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COMMUNITY ORGANIZATION IN TEMPERATE AND TROPICAL ROCKY INTERTIDAL HABITATS: PREY REFUGES IN RELATION TO CONSUMER PRESSURE GRADIENTS¹

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Abstract. The structure of a tropical rocky intertidal community on Taboguilla Island on the Pacific coast of Panama is characterized by extremely low abundances of noncrustose algae and sessile animals, indistinct vertical zonation patterns (a result of the low abundances), and the occurrence of most invertebrates (except barnacles) and upright algae in holes and crevices (as opposed to open, smooth surfaces). This contrasts strikingly with two temperate rocky intertidal communities, which have high covers of plants and animals, more obvious zones, and invertebrates and upright algae occurring both on relatively homogeneous surfaces and in holes and crevices.

Field experiments were done and observations were made in the Panama community to test the effects of different types of consumers (both predators and herbivores) on their prey and on the types of escapes utilized by the prey. Consumer exclusion experiments suggest that (1) predation and herbivory are severe at all times of the year, (2) consumer pressure is a cumulative function of many types and species of predators and herbivores, (3) the primary effect of larger fishes and crabs is to restrict most prey to three-dimensional refuges (holes and crevices), and (4) the primary effect of smaller consumers, mostly invertebrates, is to keep abundances of the prey low.

Thus, in the Panama system, three-dimensional space (holes and crevices) appears to be particularly important as a refuge from consumers, while escapes from consumers in body size, time, or two-dimensional space (e.g., in a higher zone) documented so frequently in temperate areas, assume secondary importance for many prey. This restriction of the types of escapes utilized by prey species appears to be a consequence of two main factors: the presence of fast-moving consumers (i.e., herbivorous and predaceous fishes and herbivorous crabs which are absent or rare in the two temperate communities), and the year-round foraging of all consumers.

Key words: algae; barnacles; bivalves; community structure; consumer pressure; fishes; gastropods; herbivory; predation; refugia; rocky intertidal; temperate vs. tropical; zonation.

INTRODUCTION

Differences in community structure over geographical space have long been a major concern of ecologists. Though variations in species diversity are perhaps the most striking differences and have certainly received the most attention, other aspects of community structure, including space utilization patterns, species composition, trophic structure, and body size structure can also vary. Indeed, Osman and Whitlatch (1978) argue that geographical patterns of species diversity may often be simple artifacts of the shape of the earth and the configuration of the continents and oceans, and therefore other aspects of community structure should be the real focus of geographical ecologists. Though we do not entirely agree with this viewpoint, we do feel that closer attention needs to be paid to broad-scale variations in aspects of community structure other than species diversity. For example, studies in rocky intertidal regions (e.g., Paine 1966, 1974, Dayton 1971, Menge 1976, Lubchenco and Menge 1978) suggest that patterns of space utilization and size structure can reflect the operations of important organizing agents within the community, thus of-

¹ Manuscript received 17 March 1980; revised 4 February 1981; accepted 18 February 1981.

fering a potentially useful tool to ecologists interested in understanding broad-scale patterns of community structure. Specifically, our studies in the New England rocky intertidal region suggest that much of the spatial structure of local communities depends on spatial and temporal escapes from predators and herbivores (e.g., Menge 1976, 1978a, b, Lubchenco 1978, 1980, Lubchenco and Menge 1978, Lubchenco and Cubit 1980). Furthermore, these escapes seem easily attained since predation and herbivore pressure in New England appear highly variable, most likely in response to a highly variable physical environment and the relatively few types of consumers (predators, herbivores, and omnivores) in the system (works cited above; Menge 1982). The escapes include both coexistence and noncoexistence refugia; i.e., prey occur in subhabitats which are accessible and not accessible, respectively, to consumers.

In the Pacific Northwest, the probability of escaping from consumers seems lower than in New England. Paine (1966) and Dayton (1971) found that noncoexistence spatial refugia (i.e., the high to mid intertidal mussel zone) were almost the only ones available to the prey species. The only well-documented coexistence refuge achieved by sedentary animals is the escape in large size occasionally achieved by *Mytilus* californianus (Paine 1976). Dayton (1975) suggests that many species of benthic algae achieve a coexistence refuge in size with molluscan herbivores, but that no upright (vs. crustose) algal species could escape dense concentrations of sea urchins. Since sea urchin density varies markedly over space (due in part to the patchy distribution of their predator, *Pycnopodia helianthoides*), low zones in this region are characterized by lush stands of patchy, diverse, and asynchronously developing beds of algae. Thus, consumer pressure appears both greater and less variable, and escapes fewer and less frequent, in the Pacific Northwest system. This may be because there are more species and types of both predators and herbivores.

In this paper, we extend this comparative and experimental evaluation of patterns of consumer pressure and prey escapes to a tropical rocky intertidal community located in the Bay of Panama. First, we document several striking differences in community structure between the temperate and tropical systems. Second, we offer experimental evidence supporting the notion that consumer pressure is severe in the tropical community. Third, we present experimental evidence on the changes in prey abundance and refuge utilization and abundance in response to artificial variations in local consumer pressure in the tropical community. The results suggest that refugia for sedentary species in at least this tropical community are greatly restricted by consumers. Finally, we discuss the implications of these results and other indirect evidence to broad-scale patterns of community structure. The data available suggest that variations in consumer pressure on both local and geographic scales explain a large proportion of the striking differences in community structure and patterns of refuge use observed both within and between the temperate and tropical communities.

STUDY AREAS

Data on patterns of community structure in the New England and Pacific Northwest rocky intertidal communities reported below are extracted from previously published sources (Paine 1966, 1974, Dayton 1971, 1975, Menge 1976, Lubchenco and Menge 1978). Specific study locales in New England include sites in the central coasts of Massachusetts and Maine. Sites in the Pacific Northwest are located in the vicinities of Cape Flattery and the San Juan Islands, Washington State (works cited above).

The tropical study sites are located in the Bay of Panama. The primary study site is on the southern shores of Taboguilla Island, which is 15 km south of the Pacific terminus of the Panama Canal. Secondary sites are the southern shores of Flamenco and Chitre Islands. Flamenco Island is the southernmost of a group of four islands which are at the Pacific mouth of the Panama Canal. These islands are connected to the mainland at the eastern side of the canal opening by a 2 km long breakwater. Chitre Island is located in the northern part of the Perlas Archipelago, ≈ 45 km southeast of the Panama Canal. Finally, casual observations have been made at two mainland sites, Paitilla Point and San Francisco Beach; and on Taboga Island, a larger island 1 km west of Taboguilla Island, and Naos Island, an island neighboring Flamenco Island. More quantitative information on some aspects of community structure in the mid zone are available for Paitilla Point in Reimer (1976*a*, *b*), and Southward and Newman (1977) mention patterns of barnacle distribution on the mainland and offshore islands in the Bay of Panama.

Some general physical characteristics of the Bay of Panama include the following: The tidal excursion is ≈ 6 m, compared to 3–4 m along the temperate coasts of North America. These habitats are thus comparable in the sense that all experience regular patterns of tidal fluctuation. Two seasons occur in the Panama region, a dry season (December to April) and a wet season (May to November; Glynn and Stewart 1973, Glynn 1976). Generally, the dry season is characterized by relatively strong northeast trade winds (up to 30-40 km/h), relatively low humidity, clear skies, and relatively calm seas with occasional but unpredictable periods of upwelling on the south shores of land masses (Glynn and Stewart 1973). The wet season is typified by variable winds, high humidity, variable sky cover, frequent torrential downpours, and variable seas. Southerly swells are occasionally quite severe (reaching 3-4 m) in the wet season. Sea temperatures range from a mean of 26°C (dry season) to 29°C (wet season); daily air temperatures range between 22° and 34°C year-round.

Macroscopic organisms in this community are typical of those in other rocky intertidal habitats and include gastropods, bivalves, barnacles, echinoids, asteroids, phaeophytes, rhodophytes, and chlorophytes as major components. These organisms occur in three regularly emersed zones: high, +4.6 to +6.4 m; mid, +2.4 to +4.6 m; and low, +0.6 to +2.4 m. A fourth, still lower zone, -0.85 to +0.6 m, is exposed only during the dry season when the most extreme low tides occur.

Methods

The methodology we use to quantify community structure in rocky intertidal communities is given in Menge (1976) and Lubchenco and Menge (1978). Briefly, percent cover of all sessile biota is determined using a flexible, clear vinyl quadrat with 100 dots plotted on it at random. Mobile and solitary sessile animals are also counted in each quadrat or treatment. Mean abundances are determined in each zone in 10–15 quadrats, each 0.25 m² in area. Similar techniques were employed by Dayton (1971, 1975), and the data from the temperate and tropical communities thus provide comparable quantifications of patterns of space

utilization (presented as percent cover) and abundance (numbers per square metre) of both the sessile and mobile biota.

In January 1977, we initiated experiments designed to sort out the roles of four consumer groups singly and in most combinations of two, three, or four groups. To exclude rapidly moving consumers such as fishes and crabs, we used stainless steel mesh (1-cm openings) cages or roofs (two sides open) which were $0.5 \times 0.5 = 0.25$ m² in area and 5 cm high. The more sluggish mobile invertebrates were manipulated using manual removals. We focused on groups of predator and herbivore species, rather than individuals, because of the immense difficulty of separating the effects of a single species from those of the other six to 22 commonly occurring species of consumers. The consumers were categorized according to their sizes, mobilities, manner of feeding, and diet composition into rough "functional" consumer groups. The groups whose effects we examine here are slow-moving predators (e.g., coiled predaceous gastropods, and sea stars), slow-moving herbivores (coiled gastropods, limpets, and chitons), large fishes (e.g., benthos-feeding fishes which are too large to forage in the 5-cm gap between roof and substratum), and small fishes and crabs (e.g., small, bottom-sitting fishes and crabs capable of foraging under roofs).

The experimental design involved removals of slowmoving herbivores, slow-moving predators, or both from three semi-isolated reefs. A fourth reef was selected as a control for these manipulations. On each reef, we established four control quadrats, two to four roofs, and two to four cages in the high, mid, and low zones. The sites for each replicate were selected to be as typical as possible. No attempt was made to clear each site of upright algae or sessile animals, as these were essentially already absent in most replicates (i.e., they occupied between 0-5% of the space; see Fig. 3). With one exception, this design allows us to separate out the effects of individual consumer groups (e.g., large fishes are excluded from roofs on the control reef, other species have access to this treatment); pairs of consumer groups (e.g., large fishes and slow-moving herbivores are excluded or removed from roofs on the slow-moving herbivore removal reef); sets of three consumer groups (e.g., slow-moving predators, large fishes, and small fishes and crabs are excluded or removed from cages on the slow-moving predator removal reef); and sets of four consumer groups (all consumers are removed or excluded from cages on the slow-moving predator and herbivore removal reef). The exception is the small fishes-crabs group, which we could not exclude as a single group without also excluding large fishes. In practice, exclusions were often just significant reductions and not total exclusion of individuals in a group, since small individuals often entered exclusion treatments. These small individuals were removed as often as possible, usually one to two

times monthly. Finally, several species of small-bodied consumers were not manipulated. These included several species of opisthobranchs and probably most importantly, the small (≤ 2 cm in carapace diameter), omnivorous crab *Pachygrapsus transversus*. Of these, only the latter seems abundant enough to have a potentially significant impact on our results. However, this small crab was present in all treatments, though sometimes in varying densities. Unfortunately, the possible effects of varying numbers of *Pachygrapsus* cannot be evaluated at present.

