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Effects of Differential Fish Grazing on the Community Structure of an Intertidal Reef Flat at Enewetak Atoll, Marshall Islands[1]

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ABSTRACT: The high and middle intertidal zones of the northeastern portion ("barren") of the limestone bench on the windward side of Enewetak Island, Enewetak Atoll, Marshall Islands, have a significantly higher number of herbivorous fishes grazing at high tide than the same intertidal zones of the reef flat 300 m to the southwest ("algae-covered"). This portion of the reef flat in the barren, heavily grazed area has a significantly lower coverage by erect, macroscopic algae and a lower algal biomass than the same portion of the reef flat in the algae-covered area. The removal of part of the limestone substratum by the grazing fishes as they feed and the reduced coverage by erect, macroscopic algae result in a lower topographic relief in the barren area than found in the algae-covered area. The heavily grazed area has a significantly lower number of mobile epifaunal invertebrate species and individuals per square meter than the lightly grazed area. Differences in infauna (sipunculans, polychaete worms, and tanaid crustaceans) are not so clear.

When portions of the barren area were excluded from fish grazing activity for three months, the substratum under the exclosures had 100% coverage by an algal mat; the density of mobile invertebrate epifauna was an order of magnitude higher than in quadrats outside the exclosures.

Although the high and middle intertidal community is subjected to apparently severe physical stresses (desiccation, insolation, wave shock, ultraviolet radiation, and osmotic stress from evaporation in the tide pools and rainfall), it appears to be principally structured by the grazing activities of herbivorous fishes. The high level of grazing in the barren area results in coverage by filamentous blue-green algae and a diatom-bacterial film, which may be a nutritionally more important food source to the fishes than the coralline algae in the algae-covered area.

ECOLOGICAL STUDIES of communities in recent years have gone beyond purely descriptive approaches to examine the formation and maintenance of community structure; that is, the number of species, their relative abundances, their roles in the community, and their responses to biological and physical events. Much of this effort has been with rocky intertidal communities in both temperate areas (e.g., Connell 1961, 1970, Dayton 1971, Menge 1976, 1978, Osman 1977, Paine 1966, 1971, Paine and Vadas 1969) and tropical areas (e.g., Bakus 1967, Bernstein 1974, Brander, McLeod, and Humphreys 1971, Brock 1979, Connell 1978, Kohn 1959, 1967, Kohn and Leviten 1976, Leviten 1974, Menge and Lubchenco 1981, Miller 1974, Stephenson and Searles 1960, Vine 1974).

From these and other community studies, Connell (1975) and Menge and Sutherland (1976) developed a general model that predicts in part that predation (including herbivory) is the most important biological interaction that structures physically benign communities. In communities influenced by

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disruptive physical conditions, competition becomes more important than predation. In areas with severe physical conditions (ice formation, extremes of temperature, heavy surf, etc.), the physical conditions themselves direct the development of the community structure.

Several studies have examined some of the effects of intense fish grazing on tropical intertidal rocky shores (Bakus 1967, Chartock 1972, John and Pople 1973, Stephenson and Searles 1960, Stephenson 1961) and in some tropical subtidal areas (Brock 1979, Earle 1972, Randall 1965, Vine 1974). Fish exclosures and algal transplants to heavily grazed areas have demonstrated that herbivorous fishes (primarily damselfishes [Pomacentridae], parrotfishes [Scaridae], and surgeonfishes [Acanthuridae]) reduce the abundance and number of species of algae in some intertidal habitats (Bakus 1967, John and Pople 1973, Stephenson and Searles 1960, Stephenson 1961). This grazing activity may also affect resident invertebrates because small or soft-bodied individuals may inadvertently be scraped off the substratum with the algae (Brock 1979, Stephenson 1961). Bakus (1964) suggests that fish feeding may have greatly influenced the evolution of predator avoidance mechanisms in tropical invertebrates.

On the intertidal reef flat of the windward side of Enewetak Island, Enewetak Atoll, Marshall Islands, a natural situation exists where the effects of fish grazing on the structure of the middle and high portion of an intertidal benthic community have been studied. Herein I test the hypothesis that two neighboring, intertidal sections of the reef flat have significantly different levels of fish grazing; I compare the abundance of algae, topographic relief, and the species composition and abundance of invertebrates at these two sites.

STUDY AREAS AND METHODS

Study Site

Sampling was done on the windward side of Enewetak Island, Enewetak Atoll, Marshall Islands (11°21′ N, 162°21′ E), in September 1970, January, April, and May 1971, February 1973, and January 1980. The intertidal reef flat is extensive, consisting of an essentially flat limestone bench extending 70–100 m from the sand beach to the reef crest and then dropping abruptly into deep water. The high and middle intertidal zones in the northeast section (hereafter called "barren") of Enewetak Island (Figure 1) have very little macroscopic, erect algae on the limestone substratum. The substratum is flat, covered with a thin film (less than 1 mm thick) of microscopic algae, primarily diatoms and filamentous blue-greens (probably *Schizothrix calcicola* and *Calothrix crustacea* [Webb and Wiebe 1975, Renaud 1976]). The high and middle intertidal portions of the reef flat 300 m to the southwest (hereafter called "algae-covered") is covered with large patches of macroscopic, erect (0.5–3 cm tall) algae (mostly the coralline, *Jania capillacea*, with some clumps of the brown, *Sphacelaria* sp., and several other unidentified species [Harry Calvert, personal communication]); only small patches of substratum are covered with the thin film of microscopic algae that dominates the barren portion of the reef flat to the northeast. The large clumps of erect algae and the numerous depressions and cracks occurring in the substratum create a heterogeneous topography. The portions devoid of the macroscopic algae in both areas all contain numerous scrape marks left by the hard mouth parts of herbivorous fishes as they bite into the substratum when they remove the attached algae. This barren area is within the high and middle intertidal zones of Leviten and Kohn's (1980) F4 sample area, and the algae-covered area corresponds to the high and middle intertidal portion of their F7 site.

