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STRUCTURE, PERSISTENCE, AND ROLE OF CONSUMERS IN A TROPICAL ROCKY INTERTIDAL COMMUNITY (TABOGUILLA ISLAND, BAY OF PANAMA)

Jane Lubchenco[1], Bruce A. Menge, Stephen D. Garrity[2], Peggy J. Lubchenco[3], Linda R. Ashkenas, Steven D. Gaines[3], Richard Emlet[4], John Lucas and Sharon Strauss[5]

Department of Zoology, Oregon State University, Corvallis, OR 97331, U.S.A.

and

Smithsonian Tropical Research Institute, Box 2072, Balboa, Panama

Abstract: The physical environment and patterns of distribution and abundance of macroalgae, sessile and mobile animals are described for the littoral zone of Taboguilla Island, Bay of Panama. The substratum is basaltic and heterogeneous in both texture and topography. Some physical factors vary seasonally. During the wet season, (May to mid-December) rain is frequently heavy, daily air temperatures range from 24 to 31.5 °C, surface sea-water temperatures range from 26 to 28 °C, and wind is usually low but variable in speed and direction. During the dry season (mid-December through April), rain is infrequent, daily air temperatures range from 22 to 32 °C, surface sea-water temperatures range from 18 to 27 °C, wind ranges from northwesterly to northeasterly and can reach 30 knots. Water clarity is usually poor throughout the year.

Taboguilla shores appear barren throughout the year because benthic animals and erect macroalgae are rare on exposed rock surfaces. In the high zone most surfaces are bare (91.5 to 98.1%), with small barnacles *Chthamalus fissus* (Darwin), *Euraphia imperatrix* (Pilsbry) the dominant space-occupants. In mid and low zones, encrusting algae dominate space (25.9 to 92.5% cover) and sessile animals are scarce (< 1 to 9.8% cover). Maximum cover (7.0%) of erect algae occurs in the low zone. The plants are short, < 5 cm tall. Consumers (e.g., limpets, predaceous gastropods, crabs, chitons, fishes) are diverse and abundant in all zones.

Both prey and consumer species composition and abundances change from high to low zones. Densities tend to vary more in the high, and less in lower zones. The large herbivorous crab *Grapsus grapsus* (L.) is usually most abundant at higher intertidal levels. In contrast, fishes are probably effectively denser in lower than in higher zones, at least at high tide, although many range throughout the intertidal as well as the subtidal zones. Both species richness (S) and diversity (H') increase with decreasing tidal level. Despite the seasonal changes in the physical environment, seasonal changes in community structure are small or lacking. Annual changes are sometimes larger, but still small in comparison to temperate regions. That crustose algae dominate this otherwise relatively barren shoreline seems due to: (1) intense, consistent grazing and predation by a diverse assemblage of vertebrate and invertebrate consumers on the upright algae and sessile animals, (2) desiccation, possibly ultraviolet and heat stress, especially at higher tidal levels, and (3) possible inhibition of settlement by crustose algae.

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[1] To whom reprint requests should be addressed.

[2] Present address: Department of Zoology, University of Massachusetts, Amherst, MA 01003, U.S.A.

[3] Present address: Hopkins Marine Station, Pacific Grove, CA 93950, U.S.A.

[4] Present address: Department of Zoology, University of Washington, Seattle, WA 98195, U.S.A.

[5] Present address: Department of Behavioral Biology and Ecology, University of Minnesota, Minneapolis, MN 55455, U.S.A.

INTRODUCTION

In contrast to the large body of literature concerning both qualitative (e.g., Lewis, 1964; Morton & Miller, 1968; Ricketts & Calvin, 1968; Stephenson & Stephenson, 1972) and quantitative (Dayton, 1971, 1975; Menge, 1976; Lubchenco & Menge, 1978; Underwood, 1981) patterns of temperate rocky intertidal community structure, little information exists on tropical rocky intertidal community structure (e.g., Reimer, 1976a, b; Menge & Lubchenco, 1981). The value of quantitative observational and experimental studies of such systems is potentially great. For example, evaluation of hypotheses regarding latitudinal gradients of community structure (e.g., species diversity) must rest in part on quantitative compilations of species abundance, distribution and diversity patterns at sites along the gradient. The current lack of information on tropical communities inhibits progress in this direction. Further, the design and interpretation of experimental studies is greatly enhanced by either previous or simultaneous knowledge of both biological and physical setting of a habitat. Moreover, quantitative descriptions of communities can serve as invaluable sources of information for workers with varied research interests. Finally, the availability of such information over long periods of time is also fundamental to a consideration of population and community persistence (e.g., Paine, 1974; Lewis, 1976; Menge, 1976, 1977; Connell, 1978; Lubchenco & Menge, 1978; Underwood, 1981). Because little information is available from tropical communities which would allow development of a broadly based perspective on geographic patterns of community stability, we initiated studies of community structure and organization in a tropical intertidal region on Taboguilla Island, Bay of Panama. This, and other observations and experiments from this community (e.g., Garrity & Levings, 1981, 1983; Menge & Lubchenco 1981; Gaines, 1983; Levings & Garrity, 1983; Menge *et al.*, 1983) will ultimately provide the basis for an evaluation and extension of models regarding community structure and organization in intertidal and other habitats (e.g., Menge & Sutherland, 1976; Paine, 1980; Lubchenco & Gaines, 1981; Gaines & Lubchenco 1982; Menge, 1982). Here we (1) summarize key characteristics of the physical environment, including seasonal changes, (2) quantify the structure of this community (i.e., patterns of zonation, space utilization, species composition, abundances and diversity of both sessile and mobile animals), (3) examine variation in space (vertical, horizontal) and time (seasonal, annual), and (4) present results from some consumer removal/exclusion experiments. We find that this community is dominated by algal crusts, has a rich fauna (expecially at lower tide levels) but a depauperate flora of foliose algae, a low abundance of sessile invertebrates, but a relatively high abundance of mobile invertebrates. Despite clear (but small) seasonal and annual variations in physical environment, the community changes little over space or time. Consumers prey heavily on sessile invertebrates and foliose algae and are a major factor in holding prey abundances low and maintaining the dominance of the crusts.

STUDY AREAS

The main study area is on the south side of Taboguilla Island (hereafter termed "Taboguilla", 8°48′10″N : 79°31′10″W), ≈ 16 km south of the Pacific terminus of the Panama Canal, in the Bay of Panama (Fig. 1; see Fig. 1D in Menge & Lubchenco 1981 for a photograph of Site 6). Study Sites 1 through 6 on Taboguilla consist of a series of semi-isolated stretches of heterogeneous basalt shore along a 1-km section of coast. Southern shores of this island drop steeply to ≈ − 30 to − 70 ft (− 9.1 to − 21.3 m) at which point the substratum becomes a cobble-gravel sediment mixture. Corals (mostly *Pocillopora damicornis* Dana) grow subtidally as isolated colonies and extend up into only the extreme low intertidal, so they cover a negligible portion of the intertidal substratum.

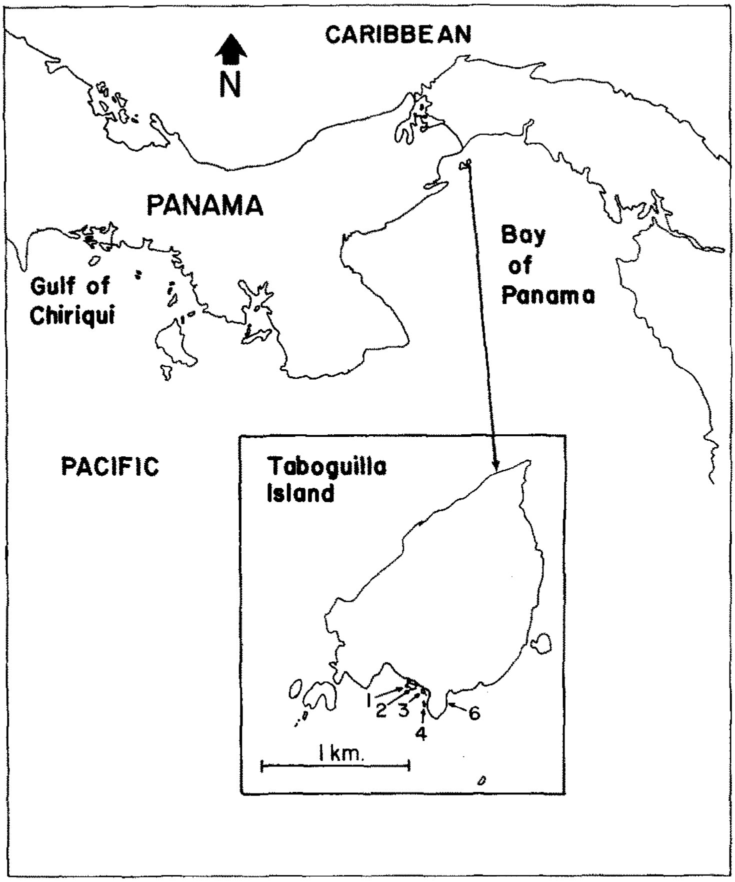

Fig. 1. Map of the Bay of Panama, showing the main study site, Taboguilla Island: numbers in inset refer to Study Sites 1–6. There is no Site 5; the line crossing the narrowest part of the isthmus is the Panama Canal.

PHYSICAL ENVIRONMENT

The Bay of Panama is characterized by two seasons, dry and wet (see Glynn, 1972; Ricklefs, 1973; Garrity & Levings, 1981; Menge & Lubchenco, 1981). The dry season (mid-December through April) is typified by periodic strong (16 to 32 km/h) north-easterly tradewinds while the wet season (May to mid-December) is characterized by mostly weak and variable winds. These differences result in several seasonal differences on the shore. During the dry season, there is little to no rainfall, skies are clear, and oceanic swells are reduced. During this study, air temperatures ranged from early morning lows of ≈22 °C to mid-day highs of 32 °C (Table I) and surface water temperatures of 18 °C to 27 °C (Table I, Fig. 2). During the wet season, there are frequent, brief, heavy rains, greater cloudiness, and changes in sea state from relatively calm seas to severe southerly swells. Such swells are unpredictable in size and time of occurrence. As a consequence the very low intertidal zone is nearly continuously submerged in the wet season, while during the dry season, it may be exposed for > 1 h at low tide. Maximal tidal excursion in the central part of the Bay of Panama is ≈21 ft (6.4 m). Tides are semidiurnal with the lowest tides occurring around midnight during the wet season and midday during the dry season (e.g., Anonymous, 1980). However, all intertidal zones except the very low zone are regularly exposed in both seasons.

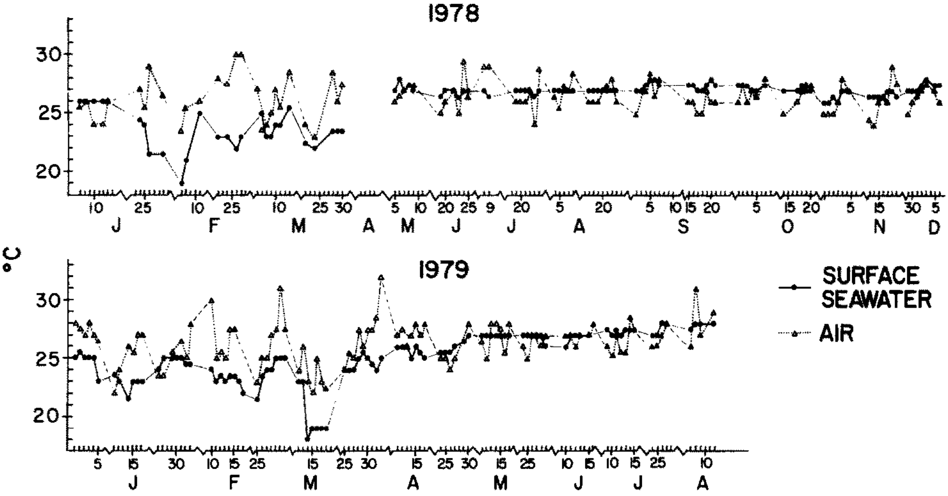

Fig. 2. Air and surface sea-water temperatures at Taboguilla Island in 1978 and 1979: zig-zags on X-axis represent periods between spring tides during which no samples were taken.

Compared to most tropical islands, water clarity is usually low in this region. Data taken at Taboguilla during 1979 indicate that there are no important seasonal differences in this characteristic, with mean lateral visibilities in dry and wet seasons of 4.0 ± 0.9 m and 3.1 ± 0.9 m, respectively (Table I). On a day-to-day basis, visibility is

TABLE I

Characteristics of the physical environment at Taboguilla Island, 1978–1980.[a]

		Dry season (January–April)				Wet season (May–December)			
Year	Statistic	Air temp. (°C)	Surface water temp. (°C)	Windspeed (km/h)	Visibility (m)	Air temp. (°C)	Surface water temp. (°C)	Windspeed (km/h)	Visibility (m)
1978	$\bar{x} \pm 95\%$ CI	26.2 ± 0.8	23.6 ± 0.7	–	–	26.6 ± 0.3	27.1 ± 0.1	–	–
	CV	7.5	7.5	–	–	4.5	1.6	–	–
	Range	23 to 30	19 to 26	–	–	24 to 29.5	26 to 28	–	–
	n	28	27	–	–	75	75	–	–
1979	$\bar{x} \pm 95\%$ CI	26.1 ± 0.5	23.9 ± 0.5	7.8 ± 2.0	4.0 ± 0.9	26.9 ± 0.4	27.2 ± 0.2	4.8 ± 2.2	3.1 ± 0.9
	CV	7.8	8.0	81.3	57.9	4.6	1.8	112.8	56.4
	Range	22 to 32	18 to 27	0 to 29	0.9 to 12.2	25 to 31	26 to 28	0 to 18	1.2 to 7.6
	n	60	63	42	28	34	34	27	16
1980	$\bar{x} \pm 95\%$ CI	–	–	–	–	27.9 ± 0.4	28.4 ± 0.1	4.1 ± 1.7	4.9 ± 1.0
	CV	–	–	–	–	4.0	1.5	116	59.2
	Range	–	–	–	–	25.5 to 31.5	27.5 to 29	0 to 20.1	0.6 to 10.7
	n	–	–	–	–	37	36	33	36

[a] Windspeed was measured on most visits to Taboguilla using a handheld gauge. Visibility was estimated by averaging subjective estimates made by each of us as we swam to shore from the boat. These estimates were occasionally checked by comparing them to objects or distances of known length (e.g. the boat).

unpredictable, and can change rapidly. Variation in visibility was large (e.g., 0.9 to 12.2 m, Table I; one instance of ≈25 m visibility observed in 1980). Several factors influenced water clarity, primarily dry season plankton blooms and suspension of sediment by waves and swells. Although some annual variation in visibility also occurred (e.g. Table I), daily variation throughout the year was so great that it is difficult to discern clear differences between either seasons or years.

The velocity of trade winds varied considerably between dry seasons. In 1977, tradewinds were strong most days. In contrast, in 1978, 1979 (Table I) and 1980–1983 (no quantitative measures), tradewinds blew strongly for only a few consecutive days.

This region exhibits little annual variation in mean surface sea-water temperature (Fig. 2, Table I). In those years for which we have data (1978–1980), mean water temperatures were similar between years for both the dry (23.6 and 23.9 °C) and the wet seasons (27.1, 27.2, and 28.4 °C). The cooler and more variable (Fig. 2, Table I) dry season temperatures are a direct consequence of the upwelling caused by the northeasterly tradewinds (e.g., Glynn & Stewart, 1973).

Similarly, mean air temperatures (taken between 0600 and 1400) change little between

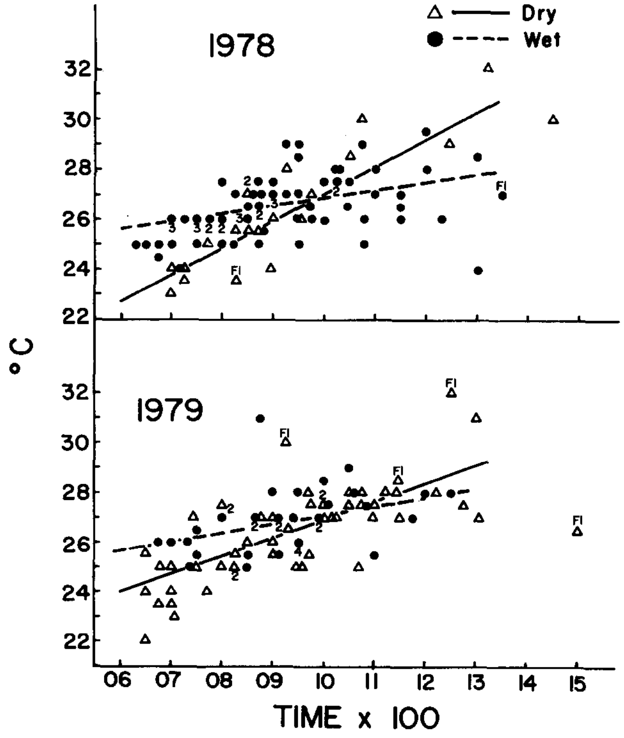

Fig. 3. Relationship between time of day and air temperature in wet and dry seasons 1978 and 1979: regression lines plotted using equations in Table II.

seasons both within and between years (Table I). However, these means mask a potentially important difference between dry and wet seasons (Fig. 3, Table II). In both years, dry season temperatures were significantly lower in the morning and higher at midday than in the wet season (analysis of covariance, 1978, season × time of day $P < 0.00001$; 1979 season × time of day $P = 0.04$; one-tailed tests used since this difference was expected). Furthermore, there are significant between-year effects in the dry season (year effect $P = 0.0015$; year × time of day $P = 0.0013$) but not in the wet season (year effect $P = 0.97$, year × time of day $P = 0.90$). This dry season difference is due to the y-intercept being lower and the slope of the line being steeper in 1978 than in 1979 (Table II). Hence, intertidal organisms on these shores are more likely to experience heat and desiccation stress during the dry season than the wet.

