

## A test of the Menge-Sutherland model of community organization in a tropical rocky intertidal food web

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**Summary.** Menge and Sutherland (1976) predicted that in physically benign habitats: (1) community structure will be most strongly affected by predation, (2) the effect of predation will increase with a decrease in trophic position in the food web, (3) trophically intermediate species will be influenced by both predation and competition, and (4) competition will occur among prey species which successfully escape consumers. These predictions were tested in a tropical rocky intertidal community on the Pacific coast of Panama. The most abundant mobile species included fishes and crabs, which occupied the top trophic level, and predaceous gastropods and herbivorous molluscs, which occupied intermediate trophic levels. The most abundant sessile organisms were encrusting algae, foliose algae, barnacles, and bivalves. Diets were broad and overlapping, and 30.3% of the consumers were omnivorous. Each consumer group had strong effects on prey occurring at lower trophic levels: (1) Fishes and crabs reduced the abundance of predaceous snails, herbivorous molluscs, foliose algae, and sessile invertebrates. (2) Predaceous gastropods reduced the abundance of herbivorous molluscs and sessile invertebrates. (3) Herbivorous molluscs reduced the abundance of foliose algae and young stages of sessile invertebrates, and altered relative abundances of the encrusting algae. The encrusting algae, although normally the dominant space occupiers, proved to be inferior competitors for space with other sessile organisms when consumers were experimentally excluded. However, the crusts escaped consumers by virtue of superior anti-herbivore defenses and competed for space despite intense grazing. Observations do not support the hypothesis that the trophically intermediate species compete. Hence, with the exception of this last observation, the predictions of the Menge and Sutherland model were supported. Although further work is needed to evaluate other predictions of the model in this community, evidence from this study joins an increasing body of knowledge supporting the model. Contradictory evidence also exists, however, indicating that aspects of the model require revision.

**Key words:** Community regulation – Experiments – Food web – Rocky intertidal – Tropics

In their model explaining the regulation of terrestrial food webs, Hairston et al. (1960), proposed that the importance of predation and competition alternated with trophic level: (1) carnivores (= top predators) are limited by the availability of prey (= herbivores), and are thereby regulated by competition for food; hence, (2) the abundance of herbivores is kept low by predation; and consequently, (3) plants, in the absence of control by herbivores, become abundant and compete for space. As used by Hairston et al. (1960), the term “regulate” referred primarily to control of abundances. Our use of this term includes this meaning, but is defined somewhat more broadly to include control of distribution, abundance, species composition, and diversity.

Inspired by these arguments, Menge and Sutherland (1976) proposed an expanded and somewhat different model. Like Hairston et al. (1960), Menge and Sutherland (1976) suggested that the top trophic level should be regulated by competition, but unlike Hairston et al. (1960), Menge and Sutherland (1976) suggested that under certain conditions, herbivores or organisms at the bottom trophic level (= basal species; Pimm 1980) may in fact be the “top” trophic level. These conditions are when the number of trophic levels (and/or consumers) effective in controlling prey are reduced by environmental harshness. Thus, whereas Hairston et al. (1960) was restricted to food webs with three trophic levels, Menge and Sutherland (1976) suggested that the number of trophic levels and consumer effectiveness varied with environmental conditions.

In contrast to the alternation between predation and competition as controlling agents proposed by Hairston et al. (1960), Menge and Sutherland (1976) suggested that the importance of predation as a regulating factor increased, and competition decreased at successively lower trophic levels. This prediction arose from the observation that in many food webs, consumers at higher levels feed on several lower trophic levels rather than on just the next lower trophic level. Finally, like Hairston et al. (1960), Menge and Sutherland (1976) suggested that basal species should compete for space or light, but only under conditions favoring an escape from predation. Thus, Menge and Sutherland (1976) proposed that the structure of the basal species assemblage is regulated by predation on juvenile stages, and that competition occurring among adults which successfully pass through this predation bottleneck has a lesser effect on basal species structure. Connell (1975) independently offered similar arguments, and suggested that es-

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capacities by prey depended, in part, on the relative sizes of predator and prey.

Recent reviews have emphasized the need for simultaneous investigation of all major structuring processes in studies of community organization (e.g., Connell 1983; Strong 1983; Schoener 1983; Sih et al. 1985). Because few such studies are available, empirical evaluation of the predictions of models of community structure is still in preliminary stages (see, e.g., Lubchenco 1986; Sih et al. 1985; Menge and Farrell 1986). Here we present a partial test of the Menge and Sutherland (1976) model. We compare model predictions with results from a recently completed study of community organization in rocky intertidal habitats in the Bay of Panama (e.g., Menge and Lubchenco 1981; Menge et al. 1983, 1985, 1986; Lubchenco et al. 1984).

### Predictions of the model

The predictions of Menge and Sutherland (1976) depend on the physical environment in the habitat of interest because the model postulates that trophic complexity depends on environmental conditions. Specifically, consumer abundance and activity appears to be more strongly inhibited by environmental harshness than is abundance of sessile prey (e.g., Connell 1975; Menge 1978a, b), and therefore effective trophic complexity should increase with decreased environmental harshness. Thus, communities in harsh environments should have few effective consumers and few trophic levels whereas communities in more moderate environments should have many effective consumers and several trophic levels.

We consider the physical environment in the low zone of the rocky intertidal region on the Pacific coast of Panama to be benign, because it experiences little seasonal variation, has "warm" (i.e., ranging from 18–26° C) water temperatures, and rarely experiences the severe wave action typical of temperate areas during storms (e.g., Lubchenco et al. 1984). Although air temperatures regularly reach "harsh" levels in the dry season (i.e., >30° C), and probably have a major influence on community structure at high and mid intertidal levels (e.g., Garrity 1984; Lubchenco et al. 1984), evidence suggests that heat and desiccation have little effect on community structure at low intertidal levels (Menge et al. 1986).

The model predicts that within food webs in benign environments: (1) food web complexity will be high and, as a result, predation will be the dominant overall biotic structuring agent; (2) the structure of the lowest trophic level will be regulated by predation; (3) well-defended basal species which escape control by consumers will compete, but this will have a minor effect on the structure of the lowest trophic level; (4) trophically intermediate species (herbivores and primary carnivores) will be controlled by both (a) predation and (b) competition; (5) top consumers will be regulated by competition, and predation will by definition have little effect at this level; and (6) the probability of escape (in space, time, size, behavior, chemical composition) from consumers will be lowest among basal species and increasingly great at higher trophic levels.

Like most models of community organization, Menge and Sutherland (1976) can be criticized because its predictions are not stated in easily falsified all-or-none terms (e.g.,

Quinn and Dunham 1983). For example, the effects of competition and predation are stated in relative terms. One could thus question how much control by a factor is necessary to be considered "important", or "dominant", or to indicate "regulation". While we agree that precisely defined null and alternative hypotheses are desirable and perhaps ideal, community-level models are less amenable to such tests than are (e.g.) population-level models (Quinn and Dunham 1983). In particular, structure typically depends on several interacting processes, not single factors like competition or predation (e.g., Connell 1983). Although we hope that community models can eventually be made more precise, we concur with Levins (1968) and Roughgarden (1983), who argue that realism and generality are most desirable, at least in the initial stages of model development. Although these are not the only criticisms of these models (see e.g., Underwood and Denley 1984), we defer further comment to the discussion.

Below, we evaluate predictions 1–6 (above) as follows: First, we describe food web structure and body sizes of consumers. Second, we evaluate the strength of links between different levels of the food web. Third, we consider whether or not, and where, interspecific competition occurs in the food web. Fourth, we summarize our results in an "interaction" web. Finally, in the discussion, we consider the strength of these "tests", and evaluate our evidence in relation to other investigations in both marine and non-marine habitats. Our data suggest that: (1) predation is the primary factor structuring the community; (2) predation is most severe on basal species; (3) trophically intermediate species are influenced by predation; and (4) competition occurs among species of crustose algae which, as a group, are competitively inferior to foliose algae and sessile invertebrates, but possess superior defenses to consumers. Since evidence regarding competition among mobile species and the probability of escape in relation to trophic level is lacking, we cannot evaluate predictions (4b), (5), or (6).

### Study sites

Descriptions of the study site, on the southern shore of Taboguilla Island in the Bay of Panama, were given in Menge and Lubchenco (1981) and Lubchenco et al. (1984). Spatial structure in this community was unlike temperature rocky intertidal habitats: the basaltic shore was covered by a pavement of crustose algae, with only a scattering of barnacles, bivalves, and foliose algae (total cover ranges from 0 to 17%). Despite the scarcity of sessile organisms, species richness was high, with many species of sponges, bryozoans, and colonial ascidians occurring in holes and crevices in the rock surface. Mobile consumers, in contrast, were abundant, and included limpets, chitons, sea urchins, herbivorous and predaceous gastropods, crabs, and herbivorous and predaceous fishes. Unlike most cold temperate rocky shores, many fishes foraged regularly in the intertidal region, feeding on both algae and sessile and mobile animals.

Physically, water and air temperatures were nearly always "warm" (i.e., >20° C). Tidal amplitude ranged between about 3 m (neap tides) and 6.4 m (spring tides). Seasonal changes were small, with the dry season (mid-December through April) having less rainfall, cooler seawater temperatures, warmer midday air temperatures, and smaller

swells than the wet season (May through mid-December; see Glynn 1972; Glynn and Stewart 1973; Lubchenco et al. 1984).

## Methods

### *Observations and measurements*

A variety of qualitative and quantitative methods, including direct field observations, gut contents, results of experiments, and the literature, were used to determine trophic relationships, and as a result, the food web in the Appendix is qualitative. This qualitative food web is sufficient for our purposes because the primary goal of this portion of the study was to identify the major consumer-prey links. (This food web should not be used by others for any quantitative purposes.)

Diets of slow-moving, invertebrate consumers were determined by examining individuals during feeding periods (e.g., Mauzey et al. 1968; Paine 1980; Menge 1972; Menge and Menge 1974). Although diet proportions so obtained may be imprecise (e.g., Peterson and Bradley 1978; Fairweather and Underwood 1983), they are sufficient for approximating the frequency of links between consumers and prey.

