Pacific Science (1980), vol. 34, no. 4

Abundance, Diversity, and Resource Use in an Assemblage of *Conus* Species in Enewetak Lagoon[1]

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ABSTRACT: Eight species of the gastropod genus *Conus* co-occur in sand substrate and an adjacent meadow of *Halimeda stuposa* in Enewetak lagoon, an unusually diverse assemblage for this type of habitat. Population density is high, and large species predominate; they represent all major feeding groups in the genus: predators on polychaetes, enteropneusts, gastropods, and fishes. Although the two most common *Conus* species eat primarily the same prey species, they mainly take prey of different sizes in different microhabitats. The results suggest that sufficient microhabitat heterogeneity and prey diversity exist to permit spatial segregation and specialization on different prey resources by the different *Conus* species present. Between-species dissimilarity in resource use thus agrees with previous observations on more diverse *Conus* assemblages of subtidal coral reef platforms. Prey species diversity is inversely related to body size, confirming and extending a previously identified pattern among *Conus* species that prey on sedentary polychaetes.

EXTENSIVE SUBTIDAL AREAS with uniform sand substratum typically support fewer species of *Conus* than other habitat types characteristically utilized by gastropods of this genus in the Indo-West Pacific tropics. Assemblages of 9–27 species ($\bar{x} = 14$) of *Conus* occur on subtidal coral reef platforms, 5–9 species ($\bar{x} = 8$) typically occupy intertidal benches, but only 1–6 species ($\bar{x} = 3$) have been found in the few subtidal sandy areas previously studied (Kohn 1967, Kohn and Nybakken 1975).

In this paper, I report on the abundance, diversity, and use of habitat and food resources in an unusually dense and diverse assemblage of eight sediment-dwelling *Conus* species in a shallow, peripheral region of the Enewetak Atoll lagoon. An effort was made to test the hypothesis that *Conus* species partition resources less, i.e., overlap more, than on subtidal coral reefs where more species co-occur in a more heterogeneous environment (Kohn and Nybakken 1975; Leviten 1978). This is one of a series of reports analyzing resource utilization by predatory gastropods in different types of marine habitats at Enewetak (Kohn and Leviten 1976; Leviten 1976, 1978; Leviten and Kohn 1980).

STUDY SITE

The study site (Sta. M19) is located in the northeastern part of Enewetak lagoon, about 150 m south of the northwest end of Aomon (also known as Aranit and Sally) Island (11°37.33′ N, 162°19.16′ E). The habitat is of Type I (Kohn 1967), "characterized by vast stretches of pure sand substratum, or sand with vegetation but without stones, coral heads, or other large hard objects." It included three very distinct microhabitats in close proximity, shown from left to right in Figure 1: (1) a very shallow area of rippled, coarse sand with some coral rubble in the troughs; (2) a channel with

[1] This research was supported by National Science Foundation grants GB-32105X and DEB-7724430, and by Atomic Energy Commission contracts AT-(29-2)-226 and AT-(26-1)-628. Manuscript accepted 21 July 1980.

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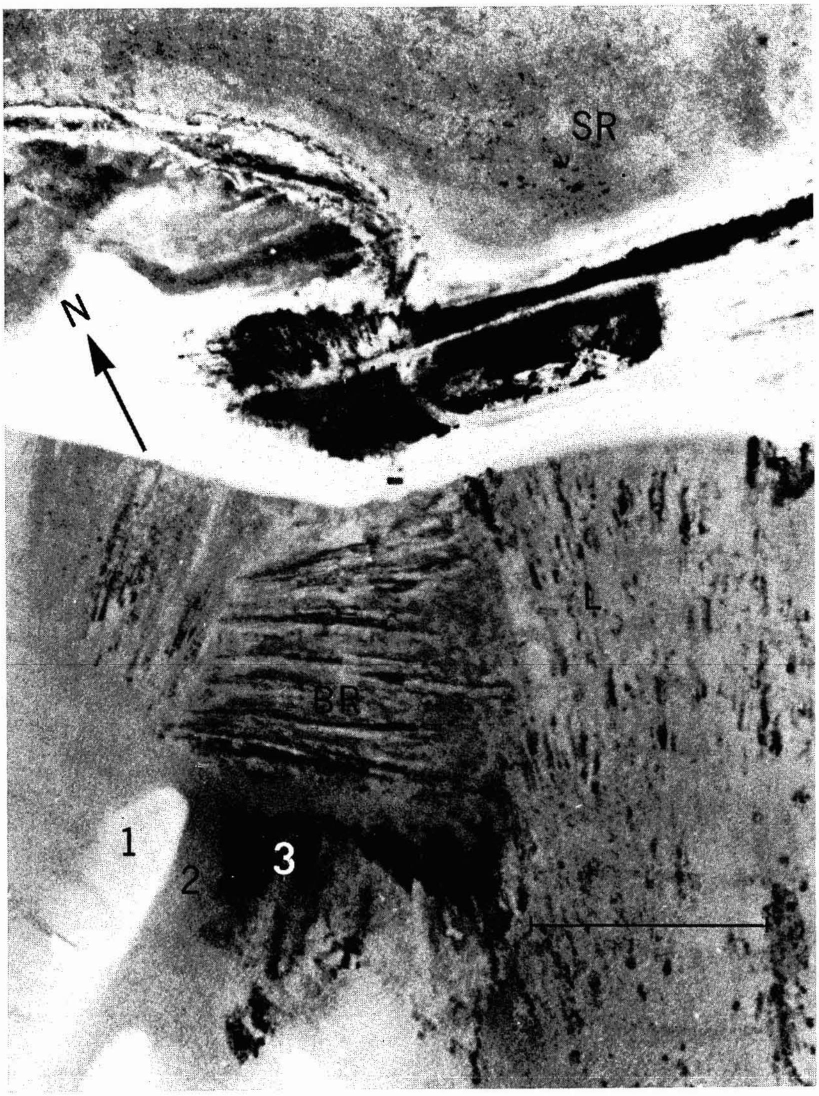

