

#10741

CAVITY DWELLERS (COELOBITES) BENEATH CORAL RUBBLE IN THE FLORIDA REEF TRACT

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ABSTRACT

Coral rubble is the most common hard substrate on coral reefs. Distribution, abundance, and diversity of cavity dwellers (coelobites) that live on rubble undersides in the Florida Reef Tract is largely controlled by (1) flushing of sub-rubble cavities, (2) rubble stability, and (3) interactions between organisms. Diversity and abundance of coelobites in terms of cover are different in the major reef environments. They are highest around the marginal reefs and lowest in the fore reef. Bryozoa, the foraminifera *Homotrema rubrum*, and vermetid gastropods are most abundant around the reef environment. Crustose coralline algae and polychaetes appear to be most abundant in the back reef. The abundance of sponges decreases from the back reef towards the fore reef. Crustose coralline algae are the most abundant organisms in terms of cover and worms in terms of individuals. Bryozoa have the highest diversity with 28% of the 67 invertebrate species identified. Diversity and abundance (cover and number of individuals) increase with rubble size. Cover is also positively correlated with relative amounts of flushing of sub-rubble cavities, which is largely a function of water depth. Lateral variations in environmental influence due to higher outflow of Florida Bay water towards the reef tract through wide channels between the Middle Keys, the impact of Hurricane Andrew and tropical storm Gordon on the Upper Keys' reefs, and the anthropogenic influence due to extensive collection of rubble ("live rock") off the Middle Keys are not reflected in the coelobite communities. There were no differences detected in coelobite abundance and diversity between reefs off the Upper, Middle, and Lower Keys. The results support the few previous large-scale studies that suggest the existence of a coelobite zonation in reefs. However, the findings indicate that coelobites are of limited use as indicators of environmental and anthropogenic impact.

Cavity dwellers (coelobites sensu Ginsburg and Schroeder, 1973) are both of biological and geological significance for coral reefs as they are important members of the food chain and contribute to the consolidation of the reef framework. Ginsburg (1983), Hutchings (1983), and Kobluk (1988) give comprehensive reviews.

Early studies were conducted in submarine caves and explained coelobite distribution according to gradients in illumination (Garrett et al., 1971; Vasseur, 1977; Logan et al., 1984). Hutchings and Weate (1977) concluded that differences in bottom characteristics and exposure to waves and currents control differences in biomass of coelobites in sites around Lizard Island, Great Barrier Reef. Martindale (1992) related coelobite distribution in Pleistocene and Holocene reefs of Barbados to gradients in water turbulence and light intensity.

Several investigations have been conducted on coelobites on the undersides of rubble in coral reefs. From their study in the Florida Reef Tract, Choi and Ginsburg (1983) concluded that flushing of sub-rubble cavities is the major factor controlling development and distribution of cavity dwellers in reefs. Meesters et al. (1991) observed a negative correlation between coelobite diversity and rubble size in the Netherland Antilles, probably indicating physical control, i.e., rubble stability and disturbance. Gischler and Ginsburg (1996) concluded that rubble stability, flushing of cavities, and biological inter-

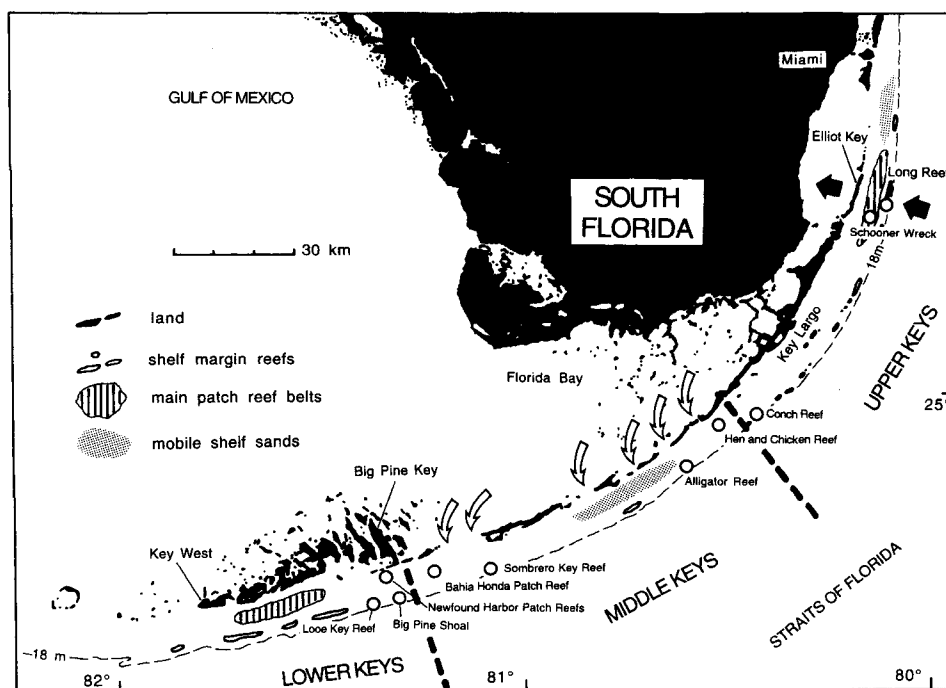


Figure 1. Map of the sample stations in the Florida Reef Tract. Sites are marked by open circles. Open arrows indicate the areas of outflow of water from Florida Bay that has higher turbidity and can reach extremely high or low temperatures and salinities. After Ginsburg and Shinn (1964). Black arrows mark the track of Hurricane Andrew and tropical storm Gordon.

actions are the most important factors influencing coelobite abundance, diversity, and distribution in southern Belize reefs. A number of studies on coastal boulder fields in temperate latitudes has revealed that intermediate levels of disturbance are imperative to maintain diversity at high levels on mobile substrates (Rützler, 1965; Osman, 1977; Sousa, 1979; Wilson, 1987). Kobluk (1988) came to the same conclusions and argued that physical disturbance is a major factor for diversity maintenance of reef cavity dwellers on mobile rubble in shallower water. In deeper, more protected and stable habitats, predation and competitive networking (Buss and Jackson, 1979) are probably decisive factors.

