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Sub-rubble communities of Curaçao and Bonaire coral reefs

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Abstract. The distribution and abundance of sessile organisms under coral rubble has been studied at Bonaire and Curaçao, Netherlands Antilles. Species richness under rubble is extremely high with at least 367 species of which sponges, tunicates and bryozoans are the most important. Shallow sub-rubble communities can be considered refuges as the majority of these species are crypt-obligate. Sub-rubble communities may also have a preserve function for sponges, but do not harbour enough corals to ensure a quick coral recolonization of the reef surface after a major disaster. Cryptic community composition is affected by depth and pollution, and differs substantially between the two neighbouring islands, possibly as a result of different bottom characteristics. Biomass of the sub-rubble communities may contribute considerably to total reef biomass. Diversity varies inversely with increased depth and increased rubble size, possibly indicating abiotic control (e. g. physical disturbance by wave action and reef slope substrate collapse).

Introduction

Cryptic reef habitats, which include cavities and the undersides of overhanging corals and dead coral rubble, have been estimated to comprise 30–50% of reef volume (Garrett et al. 1971). In contrast to the open reef, these habitats are characterized by low light levels, limited above-surface space, and reduced exposure to other environmental controls. Prominent organisms in cryptic habitats (cryptobionts sensu Kobluk 1988) belong to sessile groups such as sponges, bryozoans, filamentous and encrusting algae, tunicates, and foraminiferans, together with their predators and a variety of shelter-taking animals (Vasseur 1974, 1977; Buss and Jackson 1979; Jackson 1979b; Jackson and Winston 1982; Choi and Ginsburg 1983; Hutchings 1986; Kobluk et al. 1988; Kobluk and Van Soest 1989; Logan et al. 1984).

It appears that cryptic habitats harbour a surprisingly high number of species per unit of surface area, although

most research concentrated on species of a particular taxon or, conversely, on the distribution of groups in caves, tunnels and under foliaceous corals. Little attention has been given to quantitative all-taxon studies of communities under small pieces of dead coral rubble. However, several general statements and hypotheses have been formulated about the functional aspects of cryptic habitats and cryptobionts. These center around the questions: What function do cryptic habitats have in coral reef processes and how is the high diversity in these habitats maintained?

Concerning the first question, it has been suggested that cryptic biota may function as a reserve for reef surface corals, providing a “recruitment pool” that can accelerate recovery on a post-hurricane reef surface (Kobluk and Lysenko 1987), as a shallow-water refuge for deep-water open reef organisms (Kobluk 1988), as a shelter against predation (Wulff 1988) or as a refuge from spatial competition (Jackson 1977b). These suggestions presume that the habitat offers only limited access to larger grazers and predators.

Concerning the second question, Jackson and Buss (1975) proposed their theory of “competitive networks”, in which non-hierarchical competition within a diverse community is sufficient for maintaining high diversity. Lateral expansion by encrusting organisms is possible only by winning a competitive overgrowth battle since free space is not available (Jackson 1977a, 1977b; Buss and Jackson 1979; Jackson and Winston 1982).

Diversity in cryptic habitats also appears to be maintained by “intermediate disturbance” (Connell 1978) through abiotic factors such as mechanical disturbance, by waves and substrate collapse (Kobluk 1988), variations in flushing and sediment grain size (Choi and Ginsburg 1983), as well as through biotic factors such as predation and outgrowth of coral undersurfaces (Jackson and Winston 1982; Palumbi and Jackson 1982).

In this study quantitative data are presented on the distribution, abundance, and biomass of sessile organisms under coral rubble on Bonaire and Curaçao at nine different sites, and on the basis of the assembled data it

Fig. 1. Geographic situation and location of sampling stations (+). Curaçao: H = Hundu; B = Blauwbaai; A = St. Annabaai; C = Cornelisbaai. Bonaire: K = Karpata; Y = Yacht harbour; P = Punt Vierkant; R1 = Red Slave 5 m; R2 = Red Slave 25 m. Main wind and current directions are indicated with arrows

is discussed which of the above mentioned hypotheses may be valid for sub-rubble habitats in back reef and fore-reef environments.