Diets of fast-moving consumers (crabs and fishes) were determined by direct observation and examination of gut contents of fishes speared in dry and wet seasons 1977–1980 (e.g., Randall 1967; Hiatt and Strasburg 1960; Hobson 1974). Quantitative estimates of animal prey in fish guts were made by counting individual prey items, determining prey volume, or both. We examined gut contents for indications that prey were alive when eaten, such as gastropod opercula. Quantitative estimates of plant material were obtained by scanning aliquots of a suspension of the gut contents under  $10\times$  magnification. Algal abundance was determined from examination of one hundred consecutive fields of view.

To reduce the effects of spatial variation in diet composition, fish collection was restricted to the vicinity of Taboguilla Island, although no fishes were collected from the experimental study sites, *per se*. Because most species were relatively scarce, and migration between sampling and experimental sites was possible, sample sizes of fishes were usually small ( $n=2$  to 10 individuals/species). However, most species proved so generalized in diet that further collections would have primarily influenced dietary proportions; dietary range would either not change or increase.

To determine size structure, linear dimensions and weights of animals were estimated either in the field (mostly invertebrates), or from collections taken to the laboratory (crabs, fishes). Weight measurements included total, shell, and flesh wet and dry weights. Linear measurements depended on taxon. For gastropods, bivalves, and chitons we measured length or shell height; for sea urchins and barnacles we measured test or basal diameter; for fishes we measured standard length; and for crabs we measured carapace width.

Linear dimensions were not determined for the algae because most non-encrusting thalli were  $<3$  cm long and bound into turfs, and individual thalli of encrusting algae were usually indistinguishable. Instead, we determined algal (and sessile invertebrate) biomass at the end of the experi-

ment by scraping all sessile organisms off the rock surface in four  $10\times 10$  cm quadrat subsamples in 24 of the 32 plots (each  $0.25\text{ m}^2$ ) used in the consumer exclusion experiments described below. Abundance of sessile organisms was thus estimated in at least two of three ways: biomass/ $\text{m}^2$ , percent cover, and, for solitary sessile animals, density.

### *Experiments: effects of consumers on prey abundance*

Experiments evaluating the effects of four groups of consumers on sessile and mobile prey were done at Taboguilla Island from 1977–1980 (for details, see Menge and Lubchenco 1981; Menge et al. 1986). Briefly, the effects of (1) predaceous gastropods and (2) herbivorous molluscs were determined by quantifying changes in prey abundance in  $0.5\times 0.5$  m plots in the absence (achieved by manual removal) of neither, either, or both of these groups. The effects of (3) large fishes and (4) small fishes and crabs were evaluated by quantifying changes in prey abundance in the absence (achieved by  $0.5\times 0.5$  m stainless steel mesh enclosures) of neither, both, or one of these groups. By placing enclosures at each of the four sites at which herbivorous molluscs and predaceous gastropods were manipulated, we were able to determine the effects of most, but not all (12 of a possible 16) combinations of the four consumer groups. (We were unable to devise a method of excluding small fishes and crabs and leaving large fishes present; see Menge et al. 1986). Two to four plots of each treatment were established in the low intertidal region. Changes in percent cover of sessile organisms, here summarized for comparison to biomass, have been analyzed and presented earlier (e.g., Menge and Lubchenco 1981; Lubchenco et al. 1984; Menge et al. 1985, 1986). Changes in abundance of mobile prey species, and biomass of sessile organisms are presented here for the first time.

### *Experiments: rate of predation and effect of prey size*

Two short-term experiments were performed to determine the susceptibility to predation of sessile organisms, particularly barnacles and bivalves. First, the inside surfaces of enclosures in low and mid zones developed high densities of the small (3–5 mm basal diameter) barnacle *Chthamalus fissus* (Fig. 1). On February 14, 1980, we replaced barnacle-fouled enclosures with clean ones; the fouled enclosures were then fastened upside down to the rock, exposing barnacles to the water column. Two enclosures, one in each zone, were covered with a complete cage (which were removed during low tide) to monitor mortality from sources other than consumers, and four (two per zone) were left uncovered. *Chthamalus* abundance was estimated daily for seven days.

Second, predation rates on dense concentrations of prey and the susceptibility of different sizes of sessile prey were determined by removing enclosures from plots that had been protected from consumers for four years (1977–1981). After percent cover of sessile organisms was estimated, enclosures were removed. Although all enclosures were eventually removed (leaving none as controls for “background” mortality during the later stages of this experiment), removals were staggered so that controls were available for about six weeks at each of three sites. Ensuing changes in prey abundance were quantified whenever daily checks indicated that large changes had occurred, until May–June 1981.

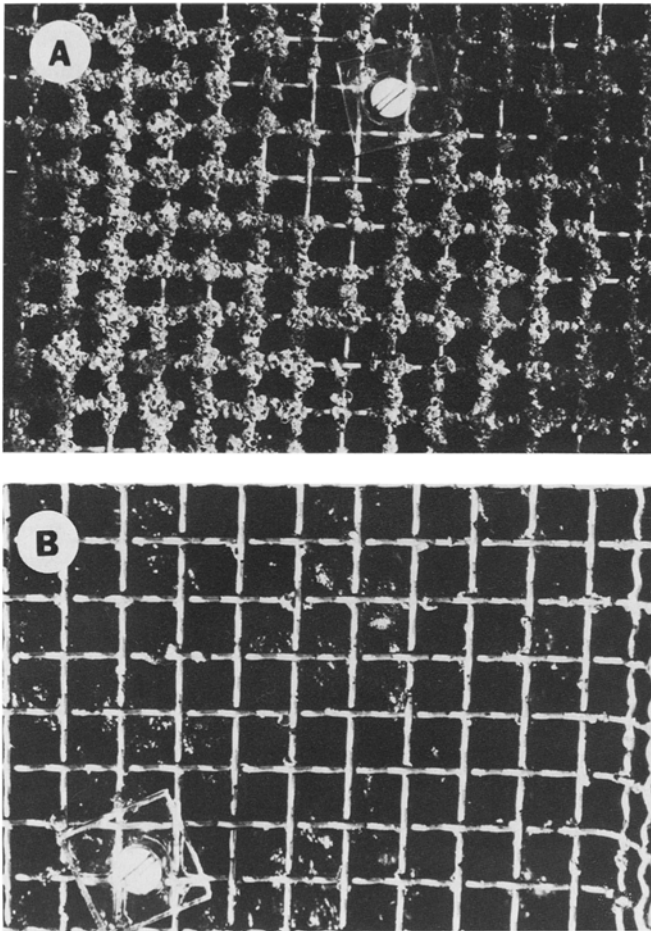


Fig. 1 A, B. Photograph of underside of mesh cage before (A) and after (B) exposure to predation by fishes. Barnacles are all *Chthamalus fissus*. Openings in the mesh are about  $10 \times 10$  mm

#### Interspecific competition

Normally, crustose algae covered more than 90% of the rock surface. Dominant space occupiers included the brown crust *Ralfsia* sp., the blue-green crust *Schizothrix calcicola*, the red crust *Hildenbrandia* sp., and encrusting coralline algae (a complex of several unidentified, difficult to distinguish species). Previous results indicated that the dominance of these crusts was a function of their superior resistance to predation; in the absence of consumers, bivalves eventually overgrew the crusts and became the dominant space occupants (Menge et al. 1985, 1986). Under normal conditions, the factors (s) preventing one of the species of crusts from outcompeting the others and monopolizing space were unknown. An obvious hypothesis considered below is that the crusts were differentially susceptible to molluscan grazers.

The best method of evaluating interspecific competition among the crusts would be to selectively remove each crust species and observe the response of the remaining crusts. We did not do this experiment because it was logistically unfeasible due to the patchiness and small patch size of each species. Less direct evidence on competition was obtained from the consumer removal experiment described above. From 1977–1980, changes in crust abundance were monitored under normal, reduced, and increased grazing

(removal of predaceous gastropods led to increased abundance and then increased size of herbivorous molluscs). Since factors other than competition can affect crust abundance, we first used stepwise linear regression to remove variation in crust cover ( $Y_i$ ) due to (hopefully all) other habitat variables (the  $X_i$ 's): season (wet or dry), a major physical variable; density of invertebrate herbivores (number invading removal plots, or resident in non-removal plots), the major consumers; and cover of both solitary sessile animals and foliose algae, the major non-crust competitors for space. Strongly negative correlation coefficients among the residuals for pairs of crusts suggests competition for space occurred, while positive, or no correlation suggests no competition occurred.

Because preliminary observations suggested that predation had the strongest biotic influence on community structure, we initially focussed on this factor. The magnitude of this task prevented simultaneous experimental tests for competition among the consumers, a major task by itself. However, the design of the study yielded information on changes in abundance of the prey of the consumers, both sessile (see above) and mobile organisms, thus providing indirect, correlative evidence regarding competition.

## Results

### *The food web*

The major consumers in this food web were fishes, molluscs (gastropods and chitons), echinoderms (sea urchins and a seastar), and crabs (Table 1, see Appendix for details). Predators (45.5% of the total number of species) occurred in each of these four taxa, while herbivores (24.2% of the total) and omnivores (30.3% of the total) occurred in two and three of the four taxa, respectively. Prominent omnivores (defined as consumers which included substantial quantities of both plants and animals in their diets), included sea urchins, grapsid crabs, parrotfishes and damselfishes, all of which are classically regarded as herbivores, and wrasses, classically considered carnivores.

As expected, mobile animals had fewer predators on average (2.1/prey species) than did sessile animals (4.8/prey) or plants (4.4/prey;  $P < 0.01$ , 99% confidence intervals do not overlap; Table 1). On average, each prey species was fed upon by  $3.8 \pm 0.4$  consumers. The diet of each consumer included an average of 8.1 prey species (Table 1).

Overlap among consumers was high; each shared prey with about 8 other species (Table 1). Further, each prey taxon in a given diet was shared with an average of 6.2 other consumers, and 95.6% of all prey were shared by 2 or more species. Thus, this food web was typified by dietary generalists whose diets tended to overlap considerably as determined by inclusion or exclusion of prey.

The large size of some of the fishes was a striking feature of this food web. At least 10 species included individuals reaching 1,000 g or more in wet weight (Fig. 2). In contrast, virtually all plants were small; it was rare to observe thalli longer than about 3 cm. Although several predaceous gastropods reached large size, the remaining consumers and animal prey in this food web were roughly comparable in size to those observed in temperate rocky intertidal food webs (author's pers. obs., unpublished data).

