Populations of Tropical Intertidal Gastropods Before and After a Typhoon

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Abstract—Structural habitat complexity in the form of cracks, crevices and boulders and rubble-filled depressions in otherwise smooth intertidal windward atoll reefrock platforms provide adequate shelter for predatory gastropod molluscs during severe storm conditions. A typhoon that struck Enewetak in January, 1979, did not reduce abundance or species richness in assemblages primarily of Conidae and Muricidae occupying refuges of these types. On a portion of the platform where a thick algal turf had provided protected sites for predatory gastropods, population density and species richness of *Conus* species were much lower after the typhoon. Muricidae, more tenacious gastropods whose shell forms are also better adapted to withstand heavy wave action, were not significantly reduced in numbers of individuals or species. Censuses more immediate than 4 years pretyphoon are unfortunately lacking, so these effects cannot be attributed with certainty to the 1979 typhoon. However, no storms of typhoon intensity had occurred during the intervening period.

Introduction

Infrequent catastrophic storms may have profound and long-lasting effects on coral reefs and atolls. Storm-caused alterations of general reef and cay morphology have been studied most (Stoddart, 1971). Quantitative before-and-after information on populations of benthic organisms is generally lacking except for some data on corals (Stoddart, 1974), although detailed comparisons are available for other unpredicted, severe hydrographic and climatic events, such as the effects of low sea stands and heavy rainstorms on corals (Loya, 1976) and gastropod molluscs (Yamaguchi, 1975a, Leviten and Kohn, 1980). In the latter report, we showed that an unpredictable, density-independent mortality factor—an unusually heavy rainstorm coinciding with low tide—severely affected populations of intertidal gastropods at Enewetak Atoll in the Marshall Islands. Earlier (Kohn and Leviten, 1976) we proposed that topographic habitat complexity protects intertidal gastropods from harsh physical environmental conditions. Typhoon Alice struck Enewetak 5 January 1979, subjecting intertidal populations to another rare, unpredictable disturbance. In this study, I test the hypotheses that 1) unusually severe storm conditions reduce abundance and species richness in intertidal assemblages of tropical predatory gastropods, and 2) the presence of refuges ameliorates these effects. The test is based on comparisons of censuses about 3 months after the typhoon (29 March-2 April 1979) with data from earlier years.

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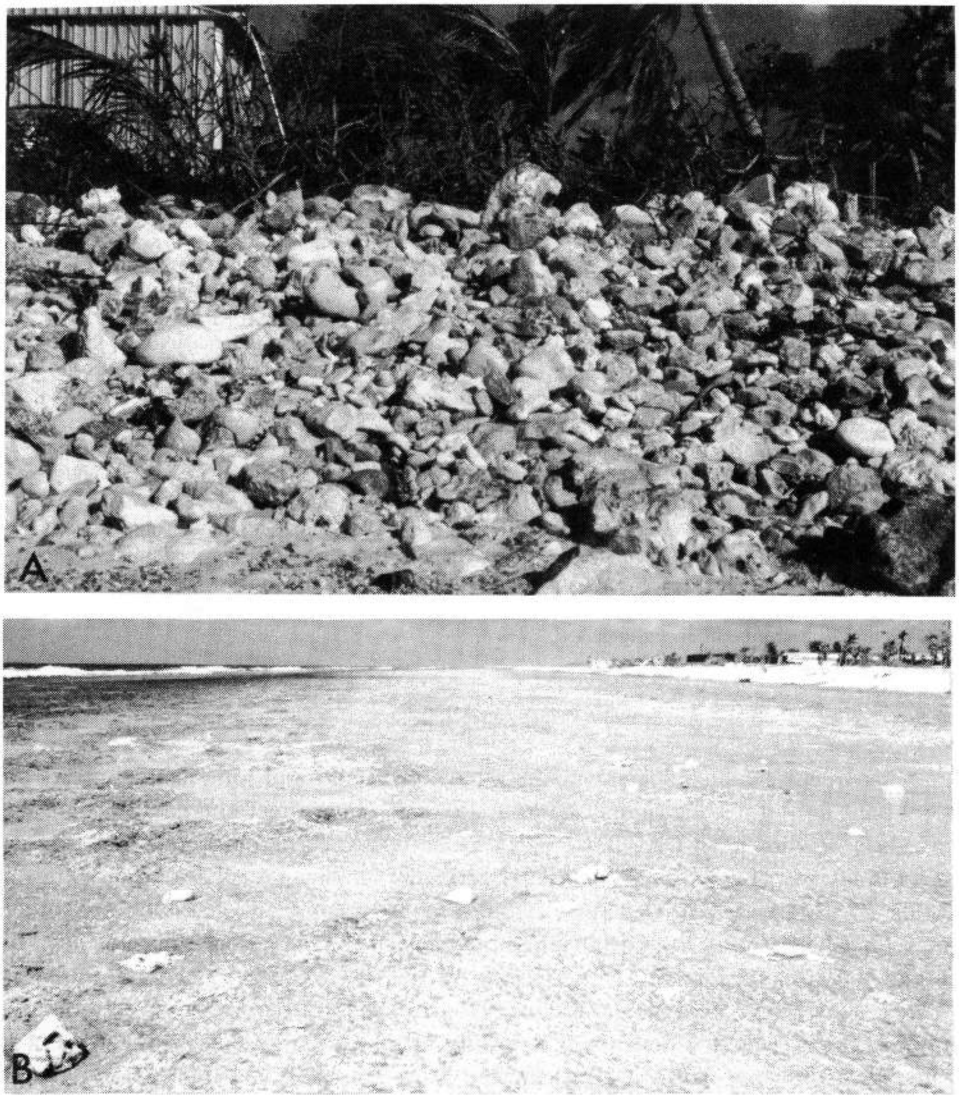