TABLE II

Linear regressions between time of day that temperature was measured (X) and air temperature (Y)[a].

Regression	r^2	a	b	n	P
1978 Dry season	0.79	16.2	1.08	20	<0.01
1978 Wet season	0.20	23.6	0.32	69	<0.01
1979 Dry season	0.51	19.7	0.72	52	<0.01
1979 Wet season	0.17	23.4	0.37	33	<0.05

[a] The best fit general linear regression model is temperature = 23.52 + 0.0034 (time of day) − 8.97 (season) − 0.062 (year) + 0.0097 (time of day × season) + 0.003 (time of day × year) + 5.35 (season × year) − 0.006 (time of day × season × year). Time of day ranges from 0600 to 1400; season and year are modeled as indicator variables (wet season = 0, dry season = 1, 1978 = 0, 1979 = 1.

SUBSTRATUM HETEROGENEITY

The basaltic shores of Taboguilla range from gently sloping sites to vertical faces. Continuous rock substratum is frequently split by crevices and channels, with a few massive stationary boulders and small sandy beaches. On a finer scale, the rock varies in surface irregularity from site to site and between tidal levels. The low zone has numerous sea urchin holes and appears much more heterogeneous than the mid and high zones (Fig. 4). Since numerous organisms appeared to live in holes and crevices, we speculated that such relief may influence abundance and diversity patterns (Leviten & Kohn, 1980). We attempted to quantify substratum heterogeneity by running line transects 30 to 50 m long parallel to the shore in each zone. At randomly determined points, 10–15 quadrats, each 0.25 m^2 in area, were sampled by centering an aluminum frame quadrat on the line. The quadrat was strung vertically and horizontally at 10 cm intervals. The intersections of these strings with each other and with the frame of the quadrat produced a regular grid of 6 × 6 = 36 intersections. At each intersection a meter stick was inserted perpendicularly through the plane of the quadrat until the substratum was contacted. The distance from the plane of the quadrat to the surface was read to

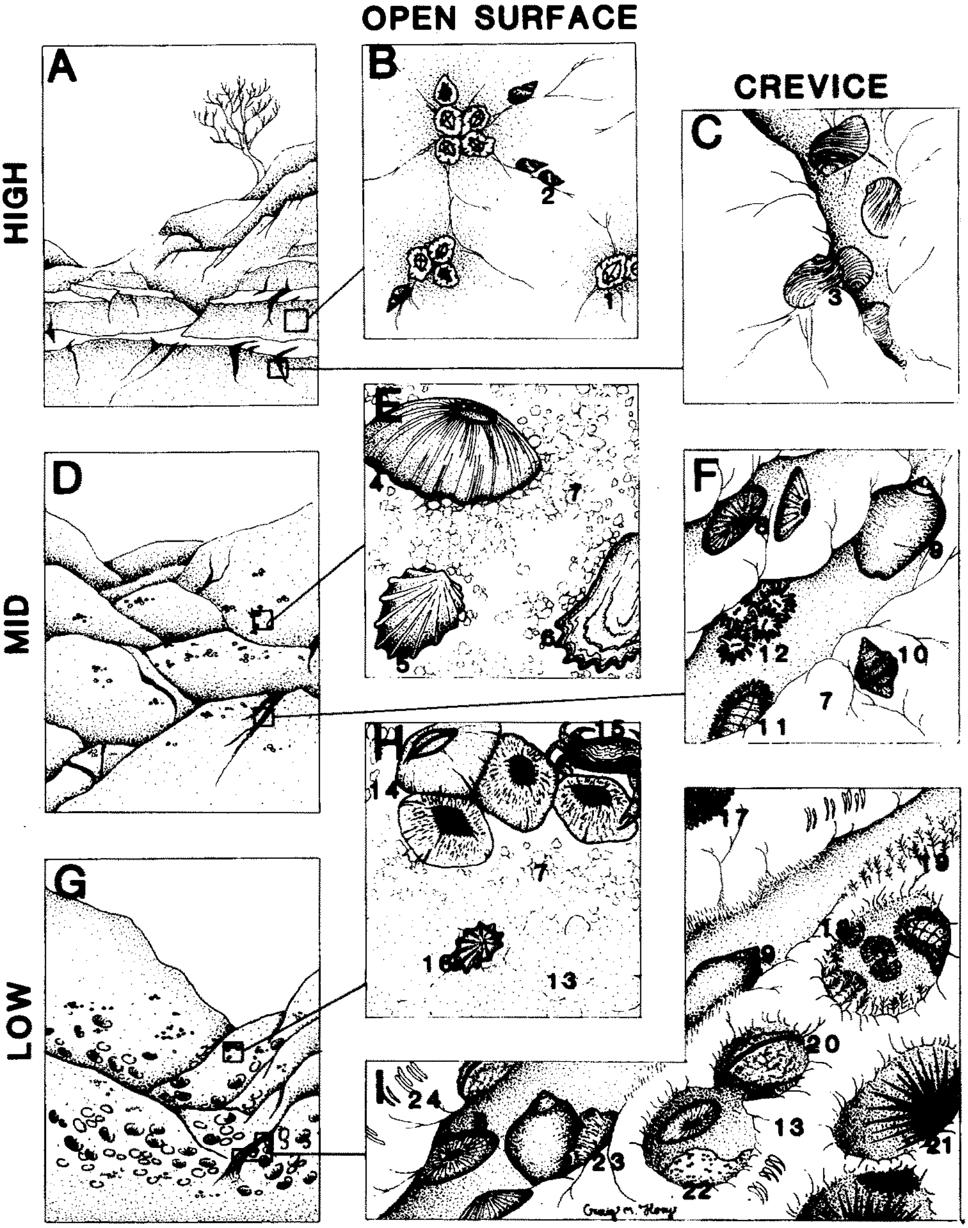

Fig. 4. Schematic illustration of the organisms and physical heterogeneity at Taboguilla Island: distant views are shown for the high (A), mid (D) and low (G) zones; each of these is ≈2 m across the foreground; close-up views are illustrated for open surfaces and crevices/holes for the high (B, C, respectively), mid (E, F) and low (H, I) zones; see text for actual organism size; animal density on open surfaces (B, E, H) is higher than in reality (see Appendix 4); species identifications are: 1, Chthamaloid barnacles (live and dead); 2, *Littorina spp.*; 3, *Nerita scabricosta*; 4, *Tetraclita*; 5, *Siphonaria gigas*; 6, *Ostrea palmula*; 7, mixed algal crusts: *Schizothrix*, *Ralfsia*, and *Hildenbrandia*; 8, *Fissurella* spp.; 9 *Thais melones*; 10, *Acanthina*; 11, *Ceratozona*; 12, anemones; 13, coralline crust; 14, *Balanus inexpectatus* (live and dead); 15, *Pachygrapsus*; 16, *Siphonaria maura*; 17, encrusting bryozoan; 18, colonial tunicate; 19, mixture of *Abietinaria* and filamentous algae; 20, *Chama*; 21, *Echinometra*; 22, sponge; 23, *Ascidia*; 24, rasp marks of grazing fishes.

the nearest 0.5 cm. If the surface of the rock was convex, the quadrat was moved about in situ to keep the edge nearest the meter stick on, or close, to the rock surface. Although this method is subject to various biases (see below), we feel that for our purposes it adequately estimates average small-scale surface irregularity in each zone.

These data were taken on Sites 2 and 6 on Taboguilla. They indicate that mean substratum irregularity is greater in the low and high zones than in the mid zone, but that variability of microtopography, as revealed by the coefficient of variation, is similar among zones (Table III). The difference between mid and high zones is partly an artifact of our sampling method and partly real. Unlike the rock surfaces in the low zone, which are more or less riddled with urchin holes, surfaces in the high zone are typically smoother on a fine scale but appear more angular on a coarser scale. Thus our quadrat frame frequently spanned irregularly shaped ledges and many "deep" readings resulted despite the lack of sea urchin holes.

TABLE III

Mean substratum depth (cm) in the high, mid and low zones at two sites on Taboguilla Island, Bay of Panama.

	Site 6	Site 2
High		
$x \pm 95\%$ CI	7.88 ± 0.61	6.58 ± 0.46
Range of $\bar{x}$'s	3.99 to 11.75	2.76 to 13.03
CI range	7.27 to 8.49	6.12 to 7.04
CV	74.62	82.83
n_1, n_2[a]	10, 360	15, 540
Mid		
$x \pm 95\%$ CI	4.28 ± 0.29	4.91 ± 0.41
Range of $\bar{x}$'s	1.83 to 6.78	2.67 to 9.61
CI range	3.99 to 4.57	4.50 to 5.32
CV	78.97	98.17
n_1, n_2	15, 540	15, 540
Low		
$x \pm 95\%$ CI	5.08 ± 0.36	6.66 ± 0.44
Range of $\bar{x}$'s	2.10 to 8.00	4.03 to 11.31
CI range	4.72 to 5.44	6.22 to 7.10
CV	84.65	77.2
n_1, n_2	15, 540	15, 534

[a] n_1 = no. of quadrats; n_2 = no. of points over entire transect.

COMMUNITY STRUCTURE AND ORGANIZATION

METHODS

Patterns of space utilization were determined using a variation of the transect-quadrat method described in detail in Menge (1976) and Lubchenco & Menge (1978). Transect lines (30 to 50 m long) marked at 1-m intervals were laid through the middle of each zone parallel to the water's edge. Ten to 15 permanently marked quadrats, initially located randomly along the transect line, were sampled in the wet and in the dry seasons each year. Percent cover (all sessile organisms) and densities (mobile and solitary sessile animals) were taken in each quadrat. Percent cover was determined using a flexible 0.5 × 0.5 m vinyl square perforated with 100 randomly plotted holes. Space occupants not hit by the projection through any hole were assigned a "trace" abundance equivalent to 0.01%. Percent covers were transformed (arcsine; Sokal & Rohlf, 1981) for parametric statistical analyses. Excepting high zone barnacles, which were often very abundant and were subsampled in a 20 × 20 cm subquadrat, densities were estimated by direct counts using an aluminum 0.25-m^2 quadrat.

Abundances of highly mobile and sometimes cryptic species, such as large crabs and fishes, were estimated by periodic censuses. Counts of crabs – mostly the Sally Lightfoot crab, *Grapsus grapsus* (L.) – were done by an observer who started at one side of a reef and systematically but quickly searched the reef, counting all crabs observed. By frequent repetition of such censuses, an average estimate of crab density was obtained. These crabs are large (average carapace width ≈ 6 cm) and tend to roam in groups at the water's edge or to hide in large, deep crevices. Our data undoubtedly underestimate true crab density since small individuals or crabs in crevices were probably missed. Numbers observed per census were converted to density estimates by dividing by the area of each site. Area was estimated using the method described in Menge (1972, p. 642). Briefly, this involved measurement of lengths from a central point on each reef to the shoreline at low tide at 5 to 15° intervals around the central point. The resulting data were plotted on polar coordinate paper and area was estimated with a planimeter.

Fish abundance was estimated while snorkeling or diving using visual "census" methods (e.g. Hobson, 1974; see Brock, 1982 for a recent critique of this method). Every 1–3 months, on days when visibility was relatively good (15–20 ft), benthos-feeding fishes were counted and identified between fixed reference points to a depth of ≈ -20 ft (-6.1 m) below MLW. Abundances were standardized to both no./linear meter of low tide shoreline length and to no./m^2 of intertidal area of each site. Both methods have obvious drawbacks (e.g., topography differs at different intertidal and subtidal levels, not all species forage extensively in the intertidal). We present both estimates for comparison. In addition to these low tide observations, we snorkelled or dove at high tide to determine which fish forage in which portions of the littoral zone.

Species identifications were made using Keen (1971; molluscs), Thompson *et al.* (1979; fishes), and Brusca (1980; most other invertebrates). Taxonomic authorities of Panamanian species not included in these works are given in the text. However, there are gaps in our identifications, especially of some algae and colonial invertebrates. We assigned descriptive names to unidentified species and collected specimens for future identification.

Experiments were performed at each tidal level, except the very low zone, to determine the effect of consumers. Details are described elsewhere (Menge & Lubchenco, 1981; in prep.). Briefly, slow-moving invertebrate consumers were removed manually from the rock at all tidal heights at experimental sites (Sites 1–4) and left undisturbed on a control site (Site 6). Large, fast-moving consumers (fishes and crabs) were excluded from 0.25-m^2 plots with cages. Here we present data only from plots which were marked but otherwise unmanipulated (controls), and from plots lacking all consumers (total exclusions). More detailed presentations of some of these results are published in Menge & Lubchenco (1981) or will appear elsewhere (e.g., Menge & Lubchenco, unpubl. data). Because time series data are not independent, results were analyzed with MANOVA (multivariate analysis of variance; Morrison, 1976), rather than ANOVA. More detailed examples of the rationale and use of this statistical procedure are in Morin (1983) and Lubchenco (1983).

RESULTS

ZONATION PATTERNS

A striking difference between Panamanian shores and those in temperate regions we have observed is the general scarcity of epibenthic animals and plants and the consequent indistinct vertical zones (as viewed from distances >5 m) in Panama (Fig. 4A, D,G). On temperate shores, there is near universal observation of dense covers of epibenthic organisms located in often sharply defined horizontal bands (see e.g., Lewis, 1964; Stephenson & Stephenson, 1972; Menge & Lubchenco, 1981). However, close inspection reveals that although sharply defined zones are not prominently visible, organisms in this tropical community are zoned vertically (Menge & Lubchenco, 1981). We delineate the splash ($> +6.4$ m), high ($+4.6$ to $+6.4$ m), mid ($+2.4$ to $+4.6$ m), low ($+0.6$ to $+2.4$ m) and very low zones ($+0.6$ to -0.8 m). Most data here are from the three middle zones. They very low zone was often dangerous or impossible to sample and we did not deal with the splash zone. The most obvious sessile animal species in each of the zones are barnacles or oysters and include *Chthamalus fissus* (Darwin) or *Euraphia imperatrix* (Pilsbry) or both in the high (Fig. 4B), *Tetraclita panamensis* Pilsbry in the mid, and *Balanus inexpectatus* Pilsbry or *Chama echinata* in the low (Fig. 4H) and very low zones. Encrusting algae are dominant space occupants in all but the high and splash zones.

SPECIES COMPOSITION

The species composition of this rocky intertidal community is listed by zone in Appendices 1 and 2. Animal species are grouped by trophic status (e.g., predator, herbivore, omnivore, etc.) and general systematic group (e.g., fishes, gastropod molluscs, etc.). At least 115 macrofaunal species occur at Taboguilla. Data reviewed in Gaines & Lubchenco (1982) suggest that compared to higher latitudes, the total number of macroalgal species will be relatively low in this community. However, until identifications are complete, values of H' and S calculated for each zone must be interpreted with caution.

SPACE UTILIZATION

Space on intertidal rock surfaces can be occupied by encrusting species (primary space occupants) or erect species which are attached to but grow away from the surface. The latter occupy both primary and secondary space, though usually less of the former. We previously considered "available" space to include bare rock and surface covered by crustose algae (e.g., Menge, 1976; Lubchenco & Menge, 1978). However, there is evidence (Garrity & Levings, 1981; Menge *et al.*, unpubl. data) that in Panama, some algal crusts inhibit significantly, albeit incompletely, settlement of at least some organ-

TABLE IV

Local spatial variation in dry season abundance (percent cover) of major space occupying groups in the high zone at four neighboring sites on Taboguilla Island, and seasonal variation for one site: data are $\bar{x}$ ± 95% confidence intervals from N number of quadrats; where appropriate, number of species in a category is given in parentheses; NP, none present; t, trace, indicates a mean abundance of <0.1%.