Materials and methods

Sampling stations

Stations were chosen based on depth and degree of physico-chemical disturbance, with 5 on Bonaire (May–October 1987) and 4 on Curaçao (November 1988–March 1989; Table 1). The yacht harbour of Bonaire was built in the early 1970's with explosives, destroying the reef near the entrance. Up to the present study there has not been any recolonization by corals. St. Annabaai lies near the mouth of the Schottegat, Curaçao, a large inland bay in which the island's main harbour and oil terminal are situated. It is characterized by a poorly developed coral reef presumably because of pollution by oil and many sewage outfalls, and sediment run-off. The other stations are relatively free of human influence.

Sampling methods

Coral rubble is most abundant on the shallow water (1–5 m) reef flat, where it is composed primarily of broken pieces of *Acropora*

palmata (Lamarck 1816). Conversely, coral rubble in deeper water (5–35 m) reef margin and fore-reef environments is composed of broken pieces of foliaceous corals and *A. palmata*. Coral rubble was selected haphazardly in each of these environments. The rubble was turned over and the total sub-rubble surface area as well as the colonizable area was measured in situ by using a 10 × 10 cm quadrat, divided into 100 squares of 1 cm² each. Areas that appeared uncolonized as a result of contact with other rubble, underlying substrate or because of burial in sand, were considered not-colonizable. Total sub-rubble surface area of individual rubble varied from 250 to 1600 cm². On each individual rubble one quadrat was positioned approximately in the middle of a colonizable area and at a minimum distance from the edge of one third of the rubble radius. This prevented many non-cryptic algae growing on the periphery of the rubble from being included in our measurements. In each quadrat the percentage cover of each organism or colony in vertical projection on the substrate was estimated, and all specimens were collected for identification to species level in the laboratory. Because the greater depth (35 m) limited diving time at station Blauwbaai, at that station rubble was at first merely collected and subsequently brought to a depth of 6 m to be sampled further. For biomass calculation (see below), it was noted whether an organism was thinly or massively (≥ 0.5 cm thickness) encrusting. Organisms cementing rubble to the underlying substrate and torn from the rubble when it was turned over, were included by estimating the cover from its remains on both substrate and rubble. Not all species, notably coralline algae and ascidians, could be identified to species level due to lack of adequate identification keys.

Sampling area

The minimal area (the minimal sample size for a representative description of the sub-rubble community) was calculated with the program MINAR described by Kaandorp (1986), which uses the Bray-Curtis dissimilarity coefficient and a logarithmic transformation to prevent too much emphasis on dominant species. MINAR calculates the similarity between each possible combination of subsets of m elements out of ten quadrats, where the same element is not used twice in one combination ($1 \leq m \leq 5$). Apart from the number of species, which is normally used in species area calculation, species cover is included as well. This method is more objective than the classical species-area curve calculation (Weinberg 1978), but needs twice the sample size for its calculation. To save time the minimal area was only calculated for one station, and assumed the same or smaller for the other stations. For its calculation, the data from Hundu, representing 70 quadrats (each 100 cm²) on 70 pieces of rubble were used. These quadrats were randomized into 10 "quadrats" each of 700 cm² to accommodate MINAR requirements.

Table 1. Station characteristics. "Bottom" is the predominant substrate underlying rubble, expressed as a percentage of the total number of sampled pieces of rubble. Human influence (see text): + present; – absent; $\pm$ in the past. Coral cover was estimated by eye. For station abbreviations see Fig. 1

Location	Bottom (%)			Depth (m)	Coral cover (%)	Impact
	Sand	Rubble	Rock			
Bonaire						
Y	50	40	10	5	0–5	±
K	40	50	10	5	20–40	—
P	60	40	0	5	0–20	—
R1	15	80	5	5	0–20	—
R2	10	90	0	25	20–40	—
Curaçao						
A	0	100	0	6	0–10	+
B	21	71	8	35	20–40	—
C	22	42	36	5	20–40	—
H	24	58	18	4	10–20	—

Diversity and species cover

To compare the stations we used the untransformed data to calculate species richness, the Shannon-Wiener diversity and evenness index (Pielou 1966), and cover for each taxon per station.

Influence of rubble size

Individual rubbles and rubble size classes larger or smaller than 400 cm² were compared on their number of species and cover, to investigate whether substrate stability (assumed greater in larger rubble) is correlated with number of species and biomass.