Study Sites

Three previously studied sites were resurveyed on broad intertidal windward bench platforms at Enewetak Atoll. Kohn and Leviten (1976) and Leviten and Kohn (1980) described the two sites on the northeast shore of Enewetak (formerly Eniwetok) Island, Stas. F4 (11°21.7′N, 162°21.3′E) and F7 (11°21.2′N, 162°21.1′E), where the platform is about 100 m wide and at the +1.8′ (+0.5 m) level. Bailey-Brock, et al. (1980) described the pretyphoon algal flora as well as the polychaete

Fig. 1. Sta. F7, Enewetak Island. A, Bank of boulders and rubble driven against *Scaevola* bushes by Typhoon Alice. 2 April 1979. B, View southwest from Sta. F7 at low tide. The algal turf in Figs. 1B and 1C is about half as thick as shown in Fig. 1B of Leviten and Kohn (1980), which was taken 8 September 1971. C, A 1-m^2 quadrat adjacent to foreground of Fig. 1B at low tide. Photos B and C, 26 April 1979.

annelids at Sta. F7. Sta. M1 is a similar but broader (157 m) bench along the northeast shore of Medren (formerly Parry) Island (11°24.5′N, 162°23.0′E). Stas. F4 and F7 had been censused 1971–1974, and Sta. M1 in 1956, 1971, and 1974.

Thus the most recent pretyphoon surveys (Dec., 1974) were four years prior to the resurveys. However, no other typhoons had occurred in the interim. The most severe weather during this period was Tropical Storm Nancy, which arrived at Enewetak as a tropical disturbance 25 April 1976, and attained tropical depression and storm status only after passing to the west (NOAA 1977). A second factor complicating interpretation of the resurvey data is that because of the use of Enewetak Island by several hundred U.S. military and civilian contract personnel commencing in 1977, gastropod populations may have been reduced by shell collecting activity. Because the animals treated in this study are small, inconspicuous, and primarily in sheltered sites during daytime low tides (Kohn and Leviten, 1976; Leviten and Kohn, 1980), this may not be important, but the magnitude of this human predation effect is unknown. Because no U.S. personnel are housed on Medren, the resurvey there controlled for this factor.