FIGURE 1. Vertical aerial photograph of the northwest portion of Aomon (=Aranit, =Sally) Island, Enewetak Atoll. Study site (Sta. M19): (1) shallow, rippled sand; (2) channel; (3) *Halimeda* meadow (BR, beachrock ridges; L, lagoon; SR, seaward reef flat; V, terrestrial vegetation). Scale line = 100 m. (Photograph by EG&G, Inc. for U.S. Energy Research and Development Administration, 1974.)

substrate grading from gravel and some pebbles and coarse and medium sand on the northwest side to primarily medium and coarse sand on the southeast side; and (3) a large meadow primarily of the calcareous green alga *Halimeda stuposa* Taylor (Hillis 1959; Hillis-Colinvaux 1977 and personal communication). I subdivided the channel into two microhabitats, characterized by high (35 percent) gravel and pebble content on the northwest side adjacent to the bank and by low gravel and pebble content (13 percent) on the southeast side adjacent to the *Halimeda* bed. The particle size distribution of sand within the *Halimeda* bed was similar to the southeast side of the channel but with

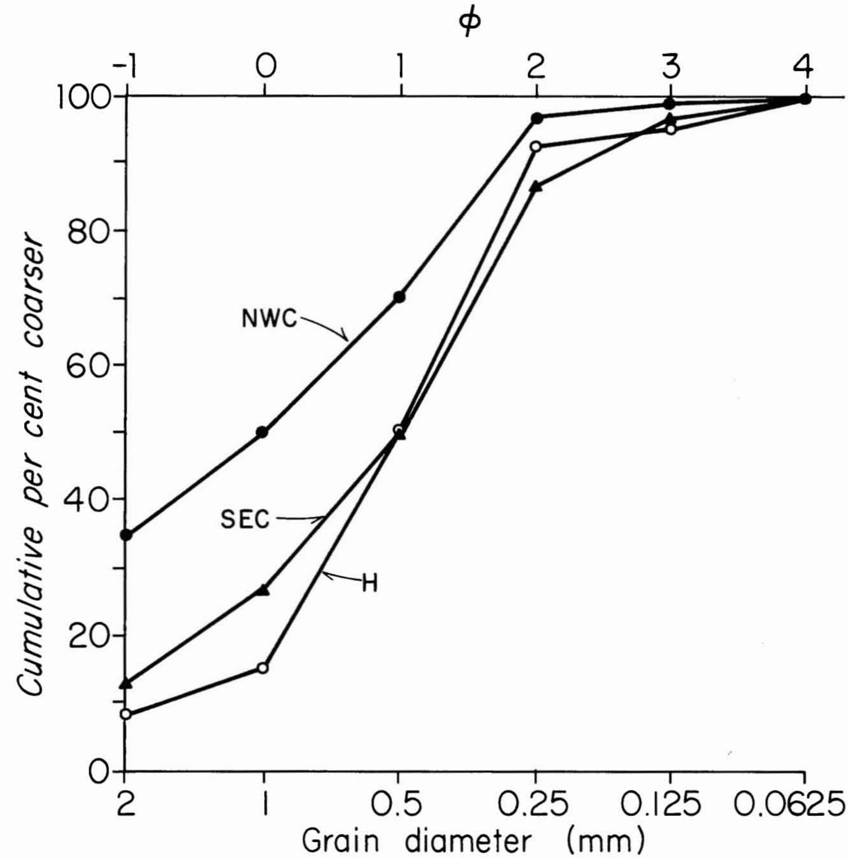

FIGURE 2. Cumulative particle size distribution of substrate at Sta. M19, 20 September 1973 (NWC, northwest side of channel, occupied by *Conus pulicarius*; SEC, southeast side of channel, occupied by *C. litteratus* and *C. leopardus*; H, *Halimeda* meadow, occupied by *C. leopardus*).

