. Figure 2 indicates the change in morphology of each anemone with respect to substrate preference. For example, S. helianthus required a large, sturdy substrate on which to attach its thick pedal disk. Therefore, it should not normally occur with L. danae, which attaches its stalk deep within entwined dead coral branches. Morphological features are then important parameters in determining the distuibution of species on different substrate types.

If niche partitioning is complete and not related to competitive interactions, other factors must be affecting anemone distributions. Figure 1 A-F show little overlap among species on the fore reef with those on the back reef. The anemones on the fore reef achieved the greatest overall densities around 30 to 40 feet. Most species appear to prefer these shallow waters, where maximal sunlight will benefit the symbiotic zooxanthellae. However, on the fore reef, little or no anemones were found at 10 to 20 feet depths. Disturbance is the major factor limiting utilization of this level. Continual battering from waves and surge would destroy the soft bodied sessile anemones. A major disturbance was Hurricane Allen . This storm created a new shallow fore reef by piling A. palmata into a reef crest. Hence these two disturbing forces, wave surge and hurricane damage restricted the anemones to deeper waters by disturbance and the creation of a new barrier.

In the calm waters of the shallow back reef, S. helianthus and C. gigantea dominate. Oddly enough, few species from the fore reef are present here. Morphological characteristics appear to be the limiting factors for colonizing this area. H. lucida, B. annulata and L. danae all require crevices within which they attach their stalks. Greater amounts of sediment filling in the back reef crevices would limit potential substrates. In addition only the heartier species could survive in the back reef where there is a fresh water surface layer from runoff. Pollution from sewage dumped into the bay (exeess nitrogen) and oil and bauxite spillage from the Kaiser Bauxite plant may also restrict anemones abundance and require adaptations for these pollutants. Finally, the transect area in the back reef may not have represented all the anemone species there. B. annulata and H. lucida have been observed to be present in the back reef.

Therefore, distribution patterns vary with substrate changes and with vertical zonation. Although interspecific competitive interactions were evident in lab, substrate partitioning appears to be a result of morphological characteristics of each anemone, and possibly other factors, and is not necessarily due to competitive interactions.

CONCLUSIONS

Substrate partitioning among sea anemones appears to be a result of either morphological characteristics or competitive interactions or both. In order for interspecific competition to exist in a hierarchy, one species must prove itself dominant. McNaughton and Wolf (1970) proposed the following generalizations about benthic marine communities: (1) dominance was characteristic of the most abundant species; (2) dominant species had broader niches than subordinate species; (3) species are added to the system by compression of niches, and (4) community dominance is minimum on the most equitable sites.

On the coral reef studied in Discovery Bay, where S. helianthus was shown experimentally to be the competitive dominant among the sea anemones, none of McNaughton and Wolf's gerneralizations seem to apply. For example, generalization (1) was only true for the inner back reef where it and C. gigantea were the only two species found. S. helianthus was virtually non-existant in the other transects. Hence, (2) cannot be true since the niche of S. helianthus was limited to the shallow back reef. Niche compression (3) would occur if anemone densities increased and space became a limiting factor. However, low anemone densities in these areas imply minimal spacial limitations. Finally, community dominance (4) was maximized, not minimized, by S. helianthus in the shallow water back reef where light is plentiful and disturbance minimal.

Based on these criteria, competition does not appear to occur among the sea anemones. Space is most likely not a limiting factor since Hurricane Allen created clear, new substrate less than four years ago. Pianka (1976, through Reichelt, 1982) appropriately summarized this type of situation by stating: "In a competitive vacuum with a surplus of resources available, niches could presumably overlap completely without detriment to the organisms concerned." Indeed sea anemone densities remained well below saturation levels, thus minimizing interspecific competition.

While competition seems to play a minor role in species distributions, the ability for competitive interactions does exist among anemones. This study proved that anemones possess the mechanisms involved for competition: (1) a competitive hierarchy, (2) selective substrate partitioning and (3) the ability to kill surrounding corals. However, none of these mechanisms were directly observed in competition for preferred substrate.

Therefore, what other factors are influencing the distribution patterns of sea anemones ? The amount of light available and disturbance levels have already been discussed as possible factors including or precluding, respectively, anemones from certain depths on the fore reef. A slow reproductive rate would restrict population expansion. Natural predation may reduce the population size or relieve the competitive strain caused by a dominant anemone. Some abiotic factors, such as man-made pollution may hamper resource exploitation in certain areas, particularly on the back reef. Certainly, substratum requirements of each anemone due to its morphology indicate that niche partitioning may have a physical component and not a competitive factor.

In summary, we contest the findings of other authors who found that competitive interactions are a result of substratum limitation. This may be the case in climax coral reef communities. Yet, reefs are continually in a successional stage due to episodic storms causing minor damage (or major destruction in the case of Hurricane Allen) and due to coral patches dying from predation or other factors. Numerous other factors appear to affect distribution patterns of these sea anemones. In particular substrate preference, vertical zonation and morphology are of major importance.

Therefore, future studies should not consider space as the sole limiting factor to sea anemone distribution on coral reefs, where frequent substrate clearing occurs. Instead they should examine a variety of other possible sources for anemone limitations.

REFERENCES

Connell, J.H. 1973. Population Ecology of Reef Building Corals. In: Biology and Geology of Coral Reefs. D.A. Jones and P. Endean, Eds. Academic Press, New York, 360 pp.

Dayton, P.K. 1971. Competition, Disturbance, and Community Organization: The Provision and Subsequent Utilization of Space in a Rocky Intertidal Community. Ecol. Monogr. 41:351-389.

Norris, T. and T. Whittington. 1981. Everything You Always Wanted to Know About Sea Anemones. Foreign Study Program Biology Report. Unpublished.

Reichelt, R.E. 1982. Space: A Non-limiting Resource in the Niches of Some Abundant Coral Reef Gastropods. Coral Reefs. 1:3-11.

Sebens, K.P. 1976. The Ecology of Caribbean Sea Anemones in Panama: Utilization of Space on a Coral Reef. Coel. Ecol. and Behav. pp67-77.

Woodley, J.D. et al. 1981. Hurrican Allen's Impact on Jamaican Coral Reefs. Science. 214:749-755.

Some very nice results, which are well-discussed with respect to current theory and other, published observations.