Typhoon Alice

Enewetak Island was exposed to nearly the full force of Typhoon Alice on 5 January 1979. The center of the storm passed about 50 km S. of the island moving about 18 km/h. Winds at Enewetak reached 145 km/h, and damage to structures and terrestrial vegetation was severe (Honolulu Star-Bulletin, 6, 7 Jan. 1979). Waves washed over the island, and water depth reached 40 cm in the Mid-Pacific Marine Laboratory. Cobble- and boulder-sized coral fragments from the seaward forereef slope were washed across the windward platform; as has occurred elsewhere (Stoddart, 1971) these formed boulder and rubble banks against *Scaevola* bushes along the windward shore of the central portion of Enewetak Island (Sta. F7; Fig. 1A).

At the time of our visit, the 2 cm-thick algal turf described by Leviten and Kohn (1980: Fig. 1B) and Bailey-Brock, et al. (1980) was reduced to about half its former thickness (Figs. 1B, 1C). However, we do not really know whether this turf was scoured by rapidly moving water containing suspended particles during the typhoon, or whether it may normally be thinner at that time of year.

At the northern part of Enewetak Island (Sta. F4) and at Medren (Sta. M1), the pretyphoon substrate was primarily smooth reef limestone, bare of macroscopic plants or with a thin algal film (Kohn and Leviten, 1976, Leviten and Kohn, 1980: Fig. 1C). Few typhoon-related changes were apparent at these localities. Some of the depressions described by Leviten and Kohn (1980: Fig. 1D, E) contained fresh rubble, and one contained a large (23 cm long), partially living fragment of the coral *Pocillopora eydouxii*, which does not normally live on the windward platform. This fragment was undoubtedly broken from a head on the forereef slope and deposited on the platform by the storm waves.

Methods

The methods in this study are essentially those described by Kohn and Leviten (1976) and Leviten and Kohn (1980), except that because of tide and weather conditions during a visit limited to part of one spring tide series it was not possible to census a minimum of 20 1-m^2 quadrats in each microhabitat type.

In order to compare population density and species richness of predatory gastropods with prior data and in different microhabitat types, the following areas (designated as in Kohn and Leviten, 1976) were recensused: Sta. F4: A_1, smooth, bare portions of bench without refuges; C_1, as A_1 but with refuges, i.e., depressions partly filled with coral rubble and sand; C_2, as A_1 but with experimentally bored depressions. Sta. M1: C_5, smooth, bare portions of bench with crevices and depressions lacking coral rubble and sand; C_6, as C_5 but with depressions containing coral rubble and sand. Sta. F7: A transect of 1-m^2 quadrats normal to the bench, from the shoreward margin to as close to the outer edge as wave action permitted. All censuses were made during daytime low tides except that the outer 14 m at Sta. F7 had to be sampled during a night low tide. We also censused Sta. F4 during a night low tide.

Because 50.3% of all individuals (N = 743) and 7 of the 21 species in the recensuses were members of the genus *Conus*, and because Kohn and Leviten (1976) treated it separately, I consider it separately here. Most (85%) of the remaining individuals were members of the family Muricidae.

Results

STA. F4. Because the pretyphoon habitats at Sta. F4 and M1 were very similar, these are treated first. As in the earlier censuses at F4, we found lowest *Conus* population density and species richness on the smoothest, barest portions of bench. Total *Conus* population densities in 20 1-m^2 quadrats at Area A_1 did not differ significantly from the 1972 census (1-way G-test; $P > 0.3$), nor did population density or species richness per quadrat, although one additional species occurred in the sample (Tables 1, 2). Density of all predatory gastropods other than *Conus* was identical to the earlier census, in which only half as many quadrats had been sampled; two additional species were present and relative abundances differed somewhat. In 1979, a census of the smooth, bare portions of bench at night, when many *Conus* leave their refuges to forage on the bench surface, revealed higher *Conus* density ($0.9/m^2$) than during the day ($0.4/m^2$), as expected. Density of other predatory gastropods was somewhat lower at night ($2.3/m^2$) than that measured during the day ($3.4/m^2$), but higher than in a comparable daytime census in 1972 (area A_2: $1.1/m^2$).