In sum, this tropical intertidal food web was character-

**Table 1.** Summary of food web characteristics. Only common species are included. See Appendix for food webs

| A. Taxonomic and trophic composition |             |             |            |           |
|--------------------------------------|-------------|-------------|------------|-----------|
| Category                             |             | Predators   | Herbivores | Omnivores |
| Consumers                            | Fishes      | 8           | 1          | 5         |
|                                      | Molluscs    | 4           | 7          | 0         |
|                                      | Echinoderms | 1           | 0          | 2         |
|                                      | Crabs       | 2           | 0          | 3         |
|                                      | Total       | <i>N</i> 15 | 8          | 10        |
|                                      | %           | 45.5        | 24.2       | 30.3      |

| B. Food web statistics |                               |                |                               |                |
|------------------------|-------------------------------|----------------|-------------------------------|----------------|
| Prey category          | Consumer species/prey species |                | Prey species/consumer species |                |
|                        | $\bar{X}$                     | $\pm 1$ SE (N) | $\bar{X}$                     | $\pm 1$ SE (N) |
| Sessile animals        | 4.8                           | $\pm 0.7$ (21) | 4.6                           | $\pm 0.6$ (22) |
| Mobile animals         | 2.1                           | $\pm 0.2$ (18) | 4.3                           | $\pm 1.4$ (8)  |
| All animals            | 3.5                           | $\pm 0.5$ (39) | 6.2                           | $\pm 1.1$ (22) |
| Plants                 | 4.4                           | $\pm 0.6$ (22) | 6.7                           | $\pm 1.5$ (16) |
| All prey               | 3.8                           | $\pm 0.4$ (62) | 8.1                           | $\pm 1.2$ (30) |

| C. Diet overlap   |  |                    |
|---|--|--------------------|
| $\bar{X}$ N consumers sharing prey/consumer species                             |  | 8.0 $\pm$ 1.2 (30) |
| $\bar{X}$ N consumers shared/prey species in each consumer diet (range=0 to 12) |  | 6.2 $\pm$ 0.4 (30) |
| % of prey shared by 2 or more consumers   |  | 95.6%              |
| % of prey not shared  |  | 4.4%               |

ized by high species richness, low density of sessile organisms, a rather high proportion of omnivores, and consumers with broad, overlapping diets, many of which grew to relatively large size.

#### Consumer-prey interactions

The strength of consumer-prey links is best evaluated by comparing changes in prey abundance, size, or other measures of population performance in the absence and presence of consumers. Here, we examine four key interactions: the effects of fishes on predaceous gastropods (i.e., the F-P link), the effects of fishes on herbivorous molluscs (the F-H link), the effects of predaceous gastropods on herbivorous molluscs (the P-H link), the effects of herbivorous molluscs on crustose algae (the H-C link), and the effects of the entire assemblage of consumers on sessile prey. Most aspects of the latter have been considered in detail elsewhere (Menge and Lubchenco 1981; Menge et al. 1985, 1986). Here, we add to a summary of these results further information on rates of predation and vulnerability of sessile invertebrate animals to predation.

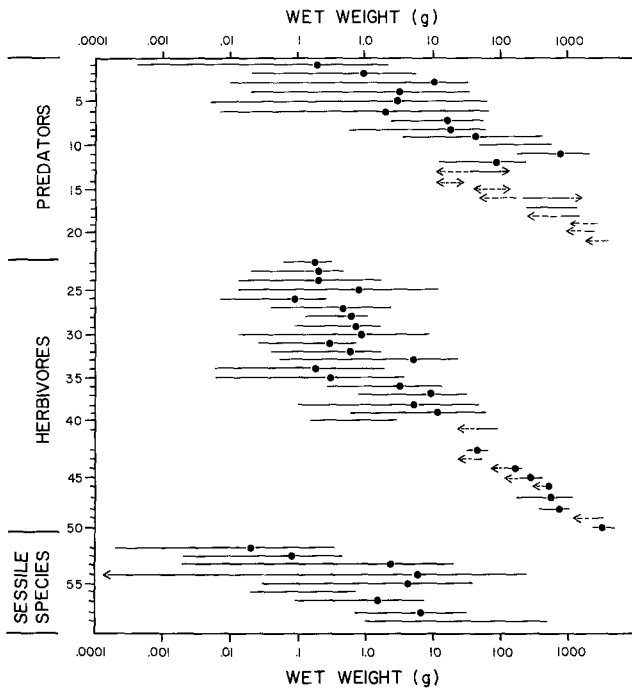
*The fishes-predaceous gastropod link.* Observations suggested that fishes reduce the abundance of predatory snails. First, predatory gastropods were denser at sites with heterogeneous rock surfaces than at sites with homogeneous surfaces (Menge et al. 1985; Gaines, unpublished work). Further, 89% of predaceous snails sampled at low tide on an unmanipulated reef were located in cracks, depressions, crevices, and holes (Table 3 in Menge and Lubchenco 1981).

Gastropods were observed remaining in these locations when covered by water (i.e., in the presence of fishes) at high tide, whether night or day. We believe that similar explanations hold for the occurrence of both mobile and sessile invertebrates in cryptic microhabitats: heterogeneous surfaces provided refuges from predation by large fishes. Their large size prevented the fishes from seizing prey occurring in crevices, holes, and small depressions in the rock (Menge and Lubchenco 1981; Menge et al. 1985; Gaines 1983).

Second, previous experimental studies indicate that predation by fishes and crabs on gastropods is strong (Bertness et al. 1981; Garrity and Levings 1981; Palmer 1979; Wellington and Kuris 1983; Zipser and Vermeij 1978). Although these investigations did not show that fishes reduced the density of gastropods, they provide convincing evidence that fishes can be a powerful source of gastropod mortality. One implication is that small gastropods are particularly vulnerable to fish predation, particularly if they are on homogeneous rock surfaces accessible to fishes.

Additional evidence for the effects of fishes on mobile invertebrates was obtained from the 1977–1980 experiments, in which invertebrate predators were removed from two sites and left undisturbed at two others. Fishes were excluded from plots at each of these sites by cages and roofs, so that we had two types of change in prey abundance to evaluate: changes in density of resident individuals, and changes in number of recruits, defined as individuals either invading from the surfaces surrounding each plot or recruiting from the plankton.

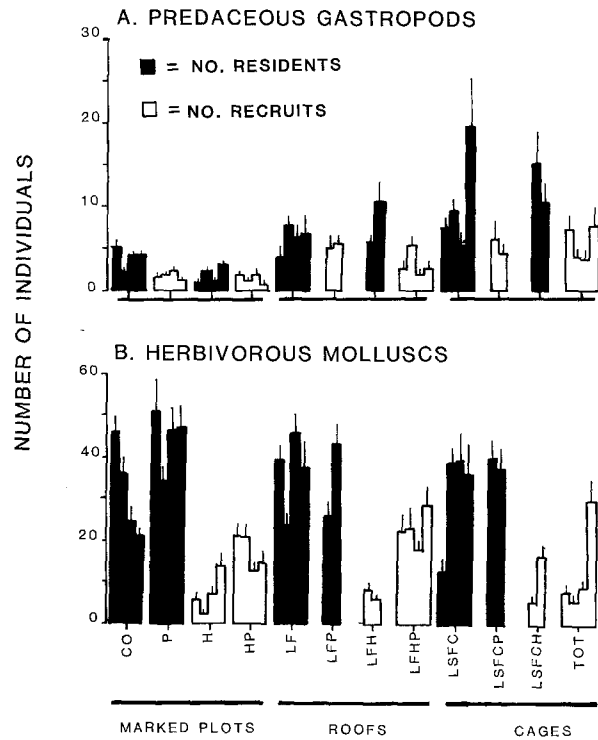
Abundance of predaceous gastropods (mostly *Thais melones* and *Acanthina brevidentata*) increased under cages and



**Fig. 2.** Mean wet weight (solid dots) and range (solid lines) in g of predators, herbivores, and sessile animals in the Taboguilla food web. Lines with dashed portions and arrows are for species with small sample sizes; arrows indicate that smaller or larger individuals occur regularly in the population but were not sampled. Species names, coded by number on the Y-axis of the figure are: 1 *Thais triangularis*; 2 *Acanthina brevidentata*; 3 *Leucozonia cerata*; 4 *Thais speciosa*; 5 *Thais melones*; 6 *Thais biserialis*; 7 *Purpura pansa*; 8 *Opeatostoma pseudodon*; 9 *Neorapana muricata*; 10 *Muricanthus princeps*; 11 *Muricanthus radix* (all predaceous gastropods); 12 *Heliaster microbrachius* (seastar); 13 *Ozius verreauxii* (predaceous crab); 14 *Canthigaster punctatissima*; 15 *Sufflamen verres*; 16 *Bodianus diplotaenia*; 17 *Arothron hispidus*; 18 *Arothron meleagris*; 19 *Diodon hystrix*; 20 *Balistes polylepis*; 21 *Pseudobalistes naufragium* (predaceous fishes); 22 *Littorina modesta*; 23 *L. aspera*; 24 *Nerita funiculata*; 25 *N. scabricosta* (coiled herbivorous snails); 26 *Collisella pediculus*; 27 *Fissurella longifissa*; 28 *Scurria stipulata*; 29 *F. microtrema*; 30 *F. virescens*; 31 *Siphonaria maura*; 32 *S. palmata*; 33 *S. gigas* (limpets); 34 *Ceratizona angusta*; 35 *Acanthochitona hirudiniformis*; 36 *Tonicia forbesi*; 37 *Chiton stokesii* (chitons); 38 *Echinometra vanbrunti*; 39 *Eucidaris thouarsi* (sea urchins); 40 *Pachygrapsus transversus*; 41 *Grapsus grapsus*; 42 *Eriphides hispida* (herbivorous/omnivorous crabs); 43 *Ophioblennius steindachneri*; 44 *Eupomacentrus flavilatus*; 45 *E. acapulcoensis*; 46 *Kyphosus elegans*; 47 *Microspathodon dorsalis*; 48 *Holacanthus passer*; 49 *Pomacanthus zonipectus*; 50 *Prionurus punctatus*; 51 *Scarus perrico* (omnivorous fishes); 52 *Chthamalus fissus*; 53 *Euraphia imperatrix*; 54 *Balanus inexpectatus*; 55 *Tetraclita panamensis*; 56 *Catophragmus pilsbryi* (barnacles); 57 *Braichidontes semilaevis*; 58 *Ostrea palmula*; 59 *Chama echinata*; 60 *Ostrea iridescens* (bivalves)

roofs compared with controls (Fig. 3A, Table 2). Both resident and recruited predaceous gastropods were denser in caged plots, and on one date, roofed plots, than in marked (uncaged or unroofed) plots (Table 2). Hence, assuming that cages and roofs have little effect besides excluding fishes and crabs, predation by either large fishes (excluded by both cages and roofs) or small fishes and crabs (excluded by cages) or both can reduce density of predaceous snails. This assumption seemed true for changes in abundance of sessile organisms (Menge et al. 1986), but needs indepen-

