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Coral cavities are sinks of dissolved organic carbon (DOC)

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Abstract

We studied the removal of dissolved organic carbon (DOC) by coral cavities of 50–250 dm^3 at a depth range of 5–17 m along the coral reefs of Curaçao, Netherlands Antilles, and the Berau area, East Kalimantan, Indonesia. We found significantly lower DOC concentrations in cavity water compared with ambient reef water. On average, DOC concentrations in cavity water were 15.1 ± 6.0 μmol L^{-1} (Curaçao) and 4.0 ± 2.4 μmol L^{-1} (Berau) lower than in reef water. When the cavities were closed, DOC concentrations in the cavities declined by 22% ± 8% and 11% ± 4% in Curaçao and Berau, respectively, within 30 min. This corresponded to average DOC removal rates per cavity surface area of 342 ± 82 mmol C m^{-2} d^{-1} in Curaçao and 90 ± 45 mmol C m^{-2} d^{-1} in Berau. Bioassays showed that bacterioplankton are not responsible for this DOC removal by coral cavities. DOC fluxes exceeded bacterioplankton carbon (BC) fluxes into cavities by two orders of magnitude. On average BC fluxes per cavity surface area were 3.6 ± 1.3 mmol C m^{-2} d^{-1} (Curaçao) and 1.9 ± 1.3 mmol C m^{-2} d^{-1} (Berau area). The net DOC removal per square meter of cryptic surface likely exceeded the gross primary production per square meter of planar reef area. We conclude that coral cavities and their biota are net sinks of DOC and play an important role in the energy budget of coral reefs.

Coral cavities are among the largest and least-known habitats in coral reef environments. Their total volume comprises up to two-thirds of the reef volume (Garret et al. 1971; Ginsburg 1983) and their inner surface represents 60–75% of the total available surface of the reef (e.g., Jackson et al. 1971; Logan et al. 1984; Scheffers 2005). Yet, hardly anything is known about the ecological role of this cryptic habitat in the carbon cycling on the reef.

The relatively sheltered cryptic habitat is inhabited by a high abundance of different organisms, called cavity dwellers or coelobites (Ginsburg and Schroeder 1973). The biomass of this cryptofaunal community might exceed that of the reef surface (Hutchings 1974; Brock and Brock 1977; Meesters et al. 1991) and the encrusting biota can cover more than 93% of the available hard substrate (Richter and Wunsch 1999; Richter et al. 2001; Scheffers 2005). As a consequence, the competition for space is high in coral cavities (Jackson et al. 1971; Buss 1979; Buss and Jackson 1979). Heterotrophic organisms generally dominate the coelobite community because of low light conditions in the cavities. Two-thirds of the cavity walls are inhabited by suspension feeders (sponges, tunicates, bryozoans, bivalves, and polychaetes), with sponges usually dominating this group. Approximately one-third of the cavity walls consists of calcareous algae (e.g., Vasseur 1974; Gili and Coma 1998; Wunsch et al. 2002).

The large area of the cryptic habitat and the high cover of encrusting organisms provide a potentially important interface in the exchange of material between the cavities and the overlying water column. Several studies have shown a depletion of phyto-, nano-, pico-, and bacterioplankton in waters overlying coral reefs (e.g., Ayukai 1995; Yahel et al. 1998; Van Duyl et al. 2002). Gast et al. (1998) were the first to describe bacterioplankton depletion and accumulation of inorganic nutrients in coral crevices of Curaçao compared with overlying reef water. On the reefs along Curaçao, bacterial abundance was usually lower inside cavities than outside and the inorganic nutrient concentrations often differed from that in overlying water. Scheffers et al. (2004) and Van Duyl et al. (2006) reported bacterial removal rates by coral cavities of Curaçao of, on average, 3 mmol C m^{-2} d^{-1}. A net influx of chlorophyll *a* was found in framework cavities in the Red Sea at an estimated phytoplankton removal rate in cavities of 75 mmol C m^{-2} d^{-1} (Richter et al. 2001).

Phytoplankton and bacterioplankton make up the major part of particulate organic matter (POM; *see* Table 1 for

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Table 1. List of abbreviations used (listed in alphabetical order).

Abbreviations	
BA	bacterial abundance
BC	bacterioplankton carbon
CW	cavity water
DOC	dissolved organic carbon
DOM	dissolved organic matter
PC	phytoplankton carbon
POC	particulate organic carbon
POM	particulate organic matter
RW	reef water
TOC	total organic carbon
TSA	total cavity surface area

a list of abbreviations) in the oligotrophic reef waters. However, by far the largest component (>97%) of organic matter is dissolved organic matter (DOM) (Benner 2002), which, in turn, is the largest carbon standing stock in the oceans (Martin and Fitzwater 1992). This fraction is operationally defined as the organic carbon passing through a fine filter, typically GF/F (Benner 2002; Carlson 2002). Dissolved organic carbon (DOC) is composed of a small labile and a much larger refractory fraction, which is not readily available to bacteria (Carlson 2002). DOC levels are usually enhanced over coral reefs and in lagoons compared to ocean surface waters (e.g., Johannes 1967; Ducklow 1990; Torréton et al. 1997), indicating that in reef waters, the production of DOC exceeds its loss (Van Duyl and Gast 2001). Sources of DOC in coral reefs are, for example, the release of DOC by benthic algae as a function of photosynthesis (Mague et al. 1980; Zlotnik and Dubinsky 1989), and release of DOC by corals through mucus production (Johannes 1967; Richman et al. 1975) or as free amino acids (Schlichter and Liebezeit 1991). The main consumers of DOC are heterotrophic bacteria (Fenchel 1988) mediating the flux of DOC through the microbial loop (Azam et al. 1983).

However, DOC may also be a potential food source for marine benthic invertebrates, as has been suggested already since the end of the nineteenth century (reviewed by Jørgensen 1976). Reiswig (1981) found a discrepancy between the supply and demand of carbon in benthic suspension feeders. However, although DOC has been suggested as the missing carbon (Reiswig 1981; Gili and Coma 1998), not much is known on the uptake of DOC by the benthic community. Yahel et al. (2003) were the first to show extensive feeding on bulk DOC by the sponge *Theonella swinhoei*. Although the potential importance of DOC in the carbon budgets of coral cavities and for the cryptofauna has been discussed (Richter et al. 2001; Yahel et al. 2003; Van Duyl et al. 2006), DOC removal by the cryptofauna has not been determined.