TABLE 1

RELATIVE ABUNDANCE AND POPULATION DENSITY OF *Conus* SPECIES AT STA. M19, ENEWETAK LAGOON

SPECIES	NUMBER OBSERVED IN QUANTITATIVE AND NONQUANTITATIVE CENSUSES	PROPORTION OF TOTAL (p_i)	PROPORTION IN QUANTITATIVE CENSUSES, $N = 93$ (p_i)
C. pulicarius Hwass *in* Bruguière	122	0.40	0.55
C. litteratus Linnaeus	105	0.35	0.26
C. leopardus (Röding)	49	0.16	0.16
C. lividus Hwass *in* Bruguière	14	0.05	0.01
C. eburneus Hwass *in* Bruguière	6	0.02	0.01
C. consors Sowerby	3	0.01	0.01
C. sugillatus Reeve	3	0.01	—
C. marmoreus Linnaeus	2	<0.01	—
	304	1.00	1.00

somewhat less very coarse sand and gravel (Figure 2). Inshore of the *Halimeda* bed, the channel bends, separating the bed from the most offshore of several beachrock ridges to the northeast (Figure 1). These apparently indicate positions of the lagoon beach of Aomon at earlier times. The islet thus appears to be migrating northeastward over the seaward reef flat. The elevations of the shallow sand, northwest and southeast sides of the channel, and *Halimeda* meadow were about -0.3 m, -0.8 m, -1.0 m, and -0.7 m, respectively, relative to tidal datum (0.5 ft $\approx$ 0.15 m below mean low water spring tides).

A sample of about 1 liter of substrate material from the northwest portion of the channel was examined for infauna. This revealed that the cirratulid polychaete *Cirriformia punctata* (Grube) was the dominant species, and that *Glycera tesselata* Grube and the enteropneust *Ptychodera flava* Eschscholtz were common. *Phyllochaetopterus* sp. cf. *P. arabicus* Grube predominated in a similar sample from the southeast portion, which also contained several *Eunice vittata* (Della Chiaje), *C. punctata*, and burrowing anemones. Censuses of *Conus* in the northwest portion of the channel also contained six individuals of the gastropod *Terebra maculata* (Linnaeus) and one each of *T. crenulata* (Linnaeus), *T.* sp., and *Oliva* sp. in 31 m^2.

Infrequent visits unfortunately permitted only a few study days widely separated in time. The site was visited 3 and 5 September 1972, 17 and 20 September 1973, and 30 December 1974.

METHODS

Population density of *Conus* was determined by censusing individuals in 1-m^2 quadrats placed randomly on the channel and *Halimeda* meadow microhabitats, and in six 1 × 5-m transects along or across apparent environmental gradients. In all, 210 m^2 containing 93 individuals of six species of *Conus* were surveyed in this manner. In parts of the habitat that were not sampled quantitatively, visual censuses of *Conus* species were made by swimming over the habitat. For each observed individual, the nature of the substrate and the gastropod's relationship to it were recorded.

Composition of the diet was determined mainly by identifying remains defecated by *Conus* kept individually in jars of clean seawater for 24 hr after collection. These animals were individually marked (by num-

TABLE 2

POPULATION DENSITY (NUMBER/10 m^2) OF *Conus* SPECIES IN DIFFERENT MICROHABITATS AT STA. M19, ENEWETAK LAGOON

SPECIES	NORTHWEST PART OF CHANNEL, ADJACENT TO COARSE SAND AREA	SOUTHEAST CHANNEL, ADJACENT TO *Halimeda* BED (+ SAND PATCHES IN *Halimeda* BED)	DENSE *Halimeda* BED	NUMBER IN SAMPLES	MEAN DENSITY
C. eburneus	0.1			1	0.05
C. pulicarius	5.8	0.2		51	2.4
C. leopardus	0.8	0.8		15	0.7
C. litteratus	0.7	1.5	1.0	24	1.1
C. consors		0.1		1	0.05
C. lividus			0.5	1	0.05
Number in samples	63	27	3	93	—
Area sampled (m^2)	84	106	20	$\Sigma = 210$	
Mean density	7.4	2.6	1.5		4.4
Total number of species present	5	6	4		
H' (in all samples)	0.7	1.3	0.8		