In addition to excluding fishes and crabs, cages and roofs may have undesirable side effects such as shading or alteration of microcurrents. We designed experiments to evaluate the importance of these secondary effects. The rationale for these experiments is expressed below in terms of shading effects but could apply to water movement effects as well. An increase in roof mesh size, from the standard 1-cm openings used in other experiments to 2.5-cm openings, should allow more light into the treatment while still excluding large fishes. If increases in percent cover of animals or algae under normal size mesh roofs are due exclusively to reduced desiccation stress in the shade of the mesh (we assume that changes in light intensity are too small to change rates of algal photosynthesis) then the larger mesh opening should result in smaller changes in percent cover.

In January 1979, we set up roofs with 1-cm and 2.5cm mesh openings, but the same gauge wire, at four sites in the low zone in the immediate vicinity of the experimental and control reefs on Taboguilla Island. We removed both slow-moving herbivores and predators from each treatment and from a 2-m wide band surrounding the treatment. Thus, the experiments were comparable to roof exclusions on the slow-moving herbivore and predator removal reef. The experiment was monitored in January, March, and May 1979, which is the period of greatest algal settlement and growth. The analysis in Table 1 is done on data from January and May (i.e., beginning and end of the experiment).

The data from this short-term experiment suggest that shading by the 1-cm mesh probably does not alter desiccation stress much below natural levels. Changes in free space, algal cover, solitary and colonial sessile animals, and total plant and animal cover in standard and large-opening mesh treatments are not statistically different (Table 1). Declines in mean free space availability in both standard and large-opening mesh from 71 to 65% (standard) and from 86 to 65% (large) were not statistically significant (Table 1). Further, though increases in abundances of animals and upright (vs. crustose) algae generally occurred in both mesh sizes from January to May, none of these increases was significant (Table 1). Note that both the decline in free space and the concomitant increase in total plant and animal cover (under standard mesh, 30 to 37%; under

TABLE 1. Results of two-way ANOVA of shade experiments evaluating effect of mesh size (see text) and time (January vs. May 1979).

		F value*	
Category	Mesh size	Time	Inter- action
Free space [†]	0.65	2.91	0.92
Algae = secondary cover‡	0.19	3.84	4.02
Solitary sessile animals§	0.84	0.98	0.97
Colonial sessile animals ¹¹	0.25	0.11	0.29
Total animal and plant cover	0.35	1.78	0.39

* Critical F value = 4.75 (df = 1,12; α = .05). None of the F's is significant. N = 4. Analyses performed on arcsine-transformed percent cover data.

† Defined as bare rock and space occupied by live and dead encrusting algae.

‡ Secondary algae include primarily opportunistic greens and browns such as *Cladophora* sp., *Enteromorpha* sp., *Ulva* sp., and *Giffordia* sp. *Jania* (a red corallinaceous alga); filamentous blue-green algae were also relatively common.

§ Includes barnacles, oysters, mussels, vermetids, anemones, solitary tunicates, and sedentary polychaetes.

"Includes sponges, hydroids, colonial tunicates, and ectoprocts.

 \P Includes secondary algae, solitary and colonial sessile animals.

large mesh, 19 to 37%) were actually greater in the large-opening roofs than in the standard opening roofs. If a decrease in desiccation by increased shading had led to our experimental results rather than to consumer exclusion, we would expect the opposite effect to occur. We do not mean to suggest here that physical stresses such as desiccation are unimportant to the organisms, but simply that our normal mesh exclosures do not appear to alter the normal physical regime by a substantial amount, at least in the low zone.

PATTERNS OF COMMUNITY STRUCTURE

Space utilization

Space occupancy patterns in the intertidal region are comparable to those in a forest. Primary space is on the rocky surface itself (i.e., like the surface of the ground), understory space is that used by short (1-5 cm) shrubby algae, colonial hydroids, and bryozoans (like shrubs), and canopy space is space occupied by taller (≥ 5 cm tall) algae (like the canopy trees). Detailed descriptions of patterns of community structure in the two temperate regions over both space and time are available in Dayton (1971, 1975), Paine (1974), Menge (1976), and Lubchenco and Menge (1978). Detailed descriptions of patterns of community structure in the tropical region will be presented in later publications. For comparative purposes, characteristic patterns of community structure in these three communities abstracted from the above-cited studies are summarized in Table 2 and Fig. 1. We emphasize that most of our experimental and observational efforts in Panama have been concentrated on one site, namely the Taboguilla Island area. However, we have examined several other sites in the Bay of Panama (see above). When patterns or results appear to apply to most sites we have seen in the Bay of Panama region, we so state. Otherwise, most comments refer to the Taboguilla study sites.

In New England, wave-exposed sites are typified by low space availability, a low cover of large algae in all but the low zone, and dense covers of barnacles and mussels (e.g., Table 2, Fig. 1). Of all the sites summarized in Table 2, patterns of community structure in the mid and low zones at wave-exposed sites in New England such as Pemaquid Point are the most seasonally variable (e.g., Menge 1976, Lubchenco and Menge 1978). Thus, in most winters, much of the mussel cover in the mid and low zones is markedly reduced by severe wave shock during storms. Barnacles settle densely in these zones in spring and may dominate space for 2-4 mo until they are outcompeted by mussels again in midsummer. Mussels then dominate space for 5–7 mo (until December to February) when they are again usually decimated. At such sites, escapes from predators in space, time, and probably size appear to be readily achieved.

Sites protected from wave action in New England characteristically have relatively high space availability in all but the low zone, high covers of algae, and relatively low covers of sessile animals (Table 2, Fig. 1). Seasonal variation is low (Menge 1976, Lubchenco and Menge 1978) and predation and herbivory have major impacts on community structure. Protected sites are usually typified by structural dominance by single species of large, long-lived fucoid algae (Table 2); this appears to result from competitive exclusion of other algae by these fucoids (Schonbeck and Norton 1980). An important consequence of the greater consumer pressure as compared to exposed sites is a reduction in the chances of escapes in time and space by prey species, although the larger algae still readily achieve refuges from the herbivores in large size or a size-related characteristic (Lubchenco and Menge 1978).

In Washington, as in New England, wave-exposed sites are typified by low space availability and in all but the low zone, low covers of algae, and dense covers of sessile animals (mostly mussels; Dayton 1971, 1975, Paine 1974, Table 2, Fig. 1). Seasonal changes occur at exposed sites but the levels of mussel decimation seen in New England are usually greater than in Washington (R. Paine, *personal communication*, authors' *personal observations*). Escapes in space and time but not size are achieved by some animal prey at exposed sites (Paine 1976). The large algae may achieve refuges in space, time, and also in size (Dayton 1975).

Protected sites in Washington usually have high space availability, low to moderate covers of algae, and low covers of sessile animals (Dayton 1971, 1975,

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			New F	England*	Washir	ngton†	Pana	ma‡
Characteristics	Tidal level		Exposed (Pemaquid Point)	Protected (Canoe Beach Cove)	Exposed (Tatoosh Island)	Protected (Colin's Cove)	Exposed (Taboguilla Island)	Protected (Flamenco Island)
Space availability	High		10.4 ± 6.8	50 ± 9.5	Unshaded $3.6 \pm$	97.3 ± 2.4	97.2 ± 1.6	67.5 ± 18.2
(percent cover of free space)§	Mid		25.0 ± 15.7	89.6 ± 6.6	Unshaded 9.0 \pm	27.2 ± 9.0	98.0 ± 1.6	65.2 ± 17.9
	Low		0.3 ± 0.5	7.5 ± 4.2	Shaded 3.8 ± 3.6 Unshaded 5.8 ± 11.1	53.5 ± 11.4 65.5 ± 25.8	98.3 ± 1.1	76.7 ± 8.5
Algal canopy ["]	High	Species	None	Ascophyllum	Postelsia	Fucus	None	None
(percent cover)		Cover	0	nodosum 84.0 ± 8.9	$palmaeformis 4.0 \pm 6.4$	$distichus 6.5 \pm 5.7$	0	0
	Mid	Species	F. distichus	A. nodosum	P. palmaeformis	F. distichus	Filamentous	Filamentous
		Cover	3.3 ± 3.3	94.2 ± 6.3	6.9 ± 8.1	53.5 ± 10.7	algae 0.01 ± 0.01	algae 0.7 ± 1.6
	Low	Species	Alaria	Chondrus	Lessoniopsis	None	Filamentous al-	Filamentous al-
		Cover	$esculenta \\ 44.4 \pm 17.4$	$\begin{array}{c} crispus\\ 91.2 \pm 4.1 \end{array}$	littoralis 62.3 ± 8.9	0	$gae 0.1 \pm 0.08$	$gae_{8.0 \pm 5.5}$
Most abundant	High	Species	Balanus	B. balanoides	Mytilus	Balanus glan-	Chthamalus	C. fissus
occupant of primary space		Cover	balanoides 85.0 ± 6.9	30.7 ± 10.6	californianus 61.1 ± 26.8	$\begin{array}{c} dula\\ 2.0 \pm 1.8 \end{array}$	fissus 1.3 ± 1.0	32.1 ± 18.1
4	Mid	Species	Mytilus edulis	Encrusting algae	M. californianus	Fugitive algal	Encrusting algae	Encrusting
		Cover	64.3 ± 13.4	64.4 ± 24.6	5 3.7 ± 20.7	species 19.3 ± 5.8	80.9 ± 1.1	algae; C. $fissus$ 55.3 \pm 17.3; 30.5 \pm 17.5
	Low	Species	M. edulis; B.	Chondrus crisp-	Algal holdfasts	Fugitive algal	Encrusting algae	Encrusting
·		Cover	balanoides 57.8 ± 21.5; 37.4 ± 23.4	us holdfasts 84.9 ± 5.6	÷	species 34.7 ± 25.6	89.6 ± 6.9	algae; Ostrea spp. 60.3 ± 7.0; 22.0 ± 10.0
* Data here and at t August 1974. See Meny † Data taken from Dr mid at Tatoosh Island i in heights of high and m	he other ge 1976, ayton 15 is 1.83-2	r sites are Lubchen 971 (Table 2.45 m (6- s are due	e \bar{x} and 95% cl. L ico and Menge 19 e 1) and Dayton 19 -8 ft); and at Colii to the uplifting eff	Data from Pemaquid 78, and Lubchenco 975 (Table 4). High o n's Cove 0.61–1.22 ect that near-continu	Point were taken 1980 for further de at Tatoosh Island m (2–4 ft); low at uous wave surge h	July 1974; those etails of communit is > 3.05 m (10 ft) both sites is -0.6 as on zones at way	from Canoe Beach y structure at these) and at Colin's Co 1 to $0 \text{ m} (-2 \text{ to } 0 \text{ fr})$ e-exposed sites. N	Cove were taken : and other sites. ve > 1.83 m (6 ft); .). The differences = 10–30 quadrats
per zone. Dash under / ‡ Data were taken in	Algal ho Januar	y 1977 at	eans no data are a Taboguilla Island	available. and January/Februs	ary 1978 at Flamer	nco Island. $N = 1$	0 quadrats in all bu	it the mid and low

most free space is bare rock; in the low zone most free space is on surfaces covered with encrusting algae. The assumption that nonbare rock surfaces are available for settlement is based on the fact that we commonly observe recruitment by barnacles, oysters, algae, and other organisms on these surfaces. This assumption is currently being tested; preliminary results suggest that at least algal settlement is actually inhibited, though not prevented, by the crustose algae in the low zone. "Note that *Chondrus crispus* in New England and the filamentous red, brown, and green algae in Panama are not true canopy species but rather are "Note that *Chondrus crispus* in New England and the filamentous red, brown, and green algae in Panama are not true canopy species but rather are "Understory" species. They are listed here because they are not overtopped by taller algae. The encrusting algae, "algal holdfasts," and "fugitive algal species" categories all include several species. They are listed here because the added detail would be confusing and is unnecessary for the purposes of this paper. § Free space includes surfaces which are bare rock, or covered with encrusting algae or the remains of dead barnacles or oysters. In the high zone, wnere zones at Laboguilla,

