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REPORT

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The effect of water exchange on bacterioplankton depletion and inorganic nutrient dynamics in coral reef cavities

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Abstract We studied the effect of water exchange on the depletion (or accumulation) of bacterioplankton, dissolved organic matter and inorganic nutrients in small open framework cavities (50–70 l) at 15 m depth on the coral reef along Curaçao, Netherlands Antilles. The bacterioplankton removal rate in cavities increased with increasing water exchange rates up to a threshold of 0.0045 s^{-1}, reaching values of 50–100 mg C m^{-2} total interior cavity surface area (CSA) per day. Beyond the threshold, bacterioplankton removal dropped. The cryptic community is apparently adapted to the average water exchange in these cavities (0.0041 s^{-1}). Dissolved inorganic nitrogen (DIN), nitrate + nitrite (NO_x) in particular, accumulated in cavity water and the accumulation decreased with increasing water exchange. Net NO_x effluxes exceeded net DIN effluxes from cavities (average efflux rate of 1.9 mmol NO_x vs. 0.8 mmol DIN m^{-2} interior CSA per day). The difference is ascribed to net ammonium losses (NH_4) in cavities at reef concentrations >0.025 µM NH_4, possibly due to enhanced nitrification. Dissolved inorganic phosphate accumulated in cavities, but was not related to water exchange. The cryptic biota in cavities depend on water exchange for optimization of consumption of bacterioplankton and removal of inorganic nitrogen. Coral cavities are an evident sink of bacterioplankton and a source of NO_x and PO_4^{3-}.

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Introduction

Coral reefs have a high structural and biotic complexity in which the reef building corals are the main structuring components. The structural complexity is three dimensional and comprised of the coral bottom roughness and relief as well as cavities and crevices, which occur under the overhangs of corals and in the reef framework. Ginsburg (1983) estimated the inner open space in reefs to encompass one to two-thirds of the total volume of reefs. Cryptic habitats make up an important part of the volume of coral reefs and their surfaces provide a very large interface for the exchange of materials, particularly when they are in open connection with the outside water column (Tribble et al. 1988). More than 93% of this large cryptic hard substratum in cavities of the reef framework has been found to be covered with encrusting organisms, typically 27% by calcareous algae and 66% by suspension feeding organisms, such as sponges, tunicates, bryozoa and polychaetes in reefs of Jordan and Curaçao (Richter and Wunsch 1999; Wunsch et al. 2002; Scheffers 2005).

Suspension feeders living on these walls in dim light depend on food from the waterborne organic matter supply in which nano- and picoplankton, and dissolved organic matter (DOM) make up the bulk. Depletions of nano- and picoplankton from waters overlying coral reefs have been reported for several sites (e.g., Ayukai 1995; Yahel et al. 1998; Van Duyl et al. 2002). Gast et al. (1998) established depletion of bacterioplankton and accumulation of inorganic nutrients in crevices compared with their respective concentrations in reef overlying water at Curaçao. Enclosure studies with cryptic sponges revealed high consumption rates of nano- and picoplankton and high mineralization rates (Kötter and Pernthaler 2002; Kötter 2003).

The challenge now lies in quantifying the fluxes into and from cavities in situ, and understanding variations in these fluxes. Richter and Wunsch (1999) report removal rates of chlorophyll-a and release rates of inorganic nutrients in water, flowing through cavities of coral reefs in the Red Sea. Scheffers et al. (2004) conducted detailed studies of the removal of bacterioplankton and the regeneration of inorganic nutrients in closed blind-end cavities under coral overhangs in the Caribbean. They (*ibid*) closed the main opening of the cavity with a cloth to reduce the exchange of water between the cavity and the ambient reef water. Since the degree to which cavities are closed to the outside environment may influence the in situ rates of organic matter uptake and inorganic nutrient regeneration, we conducted a series of experiments in open, blind-end cavities and assessed the importance of water exchange rate of cavities for the bacterioplankton removal rates, DOM dynamics and the inorganic nutrient regeneration. The aim of the study is to assess the influence of water exchange in cavities on the biogenic fluxes of matter into and out of cavities, and to assess the quantitative role cryptic biota play in removing bacterioplankton and DOM from the passing water, and in mineralization of Nitrogen (N) and Phosphorus (P).

Materials and methods

Cavity surveys

Cavities were selected along the reef slope of the SW coast of Curaçao by SCUBA-diving (Fig. 1). Two cavities were located close to each other on the reef slope at station Buoy One (BO), but with different orientation to the main current. BO4 at 15.2 m depth outcropped from the reef slope, while BO3 at 13.8 m depth was deeper into the reef. To cover a wide range of exchange rate coefficients, a cavity at the Water plant (WP) was used at 15 m depth. The chances of strong currents over the reef during experiments are larger at station WP than at station BO. Two of the three cavities in this study were also used for other experiments by Scheffers et al. (2004).

The interior surface area and volume of cavities were assessed with a cave-profiler (Scheffers et al. 2003), a simple instrument with which coordinates are taken of the walls and roof of the cavity, while positioned on the sandy and slightly seaward sloping floor of the cavity. The inventory of the cover of different cryptic organisms and substratum types in cavities was made with a Sony 900E digital CaveCam (Wunsch and Richter 1998). The cover of functional components in cavities such as bare sand, hard substratum covered with calcareous algae or suspension feeders, and the cover of different groups of suspension feeders was determined according to Scheffers et al. (2004).

Water exchange of cavities and water sampling

We used fluorescent dye (Fluorescein Sodium Salt, Sigma) to determine the water exchange rate of cavities. The dye solution (120 ml with 60 µg dye ml^{-1}) was inserted in the cavity with a 50 cm long plastic plunger device. It was agitated until the dye was homogeneously distributed within the cavity. Cavity water samples were then taken over time by inserting tygon tubing, attached to a rigid pole into the center of the cavity. The center was determined before dye addition, and was ca 30–50 cm from the front opening of the cavity and ca 20 cm over the bottom depending on cavity geometry. After insertion of the tubing, samples were taken with a 60 ml syringe every 1.5–2 min until the dye concentration in the cavity dropped to values below visible detection. In the laboratory the concentration of dye was determined from spectrometric analysis of samples compared with a

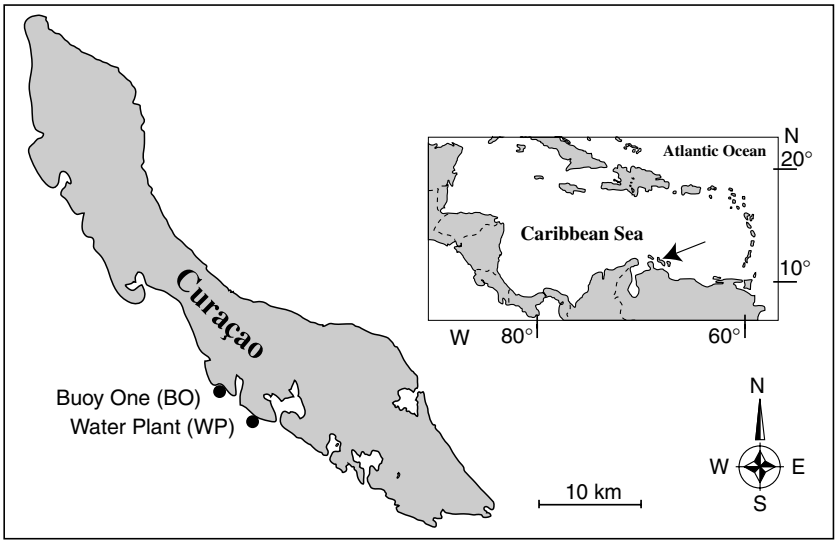


Fig. 1 Location of the island of Curaçao in the Caribbean (*inset*). Sampling stations Buoy One (*BO*) and Water plant (*WP*) along the SW coast of the island are indicated

known calibration curve of concentration versus transmittance at a wavelength of 450 nm. The water exchange rate coefficient was determined from exponential decay of concentration over time.

