

Effects of Algal Turf and Depressions as Refuges on Polychaete Assemblages of a Windward Reef Bench at Enewetak Atoll

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Abstract.—Quantitative analyses of epifaunal and infaunal polychaete assemblages from an intertidal windward reef bench at Enewetak Atoll revealed increases in species richness and abundance along a shoreward to seaward transect. The importance of refuges (shallow pools and algal turf) to the polychaete fauna was examined. Species diversity and richness and polychaete abundance were lower near shore where shallow pools, lined with sand, were the only refuges for soft-bodied invertebrates during periods of environmental harshness. Towards the ocean the bench was almost entirely covered by a thick algal turf which harbored a sizeable standing crop of polychaetes (up to 8.2 g dry wt./m²). Tube dwelling, suspension feeders and detritivores of the Sabellidae and Spionidae are most abundant in the shoreward pools while cirratulids, opheliids, errant amphinomids, and nereids, dominated the seaward samples. Thirty-one syllid species were recognized, contributing 35% of the polychaetes from epifaunal samples and the family was well represented in all algal turf and bench rock samples. Boring and burrowing polychaetes were more abundant as infauna in reef rock and coralline ridge samples as compared to samples of filamentous and turf-forming algae, and fine sediments scraped from the reef rock substratum where they were relatively few in number. The carbonate rock offered a third habitat dimension for cryptic and boring species including *Dodecaceria laddi*, eunicids and the spionid *Polydora armata*. Overall polychaete abundance and standing crop was approximately eight times greater in the algal mat habitat than in nearshore areas lacking macrothalloid algae. Shoreward refuges (shallow pools) harbored a richer polychaete fauna than the surrounding bench. Despite the harsh environmental conditions that exist nearshore during low tides, polychaete abundance was rather high (400–24,200 worms/m²). Algal turf scraped from the seaward section of bench contained an estimated 32,700 worms/m² in one of these samples, while blocks of reef rock including the overlying turf had 82,000–100,300 worms/m². These estimates indicate an increase in polychaetes with increasing macrothalloid algal cover and additionally with inclusion of the underlying hard substratum. Reef rock samples from the crest had a less abundant polychaete fauna composed of different species than those from the algal-covered section of bench. Data show that refuges affect the distribution, abundance and composition of polychaete assemblages on an intertidal, tropical bench.

Introduction

Intertidal benches of tropical islands support diverse communities of reef biota despite the apparently featureless topography typifying this environment. We attempt to explain the distribution and composition of polychaete assemblages across a windward reef bench at Enewetak Atoll, Marshall Islands. Three major habitat types

are present on this bench; shallow pools and algal turf (hereafter termed "refuges"), and nearly bare reef rock. Factors influencing the distribution of small invertebrates in this environment include tidal effects, diurnal warming and evaporation of pools at low tides, coverage and thickness of algal turf, and predation by fishes and invertebrates.

We hypothesize that (a) abundance and species richness of polychaete assemblages are greater in naturally occurring refuges (pools and algal turf) than on parts of the bench without these features and (b) species richness and abundance are greater towards the maximum thickness of algal mat, concomitant with the increased frequency of immersion, more luxuriant algal growth, and lessening of harsh physical conditions which prevail near shore. Kohn and Leviten (1976) showed that the species diversity and population density of predatory gastropod molluscs on tropical limestone benches increased with availability of refuges, described in their paper as cracks and depressions, and with increased algal turf. While the algal turf was regarded as a biotic refuge to the predatory gastropods in terms of harboring food, the topographic irregularities provided protection from the harsh physical conditions of the bench and were considered most important.

Ecological information on tropical polychaetes is of interest to coral reef ecologists because of the importance of polychaetes in the diet of vermivorous invertebrates, including gastropods (Kohn, 1959; Leviten, 1976, 1978); and reef fishes (Hiatt and Strasburg, 1960; Randall, 1967). Available data suggest that polychaetes are abundant in intertidal and shallow subtidal reef habitats (Kohn and Lloyd, 1973; Kohn and White, 1977).

Study Site

Enewetak Island lies in the S.E. sector of Enewetak Atoll, Marshall Islands ($162^{\circ} 21' 06''\text{E}$, $11^{\circ} 21' 25''\text{N}$). The almost flat, windward limestone bench is influenced by trade winds and receives constant wave action which is diminished to some extent by a coralline algal ridge. The bench is exposed during low tides, except for a shallow channel between 40–65 m from shore, that remains submerged due to waves breaking over the ridge and entering via surge channels (Leviten, 1974). Our study site is in the same vicinity as Leviten's, near the original location of the Mid-Pacific Marine Laboratory. The width of the bench here is approximately 100 m, but it narrows considerably further south.