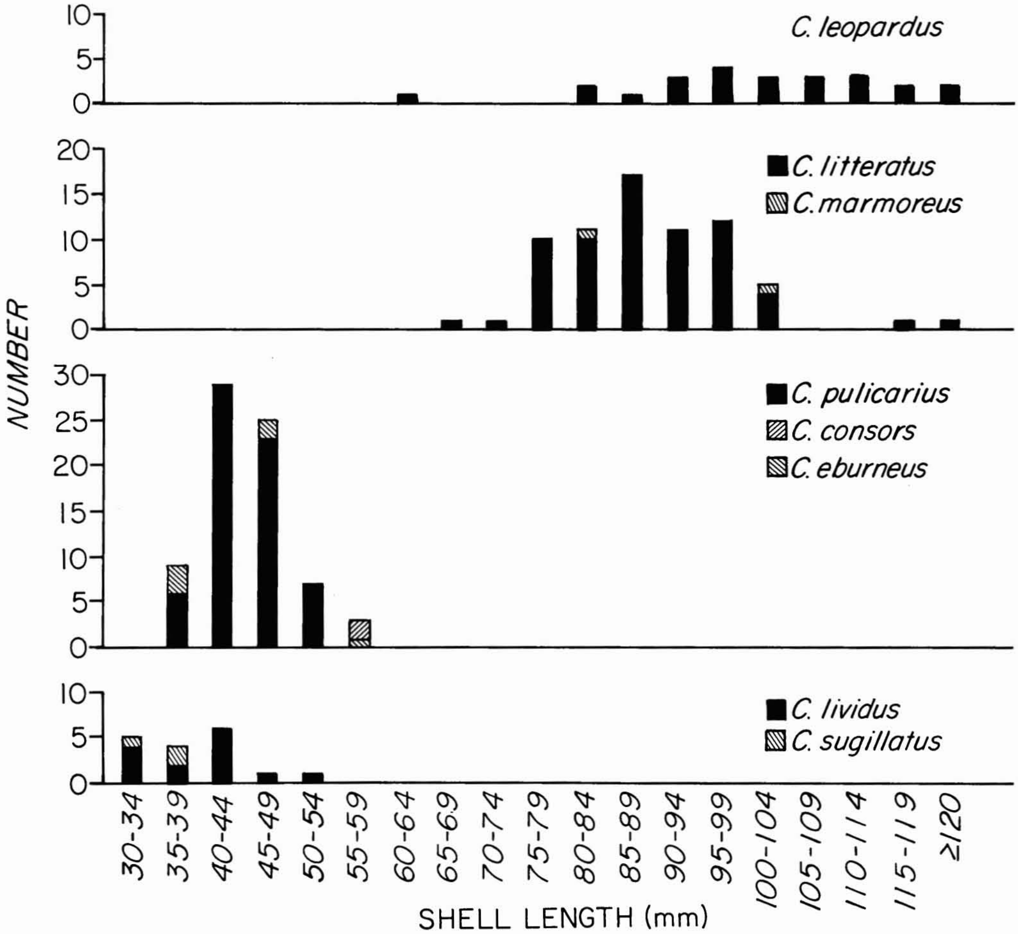

FIGURE 3. Length–frequency distributions of *Conus* species at Sta. M19, Enewetak lagoon. Mean shell length in millimeters, mean ln body volume in cubic millimeters, and sample size, respectively, follow in parentheses: *C. leopardus* (101, 11.6, 24); *C. marmoreus* (94, 11.1, 2); *C. litteratus* (89, 11.1, 68); *C. consors* (57, 9.5, 2); *C. eburneus* (44, 9.1, 6); *C. pulicarius* (44, 9.1, 65); *C. lividus* (40, 8.6, 14); *C. sugillatus* (35, 8.1, 3).

bers scratched in the periostracum) and returned to their original habitat 2–3 days later. In other cases, food organisms were recovered from dissection of alimentary tracts of specimens fixed as soon as possible after collection.

RESULTS

Abundance and Population Density

Table 1 lists the species of *Conus* present and their relative abundance in all censuses. The assemblage consists of more species (8 versus 1–6, $\bar{x} = 3$) and has a high index of diversity ($H' = 1.4$ versus 0.0–1.5, $\bar{x} = 0.5$) compared with those of similar habitats elsewhere summarized by Kohn (1967: table 1, fig. 1). The major discrepancy between the quantitative and nonquantitative censuses in Table 1 is the lower proportion of *Conus pulicarius* in the latter. This is probably because about 2/3 of the data are from the nonquantitative censuses, in which the gastropods were only observed from above; some *C. pulicarius* bury completely in sediment, and these would have been missed.