PURPOSE.— There are only two large-scale studies on the distribution of coelobites in major reef zones of one area (Choi and Ginsburg, 1983: Florida; Gischler and Ginsburg, 1996: Belize). The study by Choi and Ginsburg (1983) includes only one sample transect off the Upper Keys in the Florida Reef Tract. However, abundance and development of reefs is markedly different off the Upper, Middle, and Lower Florida Keys (Fig. 1). Both marginal reefs and patch reefs are much more abundant and developed off the Upper and Lower Keys than off the Middle Keys. This has been explained by the sheltering effect of continuous islands off the Upper and Lower Keys which protect the reefs from unfavorable currents (Ginsburg and Shinn, 1964). In the Middle Keys wide channels separate the few keys and cross-platform currents produce bottom sediment movement. Furthermore, water steadily flowing seaward from Florida Bay (Smith, 1994) has higher turbidity and temperatures can reach extremely low values (Hudson et al., 1976; Roberts et al., 1982). Both effects are inimical to reef growth.

Furthermore, recent natural and anthropogenic factors had significant impacts on certain areas in the Florida Reef Tract that are of interest regarding organisms that colonize rubble. Firstly, Hurricane Andrew and tropical storm Gordon passed over the reefs off Elliott Key in the Upper Keys in August 1992 and November 1994, respectively (Tilmant et al., 1994; Lirman and Fong, 1995). Both storms produced and moved large amounts of coral rubble. Secondly, rubble from the Florida Reef Tract is collected in large amounts in federal waters (more than 3 mi offshore) by private companies that sell it to aquaria as live rock. There are significant differences in the amounts of live rock collected between the Upper, Lower, and Middle Keys. While 150 t and 130 t were collected in the Upper and Lower Keys, respectively, more than 690 t were collected off the Middle Keys between 1990 and 1995.

This study was designed (1) to test whether there is significant variation in coelobite diversity and abundance between major reef environments, (2) to test whether the above-mentioned differences in environmental and anthropogenic influence affect distribution, abundance, and diversity of cavity dwellers and if there is significant lateral variation in coelobite development in the reef tract, and (3) to compare the results with an identical study conducted in Belize (Gischler and Ginsburg, 1996).

MATERIALS AND METHODS

STUDY AND SAMPLE SITES.—The study area is the Florida Reef Tract located seaward of the Florida Keys (Fig. 1). The major environments are (1) the discontinuous shelf margin reefs, (2) the fore reef, and (3) the back reef that can be divided in patch reef areas and grassy lagoon areas (Ginsburg, 1956; Enos, 1977). As discussed above, abundance and development of reefs is higher in the Upper and Lower Keys than in the Middle Keys, presumably because of the sheltering effects of islands. Alternatively, the study by Shinn et al. (1977) has shown that the underlying Pleistocene topography is a major factor controlling Holocene reef development in south Florida. Modern reefs are generally developing on Pleistocene highs that are presumably rare off the Middle Keys.

Samples of coral rubble were collected at 10 sites from Long Reef in the Upper Keys to Looe Key Reef in the Lower Keys. Three sites are located in the Upper Keys, four in the Middle Keys, and three in the Lower Keys. At the shelf margin reefs (Long Reef, Conch Reef, Alligator Reef, Sombrero Key Reef, Big Pine Shoal, Looe Key Reef), except for Big Pine Shoal, additional fore reef sites were sampled. The back reef sites are Schooner Wreck, Hen and Chicken Reef, Bahia Honda patch reef, and one of the Newfound Harbor patch reefs. In all, four back reef patch reefs, six reef, and five fore reef stations were sampled. Water depths at the 15 stations range from 1-5 m in the reef, from 8-15 m in the fore reef, and from 1-6 m in the back reef environment.

SAMPLING METHODS AND SAMPLE TREATMENT.—SCUBA or free diving was used to randomly collect 142 samples of coral rubble between March and June 1995. At each station 7-12 samples were taken. Rubble size ranged from 83-525 cm² and averaged 170 cm². Most of the samples from reef and fore reef areas were flat-shaped fragments of *Acropora palmata*. At back reef patch reefs fragments of foliaceous and head corals were collected. Immediately after collection, the rubble was soaked in a dilute solution of formaldehyde and later transported to the laboratory where it was stored in a refrigerated room. Rubble undersides were mapped, areas covered with attached and encrusting organisms were measured with a planimeter, and organisms were identified, in part with the help of specialists. Coelobite successions were identified by overgrowth patterns. Species and individuals were counted on each sample and diversity indices (Shannon-Wiener) and evenness were calculated for each sample. Data from the main reef environments were compared with non-parametric statistics (Kruskal-Wallis), because the data is not distributed normally even after logarithmic transformation. Some parameters (colonized area, diversity, rubble size, water depth) were

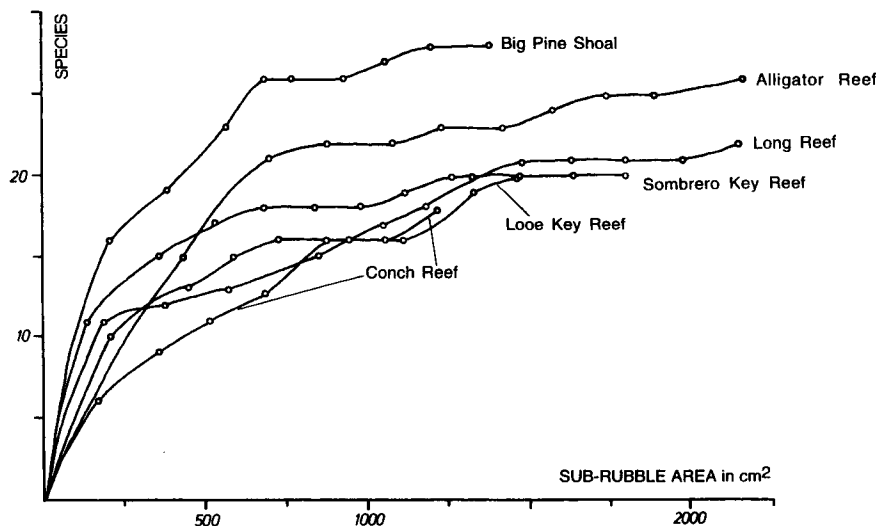


Figure 2. Selected cumulative curves with species plotted versus sub-rubble area show that the number of samples taken are sufficient as asymptotes are reached (only shallow reef sites are plotted). Samples of each site were selected in random sequence to construct the cumulative curve.