As in the previous study (Kohn and Leviten, 1976), quadrats centered on refuges (Area C_1) contained more species of *Conus* (5) and higher population densities (Tables 1, 2). Population density did not differ significantly from the pretyphoon study, and species richness was identical, although two of the rarer species were different and relative abundances differed considerably. Population densities of other predatory gastropods were not determined in the earlier census. Relative abundances differed primarily in that *Morula uva* and *Drupa morum* were commoner and *D. ricina* somewhat less common in the posttyphoon samples (Table 1).

It was possible to locate only 9 of the artificial refuges surveyed earlier (Kohn and Leviten, 1976). This was partly because waves were washing over the bench when this portion of the resurvey had to be done, but many of the boreholes seemed to have disappeared or have eroded into larger potholes during the 7 years since the first census and the 9 years since they were drilled (Bernstein, 1974). Population density of both *Conus* and other gastropods was considerably lower than in 1972 (Area C_2; Tables 1 and 2), but the refuges were shallower due to erosion (4–6 cm vs. 8 cm) (Bernstein, 1974) and probably therefore offered less protection to the gastropods (Kohn and Leviten, 1976).

STA. M1. In both 1974 and 1979 studies, quadrats centered on refuges with coral rocks, rubble, and sand (Area C_5) contained significantly more *Conus* individuals than quadrats with only crevices and depressions lacking rocks, rubble

Table 1. Abundance and diversity of intertidal predatory gastropods at Enewetak before
in the areas sampled. For descriptions, sizes, and illustrations

				Conus species — Family Conidae								
Year Censused	Census Area	Microhabitat	Area Sampled (m^2)	*C. ebraeus*	*C. chaldaeus*	*C. sponsalis*	*C. coronatus*	*C. miliaris*	*C. catus*	*C. frigidus*	*C. rattus*	Total
Sta. F4 Enewetak I., northern part, Enewetak Atoll, Marshall Islands (11°21.4′N, 162°21.1′E)												
1972	A_1	Smooth, bare portions of bench without refuges	20	7	4							11
1979	A_1		20	4	1	3						8
1972	A_2	As A_1; controls of C_2	57	12	5	32						49
1972	C_1	Smooth, bare portions of bench with natural	20	48	44	4	7	1				104
1979	C_1	refuges	20	22	40	30			1		1	94
1972	C_{1a}	As C_1	—	61	115	17	22	2	2	1		220
1972	C_2	As A_2 but with	(57)[b]	35	57	127			1	1		221
1979	C_2	experimental refuges	(9)[b]	1	6	15						22
Sta. M1 Medren (Parry I.), Enewetak Atoll, Marshall Islands (11°24.6′N, 162°20.4′E)												
1974	C_5	Smooth, bare portions of bench with refuges lacking	16	15	6	5	1			1		28
1979	C_5	sand and coral rubble	17	26	6	26	4					62
1974	C_6	As C_5, but refuges containing sand and/or	30	68	50	9	4					131
1979	C_6	coral rubble	14	46	18	23	9					96
Sta. F7 Enewetak I., central part, Enewetak Atoll, Marshall Islands (11°21.0′N, 162°20.6′E)												
1972–1974		Smooth portions of bench with algal	223	383	245	78	75	3		2		786
1979		turf	75	31	16	32	10	1		1	1	92

[a] area of sample = $10\,m^2$.

[b] data for gastropods in experimental refuges only.

and after Typhoon Alice. Values in the table are numbers of individuals observed of the species listed, see Cernohorsky (1971–1972).

Species in Other Genera																	
Family Muricidae										Family Mitridae			Buccinidae	Vasidae	Nassariidae	Epitoniidae	
Morula granulata	*Morula uva*	*Morula fiscella*	*Drupa morum*	*Drupa ricina*	*Drupa arachnoides*	*Drupa grossularia*	*Drupella cornus*	*Thais tuberosa*	*Maculotriton serriale*	*Strigatella litterata*	*Pusia cancellarioides*	*Mitra cucumerina*	*Cantharus undosus*	*Vasum turbinellus*	*Nassarius gaudiosus*	*Epitonium* sp.	Total
24[a]	8[a]			1[a]										1[a]			34
20	13		15	8	3									9			68
26	10		24	3						1				1			65
									no data								
74	14	1	15	33	7		1			3	3	1	2	7			161
30	1		1	25	6				1	1	2			3			70
98	10		20	13				4	6	1	7			16			175
5				2							1			5	2		15
11										2							13
2														2			4
42	1			1	1				3	3				1			52
23		1								1				8			33
281	55		6	67		1				16	5			3			434
62	3		3	7						4	1			7		1	88