Our main question in this study is: are coral reef cavities net sinks of DOC? If so, is DOC quantitatively an important food source for cryptic coral reef habitats? To answer these questions, we carried out a series of measurements and experiments. We compared the concentration of DOC and bacterial abundance (BA) between cavity water and overlying reef water in 19 cavities on the fringing reefs of Curaçao and 21 cavities on different types of reefs in the Berau area, East Kalimantan, Indonesia. To determine DOC uptake rates, we closed cavities in both areas and followed the removal of DOC over time and compared that with the removal of bacterioplankton carbon (BC). We estimated fluxes of DOC and BC for the cryptic habitat. The biodegradability of DOC was determined in a series of bioassays with ambient reef-water bacterioplankton as key DOC consumers.

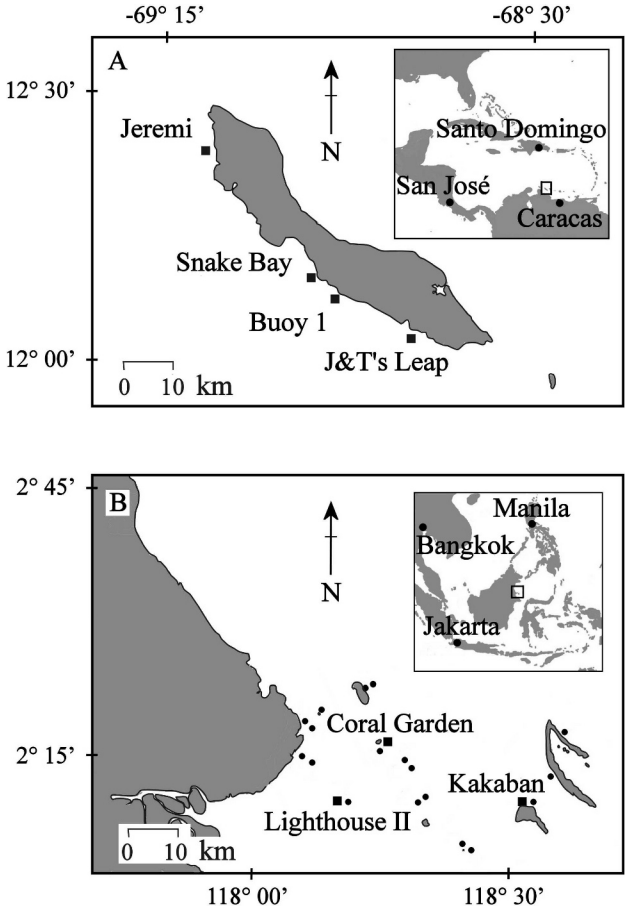

Fig. 1. (A) Map of Curaçao, locating four sites along the SW coast, with an inset of the location of Curaçao in the Caribbean Sea. (B) Map of Berau, East Kalimantan, Indonesia, with an inset of the location of Berau in Indonesia. The sampled area consists of 21 sites, of which three sites (Lighthouse II, Coral Garden, and Kakaban) were used in cavity closure experiments.

Materials and methods

Study area and sites—This study was conducted on Curaçao, Netherlands Antilles (12°12′N, 68°56′W), in the Caribbean (Fig. 1A) and in the Berau region along the east coast of Kalimantan, Indonesia (2°15′N, 118°15′E) (Fig. 1B). Most of the experimental work was performed at the fringing reefs along the leeward side of Curaçao. For station selection, the long-term mean current was taken into account running from SE to NW along the island.

Table 2. Volume, surface area, and in situ depth of seven coral cavities in Curaçao, Netherlands Antilles, and three coral cavities in Berau, East-Kalimantan, Indonesia.

Cavity	Depth (m)	Volume (dm^3)	Wall surface (m^2)	Floor surface (m^2)	Total surface (m^2)
Curaçao					
Buoy 1.1	15.2	111	1.0	0.7	1.7
Buoy 1.2*	15.0	250	1.7	0.8	2.4
Jeremi 1	16.8	175	1.3	1.0	2.3
Jeremi 2	16.3	86	0.5	0.8	1.3
Snake Bay 1	15.8	248	1.8	1.3	3.1
J&T's Leap 1	12.7	194	1.1	1.8	2.9
J&T's Leap 2	16.1	159	0.9	1.4	2.3
Berau					
Coral Garden	12.7	50			1.00
Lighthouse II	9.6	150			2.08
Kakaban	15.8	200			2.62

* Buoy 1.2 is an artificial cave.

Cavities (two per site) were selected at four sites: J&T's Leap, Buoy 1, Snake Bay, and Jeremi, along the SW coast of Curaçao (Fig. 1A; Table 2). Cavity Buoy 1.2 is an artificial cavity constructed with a steel skeleton in August 2004. It was covered with concrete plates and a coral cement top layer. The cavity was placed in the Buoy 1 area on 08 September 2004. Station J&T's Leap is upcurrent from the area around the city of Willemstad. Buoy 1, Snake Bay, and Jeremi are all downcurrent from Willemstad. Cavities were located in the fore-reef slope between 10 m and 15 m depth close to the drop-off. In Berau, 21 cavities, in a depth range of 5–17 m, were selected. Cavity volumes ranged from 50 to 250 dm^3, where a sandy bottom made up approximately one-third of the total cavity surface area (TSA) and the remainder consisted of cavity wall. The framework of the Berau reefs was more porous than the reefs of Curaçao, and cavities showed more openings to the outside reef than cavities at Curaçao. Samples were collected by scuba diving.