Biomass

Biomass, estimated as dry weight minus ash weight (i.e. ash-free dry weight), was recorded in samples of the most dominant groups of sessile cryptobionts, i.e. encrusting sponges, massive sponges (thickness ≥ 0.5 cm), coralline algae and bryozoans. For each group a number of samples of known cover were dried to constant weight at 100° C and, after weighing, combusted at 550° C for 3 h. The organic matter per unit of surface area for each taxon was then multiplied by the total cover of the corresponding group.

Distinction of sub-rubble communities

To detect possible patterns in the distribution of species, the sample data (i.e. cover of each species at the various sites) were analyzed with an unweighted pair-group method using arithmetic averages (UPGMA, Sokal and Michener 1958) and the two-way indicator species analysis using reciprocal averaging (Hill 1979). For the former method we used the program CLUSTAN (Wishart 1978) with the Bray-Curtis dissimilarity coefficient and a logarithmic transformation of the data. For the latter, the program TWINSpan (Hill 1979) was chosen. After a comparison of different clustering techniques, Gauch and Whittaker (1981) concluded that TWINSpan, because of greater robustness and objectivity, is usually superior to other ordination techniques. With marine data, good results have been obtained with both methods (Kooistra et al. 1989, TWINSpan; Kaandorp 1986, UPGMA). The programs combine similar samples into clusters. Before cluster analysis, the 70 quadrats of Playa Hundu were randomized into two subsamples of 3500 cm² (Hundu 1 and 2) to get approximately the same sample size as for the other stations.

Characteristic and dominant species were obtained by classifying species by an inverse analysis on the basis of sample clustering (Kaandorp 1986). We considered species that occurred only in one cluster, but on every station of that cluster, as characteristic. Species that also averaged more than 1% cover in a cluster (due to the extreme species richness the majority of the species averaged much less than 1%) were considered relatively dominant.

Results

Minimal area

The sessile sub-rubble community at Hundu is extremely heterogeneous, with new species – almost exclusively sponges – still occurring after reaching a sampling area of 2800 cm² (Fig. 2). Similarity values (similarity = 1 – dissimilarity) between samples of increasing size are low and the corresponding curve does not reach a clear asymptote. As a reasonable estimate of the minimal area for

Fig. 2. Similarity values (S) between samples of increasing size, illustrating the minimal sampling area for the sub-rubble community at station Hundu. Calculation with logarithmic transformation of data and the Bray-Curtis coefficient of similarity (Kaandorp 1986)

sub-rubble communities and for logistic reasons we chose to sample approximately 3000 cm² on every station.

Species richness and diversity

We found a total of 367 sessile species, of which almost 60% are sponges (Table 2). Number of species at unpolluted shallow stations on Curaçao (C and H) is much higher than at similar stations on Bonaire (K, P, and R1). Identification problems reduced the total number of crustose coralline algae species to the four that could be distinguished with confidence, thereby making the estimation of the total number conservative. Because most of the data were not normally distributed, not even after logarithmic or arcsin transformation, non-parametric statistics were applied. There was a significant difference between stations (G-test for goodness of fit, $G = 80.7$, $P < 0.001$, with lumping of Actiniaria, Bivalvia, Foraminifera, Scleractinia, Algae, Stylasteridae, Polychaeta, Octocorallia and Hydroidea into one class; Sokal and Rohlf 1981). Annabaai and Hundu had a different taxon distribution than the other stations (Table 3). For Annabaai, this is mostly caused by the relatively low number of Ascidiacea and Bryozoa and the high number of Polychaeta. Hundu differs from most stations because of its relatively low number of sponges and tunicates. There was a significant heterogeneity among the shallow unpolluted stations (C, H, K, P, R1) and the deep stations (B and R2) when considered together, but not when taken separately (unplanned tests for heterogeneity, $P < 0.05$, Sokal and Rohlf 1981). Deep stations have relatively more sponges and less crustose algae and tunicates. The higher total number of station Hundu is caused by the double sampling area, carried out to determine the minimal area.

There was a significantly different number of species per rubble between stations (Kruskal-Wallis one-way analysis of variance by ranks, $KW = 80.7$, $P < 0.001$; Siegel and Castellan 1988). There is a large difference in the total number of species (Table 2), but the difference between number of species per rubble is less (Table 4). Among unpolluted shallow stations there is only a significant difference between Curaçao and Punt Vierkant.