Table 2 indicates population density of the species encountered in the quantitative sam-

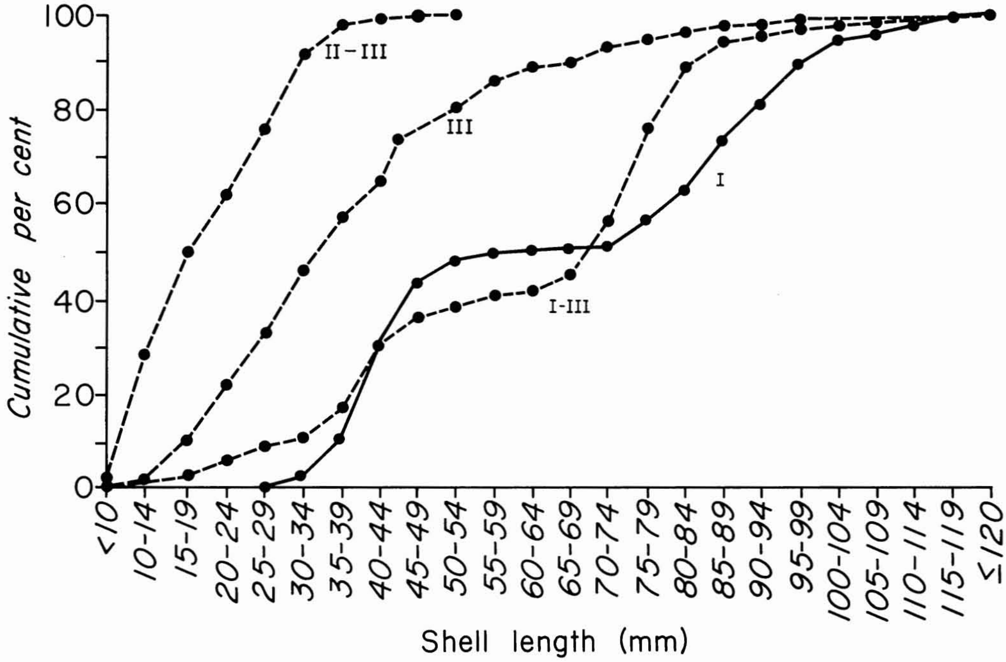

FIGURE 4. Cumulative length–frequency distributions of *Conus* species in Type I habitat (subtidal sand) at Sta. M19, Enewetak Atoll (solid line; $N = 184$), compared with data from other habitat types on Indian Ocean reefs (Kohn and Nybakken 1975: fig. 4): Type II-III, truncated reef limestone platform ($N = 469$); Type III, subtidal reefs ($N = 389$); Type I-III, subtidal reef with large sand areas ($N = 174$).

ples of the major microhabitats. Population density is highest in the northwest (outer) side of the channel, because the most common species, *Conus pulicarius*, is concentrated there. It is lowest on *Halimeda*, as most individuals occurred on sand patches—clearings within the *Halimeda* meadow.

Population density at Sta. M19 is an order of magnitude higher than at the most similar previously censused habitats—subtidal reef platforms with large areas of sand substrate (Type I-III habitat) in the Indian Ocean [0.2–0.5 individuals per 10 m^2 (Kohn and Nybakken 1975)].

Size

Analysis of size—frequency distributions (Figure 3) indicates that about half the individuals belong to a group of species (mainly *C. leopardus* and *C. litteratus*) characterized by large body size (mean shell lengths about 92 mm); the rest comprise a group of species (mainly *C. pulicarius*) with mean shell length about 45 mm. The overall size–frequency distribution (curve I, Figure 4) closely resembles that from Type I-III habitat in the Indian Ocean. The two steep rises in both cumulative curves reflect the bimodality evident in Figure 3. Both curves are displaced to the right relative to those for other habitat types characteristically occupied by *Conus* assemblages (curves II-III and III, Figure 4), indicating the predominance of larger animals in Type I and I-III habitats. Members of the large group in the Type I habitat at Enewetak are significantly larger than in the Indian Ocean Type I-III sample (one-tailed Kolmogorov–Smirnov test, $P < 0.001$). The former habitat supports the largest-size *Conus* assemblage yet studied. The caption to Figure 3 includes values of mean body volume [formula of Leviten (1978)] in order to permit comparison with sizes of species in Type II and III habitats given by Leviten (1978).