Just before the dye release in the cavity, two water samples of 700 ml were taken with 750 ml Perspex syringes, one from the water just outside the cavity (about 1 m in front of the entrance of the cavity), and subsequently one from the cavity water in the center of the cavity. Samples were kept cool in the dark during transport to the laboratory and processed within 2 h.

Matter concentrations and water exchange measurements were obtained six to eight times per cavity at different mainstream current velocities (between 0 and 50 cm s^{-1}) between 6 and 28 June 2001. Estimates of current velocities along the reef were made two to three times per experiment with a neutrally buoyant drogue. The drogue was timed twice during transport approximately 1.5 m above a 10 m long line on the reef bottom, which was placed parallel to the reef slope just below the cavity involved.

Water sample analyses

Duplicate water samples for inorganic nutrient analysis were filtered over 0.2 µm sterile Acrodisc filters and collected in 6 ml Pony vials. Vials were stored at −20°C until further processing of dissolved inorganic nitrogen (DIN) and phosphate. Concentrations of ammonium (Helder and De Vries 1979), phosphate (Murphy and Riley 1962) and nitrite, nitrate (Grasshoff et al. 1999) were measured on a Traacs auto-analyzer (Technicon).

Duplicate 10 ml samples for bacterioplankton abundance determination were fixed with buffered (sodium tetraborate, pH = 7.9), 0.2 µm filtered formaldehyde (2% end concentration) in 16 ml polystyrene tubes (Falcon). Samples were stained with acridine orange (100 mg l^{-1} final concentration) within 24 h, and subsequently collected onto 0.2 µm Sudan black prestained polycarbonate membrane filters (Poretics) and stored at −20°C. Within 1 month after slide preparation, samples were counted with an epifluorescence microscope.

Dissolved organic carbon (DOC) was gravity filtered over 0.2 µm polycarbonate filters. Filters were prewashed several times with the sample to remove organic C from the filter. After filtration, DOC samples (8 ml) were transferred in duplicate to precombusted glass ampoules, which were sealed immediately after addition of two drops of phosphoric acid (85%). DOC concentrations were determined by the high-temperature combustion method on a Shimadzu TOC−5000.

Determination of fluxes of matter

Fluxes of matter between the water mass and the substratum are dependent on hydrodynamic factors and concentration (e.g., Baird and Atkinson 1997; Thomas and Atkinson 1997). Differences in concentrations of matter in cavities and in front of cavities (just outside cavities) point to net fluxes of matter into or out of cavities. We compared reef water concentrations of variables with their concentration in cavity water, and investigated the relation between depletion of variables in cavity water (= concentration in reef water of a particular variable minus its concentration in cavity water, $C_{reef} - C_{cavity}$) and the water exchange coefficient. Negative depletion is called accumulation.

Fluxes of bacterioplankton, DOC, and inorganic nutrients between open reef water and cavity water were assessed by assuming an exponential relation between concentrations in reef water (C_{reef}) and cavity water (C_{cavity}) using the exchange rate coefficient determined by the dilution of fluorescent dye in time (t) after injection in cavities (Eq. 1). The regression exponent (t/t_c) is the exchange rate coefficient, and is analogous to the uptake rate constant (e.g., Atkinson and Bilger 1992; Thomas and Atkinson 1997; Thomas et al. 2000). t_c is the residence time of the water in the cavity and $1/t_c$ is the exchange rate coefficient. $C(t)$ is the concentration of the variable (bacterial abundance, DOC, NH_4, NO_2, NO_3, and PO_4, respectively) in cavity water at time t. If the difference between C_{reef} and C_{cavity} is 0, $C(t)$ is equal to C_{reef}. $\delta/\delta t \times C(t)$ in Eq. 2 shows the tangent of Eq. 1, which cannot be solved if t is larger than 0 and unknown. Net fluxes of matter (either into or out of cavities) were calculated as the tangent of Eq. 1 at $t = 0$ (3).

$$C(t) = C_{reef} - \left(C_{reef} - C_{cavity}\right) \times e^{-t/t_c}, \quad (1)$$

$$\frac{\delta}{\delta t} \times C(t) = -\left(C_{reef} - C_{cavity}\right) \times \left(\frac{-1}{t_c}\right) \times e^{-t/t_c} = \left(\frac{C_{reef} - C_{cavity}}{t_c}\right) \times e^{-t/t_c}, \quad (2)$$

$$\left.\frac{\delta}{\delta t}\right|_{t=0} \times C(t) = \frac{C_{reef} - C_{cavity}}{t_c}. \quad (3)$$

Solving Eq. 3 for the different variables rendered the fluxes of variables in this study, which were based on the difference in concentration of variables between reef and cavity water (depletion) and the water exchange coefficient ($1/t_c$). Negative influxes to coral cavities are considered as effluxes. For the calculations we assumed that

1. Gradients in variable concentrations from inside to outside the cavity are exponential, comparable with the dye dilution in time.
2. Differences in variable concentrations inside and outside a cavity remain constant during the 30–40 min period of individual experiments.
3. Exchange rate is constant during the 30–40 min experiments.
4. Concentrations of variables in the center of the cavity resemble the average concentration in cavity water.

To extrapolate the fluxes per unit volume to the cavity surface, we multiplied the rate by cavity volume

and divided it by the total substratum surface area to obtain rates per unit total interior cavity surface area (CSA) per day. To convert bacterial removal rates in cavities to C and N, we applied an average C-content of 30 fgC bacterium^{-1} and average N-content of 5.8 fgN bacterium^{-1} (Fukuda et al. 1998).

Statistical analysis

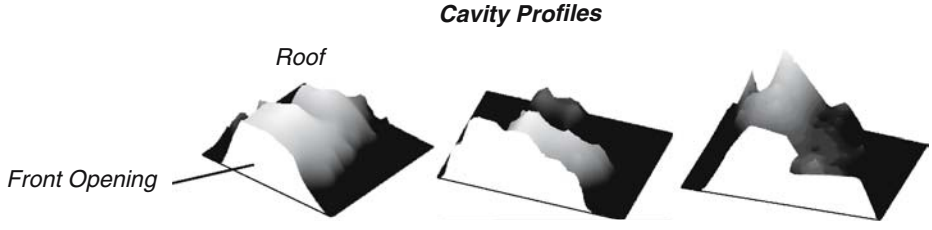
Data were analyzed using standard statistical tests (SYSTAT® 10). We ran full ANOVAs (general linear models) to determine the effects of cavity and bulk stream flow velocities along the reef on the variations in water exchange in coral cavities. Full ANOVAs were also used to explore the effect of cavity and water exchange on the variations in depletion and accumulation of matter observed in cavities. We applied paired *t* tests for comparison of matter concentrations between reef and cavity water. Linear relationships between depletions and accumulations of matter and respective reef or cavity concentrations were described with Pearson correlation tests. We used nonlinear piecewise regression for the determination of significant breaks in relationships.

Results

Cavity characteristics and hydrodynamics

The geometry of cavities is presented in 3D models which are based on the coordinates taken with the cave-profiler. Models illustrate the irregular morphology of cavities and their surface area extensions in the roof (Fig. 2). Cavities BO3 and WP1 were larger than cavity BO4. In spite of differences in volume among cavities, the total substratum surface area of the three cavities was comparable and consisted of one-third sand (on the floor) and two-thirds hard substratum (roof and walls), more than 90% of which is covered with cryptic organisms. Calcareous algae predominate at the entrance (ca 20% of total cover) and suspension feeders (43–47% of total cover) occupy most space deeper in the cavity. Sponges dominated the total cover of the suspension feeders with 19% in BO3, 33% in BO4, and 26% in WP1 of total cavity surface substratum area (Fig. 2).