compared by correlation analysis. For the comparison of the 15 sample stations, the data for each station was treated in a cumulative way. Cumulative samples of 1200-1500 cm² include between 90 and 100% of the species at a station (Fig. 2). Data from individual stations were also compared by Kruskal-Wallis analysis and cluster analysis.

ASSESSING EXPOSURE AND FLUSHING.—To assess exposure and flushing in sub-rubble cavities, the clod-card technique (Doty, 1971; Jokiel and Morrissey, 1993) was applied. At 10 stations, three samples of plaster of paris (31 cm³, cast in 35 mm film canisters) were put under pieces of rubble and recollected after approximately 20 h. The volume loss was recorded by measuring the water displacement of each clod in a beaker. On a calibration curve for the dissolution of plaster of paris in running seawater in small aquaria, that resemble sub-rubble cavities (Gischler and Ginsburg, 1996), a hypothetical flow rate was obtained for each station. From these values relative amounts of flushing in sub-rubble cavities were calculated.

RESULTS

INVENTORY AND DIVERSITY OF COELOBITES.—Sixty-seven species of coelobites have been identified. These include sponges, bryozoa, polychaetes, mollusks, crustose coralline algae, foraminifera, tunicates, and sipunculids (Table 1). Bryozoa exhibit the highest diversity and make up 28% of all the species identified. Sponges and polychaetes each account for 20 % of the species. Within the sponges, *Niphates* is most common. *Schizoporella feegensis*, *Steginoporella magnilabris*, and *Schizoporella* are the most common bryozoa. *Pseudovermilia* is the most frequently found polychaete.

Diversity has two aspects: species richness and evenness. Average species richness of coelobites per rubble sample is highest around the reef crest (7.1) and decreases landward and seaward (Table 2, Fig. 3). It is lowest in the fore reef (5.9). Values of evenness per rubble sample are similar in the major reef zones and range between 0.68 and 0.71. The correlation analysis shows that species richness increases with increasing rubble size,

Table 1. Species list of coelobites under rubble in the Florida Reef Tract.

Sponges	Sipunculids	Worms
<i>Acamus</i> sp.	sipunculid A	<i>Eunice</i> sp.
<i>Callyspongia</i> sp.	sipunculid B	<i>Filograna</i> sp.
<i>Chondrilla nucula</i>	Bryozoa	<i>Hydroides</i> sp.
<i>Clathria</i> sp.	<i>Anarthropora</i> sp.	<i>Protula</i> sp.
<i>Haliclona</i> sp.	<i>Arthropoma ceciliai</i>	<i>Pseudovermilia fuscostriata</i>
<i>Hyrtios</i> sp.	<i>Canda</i> sp.	<i>Pseudovermilia occidentalis</i>
<i>Ircinia</i> sp.	<i>Cleidochasma porcellanum</i>	<i>Serpula</i> sp.
<i>Leucosolenia</i> sp.	<i>Cranosina coronata</i>	<i>Spirorbis</i> sp.
<i>Lissodendoryx isodictyalis</i>	<i>Crassimarginatella crassimarginata</i>	<i>Vermiliopsis</i> sp.
<i>Niphates erecta</i>	<i>Epistomia bursaria</i>	terebellid A
<i>Niphates</i> sp.	<i>Hippopodina feegensis</i>	sabellid A
<i>Oligoceras</i> sp.	<i>Lichenopora radiata</i>	polychaete A
<i>Rhaphidophylus</i> sp.	<i>Microporella ciliata</i>	polychaete B
<i>Spirastrella coccinea</i>	<i>Parellisina latirostris</i>	Mollusks
sponge A	<i>Reptadeonella violacea</i>	<i>Arca imbricata</i>
Crustose coralline algae	<i>Rhynchozoon</i> sp.	<i>Barbatia domingensis</i>
<i>Peyssonnelia</i> sp.	<i>Schizoporella errata</i>	<i>Cerithium litteratum</i>
crustose coralline alga A	<i>Scrupocellaria</i> sp.	<i>Chama congregata</i>
crustose coralline alga B	<i>Steginoporella magnilabris</i>	<i>Codakia orbiculata</i>
crustose coralline alga C	<i>Stylopoma spongites</i>	<i>Dendropoma</i> sp.
crustose coralline alga D	<i>Thalamoporella falcifera</i>	<i>Isognomon radiatus</i>
Tunicates	<i>Trematoecia turrita</i>	<i>Plicatula gibbosa</i>
tunicate A		
tunicate B		
Foraminifera		
<i>Homotrema rubrum</i>		
foraminifer A		
foraminifer B		

whereas evenness decreases with increasing rubble size. Total species richness in the major reef environments is highest in the reef (40), followed by the fore reef (36), and is lowest in the back reef (33).