	Dry season (1977)				Wet season (1977)
Category	Site 1 21 Jan.	Site 2 19 Jan.	Site 3 6 Mar.	Site 6 2 Feb.	Site 6 18 July
N	10	15	10	10	10
Chthamalus fissus	1.8 ± 2.3	4.2 ± 2.4	0.7 ± 1.1	1.2 ± 1.0	0.8 ± 1.1
Euraphia imperatrix	1.5 ± 1.3	4.7 ± 4.4	6.8 ± 8.0	0.7 ± 0.8	2.5 ± 1.5
Barnacles	3.3 ± 3.5 (2)	8.3 ± 4.7 (2)	7.5 ± 7.8 (2)	1.9 ± 1.3 (2)	3.3 ± 2.0 (2)
Bivalves	NP	t (1)	NP	NP	NP
Solitary sessile animals total	3.3 ± 3.5 (2)	8.3 ± 4.7 (3)	7.5 ± 7.8 (2)	1.9 ± 1.3 (2)	3.3 ± 2.0 (3)
Crustose algae	0.5 ± 0.7 (3)	t (1)	0.3 ± 0.5 (2)	t (1)	0.2 ± 0.5 (1)
Erect algae	t (1)	t (1)	0.4 ± 0.9 (1)	NP	3.7 ± 8.4 (2)
Total algal cover	0.5 ± 0.7 (4)	t (2)	0.7 ± 0.9 (3)	t (1)	3.9 ± 8.8 (3)
Bare	93.4 ± 4.4	89.1 ± 5.9	88.4 ± 8.7	97.2 ± 1.5	91.4 ± 9.3

isms. Hence, crust-covered rock cannot be considered completely "available", although most species evidently colonize such surfaces. In lieu of estimating available space, we simply recorded bare space and algal crusts as separate entries.

In the dry season, space in the high zone is mostly bare rock, while in mid and low zones algal crusts dominate (Appendix 3, Tables IV–VI, Fig. 4B,E,H). Dominant animals in the high zone are two barnacles (*Chthamalus fissus* and *Euraphia imperatrix*; Appendix 3, Table IV). Animal cover in the mid zone is very low ($\approx 2\%$). Dominant space occupants include the crustose algae *Ralfsia* sp. (brown), *Schizothrix calcicola* (C. Agardh) Gomont (blue-green) and *Hildenbrandia* sp. (red; Appendix 3, Table V). Upright algae are essentially absent from both high and mid zones. Dominants in the low zone include the crustose algae listed above plus encrusting corallines. Total cover of other space-occupying groups is low (e.g., barnacles, 0.8%; bivalves, 1.1%; other solitary sessile animals, 0.4%; colonial sessile animals, 0.9%). Although more abundant than at higher levels, erect algae (2.7%) are scarce (Appendix 3, Table VI). Abundances in the very low zone are similar to those in higher zones with three exceptions. First, colonial sessile animals, mostly *Abietinaria* sp. (hydroid) are more abundant than at higher levels (7.1% vs. 0.9 in the low, 0 in mid and high zones; Appendix 3). Second, encrusting corallines are the dominant space occupant (live + dead = 39.3% cover). The high cover of dead coralline crust is typical of the early dry season. The onset of lower low tides coinciding with low cloud cover (Table I) evidently leads to desiccation, heat, and/or ultra-violet stress. Third, erect algal cover, mostly "algal turf" (a multi-species association of filamentous algae including *Polysiphonia* spp.) is relatively high (11.9%). Diversity (H') and species richness (S) both increase from high to lower zones while evenness (J') remains about the same (Appendix 3). Thus the increase in H' is largely due to species additions (which occur in all major organismal groupings; Appendix 3).

In summary, (1) primary space is dominated by algal crusts in the mid, low, and very low zones and by bare rock in the high zone, (2) sessile animals are scarce, (3) most species are rare or patchily abundant, (4) barnacles and large bivalves, so abundant in temperate areas, are scarce, (5) cover of erect algae is very low, (6) erect algae are short (usually < 1 cm), and (7) H' and S are greater in lower zones.

TABLE V

Local spatial variation in dry season abundance (percent cover) of major space occupying groups in the mid zone at four neighboring sites on Taboguilla Island, and seasonal variation at one site: data are $\bar{x} \pm 95\%$ confidence interval; number of species in a category is given in parentheses where appropriate; all mean abundances <0.1% are labeled t (trace).

	Dry season (1977)				Wet season (1977)
Category	Site 1 21 Jan.	Site 2 19 Jan.	Site 3 6 Mar.	Site 6 2 Feb.	Site 6 18 July
N	10	15	10	15	15
ANIMALS					
Barnacles	2.2 ± 3.6 (1)	t (1)	t (1)	t (2)	5.9 ± 0.3 (2)
Bivalves	t (1)	0.3 ± 0.5 (1)	t (3)	t (1)	0.3 ± 0.3 (2)
Other solitary sessile animals	0.1 ± 0.2 (2)	t (2)	t (2)	2.1 ± 1.7 (2)	1.2 ± 0.8 (4)
Total solitary sessile animals	2.3 ± 3.6 (4)	0.4 ± 0.5 (4)	t (6)	2.1 ± 1.7 (5)	1.8 ± 0.8 (8)
Total colonial sessile animals	t (3)	t (4)	NP	t (3)	t (4)
Total animal cover	2.3 ± 3.6 (7)	0.3 ± 0.5 (8)	t (6)	2.1 ± 1.7 (8)	2.0 ± 0.9 (12)
ALGAE					
Hildenbrandia sp.	24.9 ± 10.1	9.5 ± 5.4	7.8 ± 8.6	22.9 ± 12.2	12.3 ± 4.6
Ralfsia sp.	57.2 ± 10.3	16.9 ± 13.3	NP	23.8 ± 15.2	49.8 ± 13.1
Schizothrix calcicola (green phase)	3.1 ± 1.2	17.5 ± 7.3	16.5 ± 13.7	23.5 ± 13.9	10.4 ± 4.4
Total algal crusts	92.5 ± 6.3 (6)	50.5 ± 4.0 (5)	25.9 ± 14.7 (4)	80.7 ± 17.3 (7)	79.2 ± 13.5 (5)
Erect greens	t (1)	t (1)	NP	NP	NP
Erect browns	NP	t (1)	NP	NP	t (1)
Erect fleshy reds	0.4 ± 0.9 (2)	0.2 ± 0.2 (2)	NP	NP	t (1)
Total erect algae	0.4 ± 0.9 (3)	0.2 ± 0.2 (5)	NP	NP	t (2)
Bare	4.0 ± 4.5	43.3 ± 19.2	74.0 ± 14.7	16.7 ± 17.7	16.6 ± 14.0
Erect corallines	NP	t (1)	NP	NP	t (1)
Dead crustose corallines[a]	0.6 ± 0.9	0.7 ± 0.6	NP	0.3 ± 0.4	t

[a] See footnote d, Appendix 3.

TABLE VI

Local spatial variation in dry season abundance (percent cover) of major space occupants in the low zone at four neighboring sites on Taboguilla Island, and seasonal variation at one site: data are $\bar{x} \pm 95\%$ confidence interval; number of species in a category is given in parentheses where appropriate; all mean abundances $<0.1\%$ are labeled t (trace).

	Dry season (1977)				Wet season (1977)
Category	Site 1 21 Jan.	Site 2 19 Jan.	Site 3 6 Mar.	Site 6 2 Feb.	Site 6 18 July
N	15	15	15	15	15
ANIMALS					
Barnacles	1.3 ± 1.1 (2)	0.5 ± 0.7 (2)	2.8 ± 2.8 (4)	0.3 ± 0.4 (3)	1.3 ± 0.7 (3)
Bivalves	1.9 ± 0.8 (3)	1.9 ± 2.1 (2)	2.1 ± 1.6 (5)	0.8 ± 0.8 (2)	1.3 ± 0.9 (4)
Other solitary sessile animals	t (4)	0.1 ± 0.2 (3)	0.3 ± 0.2 (5)	0.2 ± 0.3 (6)	0.8 ± 0.7 (5)
Total solitary sessile animals	3.3 ± 0.9 (9)	2.5 ± 2.0 (7)	5.0 ± 3.3 (14)	1.3 ± 1.0 (9)	3.5 ± 1.1 (8)
Colonial sessile animals (mostly *Abietinaria* sp.)	2.4 ± 1.2 (6)	1.4 ± 1.2 (6)	4.7 ± 5.0 (7)	0.9 ± 1.5 (2)	0.7 ± 0.6 (6)
Total animal cover	5.7 ± 1.5 (15)	3.8 ± 2.6 (13)	9.8 ± 7.1 (21)	2.2 ± 1.8 (11)	4.0 ± 1.4 (14)
ALGAE					
Hildenbrandia sp.	15.8 ± 5.8	14.9 ± 5.6	15.3 ± 7.8	16.5 ± 3.4	15.2 ± 7.0
crustose corallines	10.4 ± 4.7	8.8 ± 3.1	7.5 ± 3.7	10.5 ± 4.8	18.0 ± 6.0
Ralfsia sp.	31.6 ± 5.7	33.7 ± 9.3	40.5 ± 10.8	22.4 ± 10.9	42.9 ± 7.5
Schizothrix calcicola (green phase)	1.9 ± 1.6	18.5 ± 9.9	6.3 ± 4.5	28.9 ± 10.5	4.9 ± 2.2
Schizothrix calcicola (white phase)	3.3 ± 3.0	8.9 ± 2.9	5.7 ± 3.0	9.1 ± 2.9	4.0 ± 2.5
Total algal crusts	67.3 ± 8.6 (6)	92.5 ± 2.3 (5)	80.0 ± 8.8 (6)	88.7 ± 7.2 (7)	87.9 ± 4.8 (5)
Total erect greens	t (2)	0.4 ± 0.3 (3)	0.9 ± 1.0 (2)	t (2)	t (4)
Total erect browns	t (1)	t (1)	t (1)	NP	t (2)
Total erect fleshy reds	t (4)	0.9 ± 0.8 (2)	2.4 ± 2.9 (3)	t (1)	0.3 ± 0.3 (4)
Total erect corallines	t (1)	0.1 ± 0.3 (1)	0.2 ± 0.4 (1)	t (1)	0.2 ± 0.3 (1)
Total erect algae	3.7 ± 3.1 (8)	1.4 ± 0.9 (7)	7.0 ± 7.1 (7)	0.2 ± 0.2 (4)	0.6 ± 0.7 (11)
Dead crustose corallines[a]	15.4 ± 4.2	3.5 ± 1.3	3.3 ± 1.8	2.1 ± 1.1	1.3 ± 0.7
Bare	7.7 ± 3.4	0.3 ± 0.6	0.1 ± 0.2	5.8 ± 7.4	5.0 ± 4.1

[a] See footnote d, Appendix 3.

LOCAL VARIATION IN SPACE UTILIZATION PATTERNS

In order to determine the extent to which nearby sites differ, we quantified space utilization at four sites, all within 1 km stretch of shore. Transects were taken in the dry season, 1977; data are presented by zone (Tables IV–VI) and include the site (Site 6) from which data in Appendix 3 were taken. Comparisons among sites indicate that although some variation in abundances occurs, it is usually low and probably of little ecological significance. The most striking variation was the relatively low algal crust cover on Site 3 in the mid zone (Table V). Causes of this variation are unknown. We conclude that data in Appendix 3 are generally representative of the southern shore of Taboguilla Island.

ANIMAL DENSITIES

Sessile animal density decreases in successively lower zones, while slow-moving animal density increases (Appendix 4). For both groups, H' and S are higher in lower zones (Appendix 4).

In the high zone the most numerous sessile species are the equally abundant *Chthamalus* and *Euraphia*. The small ($\approx$ 1.7 cm maximum size; sizes given are $\bar{x} \pm 1$ SE unless otherwise noted) mussel *Brachidontes semilaevis* is always rare (0.1% cover, Appendix 4). Mobile animals include mostly herbivorous gastropods: two small (0.99 ± 0.02 and 1.04 ± 0.02 cm) littorines, and a large (1.36 ± 0.08 cm) neritid (Appendix 4). Abundances of large mobile species are probably poorly estimated in our transects. For example, *Nerita scabricosta* tends to form large, patchily distributed aggregations (e.g. Garrity & Levings, 1981: Levings & Garrity, 1983) which are not well sampled by our method. Furthermore, effective abundances of the predaceous gastropods *Acanthina brevidentata* and *Thais melones* are undoubtedly not zero (Appendix 4). Where large deep crevices extend from lower to higher levels, these snails appear to forage into the high zone during high tides. This conclusion is based on (1) the large numbers of small individuals in crevices in the upper portions of the mid zone, (2) the frequent consumption of *Chthamalus* by these species (Menge *et al.*, unpubl. data), (3) the "bare zones" around crevices that run through dense patches of *Chthamalus* (in temperate regions such "bare zones" are sometimes due to foraging by predaceous snails; e.g., Menge, 1978a) and (4) dramatic increases in *C. fissus* following removal of these predators from crevices in the higher mid zone (Menge & Lubchenco, 1981).

In the mid zone, the most abundant sessile species are *Chthamalus*, the mussel *Brachidontes semilaevis*, and the anemone *Anthopleura* (Table VIII, Appendix 4). The barnacle *Tetraclita panamensis*, through not abundant, is large (2.19 ± 0.23 cm diameter). It is more abundant at some mainland sites (Reimer, 1976a,b). Among mobile animals, some herbivores, including the limpets (*Siphonaria gigas*, 3.15 ± 0.1 cm, and *Fissurella virescens*, 1.90 ± 0.08 cm) and chitons (*Chiton stokesii*, 5.43 ± 0.14 cm, *Acanthina hirudiniformis* 1.86 ± 0.06 cm) are abundant or large or both. Predators include two gastropods, *Acanthina brevidentata* (1.65 ± 0.08 cm) and *Thais melones*

(2.19 ± 0.14 cm), and the crab *Eriphia squamata* Stimpson (range of 3–6.3 cm). The asteroid *Heliaster microbrachius* Xantus initially occurred at this site (1977–1978). During successive years (transects taken through 1983), the seastar seems to have vanished from Taboguilla. In general, *Thais melones* and *Acanthina* are the most ubiquitous mid zone predators.

The low zone harbors a lower density of sessile individuals, but a greater diversity of species than either of the two higher zones (Appendix 4). Barnacles and bivalves again represent the majority of sessile individuals (Appendix 4). Most numerous are the small *Chthamalus* and *Brachidontes* (0.45 ± 0.02 cm basal diameter and 1.7 cm length, respectively), the larger rock oyster *Chama echinata*, and the barnacle *Balanus inexpectatus* (3.03 ± 0.11 and 2.03 ± 0.08 cm diameter, respectively).*Chama* occurs in holes and crevices, while *Balanus inexpectatus* occurs on open surfaces and appears more common than it actually is because the tests of dead individuals persist for some time. Additional solitary, sessile species occurring in the low zone include anemones, vermetids, sedentary polychaetes, solitary tunicates, and crevice-dwelling sea cucumbers (Appendix 4). Mobile herbivores and predators are numerous and diverse in the low zone. Abundant molluscan grazers are *Siphonaria maura* (1.42 ± 0.02 cm length), *Fissurella virescens* (1.90 ± 0.08 cm) and *F. longifissa* (1.43 ± 0.07 cm; Appendix 4). Other relatively abundant herbivores include three chiton species, the small herbivorous crab *Pachygrapsus transversus* (Gibbes), and the sea urchin *Echinometra vanbrunti* Agassiz. A fourth chiton, *Tonicia forbesi*, is also relatively common but occurs primarily in holes beneath *Echinometra vanbrunti*; since our sampling in these transects is non-destructive, such cryptic species are usually missed. Other cryptic herbivores are the crab *Eriphides hispida* (Stimpson) (5.03 ± 0.5 cm carapace width), and the sea urchin *Eucidaris thouarsi* (Valenciennes) (2.35 ± 0.12 cm diameter). Although predaceous snails have similar densities in mid and low zones, there are more species in the latter (Appendices 1, 4). Of these, only *Thais melones*, (2.19 ± 0.14 cm), *Acanthina brevidentata* (1.65 ± 0.08 cm) and *Thais triangularis* (0.96 ± 0.06 cm) are common (Appendix 1). The predaceous crab *Eriphia squamata* (5–8 cm carapace diameter) is cryptic in habitat and its density may also be underestimated. Hermit crabs are rare on these rock surfaces and more common in areas with boulder fields, tidepools or sandy areas (e.g., Abrams, 1981; Bertness, 1981).

In the very low zone, solitary sessile animals are scarcer than at higher levels, with *Chama*, vermetids, and *Balanus inexpectatus* being most abundant (Appendix 4). In contrast, mobile organisms are relatively abundant (total density = $91.2/\mathrm{m}^2$), particularly limpets, sea urchins and predaceous snails (Appendix 4). The most abundant herbivores are *Siphonaria palmata*, *Fissurella virescens*, *Echinometra vanbrunti* and *Pachygrapsus*. Like *Tonicia forbesi*, the limpet *Fissurella morrisoni* occurs in urchin holes and is undersampled by our methods. The most abundant predaceous gastropods, *Thais melones* and *Acanthina brevidentata* range into the mid and occasionally the high zone. The other relatively abundant predatory snails (*Thais triangularis*, *Opeatostoma*) are normally found in the low intertidal to shallow subtidal. Finally, ophiuroids, nudibranchs and sea cucumbers span a range of abundances, the last being most numerous (Appendix 4).