Sample collection

DOC concentration and BA in cavity water and reef water—To compare the concentrations of DOC and BA between cavity water and overlying reef water, we defined two types of water. Cavity water (CW) was sampled from the middle of the cavity and reef water (RW) ~1 m from the opening of the cavity. For each cavity, a RW sample was taken first, against the current to avoid contamination of samples, then a CW sample was taken. On Curaçao, 20 cavities were sampled along the house reef of the CARMABI Foundation (Buoy 1) in August 2003 (Fig. 1A). Samples for DOC and BA were taken between 09:00 h and 10:00 h local time with an acid-washed 750-mL polycarbonate syringe. The water was collected in acid-washed glass bottles, stored in the dark at 4°C prior to further processing in the laboratory within 4 h. In Berau, 21 cavities in the Berau area were sampled in October 2003. One-hundred milliliter polycarbonate syringes were used for sampling in the morning and afternoon around slack tide to avoid strong currents. Morning samples were processed on the boat. Afternoon samples were kept in the 100-mL syringes in the dark at 4°C prior to further processing within 4 h.

DOC and BC removal rates—To study in situ net fluxes of DOC and bacterioplankton carbon (BC) in coral cavities, water exchange was restricted by closing the cavity with a tightly woven cloth (Scheffers et al. 2004). Water samples were taken at 0, 5, 10, 15, 30, and 60 min after closing the cavities by an acid-washed silicon tube and 100-mL polycarbonate syringes. Closure experiments were performed over the course of four fieldwork periods, in July–August 2003, March–August 2004, March–May 2005, and January–April 2006. Berau cavity close-off experiments were carried out at three stations (Lighthouse II, Coral Garden, and Kakaban; Fig. 1B; Table 2) in October 2003. Volume and TSA (i.e., the sum of the surface of the inner walls and surface of the sandy bottom combined; Table 2) of the cavities along Curaçao were determined with the Cave-Profiler, a tool to measure the three-dimensional structure of cavities (Scheffers et al. 2003). In Berau, cavity volumes were estimated on basis of depth, width, and height measurements of cavities. The TSA was derived from the empirical linear relation between cavity volume (CV, in a size range of 50–250 dm^3) and TSA, given by the following equation: $TSA = 0.0084 \times CV + 0.7855$ ($R^2 = 0.774$; $F = 20.509$; df = 6; $p < 0.005$). In Curaçao, samples for DOC and BA were taken between 10:00 h and 12:00 h. Water was collected in acid-washed glass bottles, stored in the dark at 4°C prior to further processing in the laboratory within 4 h. In Berau, samples for total organic carbon (TOC) and BA were taken both in the morning and the afternoon. Samples of the morning session were directly processed on the boat. Water collected in the afternoon was kept in the 100-mL syringes in the dark at 4°C, prior to further processing in the laboratory within 4 h.

Bioassays—Bioavailability of DOC for ambient reef water bacterioplankton was determined by a series of bioassays. Water used in the bioassay was collected in August 2003 at the station Buoy 1 at 15-m depth in front of coral cavities. Aliquots of seawater (1.5 liters) were gently filtered through 0.8-μm polycarbonate filters (Millipore,

47-mm diameter) to remove grazers and incubated in acid-washed glass bottles in the dark at in situ temperature of 26°C ($n = 6$). Duplicate samples for bacterial abundance and DOC were taken at $t = 0$, 5, 10, 20, and 30 d. To keep the system C-limited, inorganic N and P (10 μmol L^{-1} N as $NaNO_3$ and 1 μmol L^{-1} P as K_2HPO_4) were added at day 1.

Sample treatment and analysis—Water samples were processed in the laboratory, prior to transportation to the Netherlands for analyses. Samples for BA (10 mL) were stained with acridine orange and filtered (maximum 20 kPa suction pressure) onto 0.2-µm black polycarbonate membrane filters (Millipore, 25 mm), mounted on slides and stored at −20°C. Bacterial numbers were counted using an epifluorescence microscope (×1,250). Per slide, 10 fields were counted or up to a minimum of 200 bacteria. In Berau, BA was determined with a flow cytometer (FCM, Beckton Dickinson FACScalibur equipped with a 15-mW, 488-nm air cooled argon-ion laser) as described by Marie et al. (1999) with the modification of using 0.2-µm filtered glutaraldehyde as a fixative (20 μL of 25% glutaraldehyde per sample, EM grade, Merck). In the field, duplicate 1-mL samples were collected in cryovials (Greiner), fixed and kept at 4°C before shock-freezing and storage in liquid nitrogen. To convert BA to carbon biomass a conversion factor of 30 fg per bacterial cell was used (Fukuda et al. 1998). BC removal rates in closed coral cavities were calculated assuming exponential clearance of prey in a closed system with homogenous mixed water (Scheffers et al. 2004).

Samples for DOC analysis were gently (maximum 20 kPa Hg suction pressure) filtered through a 0.2-µm polycarbonate filter (Millipore, 47 mm). Prior to filtration, filters, glassware and pipette tips were washed with, consecutively, acid (3 × 10 mL 0.4 M HCl), 0.2-µm filtered double distilled water (3 × 10 mL) and sample water (3 × 10 mL). Duplicate 8-mL DOC samples were collected in precombusted (4 h 450°C) glass ampoules. Ampoules were sealed immediately after acidification with 1–2 drops of concentrated H_3PO_4 (80%) and stored at 4°C until analysis. In Berau, TOC instead of DOC concentration was measured. Measurements of DOC and TOC were performed by the high-temperature combustion method, using a total organic carbon analyzer (model TOC-5000A, Shimadzu). The TOC analyzer was calibrated with potassium phthalate in Milli-Q water. As an internal control of the DOC measurements, consensus reference material provided by Hansell and Chen of the University of Miami, USA (Batch 4, 2004) was used.

TOC is composed of DOC and particulate organic carbon (POC). POC in tropical reef water consists mainly of phytoplankton and bacterioplankton. The phytoplankton carbon (PC) retention rates by reefs are comparable with (Ayukai 1995), or, in coral cavities, even lower than (Kötter and Pernthaler 2002) BC retention rates. Therefore, we assumed, for conservancy, that BC and PC retention rates were equal. DOC removal rate (RR) for the Berau area was calculated as: $DOC_{RR} = TOC_{RR} - 2 \times BC_{RR}$. DOC concentrations for RW and CW in the Berau area were calculated as: $DOC_{RW} = TOC_{RW} - 2 \times BC_{RW}$, and $DOC_{CW} = TOC_{CW} - 2 \times BC_{CW}$.