## EFFECTS OF FISHES AND CRABS ON MOBILE MOLLUSCS



**Fig. 3A, B.** Effect of fishes and crabs on mean number of predaceous gastropods (A) or herbivorous molluscs (B) per plot per sample date. Solid histograms density of resident invertebrate consumers; open histograms density of recruits and immigrants invading plots from which invertebrate consumers were removed. Treatment codes: CO controls; P predatory gastropods removed; H herbivorous molluscs removed; LF large fishes excluded; SFC small fishes and crabs excluded; TOT all consumers removed; combinations of these codes indicate removal/exclusion combinations (e.g., LFH large fishes and herbivorous molluscs removed). Bars under each panel indicate plots covered by cages, roofs, or uncovered (marked plots). Error bars are  $\pm 1$  SE

dent experimental evaluation for mobile organisms. We tentatively conclude that, pending tests of alternatives, fishes have a strong effect on abundance of predaceous gastropods.

*The fishes-herbivorous mollusc link.* Like predaceous gastropods, most chitons (99%) and conical limpets (96%) occurred in crevices and holes (Table 3 in Menge and Lubchenco 1981). Flat limpets (e.g., *Siphonaria maura*, *S. palmata*), on the other hand, were more abundant on homogeneous surfaces (Menge et al. 1985; Gaines, unpublished work). Finally, both limpets and chitons were active only during times when fishes were absent from the intertidal region (night high tides, and/or just when the advancing or receding tide covered or exposed them; Menge and Lubchenco 1981; Gaines 1983).

The effect of fishes on herbivorous molluscs was evaluated in two studies. The first was the 1977–1980 experiment mentioned above, while the second was a series of short-term experiments in the laboratory and field which tested the effects of fish predation on limpet abundance in relation

**Table 2.** Effects of LF and SFC on density (number/plot) of resident and recruited predaceous gastropods. *D* dry season, *W* wet season

| Manovas                          |                          | Multiple comparisons |        |          |          |          |          |          |          |          |       |
|----------------------------------|--------------------------|----------------------|--------|----------|----------|----------|----------|----------|----------|----------|-------|
| Response variable                | Test                     | <i>F</i>             | d.f.   | 1977     |          | 1978     |          | 1979     |          | 1980     |       |
|                                  |                          |                      |        | <i>D</i> | <i>W</i> | <i>D</i> | <i>W</i> | <i>D</i> | <i>W</i> | <i>D</i> | d.f.  |
| Resident density<br>(+H sites)   | Full model               | 3.04 <sup>a</sup>    | 14, 14 | ns       | ns       | ns       | ns       | ns       | ns       | 2, 26    |       |
|                                  | Roof effect<br>(-LF+SFC) | 2.16 <sup>ns</sup>   | 7, 7   | -        | -        | -        | ns       | -        | ns       | 1, 13    |       |
|                                  | Cage effect<br>(-LF-SFC) | 4.47 <sup>a</sup>    | 7, 7   | -        | -        | -        | b        | -        | b        | 1, 13    |       |
| Number of recruits<br>(-H sites) | Full model               | 3.92 <sup>b</sup>    | 14, 14 | ns       | ns       | a        | b        | ns       | ns       | 2, 26    |       |
|                                  | Roof effect<br>(-LF+SFC) | 4.88 <sup>a</sup>    | 7, 7   | -        | -        | ns       | b        | -        | -        | 1, 13    |       |
|                                  | Cage effect<br>(-LF-SFC) | 9.96 <sup>b</sup>    | 7, 7   | -        | -        | b        | b        | -        | -        | a        | 1, 13 |

<sup>a</sup> =  $P < 0.05$ ; <sup>b</sup> =  $P > 0.01$ ; ns =  $P > 0.05$ ; - = no test necessary since Full Model was not significant on that date

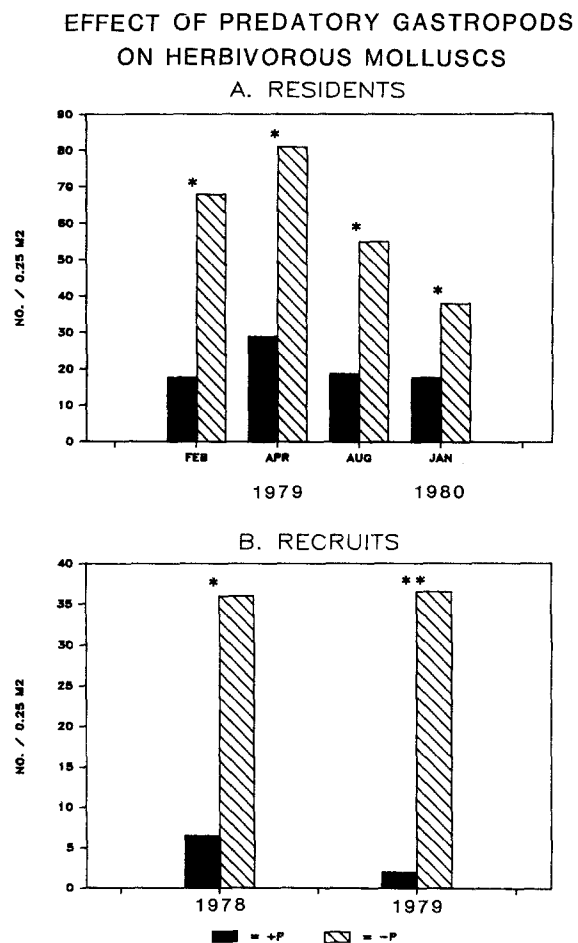
to both limpet morphology (conical vs. flat) and to substratum heterogeneity (Gaines, unpublished work).

Abundance of neither resident nor recruited herbivorous molluscs changed in the absence of fishes or fishes and crabs (Fig. 3B, MANOVA on residents,  $F = 1.26$ ; 14, 14 degrees of freedom;  $P > 0.05$ ; MANOVA on recruits,  $F = 0.81$ ; 14, 14 d.f.;  $P > 0.05$ ). However, neither substratum heterogeneity nor density of predaceous snails, (which prey on herbivorous molluscs; see below) was controlled in these particular experiments, complicating their interpretation.

The second set of experiments (by SDG) varied presence or absence of both fishes and predaceous snails, and substratum heterogeneity. The results, details of which will appear elsewhere (Gaines, unpublished work; see also Gaines 1983), indicated that predation by fishes virtually eliminated conical limpets from homogeneous surfaces while flat limpets were largely immune to this source of mortality. In contrast, predation by fishes was ineffective on heterogeneous surfaces, causing little limpet mortality. Hence, abundance, species composition, and microhabitat of herbivorous limpets was strongly influenced by predation by fishes. Although chitons were not manipulated in Gaines' experiments, and were too scarce to permit the observation of any meaningful changes in abundance in the 1977-1980 experiments, they were probably affected in the same way. They were regularly found in fish guts, were primarily nocturnal, and were exceedingly cryptic, emerging only when inaccessible to fishes.

*The predaceous gastropod-herbivorous mollusc link.* Limpets and chitons were major components of the diets of predaceous snails (Appendix, authors' unpublished data, L. West pers. comm.). Further, abundance of these herbivores was low on heterogeneous surfaces where predaceous gastropods were abundant (Menge et al. 1985; Gaines, unpublished work).

Abundance of resident limpets increased two- to three-fold in the absence of predaceous gastropods (and presence of fishes) by 1980 (Fig. 4A). Abundance of limpet recruits was also affected by predatory snails (Fig. 4B); in both



**Fig. 4A, B.** Effects of predatory gastropods on density of herbivorous molluscs. **A** Effect on residents, February 1979 to January 1980. **B** Effect on recruits, January 1978 and 1979. +P predatory gastropods present; -P predatory gastropods absent. Densities did not differ on other dates (sampled every 1 to 5 months, from February 1977 to January 1980). \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; tested using 1-way ANOVA corrected with Bonferroni approximation for multiple comparisons, 1,6 d.f. in all cases

**Table 3.** Relationship between recruitment of two limpet species ( $Y_i$ 's) and algal crusts, cover of foliose algae, dead barnacle shells, number of other herbivores, predaceous gastropods, and season ( $X_{ij}$ 's). Analysis done using stepwise linear regression

| Treatment               | $Y_i$ (no. recruits 0.25 m <sup>2</sup> ) <sup>a</sup> | Coefficients  |                                 | F (full model) <sup>b</sup> |                | % variance explained         |
|-------------------------|--|---------------|---------------------------------|-----------------------------|----------------|------------------------------|
|                         |  | ( $B_{ij}$ )  | $X_{ij}$                        | P (coeff)                   | r <sup>2</sup> |                              |
| -H-P(Site 2)            | <i>Fissurella virescens</i>                            | $B_0 = -1.60$ | (Y-intercept)                   |                             |                |                              |
|                         |  | $B_1 = 1.53$  | <i>Pachygrapsus transversus</i> | 0.00001                     | 0.712          | 71.2                         |
|                         |  | $B_2 = -2.91$ | Foliose algae                   | 0.013                       | 0.748          | 3.6                          |
|                         |  | $B_3 = 2.01$  | <i>Hildenbrandia</i> sp.        | 0.04                        | 0.763          | 73.06 <sup>b</sup><br>(3,68) |
| <i>Siphonaria maura</i> |  | $B_0 = 1.68$  | (Y-intercept)                   |                             |                |                              |
|                         |  | $B_1 = 1.08$  | <i>Pachygrapsus transversus</i> | 0.00001                     | 0.399          | 39.9                         |
|                         |  | $B_2 = -1.15$ | season                          | 0.0001                      | 0.517          | 36.88 <sup>b</sup><br>(2,69) |

<sup>a</sup> Correlation coefficient ( $r$ ) between residuals of *F. virescens* and *S. maura* = 0.302,  $P > 0.05$

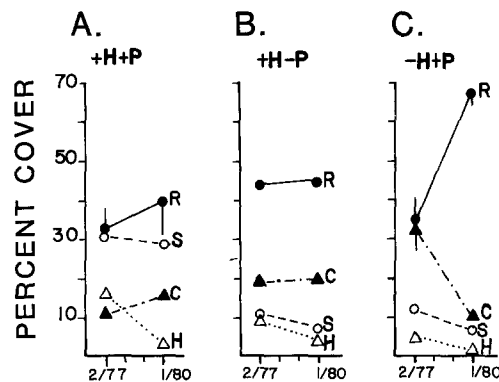
<sup>b</sup>  $P < 0.001$ . Degrees of freedom in parentheses

January 1978 and 1979 the number of invading or settling limpets was 6 to 18 × greater in plots without, than in plots with predatory gastropods.