During the cavity experiments, the dye was inserted through the front opening of the cavity. There were no other openings observed in cavities and the dye appeared to leave these cavities only via the front opening. The



	BO3	BO4	WP1
Volume (l)	70.2	53.5	73.3
Interior Cavity Surface Area (m^2)	1.32	1.38	1.52
Front Opening (m^2)	0.307	0.179	0.256
Aspect Ratio (Vol/Front Opening)	229	299	286

(cover components in % of interior cavity surface area)	BO3	BO4	WP1
Suspension feeders	43.3	46.9	44.4
Sponges	19.4	32.6	26.5
Tunicates	8.7	3.4	11.0
Bryozoans	7.0	6.3	3.4
Polychaetes	6.4	3.2	2.3
Bivalves	1.7	1.3	1.1
Calcareous algae	19.3	18.3	18.1
Bare and unidentified cover	6.5	2.8	3.8
Sand cover on cavity floor	30.9	32.0	33.8

Fig. 2 Geometry in 3D constructions of the three coral reef cavities with absolute interior surface area (including roof, walls, and floor), volume, and size of front opening and percent cover of interior cavity surface area with suspension feeders, calcareous algae, bare and unidentified cover on the roof and walls and percent cover with sand on the floor of the cavity. Scales of the 3D images differ among cavities

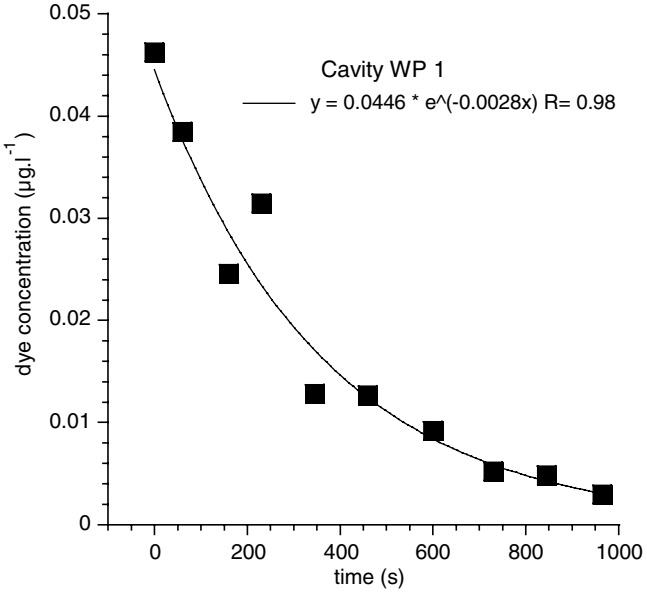


Fig. 3 Exponential decrease in dye concentration of water in a coral cavity (*WP1*) after dye injection. The exponent 0.0028 in the regression equation is the exchange rate coefficient with units per second. *R* in plot refers to multiple *R*

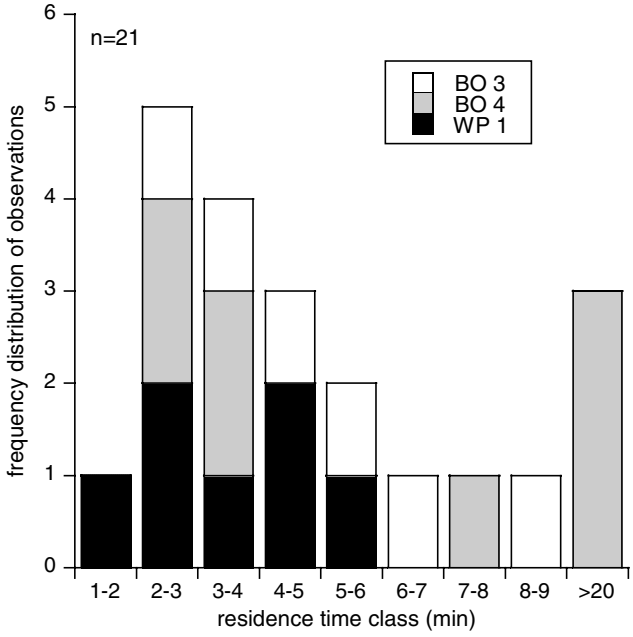


Fig. 4 Frequency distribution of water residence time classes of the three reef cavities. Six observations were made in cavity BO3, eight in BO4, and seven in WP1. Residence time is the inverse of the exchange rate coefficient

results of dye experiments indicated that the decline in dye concentration versus time is first order (Fig. 3) and exponential. Exchange rate coefficients varied between 0.00004 and 0.00880 s^{-1} corresponding to 7 h and 1.9 min residence time, respectively. The low water exchange of 0.00004 s^{-1} in the cavity BO4 during our dive of 14 June was exceptional. The average exchange rate coefficients for the different cavities ranged between 0.0034 and 0.0053 s^{-1} (4.9 and 3.1 min residence time, respectively) (Table 1). The residence time frequency distribution in Fig. 4 shows that the variation in exchange rate coefficients is larger at station BO than at station WP. The mainstream flow velocity at station WP was on an average higher than at station BO. Figure 5 shows that when the mainstream current velocity in the reef overlying water increases, the exchange rate coefficient in cavities at current velocities of up to 0.4 m s^{-1} increased as well. The relatively low exchange rate coefficient of WP1 at mainstream velocity of 0.48 m s^{-1} did not fit the regression. Cavity BO4 with the smallest volume and aspect ratio showed the steepest increase in exchange rate coefficients with current velocity. Regression slopes and intercepts were, however, not significantly different among cavities (full ANOVA, $P > 0.05$).

Combining data of different cavities

The data obtained in the three different cavities were combined to enlarge the sample size of 6–8 per cavity to up to 21 observations for each variable. Combination was done to explore the relationships between variables and water exchange rate of cavities. Combining the data of different cavities was justified because

1. No significant effect of the cavity on the relation between the concentration of matter [bacterioplankton, DOC, DIN, nitrate + nitrite (NO_x), NH_4, dissolved inorganic phosphate (DIP)] in cavity water and in reef water was established (factors: cavity and/or cavity × concentration of variable in reef water, full ANOVA step-wise regression, $P > 0.05$).
2. No significant effect of the cavity on the relation between depletion or accumulation of matter (bacterioplankton, DOC, DIN, NO_x, NH_4, DIP) and water exchange was established (factors: cavity and/or cavity × exchange, full ANOVA step-wise regression, $P > 0.05$).
3. Relative cover of functional components on the interior CSA were comparable between cavities, i.e., cover of suspension feeding organisms and of calcareous algae on the walls and roof, and the cover of sand on the floor of the cavity (Fig. 2). Also the relative cover of different groups of suspension feeders was comparable. Only the sponge cover in BO3 was 14% lower than in BO4 (Fig. 2).