LOCAL VARIATION IN ANIMAL DENSITIES

In the high zone densities are variable from site to site (e.g., barnacles range from $\bar{x}$ densities of 202 to 1083, *Littorina modesta* ranges from 5.8 to 21.1 and *Nerita scabricosta* ranges from 9.2 to 21/0.25 m^2, Table VII). However, most estimates have large confidence ranges and few differences are significant. These patterns coincide with our general impression that most high zone animals are patchily distributed.

In the mid zone, densities can vary considerably among sites (Table VIII). For example, bivalves are significantly denser at Site 1 than at the other three sites, and solitary sessile animals (mostly anemones) are more numerous at Sites 1 and 6 than at Sites 2 and 3. However, total abundance of solitary sessile animals is less variable.

TABLE VII

Local spatial variation in animal density in the high zone at four neighboring sites on Taboguilla Island and seasonal variation for one site: data are $\bar{x}$ ($\pm$95% confidence interval) no. per 0.25 m^2; number of species is given in parentheses when appropriate; total species numbers in this and Tables VIII and IX are sometimes greater than sums in the subcategories because abundances of very scarce species are not listed.

	Dry season (1977)				Wet season (1977)
Category	Site 1 21 Jan.	Site 2 19 Jan.	Site 3 6 Mar.	Site 6 2 Feb.	Site 6 18 July
SESSILE	10	15	10	10	10
Chthamalus fissus	98.1 ± 117.5	1027.0 ± 710.5	24.4 ± 36.8	97.5 ± 133.0	92.5 ± 146.9
Euraphia imperatrix	330.6 ± 474.9	55.7 ± 61.7	643.7 ± 735.0	105.6 ± 92.9	94.4 ± 107.6
Total barnacles	428.8 ± 568.4	1082.7 ± 708.5	668.1 ± 731.3	202.5 ± 177.4	186.9 ± 174.5
Other solitary sessile	1.1 ± 0.9 (3)	5.0 ± 5.4 (1)	0.3 ± 0.6 (1)	NP	0.1 ± 0.2 (1)
Total sessile	429.8 ± 568.5 (5)	1087.7 ± 707.7 (3)	668.4 ± 731.2 (3)	202.5 ± 177.4 (2)	187.0 ± 174.4 (3)
MOBILE					
Littorina modesta	21.1 ± 13.0	6.1 ± 4.8	5.8 ± 4.6	7.6 ± 6.4	3.2 ± 2.1
Nerita scabricosta	10.7 ± 6.1	12.7 ± 8.7	21.4 ± 32.2	9.2 ± 10.0	2.0 ± 1.0
Total coiled herbivores	31.9 ± 15.4 (3)	17.7 ± 9.3 (3)	27.9 ± 31.0 (4)	16.9 ± 15.7 (4)	5.3 ± 2.3 (3)
Total herbivores	32.0 ± 15.6 (4)	17.7 ± 9.2 (4)	27.9 ± 31.0 (4)	16.9 ± 15.7 (4)	5.6 ± 2.3 (4)
Total predators	0.2 ± 0.4 (2)	NP	0.1 ± 0.2 (1)	NP	NP

Further, if low covers (due to small size) of these organisms are considered, such variations are less meaningful.

Limpets, particularly *Siphonaria gigas*, *S. maura* and *Fissurella virescens* are more numerous at Site 1 than at other sites. Since *F. virescens*, chitons and *Pachygrapsus*

TABLE VIII

Local variation in animal density in the mid zone at four neighboring sites on Taboguilla Island, January, February, and March 1977: see heading of Table VII for additional details; abundances $<0.1/m^2$ are labelled p (present).

	Dry season (1977)				Wet season (1977)
Category	Site 1 21 Jan.	Site 2 19 Jan.	Site 3 6 Mar.	Site 6 2 Feb.	Site 6 18 July
N	10	15	10	15	15
SESSILE					
Chthamalus fissus	0.4 ± 0.5	3.9 ± 4.7	0.6 ± 1.3	0.5 ± 0.6	15.3 ± 15.2
Total barnacles	2.5 ± 3.1 (2)	4.1 ± 4.7 (2)	15.0 ± 11.1 (2)	1.0 ± 1.0 (3)	15.6 ± 15.1 (2)
Ostrea palmula	0.6 ± 1.1	0.1 ± 0.1	1.7 ± 1.2	p	p
Brachidontes semilaevis	11.1 ± 4.7	3.6 ± 2.1	3.7 ± 4.1	0.9 ± 0.8	0.6 ± 0.5
Total bivalves	16.5 ± 5.2 (6)	5.9 ± 2.2 (5)	5.5 ± 3.7 (3)	1.4 ± 0.9 (3)	0.6 ± 0.5 (4)
Other solitary sessile	23.2 ± 9.9 (6)	4.6 ± 3.8 (7)	3.3 ± 4.8 (3)	36.8 ± 19.8 (9)	36.3 ± 23.7 (6)
Total solitary sessile	38.7 ± 8.6 (14)	14.6 ± 7.1 (14)	23.8 ± 12.6 (8)	39.4 ± 19.3 (15)	53.1 ± 24.3 (12)
MOBILE					
Siphonaria gigas	16.3 ± 7.6	4.3 ± 3.1	2.7 ± 1.1	8.0 ± 1.9	8.5 ± 2.3
Siphonaria maura	12.6 ± 6.0	3.0 ± 1.4	0.2 ± 0.4	1.1 ± 0.8	1.3 ± 1.0
Fissurella virescens	10.2 ± 3.4	1.1 ± 0.9	NP	0.5 ± 0.3	1.6 ± 1.1
Total limpets	44.6 ± 9.2 (6)	9.5 ± 3.7 (4)	2.9 ± 1.1 (2)	9.6 ± 2.4 (6)	13.0 ± 4.5 (5)
Chitons	0.4 ± 0.7 (2)	0.9 ± 1.3 (2)	NP	0.1 ± 0.1 (1)	0.2 ± 0.3 (1)
Coiled herbivorous snails	3.8 ± 5.8 (1)	2.6 ± 4.7 (1)	5.5 ± 3.9 (4)	1.1 ± 1.3 (4)	3.9 ± 5.5 (3)
Pachygrapsus transversus	1.4 ± 0.8	0.3 ± 0.2	NP	0.1 ± 0.1	1.1 ± 0.7
Total herbivores	50.2 ± 14.1 (10)	13.4 ± 5.7 (8)	8.4 ± 4.0 (6)	10.9 ± 2.2 (12)	18.3 ± 2.7 (10)
Total predators	1.0 ± 0.8 (3)	0.5 ± 0.3 (2)	0.1 ± 0.2 (1)	0.2 ± 0.1 (2)	0.3 ± 0.3 (2)

depend on holes and crevices for shelter (Menge & Lubchenco, unpubl. data), their absence from Site 3 is probably due to low substratum heterogeneity (pers. obs.).

In the low zone, densities are less variable than in the two higher zones (Table IX). The occasionally significant differences in density of barnacles and *Brachidontes* probably have little impact on the community due to their small size and low densities (Table IX). The relatively low density of the oyster *Chama* at Site 4 may be more

TABLE IX

Local variation in animal density in the low zone at four neighboring sites on Taboguilla Island, January and February 1977: see heading of Table VII for additional details.

	Dry season (1977)				Wet season (1977)
Category	Site 1 21 Jan.	Site 2 19 Jan.	Site 3 6 Mar.	Site 6 2 Feb.	Site 6 2 Aug.
N	15	15	15	15	15
SESSILE					
Barnacles	3.4 ± 2.0 (4)	3.7 ± 2.7 (4)	5.8 ± 1.8 (4)	0.7 ± 0.7 (3)	11.9 ± 7.8 (3)
Brachidontes semilaevis	5.8 ± 2.9	19.6 ± 7.2	8.1 ± 3.7	5.5 ± 4.1	6.8 ± 8.2
Chama echinata	7.6 ± 2.5	8.3 ± 2.5	3.4 ± 1.5	8.5 ± 3.2	5.2 ± 3.2
Total bivalves	13.9 ± 4.3 (4)	29.8 ± 7.1 (7)	11.2 ± 4.8 (5)	13.6 ± 4.8 (4)	6.8 ± 8.1 (4)
Other solitary sessile	7.2 ± 3.0 (11)	5.5 ± 2.7 (7)	7.0 ± 2.2 (12)	5.7 ± 3.8 (10)	10.3 ± 4.8 (8)
Total solitary sessile	24.2 ± 3.9 (19)	39.1 ± 9.3 (18)	25.3 ± 6.3 (19)	19.5 ± 5.8 (17)	37.1 ± 10.8 (15)
MOBILE					
Fissurella virescens	3.1 ± 1.4	4.9 ± 2.4	4.4 ± 2.2	6.0 ± 1.8	23.1 ± 5.6
Total limpets	6.0 ± 1.7 (6)	12.3 ± 5.1 (6)	10.2 ± 3.7 (6)	14.4 ± 5.0 (6)	34.1 ± 9.2 (5)
Chitons	0.7 ± 0.3 (3)	0.9 ± 0.6 (4)	1.5 ± 0.7 (3)	0.8 ± 0.3 (5)	2.2 ± 0.9 (3)
Pachygrapsus transversus	1.3 ± 0.4	1.3 ± 0.5	0.6 ± 0.2	0.7 ± 0.3	2.7 ± 1.2
Echinometra vanbrunti	0.9 ± 0.5	0.9 ± 0.9	0.4 ± 0.4	0.4 ± 0.4	0.4 ± 0.6
Total herbivores	8.8 ± 2.1 (13)	15.3 ± 5.7 (14)	17.1 ± 5.7 (13)	16.3 ± 5.2 (15)	39.7 ± 10.3 (15)
Thais melones	1.6 ± 0.4	1.1 ± 0.5	1.0 ± 0.4	0.6 ± 0.6	0.9 ± 0.9
Total predators	2.7 ± 0.8 (8)	1.7 ± 0.9 (3)	1.5 ± 0.6 (4)	2.4 ± 1.4 (4)	3.2 ± 1.8 (3)

significant, since this is one of the species whose densities increase dramatically in the absence of predators (Menge & Lubchenco, 1981). *Chama* may be rare at Site 4 due to its dependence on holes or crevices and their low availability at Site 4. The remainder of the sessile and mobile animals vary little among the four sites. In summary, on a local scale, the density of animals in the high zone appears variable and patchy. In the mid zone, densities are still variable but less patchily distributed and in the low zone, densities are not very different from site to site.

ABUNDANCE: FAST-MOVING CONSUMERS

Abundances of fishes or the fast-moving crab *Grapsus grapsus* were sampled as described above. *G. grapsus* (range of 4.8 to 6.3 cm carapace width) varies in abundance from site to site and with tidal level (Table X). Data from two sites whose upper and lower portions are physically separated (Sites 1 and 2) suggest that *Grapsus* occur more abundantly on higher shore levels, (Table X; Site 1 high vs. low, one-way ANOVA, $F_{1,100} = 72.6$, $P \ll 0.001$; Site 2 high vs. low, one-way ANOVA, $F_{1,114} = 20.5$, $P \ll 0.001$). Further comparison indicates that densities can vary considerably among sites. Thus, densities range from ($\bar{x} \pm 1$ SE) 11.61 ± 3.79 (Site 3) to 0 (Site 4). This latter figure and the low value on low Site 2 indicate that isolation from the main shoreline also has a dramatic effect on density. Site 4 is a mid and low zone site which is isolated from the main shoreline at low tide by a 1.5-m wide channel. Low Site 2 is also largely isolated at low tide by a 2 m wide channel. Neither has a high or supratidal region to which crabs could retreat at high tide (*Grapsus* follow tides up and down, actively

TABLE X

Mean density of *Grapsus grapsus* at several study sites on Taboguilla Island, February 1978 to September 1979.

Site	Area (m^2)	$x \pm 95\%$ CI[a] (no./100 m^2)	CV[b]	*N*[c]
1 Steep-slope[d]	82.6	13.1 ± 2.3	60.5	49
1 Gentle-slope[d]	282.8	3.4 ± 0.6	67.8	53
2 Shoreward[e]	421.5	2.9 ± 0.5	62.1	56
2 Seaward[e]	337.9	1.2 ± 0.6	189.9	60
3	198.8	11.6 ± 3.8	51.3	12
4	178.5	0 ± 0	-	8
6	777.4	5.9 ± 1.3	63.0	34

[a] CI = confidence interval.
[b] CV = coefficient of variation or standard deviation divided by $\bar{x} \times 100$.
[c] *N* = number of dates a sample was taken.
[d] Site 1 consists of two largely distinct portions; a steep sided one encompassing high, mid and low zones and a more gently sloping, semi-isolated one occurring only in the mid and low zones.
[e] Site 2 consists of two parts separated by a 5-ft wide channel. The shoreward portion is continuous with the high shores and has steeply sloping walls, while the more gently sloping and isolated seaward portion occurs only in the mid and low zones.

avoiding immersion). These data and the low crab abundance on low Site 1 suggest that *Grapsus* spends less time at lower than at higher levels. Since the algal food of *Grapsus* is more abundant at lower levels (see above), this behavior would seem disadvantageous. This suggests that the factors causing them to avoid submergence must be strong.

The large predaceous crab *Ozius verreauxii* Sassure appears more abundant on boulder-cobble substratum than on the solid rock surfaces considered here (S. Gaines, P. Lubchenco pers. obs.). During thorough searches on night low tides at Site 6, we observe only one to three individuals each time. Daytime observations of *Ozius* are even less frequent. Fish abundances in the mid and low intertidal at high tide per m and per m^2 (Table XI) are strongly correlated ($r^2 = 0.99$; $y = 0.01 + 0.14x$, $P \ll 0.01$; $n = 48$), although topographies differ from site to site. Although all species in Table XI forage intertidally at high tide, there are consistent differences between species. For example, *Kyphosus* and *Diodon* range well into the high zone while the balistids, holacanthids, *Prionurus*, *Microspathodon dorsalis*, *Eupomacentrus flavilatus* rarely forage above the low zone. Predatory fishes which frequently forage intertidally include *Bodianus*, *Diodon*, and

TABLE XI

Relative abundance of fishes at three sites on Taboguilla Island, Bay of Panama[a].

		Site					
		1		2		6	
Species	Estimate[b]	$\bar{x} \pm 95\%$ CI[c]	CV[d]	$\bar{x} \pm 95\%$ CI	CV	$\bar{x} \pm 95\%$ CI	CV
Shoreline length (low tide, m)		41		49		73	
Intertidal area (mid and low tide, m^2)		283		338		567	
PREDATORS							
Arothron hispidus	m	0		0.7 ± 0.6		1.1 ± 1.4	
(F. Tetraodontidae)			–		138.4		118
	m^2	0		0.11 ± 0.09		0.15 ± 0.17	
A. meleagris	m	0		0.2 ± 0.3		0	
(F. Tetraodontidae)			–		367		–
	m^2	0		0.02 ± 0.05		0	
Balistes polylepis	m	0.24 ± 0.55		0.2 ± 0.3		1.1 ± 1.1	
(F. Balistidae)			316		367		90.3
	m^2	0.035 ± 0.078		0.02 ± 0.05		0.15 ± 0.13	
Bodianus diplotaenia	m	5.6 ± 3.5		13.8 ± 3.4		7.8 ± 6.4	
(F. Labridae)			87.1		38.5		78.6
	m^2	0.8 ± 0.5		1.7 ± 0.6		1.0 ± 0.8	
Diodon hystrix	m	0		0.7 ± 0.9		0.5 ± 1.2	
(F. Diodontidae)			–		208		245
	m^2	0		0.11 ± 0.13		0.06 ± 0.14	
Holacanthus passer	m	1.95 ± 2.15		3.4 ± 1.2		3.9 ± 1.7	
(F. Holacanthidae)			154		61.5		41.3
	m^2	0.28 ± 0.31		0.49 ± 0.17		0.5 ± 0.2	

TABLE XI (continued)

		Site					
		1		2		6	
Species	Estimate[b]	$\bar{x} \pm 95\%$ CI[c]	CV[d]	$\bar{x} \pm 95\%$ CI	CV	$\bar{x} \pm 95\%$ CI	CV
Pomacanthus zonipectus (F. Holacanthidae)	m	1.22 ± 2.22	254	0		2.7 ± 1.8	63.2
	m^2	0.18 ± 0.32		0		0.35 ± 0.22	
Pseudobalistes naufragium (F. Balistidae)	m	0	–	0	–	0.9 ± 0.7	77.5
	m^2	0		0		0.12 ± 0.09	
HERBIVORES							
Eupomacentrus acapulcoensis (F. Pomacentridae)	m	200.5 ± 101.1	70.5	241.8 ± 77.1	55.2	276 ± 162	55.7
	m^2	29.0 ± 14.4		35.1 ± 11.1		34.6 ± 19.3	
E. flavilatus (F. Pomacentridae)	m	2.2 ± 2.9	185	0.6 ± 1.3	376	9.8 ± 23.2	225
	m^2	0.32 ± 0.41		0.08 ± 0.18		1.3 ± 2.8	
Kyphosus elegans (F. Kyphosidae)	m	31.7 ± 43.5	192	8.9 ± 8.0	157	18.0 ± 36.0	190
	m^2	4.6 ± 6.3		1.3 ± 1.2		2.3 ± 4.4	
Microspathodon dorsalis (F. Pomacentridae)	m	1.5 ± 1.2	117	6.6 ± 1.2	32.6	7.8 ± 3.9	48.2
	m^2	0.21 ± 0.17		0.87 ± 0.22		1.0 ± 0.5	
M. bairdii (F. Pomacentridae)	m	2.0 ± 2.3	165	0.3 ± 0.6	376	2.1 ± 2.4	109
	m^2	0.28 ± 0.33		0.94 ± 0.009		0.27 ± 0.29	
Ophioblennius steindachneri (F. Blenniidae)	m	7.3 ± 4.4	83.1	11.4 ± 5.6	85.6	18.9 ± 8.8	44.2
	m^2	1.1 ± 0.6		1.6 ± 0.8		2.4 ± 1.1	
Prionurus punctatus (F. Acanthuridae)	m	0.2 ± 0.6	321	0	–	0	–
	m^2	0.035 ± 0.08		0		0	
Scarus perrico (F. Scaridae)	m	4.2 ± 5.5	186	24.0 ± 47.6	342	13.2 ± 14.7	106
	m^2	0.6 ± 0.8		3.5 ± 6.8		1.3 ± 1.9	
N[e]		10		14		6	

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[a] Other fishes present but not monitored or monitored irregularly were the small sharpnose puffer *Canthigaster punctatissima* (usually present, < 5 per site), the small Cortez rainbow wrasse *Thalassoma lucasanum* (always present, 100's per site), the small Panamic sergeant major *Abudefduf troschelii* (always present, > 10's per site), the medium-sized orangeside triggerfish *Sufflamen verres* (sometimes present < 1 per site), the loosetooth parrotfish *Nicholsina denticulata* (usually present, < 10 per site), and the large blue chin parrotfish *Scarus ghobban* (usually present, < 5 per site).