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FIG. 1. Photographs of marine rocky intertidal areas. Code to abbreviations: H = high, M = mid, and L = low zone regions at each site. A. Wave-exposed shore at Pemaquid Point, Maine. Note high cover and sharply defined zones of *Balanus balanoides* (barnacle; H), *Mytilus edulis* (mussel; M and L), and *Alaria esculenta* (kelp; L). Consumers have no effect at this site. B. Wave-protected shore at Little Brewster Cove, Little Brewster Island, Massachusetts Bay, Massachusetts. Note high covers and sharply defined zones of *B. balanoides* (H), *Fucus vesiculosus* and *Ascophyllum nodosum* (fucoid algae; M), and *Chondrus crispus* (L). Predators (*Thais lapillus*) determine the lower limit of the barnacle zone; herbivores (*Littorina littorea*) affect only the ephemeral algae. C. Wave-exposed shore on Tatoosh Island, Washington State. Note high covers and sharply defined zones of *Balanus glandula* and *Chthamalus dalli* (barnacles; upper H), *Iridaea cornucopia* (a red alga; lower H), *Mytilus californianus* (mussels; upper M), and various algae and sessile animals (L). Predators (*Pisaster ochraceus*) determine lower limit of mussels; herbivores affect abundance of algae. D. Wave-exposed site on the south shore of Taboguilla Island, Bay of Panama, Panama. Note near-barren aspect of shore and diffuse zones. White appearance of low zone is due to high cover of encrusting coralline algae.

Table 2, authors' *personal observations*). Pressure from consumers, especially herbivores, seems higher at protected sites as does desiccation stress (Dayton 1971, 1975). Presumably as a consequence of these stronger sources of mortality, few escapes by both animal and algal species occur in size, space, or time (e.g., Dayton 1971, Paine 1976).

At our sites in Panama, different relative exposures to wave shock also occur but the wave energy at the exposed sites seems considerably less (though still well worthy of respect) than in temperate regions. Wave shock thus presumably has lesser direct and indirect effects on community structure at the tropical region than at the temperate regions. Community structure at Taboguilla Island, the relatively exposed site, is characterized by an apparently high space availability, low cover of upright algae, a low cover of sessile animals and a high cover of encrusting algae (Table 2, Fig. 2). Flamenco Island, the more protected site, has a lower (but still high) level of space availability, a low cover of algae, a moderate cover of sessile animals, and in the mid and low zones, a high cover of encrusting algae (Table 2).

The temperate communities thus differ from the tropical community in several striking ways. First, compared to the relatively high sessile animal and upright algal abundances in the temperate communities, these organisms are generally very scarce in the zones discussed at Taboguilla Island and do not form a solid cover (Table 2). Sessile animals are denser at Flamen-co Island but upright algae are also virtually absent from this site. At other sites in Panama, higher covers of barnacles (*Tetraclita panamensis* at Punta Paitilla; Reimer 1976a, b, authors' personal observations), oysters (Ostrea spp. at Naos Island and on vertical walls on offshore islands; authors' personal observa-

tions), and upright algae (a 1-3 cm high mat or turf of filamentous reds, browns, and greens at Chitre Island and small patches on Taboguilla and Taboga Island; authors' personal observations, S. Gaines, personal communication) do occur. However, to us as observers trained in temperate areas, most shores in the Bay of Panama appear barren. The almost total absence of any plants longer than ≈ 10 cm (e.g., genera of canopyforming macroalgae such as Fucus, Ascophyllum, Hedophyllum, Laminaria, Lessoniopsis, Postelsia, and Alaria) is especially conspicuous.

Second, due to the low abundances of the noncrustose sessile biota, zonation appears far less distinct on Taboguilla Island than in either temperate region when viewed from distances $>\approx 5$ m. Though close inspection at Taboguilla and other sites reveals that specific species do tend to be located in specific zones, the sharply defined zones so characteristic of temperate areas seem less evident in the Bay of Panama (Fig. 1).

Third, encrusting algae are far more prominent as a space occupant at the Panama sites than at any temperate site except the mid zone at the protected site in New England (Table 2).

Finally, mussels, which are the dominant sessile animals in mid and low zones at the temperate sites, are not dominant at the Panama sites. Rather, when a spatial dominant can be said to occur, the small (up to 1 cm in diameter) *Chthamalus fissus* and the larger oysters *Ostrea palmula* (up to 4 cm in diameter), *O. iridescens* (up to 16 cm in diameter), and *Chama echinata* (up to 6.5 cm in diameter) are the most abundant sessile animals (Table 2). The significance of this replacement of mussels by barnacles and oysters lies in the competitive dominance of mussels over co-occurring animal and plant species in most temperate regions (e.g., Hoshiai 1960, 1961, 1964, Paine 1966, 1971, 1974, Menge 1976, Lubchenco and Menge 1978, Peterson 1979). We return to this point in the Discussion.

Community structure and microhabitat occupancy

Upon our first examination of this system in 1973, we observed that most organisms occurred in the holes, crevices, depressions, and cracks in the primarily basaltic substratum, and except for limpets, barnacles, and oysters, few animals occurred on



FIG. 2. A. Band of barnacles (primarily *Chthamalus fissus*; arrows) which appeared subsequent to removal of *Thais melones* and *Acanthina brevidentata* in the high intertidal of Taboguilla Island. B. Nearby control site. Note the normal absence of a barnacle zone. Arrows indicate approximate height of barnacle zone observed in A.

smoother, more homogeneous surfaces. To quantify this pattern, microhabitat occupancy was determined for both mobile and sessile invertebrate species by noting the microhabitat of all individuals of each species in a survey of mid and low zones (Table 3). Microhabitats were distinguished subjectively by the relative degree of protection that they appeared to offer from large, fast-moving consumers, primarily fishes and crabs. Subjective, rather than objective, evaluations were made because the degree of protection afforded by a microsite appears to be a function of the

TABLE 3. Relative percentages of solitary intertidal invertebrates in different microhabitats in the mid and low zones on the unmanipulated reef. Degree of protection from fast-moving consumers increases from left to right.

Organisms	Exposed	Crack	Depression	Crevice	Hole	N
Barnacles (four species)	69	2	20	0.3	9	381
Bivalves (three species)	14	6	12	29	39	197
Limpets (six species)	4	4	49	8	35	701
Chitons (three species)	1	2	1	43	52	90
Predaceous snails (four species)	11	3	15	15	56	357
Total (except barnacles)	7	3	32	16	43	1335

size and morphology of the organism. For example, to an individual of the small, relatively flat barnacle *Chthamalus fissus*, a small, shallow depression probably offers greater protection than it would to similarly sized individuals of *Balanus inexpectatus*, which are taller. The latter individuals should thus experience a great risk of being bitten or scraped off the surface, while a similar bite or scrape might pass over the flatter *Chthamalus*.

We therefore recognized five microhabitats in order of increased protection from large fast-moving consumers: open surfaces (=exposed to consumers), cracks, depressions, crevices, and holes. Open surfaces were unbroken, flat, homogeneous substrata or convexities on heterogeneous surfaces. Cracks and depressions in the rock presumably afforded some protection to small inhabitants but usually at least part of the organism extended out of the microhabitat. Crevices and holes were deeper microhabitats from which neither large nor small organisms extended. Large fishes were presumed to be unable to enter the latter two microhabitats. Small fishes and crabs could enter the larger or wider of these microhabitats but foraging in them is probably difficult due to the close confines of many of the crevices, holes, etc. Predaceous and herbivorous gastropods had access to all such habitats and indeed, most gastropods occurred primarily in holes and crevices (Table 3).

Except for barnacles, 69% of which occur on open surfaces, most individuals of most invertebrate species occur in cracks, depressions, crevices, and holes as opposed to open, more homogeneous substrata (Table 3). As will be discussed later, these patterns hold for most conditions of tide (high or low) and time (day or night). Thus, most of the benthic biota typical of open surfaces in temperate rocky intertidal regions (e.g., limpets, chitons, bivalves, predaceous snails), are at least partially hidden in surface heterogeneities at Taboguilla.

In summary, major differences in several patterns of community structure occur between the two temperate communities and the tropical community. Relative to the temperate sites, abundances of epibenthic invertebrates and plants are low, zones seem more poorly defined, and large algae are completely absent. In strong contrast to temperate regions, where both animals and plants are abundant on both homogeneous surfaces and in holes and crevices, the majority of invertebrate species (except barnacles, limpets, and oysters) and upright algae occur primarily in crevices, holes, and other substratum irregularities on Taboguilla Island.

Evidence for a Gradient in Consumer Pressure

The sources of these temperate-tropical differences in structure are suggested by comparing the physical environments and organizations of the two temperate systems. The New England community occurs in a highly variable environment (e.g., Menge 1978a). Seasonal variations in air temperature range from frequent, severe winter freezes to summer heat waves during which temperatures $>30^{\circ}$ C are often reached. Seas can change from flat calm to 7 m high within a day in any season. As noted earlier, predation and herbivore intensity are greater and have more important effects on community structure at wave-protected coves as compared to wave-exposed headlands (Menge 1976, 1978a, b, Lubchenco 1978, Lubchenco and Menge 1978). Predators have no influence at wave-exposed sites, and an increasingly strong controlling effect as protection from wave shock increases. However, as noted earlier, both coexistence and noncoexistence escapes from predators are frequent, even at protected sites (Menge 1976, Lubchenco and Menge 1978). Herbivores (primarily gastropods) are even less effective than predators in controlling their food. Algae in this community have effective spatial, temporal, size, mechanical, and chemical escapes from the herbivores and thus become dense (Lubchenco 1978, 1980, Lubchenco and Cubit 1980, Geiselman 1980). Temporal escapes (i.e., settlement and growth of the animal prev or algae during the winter when consumers are inactive) appear common and particularly important. The physical environment in New England is thus characterized by high temporal variation which presumably leads indirectly to some of the refuges enjoyed by the biota in this system.

In contrast, the physical environment in the Pacific Northwest is characterized by seasonal but less variable and more predictable changes in wave shock and temperatures. Heavy seas and storms usually occur primarily during winter, while during summer, gentle swells and relatively mild weather generally prevail. In comparison to New England, this community seems characterized by greater predation intensity, a larger percent cover of free space at protected sites, less frequent escapes from consumers, and a greater species richness (Paine 1966, 1974, 1976; Dayton 1971, 1975; Table 2). The activities of predaceous sea stars and herbivorous sea urchins and limpets have been shown to be particularly important in affecting the structure of this community (Paine 1966, 1974, 1976, Paine and Vadas 1969, Dayton 1971, 1975).