Bacterioplankton depletion

The bacterioplankton concentration was higher in all experiments in reef water than in cavity water (*t* tests for paired comparisons: $n = 21$, $t = 6.635$, $P < 0.0001$, Fig. 6a). Reef water concentrations were on an average 354×10^3 bacteria ml^{-1} and cavity water concentrations 250×10^3 bacteria ml^{-1}. Densities were on an average

Table 1 Nutrient dynamics of reef cavities on the SW coast of Curaçao, Netherlands Antilles

Average values	*n*	Cavity Buoy One (BO3)	*n*	Cavity BO4	*n*	Cavity WP1	*n*	Overall average (range)
Water exchange rate coefficient (s^{-1})	6	0.0037	8	0.0034	7	0.0053	21	0.0041 (0.00004–0.009)
Fluxes of organic matter into cavities								
Bacterioplankton (mgC m^{-2} CSA day^{-1})	6	46.0	8	19.0	7	60.3	21	40.5 (0.4 −178.5)
Bacterioplankton N (mgN m^{-2} CSA day^{-1})	6	8.9	8	3. 7	7	11. 7	21	7.8 (−127–207)
DOC (mgC m^{-2}CSA day^{-1})	5	713	7	852	6	−1	18	521 (−3661–3583)
Fluxes of inorganic nutrients out of cavities								
NO_x (mmol N m^{-2} CSA day^{-1})	6	2.73	8	1.70	7	1.43	21	1.9 (−2.1–5.5)
NH_4 (mmol N m^{-2} CSA day^{-1})	6	−1.50	8	−1.05	7	−0.55	21	−1.01 (−9.7 –5.9)
Dissolved inorganic nitrogen (DIN, mmol N m^{-2} CSA day^{-1})	6	1.16	8	0.64	7	0.75	21	0.83 (−11.3 −7.3)
Dissolved inorganic phosphate (DIP, mmol P m^{-2} CSA day^{-1})	6	0.33	8	0.30	7	0.31	21	0.31 (−0.26 –1.26)
DIN/DIP ratios								
Molar DIN/DIP ratio in reef water	6	13.5	8	11.4	7	14.3	21	12.4 (7.2–228)
Molar DIN/DIP ratio in cavity water	6	11.2	8	9.2	7	12.7	21	10.9 (2.5–19.2)
Average DIN flux/average DIP flux	1	3.5	1	2.1	1	2.4	3	2.7

Average values of water exchange coefficient of cavities, fluxes of organic and inorganic matter into and out of cavities, and ratios of DIN and DIP concentrations in reef and cavity water and the ratio of their fluxes. The overall averages of the combined data are listed with the total range of all values in the last column
CSA Interior cavity surface area

28% (range 1–59%) lower in cavities than in reef water. Bacterioplankton differences between reef and cavity water (= depletion in cavity water) were positively and significantly related to respective concentrations in the reef water (Pearson: $n=21$, $r=0.623$, $P<0.05$). At a higher concentration in reef water the depletion was larger. There were no significant differences in bacterial concentrations in cavity water between cavities.

Bacterioplankton depletion in cavity water decreased with increasing water exchange (Fig. 6b). Depletion did not gradually drop with increasing water exchange, but remained more or less equal between exchange rate coefficients close to 0–0.004 s^{-1}; beyond this, depletion clearly dropped. With nonlinear piecewise regression the significant threshold was established between water exchange rate coefficients of 0.0042 (case 12) and 0.0047 s^{-1} (case 13) (average 0.0045 s^{-1}) (Fig. 7). This threshold cavity water exchange coefficient occurred at flow velocities just outside cavities of 12–14 cm s^{-1}, while the average current velocity was 13.2 cm s^{-1} (11.5 cm s^{-1} minus the outlier in Fig. 5).

Bacterioplankton removal rates (fluxes into coral cavities) increased significantly with water exchange towards the threshold, and then dropped (Fig. 6c). Bacterial carbon and nitrogen removal rates ranged between 1 and 206 µmol C l^{-1} day^{-1} (0.38–178 mgC m^{-2} total interior CSA (day^{-1}), and between 0.1 and 41.2 µmol N l^{-1} day^{-1} (0.07–34.5 mg N m^{-2} CSA day^{-1}). The overall average of bacterioplankton C and N removal rate in cavities was 40.5 mg bact C m^{-2} CSA day^{-1} and 7.8 mg bact N m^{-2} CSA day^{-1}. The lowest average rates were measured in cavity BO4 (Table 1). The lowest measured rates in this cavity concurred with the lowest exchange rate coefficients established. There were no indications that the differences in bacterioplankton removal rates among cavities were due to differences in relative cover of certain groups of suspension feeders.

Dissolved organic carbon depletion

Dissolved organic carbon concentrations were not significantly different between reef and cavity water (*t* test: $n=18$, $t=1.501$, $P>0.05$), ranging from 68 to 114 and from 65 to 101 µM, respectively. DOC depletions were

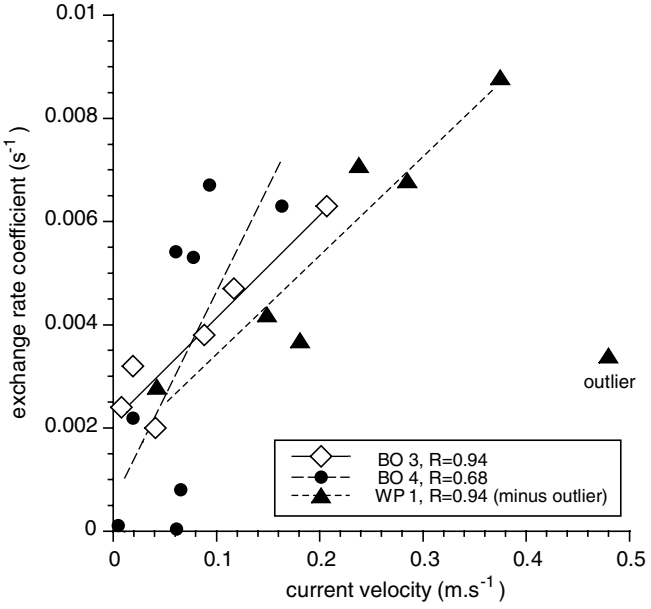


Fig. 5 Relationship between the exchange rate coefficients (s^{-1}) and the mainstream current velocity along the reef slope at 1.5 m above the bottom in front of cavities. Regression slopes of cavities were significant, but not significantly different from each other. The regression equation of the combined data without the outlier was $y=0.0019+0.019x$, multiple $R=0.79$, $P<0.05$ (not shown)