Sampling Methods

The intensity of the grazing activity in the high and middle intertidal zones in both the barren and algae-covered areas was estimated in 1980 by taking three random, close-up photographs of the substratum every 5 m along a 40 m long, randomly chosen transect line perpendicular to the shore line and projecting these pictures onto a random pattern

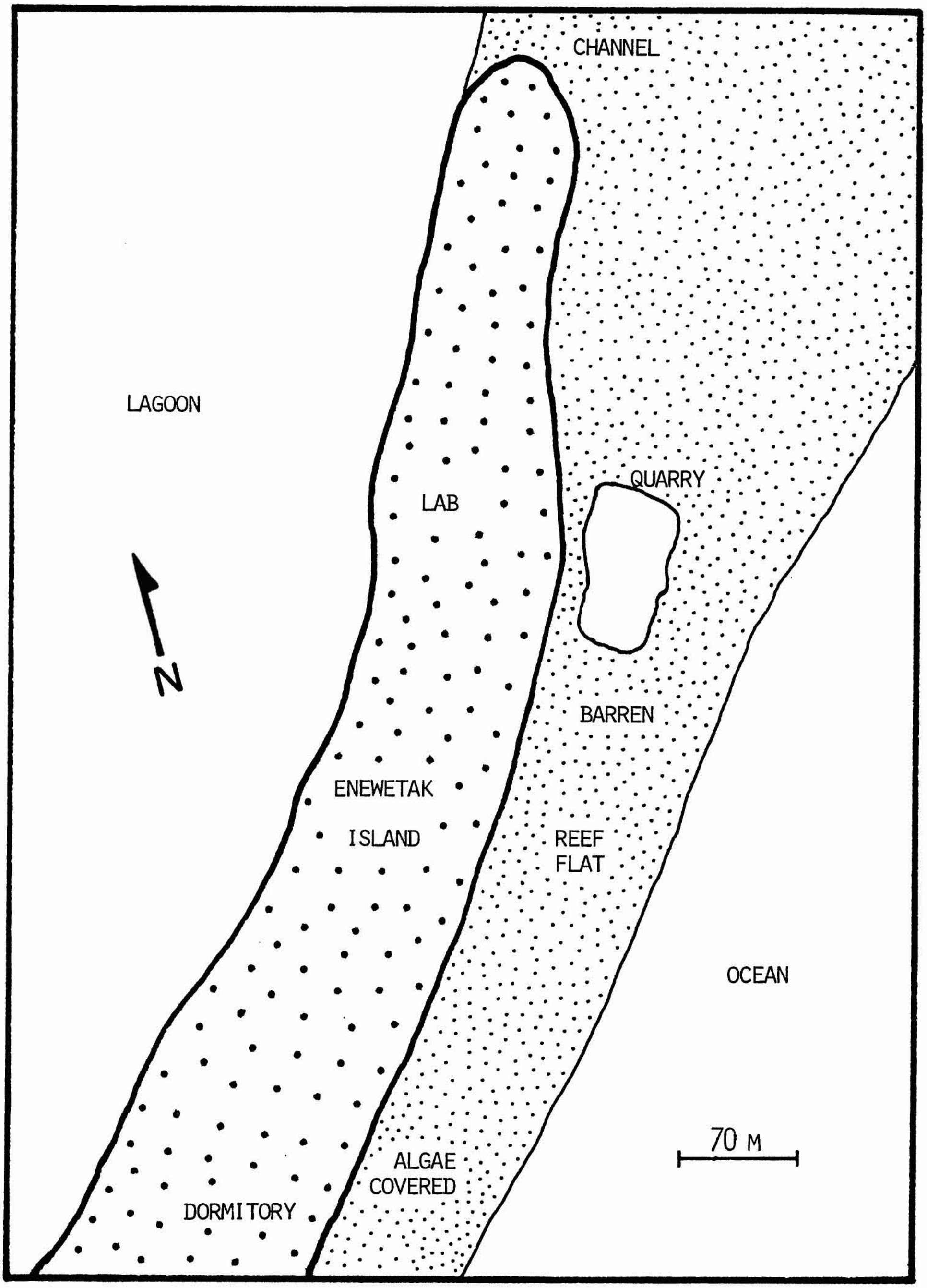

FIGURE 1. Sketch of Enewetak Island indicating the study sites. Dense stippling indicates intertidal reef flat. Scale is approximate.

of 100 points. Each picture covered a .0095 m^2 area. The percent of the grazed area was determined by counting the number of points covered by recently made fish scrape marks that exposed the white, limestone substratum. This technique was also used for the exclosure experiments.