[b] Data are expressed as either mean number of individuals/100 m of shoreline (m) or mean number/100 m^2 of mid and low intertidal area (m^2).

[c] $\bar{x} \pm 95\%$ CI = mean ± 95% confidence interval.

[d] CV = coefficient of variation.

[e] *N* = no. of dates samples were taken. *N* for *B. diplotaenia* at Site 2 was 12 rather than 14.

Arothron hispidus. Herbivorous fishes commonly foraging in the intertidal include *Eupomacentrus acapulcoensis*, *Ophioblennius steindachneri*, *Kyphosus elegans* and *Microspathodon bairdii*.

Among predatory fishes, the wrasse *Bodianus diplotaenia* is most common. Angelfishes *Holacanthus passer* and *Pomacanthus zonipectus* are next most abundant, while triggerfishes (*Balistes polylepis*, *Pseudobalistes naufragium*), puffers (*Arothron hispidus*, *A. meleagris*) and porcupine fish (*Diodon hystrix*) are scarce or seemingly absent at some sites (Table XI). However, these latter are probably always in the vicinity. Observations suggest that longer sampling periods and better visibility would probably increase these apparent densities or at least reduce coefficients of variation.

The most common herbivorous fish is the territorial damselfish *Eupomacentrus acapulcoensis*. Other common species include the chub *Kyphosus elegans* which occur in schools or as solitary individuals, the blenny *Ophioblennius steindachneri*, several species of damselfishes (*Eupomacentrus flavilatus*, *Microspathodon dorsalis*, *M. bairdii*) and the relatively huge (up to 0.5 m long) schooling or solitary parrotfish *Scarus perrico* (Table XI). The herbivores are more numerous (Table XI) and have a greater biomass (Menge & Lubchenco, unpubl. data) than the predators. In summary, fast-moving consumers are ubiquitous at Taboguilla. Crabs and fishes are generally large and abundant and range throughout the intertidal region.

COMMUNITY PERSISTENCE

TEMPORAL VARIATION IN SPACE UTILIZATION

Repeated sampling of the same permanent quadrats on Site 6 during successive dry and wet seasons, 1977–1980 yielded information on seasonal as well as annual fluctuations in space utilization patterns. Percent cover data for both individual species and functional groups indicate that there are no major, consistent seasonal fluctuations in use of primary space (Fig. 5, Tables IV–VI). Unquantified observations made in dry seasons 1973, 1974 and in both wet and dry seasons 1980–1983 indicate that this apparent lack of major change has persisted for at least a decade. Some year-to-year variation does exist, and far outweighs any seasonal changes. We summarize the patterns below. Wet season data comparable to those for Appendices 3 and 4 are available upon request.

In the high zone, solitary sessile species vary little in abundance over time, ranging from a low of 1.9% in February 1977 to a high of 8.5% in January 1979 (Fig. 5). Algal crusts always cover $<0.5\%$. In the mid zone, algal crusts fluctuate from a low of 79.2% in July–August 1977 to a high of 96.2% in January 1979. However, annual fluctuations outweigh seasonal changes. The major species in the algal crust group also show annual fluctuations greater than seasonal changes (Fig. 6). The brown crust *Ralfsia* sp., for example, occupied 65% in January 1979 and declined to 31% in January 1980. *Schizothrix calcicola* and *Hildenbrandia* sp. also fluctuate in an irregular fashion, but less so than *Ralfsia*. Some of the initial variation in crust abundance in both mid and low zones is due in part to early problems in our distinguishing the different crust species. Solitary and colonial sessile groups (Fig. 5) and their most common individual species exhibit little seasonal or annual changes in cover. Bare rock thus changes primarily as the inverse of crust abundance (Fig. 5).

Abundances in the low zone vary even less through time. Mean cover of algal crusts range from a low of 87.9% in August 1977 to a high of 93.8% in January 1979 (Fig. 5). Individual species show more fluctuations but no consistent seasonal patterns (Fig. 6).

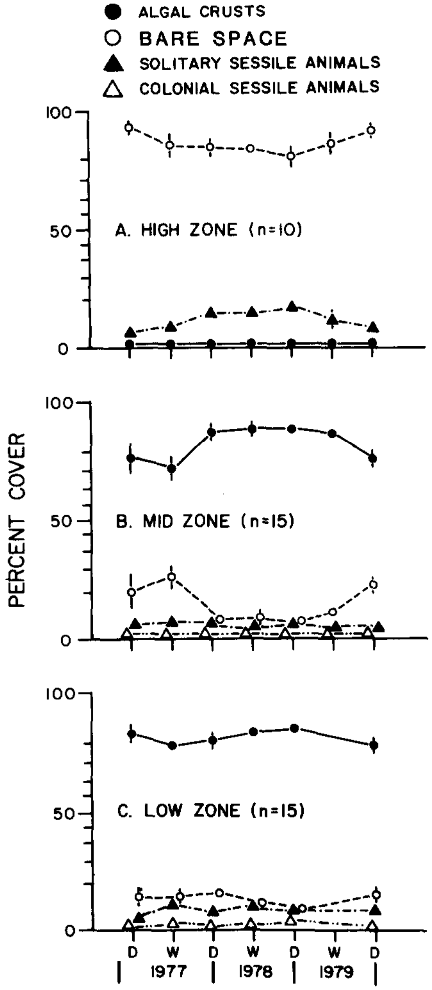

Fig. 5. Temporal change in percent cover of major primary space occupying groups in the high, mid and low zones on Site 6: mean and standard error (SE) are plotted for each date; when no SE bar is shown, the symbol is larger than the SE; number of quadrats sampled per transect is given in parentheses; in this and all subsequent figures presenting percent cover data, the units of the ordinate are transformed with the arcsine transformation (Sokal & Rohlf, 1981).

If the 1977 data are disregarded (see above), these variations are less. Coralline crusts come closest to fluctuating seasonally, with higher mean covers in the wet season, but these changes are not significantly different (as indicated by overlap in error bars in Fig. 6, and by analyses of differences from one season to next; one-way ANOVA $P > 0.05$). However, a more qualitative (i.e., does abundance increase or decrease from one season to the next?) analysis (Table XII) suggests a weak, but significant seasonal pattern in encrusting coralline algae. Specifically, abundance of encrusting corallines tends to increase in the wet and decrease in the dry seasons.

Bare rock and cover of solitary and colonial sessile animals also vary little in the low

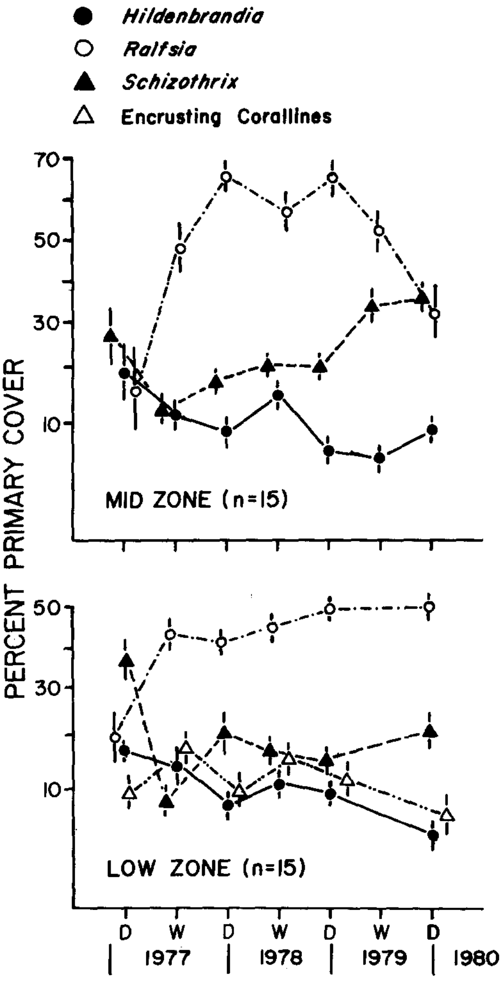

Fig. 6. Temporal change in percent cover of most abundant primary space occupying crustose algae in the mid and low zones on Site 6; no algal crusts occurred in the high zone; free space = bare rock; see caption Fig. 5 for further explanation.

zone (Fig. 5). Analyses similar to those above indicate that although no significant seasonal patterns can be detected in percent covers, significant qualitative seasonal changes in abundance of solitary sessile organisms also occur (Table XII). These are more abundant in the wet than in the dry season. Individual species in these animal groups show little seasonal or year to year change.

TABLE XII

Analysis of seasonal changes in abundance in certain categories of organisms in the high, mid and low zones at Site 6, Taboguilla Island[a].

Zone	Category	Change	Abundance		χ^2
			Increases	Decreases	
Mid	DENSITY				
	Total herbivores	Dry to wet	20	10	5.73*
	(1977–80)	Wet to dry	9	17	
	DENSITY				
	Siphonaria gigas	Dry to wet	26	13	8.90***
	(1977–80)	Wet to dry	12	25	
Low	PERCENT COVER				
	Encrusting coralline algae	Dry to wet	121	8	7.59**
	(1977–79)	Wet to dry	11	19	
	PERCENT COVER				
	Solitary sessile animals	Dry to wet	25	5	11.92***
	(1977–79)	Wet to dry	12	18	
	PERCENT COVER				
	Erect hydroids	Dry to wet	16	2	11.19***
	(1977–79)	Wet to dry	10	16	
	PERCENT COVER				
	Erect coralline algae	Dry to wet	15	3	13.49***
	(1977–79)	Wet to dry	4	14	
	DENSITY				
	Total herbivore	Dry to wet	26	4	26.79***
	(1977–79)	Wet to dry	11	19	

[a] Data entries are the number of permanent quadrats in which the change occurred. For example, if total herbivore density in quadrat 1 increased from 20/0.25 m^2 in Jan. 1977 to 24/0.25 m^2 in July 1977, a "1" was entered in the "increases" column of the "Dry to wet" row. No significant seasonal changes in abundance occurred in the high zone. No other category other than those presented exhibited significant seasonal changes.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$.

Similar patterns exist for erect species (Fig. 7). Fleshy algae increase from 0.1% cover in February 1977 to 7.7% in January 1979 and then decline again. Articulated coralline algae vary little but erect hydroids (primarily *Abietinaria* sp.) tend toward seasonal fluctuations with high covers in the wet season. These quantitative patterns are not significant (one-way ANOVA, $P > 0.05$), but qualitative seasonal changes in both hydroids and erect coralline abundances are significant (Table XII).

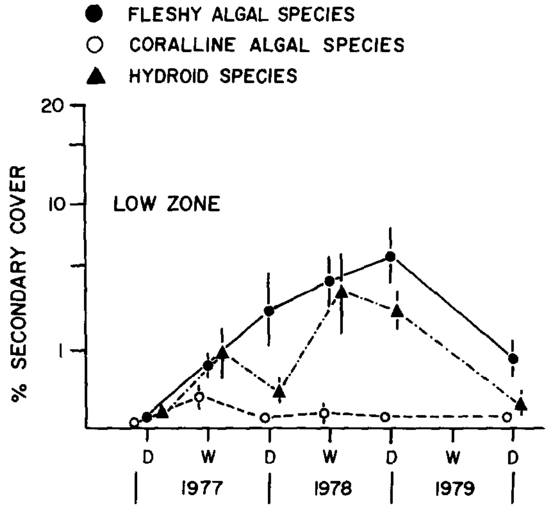

Fig. 7. Temporal change in percent cover of most abundant secondary space occupying groups in the low zone on Site 6: these groups are virtually absent from the high and mid zones; see caption Fig. 5 for further explanation.

Thus three overall patterns emerge: (1) for some species, no seasonal or annual fluctuations are apparent (high zone crusts; mid zone colonial sessile animals; and low zone colonial sessile animals and fleshy crusts); (2) for others, annual but not seasonal changes occur (high zone solitary sessile animals; mid zone crusts, *Ralfsia*, *Schizothrix*, *Hildenbrandia*; and low zone *Ralfsia*, *Schizothrix*, *Hildenbrandia* and erect fleshy algae); and (3) for yet others, slight seasonal change occurs (low zone encrusting and erect coralline algae, solitary sessile animals, hydroids). In all of the latter cases, abundance is higher in the wet than in the dry season (Table XII).

TEMPORAL VARIATION IN DENSITIES

Density and percent cover data show similar patterns: in all three zones most, but not all, species exhibit little quantitative seasonal or annual change. In the high and mid zones, densities of most sessile and mobile species change little from dry to wet season (Tables VII, VIII). Densities of *Chthamalus* in the mid zone, however, change considerably from year to year (Fig. 8). In the low zone, several species show large annual fluctuations, particularly *Brachidontes*, *Balanus*, and *Fissurella virescens* (Fig. 8). With the exceptions of significant qualitative seasonal changes of mid and low zone total herbivores and mid zone *Siphonaria gigas* (Table XII), other sessile and mobile species remain fairly constant in number (Table IX, Fig. 8). *Eupomacentrus acapulcoensis*, the

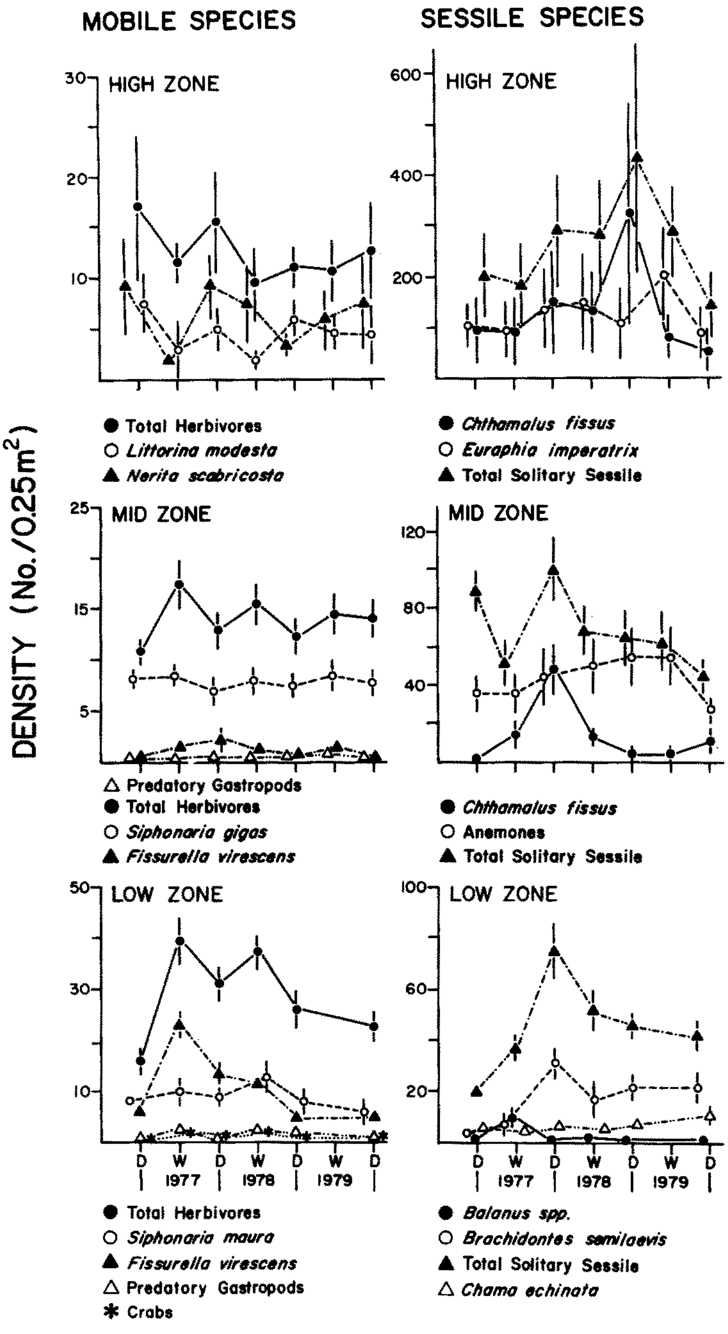

Fig. 8. Temporal change in densities of most abundant groups and species of mobile and solitary sessile animals in the high, mid and low zones on Site 6: see caption Fig. 5 for further explanation.

only fish species numerous enough to allow us to examine temporal variation in abundance, show weak seasonal patterns: at Site 2 they are more abundant during the dry season (ANOVA; $P < 0.01$, Fig. 9), but at Sites 1 and 6, seasonal differences are not significant (ANOVA; $P > 0.25$, Site 1; $P > 0.75$, Site 2; Fig. 9).