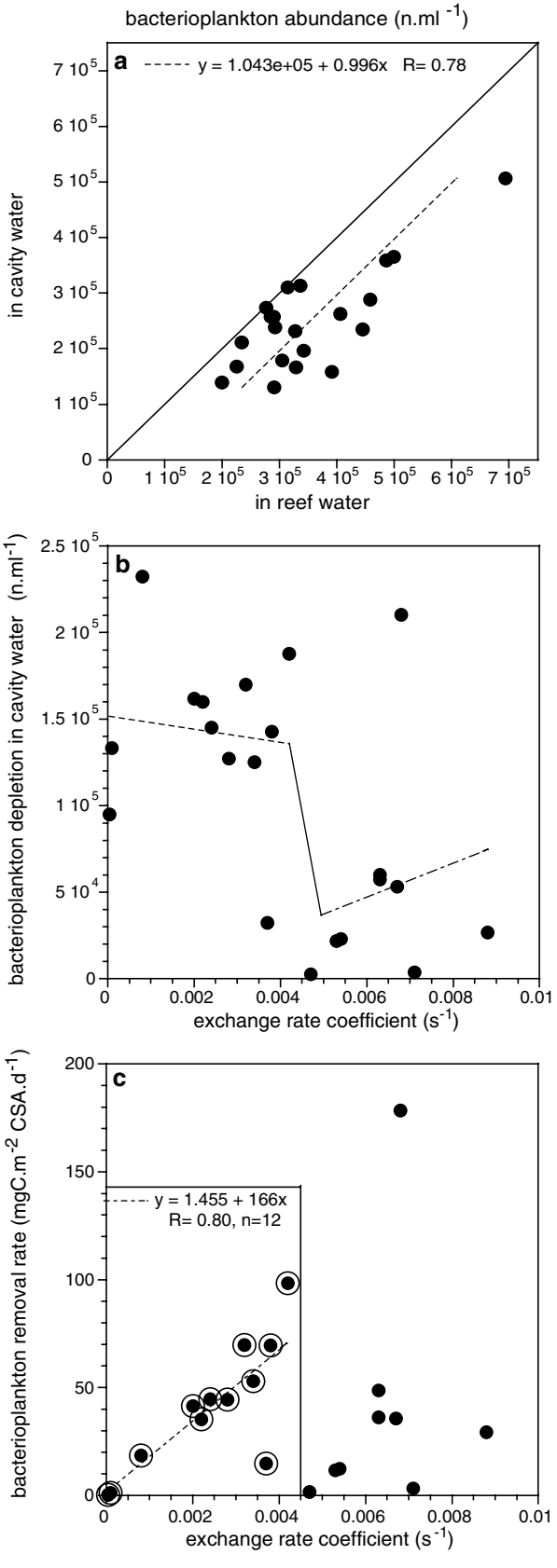


Fig. 6 Comparisons of bacterioplankton abundance between reef water and cavity water. *Diagonal line* represents the "no difference in concentration" line in the plot (**a**). Nonlinear decrease of bacterioplankton depletion (= concentration differences between reef and cavity water) in coral cavities at increasing water exchange rate coefficients. Note the truncation in the data set illustrated by the connection of two nonsignificant linear regression functions (at exchange rate <0.0045 and >0.0045 s^{-1}) (**b**). Relationship between bacterioplankton removal rate and the water exchange rate coefficient. The regression equation was applied to removal rates at exchange rates <0.0045 s^{-1} (*contoured black symbols*) (**c**). *CSA* interior cavity surface area. *R* in plot **a** and **c** refers to multiple *R*

positively and significantly related to concentrations in the reef water (Pearson: $n=18$, $r=0.803$, $P<0.01$). DOC depletions were not related to exchange rate coefficients ($P>0.05$). A broad range of DOC fluxes was found, with influxes ranging between 7.7 and -6.3 mmol C l^{-1} day^{-1} (3.6 to -3.7 gC m^{-2} CSA day^{-1}). The average fluxes for the different cavities differ substantially, with net influxes for BO3 and BO4, but no net flux for WP1 (Table 1).

Inorganic nutrient accumulation

The NO_x (NO_3 plus NO_2) concentration was significantly enhanced in cavity water compared with reef water ($n=21$, $t=-4.830$, $P<0.01$, Fig. 8a) and was on an average 0.16 µM higher in cavity than in reef water (0.21 in BO3, 0.18 in BO4, and 0.09 µM in WP1). Only in 2 of 21 experiments was the NO_x concentration in reef water higher than in cavity water. NO_3 and NO_2 concentrations were both significantly higher in cavity water than in reef water ($n=21$, $t=-4.757$, $t=-3.985$, respectively; $P<0.01$). NO_3 concentrations were on an average 0.41 µM in reef water and 0.56 µM in cavity water accounting for 90% for the NO_x.

NO_x accumulations in cavities ($C_{reef} - C_{cavity}$ is negative) were significantly related to NO_x concentrations in cavity water (Pearson: $n=21$, $r=0.565$, $P<0.01$). A high concentration in cavities coincided with a large accumulation in cavity water. NO_x accumulations in cavities were related to water exchange rate coefficients and decreased with increasing exchange (Pearson: $n=21$, $r=-0.472$, $P<0.05$, Fig. 8b).

Net efflux of NO_x from cavities increased with water exchange from low towards threshold exchange rates (Fig. 8c). The negative efflux of NO_x at exchange rate 0.0038 s^{-1} was deleted from the regression, although it was not an outlier (ANOVA). The observation that both [NH_4] and [DIN] showed outliers (ANOVA) during this experiment (see Figs. 9 and 10) justifies the deletion. At higher water exchange rates NO_x effluxes tended to decrease again. NO_x effluxes from cavities varied between -42.8 and 143 µmol l^{-1} day^{-1} (-2.05–5.54 mmol m^{-2} CSA day^{-1}). The overall average rate was 1.9 mmol m^{-2} CSA day^{-1} with the highest average rate for cavity BO3 and comparable rates for the other two cavities (Table 1).

In contrast to NO_x, the NH_4 concentrations were not significantly different between reef and cavity water considering the whole data set with one outlier removed

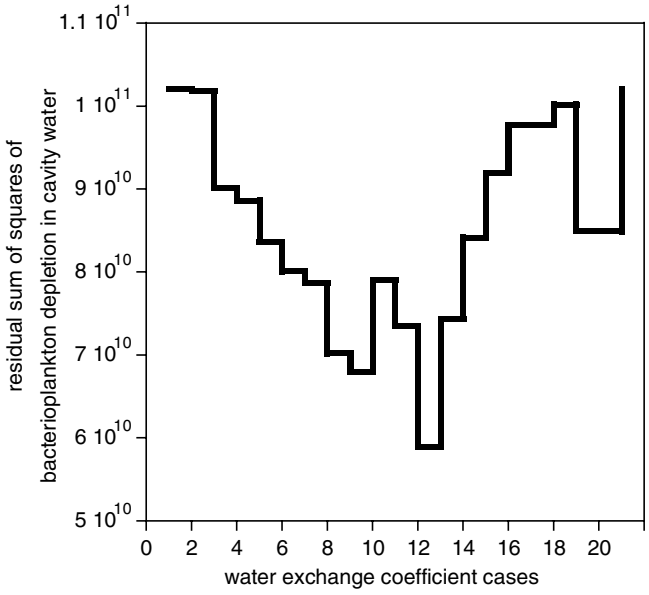


Fig. 7 Piecewise regression of the residual sum of squares of bacterioplankton depletion in cavity water on water exchange coefficient for 21 experimental cases. Cases 1–21 refer to the ranked (low–high) exchange rate coefficients, showing a significant break between case 12 and 13 (water exchange coefficients of 0.0042 and 0.0047 s^{-1}, respectively)

(Fig. 9a). At low-reef concentrations of NH_4 (< 0.25 μM), NH_4 concentrations in cavity water exceeded those in reef water (Fig. 9a); and at reef concentrations higher than > 0.25 μM, concentrations were significantly higher in reef than in cavity water (*t* test: $n = 13$, $t = 4.656$, $P < 0.01$, without the outlier in Fig. 9a). NH_4 depletions and accumulations in cavity water were not significantly related to exchange rate coefficients (Fig. 9b).

NH_4 influxes (= negative effluxes from cavities in Fig. 9c) increased with water exchange, particularly at the higher exchange rate coefficients (> 0.0045 s^{-1}). Fluxes of NH_4 range from maximal influxes of 92 μmol l^{-1} day^{-1} (5.6 mmol m^{-2} CSA day^{-1}) to maximal effluxes of 119 μmol l^{-1} day^{-1} (5.9 mmol m^{-2} CSA day^{-1}), with average influxes for all cavities (Table 1).

The DIN concentration was enhanced in cavity water (*t* test: $n = 20$, $t = -3.249$, $P < 0.01$, Fig. 10a). The average DIN concentration difference between reef (0.86 μM) and cavity water (0.96 μM) was 0.11 μM. For the cavities BO3, BO4, and WP1 separately, this was 0.23, 0.15, and 0.07 μM, respectively. The overall net influx of NH_4 and the net efflux of NO_x imply that the net outflow of DIN from cavities consists predominantly of NO_x. The DIN accumulation in cavity water decreased with increasing water exchange (Pearson: $n = 20$, $r = -0.508$ $P < 0.05$, Fig. 10b) analogous to NO_x. The net DIN efflux rate increased with water exchange (Fig. 10c). Negative effluxes of DIN at the higher range of water exchange rates coincided with enhanced influxes of NH_4 (Fig. 9c).