Counts of fishes actually grazing in both areas were made by crawling along a 100 m transect parallel to and 5 m out from the beach rock-reef interface at high tide and counting the number of fishes seen feeding. One count in the barren area would be followed immediately by a count in the algae-covered area. The presence of fishes in each area during daytime high tides was quantified by counting fishes that swam through a 3 × 5 m quadrat marked on the substratum 10 m out from the beach. Observations were 20 min long and were made from observation platforms on cement pilings about 2 m above the reef flat. Fourteen counts were made in each area; usually, one 20-min count was done in one area and the next was made in the other. Most fishes could easily be identified to species or type through the clear, shallow (0.5–1.0 m) water. Because the two common damselfishes, *Abudefduf sordidus* and *A. septemfasciatus*, are similar in size and color pattern to *Acanthurus triostegus*, they could not be distinguished from *Acanthurus triostegus* with any certainty; therefore, the three species were counted as one. In addition, the number of *Abudefduf* spp. were estimated by multiplying the total number of the three fishes by 5% since this is the relative abundance of *Abudefduf* spp. individuals to *Acanthurus triostegus* found in the transect counts of fish feeding.

In 1973 algal coverage in both areas was estimated in two ways. Color slides were taken of 0.5 × 0.5 m quadrats placed every 15 m along randomly located lines running perpendicular to the beach. The slides were projected onto heavy drawing paper, macroscopic algal patches were outlined and cut out, and the percent of the total weight of the quadrat removed by cutting was used as the estimate of percent cover of macroscopic algae. The other method involved recovering algae from the cores of the substratum used to sample infaunal invertebrates (see below) after the acid bath. These algae were dried for 24 hours at 100°C, were weighed, and were ashed at 750°C. Most of the calcium carbonate in the coralline algae was dissolved in the acid bath. Algal coverage in 1980 was estimated from pictures of the substratum, as in 1973, except that the quadrat size was 0.12 × 0.08 m and three randomly chosen pictures were taken every 5 m along a 40 m transect line placed perpendicular to the beach.

The mobile invertebrate epifauna (gastropods, crabs, and echinoderms) was sampled at low tide in each area along transects originating from random points on the reef flat fronting the beach rock in the high intertidal and extending 40 m onto the limestone bench along a line perpendicular to the beach. The transects were terminated at 40 m because this is about the limit at which fish grazing activity appears to affect the macroscopic algal coverage in the barren area. The 1970 and 1971 random transects in each area were made by counting all mobile invertebrates on the reef flat surface in 1 m^2 quadrats placed every 5 m along the 40 m lines. The 1973 and 1980 quadrats were spaced every other meter. The population of the limpet, *Siphonaria normalis*, and an unidentified, small sea anemone were not adequately sampled and have not been included in this study.

Polychaetes, sipunculans, tanaids, and vermetids were sampled by removing 4.6 cm diameter by 5 cm long cores of the substratum using a motorized drill. In 1970 two cores were drilled every 10 m along both 40 m transects, except at the 20 and 30 m positions in the barren area transect where only one core each was taken. One core was drilled every 5 m along the 40 m transects in the 1971 sample. The 1973 sample consisted of two cores, each from the 10, 20, and 30 m positions and one core from the 15 and 35 m positions from both areas. The cores were frozen and the invertebrates were extracted in the laboratory by dissolving the cores in a solution of acetic and hydrochloric acid.

In 1971 five fish exclosures consisting of four walls and a top constructed of 5 mm mesh screen were placed in each area along transect lines perpendicular to the beach. The

TABLE 1

NUMBER OF FISHES FEEDING AT HIGH TIDE*

	BARREN	ALGAE-COVERED	CHI-SQUARE
Acanthurus triostegus	202	29	$\chi^2 = 128, p < .001$
Abudefduf spp.	10	0	$\chi^2 = 8, p < .005$

* The number of *Acanthurus triostegus* and *Abudefduf* spp. feeding were counted by swimming along five 100 m transect lines in the barren and algae-covered areas during high tide.

exclosures were attached to the substratum only at the four corners, so that small invertebrates could move in and out under the edges. In the barren area, the portions of the substratum excluded from fish grazing were initially without macroscopic algal coverage and mobile epifauna. In the algae-covered area, the substratum under the exclosures had from about 85% to 100% coverage by macroscopic algae. The density and species diversity of mobile epifauna in this area were not assessed before the exclosures were put in place to avoid destroying the algal turf. Only three exclosures survived the three-month duration of the experiment: at the 15 m position in the algae-covered area (29 cm long × 27 cm wide × 8 cm high), and the 20 m (38 cm long × 28 cm wide × 8 cm high) and the 35 m (35 cm long × 28 cm wide × 8 cm high) positions in the barren area.

Topographic relief was quantified by comparing a 1 m straight line distance (a metal bar) above the substratum with actual distance covered by a chain (link length, 2 mm; link width, 1.5 mm) placed to conform to the surface of the substratum alongside the bar (the more topographic relief, the greater the chain distance over a 1 m straight-line distance). In each area, starting at the beach rock-sand interface, 31 random measurements were made in a 60 m (parallel to beach) by 30 m (perpendicular to the beach) grid.

Feeding preference in barren or algae-covered patches of substratum by *Acanthurus triostegus* and *Abudefduf* spp. was studied subtidally in the quarry. Two adjacent 40 cm × 60 cm quadrats were selected with one quadrat covered completely by an algal turf of primarily coralline algae and the other by microscopic, filamentous algae and a diatom-bacterial film. Simultaneous counts of fishes feeding in the quadrats during eight different 15-min periods were made by two divers.

Species identifications were determined from the Mid-Pacific Laboratory collections; standard references such as Fauvel (1953), Day (1967), and Reish (1968); and material made available by A. J. Kohn and M. C. Lloyd. Lists of the species sampled may be obtained from the author.

FISH ACTIVITY

Photographic analysis of fish grazing showed that, on the average, 6.2% (±1.8% S.E.M., $N = 24$) of the limestone substratum in the algae-covered area was exposed by the scrape marks left by the mouth parts of grazing fishes. In the barren area a significantly greater amount of barren limestone is exposed, on the average, (32.6% ± 1.9% S.E.M., $N = 24$) by fish grazing ($t_s = 5.670$, $p < .001$; Wilcoxon two-sample test). Counts of fishes feeding (Table 1) and the estimates of fishes present in each area at high tide (Table 2) support this conclusion. There were significant differences in the number of *Acanthurus triostegus* ($\chi^2 = 128, p < .001$) and *Abudefduf* spp. ($\chi^2 = 8$, $p < .005$) found feeding in the barren versus the algae-covered area (Table 1). In the 14 separate fish counts made to determine differences in the number of fishes active in each area at high tide (Table 2), a chi-square analysis indicated that more fishes were found in the barren area ($\chi^2 = 679$, $p < .001$).

Herbivorous fishes numerically dominate

TABLE 2

ESTIMATES OF FISHES PRESENT AT HIGH TIDE

		SURGEONFISHES					
AREA	PARROTFISHES *Scarus* SPP.	*Acanthurus guttatus*	*Acanthurus triostegus*	DAMSELFISHES *Abudefduf* SPP.	BLACK TIP SHARK *Carcharhinus melanopterus*	UNIDENTIFIED INDIVIDUALS	TOTAL*
Algae-covered	12	0	458	24	3	94	591
Barren	33	166	1347	71	7	265	1889

* The total number of fishes in 14 separate 20-min counts observed swimming through a 3 × 5 m quadrat at high tide on the reef flat in the algae-covered and barren areas. The abundance of *Abudefduf* spp. was calculated as 5% of the total fishes scored as *Acanthurus triostegus*; see text.

the fish counts. Parrotfishes (Scaridae), surgeonfishes (Acanthuridae), and damselfishes (Pomacentridae) comprise 86% of the individuals in the barren area and 84% in the algae-covered area. These percentages should be considered minimal because some unidentified individuals may also be herbivorous.

Parrotfishes and *Acanthurus guttatus* are both grazing herbivores that bite the substratum when feeding on the attached algae (Chartock 1972, Hiatt and Strasburg 1960, Hobson 1974). Parrotfishes have been described as grazing omnivores (Hiatt and Strasburg 1960) because algae and coral polyps are found in the stomach contents. *Acanthurus guttatus* feeds on the coralline alga, *Jania*, and on the blue-green, *Calothrix* (Hiatt and Strasburg 1960, Wiebe, Johannes, and Webb 1975).

Although *Acanthurus triostegus* has teeth shaped such that it can browse on filamentous algae (Jones 1968, Randall 1961), these fish also remove portions of the limestone substratum when they feed on the microscopic algae in the barren area. The tooth marks left in the substratum where *A. triostegus* have recently been feeding clearly show four to five thin, parallel scrapes that correspond to the separated teeth in the jaw of *A. triostegus*. Randall (1961) found that Hawaiian *A. triostegus* eats *Polysiphonia* sp. (a red algae) and *Enteromorpha* sp. (a green algae) in lab experiments, but found other species of algae, including blue-green algae, in the stomach contents of fish collected in the field. The filamentous blue-green, *Lyngbya majuscula*, which dominates algal cover in some reef areas (Randall 1961), is common in diets of *A. triostegus* in the Line Islands (Dawson, Aleem, and Halstead 1955).

The damselfish, *Abudefduf sordidus*, scrapes filamentous algae from the substratum; but although algae forms the major portion of the diet, crustaceans and polychaetes were also found in their guts (Hiatt and Strasburg 1960, Hobson 1974). The stomach contents of the other common damselfish, *A. septemfasciatus*, examined by Hiatt and Strasburg (1960) contained fronds of algae (like the coralline alga, *Jania*) and small crustaceans.

The reason that greater numbers of fishes, especially grazing herbivores, occur on the northeastern portion of the reef flat than on the central southwestern portion is undetermined. The proximity of a quarry (about 45 m wide, 90 m long, and 1–4 m deep [Bakus 1967] on the intertidal reef flat and a shallow channel connecting the lagoon to the open ocean may be important. Randall (1961) found that Hawaiian *Acanthurus triostegus* showed a tendency to remain in localized areas. A large resident population of *A. triostegus*, the most common fish found in this study (Tables 1 and 2), may find refuge in the quarry at low tide and may concentrate its feeding during high tide on the reef flat adjacent to the quarry. No similar refuge exists by the algae-covered area. Also, since there is not much of a reef flat on which to feed on the lagoon side of the island, fishes may swim from the lagoon through the northeastern channel (Figure 1) at high tide to feed on the expansive windward reef flat. These fishes would come to the northeastern portion of the reef flat first and may concentrate their feeding there.

ALGAL DIFFERENCES

The differences in macroscopic algal cover on the barren and algae-covered areas noted visually are confirmed when the percent cover by macroscopic algae is analyzed (Tables 3 and 4). The algae-covered area has more macroscopic algae. Differences are significant for

TABLE 3

PERCENT COVER BY ERECT, MACROSCOPIC ALGAE IN 1973*

POSITION ALONG TRANSECT	ALGAE-COVERED		BARREN	
	SERIES A	SERIES B	SERIES A	SERIES B
1 m	100	96	0	0
15 m	56	81	0	1
30 m	40	60	0	0
45 m	69	74	0.5	17
55 m	—†	—	7	—
$\bar{x}$, range‡	72.0, 40–100		2.8, 0–17	
U test	$U = 72, p < .01$, 2-tail			

* Percent cover measured in 0.5 × 0.5 m quadrats.
† Dash means no data available.
‡ Sample series A and B are lumped for each area.

TABLE 4

PERCENT COVER BY ERECT, MACROSCOPIC ALGAE IN 1980*

POSITION ALONG TRANSECT	ALGAE-COVERED			BARREN		
	SERIES A	SERIES B	SERIES C	SERIES A	SERIES B	SERIES C
5 m	100.0	100.0	100.0	0.0	0.0	0.0
10 m	100.0	100.0	100.0	0.0	0.9	0.0
15 m	97.4	90.2	57.0	11.3	0.7	6.7
20 m	33.8	89.5	55.8	8.4	0.9	1.4
25 m	88.2	97.5	22.0	4.8	0.0	2.6
30 m	88.1	85.7	33.6	16.0	14.3	23.2
35 m	92.6	89.6	98.6	5.6	17.1	52.2
40 m	98.8	65.1	100.0	49.4	66.5	54.3
$\bar{x}$, range		82.6, 22.0–100.0			14.0, 0.0–66.5	
U test			$t_s = 5.66, p < .001$, 1-tail			

*Percent cover measured in 0.12 × 0.08 m quadrats. Three quadrats were ramdomly placed at each transect position.

TABLE 5

ASH-FREE DRY WEIGHT (IN GRAMS) OF ALGAE FROM SUBSTRATUM CORES*

POSITION ALONG TRANSECT	ALGAE-COVERED		BARREN	
	SERIES A	SERIES B	SERIES A	SERIES B
10 m	.157	.200	.115	.105
15 m	.170	—†	.078	—
20 m	.117	.107	.031	.114
30 m	.134	.107	.077	.089
35 m	.234	—	.160	—
Average‡	.153 ± .016		.096 ± .013	
U test		$U = 55, p < .05$, 2-tail		

*Algae were recovered from 4.6 cm diameter cores of the substratum. Ash-free dry weight was measured after removal of the carbonate material in an acid bath.

† Dashes mean no data available.

‡ Sample series A and B are lumped for each area. $\bar{x} \pm$ one standard error.

the 1973 ($U = 72, p < .01$; Table 3) and the 1980 ($t_s = 5.66, p < .001$; Table 4) percent cover values for each area. Comparison of ash-free dry weight of algae from the substratum cores (Table 5) also indicates that the algae-covered area has a greater algal biomass ($U = 55, p < .05$).

MOBILE INVERTEBRATE EPIFAUNAL DIFFERENCES

Table 6 summarizes data on the invertebrate epifauna and its abundance. No significant differences were found for the total number of mobile epifaunal species per transect between areas for each year; however, there are significant differences in total number of individuals (Table 6). There are also significant differences in both the average number of individuals and the average number of species found in a 1 m^2 quadrat for each of the four census periods (Table 6). In each case the algae-covered area has more individuals and more species than the barren area. The percent similarity values (Whittaker 1952) are low for each year, which also suggests that there are species composition differences between areas.

INVERTEBRATE INFAUNAL AND SEDENTARY EPIFAUNAL DIFFERENCES

The data on the invertebrates from the core samples are summarized in Tables 7 and 8. Vermetid gastropods (primarily *Dendropoma psarocephala*) and a small (<1 cm diameter), unidentified sea anemone make up the majority of the sedentary epifauna occupying the high and middle intertidal zones of the reef flat. Only the vermetids are included in this analysis, since sampling techniques were not adequate to assess the sea anemone's density.

The statistical comparisons (Table 7) between the two sample areas indicate that there are no significant differences in the total num-

TABLE 6

Occurrence of Mobile Invertebrate Epifauna in the Study Areas*

	1970		1971		1973		1980	
	ALGAE-COVERED	BARREN	ALGAE-COVERED	BARREN	ALGAE-COVERED	BARREN	ALGAE-COVERED	BARREN
Number of quadrats	9	9	9	9	20	20	20	20
Total species	15	6	18	11	21	12	27	20
Chi-square	$\chi^2 = 3.05, p > .05$		$\chi^2 = 1.24, p > .05$		$\chi^2 = 1.94, p > .05$		$\chi^2 = 1.02, p > .05$	
Avg. number of species per m^2	4.3 ± 0.6†	0.9 ± 0.4	8.1 ± 0.5	2.6 ± 0.7	6.2 ± 0.5	1.8 ± 0.3	7.5 ± 0.4	2.2 ± 0.4
U test (2-tail)	$U = 76, p < .001$		$U = 79, p < .001$		$U = 381, p < .001$		$U = 392, p < .001$	
Total individuals	95	10	729	52	420	73	971	93
Chi-square	$\chi^2 = 67.2, p < .001$		$\chi^2 = 585, p < .001$		$\chi^2 = 243, p < .001$		$\chi^2 = 724, p < .001$	
Avg. number of individuals per m^2	10.6 ± 1.5†	1.1 ± 0.6	81.0 ± 20.2	5.8 ± 2.2	21.0 ± 2.4	3.6 ± 0.7	48.5 ± 5.7	4.6 ± 1.2
U test (2-tail)	$U = 78, p < .001$		$U = 81, p < .001$		$U = 392, p < .001$		$U = 396, p < .001$	
Percent similarity of species diversity	37.4%		24.6%		24.3%		24.3%	

*The quadrat size is one square meter.
† $\bar{x} \pm$ one standard error.