Table 2. Total number of species per taxon per site. $H' = \text{Shannon-Wiener diversity index: } H' = -\sum(n_i/N)\log(n_i/N)$, where n_i/N is the percentage cover of species i.e., the general evenness: $e = H'/\log S$, where S is the total number of species. For station abbreviations see Fig. 1

	Curaçao (C)					Bonaire (B)					C and B	
	A	B	C	H	Total	J	K	P	R1	R2	Total	
Actiniaria	0	0	0	0	0	0	1	2	1	0	4	4
Algae	4	1	7	9	14	0	5	3	1	2	12	18
Ascidacea	3	11	20	25	41	7	21	11	24	4	52	65
Bivalvia	0	0	0	1	1	0	1	0	0	0	1	2
Bryozoa	1	15	12	20	33	8	8	13	14	9	22	41
Corallinacea	5	5	11	26	25	4	5	7	5	5	11	4
Foraminifera	1	1	1	1	1	1	1	1	1	1	1	1
Scleractinia	1	3	2	5	7	1	1	1	6	1	8	11
Hydroida	1	0	0	1	2	0	0	0	0	0	0	2
Octocorallia	1	0	0	0	1	0	0	1	0	0	1	1
Polychaeta	10	1	5	11	17	1	3	2	0	1	5	18
Porifera	38	56	69	79	156	44	54	38	44	49	103	199
Stylasteridae	1	0	1	1	1	0	0	0	0	0	0	1
Total	66	93	128	179	299	66	100	79	96	72	220	367
H'	1.36	1.59	1.72	1.73		1.56	1.63	1.64	1.71	1.32		
e	0.75	0.81	0.82	0.77		0.86	0.82	0.86	0.86	0.71		

Table 3. Results of unplanned tests of homogeneity of the species distribution of stations using the G-statistic (Sokal and Rohlf 1981). ** = $P < 0.01$; * = $0.01 < P < 0.05$. For station abbreviations see Fig. 1

	A	B	C	H	J	K	P	R1	R2
A		**	**	**	**	**	**	**	**
B	**			**					
C	**								
H	**	**			**	*		*	**
J	**			**					
K	**			*					*
P	**								
R1	**			*					
R2	**			**		*			

Table 4. Mean number of species per rubble and results of multiple comparisons after Kruskal-Wallis one-way analysis of variance (Siegel and Castellan 1988). SD = standard deviation; N = number of stones; * = $P < 0.05$. For station abbreviations see Fig. 1

	A	B	C	H	Y	K	P	R1	R2
Mean	6.6	6.8	9.5	9.6	4.1	7.4	6.1	9	7.8
SD	2.2	2.6	2.7	3.5	2.6	3.7	2.9	3.1	3.8
N	36	35	36	70	32	38	29	32	27
A			*	*					
B			*	*					
C	*	*			*		*		
H	*	*			*		*		
Y			*	*		*		*	*
K					*				
P			*	*				*	
R1					*		*		
R2					*				

Yacht harbour (mechanically disturbed) has less species than most other stations, except for Annabaai (polluted) and Punt Vierkant. Values of the Shannon-Wiener diversity index show a comparable pattern (Table 2). They are lower for Annabaai (polluted), Yacht harbour (mechani-

cally disturbed) and the two deep stations. This is mostly caused by the lower number of species as the evenness index is similar between stations.

Cover

Sponges are the most important group in terms of cover (Table 5). They occupy 12 to 54% of the available surface area, with an average of almost 30%. The extremely high number of species, however, reduces cover per species often to less than 1%. The next most abundant group is that of the coralline algae, followed by the bryozoans. At Hundu and Punt Vierkant, the coralline algae exceed the sponges in area covered. Annabaai (polluted) has the highest cover, mostly of sponges and algae.

Comparison of the mean cover per stone between stations yielded a significant difference (Kruskal-Wallis one-way analysis of variance by ranks, $KW = 140.6$, $P < 0.001$; Siegel and Castellan 1988). Further examination by comparison tests between single stations indicated the existence of a clear difference between Curaçao and Bonaire (Table 6). Cover at stations Annabaai, Cornelisbaai and Hundu is significantly higher than that of every station on Bonaire. The two deep stations (Blauwbaai and Red Slave 2) have a higher cover than Yacht harbour (mechanically disturbed).