The DIP concentrations were significantly enhanced in cavity water (*t* test: $n = 21$, $t = -2.209$, $P < 0.05$, Fig. 11a). In reef water the average concentration was 0.07 μM and in cavity water 0.11 μM (0.09 μM without the outlier of 0.046 μM). The average difference was 0.04 μM (0.02 μM without the outlier in cavity water). The DIP accumulation increased significantly with increasing concentrations of DIP in cavity water (Pearson: $n = 21$, $r = 0.893$, $P < 0.001$). DIP accumulation in cavity water was not related to water exchange (Fig. 11b). Like the effluxes of DIN and NO_x from cavities, the net DIP efflux was positively related to the water exchange up to the threshold water exchange coefficient after deletion of the negative efflux of DIP at water exchange of 0.0038 s^{-1} (Fig. 11c). This was the same experiment in which inorganic N species gave deviating results (see above).

Relations between bacterioplankton influxes and inorganic N and P effluxes from cavities and DIN, DIP relations

We found no significant relationship between the bacterial N influx and the DIN efflux. The concentration differences between cavity and reef water for DIN and DIP were significantly related (Pearson: $n = 20$, $r = 0.631$, $P < 0.01$). The net positive effluxes of DIN, NO_x, and DIP at water exchange rates < 0.0045 s^{-1} were not related to the removal rate of bacterioplankton. The average molar DIN:DIP ratio in all three cavities was lower in cavity than in reef water. The average molar DIN:DIP ratios of fluxes were close to the molar N:P ratio in bacteria (average of different cavities range between 2.1 and 3.5, Table 1).

Discussion

It is widely recognized that cryptic biota in underwater cavities are dependent on the hydrodynamic influx of nutrients for food, and on the efflux for disposal of their waste products (e.g., Kobluk and Van Soest 1989; Gili and Coma 1998). The quantification of water fluxes between overlying water and cavity water is complex (Kays and Crawford 1993). It is difficult to determine the flow regime in irregularly shaped and blind-end coral cavities and couple this to matter fluxes. To circumvent this we determined water exchange rate coefficients in the center of the cavities at different mainstream current velocities along the reef slope. The water exchange rates of cavities increased linearly with increasing mainstream current velocity, irrespective of the geometry and size of cavities (e.g., aspect ratio). Orientation of cavity openings towards the mainstream current and turbulent energy in the vicinity of the cavity may be more important than the internal morphology of a cavity in determining exchange rates (Grant and Madsen 1979). Strong currents along the reef at station WP on 28 June placed the

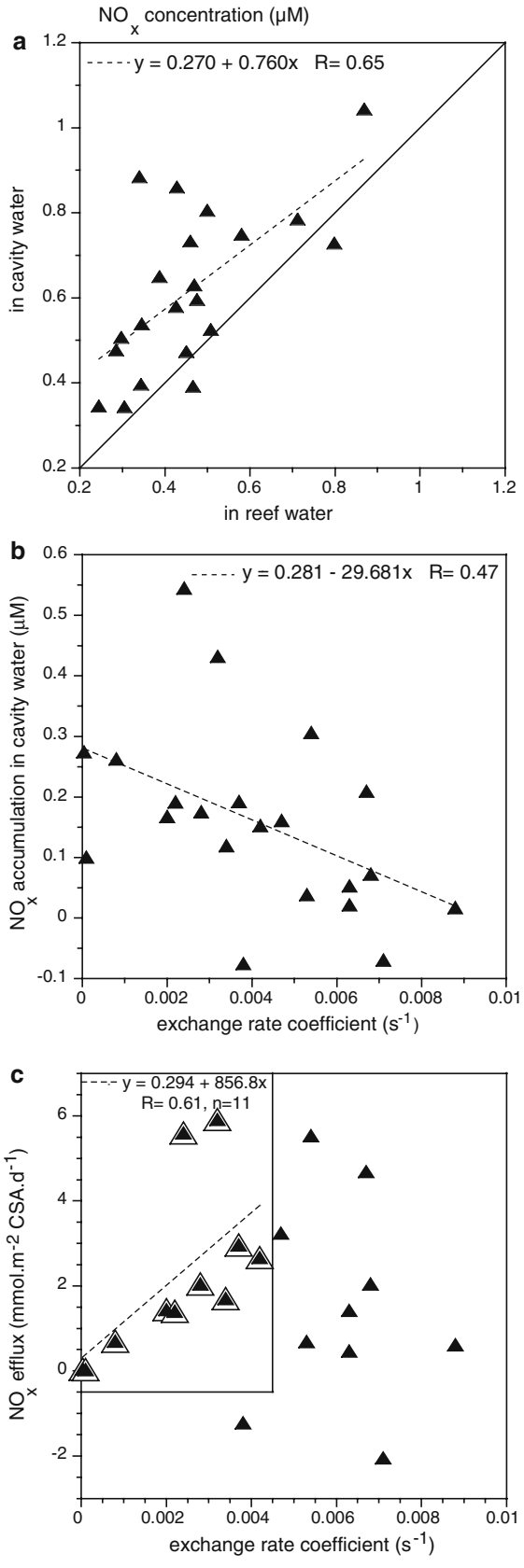


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Fig. 8 Comparisons of NO_x concentrations between reef and cavity water. *Diagonal line* represents the "no difference in concentration" line in the plot (**a**). Decrease of NO_x accumulation (= concentration differences between cavity and reef water) with increasing water exchange rate coefficient (**b**). Relationship between the NO_x efflux from cavities and the water exchange rate coefficient. The regression equation was applied to positive effluxes at exchange rates $< 0.0045\ s^{-1}$ (*contoured black symbols*) (**c**). *CSA* interior cavity surface area. *R* in plots **a**, **b** and **c** refers to multiple *R*

cavity WP1 in a leeward position, resulting in a water exchange rate much lower than expected. Water residence time in the three cavities fell in the range of 1.9 min to 7 h (exchange coefficients 0.00004–0.0088 s^{-1}). The residence time in cavity BO4 was longer than 20 min on three of the eight occasions. This result was unexpected, but corresponded with very slow mainstream currents along the reef slope during these experiments, which at that time also occurred at BO3 close to BO4. In spite of the variations, the average residence time of water in the three cavities were not significantly different (4.5, 5.0, and 3.2 min for BO3, BO4, and WP1, respectively) and were comparable to estimated residence times in coral cavities in the Red Sea with comparable coelobite cover (Richter and Wunsch 1999).

Bacterioplankton depletion and removal rates

Coral cavities are definitely sinks for bacteria. In all experiments we found bacterioplankton depletion of cavity water. This is not surprising considering the high cover of suspension feeders in cavities that can feed on bacteria (e.g., Buss and Jackson 1981; Coma et al. 2001) and the high cover and efficiency of sponges among them in taking up bacteria (Kötter and Pernthaler 2002). Relations between concentrations in reef and cavity water, and between bacterioplankton depletion in cavity water and reef water concentration suggest that the passing water is the main source of the bacterioplankton supply to cavity biota.