Two broad regions can be defined on the bench, the most shoreward, extending approximately 25 m from the shore line, is characterized by development of a thin film of filamentous, blue-green algae and conspicuous shallow pools. The second, more seaward section, consists of a thick algal turf extending to the *Porolithon* ridge approximately 80 m from shore (our observations and Leviten, 1974). Pools are indistinguishable at the seaward end of the transect area just inside the reef crest as the algal turf becomes so thick as to obscure minor topographical features. We define four zones in this paper on the basis of increasing algal cover and turf development

towards the reef crest (Table 1). The transect covered all four zones, beginning 1 m from the shore line and ending at 71 m, just shoreward of the coralline algal ridge. Wave action prevented sampling beyond this point.

Table 1. The distribution and abundance of algal species in four zones across the bench transect and from the crest. The morphology of each species is represented by F=filamentous, T=turf (1-2 cm tufts forming dense turf), Fo=foliose, E=encrusting turf forms, c=crustose corallines. Where percent cover was estimated for individual species, these figures follow the morphological designate in the appropriate column. Algal species are arranged according to their occurrence on the reef flat from shore to crest rather than taxonomically.

Zone	Shoreward			Seaward	
	1 0-20	2 20-40	3 40-60	4 60-71	Crest ~85
Distance from shore (m.)					
Algal species					
<i>Bryopsis hypnoides</i>	T				
<i>Codium edule</i>	E 2				
<i>Cladophora hemisphaerica</i>	F 2	F	F		
<i>Cladophora</i> sp.			F		
<i>Ceramium</i> sp.	F	F	F	F } 5	F
<i>Polysiphonia</i> sp.	F 5	F 5	F 5	F } 5	F
" <i>Falkenbergia</i> "	F	F	F	F	
<i>Boodlea composita</i>				E 10	
<i>Jania</i> sp.	F } 5	T 25	T 60	T 60	T 10
<i>Acetabularia clavata</i>	T } 5	T			
<i>Centroceros</i> sp.	F	F			
Blue-green mat	F				
<i>Gelidiella</i> sp.		T	T	T 10	
<i>Griffithsia</i> sp.			F		
<i>Valonia trabeculata</i>		E	E 5	E 10	
<i>V. ventricava</i>			E		
<i>V. aegagropila</i>			E	E 15	
<i>Caulerpa racemosa</i>				Fo 5	
<i>C. serrulata</i>		Fo } 5	Fo } 5		
<i>Padina japonica</i>		Fo } 5	Fo } 5	Fo 10	Fo 5
<i>Chondria</i> sp.			T		
<i>Chylocladia</i> sp.			T		
<i>Bryopsis</i> sp.				T	
<i>Dictyosphaeria cavernosa</i>					E 5
<i>Porolithon</i> spp.					C 70
Total % cover	10-15	30-40	80-95	>95	>95
X Dry wt g/m ² Platforms	65	65	625	850	
X Dry wt g/m ² Depressions	35.5	165	585	660	X 198*

* Represents wet weight (g) of crest samples.

Methods

SAMPLING PROCEDURES

One segment of the polychaete fauna was sampled by taking twenty-five, 100 cm² scrapes with a sharp blade to include sand and algal matrix from thirteen stations along the first 70 m of a transect perpendicular to the shore line in January, 1976. All materials removed from these quadrats were bagged and preserved in 10% formalin. Two samples were collected from each site, one from a shallow pool (designated 1, 2, 3, etc.) and the other from within a half meter on the first platform (designated 1A, 2A, 3A, etc.). Station 13 is represented by one sample as pools and platforms were indistinguishable due to the thick algal mat. The endolithic fraction of the polychaete fauna was sampled by chiseling six pieces of rock including the overlying algal turf from the bench. Four of these blocks of hard substratum were from 23, 30, 35 and 40 m along the transect and measured 10 × 10 × 2 cm (block A) and 10 × 10 × 1 cm (blocks B, C, D). The algal crest samples measured 12 × 8 × 7 cm (block E) and 8 × 7 × 5 cm (block F) and were collected 85 m from shore in August, 1978, during a spring low tide. Blocks were soaked in 10% formalin and processed for polychaetes.

Fifteen, 100 cm² samples of algae were removed from the four zones of the bench (4 from Zones I, II, III and 3 from Zone IV). Algae were identified following preservation, then rinsed and sieved to remove sand and finally dried for biomass estimates.

LABORATORY ANALYSES

Chiseled blocks and crest samples were measured (surface area and volume displacement) then dissolved in a bath of 4 percent nitric acid and formalin to facilitate the rapid removal of polychaetes from the hard substrata (Brock and Brock, 1977). Polychaetes are usually entire and readily identifiable following acid dissolution of the carbonate substratum, permitting quantitative estimates of biomass and numbers/m². Scraped samples were sorted with the aid of a dissecting microscope to remove worms from the sand and algal matrix.

The most pertinent taxonomic works include Day 1967, Fauvel 1953, Hartman 1954, Imajima 1966 a & b, Reish 1968, Westheide 1974 and Woodwick 1964. Algae were identified from Taylor (1950) and unpublished keys.

Species diversities were calculated using the Shannon-Weaver diversity index (H').

TEMPERATURE

Daytime temperature readings were made in eleven pools across the bench during a spring low tide. Also a continuous recorder was placed in a pool midway along the study area for a 3-day period to record diurnal temperature range.

Results

Polychaetes totaling 6,931 individuals of 79 species belonging to 24 families were found (Appendix I, Tables 2 & 3). Four families, the Sphaerodoridae, Orbiniidae,

Table 2. The abundance of polychaetes in pairs of scraped samples from the bench. Samples designated A are from the flat surface of the reef platform, the others are from adjacent, shallow pools. Results are expressed as numbers of polychaetes and number of species per sample, dry weight g/m², species diversity (H') and estimated numbers of worms/m².

Station no.	1	1A	2	2A	3	3A	4	4A	5	5A	6	6A	7	7A
Distance from shore (m)		1		3		5		8		11		17		23
No. species	11	4	16	10	7	2	14	3	17	7	5	10	10	4
Biomass g/m ²	.4	.3	.5	.4	1.6	.04	1.03	.09	.3	.09	.01	.2	.07	.23
Species diversity (H')	1.77	0.93	1.96	1.81	1.34	0.69	1.96	0.96	1.97	1.62	1.16	2.09	2.08	1.37
Polychaetes/m ²	9,800	2,000	16,300	8,500	5,800	400	24,200	700	17,700	1,500	1,100	2,700	1,900	900
Station no.	8	8A	9	9A	10	10A	11	11A	12	12A	13			
Distance from shore (m)		26		36		46		56		66	71			
No. species	10	7	6	13	21	20	14	18	27	34	27			
Biomass g/m ²	.4	.14	0	4.4	1.1	2.7	8.2	7.3	8.0	4.7	1			
Species diversity (H')	2.14	1.89	1.52	1.65	2.6	2.5	2.09	2.14	2.32	2.77	2.13			
Polychaetes/m ²	2,300	1,100	1,300	10,300	10,800	13,800	21,400	15,900	30,100	32,700	13,000			

Table 3. The abundance and diversity of polychaetes in three dimensional samples, blocks (samples A, B, C, and D) and crest samples (samples E and F) from the bench. Sample information is presented as described for Table 2.

	A	B	C	D	E	F
Distance from shore (m)	23	30	35	40	~85	~85
No. species	27	30	35	39	26	25
Biomass g/m ²	8.8	7.4	9.3	7.6	33.1*	8.95
Species diversity (H')	1.75	2.37	2.53	2.65	2.41	2.47
Polychaetes/m ²	84,400	82,300	84,700	100,300	62,416	60,010

* Figure includes three large specimens of *Eunice afra*, without this biomass = 5.37 g/m².

Paraonidae and Scalibregmidae, and 12 species represent new records for Enewetak (see Reish, 1968; Hartman, 1954). In addition, 21 of the 31 syllid species were not previously recorded and 12 have yet to be assigned specific names. Scrape samples had 59 species, with 17 exclusive to these samples. Analyses of scraped samples revealed greater species richness of syllids, spionids and capitellids than the blocks (Appendix 1). Blocks contained larger populations of amphinomids, some syllid species, eunicids and the cirratulid *Dodecaceria laddi* (Appendix 1 and Table 3). These 3-dimensional samples included the burrowing and bioeroder polychaete species of the bench community.

Blocks A-D (Table 3) averaged 88,000 polychaetes/m² (range = 82,300–100,300/m²) with 27–39 species, scrapes (Table 2) from pools averaged 11,946 polychaetes/m² (range = 1100–301,000/m²) with 5–27 species and scrapes from the platform averaged 7,962 polychaetes/m² (range = 400–32,700/m²) with 2–34 species. Blocks E-F from the crest (Table 3) had an estimated 60,000 to 62,416 polychaetes/m² and twenty-five and twenty-six species. These crest samples are very similar in faunal composition. Biomass and species diversity (H') estimates (Tables 2 and 3, Fig. 1) increased seaward. Blocks and pool scrapes from the seaward extent of the transect have comparable polychaete biomass figures of 7.4–9.3 g dry wt/m² and 8.0–8.2 g dry wt/m².

The distribution of feeding types across the bench reveals a nearshore community dominated by tube dwelling, selective deposit feeders and suspension feeders, and a seaward assemblage of errant omnivorous and carnivorous species including syllids, amphinomids and nereids (Fig. 2).

Species richness and number of polychaetes/m² in scrape samples also differs in the two sections of the bench (Fig. 3A & B). Numbers of species range from 2 to 17 near shore, with more species in the pools than on the exposed platform, and 15–31 offshore (Fig. 3B). Estimates of polychaete abundance from scraped samples reveal a broad range from 400–24,200/m² near shore to a maximum of 32,700/m² at 66 m from shore (Fig. 3A and Table 2) with more individuals recorded from the pools in the shoreward sector.

The large standing crop of polychaetes in the pools (Figs. 1 and 3) at the

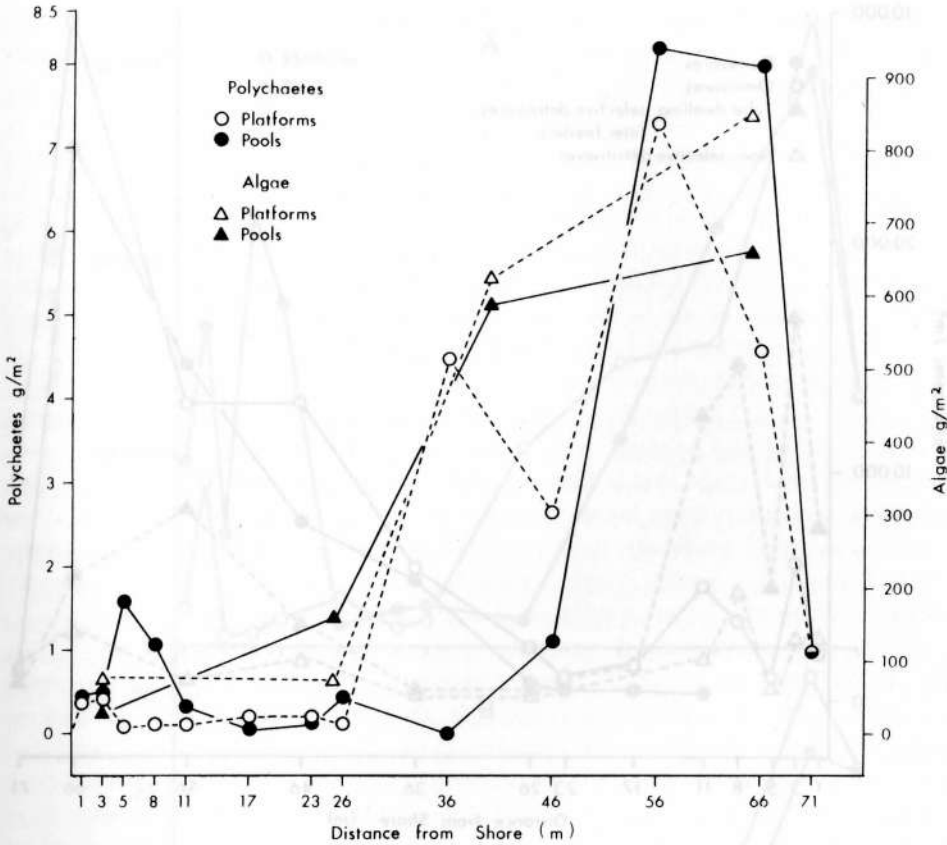


Fig. 1. Biomass of polychaetes (dry weight, g/m^2) from scape samples and the standing crop of algae (dry weight, g/m^2) along the shoreward to seaward transect on the Enewetak windward reef bench. Polychaete biomass, platforms \circ and pools \bullet ; algal biomass, platforms \triangle and pools \blacktriangle .

shoreward end of the transect is attributed to numerous spionids (Appendix 1). The spionids *Microspio microcera* and *Pseudopolydora antennata*, sabellids, capitellids and the syllids *Ehlersia cornuta* and *Opisthosyllis brunnea* form the majority of near shore polychaetes while the amphinomids, species of *Typosyllis*, nereids, chaetopterids and cirratulids are dominant forms in the turf covered section of bench (Appendix 1).

Algal turf thickness and percentage cover on the bench varies both along the shore-to-crest gradient and between platform and depressions. Twenty-six algal species were identified and the distribution and abundance of species across the bench formed the basis of the four zones defined in Table 1. It should be stressed here that algae were collected on a single occasion, and that species composition, percentage cover and standing crop of algae on the bench may vary seasonally (Tsuda and Kami, 1972). In general filamentous species predominate near shore (Zone I, Table 1) and