Although other factors affected recruitment of limpets, predation had the greatest effect (Fig. 4, recruit density with predators was 2 to 6.5 per 0.25 m<sup>2</sup>; without predators, it was 36 per 0.25 m<sup>2</sup>). In the absence of predaceous gastropods, recruitment of both *Fissurella virescens* and *Siphonaria maura* was positively correlated with density of the small, herbivorous crab *Pachygrapsus transversus* (Table 3), which explained 40% (*S. maura*) and 71.2% (*F. virescens*) of the variance. Other significant variables were cover of foliose algae and *Hildenbrandia* (negatively and positively related, respectively) and season (greatest recruitment of *S. maura* in the dry season; Table 3). The positive association between the limpets and *Pachygrapsus* is intriguing, but too little is known about the biology of this potential interaction to speculate on causation. The negative association with foliose algae is most likely due to the inability of limpets to attach to turfs (e.g., Underwood and Jernakoff 1981), and that cover of turf increased after removal of the resident herbivores from these treatments (Menge et al. 1986). The positive association with *Hildenbrandia* probably reflects the tendency of this crust to increase (or decrease) with increased (or decreased) grazing (e.g., Levings and Garrity 1983).

We conclude that abundance of both adult and recruiting herbivorous molluscs was strongly influenced by predation by gastropods.

*The herbivorous mollusc-crustose algae link.* Grazing by herbivorous molluscs (limpets and chitons) helped maintain both the high cover of crustose algae and high evenness among species of algal crusts. Normally, more than 90% of low intertidal rock surfaces were covered by several species of algal crusts. To evaluate the effects of grazing by limpets and chitons on crust abundance, we compared changes in cover after three years under normal, reduced (grazing molluscs removed), and increased grazing (predaceous gastropods removed, leading to increased abundance, and eventually, size of grazers). Under both normal and increased grazing, relative abundances of the crust species changed little, but under reduced grazing, abundance of *Ralfsia* nearly doubled while abundance of the other three crusts declined by more than half (Fig. 5). Hence, normal



**Fig. 5A–C.** Percent cover of four algal crusts at the beginning (2/77) and end (1/80) of the experiments. **A** +H+P normal grazing; both herbivorous molluscs and predaceous snails present. **B** +H–P increased grazing; herbivorous molluscs present, predaceous snails absent (leading to increased density, then size of herbivores). **C** –H+P reduced grazing; herbivorous molluscs absent, predaceous snails present. Code: *R* *Ralfsia* sp.; *S* *Schizothrix calcicola*; *C* coraline crust; *H* *Hildenbrandia* spp

to high levels of grazing prevent *Ralfsia* from monopolizing rock surfaces by displacing other algal crusts. The general effect of herbivorous molluscs was thus to maintain higher evenness, and therefore higher diversity, of species of crustose algae.

*Effect of the consumer assemblage on sessile organisms.* The entire consumer assemblage was responsible for maintaining the dominance of crusts on rock surfaces. Although *Ralfsia* displaced other crusts in the absence of herbivorous molluscs, the presence of the remaining consumers in this treatment prevented invasion and overgrowth of *Ralfsia* by foliose algae and sessile invertebrates (Menge and Lubchenco 1981; Lubchenco et al. 1984; Menge et al. 1985, 1986). Striking increases in percent cover of sessile invertebrates occurred only in treatments from which most or all consumers had been excluded, with crusts being displaced in sequence by foliose algae, barnacles, and bivalves (Menge et al. 1986). Similar increases in biomass occurred; e.g., biomass accumulated in total exclusions was 12 × that in controls, while intermediate treatments accumulated intermediate levels (Fig. 6). Average biomass of sessile invertebrates



## BIOMASS ACCUMULATION

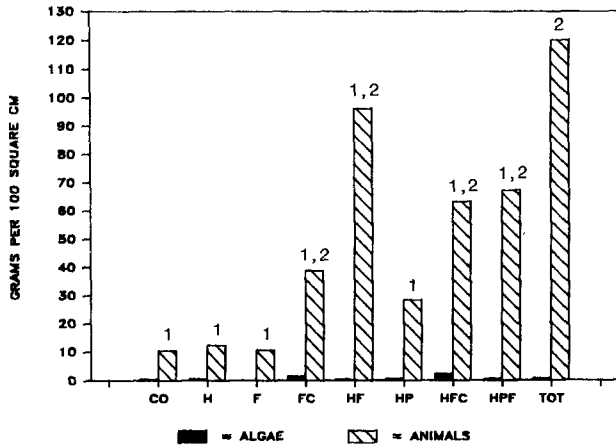


Fig. 6. Accumulation of biomass ( $\text{g}/100 \text{ cm}^2$ ) of sessile invertebrates (Animals) and algae from February 1977 to January 1981. Animal biomass differed among treatments (one-way nested ANOVA;  $F=6.98$ ,  $P<0.001$ ,  $\text{d.f.}=8,110$ ) but algae biomass did not (same test;  $P>0.05$ ). Biomass density differs between treatments if bars have different numbers above them (unplanned comparisons, GT2 method; Sokal and Rohlf 1981)

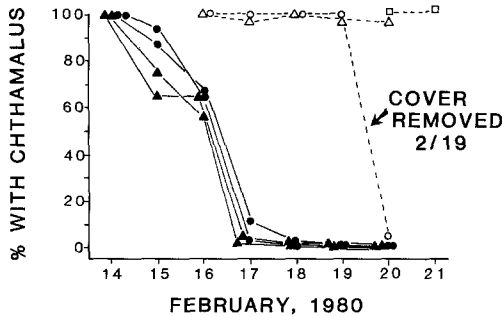


Fig. 7. Percent of mesh intersections with *Chthamalus fissus* on the undersides of enclosures with fishes present (solid symbols) and absent (open symbols) in mid (triangles) and low (circles and squares) zones. The cover was removed from one of the fish enclosures on 2/19, and left on the other. A third enclosure was established in the low zone on 2/20

per plot differed among treatments (nested one-way ANOVA;  $F=6.98$ ,  $8,110 \text{ d.f.}$ ,  $P<0.001$ ), while average biomass of foliose algae did not ( $F=2.07$ ,  $8,88 \text{ d.f.}$ ,  $P>0.05$ ; Fig. 6).

**Predation intensity and escapes in size and space.** When dense concentrations of the barnacle *Chthamalus* were exposed to fishes and crabs in February 1980, rates of predation were high. Consumers had virtually eliminated barnacles within three days of exposure of *Chthamalus* to predators (Figs. 1, 7). A fifth enclosure (February 19; Fig. 7) declined to 5% of its initial value in a single day. Although no similar experiments were carried out in the high zone, experiments reported earlier indicated that predation by both gastropods (Menge and Lubchenco 1981) and fishes (Lubchenco et al. 1984) was responsible for the low prey cover (<5%; Lubchenco et al. 1984) in this zone as well. Hence, predation on both dense and sparse concentrations of *Chthamalus*, a small prey (maximum basal diameter  $\leq 5 \text{ mm}$ ), was intense.

When the sessile prey under roofs and cages were ex-

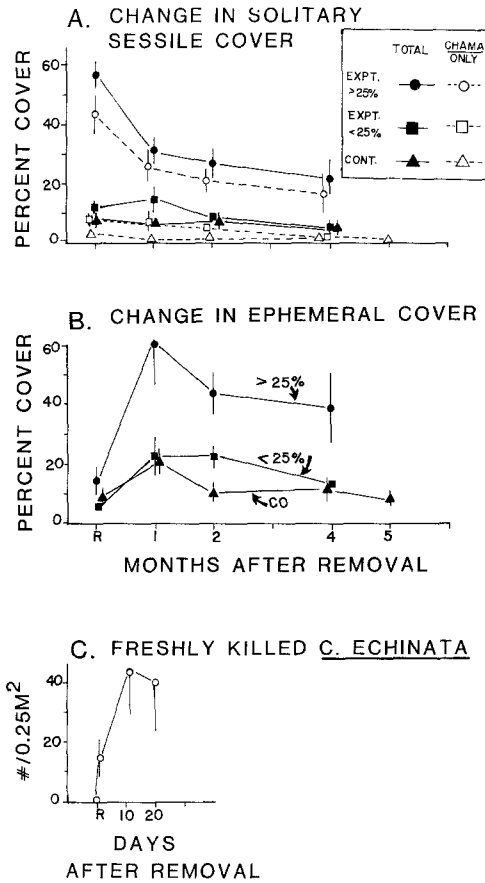


Fig. 8A-C. Changes in abundance of sessile organisms after exposure to fishes and crabs in February 1981. Sessile prey had accumulated under enclosures from 1977 to 1981. **A** Change in cover of solitary sessile animals (solid symbols) and the bivalve *Chama echinata* (open symbols) in plots with >25% initial cover, <25% initial cover, and controls. **B** Change in cover of ephemeral algae in treatments listed in A. **C** Number of recently killed *Chama* (i.e., 2-3 days prior to the observation date), as judged by appearance of the interior of the shell (recently killed individuals have shiny shell interiors, often with some flesh of the adductor muscles remaining attached, while older shells are fouled with ephemeral algae). Percent covers are untransformed, symbols and bars are mean and 1 SE. "R" on X-axis means "Removal Date"

posed to fishes and crabs in February 1981, rates of predation varied, depending on both initial abundance and average individual body size of the prey. First, after removal of enclosures, abundance of prey in patches with >25% cover declined sharply during the first month, while abundance of prey in patches with <25% cover did not change (Fig. 8). Second, abundance of prey declined more slowly in this experiment than in the *Chthamalus* experiment (compare Figs. 7 and 8), even though both experiments were done in the dry season, and in the same place. Apart from taxonomic affinity, major differences among these prey species are body size and morphology. All the abundant barnacles and bivalves in these prey patches were considerably larger than *Chthamalus* (e.g., between about 10 and 100 mm in diameter), and, with the exceptions of *Balanus* spp. and *Modiolus capax*, were flat. The survival of *Balanus* spp. remains puzzling, although fishes may avoid them because normally most *Balanus* shells observed on the shore are actually dead and empty; these remains can last for months. The mussel *Modiolus* was clearly an attractive prey; all