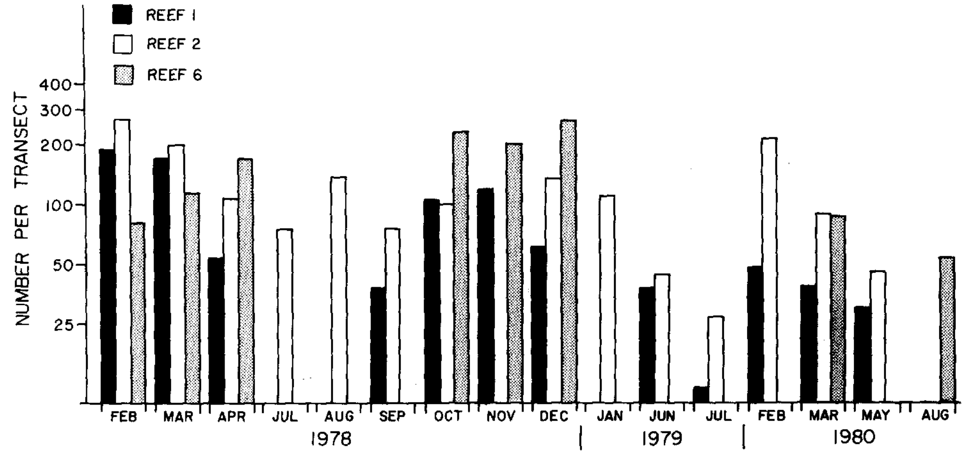

Fig. 9. Temporal change in abundance of the damselfish *Eupomacentrus acapulcoensis* on Sites 1, 2, and 6.

TEMPORAL VARIATION IN DIVERSITY

Measures of diversity (H'), evenness (J') and species richness (S) taken on percent cover (Fig. 10) and density data (Fig. 11) reveal that little significant seasonal change occurs at any tidal level. As with abundances, the most significant differences are occasional between-year differences in richness (e.g., mid and low zones, percent cover; low zone, density) and H' (e.g., low zone, density and percent cover; Figs. 10, 11). The apparent mid and low zone increases in S in 1977–1978 are probably due to improvements in our taxonomic knowledge and not to real increases in species richness. The only consistent qualitative seasonal change is in H' (percent cover) in the high zone (Fig. 10). In all other cases, apparent trends always have at least one exceptional sample date (Fig. 10, 11). We conclude that during the period of our study, little meaningful change in these parameters occurred in this community.

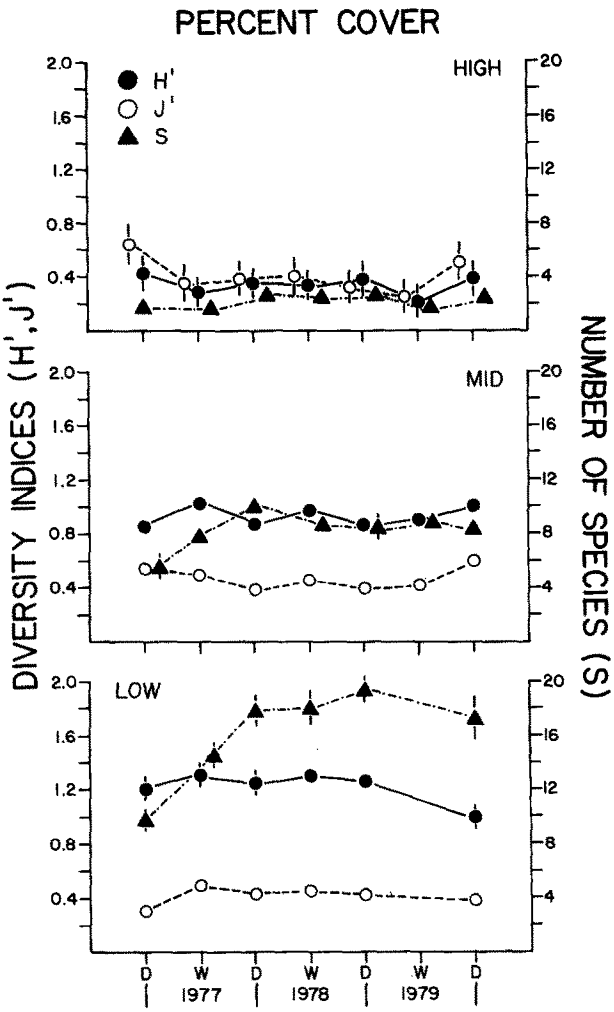

Fig. 10. Temporal change in diversity (H') and evenness (J') and species richness (S) of sessile organisms (percent cover) in the high, mid and low zones on Site 6: see caption Fig. 5 for further explanation.

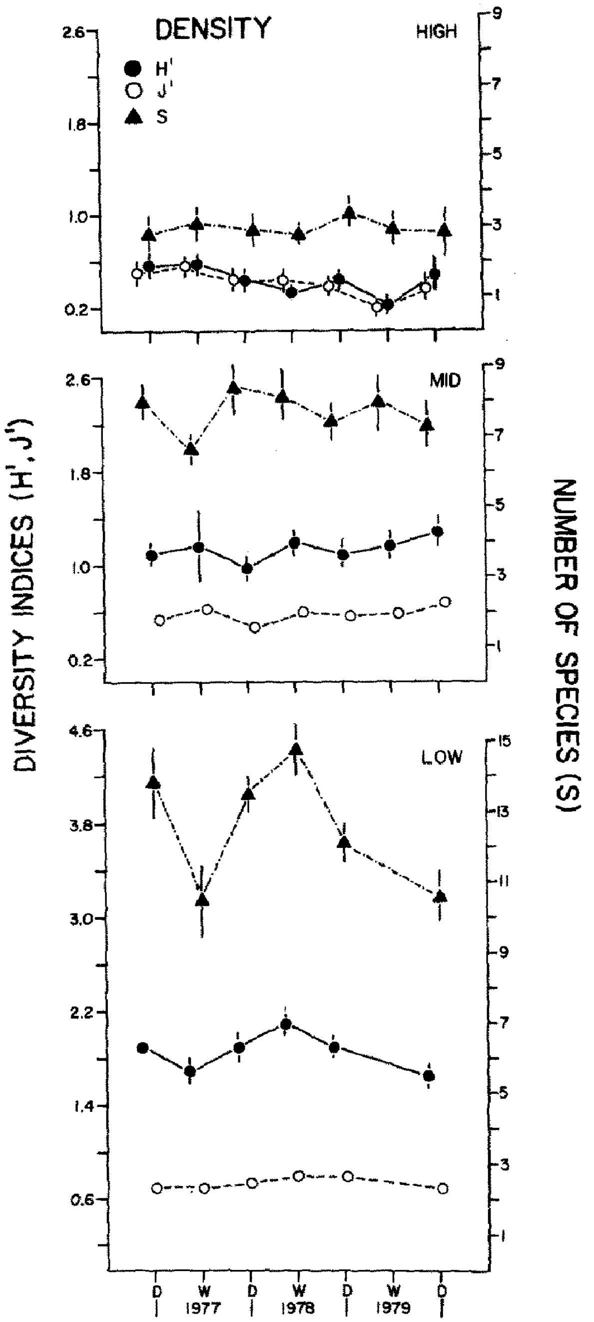

Fig. 11. Temporal change in diversity (H'), evenness (J') and species richness (S) of mobile and solitary sessile animals (density) in the high, mid, and low zone on Site 6: see caption Fig. 5 for further explanation.

ROLE OF CONSUMERS

Consumers are a major factor in maintaining the consistently low covers of noncrustose algae and sessile invertebrates (Tables XIII, XIV). Preliminary analyses (one-way ANOVA) comparing premanipulation abundances of the prey categories listed in Table XIII indicate that no initial differences occurred between control and total consumer exclusion plots with the exception of barnacles in the mid zone. In this case, percent cover and density of barnacles was initially higher in total exclusion plots ($P < 0.01$ in both comparisons). However, these differences seem biologically insignificant, since percent cover and density were 0 in all 15 control plots and 0 and 1% (cover) and 0 and $4/0.25\ m^2$ (density) in total exclusions (Table XIII). Subsequent MANOVAs detected large differences between control and total exclusion plots in abundances of prey (Table XIV). In these analyses, dry season densities of barnacles

TABLE XIII

Effects of benthic consumers on prey abundance: density of barnacles in high zone are no./0.04 m^2; all other densities are no./0.25 m^2; data are $\bar{x}$ ± 1 SE; initial date was in January or February, 1977; final date was February 1979 (high) or March 1980 (mid and low)[a].

		Control		Total exclusion	
Zone	Category	Initial	Final	Initial	Final
High	Barnacles (%)	1.1 ± 0.3	7.4 ± 0.6	1.0 ± 0	21.5 ± 8.5
	(density)	203.1 ± 81.9	434.4 ± 227.8	59.4 ± 9.4	1253.1 ± 128.1
	Bare (%)	97.2 ± 0.7	91.7 ± 0.9	95.5 ± 1.5	78.5 ± 8.5
	N	10	10	2	2
Mid	Barnacles (%)	0.1 ± 0.1	0.3 ± 0.1	0.2 ± 0.4	0.5 ± 0.7
	(density)	4.1 ± 1.8	14.8 ± 6.7	2.0 ± 2.0	10.5 ± 7.5
	Bivalves (%)	0	0.1 ± 0.1	0	6.7 ± 2.0
	(density)	1.6 ± 0.4	5.4 ± 1.4	1.0 ± 0	95.5 ± 55.5
	Algal crusts (%)	80.9 ± 8.0	84.2 ± 4.0	95.9 ± 0.6	85.5 ± 4.9
	Upright algae (%)	0	0	0	8.3 ± 3.2
	N	15	15	2	2
Low	Barnacles (%)	0.1 ± 0.1	0.2 ± 0.1	0	0 ± 0.8
	(density)	0.7 ± 0.3	0.3 ± 0.1	0	26.0 ± 3.6
	Bivalves (%)	0.3 ± 0.1	1.6 ± 0.2	0.2 ± 0.4	51.1 ± 7.1
	(density)	13.6 ± 2.2	34.5 ± 5.2	4.0 ± 0	247.5 ± 128.5
	Algal crusts (%)	91.1 ± 0.9	88.9 ± 0.8	86.2 ± 3.3	12.0 ± 0
	Upright algae (%)	0.1 ± 0.1	1.0 ± 0.2	0.5 ± 0.7	30.8 ± 7.0
	N	15	15	2	2

[a] Statistics comparing control and total consumer exclusion values for each category are presented in Table XIV.

and bivalves and cover of sessile organisms occupying primary rock surface (barnacles, bivalves, algal crusts) or secondary space above the surface (perennial algae, opportunistic algae and the hydroid *Abietinaria*) were compared (Table XIV). In the high zone, significant changes occurred in the amount of bare space and percent cover of barnacles (*Chthamalus* and *Euraphia*); a posteriori tests using one-way ANOVA with the critical level adjusted for multiple comparisons using the Bonferroni approximation (Neter & Wasserman 1974, this method was also used in mid and low zone multiple comparisons) indicate that both changes contribute to the significance of the MANOVA. Although barnacle density changes from 1977–1979 were not significant, a MANOVA indicates that cirripede density was greater in total exclusions than in controls in 1978 (Table XIV). We do not know why this difference was not maintained in 1979, although the data indicate that high recruitment variability in control plots in 1979 swamped any between-treatment differences.

TABLE XIV

Multivariate analyses of variance comparing percent covers and densities of major groups of organisms in control and total consumer exclusion plots in the high, mid and low zones from 1977–79 (high) or 1977–80 (mid, low).

Zone	Abundance category	Calculated *F*	d.f.	Critical *F*	*P*
High	% Cover (1°)				
	Barnacles and bare	53.8	6,6	20.0	<0.001
	Density				
	Barnacles	3.85 NS	3,9	3.86	>0.05
	Barnacles 1978 only	11.1	1,11	9.6	<0.01
Mid	% Cover (1°)				
	Barnacles, bivalves, algal crusts	12.0	12,5	9.9	<0.01
	% Cover (2°)				
	Perennial algae, opportunistic algae, *Abietinaria*	1.8×10^{15}	12,5	26.4	$\lll 0.001$
	Density				
	Barnacles and bivalves	68.0	8,9	10.4	$\leqslant 0.001$
Low	% Cover (1°)				
	Barnacles, bivalves, algal crusts	56.8	12,5	26.4	$\leqslant 0.001$
	% Cover (2°)				
	Perennial algae, opportunistic algae, *Abietinaria*	2.368	12,5	26.4	$\lll 0.001$
	Density				
	Barnacles and bivalves	80.8	8,9	10.4	$\leqslant 0.001$

In the mid zone, all major prey groups exhibit significant differences between total exclusions and controls (Table XIV). A posteriori tests indicate that most differences occurred in 1978 (percent cover of perennial and opportunistic algae, and of *Abietinaria*; densities of barnacles; $P < 0.05$), 1979 (percent cover of barnacles, bivalves, algal crusts and perennial algae; densities of barnacles and bivalves; $P < 0.05$) and 1980 (percent cover of bivalves, perennial and opportunistic algae; density of bivalves; $P < 0.05$). Only erect algae (both perennial and opportunistic; $P < 0.05$) were more abundant in total exclusions than controls in the first year of the experiment (1977).

Similar changes occurred in the low zone (Tables XIII, XIV). A posteriori tests indicate that only percent covers of erect algae differed between controls and total exclusions in 1977 ($P < 0.05$). By 1978, covers of barnacles, algal crusts, perennial algae and *Abietinaria* differed between these treatments, and all categories except opportunistic algae in 1979 differed in the last 2 yr (1979, 1980) of the experiment. Significant increases in organism abundance occurred in each zone with every group excepting crustose algae which decreased (Table XIII). This decrease results from the crusts being covered by foliose algae and sessile animals. In controls, changes in organism abundances from 1977–1980 were always small. Thus, consumers have a major impact on the abundance of the sessile benthos in all zones. These results indicate that crustose algae normally predominate in mid and low zones and bare rock in the high zone because consumers keep foliose algae and sessile invertebrates scarce.

DISCUSSION

SPECIES COMPOSITION

The general taxonomic composition of this community is in many respects typical of that observed in temperate rocky intertidal habitats. Carnivorous and herbivorous gastropods, limpets (or limpet-like pulmonate gastropods), chitons, seastars, crabs, sea urchins, barnacles, bivalves, anemones, sponges, bryozoans, hydrozoans, and tunicates are all relatively common.

The major differences between the Panama community and its temperate counterparts are twofold: (a) the paucity of macroalgae and (b) the abundance of herbivorous fishes and crabs and predaceous fishes in Panama. Benthos-feeding fishes seem to be minor components in temperate rocky intertidal communities, although studies specifically designed to investigate abundances and effects of fishes in these habitats are few (e.g., Choat, 1982). Fishes are prominent and important structuring agents in this (Bertness, 1981; Bertness *et al.*, 1981; Menge & Lubchenco, 1981; Gaines, 1983; Garrity & Levings, 1983: Levings & Garrity, 1983) and other tropical marine communities (e.g., Bakus, 1964, 1969; Randall, 1965; Vine, 1974; Birkeland, 1977; Vermeij, 1978; Neudecker, 1979; Wellington, 1982). Further, although the role of *Grapsus* has not been demonstrated experimentally, observations of an unusually high cover of erect algae (24 ± 8% cover vs. usual mean covers of 1 to 2%) in the mid zone at one of our experimental sites (4), which has no *Grapsus* (Table X), suggest that this very active crab is an important grazer.