Estimation of DOC removal rates—The removal rates of DOC in closed cavities were determined with a 2G-model. DOC represents a very heterogenic group of organic compounds, both in size fractions, chemical composition as in bioavailability or biodegradability. The degradation of carbon is often described as a first-order process, in which velocity of degradation is given as the product of a reaction constant and the actual carbon concentration, or:

$$\frac{dC}{dt} = -kC \tag{1}$$

This equation assumes that only one carbon fraction has a constant biodegradation. Application of this model to experimental data often gives a poor description or trend, while in fact there are multiple fractions with different degradation constants and with different concentrations within the total DOC pool. A simplified model to describe the course of carbon in time assumes that the DOC pool is composed of two major fractions, a fast removable fraction, C_f , and a slow removable fraction, C_s. These two fractions will be consumed according to characteristic removal constants, k_f and k_s. The total DOC removal will then be described as the sum of all individual removal rates, or:

$$\frac{dDOC}{dt} = -\left(k_f C_f + k_s C_s\right) \tag{2}$$

By integration of Eq. 2 in reference to time, t, we arrive at the equation describing the concentration of DOC as function of time:

$$DOC(t) = C_{f,0}e^{-k_f t} + C_{s,0}e^{-k_s t} \tag{3}$$

Using a minimalization routine, the experimental data can be described with the model by estimating the model variables $C_{f,0}$, k_f, $C_{s,0}$, and k_s. The initial uptake rate of DOC (the flux on $t = 0$) was calculated from the estimated values of these variables and is given by:

$$\text{Flux}_{DOC} = -\left(k_f C_{f,0} + k_s C_{s,0}\right) \tag{4}$$

The computed fluxes are the expected DOC fluxes in the field. For our closure experiments, we assume a well-mixed closed system without exchange with overlying reef water.

Results

The concentrations of DOC in the cavity waters (70.1 ± 5.4 μmol L^{-1}) at the Curaçao sampling sites were significantly lower than in the overlying reef water (84.9 ± 9.1 μmol L^{-1}; paired t-test: $t = -4.863$, df = 18; $p < 0.0005$; Table 3). In 15 out of 19 different cavities on Curaçao, the DOC concentrations were lower inside the cavity than outside. Out of the remaining four measurements, three showed no difference in DOC concentration (<3 μmol L^{-1}) between CW and RW. In one cavity, the concentration of DOC was higher than in RW. The average difference in DOC concentration between RW and CW was 14.8 ± 6.0 μmol L^{-1}. This corresponded to a 15.2% ±

Table 3. Overview of average concentrations of dissolved organic carbon (DOC) and bacterial abundances in reef water (RW) and cavity water (CW), for coral cavities in Curaçao, Netherlands Antilles, and coral cavities in Berau, East-Kalimantan, Indonesia (average ± SD).

DOC	Average RW (μmol L^{-1})	Average CW (μmol L^{-1})	Average difference (μmol)	Relative difference (%)
Curaçao (n=19)	84.9±9.1	70.1±5.4	14.8±6.0	15.2±6.8
Berau area* (n=21)	71.0±7.2	67.0±7.1	4.0±2.4	5.7±3.7
Bacterial abundance	Average RW ($\times 10^5$ cm^{-3})	Average CW ($\times 10^5$ cm^{-3})	Average difference ($\times 10^5$ cm^{-3})	Relative difference (%)
Curaçao (n=20)	10.5±3.4	7.2±1.6	3.3±2.8	27.9±16.7
Berau (n=21)	8.6±1.9	5.5±2.1	3.2±1.3	38.0±16.8

* Calculated from TOC.

6.8% lower DOC concentration in the coral cavities on Curaçao.

The cavities in Berau were characterized by a significantly lower concentration of DOC in CW (67.0 ± 7.1 μmol L^{-1}) than in RW (71.0 ± 7.2 μmol L^{-1}; paired t-test: $t = -3.845$, df = 20; $p < 0.005$; Table 3). In Berau, 16 out of 21 cavities showed a lower concentration of DOC in CW as compared to RW. There was no difference in four cavities (<3 μmol L^{-1}), and in one cavity the concentration DOC in CW was higher than RW. On average, difference in DOC concentrations in CW were 4.0 ± 2.4 μmol L^{-1} or 5.7% ± 3.7 % lower than in RW.

The BA was always significantly lower in CW than in RW, in cavities on Curaçao (paired t-test: $t = -4.364$, df = 19; $p < 0.0005$) and Berau (paired t-test: $t = -3.3845$, df = 20; $p < 0.005$) (Table 3). The average BA in RW in Curaçao was 10.5 ± 3.4 × 10^5 cm^{-3}, compared to an average CW BA of 7.2 ± 1.6 ×10^5 cm^{-3}. Bacterial numbers were on average 27.9% ± 16% (Curaçao) and 38.0% ± 16.8% (Berau) lower in CW compared with RW. The average BC concentration in RW of Berau was 2.2 ± 0.5 μmol L^{-1}, or 3% of the TOC pool. TOC consisted for 94% of DOC.

The DOC (Curaçao; paired t-test: $t = -9.852$, df = 22; $p < 0.001$), and TOC (Berau area; paired t-test: $t = -5.908$, df = 6; $p < 0.0025$) concentrations significantly decreased in time in cavities after closure. In all 30 time series in 10 different cavities in both regions, the concentration of DOC or TOC declined after 30 min of cavity closure (Table 4). In seven time series in different cavities on Curaçao, we measured changes in DOC concentration up to 60 min, but in all cases, the changes in DOC concentration stabilized after 30–45 min. Figure 2 illustrates the pattern of DOC concentration change in time at six different cavities at four different stations on Curaçao. Cavity Buoy 1.1 was studied in more detail. The average concentration drop of DOC after 30 min in cavity Buoy 1.1 was 20.3 ± 4.9 μmol L^{-1}; the average calculated flux per cavity surface area was 353 ± 57 mmol C m^{-2} d^{-1} (n = 12; Table 4).

Artificial cavity Buoy 1.2 was sampled in May 2005, eight months after its underwater placement. Occasional observation and underwater photography indicated that within a time frame of eight months, the artificial cavity walls had a thin veneer of encrusting cryptic organisms. The estimated DOC flux into cavity Buoy 1.2 was 324 mmol C m^{-2} d^{-1}, which was in the same order of magnitude as DOC fluxes estimated for natural coral reef cavities (Table 4).

For all cavities the average concentration drop of DOC (Curaçao) or TOC (Berau) after 30 min was respectively 25.6 ± 12.3 μmol L^{-1} and 8.1 ± 3.6 μmol L^{-1}, estimating fluxes with the 2G-model of respectively 342 ± 82 mmol C m^{-2} d^{-1} for the cavities on Curaçao (DOC; n = 23) and 93 ± 44 mmol C m^{-2} d^{-1} for the cavities in Berau (TOC; n = 7) (Fig. 3). The DOC removal rates for cavities in Berau were on average 90 ± 45 mmol C m^{-2} d^{-1}, or 96% of the TOC removal rates.

We determined the following effects on the variance in organic carbon removal rates: (1) The concentration of DOC or TOC at t = 0, (2) the cavity volume, and (3) the station (area effect). There was no significant correlation between the concentration of DOC (Curaçao) at t = 0 and the removal rate of DOC in cavities (Pearson; $r = 0.256$, df = 21, not significant (n.s.)), nor between the concentration of TOC (Berau) at t = 0 and the TOC removal rates in cavities (Pearson; $r = 0.644$, df = 5, n.s.). Cavity volume did not have a significant effect on carbon removal rates in Curaçao (General Linear Models (GLM); $F = 0.058$, df = 21, n.s.), and in Berau (GLM; $F = 0.007$, df = 5, n.s.). The location of the stations did not have a significant effect on DOC removal rates (GLM; $F = 3.236$, df = 6, n.s.), or TOC removal rates (GLM; $F = 0.826$, df = 2, n.s.).

The bacterial numbers decreased exponentially in coral cavities in Curaçao and Berau in time (Figs. 3, 4; Table 4). This decrease corresponded on average to a removal of 49% ± 11% (Curaçao) and 40% ± 20% (Berau) of bacterioplankton by coral cavities. BC removal by coral cavities of Curaçao was on average 3.6 ± 1.3 mmol C m^{-2} d^{-1} (n = 15). In the Berau area, the average BC removal was 1.9 ± 1.3 mmol C m^{-2} d^{-1} (n = 6).

The bioassays showed an average DOC removal of 19.6 ± 8.4 μmol L^{-1} after 30 d (Fig. 5). During the bioassay, bacterial numbers increased from 6.3 ± 0.25 × 10^5 bacteria cm^{-3} at t = 0 to 24.3 ± 0.77 × 10^5 bacteria cm^{-3} at t = 4 d and slowly decreased again to 6.5 ± 2.1 × 10^5 bacteria cm^{-3} at t = 30 d (Fig. 5). Inorganic N and P levels remained high after enrichment at approximately 10 μmol L^{-1} and 1 μmol L^{-1}, respectively.

Table 4. Complete list of cavity closure experiments conducted from 2003 to 2006 in seven different coral cavities at four sites in Curaçao and three different coral cavities at three sites in Berau. DOC concentration at the start of each experiment, the DOC removal rate based on both the linear (DOC_{lin}) and 2G-model (DOC_{2G}) fit, the bacterial abundance (BA) at the start of each experiment, and the bacterial carbon removal rate (BC) are given. Based on the individual time series, the averages for coral cavities in both Curaçao and Berau are presented.

Cavity	Date	DOC $t=0$ (μmol L^{-1})	DOC_{lin} removal rate (mmol C m^{-2} d^{-1})		DOC_{2G} removal rate (mmol C m^{-2} d^{-1})		$BA_{t=0}$ ($\times 10^5$ cm^{-3})	BC removal rate (mmol C m^{-2} d^{-1})
Curaçao								
Buoy 1.1	21 Aug 03	63	53		336		8.2	2.5
Buoy 1.1	22 Aug 03	101	63		386		8.3	6.1
Buoy 1.1	23 Aug 03	97	57		345		7.6	3.2
Buoy 1.1	24 Aug 03	97	75		462		6.8	2.3
Buoy 1.1	25 Aug 03	94	61		370		6.4	3.0
Buoy 1.1	19 Sep 04	98	118		340		7.8	4.9
Buoy 1.1	20 Sep 04	106	52		285		9.3	3.9
Buoy 1.1	21 Sep 04	119	101		363		7.7	5.0
Buoy 1.1	18 May 05	140	73		380		5.8	2.5
Buoy 1.1	06 Jun 05	121	42		263		6.4	2.7
Buoy 1.1	07 Jun 05	112	63		286		8.6	4.5
Buoy 1.1	11 Apr 06	112	49		419		8.9	4.7
Buoy 1.2	19 May 05	109	79		324		7.6	3.8
Jeremi 1	26 Jun 05	140	163		410		6.5	4.1
Jeremi 1	27 Jun 05	140	180		432		7.6	4.7
Jeremi 1	19 Apr 06	146	212		493		6.5	3.1
Jeremi 2	19 Apr 06	101	64		314		8.2	4.6
Snake Bay 1	25 Jun 06	122	151		444		6.5	5.4
Snake Bay 1	12 Apr 06	140	124		273		8.0	2.2
J&T's Leap 1	20 Apr 06	129	106		220		7.0	1.9
J&T's Leap 1	21 Apr 06	94	58		269		5.8	1.8
J&T's Leap 2	20 Apr 06	97	30		151		7.3	2.9
J&T's Leap 2	21 Apr 06	114	70		300		4.5	1.9
Average		113	86		342		7.3	3.6
Berau		*	*	**	*	**		
Coral Garden	18 Oct 03	84	36	34	135	133	4.0	1.0
Coral Garden	19 Oct 03	74	17	9	33	25	5.0	3.9
Lighthouse II	21 Oct 03	80	36	29	167	160	5.5	3.3
Lighthouse II	21 Oct 03	72	28	25	90	87	3.2	1.5
Kakaban	23 Oct 03	77	27	23	77	73	6.5	1.9
Kakaban	23 Oct 03	74	18	16	89	87	2.8	1.1
Kakaban	25 Oct 03	63	16	15	63	62	9.0	0.6
Average		75	28	24	93	89	5.1	1.9

* TOC.
** DOC.