Biomass

The four groups used to estimate the biomass (Table 7) were responsible for 70 to 95% of the total cover (Table 5). With the calculated percentage cover for each group the sub-rubble biomass was estimated to be between 28 and 104 gm^{-2} , depending on species cover and community composition (Fig. 3). Note that biomass is given as g ash-free dry weight per square meter of sub-rubble area and not per square meter bottom area. Yacht

Table 5. Total cover (%) per taxon and total sample size (m²) for each station, for Curaçao and Bonaire and for both islands combined. See Fig. 1 for station abbreviations

	Curaçao (C)					Bonaire (B)					C and B	
	A	B	C	H	Total	Y	K	P	R1	R2	Total	
Sample size	0.36	0.35	0.36	0.7	1.77	0.32	0.38	0.29	0.32	0.27	1.58	3.35
Actiniaria	0	0	0	0	0	0	0.2	1.8	0.5	0	0.5	0.2
Algae	13.5	6.8	1.3	7.9	7.5	0	0.5	1.3	1.1	0.4	0.6	4.3
Ascidacea	0.4	1	4.1	1.7	1.8	0.9	3.6	2.9	8.1	0.2	3.2	2.5
Bryozoa	7.2	3.6	4.5	11.7	7.7	1.9	5.7	3	6.4	17.5	6.5	7.2
Corallinacea	4.2	7.4	21.6	34	20.2	3	8.9	17.6	13.6	11.9	10.6	15.7
Foraminifera	1.3	0	2.2	1.7	1.4	0	1.1	0.6	2.3	0.1	0.8	1.1
Scleractinia	2.9	0.2	0.4	1.9	1.5	1.3	0.1	0.2	1.2	4.1	1.3	1.4
Polychaeta	2.9	0.1	5.6	1.5	2.3	0.7	0.5	1.2	0	1	0.6	1.5
Porifera	54.0	52.4	44.1	22.4	39.1	13.5	14	12.6	16.6	21.4	15.3	27.9
Stylasteridae	0.1	0	0	0.8	0.3	0	0	0	0	0	0	0.2
Total	86.5	71.5	83.8	83.6	81.8	21.3	34.6	41.2	49.8	56.6	39.6	62

Table 6. Mean species cover (%) per rubble and results of pairwise comparisons after Kruskal-Wallis one-way analysis of variance (Siegel and Castellan 1988). SD=standard deviation; N=number of stones; * = $P < 0.05$. For station abbreviations see Fig. 1

	A	B	C	H	Y	K	P	R1	R2
Mean	87	72	84	84	21	35	41	50	57
SD	19	26	20	20	26	21	33	25	27
N	36	35	36	70	32	38	29	32	27
A					*	*	*	*	*
B					*	*			
C					*	*	*	*	*
H					*	*	*	*	*
Y	*	*	*	*					*
K	*	*	*	*					
P	*	*	*	*					
R1	*	*	*	*					
R2	*	*	*	*					

Table 7. Average biomass (g ash-free dry weight m⁻² of the most abundant groups^a measured from species samples of 2–4 cm². SD=standard deviation; n=number of samples

Taxon	Biomass	SD	n
Porifera, thinly encrusting	109.7	46.8	12
Porifera, massively encrusting	198.1	98.6	3
Corallinacea	153.1	98.6	12
Bryozoa	139.8	76.8	5

^a Massively encrusting sponges were thicker than 0.5 cm

harbour and Annabaai have relatively more sponge biomass than the other stations and biomass on Curaçao is often more than twice as much as on Bonaire.