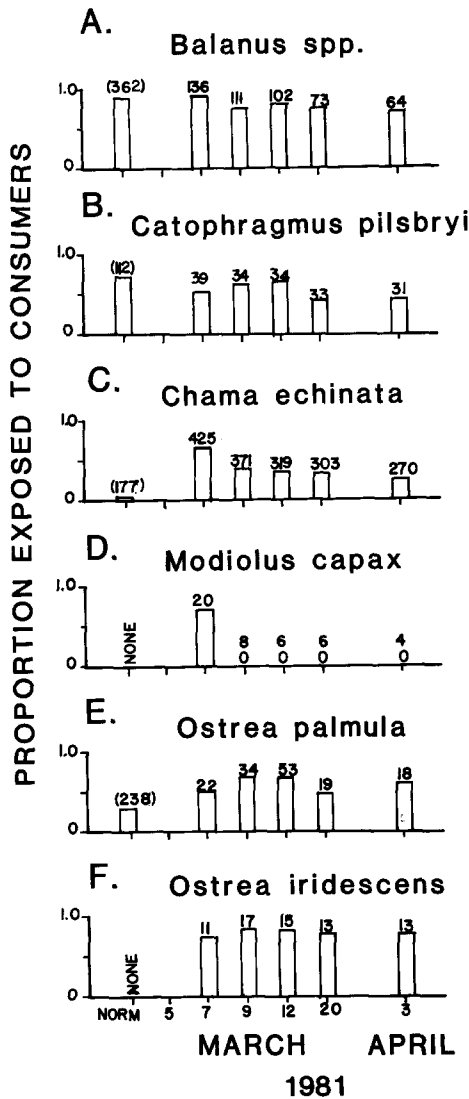


Fig. 9A-F. Proportion of individuals of six common solitary sessile invertebrates exposed to fishes and crabs (i.e., not in holes or crevices). *NORM* the proportions exposed to fishes and crabs in control plots in July 1979, is given by the first bar of each panel for comparison with experimental results. *Remaining bars* indicate changes in proportion occurring after removal of exclusions from exclusion plots that had been protected from fishes and crabs from 1977-1981 (see Fig. 8). Number of individuals (sum in 16 plots for controls; sum in 8 plots for exclusions) of each species present at each date are given above the bars

those exposed to predation by fishes were eliminated almost immediately (Fig. 9).

The lower mortality rates of the barnacle *Catophragmus pilsbryi*, and the bivalves *Chama*, *Ostrea palmula*, and *O. iridescens* (e.g., Fig. 9) was most likely due to their large size, their relatively flattened, smooth shells, and for some, their cryptic nature (*Chama* and *O. palmula* were often invisible due to a cover of foliose or encrusting algae and hydroids). Their persistence in this experiment in microhabitats exposed to predation by fishes and crabs (Fig. 9), compared to their usual near-absence from such places (Menge and Lubchenco 1981), indicates that large size lowers their susceptibility to predators. However, their steady decline in abundance (Figs. 8, 9) suggests that this refuge was tempo-

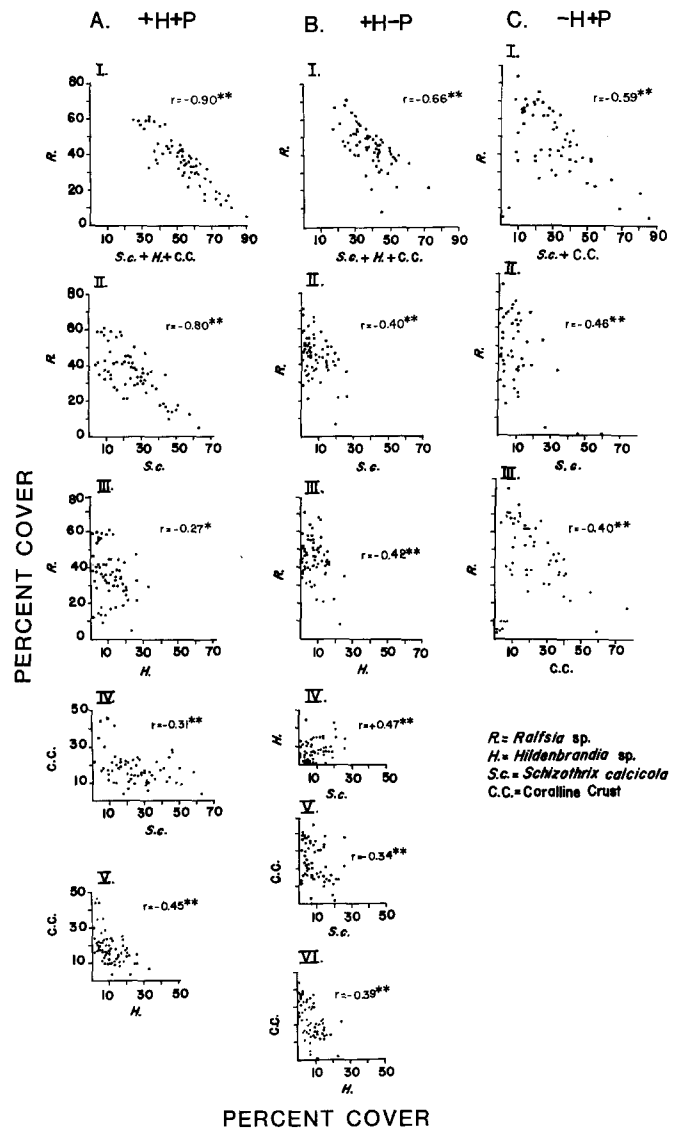


Fig. 10A-C. Scattergrams of percent covers of algal crusts under three levels of grazing. A +H+P normal grazing; both herbivorous molluscs and predaceous snails present. B +H-P increased grazing; herbivorous molluscs present, predaceous snails absent. C -H+P reduced grazing; herbivorous molluscs absent, predaceous snails present. Only significant correlations are shown. *Panels I* (in A, B, C) are plots of *Ralfsia* vs. total cover of three remaining crusts; *panels II-VI* are crust pairs

rary. Moreover, size-related refuges are probably of little importance in this community, since under normal conditions of high predation, most sessile prey occur in crevices and holes rather than open rock surfaces (Menge and Lubchenco 1981).

#### Competitive interactions

*Competition for space.* Observations indicate that competition for space occurs among the algal crusts, and that *Ralfsia* is the dominant competitor for space. For example, during colonization of artificial holes, *Ralfsia* overgrows both *Schizothrix* and coralline crust, and coralline crust overgrows *Ralfsia* (Menge et al. 1983, authors' unpublished

data). Further, both *Ralfsia* and coralline crust will settle and grow on each other, while *Schizothrix* will settle and grow on *Ralfsia*. Finally, during colonization of bare rock in crust removal experiments, near-monocultures of *Ralfsia* form in the absence of herbivorous molluscs, while crust mosaics form in their presence (although *Ralfsia* is still the most abundant species; authors' unpublished data).

Competition among the crusts is also suggested by inverse correlations between changes in their abundances in marked plots from 1977–1980 (Fig. 10). Further, differences in relative abundances of these crusts under normal, increased, and decreased grazing by herbivorous molluscs suggest that *Ralfsia* was the dominant competitor (Figs. 5, 10). For example, covers of the two most abundant crusts, *Ralfsia* spp. and *Schizothrix calcicola*, were inversely correlated under all three grazing regimes (Fig. 10), and *Ralfsia* was most abundant when grazing by limpets and chitons was low. The competitive dominance of *Ralfsia* is also suggested by the strong inverse correlations that result when its abundance is plotted against the combined cover of the other three crusts (Fig. 10A, B, C, top panels), and by the lack of correlation between each of the other crust species vs. the remaining three ( $P > 0.05$ ).

Hence, although a direct experimental test is needed, the evidence supports the hypothesis that competition for space occurred among the algal crust species, and that this competition was mediated by grazing by limpets and chitons.

**Competition among consumers.** Indirect evidence suggests that diffuse competition occurred among the consumers. Both foliose algae and sessile invertebrates, the primary food supply for most of the consumers (Appendix), were scarce (Lubchenco et al. 1984). The consumers overlapped broadly in diet (Appendix). Finally, no detectable change in abundance of sessile invertebrates occurred when only one of the four consumer groups was removed, while abundance of sessile animals changed dramatically when all four consumer groups was removed (Menge et al. 1986). This implies that the effect of the absence of one consumer group was masked by the remaining three groups by compensatory changes in abundance, diet breadth, foraging activity, or some other factor. One interpretation of this result is that diffuse competition occurs among the consumers; however, this possibility requires more direct tests.