It is evident that bacterioplankton depletion (= reef concentration minus the cavity concentration) decreases with increasing exchange across the range of water exchange coefficients measured in cavities. At a closer look there was a significant break in the data set (piecewise regression analysis). At exchange rates smaller than $0.0045\ s^{-1}$, differences in bacterioplankton abundance did not decrease with increasing water exchange as would have been expected on the basis of constant pumping activities and bacterioplankton retention efficiency. To maintain these differences in bacterioplankton abundance with increasing water exchange, their abundance in the supply water should increase. As this was not the case, it is likely that the cryptic suspension feeding community adjusted its bacterioplankton capture rate to the food supply. This could have been achieved by increasing the retention efficiency and, or the pumping activity with increasing water exchange. The latter is less likely, because pumping activities have been reported to be constant in thin-walled suspension

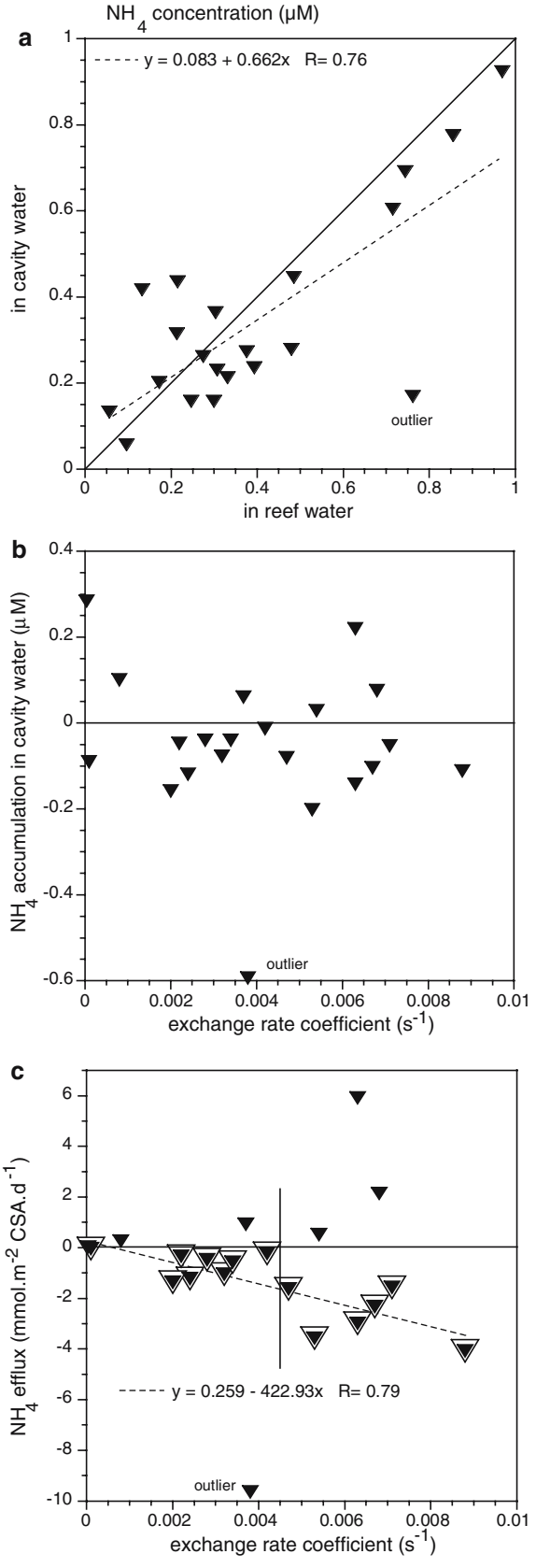

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Fig. 9 Comparison of NH_4 concentrations between reef and cavity water. The regression equation includes the indicated outlier. *Diagonal line* represents the "no difference in concentration" line in the plot (**a**). Nonrelationship of NH_4 depletion (= concentration differences between cavity and reef water) with increasing water exchange rate coefficient (**b**). Relationship between the net NH_4 efflux from cavities and the water exchange rate coefficient. The regression equation was applied to negative effluxes without the outlier (= influxes, *contoured black symbols*) (**c**). The outliers in **a**, **b**, and **c** refer to the same data pair of NH_4 concentration, with a disproportionately high [NH_4reef] versus [NH_4cavity]. *CSA* interior cavity surface area. *R* in plots **a** and **c** refers to multiple *R*

feeders (e.g., Reiswig 1971a, b; Ribes et al. 1999), irrespective of food concentration (Duckworth et al. 2003). Results suggest the dependence of consumption rate on water exchange and thus flow speed, in accordance with Fréchette et al. (1989). The threshold of 0.0045 s^{-1} was surprisingly close to the average exchange rate of 0.0041 s^{-1} of cavities, as if the suspension feeding cryptic community is adapted to the flow regime in cavities. Wildish and Kristmanson (1997) state that seston uptake rate of any benthic suspension feeder shows an optimum at intermediate values of the ambient near bottom current speed, based on physiological considerations. That the feeding strategy of the heterogeneous cryptic community in coral cavities seems to agree with the concept was remarkable. Apparently there exist exchange rates, that coincide with beneficial flows for prey capture or particle retention at which the uptake is optimized. Optimal flow rates for prey capture have been reported for corals and other suspension feeders (e.g., Riisgård and Larsen 1995; Fabricius et al. 1995; Sebens et al. 1998).

Beyond a water exchange coefficient of 0.0045 s^{-1} no further adjustments appear to be made to exploit the food more efficiently. On the contrary, bacterioplankton depletion in cavity water dropped suddenly to significantly lower levels. Rapid water exchange (i.e., flux) may negatively influence the filtration efficiency of cryptic sponges (Kötter and Pernthaler 2002). High flow forces in general may interfere with seston capture processes (Wildish and Kristmanson 1997). Therefore, it is likely that flow-induced energetic bounds to removal rates may have played a role in the sharp drop in differences in bacterioplankton beyond the exchange rate coefficient of 0.0045 s^{-1} (Fig. 6).

Under optimal water exchange conditions (0.003–0.0045 s^{-1}) bacterioplankton removal rates vary between 50 and 100 mgC m^{-2} CSA d^{-1}. Reef water concentrations were quite low during the experiments (average 353×10^3 bacteria ml^{-1}) compared with abundances found throughout the year in Curaçao reef waters (Gast et al. 1999). This implies that removal rates can be substantially higher. Beyond a water exchange rate coefficient of 0.0045 s^{-1} rates drop to 20–30 mgC m^{-2} CSA day^{-1}. At exchange rate coefficients of less than 0.0005 s^{-1} bacterioplankton removal rates were close to zero. Bacterioplankton removal rates in open cavities were 35–50% higher than removal rates in cavities of which the front opening was closed with a cotton cloth (Scheffers et al. 2004).