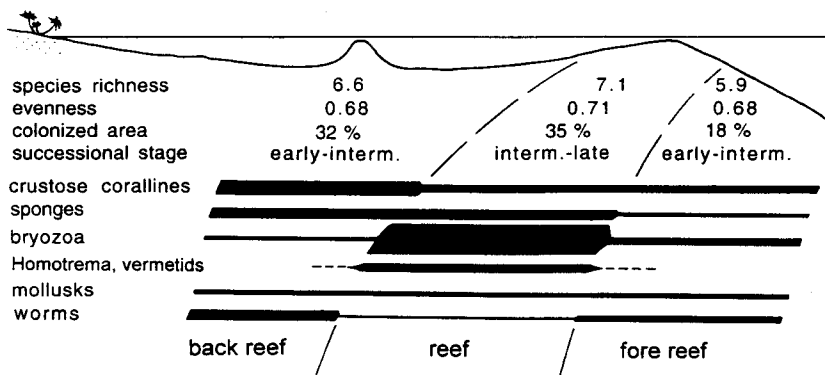
ABUNDANCE AND DISTRIBUTION OF COELOBITES IN MAJOR REEF ENVIRONMENTS.— Abundance of coelobites in terms of average cover per rubble sample is highest in the reef environment with 35% (Table 2, Fig. 3). It is a little lower in the back reef and lowest in the fore reef with an average value of 18%. The correlation analysis shows that cover is inversely correlated with water depth (Table 3). Major contributors to coelobite cover are crustose coralline algae, sponges, and bryozoa. They show a positive correlation with total cover (Table 3). Abundance of bryozoa shows a significant positive correlation with rubble size while the abundance of crustose coralline algae decreases with increasing rubble size. There are no differences in abundance in terms of average individual numbers per rubble sample in the major reef environments. Values range between 54 and 57 individuals per sample. Polychaete worms are the strongest contributors to individual numbers.

Table 2. Diversity and abundance of coelobites per rubble sample in reef, fore reef, and back reef sites. CCA = crustose coralline algae. H' = Shannon-Wiener index of diversity, e = evenness. (The raw data of the 142 samples investigated are not published for reasons of space. The author will send a list containing the data of the individual samples to interested colleagues on request.)

Variable	Mean	Standard Error
Reef (n = 57)		
CCA cover	11.8%	2.0%
sponge, cover	6.1%	1.0%
bryozoan, cover	17.2%	3.2%
mollusk, cover	0.3%	0.1%
worm, cover	0.6%	0.1%
<i>Homotrema</i> , cover	0.2%	0.05%
total cover	35.3%	3.2%
individuals	53.6	8.2
species	7.1	0.4
H'	0.57	0.02
e	0.71	0.02
Fore Reef (n = 46)		
CCA, cover	11.4%	1.9%
sponge, cover	2.3%	0.5%
bryozoan, cover	1.9%	0.5%
mollusk, cover	0.2%	0.1%
worm, cover	1.4%	0.2%
<i>Homotrema</i> , cover	0.2%	0.1%
total cover	17.7%	2.1%
individuals	56.8	11.1
species	5.9	0.4
H'	0.47	0.03
e	0.68	0.03
Back Reef (n = 39)		
CCA, cover	20.7%	3.4%
sponge, cover	5.9%	1.9%
bryozoan, cover	2.7%	0.7%
mollusk, cover	0.8%	0.2%
worm, cover	1.2%	0.2%
<i>Homotrema</i> , cover	0.3%	0.1%
total cover	31.5%	4.0%
individuals	55.2	8.0
species	6.6	0.5
H'	0.52	0.03
e	0.68	0.03

Pseudovermilia can reach values of up to 200 individuals per sample. Individual numbers increase with increasing rubble size. Individual numbers are also positively correlated with species richness (Table 3).

FLORIDA



BELIZE

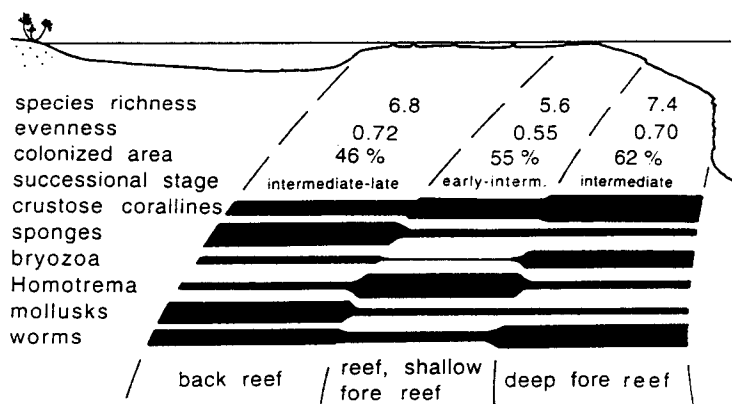


Figure 3. Distribution of major groups of coelobites under coral rubble across the Florida Reef Tract and comparison with the data obtained from rubble in Belize (schematic).

The abundance of crustose coralline algae and sponges in terms of cover decreases towards the fore reef. Bryozoa and the foraminifer *Homotrema rubrum* are most abundant in the reef environment. The abundance of worms appears to be lowest around the reef and the abundance of mollusks is more or less similar in the major reef environments, except for vermetids that are most abundant around the reef crest (Fig. 3).

Statistical comparison of abundance and diversity of coelobites in major reef environments show that most of the significant differences exist between reef and fore reef environments (Table 4). There are significant differences in total cover, cover of sponges, worms, and in diversity indices. Between reef and back reef environments, the abundance of crustose coralline algae, bryozoa, and mollusks is significantly different statistically. Between back reef and fore reef, there is only a statistically significant difference in total cover and cover by mollusks.

Table 3. Correlation matrix of a Pearson product-moment correlation of 96 samples from 10 stations where flushing was assessed. * = Correlation significant at $P > 0.20$. CCA = % cover of crustose coralline algae, SPO = % cover of sponges, BRY = % cover of bryozoans, MOL = % cover of mollusks, WOR = % cover of worms, HOM = % cover of *Homotrema*, IND = number of individuals, SPEC = number of species, COV = total cover in %, H' = diversity index, e = evenness, Flush = rel. amount of flushing in %, Size = rubble size in cm², Depth = water depth in meters.