## Discussion

Results presented here and in Menge et al. (1986) are summarized in Fig. 11. This diagram shows all statistically significant between- and within-trophic level interactions, and is here termed an "interaction" web to distinguish it from the more traditional food web. Food webs show the presence of links between consumers and prey, regardless of strength, while interaction webs show only strong links (*sensu* MacArthur 1972; Paine 1980). Although both direct and indirect interactions could be included, we show only direct links in Fig. 11 for clarity (see Menge et al. 1986 for a list of indirect interactions). Interaction webs could be sharpened further by weighting each strong link according to its ecological significance, as indicated by experiments and the importance of prey in community structure.

Although further testing is needed to clarify certain interactions in this food web, the evidence supports several

## INTERACTION WEB – PANAMA

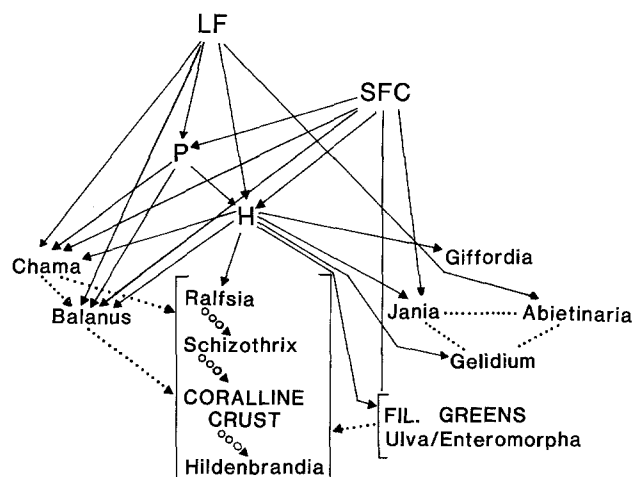


Fig. 11. Interaction web at Taboguilla Island. LF large fishes; SFC small fishes and crabs; P predaceous gastropods; H herbivorous molluscs. Strong (i.e., statistically significant) consumer-prey interactions are indicated by solid lines; arrow points to prey. Open-dot lines indicate competition for space occurring under normal conditions while solid-dot lines indicate competition for space occurring in consumer-exclusion experiments. Dotted lines without arrowheads indicate that no clear competitive dominant was apparent in the interaction. Numerous indirect interactions also occur in this web; see Menge et al. (1986), for details

predictions of Menge and Sutherland (1976). Specifically, the results support predictions (1), (2), and (3): that predation is the dominant overall structuring agent; that the sessile biota would be most strongly affected; and that competition will occur (although with a minor impact on community structure) among well-defended sessile organisms escaping consumers, respectively. Since the dominance of space by algal crusts is evidently maintained by intense predation on other sessile organisms and not competition for space, we conclude that predation is the dominant structuring agent. Moreover, most (21 of 25) links occurring under normal conditions are consumer-prey links, and 16 of these 21 links are between consumers and sessile organisms (Fig. 11). Finally, although the crusts may compete with each other for space, this competition seems mediated by grazing on the dominant crust, *Ralfsia* sp.

Prediction (4), that trophically intermediate species will be affected by both predation and competition is at least partially supported, since abundances of predaceous gastropods and herbivorous molluscs are strongly affected by predation by fishes and crabs (Fig. 11). Although no significant negative correlations (presumed to indicate competition) were detected among species in these consumer groups in Panama ( $P > 0.05$ , or significantly positive correlations; authors' unpublished data), Ortega (1985) obtained evidence for intraspecific competition in the limpets *Siphonaria gigas* and *Fissurella virescens* in Costa Rica, although Panama and Costa Rica differ in several respects (authors' personal observations, S. Ortega and J. Sutherland personal communication). Clearly, further investigation of interactions among the invertebrate predators and herbivores is needed to evaluate prediction (4b), that intermediate consumers should compete.

There is, as yet, insufficient evidence from this commu-

ity to evaluate the remaining predictions (5, 6). If competition exists among the top consumers (i.e., prediction 5), we expect that it will be diffuse and difficult to detect in pairwise experiments. As argued by Connell (1980), competition intensity is likely to be lower in species-rich than in species-poor guilds, because successive interspecific encounters are more likely to be with different species. Most convincing demonstrations of interspecific competition are in guilds of two or three species (Connell 1980, 1983; Schoener 1983, 1985). Nonetheless, a detailed study of the interactions among the fishes, in particular, would be profitable regardless of its outcome.

Prediction (6), that the probability of escape from consumers varies directly with trophic position in the web (e.g., is low among species low in the food web and vice versa) could be readily tested with field experiments. Evidence that several mobile and sessile invertebrates are susceptible to predation is already available (e.g., this study; Zipser and Vermeij 1978; Palmer 1979; Bertness et al. 1981; Garrity and Levings 1981, 1983; Levings and Garrity 1983; Gaines 1983; Wellington and Kuris 1983). We expect that such a study would support the prediction.

#### *Generality of the model: tests in other habitats*

In a recent critique, Underwood and Denley (1984) suggest that the generality of the Menge and Sutherland (1976) model "is not confirmed by subsequent investigations in other communities." Although some of their interpretations can be disputed, there appear to be some examples where model predictions are not supported (e.g., Underwood and Denley 1984; Watanabe 1984; Cubit 1984). Cubit (1984), for example, found that limpet grazing in a high intertidal site on the Oregon coast was relatively more intense during harsh (dry, warm summers) than during benign (wet, cool winters) seasons. Both productivity of ephemeral algae (the food of the limpets), and limpet grazing increased during winter and declined during summer, but algal productivity was depressed more. As a result, limpets were more effective in controlling abundance of the ephemeral algae during the harsh period, while the Menge and Sutherland model predicts the limpets would be less effective. This result suggests that future extensions of the model should include the relative influence of variation in productivity on predators and prey.

Despite such apparently contradictory results, much evidence is consistent with predictions of the Menge and Sutherland model (reviews by Sih et al. 1985; Menge and Farrell 1986; see also Lubchenco 1986; Russ 1980; Underwood 1978; Underwood et al. 1983; Fairweather et al. 1984; Paine et al. 1985; Gaines 1983, 1984; Lynch 1979; Peckarsky and Dodson 1980; Peckarsky 1983; Morin 1983; Zaret 1980; McNaughton 1983; Brown et al. 1986; Strong 1983). For instance, many of these investigations found that in communities with high effective trophic complexity, predation or grazing had important effects on prey; and that some prey species escaped control by consumers and competed for space. In fact, this latter phenomenon may explain the high frequency of competition among terrestrial plants observed by Schoener (1983, 1985) in his review of field experiments. He notes that this evidently supports Hairston et al. (1960) and not Menge and Sutherland (1976). We suggest that the high frequency of competition among plants may or may not support Hairston et al. (1960) de-

pending on whether or not the plants have passed through a predation bottleneck at small/young stages (see Introduction).

We thus suggest that the model is general in the sense that it successfully describes certain aspects of the dynamics of a wide variety of communities. Results inconsistent with the model help in identifying its limitations and are precisely those upon which revisions should be based. A revised model is currently being developed (Menge and Sutherland, in prep.), as are more rigorous methods of testing it (Menge and Farrell 1986).

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Appendix 1. Prey and their principal consumers in the low intertidal food web at Taboguilla. Only common species are included. See text for details of methods. Numbers in parentheses are number of individuals observed feeding

| A. Animal prey species                | Consumer species |        |         |        |        |        |        |        |        |        |         |        |        |          | No. consumers |         |        |         |         |                     |                     |                      |                 |    |   |
|---------------------------------------|------------------|--------|---------|--------|--------|--------|--------|--------|--------|--------|---------|--------|--------|----------|---------------|---------|--------|---------|---------|---------------------|---------------------|----------------------|-----------------|----|---|
|                                       | Ah (5)           | Am (2) | Bd (10) | Bp (4) | Dh (4) | Pn (3) | Sg (1) | Sp (6) | Hp (4) | Pz (4) | Ea (10) | Ke (4) | Pp (2) | Ab (214) |               | Tm (65) | Ti (6) | Mr (30) | Hm (19) | Pt <sup>a</sup> (3) | Gg <sup>a</sup> (4) | Eh <sup>a</sup> (12) | Ev <sup>a</sup> |    |   |
| Sessile                               |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 |    |   |
| <i>Chthamalus fissus</i>              |                  | x      |         |        |        |        |        |        | x      |        |         |        |        |          |               |         | x      |         |         |                     |                     |                      |                 | 4  |   |
| <i>Balanus</i> spp.                   | x                | x      | x       | x      | x      | x      | x      | x      | x      | x      |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 13 |   |
| <i>Catophragmus pilsbryi</i>          |                  |        |         | x      |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 3  |   |
| <i>Tetraclita panamensis</i>          |                  |        |         | x      |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 2  |   |
| <i>Arca mutabilis</i>                 |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 2  |   |
| <i>Brachidontes semilaevis</i>        | x                |        | x       |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 4  |   |
| <i>Chama echinata</i>                 |                  |        | x       | x      | x      |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 6  |   |
| <i>Ostrea palmula</i>                 |                  |        | x       |        | x      |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 6  |   |
| <i>O. iridescens</i>                  |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 4  |   |
| vermetid (red)                        |                  |        | x       | x      | x      | x      |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 1  |   |
| <i>Lithophaga</i> sp.                 |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 6  |   |
| sponge (orange)                       | x                | x      | x       |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 8  |   |
| sponge (brown)                        | x                | x      |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 3  |   |
| sponge (purple)                       |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 2  |   |
| sponge (black)                        |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 2  |   |
| sponge (white)                        | x                | x      | x       |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 10 |   |
| <i>Abietinaria</i> sp.                | x                |        | x       |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 10 |   |
| <i>Didemnum</i> sp.                   |                  | x      |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 3  |   |
| <i>Trididemnum</i> sp.                |                  | x      |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 3  |   |
| <i>Pyura vittata</i>                  | x                | x      | x       |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 1  |   |
| encrusting bryozoans                  |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 7  |   |
| Total sessile eaten                   | 6                | 9      | 6       | 6      | 5      | 5      | 1      | 3      | 4      | 6      | 3       | 4      | 1      | 8        | 10            | 3       | 2      | 3       | 4       | 1                   | 1                   | 1                    | 1               | 9  |   |
| Mobile                                |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 |    |   |
| <i>Siphonaria maura</i>               |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 |    | 3 |
| <i>S. palmata</i>                     |                  |        | x       |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 1  |   |
| <i>Fissurella virescens</i>           |                  |        | x       |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 4  |   |
| <i>F. longifissa</i>                  |                  |        | x       |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 3  |   |
| <i>F. microtrema</i>                  |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 1  |   |
| <i>Collisella pediculus</i>           |                  |        | x       |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 2  |   |
| <i>Ceratozона angusta</i>             |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 2  |   |
| <i>Chiton stokesii</i>                |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 2  |   |
| <i>Acanthochitona hirsudiniformis</i> |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 2  |   |
| <i>Echinometra vanbrunii</i>          |                  |        | x       | x      | x      |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 3  |   |
| <i>Eucidaris thouarsi</i>             |                  |        | x       | x      | x      |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 2  |   |
| <i>Pachygrapsus transversus</i>       |                  |        |         | x      | x      | x      |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 4  |   |
| <i>Grapsus grapsus</i>                |                  |        | x       |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 1  |   |
| <i>Eriphides hispida</i>              |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 1  |   |
| <i>Eriphia squamata</i>               |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 1  |   |
| <i>Acanthina brevidentata</i>         |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 1  |   |
| <i>Thais melones</i>                  |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 2  |   |
| <i>Thais triangularis</i>             |                  |        |         |        |        |        |        |        |        |        |         |        |        |          |               |         |        |         |         |                     |                     |                      |                 | 1  |   |
| Total mobile eaten                    | 1                | 0      | 6       | 3      | 12     | 2      | 0      | 0      | 0      | 0      | 0       | 0      | 0      | 1        | 9             | 0       | 0      | 3       | 0       | 0                   | 0                   | 0                    | 0               | 0  |   |
| Total animal spp. eaten/consumer      | 7                | 9      | 12      | 9      | 17     | 7      | 1      | 3      | 4      | 6      | 3       | 4      | 1      | 9        | 19            | 3       | 2      | 6       | 4       | 1                   | 1                   | 1                    | 1               | 9  |   |