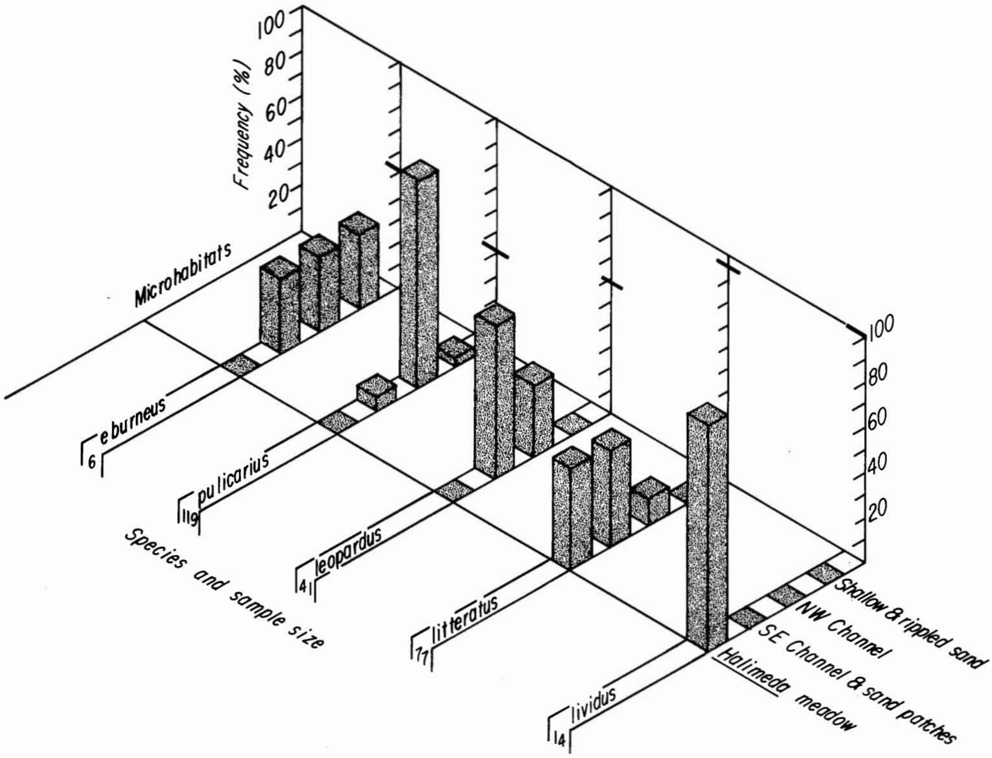

FIGURE 5. Proportions of the most common *Conus* species occupying different microhabitats at Sta. M19. Solid bars on ordinates indicate percent of epifaunal individuals.

Recovery of three marked specimens of *Conus litteratus* more than a year after their release permitted measurements of growth rate, heretofore completely lacking for any large *Conus* species. Shell lengths and maximum diameters of these (in millimeters) were: 87 × 53: 88 × 54 after 468 days; 89 × 56: no change after 380 days; 95 × 56: 99 × 59 after 469 days. Mean increases in shell length were 0.7, 0.0, and 3.1 mm/year, respectively.

Microhabitat Utilization

The most common species, *Conus pulicarius*, is highly specialized with respect to microhabitat utilization (Figure 5). All individuals occupied sand substrate, and 108 of the 119 individuals observed were in the northwest (outer) side of the channel. *Conus leopardus* also occurred exclusively on sand, primarily in the southeast side of the channel between the *Halimeda* bed and the coarser sand occupied by *C. pulicarius* (20 individuals), in the outer channel with *C. pulicarius* (13 individuals), and in sand patches within the *Halimeda* bed (8 individuals). No *C. leopardus* occurred on the dense patches of *Halimeda*. *Conus litteratus*, the second most common species, had a broad microhabitat range (Figure 5), occurring throughout the *Halimeda* bed, in the bands of the channel occupied by *C. leopardus* and *C. pulicarius*, and in the channel between the *Halimeda* bed and the beachrock outcrops (Figure 1).

The most diverse assemblage (six species, $H' = 1.3$) occurred in the inner southeast side of the channel and sand patches. In addition to the four species listed in Table 3, two of the three individuals of *Conus consors* and both *C. marmoreus* observed in the non-

TABLE 3

DIVERSITY AND SIMILARITY OF MICROHABITAT AND FOOD OF *Conus* SPECIES AT STA. M19, ENEWETAK LAGOON [EXPRESSED AS PROPORTIONAL SIMILARITY, PS $= \Sigma \min(p_{ix}, p_{iy})$, OF MICROHABITAT (LOWER LEFT HALF MATRIX, BASED ON FIGURE 3) AND FOOD (UPPER RIGHT HALF MATRIX, BASED ON DATA IN TABLE 4)]

	C. pulicarius	*C. leopardus*	*C. litteratus*	*C. lividus*
C. pulicarius		0	0.81	0
C. leopardus	0.38		0	0
C. litteratus	0.18	0.55		0
C. lividus	0	0	0.45	
Mean Microhabitat PS	0.19	0.31	0.39	0.15
Microhabitat diversity H'	0.4	0.6	1.0	0.0
Prey species diversity H'	0.7	0.0	0.1	0.9