Table 2. Population density, species richness, and relative abundance of intertidal predatory gastropods at Enewetak before (1972, 1974) and after (1979) Typhoon Alice. Symbols in the table indicate the probabilities of accepting the null hypothesis of no difference between before- and after-typhoon censuses. NS, $P>0.12$; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$. Censuses are designated as in Table 1.

		Conus species						Species in other genera					
Census Area	Year	Number of Species	Mean Density of all Species (no./m^2)	Population Density	Population Density by Quadrat	Species Richness by Quadrat	Relative Abundance	Number of Species	Mean Density of all Species (no./m^2)	Population Density	Population Density by Quadrat	Species Richness by Quadrat	Relative Abundance
				G Test	U Test	U Test	G Test			G Test	U Test	U Test	G Test
A_1	1972	2	0.6	NS	NS	NS	NS	4[a]	3.4[a]	NS	NS	NS	**
	1979	3	0.4					6	3.4				
C_1	1972	5	5.2	NS	NS	NS	***	(9)	—	—	—	—	**
	1979	5	4.7					12	8.1				
C_2^b	1972	5	3.8	—	+	*	NS	5	3.2	—	+	NS	*
	1979	3	2.4					9	1.7				
C_5	1974	5	1.8	**	*	*	NS	2	0.8	*	*	NS	NS
	1979	4	3.5					2	0.2				
C_6	1974	4	4.4	*	**	**	***	7	1.7	NS	**	***	**
	1979	4	6.9					4	2.4				

[a] Data based on 10 1-m^2 quadrats.

[b] C_2 census data include only gastropods in artificial refuges, not on the surrounding square meter.

—, Test not made due to lack of appropriate data.

and sand (Area C_6) (Tables 1, 2). Population density was considerably higher in 1979, by a factor of 2 in Area C_5 and by a factor of 1.6 in Area C_6. Both differences are significant at the 0.01 level (G tests on data from 16 and 14 quadrats, respectively). Mann-Whitney U tests on density in individual quadrats gave essentially similar results (Table 2). Population densities of other predatory gastropods were lower in 1979 than in 1974 at Area C_5 but higher at Area C_6. More species of *Conus* were present in both C_5 and C_6 quadrats in 1979. Species richness of other genera was higher in Area C_6 in 1979, because all quadrats included at least one such gastropod, while 8 of the 30 quadrats in 1974 had none. Relative abundance of both *Conus* species and species in other genera also differed between years at both areas (Tables 1, 2).