Rubble size

There was no linear relationship between rubble size and cover or number of species as the results of linear regressions were non-significant. Comparing different size classes showed that there was a significant difference in mean number of species between rubble smaller or equal

Fig. 3. Biomass of Corallinacea, Sponges and Bryozoans in sub-rubble communities (g ash-free dry weight m⁻² sub-rubble area). See Fig. 1 for station abbreviations

Table 8. Mean number of species and mean cover (%) of rubble pieces ≤ 400 cm² and > 400 cm². SD=standard deviation; N=number of stones. Results of Mann-Whitney U-test: n.s.=not significant; * = $0.005 < P < 0.01$; ** = $0.01 < P < 0.001$

	A		B		C		H	
	$\leq$	$>$	$\leq$	$>$	$\leq$	$>$	$\leq$	$>$
Cover (%)								
Mean	80.6	93.1	73.5	68.7	85.5	82.0	88.5	78.0
SD	21.9	12.6	26.3	26.6	17.8	22.0	21.1	16.0
N	19	17	20	15	19	18	36	34
P	n.s.		n.s.		n.s.		*	
Number								
Mean	6.8	6.4	6.6	7.1	10.6	8.3	11.1	8.3
SD	1.9	2.6	2.5	3.1	2.8	2.2	3.6	2.9
N	19	17	20	15	19	18	36	34
P	n.s.		n.s.		*		**	

to 400 cm² (showing a higher number) and larger than 400 cm² (showing a lower number) at the undisturbed shallow stations Cornelisbaai and Hundu (Table 8). These two classes (≤ 400 cm² and > 400 cm²) possibly represent groups of rubble relatively more and less dis-

Fig. 4. Ordination of stations after multivariate analysis of logarithmic transformed data by CLUSTAN (Wishart 1978), using the Average Linkage method combined with the Bray-Curtis dissimilarity coefficient

turbed by waves. Differences between other size distributions were not significant. The size range of Bonaire rubble was much smaller than of Curaçao rubble (250–495 cm², and 250–1600 cm² respectively), which could account for the absence of any relation between rubble size and species richness or cover of rubble on Bonaire.

Classification of sessile communities

Two major clusters emerged after analysis by the two cluster methods (Fig. 4). Again there is a clear distinction between Bonaire and Curaçao, except for Blauwbaai, the deep station on Curaçao, which has a very different community composition. On Bonaire, the deep station Red Slave 2 is also clearly separated from the shallow stations. Annabaai (polluted) and Yacht harbour (mechanically disturbed), behave quite differently. Species cover and composition at Annabaai on Curaçao differ from the undisturbed stations there, while Yacht harbour on Bonaire is even combined with Karpata, which has the highest number of species there.

Composition of sessile communities

The separation of Curaçao and Bonaire is caused by the sponges *Hyatella intestinalis* (Lamarck 1814), absent on Bonaire, and *Oscarella* spec., absent on Curaçao (a detailed table of the inverse analysis is available on request). Annabaai is dominated by just a few species. A characteristic algal association consisting of at least 2 species of unicellular brown and green algae dominates here, occupying approximately 11.4% of sub-rubble area. The scleractinian *Tubastrea aurea* (Quoy and Gaimard 1834) is also a prominent feature at Annabaai. It is found under rubble with large interstices and also in shallow open reef habitats. We suspect that available above-surface space under rubble is an important factor for its occurrence. The sponges covering more than the average surface area were *Rhaphidophylus venosus* (Alcolado 1984), *Hymedes-*

mia curacaoensis van Soest 1984 and *Eurypon* spec (8, 9, and 6% respectively). These species were sometimes found at other sampling stations (notably *R. venosus*, which is a common fouling organism), but the extremely large cover at Annabaai seems to indicate that these species profit in some way from the pollution. This appears to apply also to the bryozoan *Hippopodina feegensis* (Busk 1884), which is the only bryozoan encountered at Annabaai (7%).

Characteristic species of Cornelisbaai and Hindu (Curaçao, shallow, unpolluted) are one unidentified crustose coralline alga, and the sponges *Terpios* spec., *Iotrochota birotulata* (Higgin 1877) and *Amphimedon viridis* Duch. and Mich. 1864. The latter two species are also common in the open reef (van Soest 1980, 1984). Cover per species is much lower than at Annabaai and more evenly distributed, as almost no extremes in cover were found. A dominant species at Hindu is the bryozoan *Reptadeonella bipartita* (Canu and Bassler 1928), which was present on almost every piece of rubble.

At the shallow stations of Bonaire (J, K, P, R1) a few species (the sponges *Crella* spec., *Haliciona hogarthi* and the bryozoan *Parellisina curvirostris* Hincks 1862) are present at each station, but these species can also be found outside this cluster and are, therefore, not considered characteristic. Cover of these species did not exceed 1% at any station.