	CCA	SPO	BRY	MOL	WOR	HOM	IND	SPEC	COV	H'	e	Flush	Size	Depth
CCA	1													
SPO	0.02	1												
BRY	-0.31*	0.05	1											
MOL	0.01	0.09	-0.11	1										
WOR	-0.18	-0.17	-0.01	0.01	1									
HOM	-0.03	-0.12	-0.10	0.03	0.06	1								
IND	-0.26*	-0.08	0.17	0.05	0.63*	0.09	1							
SPEC	-0.17	0.10	0.08	0.36*	0.27*	0.11	0.51*	1						
COV	0.49*	0.43*	0.59*	-0.01	-0.15	-0.11	-0.04	0.01	1					
H'	0.07	0.26*	0.01	0.20	-0.12	-0.01	-0.07	0.55*	0.16	1				
e	0.32*	0.24*	-0.03	0.02	-0.40*	-0.10	-0.48*	-0.22*	0.28*	0.59*	1			
Flush	-0.07	0.09	0.50*	-0.19	-0.28*	-0.02	-0.04	0.05	0.36*	0.16	0.14	1		
Size	-0.21*	0.07	0.29*	0.12	0.18	0.08	0.60*	0.51*	0.12	0.06	-0.28*	0.16	1	
Depth	-0.04	-0.17	-0.35*	-0.04	0.17	-0.06	0.07	-0.04	-0.36*	-0.19	-0.14	-0.80*	-0.12	1

Table 4. Multiple comparison of samples from reef, fore reef, and back reef by Kruskal Wallis one-way analysis of variance by ranks. (* = significant difference, $p < 0.05$)

	Reef vs. fore reef	Reef vs. back reef	Back reef vs. fore reef
Crust. cor. algae	0.54	0.03*	0.06
Sponge	0.0005*	0.19	0.08
Bryozoan	0.00001*	0.0003*	0.41
Mollusk	0.45	0.04*	0.01*
Worm	0.05*	0.30	0.46
<i>Homotrema</i>	0.15	0.88	0.27
Total cover	0.0001*	0.34	0.008*
Individuals	0.39	0.83	0.43
Species	0.06	0.18	0.62
H'	0.006*	0.13	0.39
e	0.74	0.71	0.92
Success. stages	0.00001*	0.0002*	0.67

SUCCESSIONS.—Six successional stages of coelobite community development were observed on rubble undersides. The early stage is characterized by solitary organisms such as mollusks, polychaetes, *Homotrema*, and by crustose coralline algae (Table 5). Colonial organisms come in with the development of the three intermediate stages. These are dominated by scattered bryozoa (intermediate stage 1), scattered sponges (intermediate stage 2), or by both scattered bryozoa and sponges (intermediate stage 3). Within the intermediate stages there is only moderate competition by overgrowth. The two late stages are characterized by a high cover of bryozoa (late stage 1) or of sponges (late stage 2). Within the late stages, the total cover is increased markedly and there is abundant competition by overgrowth. In the late stage 1 the maximum diversity is reached. It decreases in the late stage 2 stage as the community is dominated by two or three sponge species.

The distribution of the successional stages in the major reef zones shows that intermediate 3 and late stages are most common in the reef environment (Table 5). In fore reef and back reef environments, initial and intermediate stages predominate. The statistical differences in the distribution of successional stages between reef and fore reef, and reef and back reef are significant (Table 4).

RELATIVE AMOUNTS OF FLUSHING.—Amounts of flushing are highest around the reef crest and decrease seaward and landward (Table 6). The values within the reef environment are more or less constant. An exception is the value for Big Pine Shoal that has a greater water depth than the other reef stations. Values of the fore reef are constantly low and

Table 5. Distribution of successional stages on rubble undersides in major reef zones. Numbers are in percent.

	Reef	Fore reef	Back reef
Early	8.8	19.6	17.9
Intermediate 1	8.8	23.9	15.4
Intermediate 2	8.8	19.6	20.5
Intermediate 3	40.3	34.7	43.6
Late 1	31.5	0	0
Late 2	1.8	2.2	2.6

Table 6. Results of the dissolution experiments of plaster of paris in the Florida Reef Tract. (Under # 1, 2, and 3 the volume loss of three clods of plaster of paris is given that were put out and recollected simultaneously)

Locality	Depth	# 1	# 2	# 3	Time	Flow rate	Rel. flush
	[m]	[cm ³]	[cm ³]	[cm ³]	[h:min]	[l/min]	[%]
Reef							
Long Reef crest	1	19	18	19	22:00	1.89	100
Alligator Reef crest	1.5	16	17	18	21:40	1.65	87
Big Pine Shoal	6	4	5	6	18:00	0.58	31
Looe Key crest	1	18	18	18	20:40	1.85	98
Fore reef							
Long Reef deep	15	1	1	1	19:00	0.10	5
Alligator Reef deep	10	2	1	1	19:30	0.13	7
Looe Key deep	8	1	1	2	21:00	0.12	6
Back reef							
Hen and Chicken	5	7	7.5	6	22:15	0.69	37
Nf. Harbor Patch	3	10	10	9	19:30	1.05	56
Schooner Wreck	4	6	6	7	21:00	0.60	32

range between 5 and 7%. Values from the back reef are more variable. Correlation analysis shows that relative flushing is largely controlled by water depth (Table 3). There is also a strong correlation between flushing and total coelobite cover, and between flushing and abundance of bryozoa and sponges.

COMPARISON OF LOCALITIES WITHIN THE FLORIDA REEF TRACT.—The cumulative data from individual reef stations shows that there is relatively high variation of abundance in terms of cover (Table 7). Fore reef stations are characterized by more or less constantly low values. The same holds true for the back reef with the exception of Newfound Harbor patch reef where the abundance of sponges and crustose coralline algae is relatively high. Diversity is generally high at the reef stations, lower and moderately variable in the fore reef, and variable in the back reef (Table 8). The results of pairwise statistical comparisons of cover, abundance of sponges, bryozoa, and diversity between the stations shows that there are no clear patterns in the differences between reefs from the Upper, Middle, and Lower Keys (Tables 9-12). Cluster analysis shows that stations from similar major reef environments tend to fall in the same clusters (Fig. 4). Newfound Harbor patch reef falls together with the reef stations as it has high coelobite cover. The other patch reef stations tend to accumulate in clusters with the fore reef stations.