ZONATION AND ABUNDANCE

As in other intertidal communites, most organisms on these rocky shores occur in vertical zones. However, compared to temperate shores, the Taboguilla zones are less obvious, primarily because they are dominated by algal crusts or bare rock (Tables IV–VI, Appendix 3), as opposed to sessile animals and upright macrophytes. As indicated by the consumer exclusion experiments (Table XIII, Menge & Lubchenco, 1981), the scarcity of erect sessile invertebrates and foliose algae is at least partly due to predation and herbivory. Consumers thus obscure the Taboguilla zonation patterns by preventing the development of prominent horizontal bands of sessile animals or erect macroalgae (see also Menge & Lubchenco, 1981). In the high zone, for example, temperate shores harbor a prominent barnacle zone which is indistinct at Taboguilla. Although consumer removal experiments (Tables XIII, XIV, Menge & Lubchenco, 1981) suggest barnacle abundance is strongly affected by consumers, these experiments do not allow us to evaluate which consumers may be more or less important. Feeding data (Menge *et al.*, unpubl. data) indicate that whelks (*Thais melones, Acanthina brevidentata*) and several fishes are probably the major predators. Further, invertebrate grazers may indirectly affect barnacle abundance (e.g., Garrity & Levings, 1981), by their interference with survival of settling stages. Other factors which could affect barnacle abundance in the high zone are mortality from physical stresses, larval scarcity, and recruitment irregularity. We have no evidence on the first two factors; unpublished data indicate that recruitment is indeed irregular.

In the mid zone, fleshy encrusting algae (at least three abundant species) cover most rock surfaces (Table V, Appendix 3). Mussels, barnacles and foliose macroalgae, typically abundant in the mid zones of many temperate shores (e.g., Hoshiai, 1964; Lewis, 1964; Hoshiai *et al.*, 1965; Dayton, 1971; Menge, 1976) are scarce. In contrast to the scarcity of erect sessile organisms, mobile invertebrates are common (Table VIII, Appendix 4) and in this respect these Panama shores differ little from most other quantitatively studied mid intertidal zones. Comparisons with other investigations indicate that this tropical mid zone is most similar to the most wave-protected mid zone examined by Underwood *et al.* (1983) in a warm temperate intertidal habitat (eastern Australia). Here, mid shores are covered by encrusting algae (primarily *Hildenbrandia prototypus*) and mobile invertebrates (mostly herbivorous gastropods) are abundant. Underwood *et al.* (1983) argue that whelk predation, limpet grazing and disturbance and sparse settlement of barnacle larvae are primarily responsible for observed patterns of mid zone community structure. In Panama, invertebrate and vertebrate consumers all have demonstrable effects (e.g., Menge & Lubchenco, 1981; Gaines, 1983, Garrity & Levings, 1983; Levings & Garrity, 1983; this paper). The failure of covers of upright organisms to reach 100% cover in the mid zone consumer removal experiments (e.g.,

Table XIII) suggests that other factors are also important. As mentioned above for the high zone, we suggest that mortality from physical stresses (heat, desiccation), larval scarcity, and recruitment variability may contribute to the overall pattern.

The low zone also has a very low cover of sessile animals and foliose algae (e.g. Table VI, Appendix 3). Mobile invertebrates are abundant in this zone (e.g. Table IX, Appendix 4), and fish frequently forage over the lower shore (Table XI, personal observations). Our experiments (Table XII, XIV, Menge & Lubchenco, 1981; unpubl. data) suggest that consumer pressure is high with total plant and animal covers of 100% achieved in some total exclusion plots after 3 yr. Mortality due to physical factors appears infrequent here (Menge & Lubchenco, 1981; unpubl. data). We know of no temperate intertidal community with a low zone of structural patterns comparable to those presented here. Temperate low zones usually have high covers of foliose algae (e.g., Hoshiai, 1964; Lewis, 1964; Hoshiai *et al.*, 1965; Menge & Lubchenco, 1981; Underwood, 1981) or sessile animals (e.g., Lewis, 1964; Lubchenco & Menge, 1978; Underwood, 1981). In view of our results, we have suggested that this difference is largely due to the presence of large, mobile fishes as important sources of mortality for all organisms but encrusting algae (e.g., Menge & Lubchenco, 1981; unpubl. data). Although fishes do occur in temperate habitats, herbivorous species are usually small and few while predaceous fishes seem restricted to subtidal and calm-water intertidal regions (e.g., Choat, 1982). Why herbivorous fishes are rare and predaceous fishes are more restricted in habitat in temperate regions is a problem deserving of future study (see also Gaines & Lubchenco, 1982).

VARIATION OVER HORIZONTAL SPACE

Two aspects of horizontal spatial variation are interesting to consider: (1) how typical is Taboguilla of the Eastern Pacific in general? and (2) how does variation in community structure along a stretch of shore at Taboguilla compare with variation along a comparable section of a temperate coast?

Although community structure varies little over horizontal space at the Taboguilla sites presented here (Tables IV–IX), transects taken further afield in the Bay of Panama and Gulf of Chiriqui and observations in Costa Rica indicate that greater variability occurs in East Pacific tropical rocky intertidal regions than is documented here (e.g., Menge & Lubchenco, 1981; unpubl.). Specifically, barnacle, oyster and foliose algal covers are sometimes greater than shown in this paper (see, for example, Flamenco Island data in Menge & Lubchenco, 1981). Furthermore, algal cover fluctuates seasonally, with higher cover during the wet season. Although abundance of these organisms does not approach temperate abundances, some species are sufficiently more common than at Taboguilla to suggest an important difference in structuring agents. Such differences most usually occur at sites that are either considerably more, or less wave-exposed than Taboguilla (and the essentially similar neighboring islands) or at sites in the Perlas Islands that harbor oystercatchers (unpubl. data and observations).

We hypothesize that these differences in community structure are a consequence of shifts in the intensity of consumer pressure. For example, fish may be much less effective foragers in the turbid waters characteristic of wave-protected sites (e.g., Flamenco, Menge & Lubchenco, 1981; mainland Bay of Panama areas) or in the turbulent waters characteristic of more wave-exposed sites (e.g., exposed headlands in the Gulf of Chiriqui). At both ends of the wave exposure spectrum, barnacles and algae are abundant relative to our Taboguilla sites (Menge & Lubchenco, 1981; unpubl. data; pers. obs.). A different sort of shift in consumer pressure is apparent at several sites in the Perlas Archipelago, where oystercatcher predation on herbivorous snails, limpets and chitons (pers. obs., S. Levings, pers. comm.) appears to result in a low abundance of these grazers and consequent increase in filamentous algae (unpubl. data). Why oystercatchers are present on some islands but absent at most other sites is unknown. Oystercatcher predation in Oregon has strong effects on limpets, and, indirectly, algal composition and abundance (Frank, 1982; Marsh, 1983).

Thus, all sites examined (this paper plus Menge & Lubchenco, unpubl. data, pers. obs.) in the Eastern Pacific (Panama and Costa Rica) appear relatively barren and are dominated by algal crusts (mid and low) or bare rock (high zone). The Taboguilla sites are among the most barren, perhaps because physical conditions are conducive to intense fish foraging. More protected and more exposed sites or those with oystercatchers may have slightly higher abundances of barnacles, oysters or erect algae, but are still quite barren compared to most temperate shores described. Our hypotheses about shifts in intensity of fish foraging as a function of wave action or turbidity remain to be tested.

Spatial variation in community structure over a given distance of shoreline seems less in Panama than in the temperate communities for which appropriate comparable information is available. For example, the transects reported in Tables IV–IX and Appendices 3 and 4 were done at sites along an ≈ 1 km stretch of shore; as noted, differences between these sites were few. In contrast, along stretches of shore of similar length in New England, Washington, Oregon, California and New South Wales, between-site differences can be large (e.g., Dayton, 1971, 1975; Menge, 1976; Lubchenco & Menge, 1978; Underwood *et al.*, 1983; Menge & Lubchenco, unpubl. data, pers. obs.). Neighboring sites can differ completely, with different species compositions, diversities, relative abundances and trophic structure. Such differences are sometimes correlated to differences in wave action and topography and some of the apparent difference is probably attributable to such factors. We postulate that the presence of fishes as important predators in Panama but not (apparently) the temperate sites introduces an additional factor. Fishes are fast-moving, presumably have large perceptual fields relative to invertebrate consumers, and thus are capable of rapidly locating and decimating aggregations of prey which might escape the attention of slow-moving, perceptually limited invertebrate consumers for long periods. Furthermore, the fishes in the vicinity of Taboguilla are large (see above) and forage over much larger stretches of shoreline than do the substratum-bound invertebrate consumers. Thus, small-scale variations in consumer pressure on open surfaces like those documented in temperate, invertebrate-consumer dominated sites (e.g., Menge 1978a,b, 1983) are less likely in Panama. In Panama, the high mobility and large perceptual fields of fishes effectively eliminates horizontal and vertical prey refuges and restricts most of the sessile and mobile invertebrates and macroalgae to three-dimensional refuges in the rock surface (Menge & Lubchenco, 1981; Gaines, 1983; Levings & Garrity, 1983) or to supratidal levels (e.g., Levings & Garrity 1983). Those few species occurring on smoother two-dimensional surfaces appear to have effective defenses against fish predators (Palmer, 1979; Menge & Lubchenco, 1981; Gaines, 1983; Garrity & Levings, 1983). A corollary effect of fish grazing limiting invertebrate herbivores and predators to holes and crevices is the creation of highly localized variation in invertebrate consumer pressure (Menge *et al.*, 1983). Thus, fishes create regions of uniformly high consumer pressure on open surfaces and, simultaneously, promote variation in consumer pressure in cracks, crevices and holes.

These postulated differences in consumer pressure in Panama compared to several temperate sites may have far-reaching implications regarding patterns of species diversity and other aspects of community organization (e.g, Menge & Lubchenco, unpubl. data).

COMMUNITY PERSISTENCE

Results presented earlier suggest that this community varies little over time, at least from 1977–1980. Indeed, if a transect done at Site 2 in 1974 and our unquantified observations from 1973 and 1981–1983 are considered, the community at Taboguilla appears to have changed surprisingly little over a 10-yr period. Although some aspects of community structure in temperate sites may exhibit comparable lack of change (e.g., Paine, 1974), temperate rocky intertidal communities often exhibit strong seasonal and annual changes in species abundances and composition (e.g., Menge, 1976; Lubchenco & Menge, 1978; Paine & Levin, 1981; Underwood, 1981). Thus it appears that the Taboguilla rocky intertidal community has high persistence stability compared to temperate intertidal habitats. This persistence is probably ultimately, but indirectly due to a relatively constant physical environment. Although seasonal and annual changes occur (e.g., Tables I, II, Figs. 2, 3), these rarely lead to a decline in water temperature below $\approx 20\,^{\circ}$C. We suggest that an important consequence of this is that animal acitivity is rarely, if ever, as affected by reduced water temperature as it is in temperate regions. (The activity of benthic consumers is sometimes affected by physical factors during daytime low tides, Garrity, unpubl. data.) The activity of fast-moving consumers like fishes and some crabs can be consistently high regardless of seasonal or annual changes in physical environment. (We cannot comment on the possible effects of higher than usual water temperatures, although obviously heat-related stress could have a serious effect on animal activity.) Thus, we propose that the high persistence of this community is due to consistent, spatially uniform and high consumer pressure with the large, fast-moving fishes as a major component of this pressure.

In summary, community structure in this tropical rocky intertidal habitat exhibits several major differences from most temperate intertidal communities. Zonation is diffuse and abundance of sessile organisms is very low. These patterns exhibit little local variation in space or time. Intense and year round consumer pressure is postulated to be a major biotic factor responsible for these structural patterns.

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APPENDIX 1

Component guilds of animals at Taboguilla Island, Bay of Panama, by trophic status, taxon and intertidal zone: the very low zone is omitted because samples and observations there were infrequent; this list omits species which are very rare, occasional visitors, or do not appear to feed on benthic intertidal prey.

		Zone		
Trophic status[a]	Taxon	High	Mid	Low
Predators	Fishes			
	Alutera scripta (filefish)			×
	Arothron hispidus (puffer)	×	×	×
	A. meleagris (puffer)			×
	Balistes polylepis (triggerfish)			×
	Bodianus diplotaenia (wrasse)		×	×
	Diodon hystrix (porcupinefish)	×	×	×
	Canthigaster punctatissima (sharpnose puffer)			×
	Pseudobalistes naufragium (triggerfish)		×	×
	Sufflamen verres (triggerfish)			×
	Thalassoma lucasanum (wrasse)			×
	Crabs			
	Eriphia squamata		×	×
	Ozius verreauxii	×	×	×
	Seastar			
	Heliaster microbrachius	×	×	×

APPENDIX 1 (continued)

Trophic status[a]	Taxon	Zone		
		High	Mid	Low
	Gastropods			
	Acanthina brevidentata	×	×	×
	Columbella labiosa			×
	Conus nux			×
	C. princeps			×
	C. virgatus			×
	Leucozonia cerata			×
	Mitra tristis		×	×
	Muricanthus princeps			×
	M. radix			×
	Neorapana muricata			×
	Opeatostoma pseudodon			×
	Purpura pansa	×		
	Thais biserialis			×
	T. melones	×	×	×
	T. speciosa			×
	T. triangularis		×	×
Omnivores	Fishes			
	Holacanthus passer (angelfish)			×
	Microspathodon dorsalis (damselfish)			×
	Pomacanthus zonipectus (angelfish)			×
	Scarus perrico (parrotfish)		×	×
Omnivores	Crabs			
	Eriphides hispida		×	×
Herbivores	Fishes			
	Eupomacentrus acapulcoensis (damselfish)		×	×
	E. flavilatus (damselfish)			×
	Kyphosus elegans (sea chub)	×	×	×
	Microspathodon bairdii (damselfish)		×	×
	Nicholsina denticulata (parrotfish)			×
	Ophioblennius steindachneri (blenny)		×	×
	Scarus ghobban (parrotfish)			×
	Gastropods: limpets			
	Collisella pediculus		×	
	Fissurella longifissa		×	×
	Fissurella morrisoni			×
	Fissurella microtrema			×
	Fissurella virescens		×	×
	Notoacmaea filosa		×	×
	Scurria stipulata		×	
	Siphonaria gigas		×	
	Siphonaria maura		×	×
	Siphonaria palmata			×
	Gastropods: coiled snails			
	Fossarus attratus	×	×	
	Littorina aspera	×		
	Littorina modesta	×		
	Nerita funiculata	×	×	
	Nerita scabricosta	×	×	

APPENDIX 1 (continued)

Trophic status[a]	Taxon	Zone		
		High	Mid	Low
	Chitons			
	Acanthochitona hirudiniformis		×	×
	Ceratozona angusta		×	×
	Chaetopleura sp.		×	×
	Chiton stokesii		×	×
	Tonicia forbesi			×
	Echinoids			
	Echinometra vanbrunti			×
	Eucidaris thouarsi			×
	Crabs			
	Grapsus grapsus	×	×	×
	Pachygrapsus transversus		×	×
Microcarnivores (presumed) – sessile; solitary and colonial	Anemones			
	Anthopleura dowii[b]		×	
	Diadumene leucolena[b]		×	
	Gorgonians			
	gorgonian sp. 1 (pink)			×
	gorgonian sp. 2 (orange)			×
	Hydrozoans			
	Abietinaria sp.			×
	Obelia sp.		×	×
	hydroid sp. 1			×
	Zoanthid			
	zoanthid sp. 1 ("brown")		×	×
Particle feeding sessile, solitary and colonial animals	Barnacles			
	Balanus inexpectatus[b]			×
	balanomorph sp. 1			×
	Catophragmus pilsbryi		×	×
	Chthamalus fissus	×	×	×
	Euraphia imperatrix	×		
	Tetraclita panamensis		×	×
	Bivalves			
	Arca mutabilis (hole-dwelling clam)			×
	Brachidontes semilaevis (mussel)		×	×
	Chama echinata (rock oyster)		×	×
	Modiolus capax (mussel)		×	×
	Ostrea iridescens (oyster)		×	×
	Ostrea palmula (oyster)		×	×
	Plicatula penicillata (oyster)[b]		×	×
	Pinna sp.			×
	Bryozoans			
	Membraniopora sp.			×
	erect bryozoan sp. 1			×
	Gastropod			
	Hipponix sp.			×

APPENDIX 1 (continued)

Trophic status[a]	Taxon	Zone		
		High	Mid	Low
Particle feeders (continued)	Sponges			
	sponge sp. 1 ("orange")			×
	sponge sp. 2 ("lavendar")			×
	sponge sp. 3 ("black")			×
	sponge sp. 4 ("brown-ridged")			×
	sponge sp. 5 ("white")			×
	sponge sp. 6 ("red")			×
	Tunicates			
	Pyura vittata (solitary)			×
	Ascidia sp. (solitary)			×
	Rhopalea birkelandi (solitary)			×
	Amaroucium sp. (colonial)			×
	Didemnum sp. (colonial)			×
	Eudistoma pachecae (colonial)			×
	Trididemnum sp. (colonial)			×
	Protozoans			
	Homotrema sp.			×
	Polychaetes			
	Spirorbis sp.			×
	Serpula sp.[b]			×
	terebellid sp.		×	×
	sabellid sp.			×
	Vermetids			
	Petaloconchus macrophragma[b]		×	×
	Tripsycha tulipa[b]		×	×
	Vermetus contortus[b]		×	×
	vermetid sp. 1			×
	vermetid sp. 2			×
	Echinoderms			
	ophiuroid sp. 1			×
	holothurian sp. 1			×
Number of species (without fishes)		13	41	82
Number of species (with fishes)		16	50	103

[a] Trophic assignments are made using two or more of the following criteria: (1) direct observation, (2) observation by other workers, (3) gut contents, or (4) known trophic status of particular groups (e.g., barnacles are known to be suspension feeders).