Finally, the physical environment in Panama, though still distinctly seasonal, appears to be least variable of the three systems. Water and air temperatures are always relatively high throughout the year (see above). The seasons differ in rainfall patterns, with frequently heavy tropical downpours occurring almost daily from May to November and very little rainfall from mid-December through March (Glynn and Stewart 1973). In our experience patterns of wave shock severity are correlated with these rainfall patterns. Wave shock (from lengthy oceanic swells) in the wet season is variable but often severe at oceanfacing sites. In the dry season, wave shock at oceanfacing sites is minimal.

We suggest that the two temperate systems are the first two points along a gradient of environmental stability and predictability with the Bay of Panama system as a third point. We further contend that the gradient in community structure noted in the previous section is paralleled by a gradient in the mechanisms determining the structure. Specifically, we believe that consumer pressure increases from New England to the Pacific Northwest to Panama, and that escapes from consumers grow increasingly less likely. Thus the general scarcity of sessile animals, the total lack of canopy-forming algae, and the occurrence of most species in holes and crevices at our sites in Panama are postulated to be at least a partial consequence of nearly continuous, severe predator and herbivore pressure. Predators and herbivores appear effective at controlling plant and animal abundance throughout the year and as a result, escapes from consumers in time, twodimensional space, or size seem very infrequent. The only major available refuge from at least some consumers is the third spatial dimension, depth in the substratum. Note that we do not exclude the possibility that physical factors may have important effects on this system. In fact, as noted below, in some instances heat and desiccation may have important direct and indirect effects on patterns of community structure in this system.

Below we offer experimental evidence to support the hypothesis that consumer pressure is continuous and severe. This includes responses of plant and animal abundances to experimental removal or exclusion of various consumers and changes in patterns of microhabitat use in response to exclusions of large pelagic consumers. Indirect observational evidence and literature information supporting the hypothesis are given in the Discussion.

Consumer pressure at Taboguilla

Observations of predator and herbivore activities during both high and low tides at various sites in Panama throughout the year suggest that foraging of these consumers is aseasonal, though some species have restricted daily or tidal foraging periods (B. Menge et al., personal observations, Garrity and Levings 1981). Specifically, fishes appear active during most times of the day regardless of season. Some are even active at night (e.g., the porcupine fish, Diodon hystrix; Hobson 1974; B. Menge et al., personal observations). Predaceous gastropods may be found feeding any month of the year, though at low rates. Herbivorous crabs, limpets, and chitons also exhibit no distinguishable changes in activity related to season, though daily and tidal activity patterns do vary. These observations suggest that little seasonal variation in consumer activity occurs. The low covers of plants and animals observed at several sites indicate that variations in consumer pressure seem minor from one intertidal site to another, though there is indirect evidence that regional variations in consumer pressure do occur in Panama. For example, the higher cover of animals at Flamenco Island compared to Taboguilla (Table 2) suggests that predation intensity may be less at Flamenco. We tentatively discount the possibility that this difference is due to differences in physical stress, since heat, desiccation, and rainfall seem greater and wave action less at the more protected Flamenco Island site. These differences need more study and we will not discuss them further, except to note that they appear to be relatively small variations around a consistently high consumer pressure, not large drops in such pressure.

On the other hand, qualitative and perhaps quantitative variation in consumer pressure over vertical space undoubtedly occurs. Fish predation is most likely greatest in the low intertidal due to the longer immersion time experienced by this region relative to higher tidal levels. However, predation by invertebrates occurs in the high zone (B. Menge and J. Lubchenco, personal observations; Garrity and Levings 1981) and evidently has a major effect on abundance and zonation of barnacles. Thus, experimental removals of the predators, primarily gastropods (i.e., Acanthina brevidentata, Thais melones, Purpura pansa) from two reefs over a 2-vr period have led to the gradual appearance on each reef of a distinct "zone" of Chthamalus fissus (e.g., Fig. 2). Such zones have not appeared on control reefs. This suggests that the vertical, noncoexistence refuge from predators enjoyed by barnacles in temperate areas (e.g., Connell 1961, 1970, Menge 1976) is normally unavailable at Taboguilla.

To test the hypothesis that the barrenness of the rocky shores of Taboguilla Island is a consequence of severe consumer pressure, we initiated the field experiments outlined earlier. In Fig. 3 we plot the changes in "free" space that have occurred in the low zone as a consequence of the exclusion or removal of one, two, three, and all four consumer groups in comparison to the control. Analysis of variance indicates that the changes in "free" space from 1977 to 1980 vary significantly among the treatments (Table 4). To determine which of the treatment means are significantly different, we performed a Student-Newman-Keuls multiple comparisons test (Table 5). Note that the absence of a single consumer group (i.e., slowmoving herbivores, slow-moving predators, or large fishes) never results in a significant change in free space availability (Table 5). This implies that removals or exclusions of single groups of consumers do not lead to statistically detectable increases in abundance of the epibenthos or decreases in availability of free space. However, the numbers of replicates are low and the trends toward decreased free space and in-



FIG. 3. Changes in mean percent free space in experiments excluding one, two, three, and four consumer groups over a 2-yr period. D = dry season; W = wet season. The first and second dry season 1977 points are pre- and post-manipulation, respectively. Code to consumer groups: SMP = slow-moving predators, SMH = slow-moving herbivores, LF = large fishes, SFC = small fishes and crabs. Control data (C) are the same for each panel. One standard error is plotted for all control means and for the initial and final means of one-, two-, and three-group removals. Where no error bars appear for these points, the bars are smaller than the symbol.

creased epibenthos cover suggest that larger sample sizes might lead to statistically significant declines. At present, we conclude that at most, exclusions of single consumer groups lead to relatively small increases in cover of the epibenthos.

The results of removals or exclusions of two, three and four consumer groups suggest that these groups have a cumulative (but not necessarily additive) impact on cover of epibenthos (Figs. 3B, C, and D, Table 5). Thus, in general, the more consumer groups removed or excluded, the greater and faster the decline or increase in available free space or benthos cover, respectively (Fig. 3, Column 1 in Table 5, Table 6). Of these changes, one of the two-group removals, two of the three-group removals, and the four-group removal are significantly different from the control (Row 1, Table 5). These results suggest that the effects of single groups of consumers may be masked by compensatory changes in other consumer groups, occluding the effect of the absent group. The significance of this result will be considered further in the Discussion.

Removal of all four consumer groups results in a rapid and great increase in the abundance of the epi-

benthos (Fig. 3D) including species of barnacles, ovsters, mussels, vermetids, hydroids, and upright algae (see e.g., Tables 7 and 8 below). This result supports our hypothesis that at least in the low zone, the consistently high level of available free space at Taboguilla Island is due to intense predation and herbivory. In other words, the barrenness of the shore and scarcity of both plants and animals is evidently a consequence of the foraging activities of many species of predator and herbivore. No one group (and presumably no one species) seems to exert an inordinately greater effect on overall abundance of the benthos than any other. This suggests that the keystone species concept supported by several studies in temperate areas (e.g., Paine 1969, 1976, Menge 1976, Lubchenco 1978) may not apply in this tropical system (see also comments in Menge 1981).

In summary, these data support our hypothesis that the high availability of free space at Taboguilla Island is at least partly a function of severe grazing and predation. However, they also raise the question of how prey species persist in this system. In the next section, we suggest that species persistence depends to a great

TABLE 4. One-way ANOVA on change in "free space" in control and experimental treatments from initiation of the experiments (January and February 1977) to January and February 1980.*

Source of variation	df	SS	мѕ	F
Treatments	11	6862.23	623.84	19.01***
Error	20	656.29	32.81	
Total	31	7518.52		

* Data were taken on percent cover of all plants, sessile animals, and unoccupied space in each year. The ANOVA test was done on between-treatment differences in the change in percent cover of free space from 1977 to 1980. Mean percent covers (+9 to eliminate negative differences) were transformed using the arcsine transformation (Sokal and Rohlf 1969). Tests were done on the change in free space because the treatments were not scraped clean when the experiments were started and small differences initially existed between treatments (see Fig. 3). These initial differences were not significant (one-way ANOVA, F = 1.30; critical $F_{11,20} = 2.72$ ($\alpha = .05$, two-tailed). **** P < .005.

extent on substratum heterogeneity, which provides most prey species a refuge from predation and herbivory by fishes and crabs.

Experimental shifts in patterns of microhabitat use and abundance

The patterns of microhabitat use documented in Table 3 suggest that most organisms on the shore occupy holes or crevices. There are at least three possible causes of this pattern. First, organisms on open surfaces may experience excessive heat and desiccation. Second, wave shock may be too severe to allow attachment to open substrata. Third, predators too large

TABLE 6. Number of significant and nonsignificant differences in Table 5. Treatments are categorized by the number of consumer groups by which they differ.

		Diff	erence i consume	n numbe er group	er of s
Probability		0	1	2	≥3
P < .05	Observed	0	4	8	6
	Expected*	0	1	1	0
P > .05	Observed	12	26	9	1
	Expected	12	29	16	7

* Calculated by assuming H_0 : outcomes are random and independent of the number of consumer groups removed. Thus, 5% of the total number of observed outcomes in each column should be in the P < .05 row, the other 95% in the P > .05 row. Since proper application of a χ^2 test requires that all expected entries be >0, we have adjusted all 0's to 1's (with appropriate adjustments to keep column totals the same). The more conservative χ^2 which results (with Yates continuity correction applied), is highly significant ($\chi^2 =$ 75.25; $P \ll .005$; critical $\chi^2_3 =$ 7.815 with $\alpha = .05$).

to feed in the holes and crevices may consume only those individuals occurring on open surfaces.

We have not studied direct effects of heat and desiccation on patterns of space utilization in this system. Indirect evidence suggests that at least for solitary sessile animals, such effects may be less important than other factors. Since numerous kinds of barnacles (four species), oysters (two species), and limpets (four species) occur on substrata which are exposed to direct sunlight (open, cracks, depressions), in the mid and low zones (Tables 3, 13) other hard-shelled invertebrates in the same and different groups might also be expected to be able to live in the open. Further-

TABLE 5. Results of Student-Newman-Keuls test (for multiple comparisons among means of unequal sizes; Sokal and Rohlf 1969) comparing differences in the mean change of "free" space availability among control and experimental treatments from 1977 to 1980.⁺

					the second s	and the second se				and the second sec		
Treatment	Control (0)	-SMP (1)	-LF (1)	-SMH (1)	-SMP LF (2)	-SMH SMP (2)	-LF SFC (2)	-SMH LF (2)	-SMP, LF SFC (3)	-SMP, SMH, LF (3)	-SMH LF, SFC (3)	,-SMH, SMP, LF, SFC (4)
Control (4)		NS‡	NS	NS	NS	NS	NS	*	*	**	NS	**
-SMP(4)	5.43	•	NS	NS	NS	NS	NS	NS	NS	*	NS	**
-LF (2)	7.57	2.14		NS	NS	NS	NS	NS	NS	NS	NS	**
-SMH (4)	0.90	6.33	8.47		NS	NS	NS	*	*	**	NS	**
-SMP, LF (2)	17.40	11.97	9.83	18.30		NS	NS	NS	NS	NS	NS	**
-SMH, SMP(4)	11.25	5.82	3.68	12.15	6.15		NS	NS	NS	NS	NS	**
-LF, SFC(2)	11.04	5.61	3.47	11.94	6.36	0.21		NS	NS	NS	NS	**
-SMH, LF (2)	22.85	17.42	15.28	23.75	5.45	11.60	11.81		NS	NS	NS	**
-SMP, LF, SFC (2)	25.58	20.15	18.01	26.48	8.18	14.33	14.54	2.73	1.0	NS	NS	**
-SMP, SMH, LF(2)	28.26	22.83	20.69	29.16	10.86	17.01	17.22	5.41	2.68		NS	**
-SMH, LF, SFC (2)	20.03	14.60	12.46	20.93	2.63	8.78	8.99	2.82	5.55	8.23	1.0	**
-SMP, SMH, LF, SFC (2)	57.81	52.38	50.24	58.71	40.41	46.56	46.77	34.96	32.23	29.55	37.78	

⁺ See caption of Fig. 3 for code to abbreviations. –SMH is read as "minus slow-moving herbivores." In the treatment column, number of replicates is given in parentheses; in the treatment row, number of groups removed is indicated in parentheses. Significance levels are above diagonal and differences between coded and transformed means (see Table 4) are below diagonal.