DISCUSSION

A combination of physical and biological factors controls development, abundance, and diversity of coelobites living on rubble undersides in the Florida Reef Tract. Flushing of sub-rubble cavities which is largely controlled by water agitation and depth, respectively. Rubble stability, a function of rubble size and water agitation, controls the frequency of rubble overturn and disturbance. Biological interactions between organisms that result in the development of successional stages of coelobite community development are also influenced by rubble stability.

Table 7. Cover of coelobites for individual sample sites (percentages). n = number of samples, A = sub-rubble area in cm²; S = shallow, D = deep; CCA = crustose coralline algae, SPO = sponge, BRY = bryozoan, MOL = mollusk, WOR = worm, HOM = *Homotrema*; TOT = total cover

	n	A	CCA	SPO	BRY	MOL	WOR	HOM	TOT
Reef									
Long Reef, S	12	2157	0.7	7.7	40.8	0	0.6	0.2	50.0
Conch Reef, S	7	1221	4.6	6.4	10.8	0.1	0.3	0.3	22.5
Alligator Reef, S	10	2157	12.1	2.2	28.5	0.2	1.5	0.6	45.0
Sombrero Reef, S	10	1804	18.9	3.6	3.5	0.9	0.2	0.3	27.3
Big Pine Shoal	9	1386	21.5	14.2	10.1	0	0.5	0.1	46.3
Looe Key Reef, S	9	1486	11.2	4.2	10.3	0	0.5	0.1	26.2
Fore reef									
Long Reef, D	12	2012	15.7	4.4	1.2	0	1.3	0	23.0
Conch Reef, D	9	1461	10.1	3.6	3.6	0.1	1.7	0	16.8
Alligator Reef, D	8	1082	7.5	0.7	4.7	0.4	1.5	0.8	15.6
Sombrero Reef, D	9	1316	7.9	2.4	1.4	0.4	0.6	0.1	12.8
Looe Key Reef, D	8	1104	7.7	0.9	3.9	0	2.5	0.2	15.3
Back reef									
Schooner Wreck	9	1588	14.4	4.3	2.3	1.1	1.1	0.9	24.2
Hen and Chicken Reef	10	1861	10.6	5.6	1.7	1.4	2.4	0.2	22.1
Bahia Honda Patch	11	1435	14.0	1.8	2.0	0.4	1.0	0	19.2
Nf. Harbor Patch	9	1288	41.9	16.4	5.6	0.2	0	0.2	64.4

Table 8. Species and diversity of coelobites for individual sample sites. CCA = crustose coralline algae, SPO = sponge, BRY = bryozoan, MOL = mollusk, WOR = worm; TOT = total number of species, H' = Shannon-Wiener index of diversity, e = evenness

	CCA	SPO	BRY	MOL	WOR	TOT	H'	e
Reef								
Long Reef, S	1	8	6	0	6	22	0.93	0.69
Conch Reef, S	1	6	5	0	5	18	0.91	0.72
Alligator Reef, S	1	7	6	6	5	26	0.87	0.61
Sombrero Reef, S	2	7	5	1	4	20	0.87	0.67
Big Pine Shoal	3	8	7	3	4	26	1.01	0.75
Looe Key Reef, S	3	6	4	0	5	19	0.99	0.77
Fore reef								
Long Reef, D	3	8	5	1	5	23	0.60	0.44
Conch Reef, D	3	4	5	3	6	22	0.74	0.56
Alligator Reef, D	1	3	5	2	4	16	0.83	0.69
Sombrero Reef, D	3	5	3	1	5	18	0.66	0.52
Looe Key Reef, D	2	3	4	1	6	17	0.78	0.63
Back reef								
Schooner Wreck	3	8	5	4	5	26	0.96	0.68
Hen & Chicken Reef	3	8	6	5	5	28	0.65	0.45
Bahia Honda Patch	3	7	3	3	5	22	0.60	0.45
Nf. Harbor Patch	1	5	2	1	2	12	0.88	0.82

Table 9. Multiple comparison of cover at individual sites. Kruskal Wallis one-way analysis by ranks. * = significant differences at $P < 0.05$. LRS = Long Reef shallow, CRS = Conch Reef shallow, AS = Alligator Reef shallow, SOS = Sombrero Reef shallow, BPS = Big Pine Shoal, LOS = Looe Key Reef shallow, LRD = Long Reef deep, CRD = Conch Reef deep, AD = Alligator Reef deep, SOD = Sombrero Reef deep, LOD = Looe Key Reef deep, SW = Schooner Wreck, HC = Hen and Chicken Reef, BH = Bahia Honda Patch Reef, NFH = Newfound Harbor Patch Reef

	LRS	CRS	AS	SOS	BPS	LOS	LRD	CRD	AD	SOD	LOD	SW	HC	BH	NFH
LRS		*		*				*	*	*	*		*	*	*
CRS	*				*										*
AS					*			*	*	*	*		*	*	*
SOS	*					*	*								*
BPS		*	*					*	*	*	*	*	*	*	*
LOS				*											*
LRD				*		*									*
CRD	*		*		*										*
AD	*		*		*										*
SOD	*		*		*										*
LOD	*		*		*										*
SW					*										*
HC	*		*		*										*
BH	*		*		*										*
NFH	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*

FLUSHING.— Most of the coelobites identified are filter-feeders and suspension-feeders. They are dependent on water flushing their habitat to be able to obtain food. Flushing of sub-rubble cavities controls coelobite abundance in terms of cover. There is a good correlation between flushing and total cover. Furthermore, abundance of bryozoa and sponges also increases with increasing amounts of flushing (Table 3). Flushing of sub-rubble cavities is highest in the reef environment where the highest values of cover occur. At Newfound Harbor patch reef, where higher amounts of flushing were measured than at the other back reef stations, cover is even higher than at stations in the reef environment. Several studies have shown the importance of food-availability for suspension-feeding organisms. Brock and Smith (1983) showed that the biomass of coelobites in Kanehoe Bay, Hawaii, decreased with decreasing amounts of organic matter in the water column. Winston (1976) found an increased growth of a bryozoa due to increased food supply. Wilkinson and Vacelet (1979) demonstrated that a decrease in water flow results in slower growth of several sponge species.