TABLE 4

NUMBER OF PREY ORGANISMS CONSUMED BY THE EIGHT SPECIES OF *Conus* AT STA. M19, ENEWETAK LAGOON

	Conus SPECIES AND NUMBER OF EACH EXAMINED							
PREY SPECIES	*lividus* (14)	*sugillatus* (3)	*eburneus* (6)	*pulicarius* (65)	*litteratus* (68)	*leopardus* (26)	*marmoreus* (2)	*consors* (3)
Nereidae								
Platynereis dumerilii (Audouin & Milne Edwards)	4							
Perinereis sp. 3066	1							
Ceratonereis mirabilis Kinberg		1						
Unidentified Nereidae				1				
Eunicidae								
Eunice vittata (Della Chiaje)		1						
Palola siciliensis (Grube)				2				
Arabella mutans (Chamberlin)				1				
Phyllodocidae (unidentified)			1					
Glyceridae								
Glycera sp.			1					
Syllidae (unidentified)					1			
Spionidae (unidentified)	1							
Capitellidae								
Dasybranchus caducus (Grube)				17	39*			
Chaetopteridae								
Mesochaetopterus minutus Potts			1					
Enteropneusta								
Ptychodera flava Eschscholtz						11*		
Gastropoda								
Conus litteratus Linnaeus							1	
Pisces (unidentified)								1
Total identified food items	6	2	3	21	40*	11*	1	1

*Of the total, five identified tentatively.

quantitative censuses (Table 1) occurred in this microhabitat. All three *C. sugillatus* occurred in the dense *Halimeda* bed, which had the fewest species. Species diversity of the outer channel microhabitat was lowest, due to the predominance of *C. pulicarius*. The six *C. eburneus* occurred on, or buried in, sand throughout the study area. Some individuals of this species carried sea anemones, *Anthothoe* sp., dorsally on the shell.

Among species represented by sample sizes greater than ten, *Conus litteratus* was the most generalized and *C. lividus* the most specialized with respect to microhabitat use. *Conus leopardus* and *C. litteratus* were the most similar to each other. *Conus litteratus* had the highest average similarity with all other species, while *C. lividus* and *C. pulicarius* were the most distinct, with less than 20 percent mean overlap with the others (Table 3).

Food

Leviten (1978) predicted that competition for food may be important in the ecology of subtidal reef assemblages of *Conus* on the grounds that large *Conus* individuals are more specialized predators and eat larger prey items than small individuals, and large prey organisms are not abundant in their environment (Leviten 1976).

The assemblage of eight *Conus* species studied in Enewetak lagoon is characterized by larger body size than any studied previously (Figure 4) and also includes representatives of all major feeding groups, i.e., predators on polychaete and enteropneust worms, mollusks, and fishes. The two most common species, *C. pulicarius* and *C. litteratus*, appear to prey primarily on the same species of polychaete, the capitellid *Dasybranchus caducus* (Grube) (Table 4). Unfortunately, identification of this prey organism is not certain in many cases, as it is based solely on setae and hooded hooks in fecal and alimentary tract content samples. One specimen of *C. litteratus* (shell 99 × 58 mm) regurgitated a nearly intact polychaete determined definitely as *D. caducus*, 290 mm long and 3.9 mm in diameter! All other determinations were based on hooded hooks, following comparisons with this specimen, the criteria in Day (1967), and the detailed figures of Thomassin and Picard (1972).

Of the two predators on *Dasybranchus*, *Conus litteratus* is the more specialized; if all prey categories other than *D. caducus* are lumped and the correction for continuity applied, the difference from *C. pulicarius* is significant at the 0.08 level ($\chi^2 = 3.05$, df $= 1$). In order to relate predator size to the size of a prey species that lacks jaws, the lengths of 20 hooded hooks from each meal of *D. caducus* were measured. Analyses of these data indicated that predator shell length and prey size are not significantly correlated within species, but *C. litteratus* preys on significantly larger *D. caducus* than does the much smaller *C. pulicarius* (Figure 6).

In other geographic regions, *Conus litteratus* also preys predominantly on *Dasybranchus caducus* (Kohn and Nybakken 1975). The only prior data on the diet of *C. pulicarius* elsewhere are from Hawaii, where it also eats *D. caducus* [listed as capitellid No. 1040 in Kohn (1959)] and an echiuroid. These two species of *Conus* had not previously been found in the same habitat.

Other than *Conus pulicarius* and *C. litteratus*, no two species shared a common prey organism, but too few data were obtained from the other polychaete feeders to be more than suggestive (Table 4). The largest species, *C. leopardus*, appears to prey exclusively on the enteropneust *Ptychodera flava*, as it does elsewhere (Kohn 1959, 1968; Kohn and Nybakken 1975).

Although ten or more observations of identified prey are available for only three species, the inverse relationship between size (Figure 3) and prey species diversity (Tables 3, 4) conforms closely to the general pattern illustrated by Leviten (1976: fig. 6B) for *Conus* species that prey on sedentary polychaetes, and extends it to predators of larger size.