 \pm NS = not significantly different, P > .05. * P < .05; ** P < .01.

TABLE 7. Effects of fast-moving (fishes and crabs) and slow-moving (mostly molluscs) consumers on microhabitat occupancy patterns of solitary sessile invertebrates in the mid zone.[†]

					Quadra	at treat	ments§						
		Ca	ge con	trol	Fish (F	exclu: E) (roo	sions	Fisl ey (FC	h and (clusio (E) (ca	crab ns ges)	Si	gnifican	ce
Organisms‡	Reef treatment§	Exp	(00)	Prot	Exp	2) (100	Prot	Exp	2) (04	Prot	CO vs FE	. CO vs. FCE	FE vs. FCE
Barnacles	Control (two species) SMP (one species) SMH (one species) SMC (three species)	0 16 9 114	[4] [4] [4] [4]	12 32 29 234	2 1 7 251	[4] [2] [2] [4]	7 11 10 317	1 6 8 668	[4] [2] [2] [4]	1 1 23 238	NS NS NS **	NS * NS **	NS ** NS **
Bivalves	Control (three species) SMP (three species) SMH (two species) SMC (four species)	0 1 0 0	[4] [4] [4] [4]	21 135 14 147	0 15 4 23	[4] [2] [2] [4]	5 102 54 142	1 41 2 110	[4] [2] [2] [4]	20 105 37 386	NS ** NS **	NS ** NS **	NS ** NS *

† Data are numbers of individuals observed in microhabitats exposed to (Exp) or protected from (Prot) fast-moving consumers. Number of treatments is indicated in square brackets.

‡ Numbers of species of each organism type occurring in the treatments are shown in parentheses. The greatest increases in abundance occurred with the barnacles *Chthamalus fissus* and *Tetraclita panamensis*, the oyster *Ostrea palmula*, and the mussel *Brachidontes semilaevis*.

§ Reef treatments are separate reefs: Control = no manipulations of slow-moving consumers; SMP = slow-moving predators removed; SMH = slow-moving herbivores removed; SMC = both slow-moving predators and herbivores removed. The quadrat treatments are controls (no cage or roof), roofs, or cages on each of these reefs.

^{II} Tests were done on data from equal numbers of treatments, i.e., numbers from controls of slow-moving herbivores or predator removals were divided by two. Fisher's Exact Probability Test (Siegel 1956) was done when the total N for the 2 \times 2 comparison was <40; χ^2 with Yates correction for continuity was done when the total N was \geq 40 and n of the smallest class was \leq 10. NS = not significant, P > .05; * = .01 < P < .05; ** = P < .01.

more, occasional individuals of all sizes of most species are found in exposed microhabitats (Table 3), suggesting that these species can cope with the physical rigors in this environment. We tentatively conclude that heat and desiccation are not the agents primarily responsible for microhabitat occupancy patterns of these invertebrates. The possibility that upright algal abundance, size, or both are affected by heat and desiccation remains viable.

At Taboguilla Island, if wave shock has an effect, it should be greatest on mobile organisms. Oysters, vermetids, barnacles, mussels, and other sessile fauna usually occur as firmly attached solitary individuals. Thus, waves must act on individuals, which probably present little resistance and in our experience are difficult to dislodge from the rock. This is very unlike temperate areas, where mussels, barnacles, oysters, and other species may form dense stands of tightly interconnected individuals which are subject to exfoliation by wave action. Further, some mobile species such as limpets and chitons are usually flat or of a depressed, conical shape and present little resistance to waves. Thus, we suggest that it is the predaceous snails, sea urchins, and other globose organisms which should be most influenced by wave shock. The facts that 11% of the snails are found in the open (Table 3) and waves are not always severe, especially during the dry season (see above), suggest that wave shock may not be one of the more important selective agents affecting these species. We thus conclude that wave action is not the agent restricting the epibenthos to holes and crevices.

Fishes and possibly large crabs appear to have a strong effect on microhabitat occupancy of many sessile prey species (Tables 7, 8). During the 1st 2 yr of these experiments, we noticed that in mid and low zone fish exclusion (FE) and fish and crab exclusion (FCE) treatments, barnacles, oysters, algae, hydroids, and other sessile organisms settled and survived on all rocky surfaces, not just in holes and crevices. To quantify this, we categorized every space occupant (except encrusting algae) according to its microhabitat as either being protected from, or exposed to, predation from large mobile consumers in the mid and low zone experiments in the 1979 dry season. (Similar quantifications in the high zone suggested no differences in microhabitat occupancy.) In taking these data, we assumed that the relative proportions of exposed and protected microhabitats in each treatment were similar. In fact, the treatment sites were originally selected so that they were as similar to each other as possible. Despite this, there appeared to be some variation in substratum heterogeneity between replicates, treatments, zones, and reefs. Thus, in general the mid zone seems less heterogeneous than the low zone. More importantly, in the low zone, the slowmoving predator removal reef appeared more heterogeneous and the slow-moving herbivore removal reef less heterogeneous than both the slow-moving consumer and control reefs, which seemed similar in sub-

Γ_{ABLE} 8. Effects of fast-moving (fishes and crabs) and slow-moving (mostly molluscan herbivores and predators) consumer
on microhabitat occupancy patterns of solitary and colonial sessile invertebrates and algae in the low zone.†

			(Quadrat t	reatments	S ¹¹				
		Cage (control	Fish ex (roofs	clusions	Fish an exclu (cages)	nd crab isions (FCE)	Si	gnificanc	e¶
Organisms‡	Reef treatment§	Exp	Prot	Exp	Prot	Exp	Prot	- CO vs. FE	CO vs. FCE	FE vs. FCE
Barnacles (solitary)	Control (two species) SMC (four species)	0 110	0 178	4 298	3 132	3 238	2 37	#	•••• **	NS **
Bivalves (solitary)	Control (four species) SMC (six species)	1 4	94 182	3 55	109 277	21 251	142 158	NS **	** **	** **
Other solitary invertebrates (solitary)	Control (six species) SMC (five species)	0 7	19 32	5 40	92 44	2 29	21 25	NS **	NS **	NS NS
Colonial hydroids (<i>Abietinaria</i> sp.)	Control SMC	2 6	10 10	18 24	12 8	51 35	30 8	*	** **	NS NS
Fleshy algae††	Control SMC	1 27	7 34	2 33	7 10	7 12	17 7	NS **	NS NS	NS NS
Calcareous algae‡‡	Control SMC	0 5	1 12	0 14	2 5	36 144	16 34	**	**	 NS

† Data are number of solitary animals (individuals) or number of random dots hitting colonial animals and algae in microhabitats exposed to (Exp), or protected from (Prot) fast-moving consumers. Number of treatments is four in each case.

‡ Organisms with the greatest increases in abundance in experimental treatments are barnacles (*Chthamalus fissus*, *Balanus* spp.); bivalves (*Chama echinata*, *Ostrea palmula* [oysters], *Brachidontes semilaevis* [mussel]); other solitary invertebrates (*Petaloconchus* sp. [vermetid gastropod]); hydroid (*Abietinaria* sp.); fleshy algae (*Gelidium pusillum* [red]); calcareous algae (*Jania* spp. [corallinaceous red]).

§ Treatments are separate reefs; control = no manipulations of slow-moving consumers, SMC = slow-moving consumers removed. Numbers of species of each type of organism occurring in the treatments is indicated for barnacles, bivalves, and other solitary invertebrates. These numbers are not given for hydroids because only one species is involved, or for algae, because of taxonomic uncertainty for many species of algae.

^{\parallel} Treatments are the 0.25-m² areas in which fast-moving consumer manipulations were done. Control = unmanipulated plots, fish exclusions = roofs, and fish and crab exclusion = cages.

¶ See footnote †, Table 7 for statistical tests and criteria used and footnote §, Table 7 for keys to column abbreviations and significance symbols.

Dash means numbers are too low to test.

⁺⁺ Fleshy algae include those reds, browns, and greens judged to be relatively long lived (such genera as *Hypnea*, *Gelidium*, *Dictyota*, *Laurencia*, and *Caulerpa*). Ephemeral algae (e.g., *Cladophora*, *Ulva*, *Enteromorpha*, and *Giffordia*) were not analyzed because they appeared to occur uniformly in all microhabitats.

‡‡ Calcareous algae were species of Jania, Corallina, and Amphiroa.

stratum irregularity. Such variability in substratum heterogeneity could lead to significant variation among treatments in the relative amount of substratum which is protected from fast-moving consumers and thus introduce a bias in our results (Tables 7 and 8). We therefore quantified the relative proportion of substratum exposed to and protected from fast-moving consumers in all replicates of each treatment using the random-dot technique described earlier. Relative exposure of substratum to fast-moving consumers was also quantified in 15 permanent quadrats in each of the mid and low zones on the control and slow-moving consumer removal reef. Unlike the treatment quadrats, the sites of which were deliberately selected to be amenable to cages, roofs, or controls for these treatments, the sites of the permanently marked quadrats along horizontal transects were determined using a random numbers table. Hence, the mean relative exposure to fast-moving consumers in the permanent quadrats should be representative of the average for

that level on that reef. We do not have permanent quadrats on the slow-moving predator or slow-moving herbivore removal reefs.

Though the mid zone tends to have more substratum exposed to fast-moving consumers than the low zone, the differences are not significant (at the 5% level) on either the control or slow-moving consumer removal reefs (Table 9; significance determined by non-overlap of 95% confidence intervals). Moreover, within-zone differences between these two reefs are also not significant (Table 9).

In the quadrat treatments within each zone on each reef, no treatment is different from any other treatment in mean exposure to fast-moving consumers (Table 9). However, in each zone, there is one set (i.e., control, fish exclusion, and fish and crab exclusion) of quadrat treatments on one reef which is different from the sets on the other three reefs (Table 9). In the mid zone quadrat treatments on the control reef, an average of 86.6% of the substratum is exposed to TABLE 9. Relative exposure of substratum to fast-moving consumers on each reef and in quadrat treatments. Data are mean percent cover $\pm 95\%$ confidence interval except where there are only two replicates of a treatment. In this case the mean is given with the values of the two replicates beside it in parentheses. See caption to Fig. 3 for code to abbreviations.