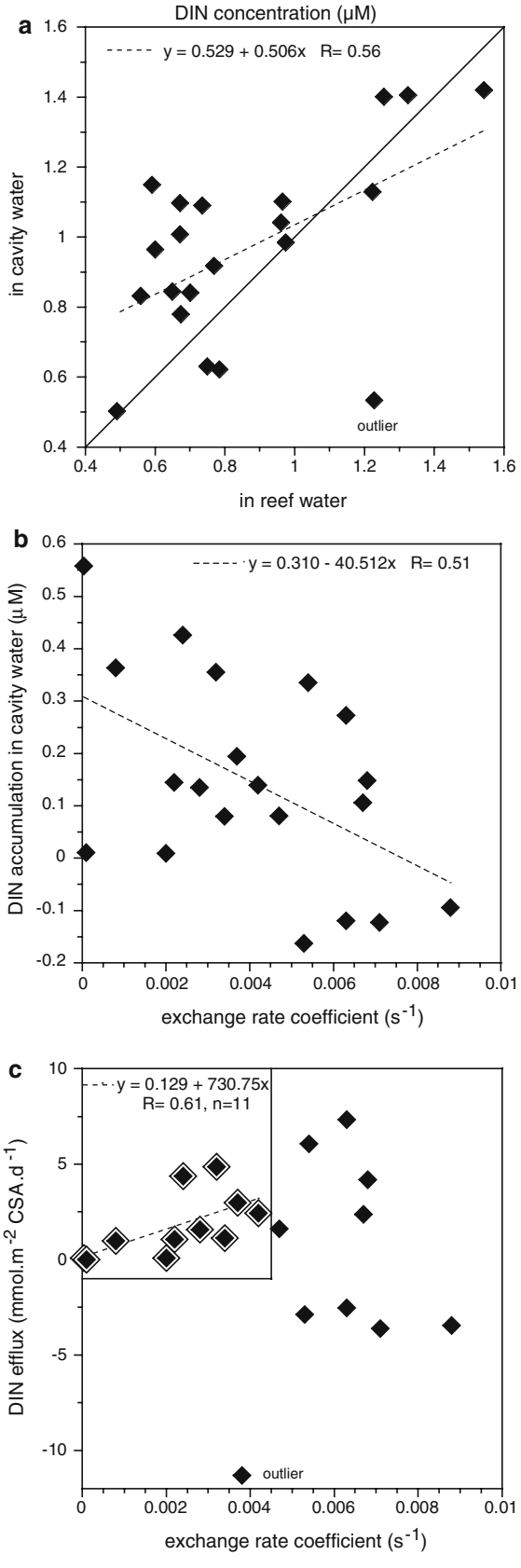

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Fig. 10 Comparisons of dissolved inorganic nitrogen (DIN) concentrations between reef and cavity water. The regression equation includes the indicated outlier. *Diagonal line* represents the "no difference in concentration" line in the plot (**a**). Decrease of DIN accumulation (= concentration differences between cavity and reef water) with increasing water exchange rate coefficient without the outlier of −0.7 µM (not shown) in previous plot (**b**). Relationship between the DIN efflux from cavities and the water exchange rate coefficient. The regression equation was applied to positive effluxes at exchange rates $< 0.0045\ s^{-1}$ (*contoured black symbols*) (**c**). The outliers in **a**, **b**, and **c** refer to the same data pair of DIN concentration with a disproportionately high [DINreef] versus [DINcavity]. *CSA* interior cavity surface area. *R* in plots **a**, **b**, and **c** refers to multiple *R*

Underestimation of fluxes in "closed" cavities is conceivable because of the "long" water residence time (no water exchange during the experiment) compared with that in open cavities. Extrapolating our conservative overall average rate to the maximum cryptic surface on reefs per meter square projected reef at 15 m depth (maximum 8 m^2 cryptic surface area m^{-2} vertically projected reef, Scheffers et al. 2004) renders a bacterioplankton removal rate of 324 mgC m^{-2} projected reef area per day. This high demand cannot be met by the bacterioplankton production along Curaçao reefs, which is low (Gast et al. 1999). Besides bacterioplankton, cryptic suspension feeders also feed on phytoplankton (Richter and Wunsch 1999; Van Duyl et al. 2002) and probably also on protists and detritus (Gast et al. 1998; Wild et al. 2004). The particulate organic carbon removal by cryptic biota may well be twice as large as the bacterioplankton removal in coral cavities and thus may exceed the net production of coral reefs (e.g., Crossland et al. 1991). Therefore, it is likely that exogenous advection of particulate organic matter to the reef from the adjacent oceanic waters, i.e., an allochthonous source is required to supplement the nutrition of suspension feeders on reefs in cryptic habitats.

DOC depletion

Unlike bacterioplankton, DOC depletion and accumulation in cavity water was not a function of exchange rates. DOC concentrations in reef water (ca 80 µM) exceeded concentrations of C in bacterioplankton biomass by up to 100 times. Up to 10–30% of bulk DOC is labile and readily available in reef waters (Van Duyl and Gast 2001). DOC uptake by microbes living in the water column and on the substratum can be substantial (e.g., Carlson et al. 2002; Fisher 2003), but also DOC uptake by higher trophic levels, such as sponges, ascidians, and polychaetes has often been proposed (e.g., Jørgensen 1976; Gili and Coma 1998). Yahel et al. (2003) report bulk DOC to be the major source for carbon of a symbiont-bearing sponge. The aforementioned groups of organisms are well represented in coral cavities (Kobluk and Van Soest 1989; Wunsch et al. 2002; Scheffers 2005). Therefore, we considered DOC to be a potential source of energy for the cryptic biota. Consistent patterns of depletion

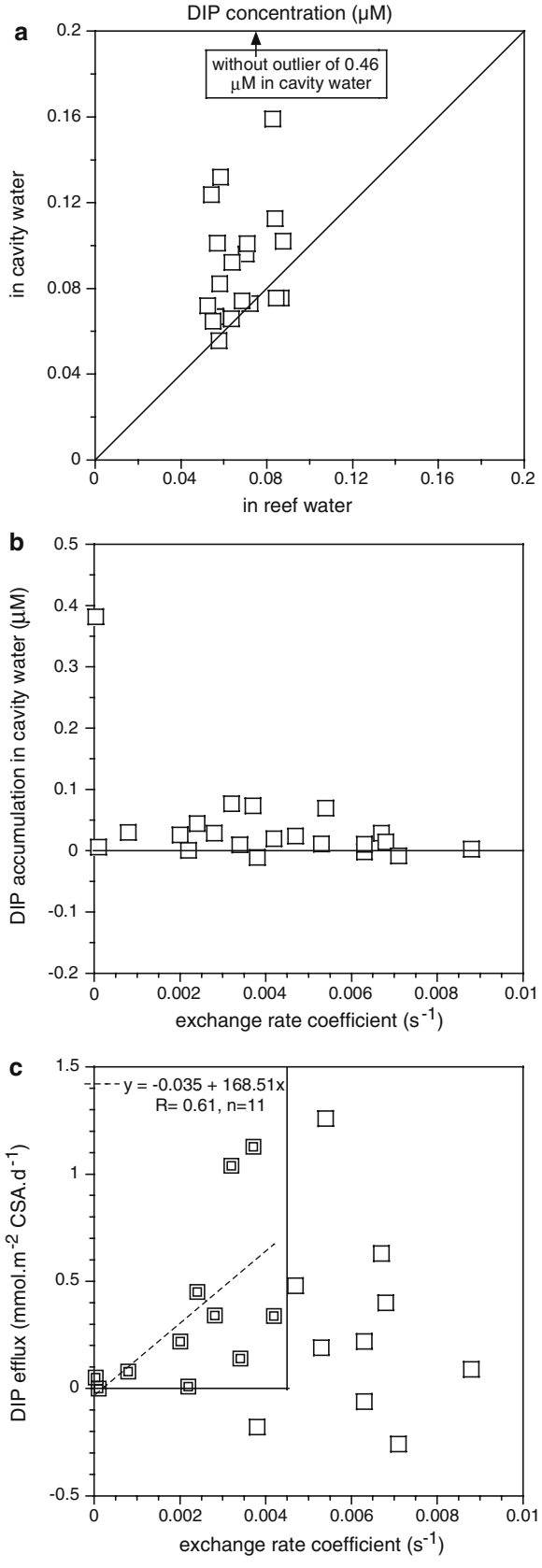

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Fig. 11 Comparisons of dissolved inorganic phosphate (DIP) concentrations between reef and cavity water. *Diagonal line* represents the "no difference in concentration" line in the plot (**a**). Nonrelationship of DIP accumulation (= concentration differences between cavity and reef water) with increasing water exchange rate coefficient (**b**). