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CORAL REEF FRAMEWORK CAVITIES: IS FUNCTIONAL SIMILARITY REFLECTED IN COMPOSITION OF THE CRYPTIC MACROFAUNAL COMMUNITY?

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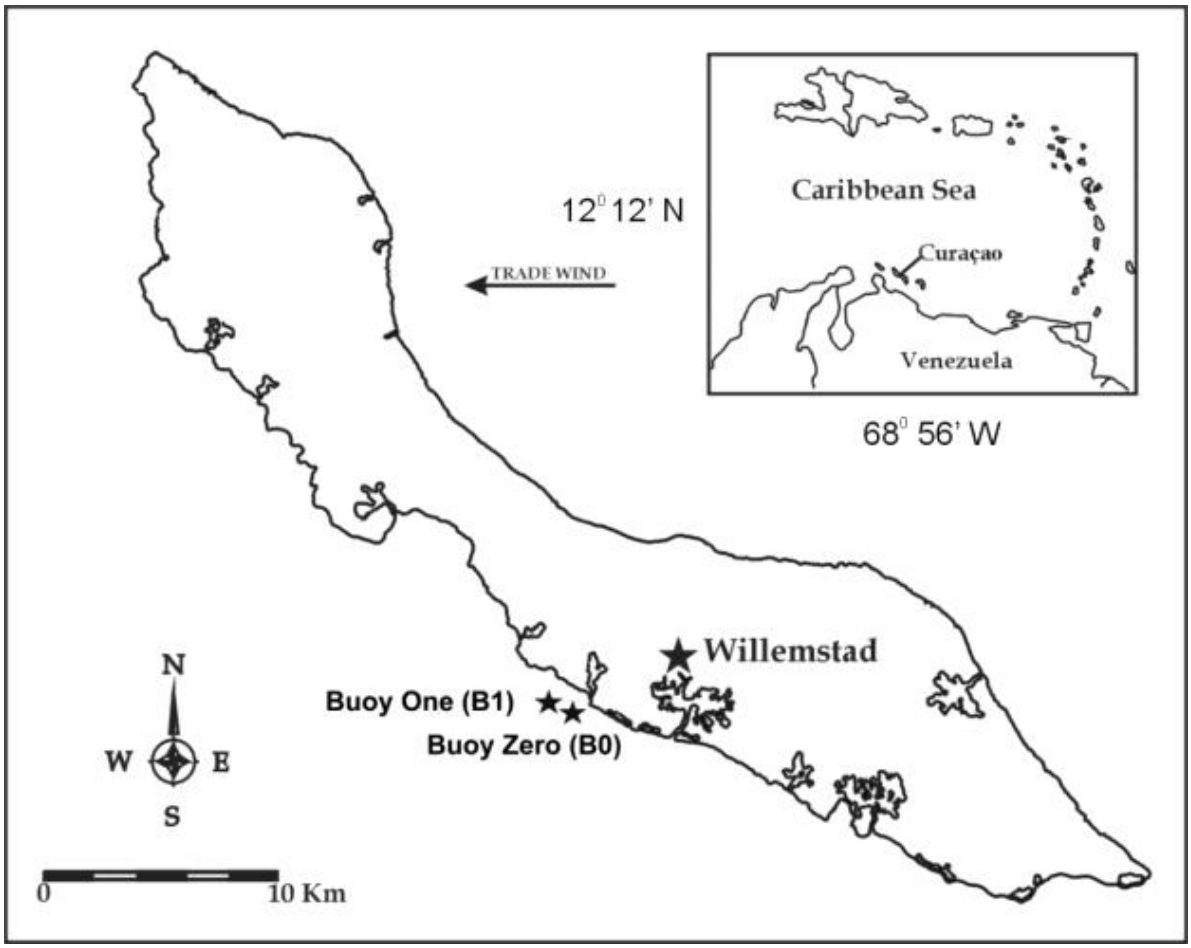

Figure 1. Map of Curaçao indicating the position of the experimental cavities. Cavities B0C1-4 are located on the reef Buoy Zero (B0) and cavities B1C1-4 are located on the reef at Buoy One (B1).

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ABSTRACT

Hard substratum surface area of framework cavities constitutes a major habitat in coral reefs. We studied the community composition and distribution of cryptic sessile macro-organisms in framework cavities in relation to abiotic parameters on a reef slope in Curaçao. Spatial characteristics were measured with a CaveCam (video) cave–explorer to investigate the macro-faunal community composition. Light intensity and water movement were measured. Bacterial densities were counted in- and outside the cavities over a year. Cover of the fauna and flora in cavities was about 95% of total hard surface area. Cavities harbored a distinctive macro-fauna. Species composition was very diverse, with a total of 88 species/taxa found. Diversity (*H'*) was high and evenness (*V'*) low, indicating the presence of dominant species. Community composition was related to abiotic parameters. Light intensity decreased with a factor of 10 from front to back of cavities, with a consequent decrease in crustose coralline algae in the same direction, but there was no other relation between light and distribution of organisms. Water motion and turbidity, generally less in cavities than on the open reef, were significantly related to biotic distribution. Inside cavities we found sponge and total suspension-feeder cover to decrease with increasing water movement and turbidity. There was an average depletion of bacteria of 40% in cavity water. In a functional sense reef framework cavities are a uniform trophodynamic environment characterized by high bacterioplankton removal rates and efflux of DIN and it is surprising to find each cavity having a different species composition and abundance.

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INTRODUCTION

Cavities are a prominent feature of coral reefs, and include the spaces and surfaces under rubble, the undersurfaces of skeletal organisms such as corals, the interior of vacated borings, the shaded undersides of overhangs, and framework cavities. Together these cavities may make up a substantial part of the volume of a reef, exceeding 30-75% of the total reef volume (Ginsburg 1983). The cavities provide a surface area for colonization by sessile organisms that may be equal to or greater than the area of the exposed reef surface (Garrett et al. 1971, Jackson and Winston 1982, Logan et al. 1984, Kobluk and van Soest 1989, Richter et al. 2001). Cryptic habitats appear to harbor a surprisingly high number of species per unit of surface area. The species composition within cavities has been extensively studied. Meesters et al. (1991), and Wunsch and Richter (1998) found sessile groups such as sponges, crustose coralline and filamentous algae, polychaetes, bryozoans, ascidians, corals and foraminifera covering almost the entire available hard substratum.

Most of these organisms are attached suspension feeders and depend upon water flow to receive dissolved and particulate nutrients (Reiswig 1971, Abelson 1991, Sebens and Johnson 1991, Eckman and Duggins 1993). Because most cavities are to some degree enclosed, with restricted access, water flow in cavities may be reduced or even non-existent in the deepest recesses. This could have important implications for some crypto-faunal groups, such as sponges, which must rely entirely upon the water movement in the cavities. Wilkinson and Vacelet (1979) have shown that reduced water movement has the effect of reducing sponge growth, and there may be a direct relationship between the size/abundance of sponges in cavities and the rate of water movement and/or water exchange.

Some sponges have symbionts with beneficial qualities (Osinga et al. 2001) such as phototrophic microorganisms (cyanobacteria, Wilkinson 1978a, zooxanthellae, Hill 1996) and light may control the distribution of photosynthetic symbiont-containing sponges within cavities. Sponges are known to be sensitive to sedimentation or turbidity, which has the effect of clogging up canals and reducing pumping rates (Burns and Bingham 2002). This sensitivity may have an effect on sponge distribution (Gerrodette and Flechsig 1979), probably also on sponges in cryptic habitats. Wilkinson (1983) concluded that sponges are not common on the floors of cavities but prefer the walls and roofs, where sedimentation is usually less intensive. Fagerstrom (1984) suggested that the low turbidity in cryptic environments compared to the exposed reef, is the prime controlling factor in the distribution of sclerosponges.

Biodiversity in cavities is dependent on species characteristics and available space. The most important problem that sessile organisms have to deal with is finding space for settlement and growth, and then, when established, defending that position. In cavities where hard substratum is a limited resource these processes result in strong competition. “Competitive networks’ have been proposed as a mechanism to reduce competition (Jackson and Buss 1979). Non-hierarchical competition within a diverse community would be sufficient for maintaining high diversity (Buss and Jackson 1979, Jackson and Winston 1982). Diversity in cavities could also be maintained by ‘intermediate disturbance’ (Connell 1978) through abiotic factors such as substrate collapse (Kobluk 1988), variations in exchange rates (with the overlying reef water) and sedimentation (Choi and Ginsburg 1983), or through biotic factors such as predation

(Palumbi and Jackson 1982). Size of area availability *per se* may be a factor in increased biodiversity (Rosenzweig 1995).