			Zo	one		
	Quedrot	М	id	Lo	ow	
Reef treatment	treatment	Exposed	Protected	Exposed	Protected	Ν
Control	Permanent quadrats	81.8 ± 4.1	18.2 ± 4.1	77.3 ± 6.6	22.7 ± 6.6	15
Slow-moving consumer removal	Permanent quadrats	73.3 ± 4.9	26.7 ± 4.9	68.3 ± 5.4	31.7 ± 5.4	15
Control	Cage control Fish exclusion Fish and crab exclusion Total	$\begin{array}{l} 83.5 \pm 7.6 \\ 87.8 \pm 9.7 \\ 88.5 \pm 8.8 \\ 86.6 \pm 3.4 \end{array}$	$\begin{array}{c} 16.5 \pm 7.6 \\ 12.2 \pm 9.7 \\ 11.5 \pm 8.8 \\ 13.4 \pm 3.4 \end{array}$	$\begin{array}{l} 67.0 \pm 11.1 \\ 70.5 \pm 9.9 \\ 67.8 \pm 10.2 \\ 68.4 \pm 3.7 \end{array}$	$\begin{array}{r} 33.0 \pm 11.1 \\ 29.5 \pm 9.9 \\ 32.2 \pm 10.2 \\ 31.6 \pm 3.7 \end{array}$	4 4 4 12
SMP removal	Cage control Fish exclusion Fish and crab exclusion Total	$\begin{array}{r} 69.8 \pm 13.7 \\ 74.5 \ (70, \ 79) \\ 73.0 \ (71, \ 75) \\ 71.8 \pm 5.4 \end{array}$	$\begin{array}{r} 30.2 \pm 13.7 \\ 25.5 \ (21, \ 30) \\ 27.0 \ (25, \ 29) \\ 28.2 \pm 5.4 \end{array}$	$71.8 \pm 11.3 \\76.0 (75, 77) \\80.0 (78, 82) \\74.9 \pm 5.1$	$\begin{array}{r} 28.2 \pm 11.3 \\ 24.0 \ (23, \ 25) \\ 20.0 \ (18, \ 22) \\ 25.1 \pm 5.1 \end{array}$	4 2 2 8
SMH removal	Cage control Fish exclusion Fish and crab exclusion Total	$\begin{array}{r} 79.0 \pm 15.3 \\ 77.5 \ (66, \ 89) \\ 77.5 \ (68, \ 87) \\ 78.2 \pm 11.5 \end{array}$	$\begin{array}{l} 21.0 \pm 15.3 \\ 22.5 \ (34, \ 11) \\ 22.5 \ (32, \ 13) \\ 21.8 \pm 11.5 \end{array}$	$\begin{array}{l} 89.0 \pm 7.5 \\ 86.0 \ (84, 88) \\ 91.0 \ (90, 92) \\ 88.8 \pm 3.2 \end{array}$	$\begin{array}{l} 11.0 \pm 7.5 \\ 14.0 \ (16, \ 12) \\ 9.0 \ (8, \ 10) \\ 11.2 \ \pm \ 3.2 \end{array}$	4 2 2 8
SMC removal	Cage control Fish exclusion Fish and crab exclusion Total	$73.5 \pm 11.8 \\ 70.5 \pm 2.7 \\ 76.2 \pm 11.8 \\ 73.4 \pm 3.7$	$\begin{array}{c} 26.5 \pm 11.8 \\ 29.5 \pm 2.7 \\ 23.8 \pm 11.8 \\ 26.6 \pm 3.7 \end{array}$	$\begin{array}{c} 66.0 \pm 5.4 \\ 71.5 \pm 22.8 \\ 77.0 \pm 11.1 \\ 71.5 \pm 6.2 \end{array}$	$\begin{array}{r} 33.0 \pm 5.4 \\ 28.5 \pm 22.8 \\ 23.0 \pm 11.1 \\ 28.5 \pm 6.2 \end{array}$	4 4 4 12

fast-moving consumers while averages on the other reefs are significantly less (71.7, 78.2, and 73.4%). In the low zone quadrat treatments on the slow-moving herbivore reef, an average of 88.8% of the substratum is exposed to fast-moving consumers while averages on the other reefs are significantly less (68.4, 74.9, and 71.5%).

Only one of these differences might affect the analyses in Tables 7 and 8. The difference in relative exposure of the substratum to fast-moving consumers in the mid zone suggests that the expected values in our χ^2 or Fisher Exact Probability tests in Table 7 should be determined by the proportion of substratum exposed to and protected from fast-moving consumers in each treatment. However, though the control reef treatments have a higher proportion of exposed substratum than the various removal reef treatments, the latter have a greater proportion of organisms in exposed sites than do the control reef treatments (Table 7). This is the opposite of what would be expected if the proportions of organisms exposed to fast-moving consumers was a simple reflection of substratum availability and not related to differential access to these prey by fast-moving consumers. If substratum availability had produced these results, the control reef treatments should have the highest proportion of organisms in sites exposed to fast-moving consumers.

This leads to a final caution about these data. In a few cases, sample size (number of organisms in each treatment category; Tables 7 and 8) is small. This could lead to incorrect conclusions regarding the im-

plications of the data. However, we note that most sample sizes are adequate or better and that we attempt to interpret our results conservatively. For example, low-zone data from the slow-moving predator and slow-moving herbivore removal reefs are omitted from the analysis in Table 8 in part because of small sample sizes (and also because of the high proportion of substratum exposed to fast-moving consumers on the slow-moving herbivore removal reef; Table 9).

With these qualifications in mind, these data (Tables 7 and 8) indicate that in general, the main effect of the large, fast-moving consumers is on the microhabitat occupied by sessile organisms while the main effect of slow-moving consumers is on the abundance of sessile prey. For example, seven of 16 comparisons between control and fast-moving consumer exclusion treatments (i.e., CO vs. FE and CO vs. FCE comparisons) in the mid, and 14 of 20 comparisons between these treatments in the low zone, indicate that significantly greater proportions of most groups survived in exposed microhabitats in exclusions than in control treatments (Tables 7 and 8). Further, in many of those cases where differences were not significant, the sample sizes in treatments on the control reef were probably too small to allow much confidence in the tests. Note also that crabs seem to have a greater effect on microhabitat use in the mid zone than they do in the low zone. That is, proportions of significant differences in CO vs. FE (i.e., there is a fish effect) as opposed to FE vs. FCE (i.e., there is a crab effect) comparisons are similar in the mid zone (three of eight TABLE 10. Analysis of effect of slow-moving consumers (predators and herbivores) on microhabitat use by benthic animals and plants. Data are numbers of individuals or points in "control" and "slow-moving consumers removed" rows of control, fish exclusion, and fish and crab exclusion columns in Tables 7 and 8.

			Significant	ce
Zone	Prey group†	Control	Fish exclusion (roofs) (FE)	Fish and crab exclusion (cages) (FCE)
Mid	Barnacles	*	NS	NS
	Bivalves	NS	NS	NS
Low	Bivalves	NS	**	***
	Other invertebrates	NS	***	***
	Abietinaria sp.	NS‡	NS	NS
	Fleshy algae	NS	**	*‡
	Calcareous algae	NS‡	NS‡	NS

TABLE 12. Cell totals for two-way ANOVAS on those prey groups having significant interaction terms in Table 11.

			Quadrat	treatment
Reef treat- ment	Zone	Prey group*	Cage control	Cage (FMC exclusion)
Control	Mid Low	Bivalves Algae-ephemeral Algae-fleshy Algae-corallinaceous	21 56 8 1	21 73.5 25 53
SMC removal	Mid Low	Bivalves Algae-ephemeral Algae-fleshy Algae-corallinaceous	147 56.5 59 16.5	496 12.5 21.5 178

* Data are numbers (bivalves) or percent cover (algae).

 \dagger Barnacles in the low zone could not be tested since N's were too low in the control reef treatments.

‡ Fisher's Exact Probability test used in these cases; otherwise significance is based on χ^2 tests with Yates continuity correction applied. Ns = not significant (P > .05); * = .01 < P < .05; ** = P < .01.

vs. four of eight) but quite dissimilar in the low zone (seven of 10 vs. three of 11). This may reflect the likelihood that fishes forage proportionately more, and crabs feed less in the low zone than in the mid zone.

Slow-moving consumers may also have an effect on microhabitat use of some prey groups (Table 10). The comparisons in Table 10 were made down columns in Tables 7 and 8; i.e., they test for the effect of removing

slow-moving consumers while holding fast-moving consumer effects constant. These tests suggest that in one of seven cases in cage controls and in three of seven cases in each of the fish and fish and crab exclusions, significant differences in prey microhabitats occurred. Note that only one of the comparisons among the cage controls (mid zone barnacles) is significant while the bivalve, other invertebrate, and fleshy algae comparisons are significant in the fish and fish and crab exclusion columns. We suggest that the cage control column comparisons may in some respects be the more appropriate comparisons, since prey abundance in the fast-moving consumer quadrat treatments was often high ($\approx 30-100\%$ cover as suggested by taking the inverse of percent free space in FMC treatments in Fig. 3) and hence inter-individual

TABLE 11. F values and significance of two-way ANOVAS testing effect of slow-moving and fast-moving consumers on abundances of sessile prey organisms.

Zone		Group affecting abundance						
		Slow-moving consumers		Fast-moving consumers		Interaction		
	Group	F^{\dagger}	Signifi- cance‡	F	Signifi- cance	F	Signifi- cance	
Mid	Barnacles Bivalves	1.87 22.20	NS ***	0.37 7.49	NS *	0.39 7.49	NS *	
Low	Barnacles Bivalves Other solitary invertebrates <i>Abietinaria</i> sp. Algae-ephemeral [#] Algae-fleshy Algae-corallinaceous Algae-total#	30.03 2.73 7.57 0.81 4.77 5.55 12.45 5.07	*** NS * NS * *	0.23 2.07 0.91 6.41 0.91 1.03 27.74 8.94	NS NS * NS NS **	0.36 0.58 0.16 1.13 4.92 7.31 7.56 0.001	NS NS NS * *	

 \dagger Two-way ANOVA with replication (n = four replicates per cell) was done on total abundances of each prey group in cage controls and cages (fast-moving consumer effect) on the control and slow-moving consumer removal reefs (slow-moving consumer effect); df = 1,12 in all cases. Data tested were numbers (barnacles, bivalves, other solitary invertebrates) or percent covers (*Albietinaria*, algae).

 $\pm NS = P > .05; * = P < .05; ** = P < .01; *** = P < .001.$

§ Includes vermetids, solitary tunicates, anemones, and serpulid polychaetes.

^{II} Primarily green (*Enteromorpha*, *Cladophora*, and *Ulva*) and brown (*Giffordia*) algae which our observations indicate are very fast to colonize and disappear.

¶ Algae such as *Gelidium, Gelidiella, Dictyota, Laurencia,* and *Hypnea* (reds) which persist for longer periods of time. # Total abundances are three algae categories lumped.