TABLE 7

VERMETID GASTROPODS IN CORES OF THE SUBSTRATUM*

	1970		1971		1973	
	ALGAE-COVERED	BARREN	ALGAE-COVERED	BARREN	ALGAE-COVERED	BARREN
Number of cores	10	8	9	9	8	8
Number of vermetids	16	14	7	6	5	2
Chi-square	———		$\chi^2 = .08, p > .05$		$\chi^2 = 1.28, p > .05$	
Avg./core†	1.6 ± 1.3	1.8 ± 0.9	0.8 ± 0.8	0.7 ± 0.4	0.6 ± 0.3	0.2 ± 0.2
U-test (2-tail)	$U = 48, p > .05$		$U = 48, p > .05$		$U = 40, p > .05$	
Avg./m^2	963.3	1083.7	481.6	421.4	373.2	150.5

*Each core is 4.6 cm in diameter and about 5 cm long.
† $\bar{x} \pm$ one standard error.

TABLE 8

NUMBER AND ABUNDANCE OF INFAUNA SPECIES (SIPUNCULANS, POLYCHAETES, AND TANAID CRUSTACEANS COMBINED) FOUND IN CORES FROM THE REEF FLAT*

	1970		1971		1973	
	ALGAE-COVERED	BARREN	ALGAE-COVERED	BARREN	ALGAE-COVERED	BARREN
Number of cores	10	8	9	9	8	8
Total species	20	21	29	14	19	11
Chi-square	———		$\chi^2 = 5.23, p < .05$		$\chi^2 = 2.13, p > .05$	
Avg. spp./core†	6.6 ± 1.1	5.0 ± 1.5	8.4 ± 1.7	3.6 ± 0.4	8.9 ± 1.4	2.4 ± 0.8
U test (2-tail)	$U = 36, p > .05$		$U = 64, p < .05$		$U = 59, p < .01$	
Total individuals	330	248	331	205	370	151
Chi-square	———		$\chi^2 = 30, p < .001$		$\chi^2 = 92, p < .001$	
Avg. individuals per core	33.6 ± 6.7	31.0 ± 7.9	36.8 ± 5.6	22.8 ± 4.3	46.2 ± 6.4	18.9 ± 10.4
U test (2-tail)	$U = 37, p > .05$		$U = 60, p < .10$		$U = 55, p < .05$	
Projected individuals per m^2	19,866	18,662	22,140	13,712	27,842	11,363
Percent similarity of species diversity	75.5%		57.1%		70.0%	

*Each core is 4.6 cm in diameter and about 5 cm long.
† $\bar{x} \pm$ one standard error.

ber of vermetids per transect (1971, 1973) or in the vermetid density (1970, 1971, 1973). Compared to epifaunal invertebrate densities (Table 6), the estimated average number of vermetids per square meter extrapolated for each area (Table 7) is very high. The occurrence of vermetids in such high densities in both areas when mobile epifaunal numbers are so low in the barren area may be the result of the vermetids' relatively thick shells which are firmly attached to the substratum.

Although sipunculans, polychaete worms, and tanaid crustaceans are treated as infauna, this does not mean that all species live exclusively in the limestone. The sipunculans and some polychaete worms are found in burrows in the limestone. Some polychaetes, however, build tubes or crawl around in the algae on

TABLE 9

LIMESTONE SUBSTRATUM EXPOSED UNDER AND ADJACENT TO FISH EXCLOSURES AFTER THREE MONTHS

EXCLOSURE POSITION		QUADRAT SIZE	% BARE LIMESTONE	
			UNDER	ADJACENT
Algae-covered	15 m	11.6 cm × 17.1 cm	0%	9.5%
Barren	20 m	18.0 cm × 26.6 cm	0%	42.8%
	35 m	16.1 cm × 30.8 cm	0%	44.4%

top of the substratum (Bailey-Brock, White, and Ward 1980). Errant polychaetes may shelter in holes and cracks in the substratum during the day or at low tide and crawl around on the surface only at night (Vivien and Peyrot-Clausade 1974) or at high tide. Bernstein (1974) found that most worms in his cores taken in the algal ridge area on the reef flat at Enewetak were in the limestone, not on the surface in the algae. Kohn and White (1977) and Bailey-Brock, White, and Ward (1980) found fewer polychaetes in samples when the surface of the reef flat had been scraped compared to samples of the reef rock that included the algae.

The infauna, primarily polychaetes, are extremely abundant in both areas (Table 8). The projected densities per square meter are of the same order of magnitude as Kohn and Lloyd (1973) obtained for polychaetes alone from Eastern Indian Ocean reef flats and as Bailey-Brock, White, and Ward (1980) found at Enewetak in samples from the reef flat in the same general area as the algae-covered site. The results of the statistical comparisons are ambiguous (Table 8). For the total number of species found in the transects, only 1971 shows a significant difference between areas. In both 1971 and 1973 significant differences in the average number of species found in a core appear, but the average number in 1970 is not significant. Significant differences exist in the total number of infaunal invertebrates (Table 8) found in the transects between the algae-covered and the barren areas for 1971 and 1973 (1970 cannot be compared because of unequal sample sizes), but only in 1973 is there a significant difference in the number of individuals per core (although the 1971 difference is significant for $\alpha = .10$, 2-tail test).

Although not significant, the trends are for the number of species and individuals per core to be larger in the algae-covered area. A larger sample size might have resulted in more obvious trends. Several polychaete worm species are represented by only one individual and more samples are probably called for. However, the fact that these results are not so clear cut as for the mobile invertebrate epifauna and the high percent similarity values suggest that the infauna is not so drastically affected by fish feeding activities as are the exposed invertebrates.

FISH EXCLOSURE RESULTS

The only fish exclosures that survived the three-month duration of this experiment in the barren area were at the 20 m and 35 m positions. The substratum under the cages (originally barren of macroscopic algae) was covered by a mat of algae ($\sim$5 mm thick), whereas the substratum adjacent to but outside of the exclosures had no algal mat and had a high proportion of bare limestone rock (Table 9). When the densities of mobile epifauna under the exclosures in the barren area are extrapolated to 1 m^2 (Table 10), the resulting densities are an order of magnitude greater than any density obtained in individual sample quadrats from this area (range: 0–17 individuals/m^2) and two orders of magnitude greater than the average density per square meter (Table 6). The density under

TABLE 10

MOBILE INVERTEBRATE EPIFAUNA UNDER FISH EXCLOSURES AFTER THREE MONTHS

	ALGAE-COVERED	BARREN	
Position along transect	15 m	20 m	35 m
Number of species	5	8	10
Number of individuals	18	22	31
Number of individuals per m^2	229.9	206.8	316.3

the 35 m exclosure is even greater than the greatest density found in the individual square meter samples in the algae-covered area (213 individuals). The number of species found under the exclosures is greater than any of the individual square meter samples from the barren area (range: 0–6 species/m^2) but falls within the range found in samples from the algae-covered area (1–11 species/m^2).

The substratum under the one surviving exclosure in the algae-covered area was completely covered by macroscopic algae, while some adjacent areas had exposed limestone rock (Table 9). The density per square meter under this exclosure (Table 10) was slightly greater than the greatest density found in individual square meter samples from the algae-covered area (range: 1–213 individuals/m^2) and was an order of magnitude greater than the average density per square meter (Table 6). The number of species found under this exclosure is within the range of species collected from individual square meter samples from this area (1–11 species).

The lush growth of algae and high density of mobile epifaunal invertebrates found after three months under the fish exclosures in the barren area were not found anywhere else in the barren study site, nor was such a growth found behind concrete pilings (about 1.5 m wide × 1.5 m long × 2 m high), which provide shelter from wave shock, or under a wooden platform (about 3 m wide × 3 m long × 2.5 m high), which shaded a portion of the barren substratum.

DISCUSSION

Although it has been said that predation is the important biological structuring force in communities not often stressed by severe physical disturbances (Connell 1975, Menge and Sutherland 1976), the situation on the intertidal reef flat at Enewetak suggests that predation (herbivory) may also be a very important community structuring force in areas where severe physical forces occur with some frequency.

The windward, intertidal habitat on Enewetak Island is not here considered physically benign. The reef flat is exposed to severe surf (Kohn 1980), and during low tides the exposure to the tropical sun can result in high levels of ultraviolet radiation (Jokiel 1980), high temperatures, and elevated salinities in tide pools. Osmotic problems can also arise when heavy rainfall covers the intertidal area with a thin layer of fresh water, resulting in the deaths of some of the invertebrates (Leviten and Kohn 1980).

Despite the physical stresses, the biological act of herbivory appears to be the major structuring force operating in this community. The lush growth of algae under the fish exclosures in this study and that of Bakus (1967) and the significant differences in abundance and types of algae growing in the barren area (Tables 3, 4, and 5) where there is more fish grazing pressure than in the algae-covered area (Tables 1 and 2) suggest that grazing fishes are controlling algal abundance and relative cover by different algal species.

The higher numbers of individuals and species of mobile invertebrate epifauna per square meter in the algae-covered area (Table 6) and under the fish exclosures (Table 10) indicate that the fish grazing probably has direct and indirect effects on these animals. Fish inadvertently picking up small invertebrates when they bite the substratum is a direct effect. Stephenson (1961) similarly found increased survival of barnacles on rocks inside his fish exclosures compared to barnacles on rocks outside of cages at Heron Island, Australia. Parrotfishes remove invertebrates when grazing on algae (Brock 1979, Hiatt and Strasburg 1960); damselfishes are

TABLE 11

TOPOGRAPHIC RELIEF* OF STUDY AREAS

SITE	N	$\bar{x} \pm$ SEM	t' TEST
Barren	31	102.8 ± 0.4	$t' = 4.78, p < .001$
Algae-covered	31	106.6 ± 0.7	

*The average distance (in cm) that a line conforming to the surface topography travels over a 100 cm straight line distance. The longer the distance traveled, the greater the topographic relief.

known to eat invertebrates as well as filamentous algae (Hiatt and Strasburg 1960); and invertebrates have been found in the guts of the surgeonfish, *Acanthurus triostegus* (Miller, personal observation).