Our previous and other studies showed reef cavities to be very similar in trophic function. Cavities are a net sink for bacterioplankton, a net source for dissolved inorganic nitrogen (Scheffers et al. 2004, Van Duyl et al. 2005) and a net sink for dissolved organic carbon (de Goeij et al. 2008). Reef and cavity water acquires a distinct signature in terms of inorganic nutrients (Scheffers et al. 2005) and dissolved organic carbon (de Goeij et al. 2008).
Cavities are a key factor in the benthic-pelagic coupling process of coral reefs.

In the present study our question is: are these cavities, so similar in function, also similar in macro-faunal species composition? We returned to the same cavities we studied previously for functional trophodynamics and now investigated cover, composition and distribution of the cavity macro-faunal community in relation to the abiotic environment.

MATERIALS AND METHODS

Experimental Sites

The framework cavities used in our study were located on the fringing reef of Curaçao, Netherlands Antilles (12°12'N, 68°56'W). We studied eight different cavities at a depth of approximately 15 meters (Fig. 1) on the reef slope at CARMABI Buoy Zero/ Buoy One (Bak 1977, Van Duyl 1985). The cavities were scattered over 200 meters along the coastline. To link microbial and nutrient dynamics to cryptofauna we used the same cavities as described in Scheffers et al. (2003) and Scheffers et al. (2004). For comparing cavity surface to open reef surface area we studied 15 different cavities, scattered along the coastline of Curaçao.

Cavity Structure

We used the 'cave explorer' to determine the inner structure of the crevices (Scheffers et al, 2003). It measures points in space (i.e. distances from the bottom-center axis to the cavity wall) along the cavity bottom middle-axes. Putting these coordinates in LISA (a Geographic Information Systems program), a 3-D image is obtained. LISA determines the best suitable algorithm with a given set of coordinates to give a direction and angle to vectors, which create a digital model of the main chamber of the cavity. The obtained model provides data on hard substratum surface area, volume, and aspect ratio (main opening surface area/ total area). The aspect ratio is used as a measure of water Throughflow.

Each cavity was subdivided in three equal compartments (in reference to the bottom middle-axes), in order to differentiate the sessile macro-faunal community composition in these separate sectors and their relation to abiotic factors.

Cavity Abundance

In order to compare the cryptic surface area, the "inside" of the reef, to the projected surface area of the "outside" reef, we measured the depth (i.e. distance from cave opening to back wall) of all visible cavities within four 1 m wide belt transects, 25 meter long, at each depth (5, 10, 15, 20, 25, 30 meters) between Buoy 0 and Buoy 1 with a ruler. We measured a sub sample of 15 cavities with the cave profiler and plotted the depth of each cavity against the respective surface area. Depth of a cavity was an accurate measure for cavity surface area. (Fig 2a, linear regression fit $p < 0.03$, $R^2 = 0.83$) and the formula for this correlation is used to calculate total cavity surface area. Cavity surface area is compared with the surface area of the outside reef. This is defined as projected bottom surface, i.e. a two-dimensional plane, which in our comparison had the size of transects: 100 x 1 m, at each depth.

Water Motion

We used the clod card method (Jokiel and Morissey 1993) to obtain a relative measure of water movement in the different parts of the cavities. Plaster-of-Paris (mixed with water in the ratio 1:2) was poured in plastic cups of 3 ml, producing almost identical clod cards. All air bubbles were removed, and the mix was hardened at room temperature (30 ^{0}C) until no loss of weight occurred. Each clod weighed approx. 2.5 g. Plastic plates were attached to the base of clods and this construction determined initial weight. The plates were then attached to a cave-specific (using the digital model LISA) construction, consisting of stalks placed exactly in the middle of the respective compartment of each cavity. This construction was pre-soaked for 12 hours. Triplicate clod cards were put in each compartment in each cavity, as well as directly outside the cave. This experiment was performed twice.
After 24 hours *in situ*, the blocks (with attached plastic plates) were dried at room temperature until no loss of weight occurred, and final weight was determined. The weight loss or dissolution rate is used as a measure for water movement.

Light Intensity

Light intensity was recorded with a specially adapted underwater LI-COR Photocell 192SA and a LI-1000 Data-logger. Measurements were inside cavities at the same positions as used for the water motion clod card measurement. In order to relate the light intensities to water depth, extinction profiles, with intervals of 3 meters, were made from the reef water surface down to the cave frontal opening. Measurements were conducted on days with constant cloud cover.

Turbidity

Turbidity measurements were taken with an OBS (Optical BackScatter infrared SeaPoint continuous turbidity meter (SeaPoint sensors, Inc. USA)) inside the cavities.

Data was read using LINK software. The sensors were put at the same locations used for measurement of water motion and light intensity and left *in situ* for 5 days. Readings were calibrated with dilution series using 0.2 µm filtered water. Dilution series were measured with the OBS and water samples were filtered (GF/F), dried (5 days, 40 ^{0}C) and weighted. This results in a calibration of readings to milligrams of suspended solids per liter of seawater (mg/l).

Bacterial Densities in Cavity and Reef Water

We sampled each of the 8 cavities at one-month intervals for one year between the hours of 10.00 to 14.00 for heterotrophic bacterial density. Samples (10 ml) were fixed with 0.2 µm filtered and buffered (sodium tetraborate, pH = 7.9) formaldehyde (final concentration 0.7 %). In the lab, the samples were stained with acridine orange and subsequently filtered (0.03 bar under pressure) onto 25 mm 0.2 µm polycarbonate filters (Nuclepore) supported by a 0.45 µm cellulose acetate filter, within 24 hours after sampling (Hobbie et al. 1977). The filters were mounted on microscopic slides in non-fluorescent immersion oil (Olympus) and then stored in a freezer (-20^{o}C). Bacteria were counted and sized with a Zeiss Axiophot epifluorescence microscope (1250x magnification). We used a grid of 36 x 36 µm, divided in 10 rows and 10 columns, for counting and sizing bacteria. At least 10 random grids per filter and at least 200 cells were counted. All cavity water samples were taken from the center of a cavity. Open reef water was sampled directly in front of a cavity opening, one meter away from the substrate. Reef water was sampled before cavity water to avoid disturbance of the water properties. The samples were kept cold in the dark until processing.

Cryptofauna Cover and Composition

We used a CaveCam to film cryptic macrofauna on the hard substratum inside cavities. The CaveCam (adapted after Wunsch and Richter 1998) consisted of a Sony DCR-TRV900E in an Amphibico underwater housing. This was attached to a digital Panasonic endoscopic video camera with underwater housing. The Sony camera was needed to record- and track in real time- what was filmed in the cavity. The CaveCam, mounted on a rod with centimeter markings, was inserted into the cave. We made photo transects over the cavity walls in front, middle and backside compartments of each cavity. Transects were oriented inside cavities using the information of the 3D-model (LISA). Digital pictures were randomly taken along these transects, using a Sony DV capture board.

For each of the three cavity compartments 16 non-overlapping, sharp pictures were analyzed with Adobe PhotoShop 4.0. 100 Points were projected over the image and all structures (biotic and a-biotic) lying directly beneath these points are noted. Depth of field of the 3.5mm wide-angle Panasonic lens is low and with a set focus distance, a sharp picture had a fixed surface area of 16 cm^2. We determined the minimal area to be analyzed per compartment using the software MINAR (based on Weinberg 1978). Using 16 pictures (256 cm^2) per compartment we covered more than 70% of all species present.

Cover percentages were recalculated (as not the whole compartment could be filmed) to absolute cover per area unit, using the hard surface area (HSA) measurements of the cavities.

Statistical Analyses

One-way ANOVA were performed to test for differences in macro-fauna/flora cover, species number and cover per individual between different cavities and between compartments. Data obtained from photographs was also used to calculate species and taxonomic richness and dominance diversity indices. The Shannon-Weaver diversity index (Krebs 1989) was computed using proportional area coverage for "importance" values (p_i).

$H' = - \Sigma p_i \ln p_i$
p_i = proportion of i^{th} cover (cover species i / cover of all species)
H' = Diversity

To investigate whether certain species have a preference for specific water movement, turbidity, and light intensity regimes or depth inside the cavity, we recreated the obtained species cover data in a Bray-Curtis dissimilarity matrix (Kaandorp 1986). The cover data was double root transformed. The matrix obtained was used to plot hierarchical clusters with Euclidean distance and Ward minimum variance method linkage. Rare species, i.e. species occurring in 1-3 cases in the filmed transects, and crustose coralline algae were left out. Data on crustose coralline algae were used in the analysis of light intensity impact.

Groups (species/taxa) of organisms were plotted against the various abiotic factors to obtain information on habitat preference. Significance levels were obtained using linear regressions.

RESULTS

Cavity Structure

The cavities measured consisted of a large main chamber with numerous small pipes and inclined chimneys, connecting the main chamber to other cavities or to the overlying reef water. The main chambers had sandy bottoms and each had one large frontal opening facing off the reef slope. The most important structural cavity features such as cavity volume, hard substratum area (HSA), and horizontal depth (measured from cave opening to back wall over the sandy bottom) ranged from 53 - 229 l, 9410 – 25334 cm^2, and 60 - 110 cm respectively (see Table 1).

Cavity Abundance

The depth of cavities measured in our sub sample was significantly (N = 15 cavities, linear regression fit, $p < 0.03$; $R^2 = 0.82$) correlated to cavity surface area (Fig. 2a).

Table 1. Structural features of cavities. Depth = vertical depth of cavity on reef; Or. FOA = Orientation of Frontal opening on the reef slope; DepthC = Distance cave opening to back wall; HSA = Hard substratum area, SA = Sandy area;FOA = Frontal opening area; Aspect ratio = Volume / FOA

Cavity	Depth (m)	Or. FOA (^{o}North)	DepthC(cm)	Volume (l)	HSA (cm^2)	SA (cm^2)	FOA (cm^2)	Aspect ratio
B0C1	12.8	195	70	104	17003	7679	2460	42
B0C2	15.2	210	90	107	18255	8287	4600	23
B0C3	12.9	240	110	176	25334	10368	3718	47
B0C4	14.1	140	90	177	17754	7688	2394	73
B1C1	14.6	200	100	229	24696	12684	4680	48
B1C2	13.8	210	70	70	9789	3813	3072	22
B1C3	15.2	220	60	53	9410	4418	1785	29
B1C4	15.8	180	80	55	11311	4702	1542	35

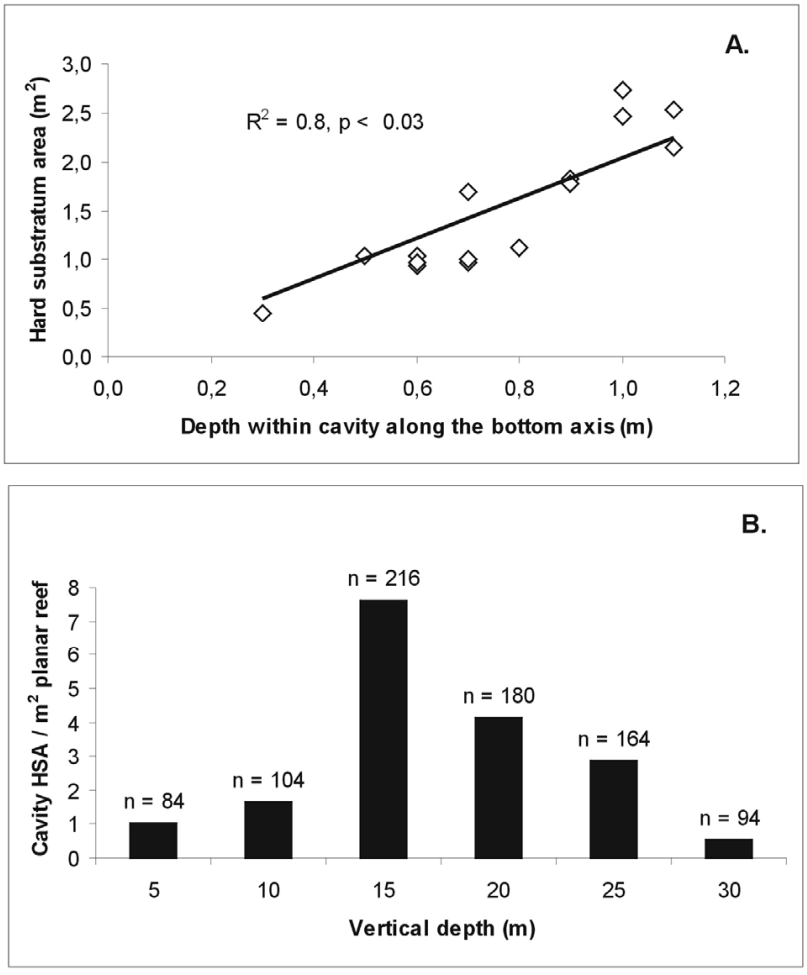

Figure 2. Cavity abundance over the reef slope. (a) The significant (linear regression fit; R2 = 0.82, p < 0.03) relationship between the horizontal depth (front opening to back wall) and hard substratum area (HSA) of a cavity (n = 15). (b) Ratio Cavity HSA/ Reef projected HSA at different depths on the reef slope. Buoy Zero. Data labels indicate the number of cavities encountered within transects at each depth.

The abundance of reef framework cavities was highest around depth of 15-meter and decreased shallower and deeper on the reef. The total surface area of cavities over the reef slope, the "inside" of the reef, exceeded the surface area of the reef projected bottom surface, by a factor of eight at 15-meter depth. At 5 and 30 meters the total cavity surface area was only slightly larger then the two-dimensional surface area of the exposed reef (Fig. 2b). Over the whole reef slope (0-30 meters), cavities provide a three times larger surface area than the projected exposed reef.

Water Movement

Water movement showed a heterogeneous and highly variable pattern over the compartments within the eight different cavities and between cavities. In general, water

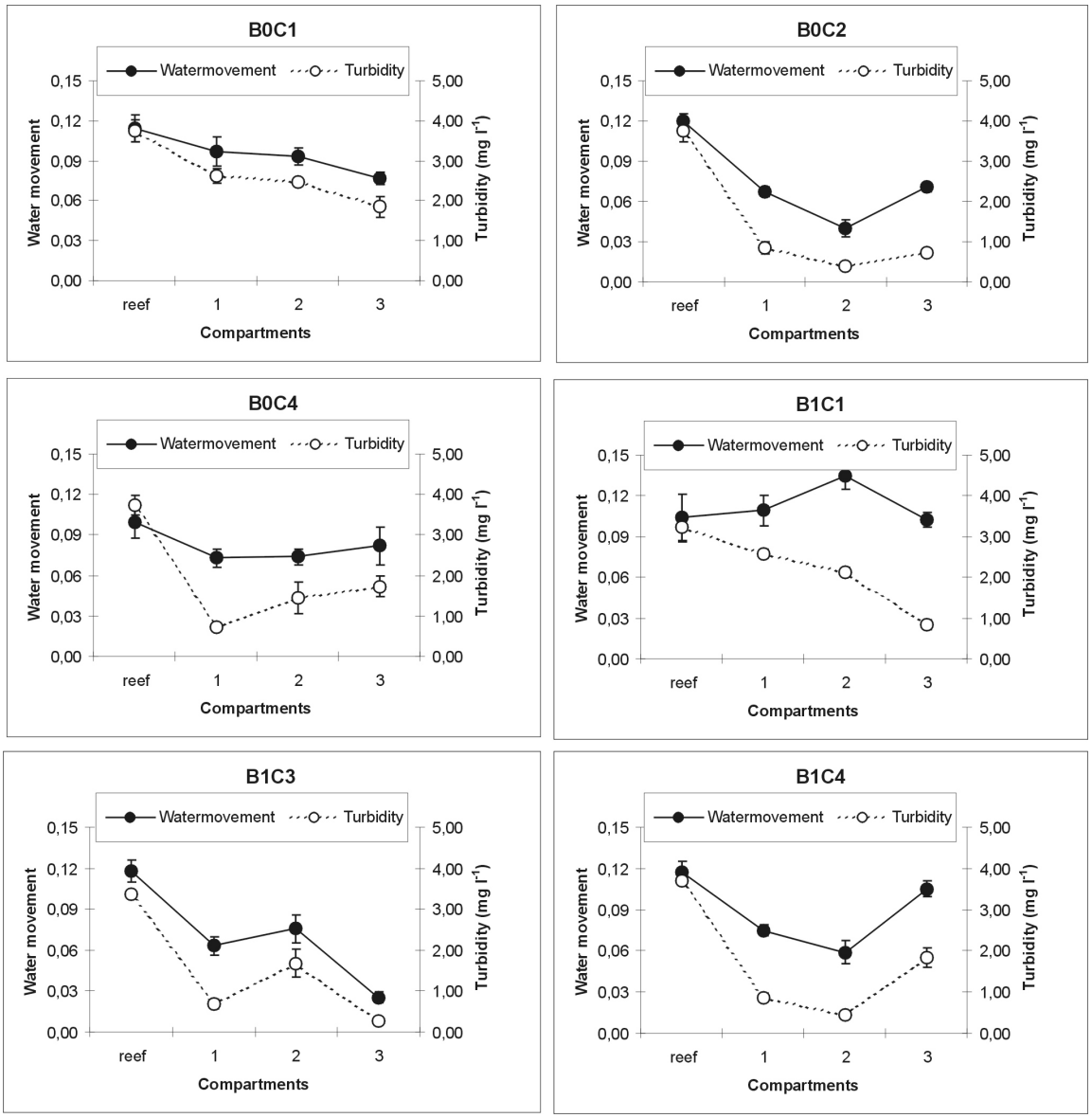

Figure 3. Panels show water movement and turbidity levels within and outside the 8 cavities and for the 8 cavities combined. X-axes show the location, y-axes show water movement and turbidity level

movement was highest outside on the open reef, decreasing inside the cavity, becoming extremely variable towards the back compartment (Fig. 3). Water movement is not significantly correlated to aspect ratio.

Turbidity

In general, turbidity was higher on the reef (3.5 mg l^{-1}) and decreasing towards the back of the cavities (1.3 mg l^{-1}). Turbidity patterns were highly variable and different between cavities (Fig 3). Water movement and turbidity were positively correlated (One-sample t-test; $R = 0.73$, $p < 0.01$) (Fig 8a).

Light Intensity

Light intensity was highest on the reef, lower inside and rapidly decreasing towards the back of the cavity. Variation in light intensity between cavities was high (Fig. 4, note logarithmic scale ordinate). Compared with extinction coefficients measured in the reef water column the light intensity in the back of a cavity is equivalent to the light intensity at a depth of 90 m.

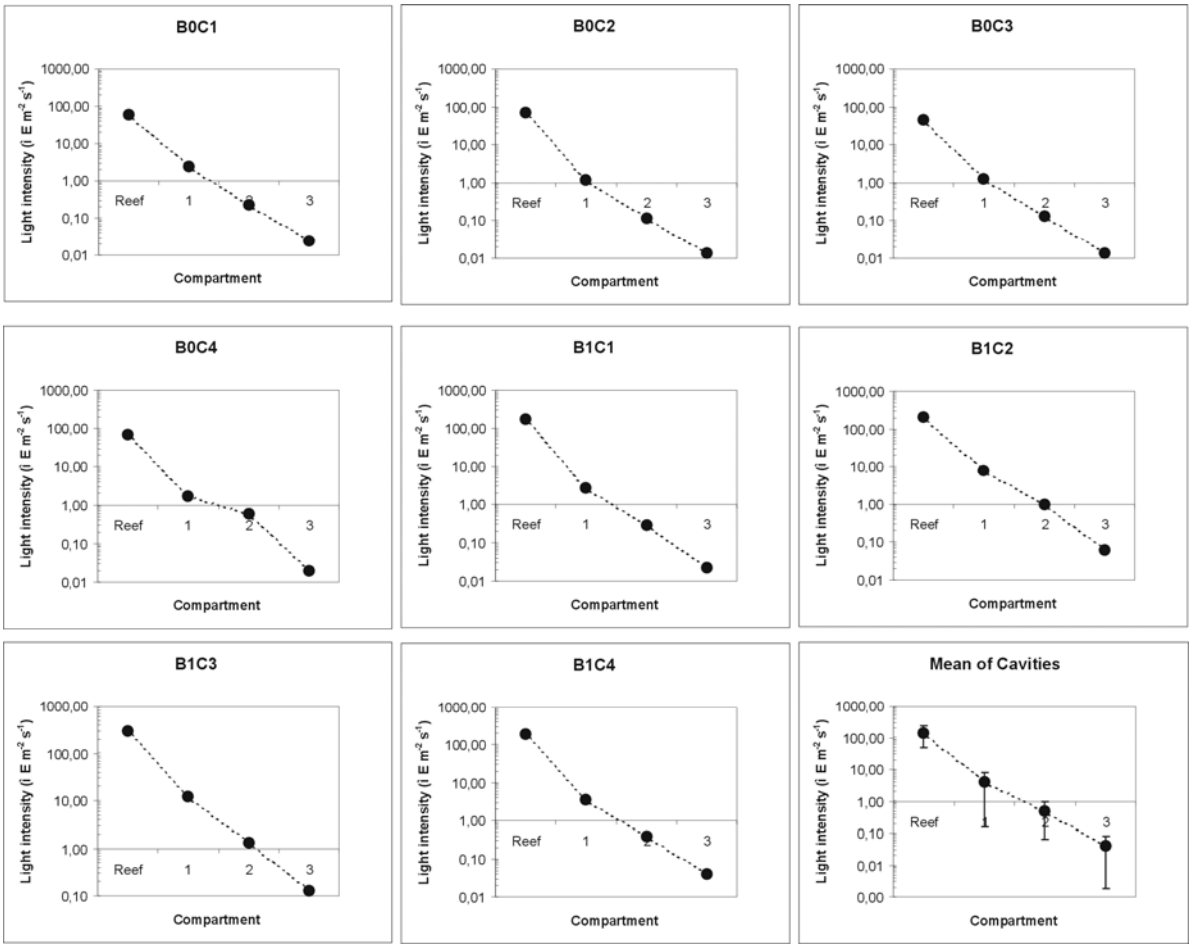

Figure 4. Panels show light intensity levels within and outside the 8 cavities and for the 8 cavities combined. X-axes show the location, y-axes show light intensity level (note logarithmic scale)

Year-round Bacterial Abundance in Cavity Water and Reef Water

Reef water bacterioplankton abundance varied highly between sampling sites (cavities) and throughout the year (not shown). Bacterial abundance was significantly (two-sample t-test, $t = -5.4$, $p < 0.0001$) lower in cavity water than in reef water. Throughout the year, the average depletion of bacterioplankton in cavity water was 40% (for all cavities at B0 and B1 monthly compiled, Fig. 5).

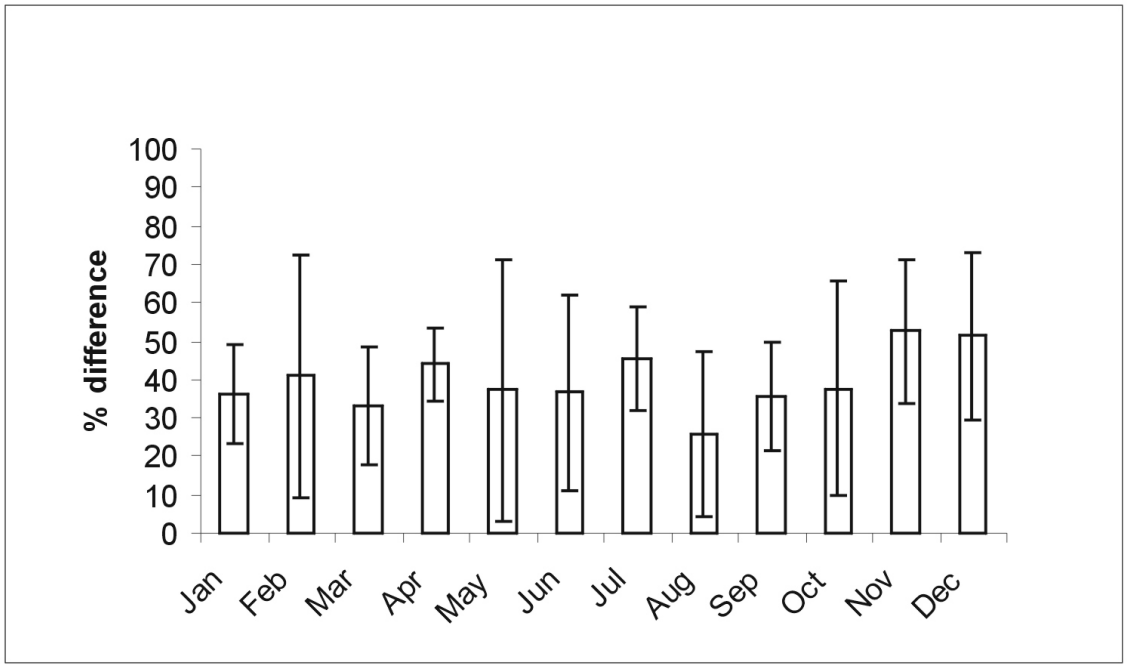

Figure 5. Bacterioplankton concentration in reef and cavity water (1 year time interval, 8 paired sampling points month-1) Y-axis shows cavity water bacterioplankton concentration as percentage of reef water bacterioplankton concentration

Cryptofauna Cover, Composition and Distribution

In the whole data set a total of 88 different species were counted representing 11 different groups (Table 2). The most numerous were the demosponges (44 species), followed by the ascidians (21 species), calcareous and sclerosponges (together 6 species), polychaetes (5 species), algae (3 species), bryozoans (2 species), anthozoa (2), hydroids (2 species), corals (1 species), bivalves (1), and foraminiferans (1). Over all cavities the mean cover of sponges was the highest (0.37 m^2 /m^2 HSA), followed by algal cover (0.27 m^2 /m^2 HSA, and ascidian cover (0.27 m^2 /m^2 HSA). Sponge cover was highest in the back of the compartments, algal cover decreased from the front of cavities to the back, and ascidian cover remained the same throughout all compartments (Fig. 6). The 5 taxa with the highest mean cover were: Crustose Coralline Algae (2720 cm^2 /m^2 HSA), Unidentified Bryozoan 1 (711 cm^2 /m^2 HSA), *Desmanthus incrustans* (573 cm^2 /m^2 HSA), *Trididemnum spec* (544 cm^2 /m^2 HSA) and *Leucetta spec* (442 cm^2 /m^2 HSA).

Table 2. Species encountered in the 8 framework cavities, presented in phylogenetic order.

Algae	**Ascidia**	**Demospongiae**
Crustose Coralline Algae	*Clavelina spec.*	*Anthosigmella varians*
Galaxaura spec	*Didemnum spec 1*	*Batzella spec*
Rhodophyta spec	*Didemnum spec 2*	*Ceratopsion spec.*
	Didemnum spec 3	*Chelonaplysilla batimensis*
Bivalva	*Distaplia spec 1*	*Chondrilla nucula*
Lithophaga sp.	*Distaplia spec 2*	*Clathria (Colloclathria) spec*
	Polyandrocarpa spec	*Clathria (Microciona) bulbotoxa*
Bryozoa	*Symplegma spec. 1*	*Clathria (Microciona) microchela*
Unidentified Bryozoan 1	*Symplegma spec. 2*	*Clathria (Thalysias) raraechelae*
Unidentified Bryozoan 2	*Symplegma spec. 3*	*Cliona delitrix*
	Symplegma spec. 4	*Cliona janitrix*
Scleractinia	*Trididemnum spec.*	*Desmanthus incrustans*
Colangia simplex	*Unidentified Ascidian 1*	*Desmapsamma anchorata*
	Unidentified Ascidian 2	*Diplastrella megastellata*
Calcarea	*Unidentified Ascidian 3*	*Dragmaxia undata*
Clathrina canariensis	*Unidentified Ascidian 4*	*Dysidea spec.*
Clathrina primordialis	*Unidentified Ascidian 5*	*Ectyoplasia ferox*
Clathrina spec	*Unidentified Ascidian 6*	*Haliclona amphioxa*
Leucetta aff. floridana	*Unidentified Ascidian 7*	*Halisarca caerulae*
Leucetta sp.	*Unidentified Ascidian 8*	*Halisarca spec*
Leucilla uter	*Unidentified Ascidian 9*	*Hymeniacidon spec.*
		Iotrochota birotulata
Foraminifera	**Polychaetae**	*Ircinia felix*
Spiculodendron corallicolum	*Filograna spec*	*Merlia normani* (Sclerosponge)
	Phoronidae	*Monanchora arbuscula*
Hydrozoa	*Unidentified Polychaete 1*	*Mycale laevis*
Unidentified Hydrozoan 1	*Unidentified Polychaete 2*	*Mycale laxissima*
Unidentified Hydrozoan 2	*Unidentified Polychaete 3*	*Myrmekioderma sp. 1*
		Myrmekioderma sp. 2
	Anthozoa	*Niphates amorpha*
	Cirripathes spec	*Niphates digitalis*
	Palythoa caribaeorum	*Niphates erecta*
		Phorbas amaranthus
		Placospongia sp. 1
		Placospongia sp. 2
		Pseudosuberites spec
		Scopalina ruetzleri
		Siphonodictyon coralliphagum
		Spirastrella coccinea
		Spirastrella spec.
		Terpios belindae
		Timea spec.
		Unidentified Sponge 1
		Unidentified Sponge 2

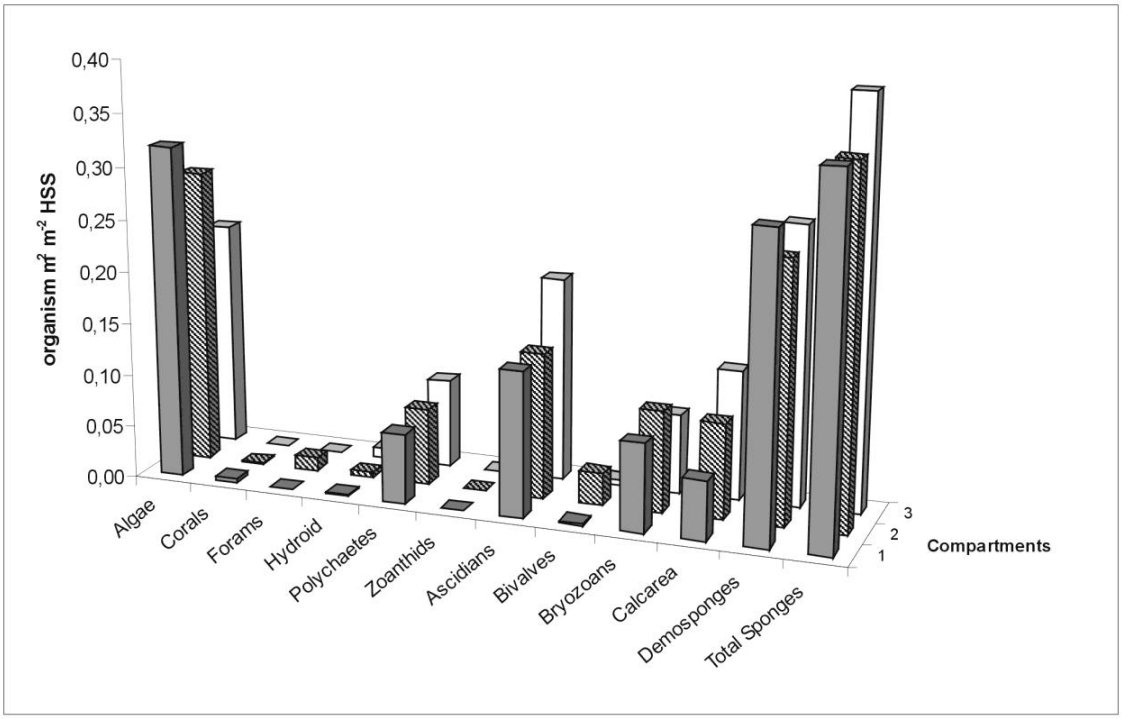

Figure 6. Distribution of average cover of groups of organisms over cavity compartments. X-axes shows groups, y-axes shows compartments (compartment 1 = front part cavity, compartment 2 = middle of cavity, compartment 3 = back of cavity), z-axes shows the cover of groups

Table 3. Significance levels of differences in species richness, species cover and cover per individual between compartments and cavities (one-way Anova's).

Parameter	Cavity	Compartment
Species richness	$R = 0.808$, $p < 0.007$	$R = 0.216$, $p < 0.605$
Species cover	$R = 0.763$, $p < 0.026$	$R = 0.223$, $p < 0.584$
Cover per individual	$R = 0.767$, $p < 0.023$	$R = 0.331$, $p < 0.295$

Table 4. Species diversity and evenness for all organisms (Diversity calculated with Shannon-Weiner diversity index and proportional cover)

Cavity	H' comp 1	H' comp 2	H' comp 3	H' cavity	Evenness comp 1	Evenness comp 2	Evenness comp 3	Evenness cavity
B0C1	2.16	2.01	1.99	2.36	0.24	0.22	0.22	0.23
B0C2	2.35	2.54	2.37	2.72	0.26	0.27	0.26	0.26
B0C3	230	2.28	2.27	2.76	0.25	0.25	0.25	0.27
B0C4	2.47	2.39	2.37	2.65	0.27	0.26	0.26	0.26
B1C1	2.18	1.99	1.99	2.31	0.24	0.22	0.22	0.22
B1C2	1.84	2.22	2.05	2.42	0.20	0.19	0.22	0.21
B1C3	1.80	2.15	2.12	2.43	0.20	0.23	0.23	0.24
B1C4	2.39	2.52	2.41	2.96	0.26	0.27	0.26	0.29

Table 5. Species diversity and evenness for sponges (Diversity calculated with Shannon-Weiner diversity index and proportional cover)

Cavity	H' comp 1	H' comp 2	H' comp 3	H' cavity	Evenness comp 1	Evenness comp 2	Evenness comp 3	Evenness cavity
B0C1	1.87	1.66	1.34	2.29	0.24	0.22	0.17	0.26
B0C2	1.97	2.42	2.06	2.48	0.24	0.29	0.24	0.26
B0C3	1.82	1.69	1.89	2.36	0.22	0.20	0.24	0.25
B0C4	2.03	2.12	2.05	2.50	0.24	0.26	0.25	0.27
B1C1	1.89	1.66	1.34	2.16	0.24	0.22	0.17	0.24
B1C2	1.34	1.03	0.76	1.56	0.18	0.10	0.09	0.15
B1C3	0.81	1.27	1.40	1.78	0.10	0.15	0.16	0.19
B1C4	1.69	1.72	1.40	2.31	0.21	0.20	0.18	0.25

Table 6. Significance levels of total species diversity, species diversity sponges, total evenness, and evenness sponges between compartments (one-sample t-test).

Parameter	Compartment
Total species diversity	$t = -0.218$, $p < 0.834$
Species diversity sponges	$t = -0.701$, $p < 0.506$
Total species evenness	$t = 0.000$, $p < 1.000$
Evenness sponges	$t = -0.656$, $p < 0.533$

The hard substratum area of cavities showed over 95% biotic coverage. Species richness, total biotic cover and cover per individual organism was significantly different between the 8 cavities. Within the cavities species richness, total biotic cover and cover per individual organism was not significantly different between the three different compartments (Table 3). Species richness did not significantly increase with increasing available hard substratum area.

All cavities and compartments showed a high variability in species diversity (ranging from 1.80 – 2.96) and evenness (ranging from 0.19 –0.29) (Table 4). Sponge species diversity and evenness followed the same pattern (Table 5), with diversity ranging from 0.81- 2.50 and evenness ranging from 0.10- 0.29.

Species diversity and evenness, for all species grouped and sponges as a group, was not significantly different between compartments (Table 6).

Rank-abundance graphs (Fig. 7) visualize the homogeneity in evenness between compartments and cavities, and the heterogeneity in species richness between cavities. Biodiversity in the cavities was high, but evenness relatively low. Potential species richness (x- intercept in Fig. 7) is much higher than the measured species richness.

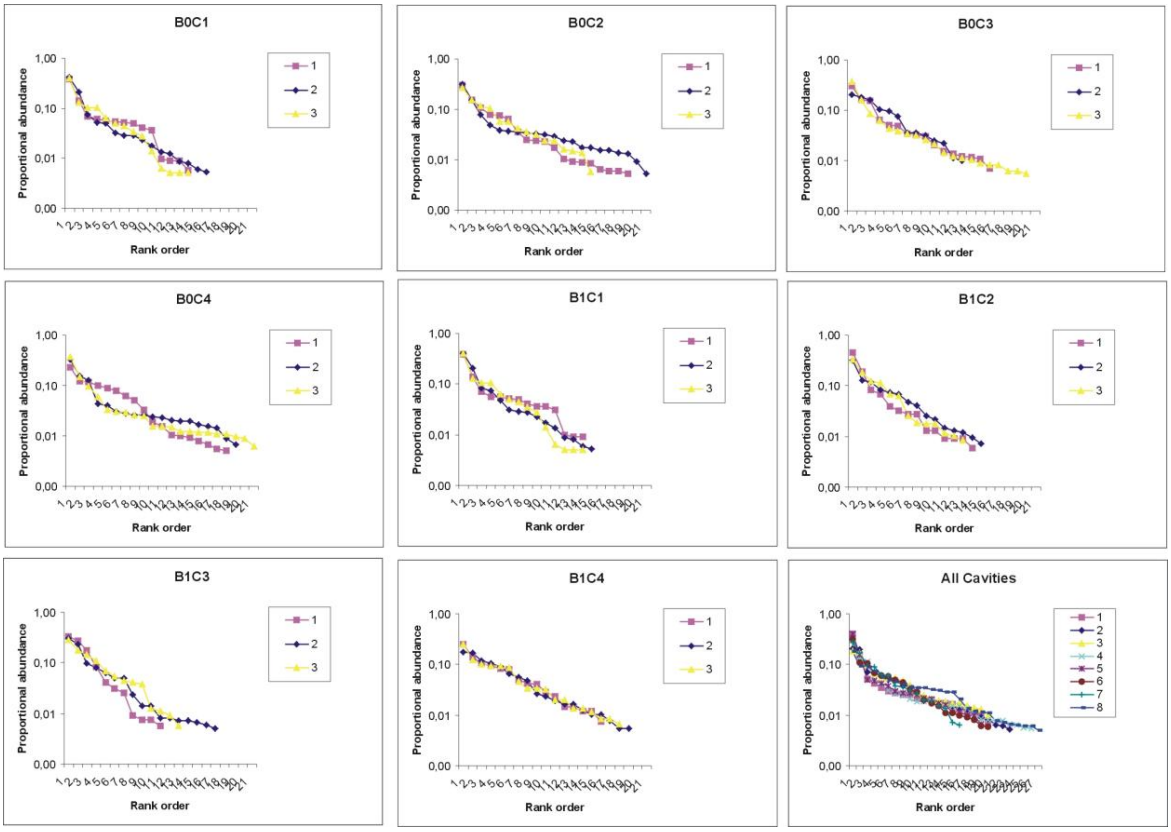

Figure 7. Rank-abundance graphs for each cavity separate and for all cavities combined (for taxa see Table 2). X-axes shows rank order of species, y-axes shows proportional abundance of species. The slope is related to evenness (steep slope- low evenness), x- intercept is potential richness

Hierarchical cluster graphs show no pattern when species are clustered with compartments (Fig. 8a), or with horizontal distance in the cavity, cave opening to back wall (Fig. 8b). Cluster graphs show no discernable pattern when species are clustered with light intensity (Fig. 8d), save for crustose coralline algae (CCA), which are present at all light levels. A weak pattern is visible when species are clustered with water movement (Fig. 8e), where a small group of sponges (*Mycale laxissima, Mycale laevis, Monanchora arbuscula, Halisarca caerulae,* and *Anthosigmella varians*), and the ascidian *Didemnum spec2* are clustered together in a group preferring moderate water movement. The same pattern is visible in the cluster graphs when species are clustered with turbidity (Fig. 8c). The group of sponges (*Mycale laxissima, Mycale laevis, Monanchora arbuscula, Halisarca caerulae,* and *Anthosigmella varians*) and the ascidian *Didemnum spec2* are clustered within the group with intermediate turbidity levels.

To look for possible patterns in habitat preference we grouped sponges (cover of all demosponges and calcareous/ sclerosponges) and suspension feeders (all cryptic organisms minus algae) and plotted these groups against the various a-biotic factors (Fig. 9). Total sponge cover plotted against water movement showed a significant (linear regression; $R = 0.78$, $p < 0.05$) decrease in sponge cover with increasing water movement (Fig 9b). Water movement outside the cavity is indicated with an arrow (Fig. 9b) and indicates the adverse water movement conditions for cryptic sponges. The same pattern

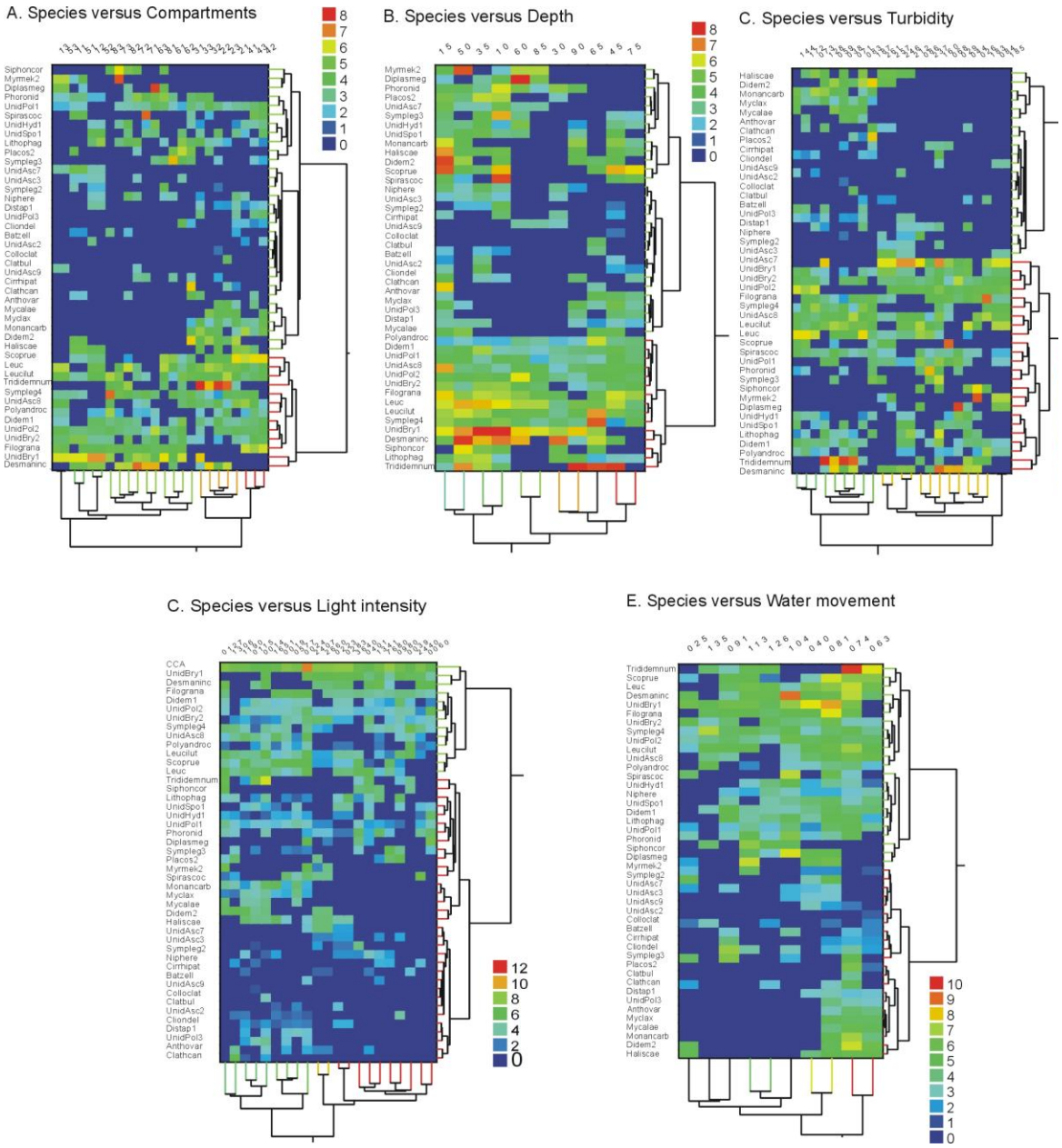

Figure 8. Hierarchical cluster analyses graphs, with complete linkage and Euclidean distance, based upon a Bray-Curtis transformed matrix. (A). X-axes show all cavity compartments. First number indicates the cavity (1-8), second number indicates the compartment (1-3). (B). X-axes show horizontal depth (cm, front to back) inside the cavity. (C). X-axes show turbidity level (in mg l-1). (D). X-axes show light intensity (µE m-2 s-1). (E). X-axes show water movement. All Y-axes show abbreviation of species name (Anthova = Anthosigmella varians, Batzell = Batzella spec, Cirrhipat = Cirrhipates spec, Clatbul = Clathria (Microciona) bulbotoxa, Clathcan = Clathrina canariensis, Cliondel = Cliona delitrix, Colloclat = Clathria (Colloclathria) spe, Desmaninc = Desmanthes incrustans, Didem1 = Didemnum spec1, Didem2 = Didemnum spec2, Diplasmeg = Diplastrella megastellata, Distap1 = Distaplia spec1, Filograna = Filograna spec, Haliscae = Halisarca caerulae, Leuc = Leucetta sp , Leucilut = Leucilla uter Polejaeff , Lithophag = Lithophaga spec, Monancarb = Monanchora arbuscula , Mycalae = Mycale laevis, Myclax = Mycale laxissima, Myrmek2 = Myrmekioderma spec2, Niphere = Niphates erecta, Phoronid = Phoronidae, Placos2 = Placospongia spec2, Polyandroc = Polyandrocarpa spec, Scoprue = Scopalina ruetzlerii, Siphoncor = Siphonodictyon coralliphagum Spirascoc = Spirastrella coccinea , Sympleg2 = Symplegma spec2, Sympleg3= Symplegma

spec3, Sympleg4 = Symplegma spec4. Tridemnum = Tridemnum spec, UnidAsc2 = Unidentified Ascidian2, UnidAsc3 = Unidentified Ascidian3, UnidAsc7 = Unidentified
Ascidian7, UnidAsc8 = Unidentified Ascidian8, UnidAsc9 = Unidentified Ascidian9, UnidBry1 = Unidentified Bryozoan1, UnidBry2 = Unidentified Bryozoan2, UnidHyd1 = Unidentified Hydrozoan1, UnidPol1 = Unidentified Polychaete1, UnidPol2 = Unidentified Polychaete2, UnidPol3 = Unidentified Polychaete3, UnidSpo1 = Unidentified Sponge1).
The color display shows the original data matrix in which rows and columns are permuted according to an algorithm in Gruvaeus and Wainer (1972). Different colors represent the magnitude / strength (0 - 12) of the linkage between cases (species) and variables (a-biotic factors) in the matrix (Ling, 1973).

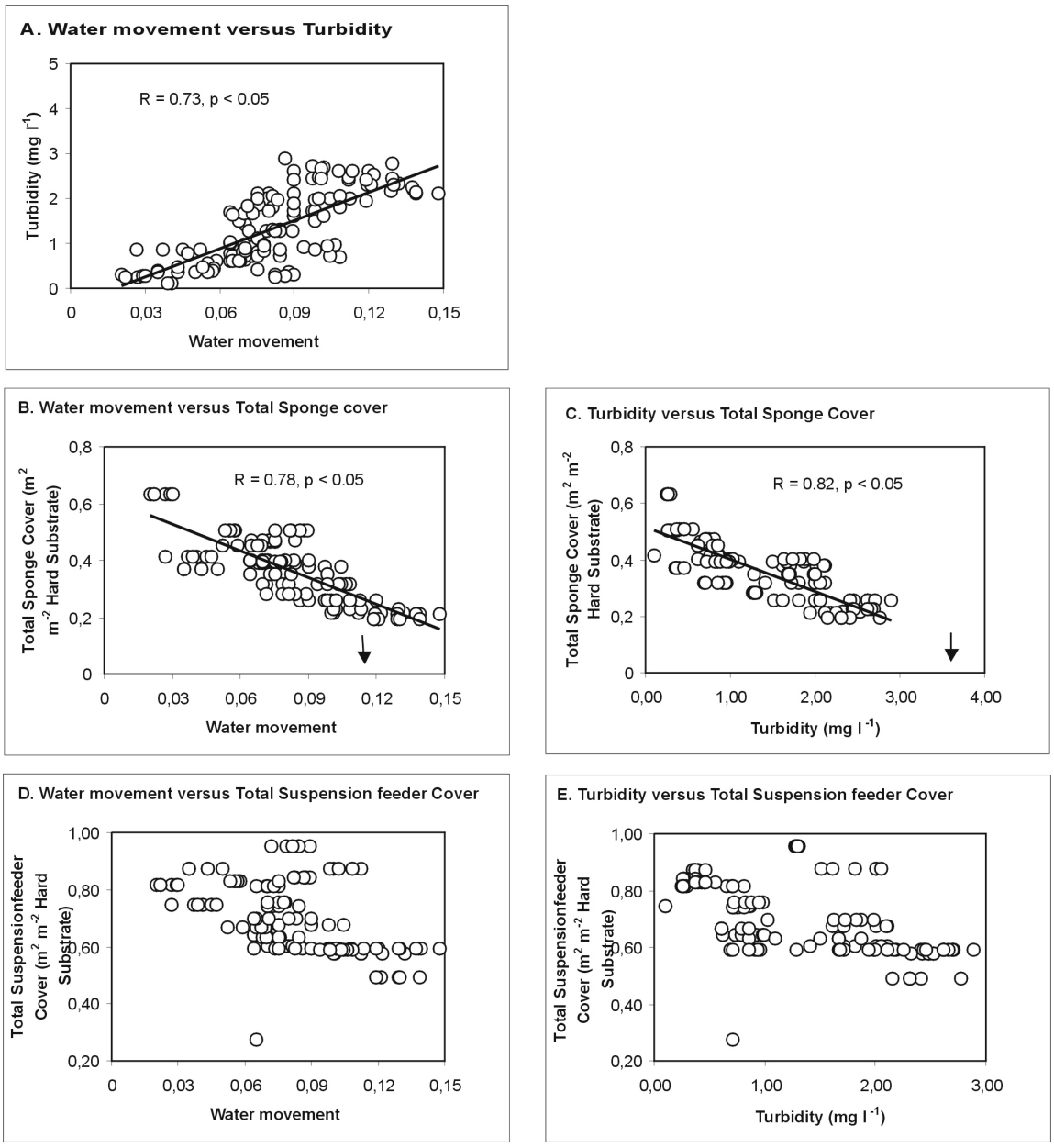

Figure 9. Relationships between water movement, turbidity, total sponge cover and suspension feeder cover. Lines are linear regression fits. Turbidity in mg l-1, water movement is given in erosion.

is discernable when plotting total sponge cover against turbidity; there is a significant (linear regression; $R = 0.82$, $p < 0.05$) decrease in total sponge cover with increasing turbidity (Fig 9c). Turbidity outside the cavity is indicated with an arrow (Fig 9b) and indicates possibly adverse turbidity conditions for cryptic sponges. Total suspension feeder cover shows a possible, though not significant, decrease with increasing water movement and turbidity (Fig. 9d and 9e). All other taxa or groups of organisms tested against the various a-biotic factors such as turbidity, water movement, light intensity, horizontal depth inside the cavity, and aspect ratio, did not display any (significant) trends.

DISCUSSION

Community Composition and Diversity

Our results show that the "inside", invisible surface area of the coral reef framework (comprised of cavities) exceeds the projected bottom surface of the 'visible' reef up to eight times. Richter et al. (2001) present a comparable area increase for cavity surface, a factor 2.5- 7, for the Red Sea. The hard substrata in framework cavities are covered for more than 95% by suspension feeders and algae: these specific organisms are scarcely encountered on the visible outside of the reef. This indicates the importance of this cryptic habitat for total reef community composition; even more so because the cryptofauna cover we measured is an underestimate of the real cover. Many organisms are overgrowing other organisms (understory species) or protruding from (e.g. polychaetes) the tissue of other organisms, forming a multilayered community. Such phenomena are not measured with our methods. Nevertheless our study shows a high density and diversity of organisms to exist in cryptic communities in coral reef framework cavities. Total species richness was comparable to Choi and Ginsburg (1983) who found 80 different species beneath coral rubble in Florida sand channels. Corriero et al. (2000) found much lower species richness in Mediterranean caves, but richness inside was much higher than outside caves. Wunsch et al. (2000) found in the Gulf of Aqaba much higher species richness compared to our Curaçao data set, probably due to much larger size of the cavities they studied. Our study was focussed on cavities around 15 meters water depth at one reef, the B0 /B1 Carmabi study reef, therefore we encountered far fewer sponge species than Kobluk and van Soest (1989), who sampled the whole reef slope and a series of stations around Bonaire and Curaçao.

Our study is the first to present diversity data for reef framework cavities, and we found species diversity in the cavities to be relatively high. Diversity was high (Shannon-Wiener, $H' \sim 2.6$), yet evenness is low, indicating the presence of dominant species. Gischler and Ginsburg (1996) found low biodiversity values and high evenness (0.57, 0.72 respectively.) for cryptic rubble habitats in Belizean reefs. Meesters et al. (1991) found a slightly lower diversity (1.73), yet a higher evenness in cryptic rubble habitats around Bonaire and Curaçao. This pattern also holds for sponge diversity *per se*. Barnes and Bell (2002) found low sponge diversity (1.7- 2.2) and high evenness in caves of the West Indian Ocean (Mozambique). In comparison, Alcolado (1994) presented sponge

diversity of 3.5 at 20 meters depth and declining to 0 at 2 meters depth on the reefs of Cuba, indicating that in terms of biodiversity cavities are at least as important as the open coral reef.

Cryptofauna diversity in the studies of Gischler and Ginsburg (1996) and Meesters et al. (1991) seems to be related to rubble size, i.e. space. Since space is a limiting factor in marine hard substratum environments, monopolization by just a few superior competitors can only be avoided when free space become available at regular intervals (Connell 1976, Loya 1976). We did not find a significant relationship between diversity and substratum area and more than 95% of available substratum was covered with organisms. There are no data to suggest either the "intermediate disturbance" (Connell 1976, 1978) or "competitive networks" (Buss and Jackson 1979) as being the main structuring force in the cavity community. In the open reef, intermediate disturbance often reduces dominant species proportionally 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 (Connell 1976, 1978, Loya 1979). Disturbance such as predation may act to make new space available on substrates (Wulff 1997), but we never encountered signs of damage to cryptofauna tissue. Physical disturbance caused by wave action is less likely to play a role creating free space in framework cavities than it is with rubble, although infrequently severe storms, and resulting high waves, may collapse cavities at depths of 10-15-meters. The competitive networks theory suggests a dynamic process in which species are constantly trying to obtain more space in competition with neighbouring species, but competitive abilities are non-hierarchical. Such a process is more likely to occur than a steady state with species, once settled, staying constantly in the original area of settlement. It is interesting to note that cryptofauna removes high amounts of bacterioplankton (Scheffers et al. 2004) and DOM (de Goeij et al. 2008a,b) from the reef water column. This is suggested to flow into the large energy demands of reproduction and organism maintenance cryptic species (de Goeij et al. 2009). Remaining energy should be available for spatial competition in these crowded reef habitats.

That cryptofauna removes high amounts of bacteria from the reef water is reflected in the continuous difference (year-round) in bacterioplankton abundance between cavity water and reef water. This difference in bacterial densities (on average 40% of reef water bacteria disappears from the water column) suggests that cavities in general generate a strong bacterioplankton influx (see Scheffers et al. 2004) and therefore should be considered as an important sink for carbon. Gradients were highly variable between cavities, which may be caused by variations in uptake rates of individual cryptofauna. Kötter and Pernthaler. (2002), found indeed strong differences in uptake rates between several sponge species. Changes in the difference between cavity and reef water bacteria concentrations over the year suggest that variation in water exchange (dependent on the bulk flow passing the reef) plays a role.

Determining Parameters for Cryptofauna Distribution

We distinguished three compartments, front, middle and back part, in our experimental cavities as possibly representing different physical cavity conditions. We measured light intensity, water movement and turbidity in each compartments. Irradiance

has been mentioned as an important factor affecting biotic distribution in cryptic habitats elsewhere (Jaubert and Vasseur 1974, Vasseur 1974, 1977). In Curaçao the concentration of crustose coralline algae around the entrances of cavities, or in areas where inclined chimneys allow light to penetrate the cavities, shows the importance of light for the distribution of CCA's. Organisms with phototrophic symbionts may also prefer a well-lit habitat. On the other hand members of the sponge community may actually avoid light (Wilkinson and Vacelet 1979) or be adversely affected by UV radiation (Jokiel 1980). We did not find any relationship between light intensity and cryptofauna, neither on species level (Fig 8d), nor on the level of groups of taxa. As light and UV-radiation levels co-vary with other environmental parameters, irradiance effects may be confused with water movement, turbidity, abrasion, predation, or algal competition (Jokiel 1980). Distance from cave opening into the cavities was not significantly related with light intensity. This is reflects the fact that our cavities are not closed entities with light only penetrating from the frontal opening and diminishing with distance. This also explains the high variance in light intensities between cavities.

Water movement and turbidity inside cavities were positively correlated (Fig. 9a) and possibly related to cavity structure (rugosity and number of chimneys) or sediment resuspension. Both were highly variable between cavities and compartments and not dependent on depth inside the cavity. All the cryptofauna are filter or suspension-feeders and are dependent upon water flushing their habitat and supplying them with food. High water-exchange rates between the cavity and the overlying reef water have been reported elsewhere for our experimental cavities (Van Duyl et al. 2005). Flushing (water exchange with the overlying reef water) of cavities is positively correlated to cryptofauna cover (Wilkinson and Vacelet 1979, Gischler 1997, Richter et al. 2001) and to particle removal by cryptic organisms (van Duyl et al. 2005). Water exchange and water movement in cavities are not necessarily correlated. Exchange rates appear to be dependent on aspect ratio (van Duyl et al. 2005), while water movement seems to be dependent on inner cavity parameters such as rugosity, and connectivity to other cavities. When water exchange is beneficial, water movement can be detrimental to cryptofauna growth, especially since it is correlated to turbidity. Too much water movement can damage the fragile tissue of cryptic sponges (Bell and Barnes 2000) and too much sediment in the water column can reduce pumping rates (Reiswig 1971, Gerrodet and Flechsig 1979, Fagerstrom 1984). This sensitivity is probably a control on the distribution of sponges in general and without doubt has an effect on sponges in cryptic habitats (Kobluk and van Soest 1988). On species level we did find a correlation between some species and moderate water flow and turbidity. On group level we found a strong significant relationship between decreasing sponge cover and increasing water movement/ turbidity. The same trend, although weaker, is visible when all suspension feeders are grouped. A possible explanation for such a correlation is that capture mechanisms of some specific suspension feeders are less susceptible to sediment loading than others. Both water movement and turbidity are higher outside on the reef, which suggests that for cryptic organisms the framework habitat is a refuge from the relative strong water movement and high turbidity occurring in the open coral reef environment.

We conclude that each framework cavity has a unique set of environmental parameters (light levels, water movement, and turbidity), which is related to variation in the inner cavity structure. The cryptofaunal community composition is very diverse and

different between cavities and parts of cavities. Community composition did not reflect variation in distribution of environmental parameters, suggesting factors such as chance of settlement and predation, intermediate disturbances and active competitive networks to be important.

That all experimental cavities removed more or less equal amounts of bacterioplankton and that all excrete inorganic nitrogen (Scheffers et al. 2004, 2005, van Duyl et al. 2005) shows them to be functionally uniform despite the biological and structural differences.

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