RUBBLE STABILITY.— Rubble size and water agitation determine rubble stability. Within the investigated samples, both numbers of individuals and species richness increase with increasing rubble size. There is a strong positive correlation between the three variables (Table 3). The larger the size of a piece of rubble, the higher its stability and the longer it is available for colonization and community development without disturbance by overturning. Evenness decreases with rubble size, presumably because of extremely high individual numbers that were observed in several larger samples. Unlike several other studies on mobile substrates, no maximum diversity was observed at a certain rubble size above which diversity decreases again (Rützler, 1965; Osman, 1977; Meesters et al., 1991). These workers explained their observations with the intermediate disturbance hypothesis

	LRS	CRS	AS	SOS	BPS	LOS	LRD	CRD	AD	SOD	LOD	SW	HC	BH	NFH
LRS			*	*				*	*	*	*		*	*	
CRS															
AS	*				*										*
SOS	*				*										
BPS			*	*		*	*	*	*	*	*	*	*	*	
LOS					*				*		*				
LRD					*				*		*				
CRD	*				*										
AD	*				*	*	*					*			*
SOD	*				*										*
LOD	*				*	*	*								*
SW					*				*						
HC	*				*										
BH	*				*										
NFH			*						*	*	*				

The negative correlation between the abundance of crustose coralline algae and rubble size (Table 3) is caused mainly by small samples. Small pieces of rubble are often over-

[illegible]

Table 12. Multiple comparison of diversity (Shannon Wiener diversity index H') at individual sites. Kruskal Wallis one-way analysis by ranks. * = significant differences at $P < 0.05$. (Abbreviations as in Table 9)

	LRS	CRS	AS	SOS	BPS	LOS	LRD	CRD	AD	SOD	LOD	SW	HC	BH	NFH
LRS					*	*						*			
CRS					*	*									
AS					*	*									
SOS															
BPS	*	*	*				*	*	*	*	*		*	*	*
LOS	*	*	*				*	*	*	*	*		*	*	*
LRD					*	*						*			
CRD					*	*									
AD					*	*				*				*	
SOD					*	*			*			*			
LOD					*	*						*			
SW	*						*			*	*			*	
HC					*	*									
BH					*	*			*			*			
NFH					*	*									

turned and disturbed and only available for colonization for a short time span. Therefore, they are dominated by early, robust taxa such as crustose coralline algae that can withstand frequent overturning. Similar observations were made by Osman (1977) and Sousa (1979) in coastal boulder fields.

BIOLOGICAL INTERACTIONS.—As observed in other studies, the succession of coelobites is characterized by a transition from solitary organisms that are the first colonizers to colonial organisms that dominate later stages (Jackson, 1977; Choi, 1984). Jackson (1977) suggests that reproduction and growth rates, defensive mechanisms, and life spans of colonial organisms favor them to play the late role in succession during competition on marine hard substrata, as opposed to solitary organisms that play the early role. For example, sponges are by far the best competitors for space. It is unclear why this does not hold true for boring coelobite communities that are dominated in all stages by polychaete worms (Hutchings, 1983).

The distribution of successional stages in the major reef environments is not fully understood. The majority of samples that are in late successional stage 1 that yield the highest diversity occur in the reef environment. Following the intermediate disturbance hypothesis, the reef environment presumably is the optimal zone of intermediate disturbance or stability, respectively. On the one hand, pieces of rubble are given a certain time to be colonized and to develop a diverse coelobite community. On the other hand, rubble is turned over often enough to prevent a few dominant taxa, such as sponges, from outcompeting and overgrowing other taxa. There should be a tendency to more abundant development of late successional stages both in the back reef and in the fore reef where rubble stability is higher and longer times for undisturbed colonization are available due to lower values of water agitation. However, this is not the case.

COMPARISON WITH A FORMER STUDY IN FLORIDA AND WITH SOUTHERN BELIZE REEFS.—Based on variations in occurrence and abundance of coelobites in the Florida Reef Tract, Choi and Ginsburg (1983) distinguished between lagoon, lagoon-reef, reef, and fore reef coelobite zones. In accordance with my study, Choi and Ginsburg (1983) found abun-

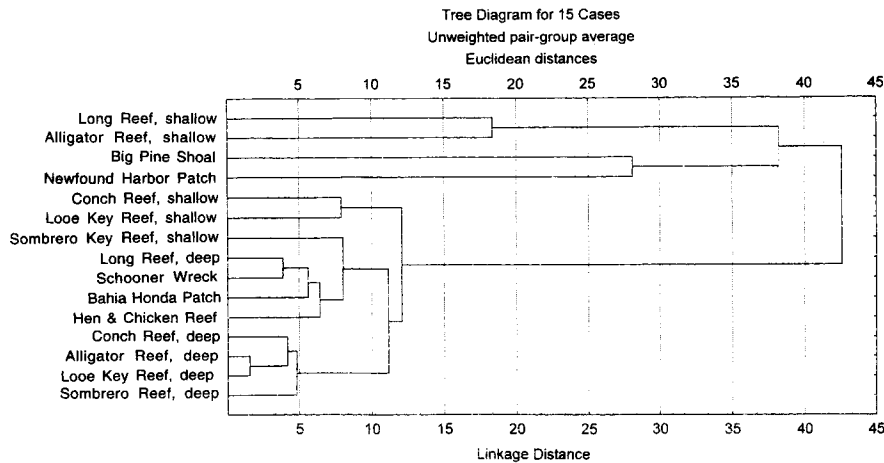


Figure 4. Tree diagram of a cluster analysis of the 15 stations in the Florida Reef Tract. The cluster analysis includes the variables: total cover, sponge cover, bryozoan cover, cover by crustose coralline algae, mollusk cover, worm cover, *Homotrema* cover, diversity index, and evenness.

dance (cover) and biomass to be highest in the reef environment, with bryozoa being most diverse and abundant and *Homotrema* reaching high individual numbers. Choi and Ginsburg (1983) also found abundance to be lowest in the fore reef, but they discovered highest values in the deeper fore reef around 25 m water depth. As no samples were taken from that depth in my study, no comparison is possible. The distribution of sponges also came out differently in the two studies. While sponge abundance decreases towards the fore reef according to the present data, Choi and Ginsburg (1983) found maxima in back reef and fore reef. An explanation for this difference might also be the lack of deep fore reef samples in my study.

There are significant differences between my data from the Florida Keys and data from coelobites on rubble undersides in the southern Belize reefs (Gischler and Ginsburg, 1996). There is generally a higher abundance in terms of cover and a higher diversity of coelobites in Belize (Fig. 3). The average cover per rubble sample in the major reef environments in Belize ranges between 46 and 62%. This difference is probably the consequence of lower amounts of flushing in the Florida Reef Tract. In all major reef environments in Florida, measured flow rates are lower than in Belize (Table 6; Gischler and Ginsburg, 1996). Highest values in Belize reach 2.7 cm s^{-1} as opposed to 1.9 cm s^{-1} in Florida. 80 species were identified in Belize as opposed to 67 in Florida. Again, this might be a consequence of the lack of deep fore reef samples in Florida as opposed to Belize where samples down to 40 m depth were taken. The average diversity per rubble sample is more or less similar between the two areas. The distribution of certain taxa such as sponges, polychaete worms, *Homotrema*, and vermetid mollusks is identical. However, the distribution of crustose coralline algae and bryozoa is different. There were more samples in late stages of succession found in Belize than in the Florida Reef Tract. The distribution of successional stages in major reef environments is also different. In Belize, intermediate, high diversity stages occur in the deeper fore reef, early stages reach highest numbers around the reef, and late stages are most common in the back reef. The deeper fore reef was interpreted as the optimal environment with intermediate disturbance. Around the reef, no late stages

can develop because of frequent disturbance and in the back reef, frequency of disturbance is too low. In Florida, the reef environment appears to be the optimal area of intermediate disturbance. One explanation for this difference is probably the different reef morphologies of the two areas and the differences in exposure to waves and currents. In Belize, the surface-breaking barrier reef is continuously developed over almost 250 km and open to the Caribbean Sea. The marginal reefs in Florida are more or less small, isolated reefs that in some cases are not surface-breaking and they are protected from the open ocean swell by the Bahamas and the Greater Antilles. Water agitation around the marginal reefs in Florida is lower than in Belize, which is shown in the lower values of flushing. As a consequence, the zone of intermediate disturbance is shifted to the reef environment. The distribution of bryozoa might be tied to variation in disturbance as both in Belize (fore reef) and in Florida (reef), they reach highest abundance and diversity in supposed zones of intermediate disturbance. The differences in reef morphology between the two areas are also reflected in the degrees of the differences in coelobite abundance and diversity in the major reef environments of the two areas. As the major reef zones are more distinctly developed and defined in Belize, much more statistically significant differences are observed (Gischler and Ginsburg, 1996).

ENVIRONMENTAL AND ANTHROPOGENIC INFLUENCE.— The comparison of data from reefs investigated in the Florida Reef Tract does not indicate geographical differences in coelobite communities. The steady influx of water from Florida Bay (Smith, 1994), mainly through the Middle Keys, seems to have no major influence on abundance and diversity of coelobites. Outflows of extremely cold water that severely damaged the reef community only occurred in intervals of 5 to 15 yrs between 1941 and 1978 (Hudson et al., 1976; Roberts et al., 1982). The development of a diverse coelobite community takes only 3 yrs at the most (Choi, 1984). Observations on barren substrates put out in southern Belize reefs even showed that in the shallow fore reef, the development of a diverse coelobite community under rubble only takes approximately 6 mo (Gischler, unpubl. data). Therefore, environmental impact can only be expected to be preserved in coelobite community structure for a limited time. For the same reason, the disturbing impact of Hurricane Andrew and tropical storm Gordon on the sub-rubble communities of the reefs in the Upper Keys are not discernible from the data. The storms presumably produced large organism-free sub-rubble areas by overturn and breakage, but those areas became colonized within a time span of several months to 3 yrs. However, Choi (1982) could still show the impact of offshore drilling on coelobite development in the Philippines after 15 mo, but only in a radial distance of about 100 m from the borehole.

The impact of much more intensive live rock collection off the Middle Keys as opposed to the Upper and Lower Keys is also not visible in the data. Even though live rock is only collected more than 3 mi offshore around the marginal reefs, but not from back reef and fore reef environments, the majority of samples with high diversity and cover that are in late stages of succession were found in the reef environment. However, the fact that the collection of live rock ended by the end of 1995 is to be supported as rubble is the most common hard substrate on coral reefs and not only a potential habitat for cavity dwellers but also for surface dwellers of the reef community.

CONCLUSIONS

Distribution and diversity of coelobites living on undersides of coral rubble in the Florida Reef Tract is largely controlled by flushing of sub-rubble cavities, rubble stability, and biological interactions between organisms.

The reef environment is presumably an "optimal" area of intermediate disturbance (*sensu* Connell, 1978) where highest diversity and abundance of coelobites occurs.

Potential differences in coelobite abundance between reefs off the Upper, Middle, and Lower Keys due to lateral gradients in "bad water" influence from Florida Bay, due to the effects of Hurricane Andrew and tropical storm Gordon, and in live rock collection were not detected.

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