| B. Algal species                             | Consumer species |           |            |           |           |           |                        |                        |                 |                 |                 |                 |                 | No. consumers |                 |                 |                 |
|--|------------------|-----------|------------|-----------|-----------|-----------|------------------------|------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|---------------|-----------------|-----------------|-----------------|
|  | Sg<br>(1)        | Sp<br>(6) | Ea<br>(10) | Ke<br>(4) | Pp<br>(2) | Os<br>(6) | Pt <sup>a</sup><br>(3) | Gg <sup>a</sup><br>(4) | Ev <sup>a</sup> | Fv <sup>a</sup> | Fl <sup>a</sup> | Sm <sup>a</sup> | Sp <sup>a</sup> |               | Ah <sup>a</sup> | Ca <sup>a</sup> | Cs <sup>a</sup> |
| microalgae, sporelings                       | x                | x         |            |           |           |           | x                      | x                      | x               | x               | x               | x               | x               | x             | x               | x               | 12              |
| Rhodophyta                                   |                  |           |            |           |           |           |                        |                        |                 |                 |                 |                 |                 |               |                 |                 |                 |
| corallines, foliose                          |                  |           |            |           |           |           |                        |                        |                 |                 |                 |                 |                 |               |                 |                 |                 |
| <i>Jania</i> spp.                            | x                | x         | x          | x         | x         | x         | x                      | x                      |                 |                 |                 |                 |                 |               |                 |                 | 8               |
| <i>Amphiroa</i> sp.                          | x                | x         | x          |           |           |           |                        |                        | x               |                 |                 |                 |                 |               |                 |                 | 4               |
| <i>Boswellia</i> spp.                        | x                | x         | x          |           |           |           |                        |                        | x               |                 |                 |                 |                 |               |                 |                 | 2               |
| non-coralines, foliose                       |                  |           |            |           |           |           |                        |                        |                 |                 |                 |                 |                 |               |                 |                 |                 |
| <i>Gelidium pusillum</i>                     |                  | x         | x          | x         | x         | x         | x                      | x                      | x               |                 |                 |                 |                 |               |                 |                 | 8               |
| <i>Gelidiella</i> sp.                        |                  | x         | x          | x         | x         | x         | x                      | x                      | x               |                 |                 |                 |                 |               |                 |                 | 5               |
| <i>Hypnea</i> spp.                           |                  | x         | x          | x         | x         | x         | x                      | x                      | x               |                 |                 |                 |                 |               |                 |                 | 5               |
| <i>Laurencia</i> sp.                         |                  | x         | x          | x         | x         | x         | x                      | x                      | x               |                 |                 |                 |                 |               |                 |                 | 2               |
| polysiphonous spp.                           |                  | x         | x          | x         | x         | x         | x                      | x                      | x               |                 |                 |                 |                 |               |                 |                 | 7               |
| <i>Spyridia</i> sp.                          |                  | x         | x          | x         | x         | x         | x                      | x                      | x               |                 |                 |                 |                 |               |                 |                 | 2               |
| other filamentous spp.                       |                  | x         | x          | x         | x         | x         | x                      | x                      | x               |                 |                 |                 |                 |               |                 |                 | 9               |
| crusts                                       |                  |           |            |           |           |           |                        |                        |                 |                 |                 |                 |                 |               |                 |                 |                 |
| corallines                                   |                  |           |            |           |           |           |                        |                        | x               |                 |                 |                 |                 |               |                 |                 | 1               |
| <i>Hildenbrandia prototypus</i>              |                  |           |            |           |           |           |                        |                        | x               |                 |                 |                 |                 |               |                 |                 | 1               |
| Phaeophyta                                   |                  |           |            |           |           |           |                        |                        |                 |                 |                 |                 |                 |               |                 |                 |                 |
| foliose                                      |                  |           |            |           |           |           |                        |                        |                 |                 |                 |                 |                 |               |                 |                 |                 |
| <i>Dictyota</i> sp.                          |                  |           | x          | x         | x         | x         | x                      | x                      | x               |                 |                 |                 |                 |               |                 |                 | 4               |
| <i>Giffordia mitchelliae</i>                 |                  |           |            |           | x         | x         | x                      | x                      | x               |                 |                 |                 |                 |               |                 |                 | 5               |
| <i>Sargassum</i> sp.                         |                  |           | x          |           |           |           |                        |                        |                 |                 |                 |                 |                 |               |                 |                 | 1               |
| crustose                                     |                  |           |            |           |           |           |                        |                        |                 |                 |                 |                 |                 |               |                 |                 |                 |
| <i>Ralfsia</i> sp.                           |                  |           |            |           |           |           |                        |                        | x               | x               | x               | x               | x               | x             | x               | x               | 6               |
| <i>Schizothrix calcicola</i>                 |                  |           |            |           |           |           |                        |                        | x               | x               | x               | x               | x               | x             | x               | x               | 6               |
| Chlorophyta                                  |                  |           |            |           |           |           |                        |                        |                 |                 |                 |                 |                 |               |                 |                 |                 |
| <i>Bryopsis</i> sp.                          |                  |           | x          |           |           |           |                        |                        | x               |                 |                 |                 |                 |               |                 |                 | 2               |
| <i>Chaetomorpha</i> sp.                      |                  |           | x          |           |           |           |                        |                        | x               |                 |                 |                 |                 |               |                 |                 | 2               |
| <i>Cladophora</i> spp.                       |                  |           | x          |           |           | x         | x                      | x                      | x               |                 |                 |                 |                 |               |                 |                 | 5               |
| <i>Enteromorpha</i> spp.                     |                  |           | x          | x         | x         | x         | x                      | x                      | x               |                 |                 |                 |                 |               |                 |                 | 4               |
| <i>Ulva</i> sp.                              |                  |           | x          | x         | x         | x         | x                      | x                      | x               |                 |                 |                 |                 |               |                 |                 | 4               |
| Others                                       |                  |           |            |           |           |           |                        |                        |                 |                 |                 |                 |                 |               |                 |                 |                 |
| diatoms                                      |                  |           |            |           |           |           |                        |                        | x               |                 |                 |                 |                 |               |                 |                 | 5               |
| <i>Microcoleus lyngbaeaceus</i> (blue-green) |                  |           |            |           |           |           |                        |                        | x               |                 |                 |                 |                 |               |                 |                 | 2               |
| Total algae eaten                            | 4                | 7         | 16         | 9         | 10        | 11        | 7                      | 8                      | 22              | 2               | 2               | 2               | 1               | 2             | 2               | 2               | 2               |
| Total algae + animals eaten                  | 5                | 10        | 19         | 13        | 11        | 11        | 11                     | 9                      | 31              | 2               | 2               | 2               | 1               | 2             | 2               | 2               | 2               |

Consumer species code: A. Fishes; Ah *Arothron hispidus*; Am *A. meleagris*; B. Fish: Os *Ophioblennius steindachneri*; Bp *Balistes polylepis*; Dh *Diodon hystrix*; Pn *Pseudobalistes naufragium*; Sg *Scarus globban*; Sp *S. perrico*; Hp *Holacanthus passer*; Pz *Pomacanthus zonipectus*; Ea *Eupomacentrus acapulcoensis*; Ke *Kyphosus elegans*; Pp *Prionurus punctatus*; Predaceous snails: Ab *Acanthina brevidentata*; Tm *Thais melones*; Tt *T. triangulata*; Mr *Muricanthus radix*; Seastar: Hm *Heliaster microbrachius*; Crabs: Pt *Pachygrapsus transversus*; Gg *Grapsus grapsus*; Eh *Eriphides hispidus*; Sea urchins: Ev *Echinometra vanbrunni*. B. Fish: Os *Ophioblennius steindachneri*; Limpets: Fv *Fissurella virescens*; Fl *F. longifissa*; Sm *Siphonaria maura*; Sp *S. palmata*; Chitons: Ah *Acanthochitona hirudiniformis*; Ca *Ceratozona angusta*; Cs *Chiton stokesii*

\* N's for Pt, Gg indicate number of individuals dissected; N for Eh indicates number of *Eriphides* observed feeding in the field; feeding of Ev (*Echinometra*) was determined by comparing treatments with and without these urchins in experiments reported in Menge et al. (1983); feeding of herbivorous molluscs (Fv, Fl, Sm, Sp, Ah, Ca, Cs) was determined from their effects in experiments reported earlier (Menge et al. 1986)