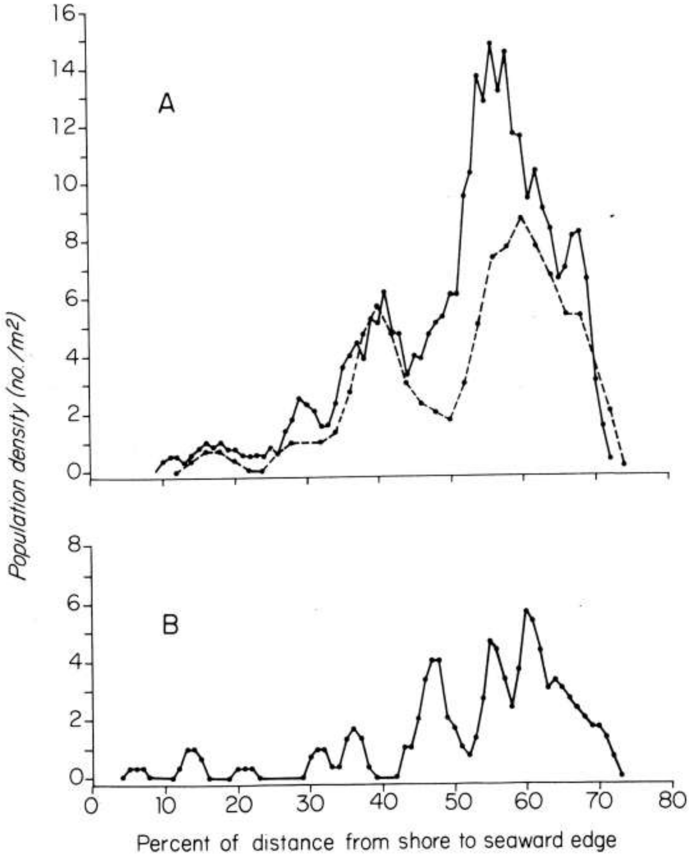

Fig. 2. Abundance distributions (3-place sliding averages) of all *Conus* species in censuses across the bench platform at Sta. F7, Enewetak Island. Plotted lines that do not intersect abscissa indicate termination of transects. A, Pretyphoon data. Solid line, mean of 4 censuses 1972–1974; dashed line, census of 28 December 1974 only. B, Post-typhoon data. Census of 30 March 1979. Statistical analyses by quadrats (Table 3) indicate a highly significant reduction in density in 1979.

STA. F7. Of the bench habitats studied, only Sta. F7 seemed visibly affected by Typhoon Alice. Prior to the typhoon, a band 50–65 m from shôre, covered by a few cm of water even at low tide, supported "a healthy 2 cm-thick algal turf" (Leviten and Kohn, 1980; see also Bailey-Brock, et al., 1980). In March, 1979, this turf was only about 1 cm thick. Because of the lack of prior algal samples from the bench during March–April, it is not certain that this loss was due to scouring during the typhoon. In previous years we observed the turf to be about 2 cm thick during December, January, and May, but Dr. P. J. Leviten stated in field notes for 28 December 1974 that the turf appeared thin. Dr. K. L. Webb, who was at Enewetak during Typhoon Alice, stated (verbal communication) that the appearance of this portion of the platform changed from green to brown following the typhoon. It was still brown in March–April. The tufted calcareous rhodophyte *Jania* appeared to be the dominant alga, and species of *Valonia, Boodlea* and *Cladophora* were prominent components of the turf after as well as before the typhoon (Bailey-Brock, et al., 1980).

Conus populations were reduced more seriously at the F7 transect site than anywhere else. Fig. 2 shows that while the pattern of distribution of *Conus* species across the bench was little altered, density was much reduced. In the band 35–65 m from shore, where the algal turf was formerly thickest and *Conus* density highest, mean number per m^2 declined from 6.9 to 2.3. Wilcoxon matched-pairs signed-ranks tests show that the density differences of *Conus* species by quadrat were highly significant in this region in comparisons of 1979 data with the means of all pre-typhoon censuses and with the most recent and least dense pretyphoon census of 1974 (Table 3). *Conus* species richness by quadrat was also significantly reduced (Table 3). Population density and species richness of other predatory gastropods at Sta. F7 were reduced less than *Conus* spp. following Typhoon Alice (Table 3). This result is as expected, because 94% of these belonged to the family Muricidae. Intertidal members of this family are much more tenacious than *Conus*; some (*Drupa* spp.) are quite limpet-like in form with a broad, disc-shaped foot (Miller, 1974; Kohn and Leviten, 1976).

SHELL SIZE. Prior to the recensus, it seemed conceivable that Typhoon Alice could have eliminated most or all adult predatory gastropods from the windward platform, but that recruitment during the ensuing 12 weeks could have restored the depleted populations to their former densities. Because there is no protected, subtidal source of large numbers of adults adjacent to the habitats studied, recruitment would have to be from settlement of planktonic veliger larvae.

Little is known of the early growth rates of *Conus* in nature. According to the formula of Frank (1969) for *C. miliaris*, a 3-month-old individual would be expected to be about 3 mm long. However, this estimate is probably maximal, as it is based on the Von Bertalanffy growth curve, which overestimates early growth rates of marine invertebrates (Yamaguchi, 1975b).