[b] Identification is tentative.

APPENDIX 2

Algal species occurrence at Taboguilla Island, Bay of Panama, by taxon and intertidal zone.

		Zone		
Taxon		High	Mid	Low
Greens (erect)	*Ulva* spp.		×	×
	Enteromorpha spp.		×	×
	Cladophora spp.	×	×	×
	Bryopsis spp.			×
	Chaetomorpha sp.			×
	Cladophoropsis sp.			×
	Caulerpa botryoides		×	
	C. peltata		×	
Browns (erect)	*Giffordia* sp.		×	×
	Dictyota spp.			×
	Padina sp.			×
(encrusting)	*Ralfsia* spp.		×	×
	Mesospora sp.		×	×
	Lobophora sp.			×
Reds (erect)	*Centroceros clavulatum*			×
	Gelidiella sp.			×
	Gelidium pusillum			×
	Hypnea sp.			×
	Jania spp.			×
	Amphiroa spp.			×
	Corallina spp.			×
	Laurencia spp.			×
	Polysiphonia pacifica			×
	Polysiphonia spp.			×
	Spyridium sp.			×
	plus several unidentified species			
(encrusting)	*Hildenbrandia* spp.		×	×
	crustose coralline spp.		×	×
Blue-green (encrusting)	*Schizothrix calcicola*	×	×	×
(erect)	*Microcoleus lyngbyaceae*	×	×	

APPENDIX 3

Space occupancy by species in the high, mid, low, and very low zones at Site 6, Taboguilla Island, Bay of Panama: data are mean percent cover ±95% confidence interval; in this and Tables IV–IX, instances where the sums of means do not add up exactly to group totals are due to rounding error; *N*, number of quadrats[a].

Species	High (25 Jan. 1978)	Mid (13 Jan. 1978)	Low (25 Jan. 1978)	Very low (5 Feb. 1977)
N	10	15	15	15
ANIMALS				
Balanus inexpectatus	0	0	0.7 ± 1.0	0.2 ± 0.3
Catophragmus pilsbryi	0	t	t	0.1 ± 0.2
Chthamalus fissus	2.0 ± 2.7	0.5 ± 0.6	t	0
Euraphia imperatrix	4.1 ± 4.0	0	0	0
Tetraclita panamensis	0	0.1 ± 0.1	t	0
Total barnacles	6.1 ± 4.6	0.5 ± 0.6	0.8 ± 1.0	0.3 ± 0.3
Arca mutabilis	0	0	t	t
Brachidontes semilaevis	t	t	t	t
Chama echinata	0	t	0.6 ± 0.5	0.6 ± 0.5
Ostrea palmula	0	t	0.5 ± 0.5	0
Plicatula penicillata	0	t	t	t
Pinna sp.	0	0	0	t
Total bivalves	t	0.2 ± 0.2	1.1 ± 0.8	0.6 ± 0.5
Anthopleura dowii	0	1.5 ± 1.1	0.4 ± 0.35	0
Ascidia sp.	0	0	t	t
Diadumene leucolena	0	t	t	t
Pyura vittata	0	0	t	t
sabellids	0	0	t	0
serpulid	0	0	t	t
Spirorbis sp.	0	0	t	0
terebellid	0	t	0	t
vermetid (brown-white keel)	0	0	t	t
vermetid (gray)	0	t	t	t
vermetid (pink)	0	t	t	0
vermetid (red)	0	0	t	t
vermetid (white)	0	0	t	0.1 ± 0.3
Other solitary sessile animals	0	1.5 ± 1.1	0.4 ± 0.4	0.3 ± 0.3
SOLITARY SESSILE ANIMALS – TOTAL COVER	6.1 ± 4.6	2.2 ± 1.3	2.3 ± 1.3	1.2 ± 0.6
Abietinaria sp. (2°)[b]	0	t	0.7 ± 0.6	6.3 ± 2.5
Amaroucium sp.	0	0	t	t
encrusting bryozoan	0	0	t	0.6 ± 0.6
erect bryozoan (2°)	0	0	0	0.1 ± 0.3
gorgonian (pink) (2°)	0	0	t	t
gorgonian (orange) (2°)	0	0	t	0
Homotrema sp.	0	0	t	0
Obelia sp. (2°)	0	0	t	0
sponge (orange)	0	t	0.1 ± 0.2	t
sponge (purple)	0	t	t	0
sponge (tan)	0	t	t	0
sponge (white)	0	t	t	t
zoanthid (brown)	0	t	0	0

APPENDIX 3 (continued)

Species	High (25 Jan. 1978)	Mid (13 Jan. 1978)	Low (25 Jan. 1978)	Very low (5 Feb. 1977)
COLONIAL SESSILE ANIMALS – TOTAL COVER	0	t	0.9 ± 0.6	7.1 ± 2.9
TOTAL ANIMAL COVER	6.1 ± 4.6	2.2 ± 1.3	2.5 ± 0.8	8.0 ± 2.7
ALGAE				
blue green (fleshy crust)	0	0	0.1 ± 0.3	0
coralline crust No. 1	0	0.3 ± 0.4	3.6 ± 3.0	0
Hildenbrandia sp.	t	10.5 ± 5.0	9.7 ± 4.8	5.7 ± 4.0
other crustose corallines	0	1.8 ± 1.9	12.5 ± 6.2	20.6 ± 7.5
Ralfsia sp.	0	65.2 ± 7.7	41.5 ± 6.5	18.3 ± 9.0
Schizothrix calcicola (green phase)	0	13.6 ± 3.3	13.7 ± 7.1	13.8 ± 6.6
Schizothrix calcicola (white phase)	0	3.8 ± 1.4	8.4 ± 4.8	t
Algal crusts	t	95.7 ± 1.3	89.6 ± 3.8	53.7 ± 9.3
Bryopsis sp. (2°)	0	t	0	0
Chaetomorpha sp. (2°)	0	0	t	0
Cladophora sp. (2°)	t	0.1 ± 0.2	1.2 ± 0.8	0.6 ± 0.7
Ulva sp. (2°)	0	0	t	1.0 ± 1.3
Erect greens	t	0.1 ± 0.2	1.2 ± 0.8	1.8 ± 1.5
Dictyota sp. (2°)	0	0	t	0
Giffordia sp. (2°)	0	t	0.2 ± 0.4	0.3 ± 0.4
Erect browns	0	t	0.2 ± 0.4	0.5 ± 0.5
algal turf (2°)[c]				
filamentous red (2°)				
Gelidium pusillum (2°)	0	0	0	6.4 ± 3.3
Hypnea sp. (2°)	0	0	0.7 ± 1.0	t
	0	t	0.5 ± 0.5	0.5 ± 0.5
	0	t	t	0
Erect fleshy reds	0	t	1.3 ± 1.2	6.9 ± 3.5
Jania sp. (2°)	0	0	t	2.1 ± 1.4
Erect corallinaceous reds	0	0	t	2.1 ± 1.4
Microcoleus lyngbyaceae (blue-green)	0	0	t	0
filamentous diatoms	0	0	t	0
ERECT ALGAE – TOTAL	t	0.1 ± 0.2	2.7 ± 1.6	11.9 ± 5.3
MISCELLANEOUS				
bare	93.2 ± 4.9	0	t	0.7 ± 0.8
scar	0	1.5 ± 0.7	0.7 ± 0.4	0
dead crustose corallines[d]	0	0.1 ± 0.2	5.7 ± 3.2	18.7 ± 5.2
dead sessile animals[e]	0.7 ± 0.8	0.3 ± 0.2	0.8 ± 0.6	9.1 ± 3.6
DIVERSITY – H'	0.96	1.62	2.61	2.67
J'	0.37	0.25	0.40	0.43
S	5	29	50	34

[a] All abundances <0.1% are labelled t for trace.

[b] 2° (secondary) refers to erect organisms.

[c] Algal turf is a mixed-species turf of filamentous reds, browns and greens.

[d] "Dead" crustose corallines are white, bleached and often flake off the substratum. However, it is uncertain if all such crusts are truly physiologically dead.

[e] Most of the dead sessile animal cover is composed of attached, empty *Balanus inexpectatus* shells.

APPENDIX 4

Animal density in the high, mid and low and very low zones at Site 6 on Taboguilla Island in the Bay of Panama: data are number per 0.25 m^2 ± 95% confidence interval except where otherwise indicated.

Species	High (25 Jan. 1978)	Mid (13 Jan. 1978)	Low (25 Jan. 1978)	Very low (5 Feb. 1977)
N	10	15	15	15
SESSILE ANIMALS				
Balanus sp.	0	0	0	0.5 ± 0.5
Balanus inexpectatus	0	0	0.6 ± 0.1	3.9 ± 4.1
Catophragmus pilsbryi	0	0.1 ± 0.1	0.1 ± 0.1	1.5 ± 0.8
Chthamalus fissus	24.4 ± 34.4[a]	48.3 ± 31.6	12.2 ± 13.6	0
Euraphia imperatrix	22.0 ± 27.7[a]	0	0	0
Tetraclita panamensis	0	0.3 ± 0.4	0.2 ± 0.2	0
Total barnacles	46.4 ± 39.4[a]	48.7 ± 31.4	13.7 ± 13.2	5.9 ± 4.5
Arca mutabilis	0	0	0.4 ± 0.7	0.7 ± 0.4
Brachidontes semilaevis	0.1 ± 0.2	3.0 ± 1.9	31.0 ± 13.2	0.4 ± 0.6
Chama echinata	0	1.0 ± 0.8	6.9 ± 2.9	8.8 ± 4.6
Chama juveniles	0	0	0.1 ± 0.1	0
Ostrea palmula	0	0.5 ± 0.6	2.2 ± 1.3	0
Plicatula penicillata	0	1.3 ± 1.1	3.3 ± 1.5	0.3 ± 0.4
Pinna sp.	0	0	0	0.1 ± 0.2
Total bivalves	0.1 ± 0.2	5.8 ± 2.5	43.8 ± 12.5	10.3 ± 4.8
vermetid (brown & white)	0	0	0	0.7 ± 0.4
vermetid (gray)	0	0.1 ± 0.1	0.9 ± 0.6	0.9 ± 0.7
vermetid (pink)	0	0.1 ± 0.2	0.1 ± 0.3	0
vermetid (red)	0	0	0.9 ± 0.6	8.6 ± 5.1
vermetid (tan)	0	0	0.3 ± 0.3	0
vermetid (white)	0	0	0.2 ± 0.3	1.8 ± 1.0
terebellid	0	0.6 ± 1.0	0	0.1 ± 0.1
sabellid	0	0	0.1 ± 0.2	0
Spirorbis sp.	0	0	1.9 ± 4.2	0
serpulid	0	0	0.1 ± 0.2	0.2 ± 0.2
Anthopleura dowii	0	46.1 ± 29.6	11.1 ± 9.8	0
Diadumene leucolena	0	0.8 ± 1.4	1.2 ± 1.2	0.1 ± 0.3
Ascidia sp.	0	0	0.1 ± 0.2	1.9 ± 1.1
Pyura vittata	0	0	0.1 ± 0.2	1.5 ± 1.1
sea cucumber sp. 1	0	0.5 ± 0.8	0.8 ± 1.7	14.6 ± 7.0
sea cucumber sp. 2	0	0	0	5.2 ± 7.7
sea cucumber sp. 3	0	0	0	0.3 ± 0.6
Other solitary invertebrates	0	48.2 ± 30.0	17.9 ± 9.8	35.6 ± 6.5
TOTAL SESSILE ANIMALS (no./0.25 m^2)	290 ± 247[b]	102.7 ± 32.2	75.5 ± 23.1	51.5 ± 11.6
H'	1.02	1.55	2.73	3.18
J'	0.18	0.23	0.44	0.56
S	3	13	22	20
MOBILE ANIMALS				
Fossarus spp.	0	0	0.3 ± 0.4	0
Littorina aspera	1.1 ± 2.5	0	0	0
L. modesta	5.0 ± 4.8	0.2 ± 0.2	0	0
Nerita scabricosta	9.5 ± 8.6	0	0	0
N. funiculata	0	0.2 ± 0.3	0	0

APPENDIX 4 (continued)

Species	High (25 Jan. 1978)	Mid (13 Jan. 1978)	Low (25 Jan. 1978)	Very low (5 Feb. 1977)
Total coiled herbivorous gastropods	15.6 ± 11.5	0.6 ± 0.7	0.3 ± 0.4	0
Calyptraea sp.	0	0	0	0.1 ± 0.1
Collisella pediculus	0	0.2 ± 0.2	1.7 ± 1.2	0
Fissurella virescens	0	2.2 ± 2.5	13.8 ± 4.3[c]	7.8 ± 4.2
F. longifissa	0	0	0[c]	1.3 ± 0.8
Scurria stipulata	0	0.8 ± 0.7	0.1 ± 0.2	0.1 ± 0.2
Siphonaria maura	0	0.9 ± 0.5	9.5 ± 4.4	0
S. gigas	0	6.9 ± 2.7	0	0
S. gigas juveniles	0	0.7 ± 0.6	0	0
S. palmata	0	0	0	13.7 ± 8.4
Total limpets	0	11.7 ± 4.4	25.1 ± 7.2	23.1 ± 9.0
Acanthochitona hirudiniformis	0	0.2 ± 0.4	1.6 ± 0.8	0
Ceratozona angusta	0	0	1.2 ± 1.1	0.8 ± 0.6
Chiton stokesii	0	0.1 ± 0.1	0.1 ± 0.1	0
Tonicia forbesi	0	0	0	0.9 ± 0.4
Total chitons	0	0.3 ± 0.4	2.9 ± 1.1	1.9 ± 0.9
Diadema mexicanum	0	0	0	0.1 ± 0.1
Echinometra vanbrunti	0	0	0.3 ± 0.3	29.0 ± 5.6
Eucidaris thouarsi	0	0	0	0.9 ± 0.8
Total sea urchins	0	0	0.3 ± 0.3	29.9 ± 5.7
Pachygrapsus transversus	0	0.6 ± 0.5	2.5 ± 0.9	4.7 ± 1.6
TOTAL HERBIVORES	15.6 ± 11.5	13.1 ± 4.5	31.0 ± 7.4	59 ± 11.6
Acanthina brevidentata	0	0.3 ± 0.3	0.1 ± 0.2	2.4 ± 1.4
Conus princeps	0	0	0	0.1 ± 0.2
C. nux	0	0	0	0.2 ± 0.2
Leucozonia cerata	0	0	0	0.2 ± 0.2
Opeatostoma pseudodon	0	0	0	0.6 ± 0.3
Thais melones	0	0.1 ± 0.1	0.7 ± 0.9	5.3 ± 1.5
T. triangularis	0	0	0.3 ± 0.4	1.7 ± 0.6
Total coiled predaceous gastropods	0	0.4 ± 0.5	1.2 ± 1.2	10.5 ± 2.8
Eriphia squamata	0	0.1 ± 0.1	0.1 ± 0.2	0
Hermit crab	0	0	0.1 ± 0.3	0
Nudibranch sp. 1	0	0	0	0.4 ± 0.4
Nudibranch sp. 2	0	0	0	0.2 ± 0.2
Ophiuroids	0	0	0	0.2 ± 0.3
Trichadiella sp. (nudibranch)	0	0	0	0.1 ± 0.3
TOTAL MOBILE ANIMALS (no./0.25 m^2)	15.6 ± 11.5	13.6 ± 4.7	32.5 ± 7.1	91.2 ± 13.0
H'	1.23	2.23	2.38	2.77
J'	0.31	0.60	0.47	0.45
S	3	13	15	22

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[a] Number per 0.04 m^2.

[b] Barnacle densities adjusted to no./0.25 m^2 in this calculation.

[c] The value for *Fissurella virescens* on this date includes individuals of both *F. virescens* and *F. longifissa*, which were not distinguished in this sample. An indication of their relative abundances is given by data from a sample taken on 19 Aug. 1978. On this date, density of *F. virescens* was 11.8 ± 2.8 and that of *F. longifissa* was 3.2 ± 1.9.

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