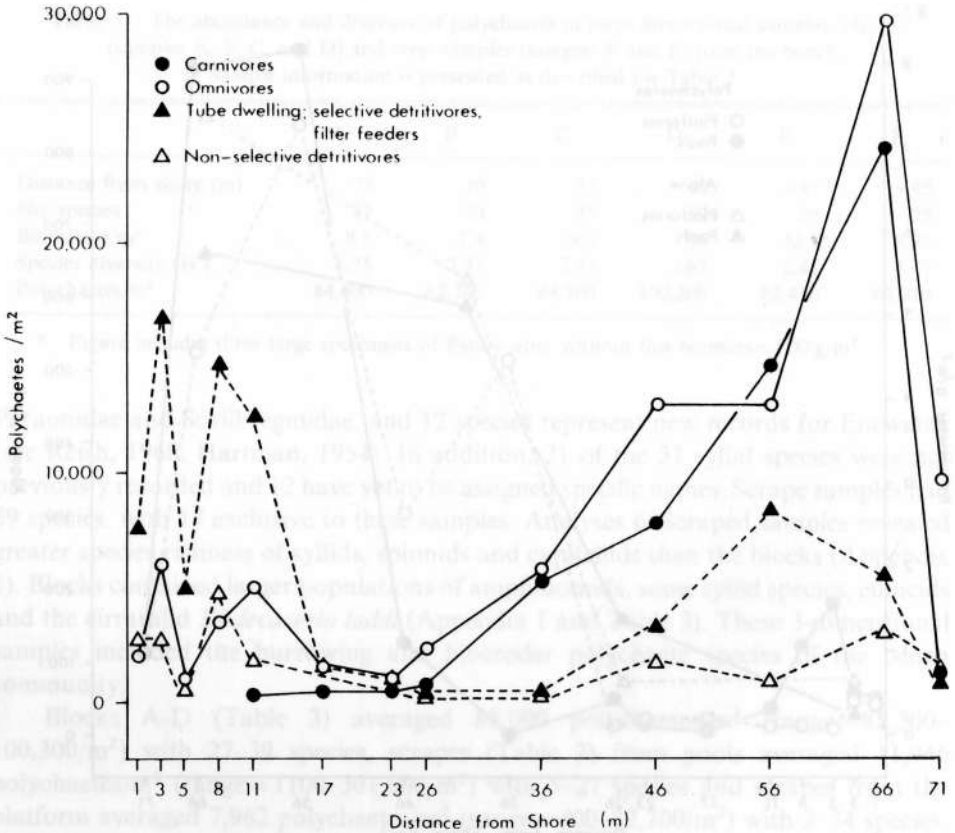


Fig. 2. The distribution of polychaete feeding categories across the bench transect. Polychaetes at the familial level are categorized as omnivores, carnivores, non-selective detritivores or tube dwelling, selective detritivores and filter feeders.

encrusting, tufted and foliose species form larger proportions of the sample with increasing distance offshore (Zones 2, 3, and 4, Table 1). Percent cover and biomass (dry wt g/m^2) of algae (Table 1 and Fig. 1) was approximately eight times greater on the seaward, as compared to the shoreward region of the bench. Filamentous *Polysiphonia* sp., *Ceramium* sp. and "*Falkenbergia*" occur in all samples, and *Cladophora hemispherica* and the blue-green *Entophysalis* sp. contributes significantly to the algal veneer of zone 1. The tufted, calcareous rhodophyte *Jania* sp. is the dominant form in zones 2, 3 and 4. The encrusting species of *Valonia* and *Boodlea* are predominant turf species in zones 3 & 4. The only foliose species *Padina japonica*, *Caulerpa serrulata* and *C. racemosa* contribute a small amount to the total cover in zones 2, 3 and 4 respectively. Encrusting *Porolithon* spp. form most of the crest with 70% coverage (Table 1).

Water temperature of pools during a midday low tide in August were 37.1°C, 35.5°C and 29.6°C at shoreward, middle and algal crest stations respectively. Air