One *Conus marmoreus* (shell 101 × 59 mm) was observed shortly after it had eaten a

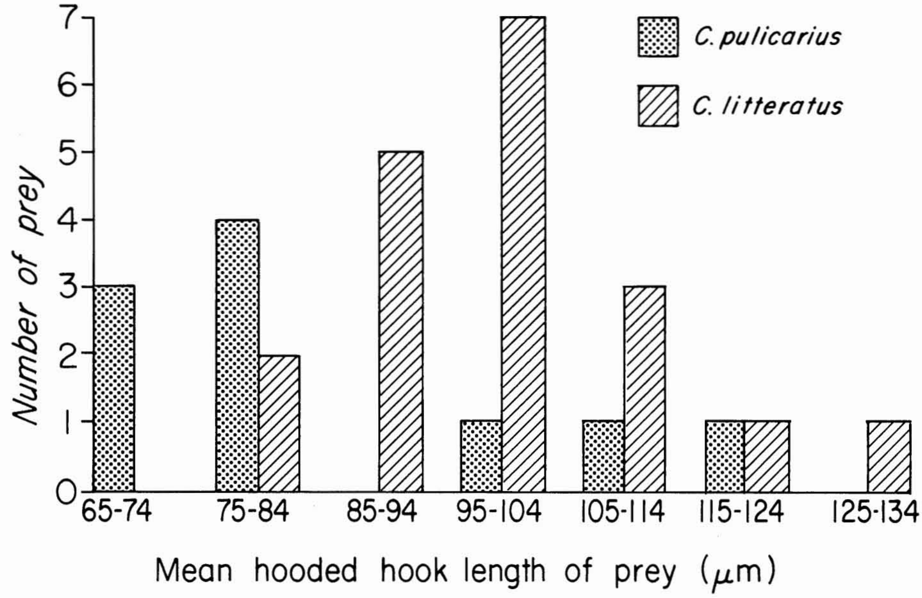

FIGURE 6. Relationship between size of *Dasybranchus caducus* eaten by *Conus pulicarius* and *C. litteratus*, estimated by mean length of hooded hooks in *Conus* alimentary tracts. *Conus litteratus* eats *D. caducus* with significantly larger hooks than does *C. pulicarius* (Mann–Whitney *U* test, $P < 0.025$).

C. litteratus (83 × 51 mm); it regurgitated the prey after being collected. *Conus marmoreus bandanus* preys exclusively on other *Conus* species in Hawaii as far as is known (Kohn 1959). One *C. consors* contained unidentified fish scales. This is the first record of the prey of this species, but it is not unexpected because the radula tooth closely resembles that of known piscivores such as *C. striatus* (Kohn, Saunders, and Wiener 1960: fig. 1).

DISCUSSION

Habitat heterogeneity, physical environmental stresses, and partitioning of food and space resources are important determinants of species diversity patterns in assemblages of *Conus* inhabiting tropical intertidal benches (Type II habitats) and subtidal coral reef platforms (Type III habitats) (Kohn 1959, 1967, 1968, 1971; Kohn and Leviten 1976; Kohn and Nybakken 1975; Leviten 1976, 1978; Leviten and Kohn 1980). Extensive subtidal areas of sand substrate (Type I habitats) have been less well studied, but their *Conus* assemblages typically have very low diversity (Kohn 1967).

Although it is not possible to define the limiting resources for the set of ecologically and morphologically similar congeners studied in the shallow, subtidal sediment habitat in Enewetak lagoon, the high degree of specialization and low overlap in use of available substrate types by the most common species suggests the importance of microhabitat resource partitioning. The two most abundant species eat primarily the same prey species, *Dasybranchus caducus*, but they take mainly different-sized prey (Figure 6) in different microhabitats (Table 3). The absence of dietary overlap in the limited data that could be obtained for three other species that prey on polychaetes suggests specialization on different prey species. The remaining three *Conus* species also exhibit no dietary overlap with any others, as they specialize on enteropneusts, gastropods, and fishes, respectively. Thus, all other species pairs show nonoverlap with respect to use of food species or both food and microhabitat resources (Tables 3, 4). The general pattern of differential specialization on these important resources agrees closely with that observed in much more diverse *Conus* assemblages on Indian Ocean reef platforms (Kohn and Nybakken 1975: 229–230, fig. 12). Higher overlap values were not associated with the lower species diversity observed at Sta. M19.

The results of this study suggest that sufficient microhabitat heterogeneity and prey diversity may exist in Type I habitats to permit sets of *Conus* that are more diverse in species than heretofore suspected to co-occur and to specialize on different microhabitat and food resources. These assemblages may be characterized by high population density, the predominance of species with large body size, and the presence of all major types of dietary specialists known in the genus—predators on polychaetes, enteropneusts, gastropods, and fishes.

ACKNOWLEDGMENTS

I thank Philip Helfrich for informing me of the presence of the assemblage studied, the late Paul Leviten for field assistance, Margaret Lloyd for identifying polychaete prey organisms, Llewellya Hillis-Colinvaux for identifying *Halimeda*, and Charles Cutress for identifying the anemones. I thank Alan C. Riggs for helpful discussion and suggestions, and David G. Jackson for providing the photograph from which Figure 1 was reproduced.

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