All species of *Conus* inhabiting intertidal benches tend to be small and similar in adult shell size (Fig. 3; Kohn, 1971). The bench environment is physically harsh even in the absence of typhoons, being subject to desiccation and inundation by fresh water

Table 3. Differences in population density and species richness of predatory gastropods in transects of 1-m^2 quadrats across Sta. F7 before and after Typhoon Alice. Symbols in the body of the table indicate one-tailed probabilities of the null hypothesis that density or species richness values are not greater in pretyphoon than posttyphoon quadrat samples, by the Wilcoxon Matched-Pairs Signed-Ranks Test. NS, $P>0.10$; +, $P<0.10$; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

Sampling Region	Taxon	1979 vs. mean of 1972–74	Number of 1-m^2 quadrat samples	1979 vs. 1974 only	Number of 1-m^2 quadrat samples
Population Density					
Inner portion (1–34 m)	Conidae	**	34	NS	17
	Muricidae, etc.	NS		NS	
Region of maximum density (35–65 m)	Conidae	***	31	**	15
	Muricidae, etc.	**		NS	
Outer portion (66–75 m)	Conidae	*	9	—	3
	Muricidae, etc.	NS		—	
Total transect (1–75 m)	Conidae	***	74	***	35
	Muricidae, etc.	**		NS	
Species Richness					
Total transect (1–75 m)	Conidae	**	74	*	35
	Muricidae, etc.	NS		+	

'Muricidae, etc.' includes the following proportions of Muricidae: 1972–74: 94%; 1974 only: 93%; 1979: 85%. Other families represented are indicated in Table 1.

from rain during low tide periods, and heavy wave action and rapid water movement at high tide. Individuals larger than about 25 mm in shell length are probably selected against by the restricted size of available protected sites; members of the genus characteristically attain considerably larger size in subtidal habitats (Kohn, 1971: Fig. 4).

Comparisons of size-frequency data for the 3 commonest *Conus* species before and after Typhoon Alice (Table 4, Fig. 3) indicate the absence of any shifts to smaller-sized individuals that would suggest recruitment of juveniles following defaunation. In fact, all 1979 means were larger, although most of the differences are not statistically significant. This result leads to the conclusion that the adult gastropods survived the typhoon.

Discussion

The general result of this resurvey is that the predatory gastropods protected by