		Protected surfaces (%)				
Organisms	Exposed	Crack	Depression	Crevice	Hole	Ν
Barnacles (four species)	43	1	45	6	6	974
Bivalves (two species)	0	0	18	21	61	415
Limpets (seven species)	9	0	17	11	63	99
Chitons (three species)	0	0	0	48	52	33
Predaceous snails (four species)	0	0	0	48	52	31
Fotal (except barnacles)	2	0	16	22	60	578

TABLE 13. Relative proportions of solitary intertidal invertebrates in different microhabitats on total removal reef (mid and low zones).*

* Note that although this is the slow-moving consumer removal reef, there are still limpets, chitons, and other gastropods present. This is because, as noted in the text, total removals of such consumers from entire reefs is not possible. However, the numbers of these consumers are greatly reduced compared to control reefs (see e.g., Table 3). Degree of protection from fast-moving consumers increases from left to right.

contact was probably frequent among the sessile organisms. Thus, the comparisons between treatments with and without slow-moving consumers (i.e., control vs. SMC in Tables 7 and 8) in the FE and FCE columns may be complicated by competitive interactions among both the prev species and higher order interactions among the different predator groups. The counterargument to these possible complications is that sample sizes in the fish or fish and crab exclusions are often larger than in the cage controls, which may strengthen the statistical comparisons. We conclude from this analysis that in general, slow-moving consumers have a relatively small effect on microhabitat occupancy of prey in the mid zone (only one of six comparisons significant) and apparently a stronger effect in the low zone (six of 15 comparisons significant; Table 10). This latter interpretation should be viewed cautiously given the potential artifacts mentioned above.

The effects of slow- and fast-moving consumers on abundance of each prey group appear somewhat more complex (Table 11). Two-way analyses of variance on each prey group listed in Table 11 indicate that both slow- and fast-moving consumers keep mid zone bivalve densities and low zone coralline and total algal covers low. Note that the interaction terms in the former two cases are significant. Examination of the data (Table 12) suggests that for bivalves, fast-moving consumers have an effect only if slow-moving consumers are also removed. For upright corallinaceous algae, the interaction seems due to the apparently greater effect of fast-moving consumers in the presence of slow-moving consumers (53-fold increase in algae cover) than in their absence (11-fold increase). However, the interpretation of this interaction is obscured by the extremely low covers of upright coralline algae in the control treatments (0, 0, 0, and 1% cover).

Slow-moving, but not fast-moving consumers affect abundances of low zone barnacles, other solitary invertebrates, ephemeral algae, and fleshy algae (Table 11). However, only the former two cases represent clear inhibitory effects by slow-moving consumers on

abundance. The effects on the algae are more complicated. With the ephemeral algae, there is no slowmoving consumer effect in the cage control treatments and their removal actually decreased cover of ephemeral algae by >80% in cage treatments (Table 12). In cage controls, removal of slow-moving consumers leads to a large increase in cover of fleshy, longerlived algae but in the cage treatments there is no change in cover of these algae (Table 12). As with some of the data in Table 10, we attribute these significant statistical interactions to biotic interactions among the sessile prey. Thus, in the absence of both types of consumer, abundances are high (e.g., Fig. 3, Tables 7, 8) and competitive or other interactions undoubtedly lead to decreased, rather than increased covers of some groups, such as the fleshy and ephemeral algae. Thus, if total algal cover is analyzed (Table 11), both groups of consumers have strong effects and the interaction term is not significant.

In addition to the above effects, slow-moving consumers appear to have a strong but variable effect on mid zone barnacle abundance. Total numbers of barnacles in four replicates each on the control reef were 12 (cage controls) and two (cages), while those on the slow-moving consumer reef were 348 (cage controls) and 906 (cages). However, variation among replicates was so great that these apparent differences are not significantly different.

Fast-, but not slow-moving consumers affected the cover of *Abietinaria* sp. (Table 11). Evidently some fishes and crabs prey actively on this hydroid but most benthic invertebrate predators and herbivores ignore or avoid it.

We thus conclude that, though both groups of consumers affect abundances of certain of the prey groups, the effect of slow-moving consumers on abundance generally seems greater than the effect of fastmoving consumers. Slow-moving consumers reduce abundances of five or six groups (bivalves and maybe barnacles in the mid; barnacles, other solitary invertebrates, fleshy algae, and corallinaceous algae in the low zone) while fast-moving consumers affect abundances of three or four prey groups (bivalves in the mid, *Abietinaria* sp., corallinaceous algae, and maybe fleshy algae in the low zone; Tables 11, 12). Note again that in some of these cases, the slow-moving consumers can mask the effect of the larger, more mobile consumers by keeping prey abundances or covers low (Table 8).

Further evidence that slow-moving consumers primarily affect abundance as opposed to microhabitat use is given in Table 13. These data represent a survey of microhabitat use patterns on the slow-moving consumer removal reef. Note that the same general pattern observed on the control reef with slow-moving consumers present (Table 3) is also evident when slow-moving consumers are absent (Table 13). On both reefs a relatively large proportion of barnacles occurs in the open but nearly all other invertebrates are located primarily in protected microhabitats. These data further suggest that patterns of microhabitat use are primarily a result of attacks by fishes and large crabs on those sessile organisms which settle and begin growing on microsites accessible to these consumers. The apparent difference in the microhabitats of the sessile animals suggested by comparing Tables 3 and 13 is most likely due to differences in size of the barnacles and bivalves on each reef. On the removal reef, the majority of barnacles and bivalves are recently settled and thus small in relation to those on the control reef. Most settling larvae appear to settle in small depressions and near cracks. Through growth, the microhabitats of such individuals gradually change from these protected categories to the exposed category. Thus, differences in size structure may account for these apparent differences in microhabitat. Since mobile organisms are being manipulated and are thus small and scarce on the total removal reef, comparisons between these groups in Tables 3 and 13 are not appropriate. However, the apparent differences suggested in these tables need further study.

These results suggest that this system may be typified by so-called higher order interactions among the consumer groups (i.e., interactions whereby the effect of one group on a second depends on other groups). In addition, the suggestion that the small invertebrate consumers most strongly affect abundance and that the larger, more active fishes and crabs most strongly affect use of microhabitats further implies that the diversity of consumer types represented by these consumer groups is an important component of predation pressure in this system.

DISCUSSION

Refuges and defenses in temperate and tropical communities

Escapes in space, time, and size.—Our data and observations suggest that most types of escapes or refuges used by species in the temperate marine rocky intertidal communities are unavailable to their coun-

terparts in the tropical community. Thus, the presence of continuously active, visually oriented, fast-moving consumers evidently makes escapes in both two-dimensional space and time unlikely in Panama. In temperate regions, prey often have a noncoexistence refuge zone above the foraging range of their (mostly sluggish asteroid and gastropod) predators (Connell 1961, 1970, Paine 1966, 1969, 1971, 1974, Menge 1976; Fig. 1B, C). In addition, these nonvisual predators often "miss" prey within their foraging range (e.g., Menge 1976, Lubchenco and Menge 1978). Finally, most consumers in temperate areas exhibit seasonal reductions of activity (e.g., Menge and Menge 1974, Paine 1974, Spight 1974, Menge 1976, 1979, Lubchenco and Menge 1978, Lubchenco and Cubit 1980), thus providing time periods when mortality from biotic agents, at least, is greatly diminished.

In Panama, the very mobile and visually oriented fishes and crabs forage throughout the intertidal region (B. Menge et al., *personal observations*) and evidently can locate any animal or algal prey missed by the sluggish, slow-moving consumers. Seasonal temporal refuges seem minor in this system. Thus much of the difference in structure that we have observed between temperate and tropical intertidal communities (e.g., Table 2) may be a direct consequence of the addition of new types of consumers plus the year-round foraging of all consumers, both of which result in a reduction of space and time refuges for sessile organisms.

In contrast to the temperate communities, size escapes seem rare in the tropical community (B. Menge and J. Lubchenco, personal observations). For a size escape to be feasible, an organism must survive through an initial vulnerable period until it reaches a size at which it is no longer (or less) susceptible to being eaten. The intensive, year-round activity of the many different consumers probably greatly reduces the likelihood of many animals or algae surviving through the vulnerable small stages. In addition, various characteristics of the different consumers enable them to handle even large, well-defended prey. For example, the relatively great sizes and massive jaw apparatuses of the predaceous fishes, along with their mobility and year-round activity suggest that sessile invertebrates rarely escape the attention of large fishes (several fish species reach at least 3.6 kg and 0.58 m standard length; B. Menge and J. Lubchenco, personal observations). Those prey individuals that do reach large sizes and may have escaped predation by fishes (e.g., the barnacles Tetraclita panamensis and Catophragmus pilsbryi reach basal diameters of 7 cm; the oyster Ostrea iridescens can reach a diameter of at least 16 cm) may still be eaten by gastropod and asteroid predators (e.g., Thais melones, Acanthina brevidentata, Muricanthus princeps, M. radix, Heliaster microbrachius).

Size escapes by algae also appear unlikely. The

near-total absence of large fleshy algae from this system, in striking contrast to the temperate areas (Table 2), appears to be a consequence of intensive yearround grazing by many species and types of herbivores.

The results in Tables 7 and 8 indicate that refuges in three-dimensional space are available to numerous prey species. In addition to the species discussed above, sea urchins avail themselves of this refuge. Echinometra vanbrunti and the less common Eucidaris thouarsi occur exclusively in holes (100% of all urchins observed, N = 235) in the low and the very low zones. The cause(s) of these holes is (are) unclear but the urchins seem to be the most likely candidates. The most heterogeneous substratum occurs in the range of these species and sea urchins are known to erode the substratum (e.g., Ebert 1968). We have found fragments of both urchin species in the guts of porcupine fishes, parrotfishes, wrasses, and triggerfishes, and Glvnn et al. (1979) suggest that the triggerfish Balistes polylepis is the major predator of these echinoids in the East Pacific region. Since they ultimately appear to generate much of the three-dimensionality of the substratum, these sea urchin species may thus be particularly important in the long-term development of this community.

Escapes in behavior and structure.-Though spatial and temporal escapes seem greatly restricted at Taboguilla, other sorts of escapes or defenses are potentially available to organisms. Before any conclusions can be reached about refuge availabilities in this system, chemical, behavioral, and morphological defenses must be considered, as well as their relative uniqueness to tropical vs. temperate communities. We do not yet know whether or not any of the more common species in this system have chemical defenses (e.g., Bakus and Green 1974), though it seems highly probable that some do. Behavioral defenses such as running responses from predators, often observed in temperate species (e.g., see reviews in Feder 1967, Menge 1982), also occur in some gastropod species in Panama (e.g., Nerita scabricosta, Fissurella virescens, F. longifissa). In at least one case (N. scabri*costa*), the response seems due to predation (Garrity and Levings 1981). Such defenses are of course unavailable to the sessile benthos.

Another apparent behavioral defense, also not unique to the tropics, is that the limpets or limpet-like pulmonates appear to home and fit tightly to scars on the rock (B. Menge and J. Lubchenco, *personal observations*, C. Lubchenco, S. Garrity, S. Gaines, *personal communication*). What does seem unique to at least some tropical systems are the very restricted activity periods in these gastropod groups. Thus, in daytime they are active only when being splashed by waves on ebbing and flowing tides; during high and low tides they are inactive (B. Menge and J. Lub-

chenco, personal observations). Inactivity at low tide is probably an adaptation to avoid desiccation. Inactivity at high tide may hinder visual predators from removing or even seeing the limpets, since they are often quite cryptic. Activity when being washed by waves may be safer because neither crabs nor fishes seem to be able to operate efficiently in the turbulent surf zone. In addition, as has been noted for invertebrates in other tropical marine systems (e.g., Ogden et al. 1973, Abbott et al. 1974), many invertebrates in this system are most active at night. This is especially true of chitons, sea urchins, large crabs, the limpets, the nerites, and the littorines. Though other factors could certainly be at least partly responsible for such behavioral patterns, predation by diurnally active predators is a major potential cause.