The two deep sites, Blauwbaai and Red Slave 2, cluster separately and share also only a few species, viz. the sponges *Hyrtios violacea* (Duch. and Mich. 1864), *Pleraplysilla stocki* van Soest, 1978 and *Aplysilla* aff. *sulfurea* Schulze 1878 (the latter was most dominant at Blauwbaai with a cover of 6.2%). The most common species at Red Slave 2 is the bryozoan *Stylopoma spongites* (Pallas 1766) which covered 15% and was also noted by Kobluk et al. (1988) to be one of the most common bryozoans in deeper water. Other dominant species are the scleractinian *Madracis decactis* (Lyman 1859) and the sponge *Spongosorites* cf. *ruetzleri* (van Soest and Stentoft 1988). Characteristic species are the sponges *Spirastrella* sp.1, *Clathria echinata* (Alcolado 1984), *Mycale diversisigmata* van Soest 1984 and *Aplysilla* aff. *rosea* (Barrois 1876). Blauwbaai, which was located some 10 m deeper than Red Slave 2, has more characteristic species. With the exception of the bryozoan *Stylopoma duboisii* (Audouin 1826) all species are sponges, including the dominant species *Agelas* spec.1, *Desmacella polysigmata* van Soest 1984, *Agelas* sp.2, *Pseudosuberites* spec., *Jaspis* spec., *Desmantisus incrustans* Topsent 1889, *Myrmekioderma styx* De Laubenfels 1953, and the characteristic species *Dendroxea* spec., *Xestospongia muta* (Schmidt 1870), *Chondrosia* aff. *collectrix* (Nardo 1833), *Rhabderemia pusilla* (Carter 1876), *Acarnus souriei* (Levi 1952), and *Clathrina coriacea* (Montagu 1818). Many of these sponges can also be found in the surrounding open deep reef habitat (van Soest 1978, 1980, 1981, 1984) and were also found by Kobluk and van Soest (1989) on Bonaire in reef cavities at comparable depths. Both Blauwbaai and Red Slave 2 share many species with the other sites. Most universal are the foraminiferan *Homotrema rubrum* (Lamarck, 1814), the bryozoans *Smittipora levinsini*

(Canu and Bassler 1917) and *Steginoporella magnilabris* (Busk 1854), many unidentified corallines and the sponges *Spirastrella coccinea* (Duch. and Mich. 1864), *Rhaphidophylus minutus* van Soest 1984, *Rhaphidophylus juniperinus* (Lamarck 1814), *Scopalina ruetzleri* (Wiedenmayer 1977), *Terpios fugax* Duch. and Mich. 1864, *Hy-medesmia* cf. *agariciicola* van Soest 1984 and *Batzella* spec.

Discussion

Species number, minimal area, and community composition

The high diversity of the sub-rubble communities seems to be in sharp contrast to the apparent simplicity and uniformity of the habitat. Species richness reported for other cryptic habitats seems to be lower, but this is probably because the area sampled was too small. From our minimal area calculation (Fig. 2), it is clear that a large area has to be sampled to give an accurate description of the cryptic community. Even in this study the minimal sampling area was not completely met, mostly because of the great number of sponge species, which still increased after having sampled 3500 cm².

Choi and Ginsburg (1983) only found a total of 80 species, while we found 367 species of sessile coelobites under coral rubble. For sponges, we found 156 species on Curaçao and 103 species on Bonaire, with a combined total of 199 different species. We encountered 41 bryozoans, whereas Kobluk et al. (1988) collected 67 bryozoans at equal depths from the undersides of coral cobbles (30–50 cm²) and coral boulders (> 50 cm²). This lesser number of bryozoans probably reflects differences in habitat.

Curaçao and Bonaire differ in composition, cover, and biomass. This could be due to different bottom characteristics (the bottom on which the rubble is situated is more often sand on Bonaire, Table 1). One can easily imagine that fine-grained sediment restricts supply of food and oxygen, will smother species sooner, and generally allows very limited above-surface space.

Significance of rubble communities for the reef system; biomass

We estimate that sponges, bryozoans, and coralline algae contribute between 28 and 104 g.m⁻² of sub-rubble area to the total biomass of the sub-rubble community, depending on community composition and cover (Fig. 3). Polovina (1984) estimates an average biomass of reef surface dwellers of 391 g.m⁻². This means that in areas with much rubble, sub-rubble communities may represent a major contribution to total reef biomass. The contribution of all cryptic habitats together could even be more substantial, as cryptic voids are estimated to constitute from 30–50% of reef volume (Garrett et al. 1971).

Biomass was not found to be adversely affected by pollution, and is apparently largely independent of diver-

sity, since Annabaai (very polluted) had the lowest diversity but the third highest biomass.

Refuge function

In response to the question whether cryptic communities function as a refuge (Kobluk 1988; Wulff 1988) we conclude that the majority of the shallow water cryptobionts appear to be specialist organisms not normally occurring in the open reef habitat (van Soest 1978, 1980, 1981, 1984; Winston 1986). At the shallow locations, 68% of the encountered sponge species can only be found in the sub-rubble habitat, while at greater depths this is about 50% (van Soest 1978, 1980, 1981, 1984). An explanation for such observations would be that rubble undersides provide protection against predation from and/or competition with open reef organisms (Jackson 1977a; Wulff 1988). Deep locations have fewer predators, which probably results in the lower number of crypt-obligate species (Hughes and Jackson 1985).

For deep water reef surface sponges (Kobluk 1988) rubble is not of any significance as a shallow-water refuge. At the shallow stations, only 2 uncommon species could be considered deep-water species (*Agelas schmidtii* Wilson 1902 and *Calyx podatypa* (De Laubenfels 1934).

Preserve function

Rubble undersides at Curaçao and Bonaire do not harbour large quantities of reef corals that could facilitate recovery of damaged reefs [cf. Kobluk and Lysenko (1987) in Fiji reefs]. In fact, of the major reef corals of Curaçao and Bonaire [*Agaricia* spp., *Montastrea* spp., *Madrina meandrites* (Linnaeus 1758)], *Diploria* spp., *Acropora* spp.; Bak 1977; van Duyl 1985) only *Montastrea annularis* (Ellis and Solander 1786), *Agaricia agaricites* and *Agaricia lamarcki* Milne Edwards and Haime 1851 appeared in very low frequencies in our samples. This preserve function may only apply to sponges, since we found that about 32% of the species under rubble also occur on the open reef.

Maintenance of diversity

Space is a limiting resource in marine hard substrate environments, and to avoid monopolization by just a few superior competitors free space should become available at regular intervals (e.g. Paine and Vadas 1969; Connell 1976; Loya 1976). Although we occasionally found rubble completely covered by sessile organisms, most rubble showed some free space (Table 6). Therefore, although we cannot exclude the existence of "competitive networks" (Buss and Jackson 1979), it seems unlikely that such networks are the main cause for the high diversity.

Predation may act to make space available on substrates (e.g. Paine 1966, 1971, 1974). Although the rather

restricted nature of the sub-rubble habitat makes it inaccessible to larger predators, the possibility remains that frequently noted small predators such as prosobranchs and polychaetes have an influence on diversity.

In the open reef, intermediate disturbance often reduces dominant species proportionately more than less dominant species and provides open space for settlement of new species (Connell 1976, 1978). Without disturbance, communities will develop into an equilibrium state dominated by a low number of species (Loya 1976; Connell 1978). Rubble stability is probably related to rubble size, with larger rubble being more stable and less influenced by waves and swell, thereby giving competitively superior organisms more opportunity to out-compete others. Some evidence in favor of this hypothesis was found (Table 8). Small rubble at shallow locations had more species than larger rubble, while this difference was absent on the deep and the polluted station. The rubble at the polluted station was firmly consolidated, which could be the reason for the absence of such a relationship at station Annabaai. Deeper rubble is less influenced by waves. Factors other than size (e.g. gravity) may determine stability of rubble there. Another result supporting this hypothesis is the lower species diversity at the deep station.

Choi (1984) predicts that rubble succession terminates within three years in a climax stage dominated by tunicates, solitary bivalves, and sabellid worms, which would overgrow and outcompete all other organisms. Our samples, dominated by encrusting sponges, coralline algae, and bryozoans, were similar to a combination of Choi's "encrusting" and "climax" stages, which points to a prolonged intermediate disturbance state.

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