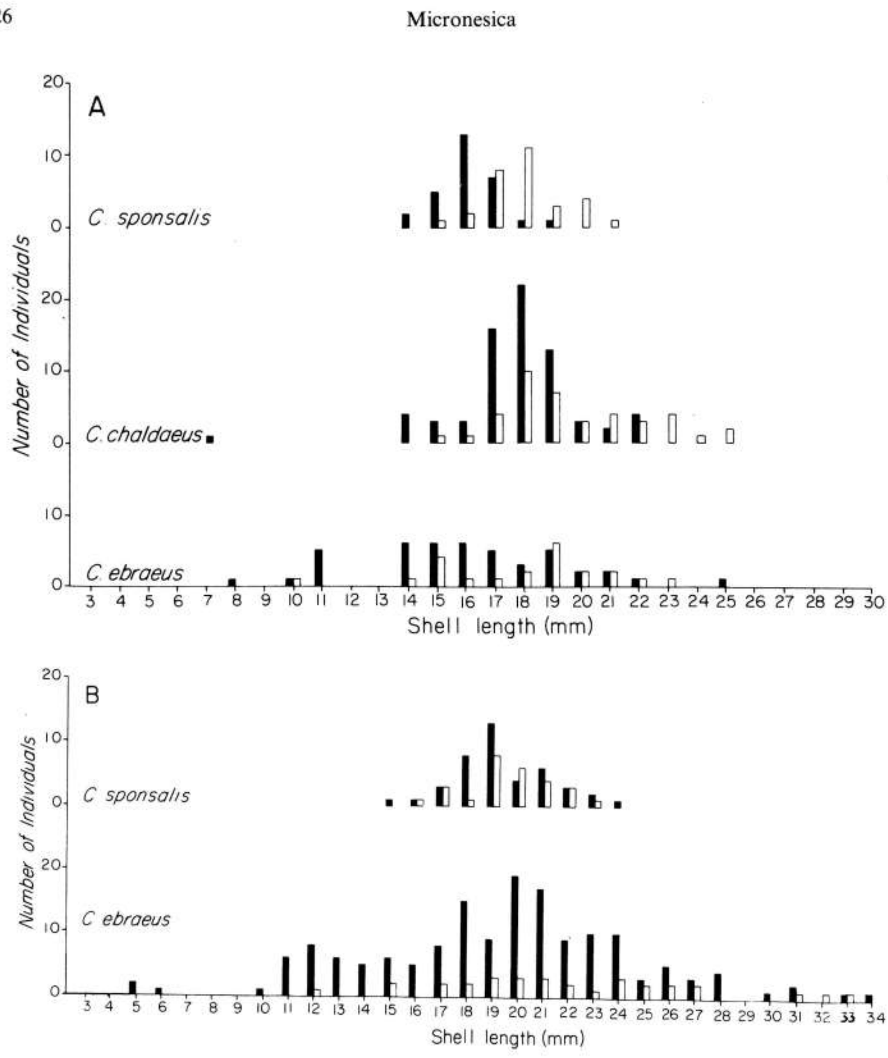

Fig. 3. Examples of size-frequency distributions of the commonest species of *Conus* before and after Typhoon Alice. A, Sta. F4. solid bars, 1972–73; open bars, 1979. B, Sta. M1. solid bars, 1956; open bars, 1979. Table 4 presents statistical analyses of these data.

refuges of physical origin—cracks, crevices, and depressions—in the windward reefrock platform at Enewetak are able to survive the most severe weather conditions likely to be encountered there. At the two stations (F4 and M1) having refuges of these types, disturbance of the environment by Typhoon Alice was insufficient to reduce abundance or species richness of the dominant predatory gastropod families, the Conidae and Muricidae.

Only in the transect at Sta. F7, where biogenic habitat structure in the form of a thick algal turf was an important source of protected sites for the gastropods, were

Table 4. *Conus* species at Enewetak before and after Typhoon Alice. Symbols in the table indicate the probability of accepting the null hypothesis of no difference in mean shell length between before- and after-typhoon censuses. NS, $P>0.10$; +, $P<0.10$; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$. (t tests for unequal variances.)

Sta.	Species	*C. ebraeus*		*C. chaldaeus*		*C. sponsalis*	
	Shell length	$\bar{Y}$ (S) n	P	$\bar{Y}$ (S) n	P	$\bar{Y}$ (S) n	P
F4	Before typhoon (1972–1973)	16.0 (3.4) 44		17.7 (2.2) 71		15.9 (1.1) 29	
		t=2.3	*	t=4.3	***	t=6.3	***
F4	After typhoon (1979)	17.9 (3.0) 22		19.7 (2.5) 40		18.0 (1.4) 30	
M1	Before typhoon (1956)	19.4 (5.2) 157				19.4 (1.9) 42	
		t=2.7	**			t=0.5	NS
M1	After typhoon (1979)	22.0 (5.0) 31				19.6 (1.7) 27	
F7	Before typhoon (Total 1971–74)	15.9 (3.3) 299		17.1 (2.1) 170		16.0 (2.5) 53	
		t=4.3	***	t=1.4	+	t=6.3	***
F7	After typhoon (1979)	19.6 (4.2) 25		19.9 (5.3) 7		19.1 (1.7) 24	
		t=0.5	NS	t=0.15	NS		
F7	Before typhoon (1974 only)	19.0 (4.6) 26		20.2 (1.5) 13			

densities significantly reduced. This reduction was most pronounced in the central part of the bench (35–65 m from shore); it may be due to removal of about one-half of the turf by scouring action during the typhoon. However, we unfortunately lack samples taken shortly before the typhoon, so that the reduction in turf thickness cannot be attributed with certainty to the storm.

I conclude that refuges of physical origin, such as crevices and depressions on the bench surface not affected by typhoon conditions, afford predatory gastropods adequate protection from the stress of severe storms. However, biogenic protective sites that are diminished during a typhoon, in this case probably by shearing of an algal turf, protect the gastropods less well from such natural disturbances, with resulting high mortality.

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