Discussion

This is the first study on the flux of DOC in coral cavities, and two independent methods indicated that they are sinks of DOC. DOC removal rates in coral cavities were on average two orders of magnitude higher than bacterioplankton removal rates. All our results strongly support a net influx of DOC and bacterioplankton into cavities. While Richter et al. (2001) suggested phytoplankton and, indirectly, bacterioplankton as the most important organic matter sources for biota in cryptic habitats on coral reefs, we, however, find that the removal of DOC in cavities is more likely to be one to two orders of magnitude larger than these particulate sources.

The concentration of DOC in cavity water compared to reef water is 15% and 6% lower than the bulk DOC concentration in ambient reef water in Curaçao and in Berau (Table 3). Depletion of bacterioplankton (29% at Curaçao and 38% at Berau) is higher than of DOC. Bacterioplankton is apparently more efficiently removed from cavity water than bulk DOC in coral cavities. These findings may not be surprising because the cryptic biota is dominated by suspension feeders, particularly by sponges (e.g., Vasseur 1977; Richter and Wunsch 1999; Wunsch et al. 2002). Sponges are very efficient filter feeders, especially in feeding on particles smaller than 2 μm, like bacterioplankton (e.g., Reiswig 1974; Pile et al. 1996; Kötter and Pernthaler 2002). Smaller differences between cavity and reef water DOC concentrations in Berau as compared to those in Curaçao could be explained by shorter residence times of water in the cavities of the Berau area. This argument is supported by the observation that the coral cavities in Berau had more openings to the ambient reef water compared with those in Curaçao, allowing enhanced

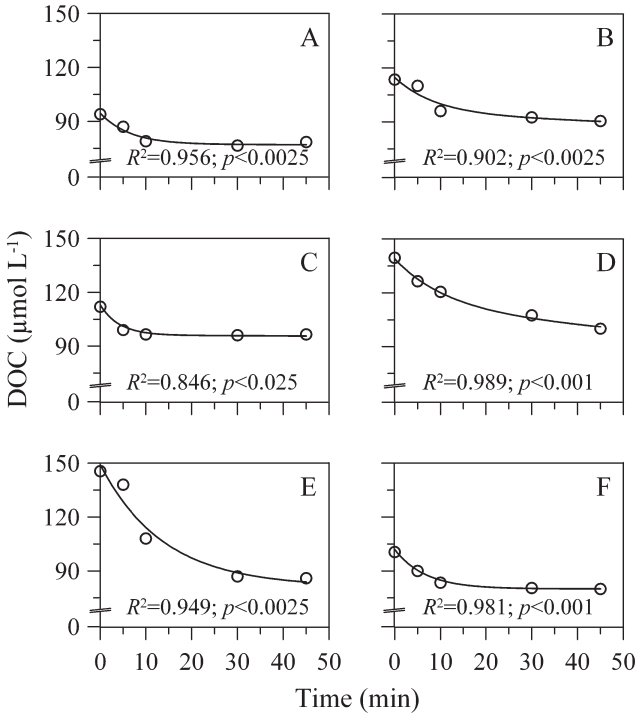

Fig. 2. The decrease of DOC concentration in time in six different coral cavities after cavity closure at four different stations: (A, B) J&T's Leap, (C) Buoy 1, (D) Snake Bay, and (E, F) Jeremi, along the SW coast of Curaçao. Trend lines are given by a 2G-model fit.

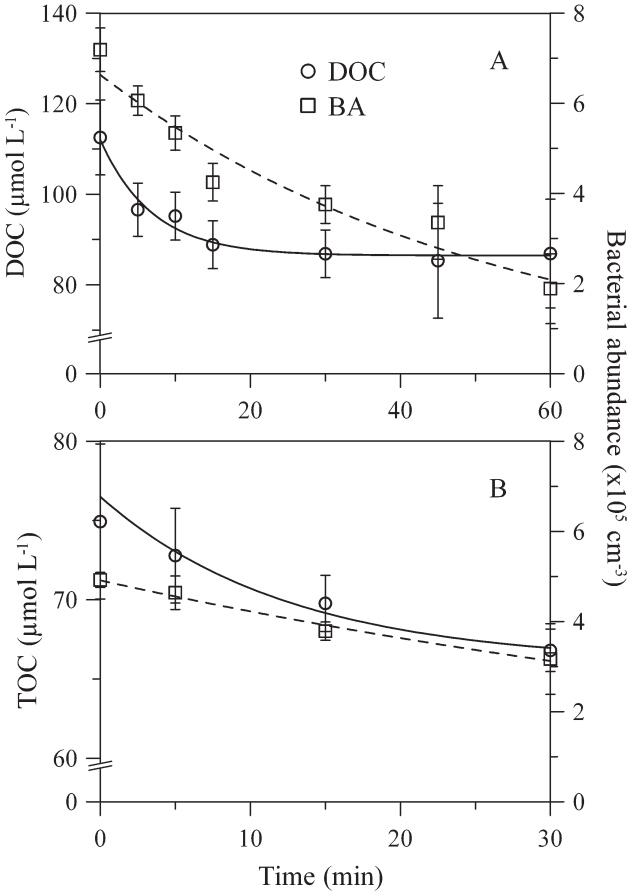

Fig. 3. (A) Curaçao: The average decrease of DOC concentrations (n = 23; trend line is given by a 2G-model fit) and BA (n = 23; trend line is given by an exponential fit) in time in coral cavities after closure. (B) Berau: The average decrease in TOC concentrations (n = 7; trend line is given by a 2G-model fit) and BA (n = 7; trend line is given by an exponential fit) in time in coral cavities after cavity closure; mean ± standard deviation.

water exchange. It is also possible that DOC is less efficiently removed from the water in the cavities in Berau as compared to the cavities in Curaçao. The ratio DOC : BC in reef water is comparable in both regions, i.e., 33.3 and 34.5 for Curaçao and Berau, respectively, but not in cavity water, i.e., 38.9 for Curaçao and 50.7 for Berau. There is no clear discrimination in DOC and BC uptake in cavities of Curaçao. Cavities in Berau, however, remove relatively more bacterial carbon than DOC. The composition of DOC in Berau could be less favorable in terms of utilization by cryptic organisms, and this could explain the positive discrimination for bacterioplankton in cavities of the Berau area.

DOC fluxes in cavities found in this study are high and unequaled in the literature, with estimated removal rates per cryptic surface area of 342 ± 82 mmol C m^{-2} d^{-1} (range: 151–493) in Curaçao and 90 ± 45 mmol C m^{-2} d^{-1} (range 33–167) in Berau. After closure of cavities organic carbon is clearly removed in two major fractions, a fast removable fraction C_f of 28 ± 12 µmol L^{-1} (Curaçao) and 12 ± 4 µmol L^{-1} (Berau), and a slow removal fraction C_s of 84 ± 14 µmol L^{-1} (Curaçao) and 65 ± 4 µmol L^{-1} (Berau) (Figs. 2, 4). Therefore, fluxes based on a linear model are grave underestimations and are presented here only as the most conservative values of DOC fluxes into coral cavities. Another approach to determine fluxes of matter into coral cavities is given by Van Duyl et al. (2006). They calculated fluxes in an open system based on the relation between differences in concentration of matter in cavity water and overlying reef water and the water exchange coefficient of a series of cavities at different current velocities along the reef bottom. They found an average water exchange coefficient of 0.0041 s^{-1}, which is equivalent to an average residence time of water in coral cavities in Curaçao of 4.07 min. This approach rules out any possible closure effects. The average difference between cavity and reef water DOC concentration in this study is 14.8 µmol L^{-1}. Using the average water exchange coefficient of 0.0041 s^{-1}, the weighed average volume (148 dm^3), and total cavity surface area (2.11 m^2), the DOC flux into cavities is 367 mmol C m^{-2} d^{-1}, which is surprisingly close to the average DOC flux calculated with a 2G-model, namely 342 mmol C m^{-2} d^{-1}. This implies that DOC fluxes based on the 2G-model are reliable.

Bacterioplankton abundance declines exponentially in closed cavities. This supports our assumption that the suspension or filter feeding activity by the cryptofauna is not arrested nor inhibited by closure of the cavities. Bacterial carbon uptake rates by coral reef cavities (Table 4) closely resemble those reported in literature. Scheffers et al. (2004) found significant bacterioplankton depletion within cavities on Curaçao of on average 2.5 mmol C m^{-2} d^{-1}; Van Duyl et

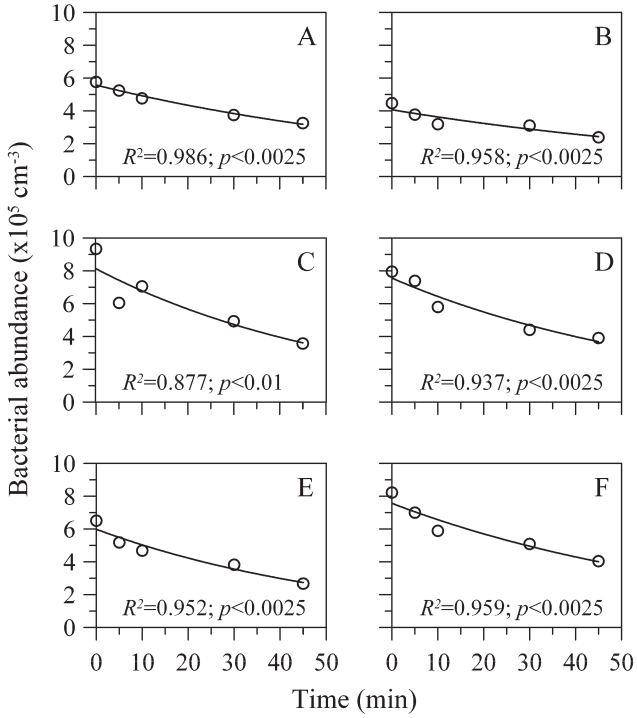

Fig. 4. The decrease of BA in time in six different coral cavities after cavity closure at four different stations: (A, B) J&T's Leap, (C) Buoy 1, (D) Snake Bay, and (E, F) Jeremi, along the SW coast of Curaçao. Trend lines are given by an exponential fit.

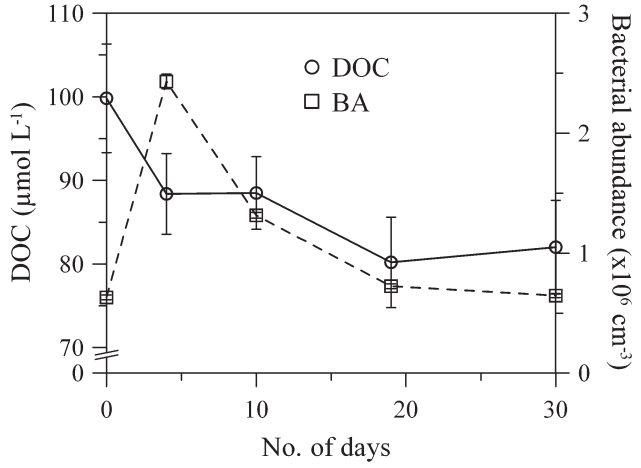

Fig. 5. Bioassays (n = 6) of grazer free seawater cultures showing the uptake of DOC by bacterioplankton in time and the BA in time; mean ± standard deviation.

al. (2006) found a bacterial carbon flux into cavities in the same area of 3.8 mmol C m^{-2} d^{-1}. Ayukai (1995) found BC retention rates on the Great Barrier Reef of on average 2.2 mmol C m^{-2} d^{-1}. The average BC removal in cavities in this study is 3.6 ± 1.3 mmol C m^{-2} d^{-1} (range: 1.8–6.1) and 1.9 ± 1.3 mmol C m^{-2} d^{-1} (range: 0.6–3.9) for cavities on Curaçao and Berau, respectively. This represents only 1–2% of the DOC removal. It is evident that DOC is quantitatively a far more important organic carbon source for coral cavities than bacterioplankton in Curaçao as well as in Berau.