Morphological adaptations can be another important type of defense against predation. For example, many species of gastropods develop a massive or knobbed shell or skeleton in apparent adaptive responses to fish or crab predation or both (e.g., Vermeij 1976, 1977, 1978, Zipser and Vermeij 1978, Palmer 1979). Other organisms such as certain species of barnacles and sea stars also develop massive tests or skeletons in this community (B. Menge and J. Lubchenco, personal observations). Such apparent defenses may explain how 43-67% of the barnacles (Tables 3, 8) and 1-14% of the bivalves, limpets, chitons, and globose gastropods (Table 3) can persist in microhabitats unsheltered from fishes and crabs. Thus, for example, for the gastropod Thais melones the shell constitutes $92.8 \pm 0.8\%$ $(\bar{x} \pm sE; N = 37)$ of the total wet mass, while for the temperate (New England) Thais lapillus, the shell constitutes only $65.2 \pm 0.8\%$ (N = 50) of the total wet mass. This pattern holds over all sizes sampled in the two habitats (Fig. 4). The relationships between shell mass and flesh dry mass are significantly different for these two snails. Analysis of covariance reveals that the regression lines for the two species are significantly different (F = 326.9; 1, 84 df; P < .001). Note that this difference is due to differences in y-intercept (7.5 for T. lapillus; 26.6 for T. melones); the slopes of the lines are virtually identical (1.09 for T. lapillus; 1.13 for T. melones; Fig. 4). Thus a T. lapillus of 1 g flesh dry mass would have a shell of 7.51 g while a 1-g T. melones would have a 26.6-g shell. This example is not unique. Other (though not all) common predaceous snails in the Panama rocky intertidal also have massive shells. Opeatostoma pseudodon, Thais speciosa, T. triangularis, and Acanthina brevidentata have shells which may range up to 90% of the total body mass (authors' personal observations). In addition to shell mass, many of these gastropod species develop thick knobs which evidently serve as a defense against fishes which crush their prey (Palmer 1979). Moreover, there is some evidence that both latitudinal and longitudinal gradients of increased shell massiveness are paralleled by gradients of increased predation pressure (Vermeij 1976, 1978, Zipser and Vermeij 1978, Palmer 1979). Such evidence lends further support to the hypothesis that consumer pressure increases with decreasing latitude.

Shape is another potential morphological adaptation against predation by fishes and crabs. For example, many of the barnacles occur in microhabitats exposed to fishes or crabs (Tables 3, 13). However, the flattened conical shapes of two of the four species may prevent fish beaks or teeth or crab claws from obtaining a firm purchase on the barnacles (Fig. 5; no individuals at either the tropical or temperate sites were in contact with another organism and thus presumably grew uninfluenced by intra- or interspecific crowding). Chthamalus fissus is not only small (up to 8 mm in basal diameter), but it is also relatively flat. Though temperate Chthamalus spp. are also relatively flat, they do not tend to be the most conspicuous barnacles in their habitats, as are C. fissus at our Panama sites. The large Catophragmus pilsbryi and Tetraclita panamensis (up to 7 cm in basal diameter; Fig. 5) have massive shells with broad bases and gently sloping sides. All of these shells appear difficult for fishes to grasp firmly or to crush or both. In contrast, barnacles of the genus Balanus have steeply sloping sides and less massive shells (Balanus balanoides from New England, Balanus inexpectatus from Panama; Fig. 5, authors' personal observations) and appear more susceptible to fish or crab predation. Indeed, we have often found individuals or test fragments of Balanus spp. in Panama fish guts. Further, this is the barnacle genus we most frequently observe crushed in the field. Crushed Tetraclita, Catophragmus, and Chthamalus are observed less often at our study areas. Note that the tropical Balanus inexpectatus has a lower shell height : basal diameter ratio than does the temperate B. balanoides. This intrageneric pattern is consistent with (but does not prove) the notion that increased predation pressure in Panama selects for lower, broader barnacle shapes.

Hence, there is a substantial amount of indirect evidence which supports the view that predation and herbivory exert strong effects on most intertidal animal and plant species at Taboguilla. Moreover, shelter of some sort seems essential for continued persistence of most species in this community.

Heterogeneity and community structure

Ecologists have long known that environmental heterogeneity is related to diversity (e.g., Hutchinson 1959, Mac Arthur and Mac Arthur 1961, Mac Arthur 1972, Wiens 1976). The actual mechanisms behind such correlations are rarely known though both competition (Mac Arthur 1972) and predation (Connell 1975) are stressed as major potential driving agents. Experimental examination of the relation between di-



FIG. 4. Regressions of flesh dry mass (g) on shell mass (g) in temperate (*Thais lapillus*) and tropical (*T. melones*) carnivorous snails. Both species are the most abundant predatory gastropods in their respective habitats. The regression lines are significantly different with common slopes but different y-intercepts (see text).

versity and heterogeneity is rare (but see e.g., Kohn and Leviten 1976, Woodin 1978). Tests of the mechanisms responsible for the relationship are even less common (but see e.g., Woodin 1978).

Our experiments and observations suggest that, relative to the temperate rocky intertidal communities, the types of available refugia are more restricted in the tropical rocky intertidal community at Taboguilla. Thus, escapes in numbers, size, and time seem largely unavailable. Escapes in space also seem more restricted, and the only fairly reliable type of spatial escape seems to be three-dimensional space (depth within the substratum). However, even this refuge can be entered by the smaller invertebrate predators. Finally, though we can say little about behavioral, chemical, and morphological refuges, some evidence suggests that some of the species in this system depend on such defenses.

Holes and crevices thus seem of unusually great importance to patterns of community structure in this system. There are several implications of this result. First, were such refugia unavailable, fishes and crabs would probably completely eliminate many plant and animal species from this community, and hence would lower overall community diversity. Second, though substratum heterogeneity seems to be a major physical dimension for soft-substratum communities (Woodin 1978, Peterson 1979), it evidently plays a less important role for the epibiota in temperate hard-substratum communities. Thus, most of the algal and animal



FIG. 5. Scattergrams of basal diameter (cm) on shell height (cm) for three tropical (*Catophragmus pilsbryi, Tetraclita panamensis*, and *Balanus inexpectatus*) and one temperate (*B. balanoides*) barnacle species. Linear regression equations (y = height, x = basal diameter) are y = 2.53 + 1.44x (*B. balanoides*, N = 23), y = -0.06 + 0.84x (*B. inexpectatus*, N = 50), y = -1.65 + 0.62x (*T. panamensis*, N = 60), and y = 0.19 + 0.32x (*C. pilsbryi*, N = 172). Analysis of covariance indicates that there are differences among the regression lines ($F_{\text{common line}} = 39.76$; 8,279 df; P < .001). These differences are primarily in slope ($F_{\text{common slope}} = 26.26$; 4,279 df; P < .001); the y-intercepts for all species except *Tetraclita panamensis* (t = 2.73, P < .004) are ≈ 0 (t tests, P > .05 or greater). Examination of 95% confidence intervals for slopes indicates that the regression line for *Catophragmus* differs from all other species; the line for *B. inexpectatus* differs from all but *Balanus inexpectatus*.

species which would occur out in the open in a temperate rocky intertidal community seem to occur almost exclusively in holes and crevices in this tropical rocky intertidal community. One interesting consequence of this is that in the tropical community, the cryptofauna (i.e., sponges, bryozoa, hydrozoa, tunicates), which normally occupy holes and crevices in both temperate and tropical areas, co-occur more intimately with organisms (such as barnacles, oysters, limpets, etc.) which more typically occur on exposed surfaces. The interactions among these species are not yet known and will be a focus of our future research efforts.

Finally, the results reported here lead to the conclusion that the population dynamics of most sessile species in this tropical system are likely to be quite different from those of comparable temperate species. Thus, since most sessile species are rare, inter-individual contact is infrequent and occurs primarily in the holes and crevices. However, even these refuges are rarely packed with algae or sessile animals; much space is either bare or covered with encrusting algae. Hence, space competition among non-encrusting forms in this tropical system would seem less important to the ecology of most of these species. This is in strong contrast to most temperate communities, where competition for space is a relatively frequent event, especially in high zones and on wave-exposed shores (e.g., Dayton 1971, 1975, Menge 1976, Lubchenco and Menge 1978).

Second, since holes and crevices represent discrete, largely discontinuous patches within a large expanse of relatively more homogeneous rock substratum, habitat patchiness, as perceived by the organisms dwelling on the shore, may be greater in this tropical system as compared to the temperate communities. This may lead to differences in dispersal, competitive abilities, and larval characteristics.

Third, those organisms which are usually so enormously abundant in temperate communities (e.g., mussels, barnacles, macroalgae) are scarce or almost completely lacking in this system. For example, mussel species which can reach large size dominate much space in many temperate communities (e.g., Table 2) while in this tropical system, the most common mussel, Brachidontes semilaevis is small (usually <1 cm), scarce (usually $\leq 1\%$ cover), and almost invariably occurs in shallow, narrow cracks in the rock. The only individuals we have observed not in cracks occurred in our fast-moving consumer exclusion treatments (Tables 7 and 8). Moreover, a larger mussel Modiolus capax (\approx 4–5 cm long) has been observed to invade and persist in exposed microhabitats only in our fastmoving consumer exclusion treatments. Modiolus is normally exceedingly scarce. The only individuals of this species we have seen were in these treatments or December 1981

co-occurring with another mytilid (unidentified) in a small clump of 100 individuals in a high intertidal tidepool in a cave on a reef south of Taboga Island (≈ 4 km southwest of Taboguilla Island). The virtual absence of such mussels from these tropical sites and their settlement on substrata lacking fishes and crabs thus seems attributable to much greater predation intensity on these bivalves in tropical as opposed to temperate regions. Although temperate mussels are preyed upon by fishes (e.g., cunners in New England, authors' personal observations; pile perch in the Pacific Northwest, Brett 1979), these predators seem to have little effect on mussel abundance, at least along rocky shores, perhaps due in part to restriction of activity by wave surge. The near-absence of large mussels further suggests that the dynamics of this tropical community are different in major ways from wellknown temperate communities. The ways in which the Taboguilla community differs from the temperate ones thus include this lack of large mussels, the apparent lack of "keystone species," the overwhelming influence of consumers on patterns of refuge availability, the importance of diversity in types as well as numbers of consumer species, and the reduced importance of macroalgae as structural and organizational components of the community. Although we now have some insight into these differences, determination of the extent and general significance of many of them must await further research.

Acknowledgments

We thank many people, but particularly L. Ashkenas, R. Emlet, S. Gaines, S. Garrity, P. Lubchenco, J. Lucas, and S. Strauss for able and devoted field assistance. J. Cubit made numerous clever suggestions regarding technique which we adopted. We acknowledge the government of the Republic of Panama for allowing us to work unimpeded in their waters. I. Rubinoff provided access to Smithsonian Tropical Research Institute (STRI) facilities and we thank several STRI personnel and staff members for various acts of assistance and kindness; in particular, T. Borges, J. Budria, P. Glynn, E. G. Leigh, I. Rubinoff, and V. Vergel have been supportive. Numerous useful comments and constructive criticisms were offered by A. J. Southward, P. S. Dawson, the members of the Oregon State University Ecology Discussion Group, and an anonymous reviewer. The latter and W. Rice gave especially useful advice on statistical procedures. This research has been supported by NSF grants OCE76-22251, and OCE78-17899 to the authors.

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