The probable indirect effects of fish grazing on survival of these mobile invertebrates come about from changes in topographic heterogeneity. When a parrotfish, *Acanthurus guttatus*, or *A. triostegus* grazes, it removes part of the limestone rock substratum along with the attached algae. The barren area, which has a greater level of grazing pressure by fishes (Tables 1 and 2) than the algae-covered area, has a significantly lower topographic relief than the algae-covered section of the reef flat (Table 11). The reduced topographic relief and the low percentage of cover by clumps of macroscopic algae (Tables 3 and 4) in the barren area limit the available shelter for invertebrates from desiccation, wave force, osmotic stress, and predators (Bailey-Brock, White, and Ward 1980, Kohn 1980, Kohn and Leviten 1976, Menge and Lubchenco 1981).

Stephenson and Searles (1960) using fish exclosures at Heron Island, Australia; Kohn and Leviten (1976), who related topographic complexity to density of several species of carnivorous gastropods at Enewetak Island; Bailey-Brock, White, and Ward (1980), who worked with polychaete worms at Enewetak Island; and Menge and Lubchenco (1981), who excluded fishes and crabs from sections of the rocky intertidal zone in Panama, found that more species and individuals occurred in the artificial shelters or in areas with natural shelters than in areas without such refuges. Brock (1979) found a larger biomass of attached organisms in his microcosm tanks with low densities of parrotfish than in tanks with high parrotfish densities. The results of this study support these relationships and extend the relationship to include most of the invertebrates (gastropods, crabs, and echinoderms) living on the surface of the reef flat (Table 6).

Another explanation for the reduced density of individuals and species in the barren area is that there is insufficient food to support as many individuals in a population as can be supported in the algae-covered area. It is possible that a specialist's food is missing entirely, which would thereby eliminate that species altogether. Without detailed knowledge of the diets of the invertebrates and the availability of their food in the two sections of the reef flat, the food limitation explanation is difficult to validate.

The effect of grazing on the infaunal invertebrates (sipunculans, polychaetes, and tanaid crustaceans) is not so obvious as with the mobile epifauna, and percentage similarity values were higher than found in the mobile epifauna comparisons (Tables 6 and 8). Although the trend in 1971 and 1973 was for there to be more species and larger numbers of individuals in the transects and cores in the algae-covered area, more samples are needed to confirm this trend. I conclude that the infauna may be more protected from fish predation and physical factors. The heavy-shelled vermetid gastropods living attached to the surface of the limestone bench seem to occur in equal numbers in both areas (Table 7), and this may indicate a high resistance to mortality from fish grazing and physical forces.

Although the greater concentration of feeding activity in the barren area on the northeastern side of Enewetak Island may be due to the proximity of shelters for the fishes at low tide (i.e., the quarry and the channel to the lagoon), the significantly larger number of grazing fishes that are found here (Tables 1 and 2) may be due to a feeding preference for the nutrient-rich blue-green algae and diatom-bacterial film that covers the barren area. Since coralline algae contains calcium carbonate, which may limit the energy and/or nutrition available per bite, the fishes may obtain more energy per unit effort by feeding in areas with an abundance of filamentous algae and diatom-bacterial film.

TABLE 12

NUMBER OF FISHES FEEDING IN ADJACENT QUADRATS*

	BARREN	ALGAE-COVERED	CHI-SQUARE
Acanthurus triostegus	566	205	$\chi^2 = 161, p < .001$
Abudefduf spp.	42	38	$\chi^2 = 0.11, p > .05$

*Totals are the number of individuals counted feeding in adjacent barren and algae-covered quadrats during eight 15-minute periods.

Randall (1961) and Vine (1974) indicate that under some circumstances, surgeonfishes, parrotfishes, and damselfishes prefer to feed on filamentous algae. In my subtidal algal preference study (Table 12), *Acanthurus triostegus* preferred to feed in the quadrat covered with filamentous algae and a diatom-bacterial film ($\chi^2 = 161$, $p < .001$); but *Abudefduf* spp. did not prefer either the algae-covered or the barren quadrat ($\chi^2 = 0.11$, $p > .05$).

Brock (1979) found that with low to medium densities of parrotfish in his microcosm tanks, filamentous algae were common, but that at high fish densities the percent coverage by filamentous forms decreased to zero and there was an increase in coverage by calcareous algae. This may result from overgrazing of the filamentous algae by the parrotfish. Vine (1974) noticed that filamentous algae were common only within feeding territories of damselfish and that these algae limit the settlement of calcareous algae and invertebrates. He found that the grazing by surgeonfishes and parrotfishes outside of the damselfish territories severely reduced the abundance of filamentous algae and this favored the settlement of calcareous algae.

The situation on the intertidal reef flat at Enewetak is different than the studies by Brock (1979) and Vine (1974) in that the filamentous algae are favored in the area with the greatest grazing pressure, and macroscopic algae, including calcareous algae, have a greater coverage in the area of low grazing pressure. This difference may be due to intertidal versus subtidal physical differences. It might also be possible that this heavy grazing pressure results in removal of portions of the limestone substratum frequently enough so that calcareous algae never get a chance to grow. It was estimated that an average of 32.6% (±1.9% S.E.M.) of the reef flat surface in the barren area is bare limestone exposed by fish grazing; the rest of the substratum is covered by an obvious film of algae. Thus, in the barren area the grazing fishes keep cropping existing algae and opening new portions of the substratum for algal colonization. This encourages the settlement and rapid growth of the filamentous algae (Bakus 1967, Chartock 1972); keeps them in a high-growth phase (Wiebe, Johannes, and Webb 1975); and prevents the monopolization of space by less productive or energetically less desirable algae.

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