In our bioassays in the reef water of Curaçao, we recorded a 20 μmol L^{-1}, or 19%, uptake of DOC by bacterioplankton in 20 d. We consider this fraction to be the average readily available part of the DOC. Because this percentage is close to the average DOC concentration reduction in closed cavities, it is tempting to suggest that the depletion in DOC concentration in CW as compared to RW was due to removal of labile DOC. The most likely candidate to remove labile DOC from cavity water is bacterioplankton. In the bioassays, it takes bacterioplankton 20 d to take up 19% of the total DOC, while cavities (with a 10-fold lower abundance of bacterioplankton as compared to the bacterial abundance in the bioassays) remove the same amount of DOC within 30 min. In addition, the residence time of water in our coral cavities was more in the range of minutes than days (Van Duyl et al. 2006). It is, therefore, unlikely that bacterioplankton was responsible for the DOC depletion in coral cavities.

Uptake of DOC by coral cavities appears to have been an overlooked general function in coral reef ecology. Considering the sheer size of the cryptic habitat and the significance compared to other sources of organic matter, DOC may be a key factor in the carbon and energy budget on coral reefs. Net influx of DOC into cavities is shown in a wide variety of cavities in two distinct coral reef regions, i.e., an Atlantic and Indo-Pacific region. Bulk DOC uptake rates by coral cavities vary in time and between cavities sampled in different areas. Neither the concentration of bulk DOC at the start of an experiment, nor cavity geometry accounts significantly for the variation in DOC fluxes. The difference in DOC flux size between the sampled areas can be explained by differences in composition and quality of DOC. The composition of the DOM pool is very diverse with a size range of low-molecular-weight organic molecules like amino acids, to high-molecular-weight molecules (e.g., mucus, polysaccharides), to minute particles like viruses and colloids. At least 10% of oceanic DOM is colloidal material (>95% consists of nonliving particles) in the size range 0.4–1.0 μm that easily passes the pores of the GF/F filters commonly employed in the separation of DOM and POM, and a significant part still passes through the pores of the 0.2-μm filters that we used (Isao et al. 1990). It could well be that the cryptofauna mainly takes up colloidal material in this size range. Sponges can take up minute particles like viruses (Hadas et al. 2006) and 0.1-μm sized beads from ambient water (Leys and Eerkes-Medrano, 2006). Pile et al. (1996, 1997) showed that the sponges used in their studies did not show selective feeding on any component of the plankton community. They suggested that the composition of the plankton community and the variability in the water column can affect sponge nutrition. The opportunistic feeding of sponges is further strengthened by Ribes et al. (1999), who argued that the composition of the ingested carbon by *Dysidea avara* mainly varied according to the availability of the different prey types in the water column. In this respect, DOM should also be taken into account as available food source for the cryptic biota, which is dominated by suspension feeders. There is evidence of extensive DOM feeding by suspension feeders. DOC intake can explain up to 50% of the carbon demand of

zebra mussels (Roditi et al. 2000; Baines et al. 2005). Yahel et al. (2003) showed evidence of extensive in situ DOC feeding (more than 90% of the total carbon intake) by the marine sponge *Theonella swinhoei*.

The variation in DOC removal rates between cavities may be attributed to differences in cryptofaunal composition. Interestingly, we know from previous data that each cavity investigated on Curaçao has its unique cryptofaunal composition (Scheffers 2005). Yet, there is no significant difference in carbon fluxes between cavities on Curaçao, and the proportion of the main functional groups, like sponges, (calcareous) algae, ascidians, bryozoans, and polychaetes, that might influence variation in DOC removal rates is relatively constant in coral cavities on Curaçao.

Depending on reef zone, the cryptic surface may range from less than 1× to 8× the planar reef area (Richter et al. 2001; Scheffers 2005). Hatcher (1997) reviewed the importance of regenerative spaces in reefs for the carbon budget of coral reefs. His gross primary production rates of entire reefs, where back reefs were the most productive reef zones (Hatcher 1990), may, however, be insufficient (200–500 mmol C m^{-2} planar reef d^{-1}) to meet the organic carbon demands of cryptic biota. We measured removal rates of 1,000 mmol C m^{-2} planar reef d^{-1}, assuming an average cryptic surface of 2.8 m^2 m^{-2} planar reef for the entire Curaçaoan reef (Scheffers 2005), omitting the particulate organic carbon removal by cryptic habitats and omitting the DOC consumption by benthos of the open reef. So removal of DOC by cryptic habitats alone is already 2× more than the gross primary production. Where is all this carbon coming from? Because bulk DOC concentrations are usually higher in reef overlying waters than in adjacent ocean (Ducklow 1990; Torréton et al. 1997; Van Duyl and Gast 2001), the carbon budget is unlikely to be matched by net import of bulk DOC from the ocean to the reef, unless organic carbon is actively taken up against a concentration gradient. This implies that DOC production by reefs and reef overlying waters, and possibly DOC supply from land-based sources is probably larger than currently anticipated. A net input of external POM to the reef, for instance by trapping of oceanic plankton and other particles by the reef (Hamner and Wolanski 1988; Richter et al. 2001), may possibly result in extra DOC supply via the benthic food web. This, however, may not be sufficient to cover the gap between gross primary production and consumption. Coral mucus, a part of colloidal DOC, has been suggested to be an important carrier of energy to the benthic food chains of the reef (Wild et al. 2004). Therefore, we hypothesize that the bulk DOC production by noncryptic reef communities is significantly higher than presently assumed. It is evident that the high DOC removal rates we measured in cryptic habitats of coral reefs in Curaçao and Berau influence our present understanding of energy budgets of coral reefs.

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