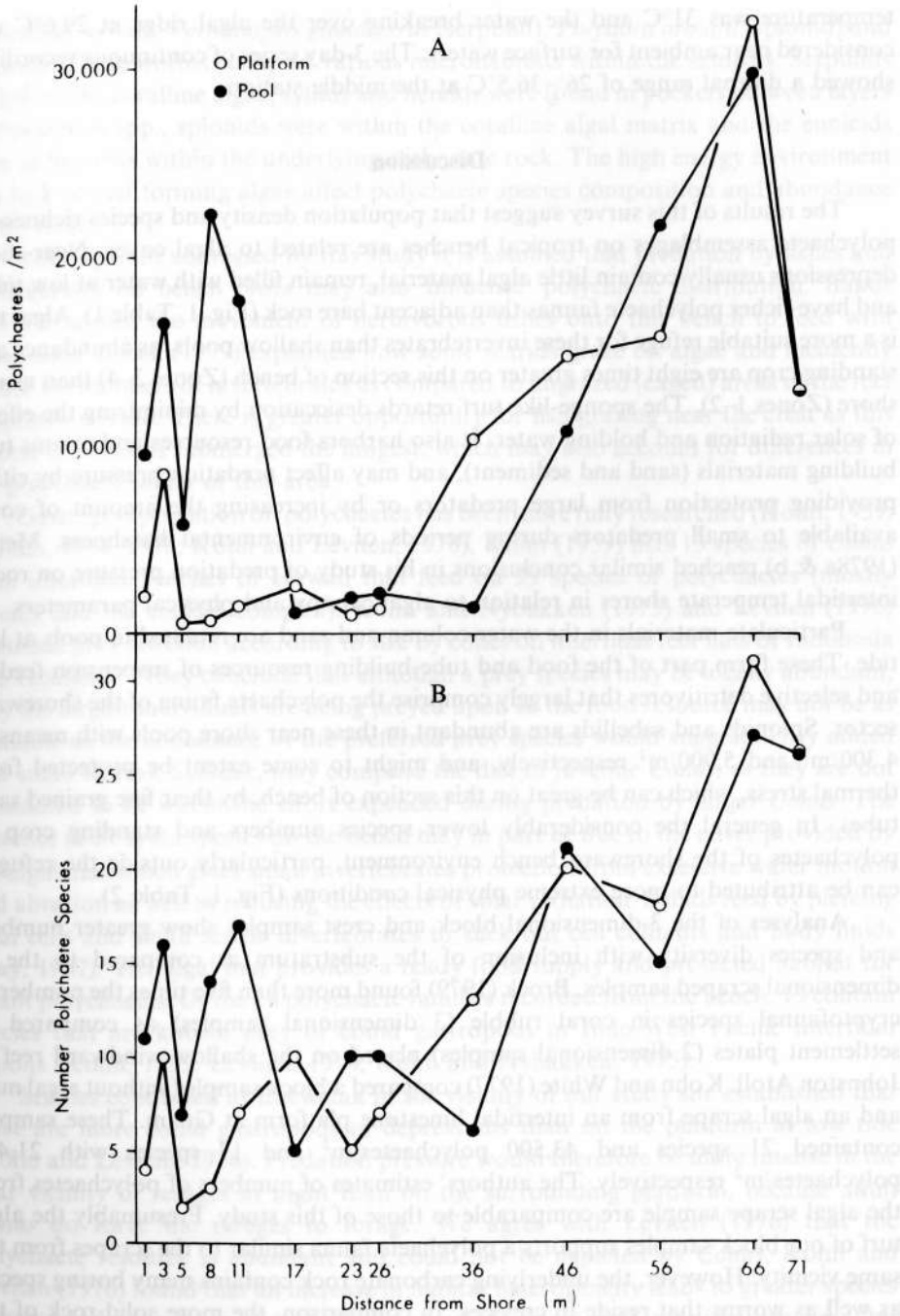


Fig. 3. The abundance of polychaetes (A) and polychaete species (B) in scape samples from both pools and adjacent platform areas.

temperature was 31°C and the water breaking over the algal ridge at 29.6°C was considered near ambient for surface waters. The 3-day series of continuous recordings showed a diurnal range of 26°–36.5°C at the middle station.

Discussion

The results of this survey suggest that population density and species richness of polychaete assemblages on tropical benches are related to algal cover. Near-shore depressions usually contain little algal material, remain filled with water at low tides, and have richer polychaete faunas than adjacent bare rock (Fig. 1, Table 1). Algal turf is a more suitable refuge for these invertebrates than shallow pools, as abundance and standing crop are eight times greater on this section of bench (Zones 3–4) than nearer shore (Zones 1–2). The sponge-like turf retards desiccation by minimizing the effects of solar radiation and holding water. It also harbors food resources and retains tube building materials (sand and sediment), and may affect predation pressure by either providing protection from large predators or by increasing the amount of cover available to small predators during periods of environmental harshness. Menge (1978a & b) reached similar conclusions in his study of predation pressure on rocky intertidal temperate shores in relation to algal canopy and physical parameters.

Particulate materials in the water column and sand are retained in pools at low tide. These form part of the food and tube-building resources of suspension feeders and selective detritivores that largely comprise the polychaete fauna of the shoreward sector. Spionids and sabellids are abundant in these near shore pools with means of 4,300/m² and 5,900/m² respectively, and might to some extent be protected from thermal stress, which can be great on this section of bench, by their fine grained sand tubes. In general the considerably lower species numbers and standing crop of polychaetes of the shoreward bench environment, particularly outside the refuges, can be attributed to more extreme physical conditions (Fig. 1, Table 2).

Analyses of the 3-dimensional block and crest samples show greater numbers and species diversity with inclusion of the substratum as compared to the 2-dimensional scraped samples. Brock (1979) found more than five times the number of cryptofaunal species in coral rubble (3 dimensional samples) as compared to settlement plates (2 dimensional samples) placed on the shallow windward reef at Johnston Atoll. Kohn and White (1977) compared a block sample (without algal mat) and an algal scrape from an intertidal limestone platform at Guam. These samples contained 21 species and 43,500 polychaetes/m² and 17 species with 21,400 polychaetes/m² respectively. The authors' estimates of numbers of polychaetes from the algal scrape sample are comparable to those of this study. Presumably the algal turf of our block samples supports a polychaete fauna similar to the scrapes from the same vicinity. However, the underlying carbonate rock contains many boring species as well as worms that reside in crevices. In comparison, the more solid rock of the crest, which lacked an algal mat and was covered by thick layers of smooth, encrusting corallines (*Porolithon* spp.) contained a different polychaete fauna typified

by nereids, syllids, *Vermiliopsis glandigerus* (serpulid), *Polydora armata* (spionid) and eunicids. These worms occupied various microhabitats within the samples. Serpulids settled on the coralline algae, syllids and nereids were found in pockets between layers of *Porolithon* spp., spionids were within the coralline algal matrix and the eunicids were in burrows within the underlying carbonate rock. The high energy environment and lack of turf forming algae affect polychaete species composition and abundance at the crest.

Although not addressed by this study it is assumed that predation by fishes and invertebrates on bench biota may also influence polychaete distribution. Bakus (1967) observed the movement of herbivorous fishes onto this bench to feed with rising tides. Brock (1979) explained how some scarids graze on algae and incidently reduce the numbers of invertebrates as compared to ungrazed (caged) areas of the reef at Johnston Atoll. There is greater opportunity for fish grazing near the crest as this section of bench is submerged the longest, which may also account for differences in the polychaete fauna of this area.

Gastropod predation on polychaetes has been more fully researched (Kohn, 1959; Leviten, 1974, 1978; Kohn and Leviten, 1976). Kohn (1959) lists 13 species of *Conus* from intertidal benches of Hawaii that feed on 29 species of polychaetes (mostly nereids and the eunicid complex). Kohn and Nybakken (1975) and Leviten (1976) discussed prey selection according to size by cones on intertidal reef flats of Indonesia and Thailand. They conclude that although a prey species may be locally abundant, only the largest individuals are being preyed upon so the food resource may not be as available as the abundance of the preferred prey species would suggest. They added that small worms, Syllidae, may comprise the diet of juvenile *Conus*, as they are not considered to be worth the effort expended during predation by larger *Conus*. The presence of 31 syllid species on the bench may in part be due to the cover provided by the algal mat which gives small invertebrates protection from excessive water motion and abrasion as well as reducing the effects of solar radiation. Syllids feed by piercing algal cells and small sessile invertebrates to suck out cell contents and body fluids (Day, 1967). The algal mat provides a ready food supply and protected habitat for errant polychaetes. Of the 24 polychaete families recorded from the bench, 13 contain species that are known prey of conid gastropods in Indo-West Pacific intertidal regions (Kohn, 1959; Leviten, 1974; Kohn and Nybakken, 1975).

Studies conducted at Enewetak in the vicinity of our study site established that there are more conid gastropods in depressions than on the platform at low tide (Kohn and Leviten, 1976). Predation pressure would therefore be more intense in the near vicinity of refuges at night than on the surrounding platform, because adult *Conus* do leave the refuges to forage. We agree with Leviten (1976) that the polychaete resource is abundant and could not be depleted by *Conus*. Kohn and Leviten (1976) found that an increase in habitat heterogeneity leads to greater species richness and abundance of predatory gastropods on tropical intertidal benches. Our data indicate that this is also true for polychaetes.

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[The table content is extremely faint and illegible due to low contrast and bleed-through from the reverse side of the page. It appears to be a large grid or data table.]

Appendix 1. Total species list and record of collections along the shore to crest transect, windward reef flat, Enewetak.

Numbers 1, 2, 3, etc. refer to scrape samples from pools, numbers 1A, 2A, 3A, etc. refer to scrape samples from the platform. Blocks (A-F) were collected at the following distances from shore: A=23 m, B=30 m, C=35 m, D=40 m, E and F=algal crest samples (85 m from shore).

Family	Distance from shore m	Blocks																				TOTAL												
		1	3	5	8	11	17	23	26	36	46	56	66	71	23	30	35	40	85	85														
	Polychaete species	1 1A	2 2A	3 3A	4 4A	5 5A	6 6A	7 7A	8 8A	9 9A	10 10A	11 11A	12 12A	13	A	B	C	D	E	F														
CHRYSOPETALIDAE	<i>Palaeonotus debilis</i>										1		4	1	1	1					8													
AMPHINOMIDAE	<i>Eurythoe complanata</i>					1		3	1	3	4	2		52	11	26	54	62	106	66	4	31	25	64	63							578		
	<i>Pseudeurythoe oculifera</i>									2					1	19	20	18	12	22	27	1	16	38	41	1						218		
PHYLLODOCIDAE	<i>Eulalia viridis</i>																															2		
SYLLIDAE	<i>Haplosyllis spongicola</i>																												1	32	30	63		
	<i>Parasphaerosyllis indica</i>													2		2				1	3	2	11	12	36	14	20	103						
	<i>Ehlersia cornuta</i>	3	6	4	2	2	2	5	1	3			3	2	4	2	15	18	8	6	13	37	11	98	169	159	252	13	11	849				
	<i>Ehlersia A</i>		5			10	13	1		1		1			2								2	8	3	10					56			
	<i>Ehlersia B</i>																															56		
	<i>Typosyllis alternata</i>																															15		
	<i>Typosyllis armillaris</i>		4	3						1				20		4				9	1	18		18	6	18	1			2	105			
	<i>Typosyllis bouvieri</i>					2									1		1															6		
	<i>Typosyllis exilis</i> (?)											2																				2		
	<i>Typosyllis hyalina</i>	1				3						3			6	2	6	1	31	12	1	10	15	22	81	26	20	242						
	<i>Typosyllis prolifera</i>		4				2			1	1		5	3	11	14	33	4	35	28	65	6	5	8		45	13	283						
	<i>Typosyllis taprobanensis</i> (?)																															1		
	<i>Typosyllis variegata</i>			4		3		2			2	2	2	1		9	20	9	21	2	28	3	5	5	8	7	3	4	140					
	<i>Typosyllis A</i>									2		1		9		4				2	18	12		1	14	12	8				83			
	<i>Typosyllis B</i>																															9		
	<i>Typosyllis C</i>																															55		
	<i>Typosyllis D</i>																															14		
	<i>Opisthosyllis brunnea</i>	6	5	5	14	7	2	6	4	16	7	1	8	1	2	5		2	6	4			1		9	7	23	36	41	25	5	1	249	
	<i>Opisthosyllis corallicola</i>																																23	
	<i>Opisthosyllis australis</i>																																1	
	<i>Exogone verugera</i>															1																	10	
	<i>Exogone A</i>							1							1																		4	
	<i>Sphaerosyllis ovigera</i>																																1	
	<i>Sphaerosyllis sublaevis</i>																																1	
	<i>Sphaerosyllis A</i>			2																													17	
	<i>Brania rhopalophora</i>	3		1				1																									43	
	<i>Brania A</i>			1				1																									8	
	<i>Brania B</i>																																3	
	<i>Autolytus sp.</i>																																8	
	Unk. sp. A																																19	
	Unk. sp. Y																																19	
																																		1

SPHAERODORIDAE																			1																	
Sphaerodoropsis capense																			1																	
NEREIDAE																																				
Micronereis eniwetokensis																			1																	
Ceratoneis mirabilis		1	2	4	1	4	1	1	3	2	1	1	4	8	24	1	3	7	2	5	4	4	11	2	3	2	3	2	13							
Pseudoneis variegata																			6																	
Platynereis pulchella																			1	2	3															
Nereis zonata perisca																			65	103	168															
Nereis sp. A																			6	1	7															
Nereis ? sp.																			3	4	7															
GLYCERIDAE																																				
Glycera tessellata																			2				2													
EUNICIDAE																																				
Palola siciliensis																			1				5	11	17											
Lysidice collaris																			2	2	9	5	6	6	28	9	67									
Nematoneis unicornis																			2	2	8	1	17	13	1	22	68	43	177							
Eunice afra																			1	1	8				10											
LYSARETIDAE																																				
Oenone fulgida																			1	1				1				3								
LUMBRINERIDAE																																				
Lumbrineris latreilli																			1				1				1									
ARABELLIDAE																																				
Arabella iricolor																			1	2				3	3				4				13			
DORVILLIDAE																																				
Dorvillea similis																			1				1				1				1					
SPIONIDAE																			1				201	21	223											
Polydora armata																			1				9	5	6				107							
Pseudopolydora antennata		9	13	26	3	2	23	5	1	5								1				2														
Pseudopolydora reishi																			1				1				2									
Microspio microcera		46	1	18	30	28	2	41	39	1	7	2	2	2	1	6	2	1	6	10	1	9				255										
CHAETOPTERIDAE																																				
Phyllochaetopterus racemosus																			7	4	45	6	25	2	1	15	1	4				110				
Mesochoetopterus sagittarius																			1				6				7				14					
ORBINIIDAE																																				
Scoloplos sp.																			2				1				3	1	4	10	35				56	
PARAONIDAE																																				
Paraonis gracilis																			1				3				4				4					
CIRRATULIDAE																																				
Dodecaceria laddi																			11				1	1	1	501	258	243	175	2	3				1196	
Cirriformia semicincta																			1	1				1	9	9	15	3	23	7	2	1				72

Appendix 3. Total species list and record of collections along the shore to great channel, southwest reef flat, Eniwetok.

Numbers 1, 2, 3, etc. refer to scrape samples from grazers, numbers 1A, 2A, 3A, etc. refer to scrape samples from

the phytobenthos. Blocks (A-F) were collected in the following locations from about A = 25 m

from Wagon C = 20 m, D = 15 m, E and F = deep areas (20 m from shore)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30							
OPHELIIDAE																																					
Polyopthalmus pictus						2							2	6	2	6	8	3	7										1		6		43				
SCALIBREGMIDAE																																					
Hyboscolex longiseta																	1																	1			
CAPITELLIDAE																																					
Capitella capitata	1	1	1			3						1			1				2															10			
Pullia sp.																								1										45	46		
Decamastus sp.												1							3	2														6			
Notomastus latericeus			1			1																1	12	33	42									90			
Heteromastides bifidus	9	5			24	2						4	1					4	1											1	5		56				
Dasybranchus sp.											1		1																					2			
Leiochrides sp.	10	13	1	1	40	8																	1											74			
Capitellid sp.																															51	41		92			
MALDANIDAE																																					
Maldanid sp.																																65		65			
TEREBELLIDAE																																					
Leania minuta																																			1		
Terebellid sp.												1																							1		
SABELLIDAE																																					
Sabellid sp.	9	69	20	17	81	1	67	1	3	4	1	1													30	72	47	63					1	487			
SERPULIDAE																																					
Vermiliopsis glandigerus																																5	4	9			
Serpuline																																			4		
Spirorbine																																			4		
																			2												1				24	3	30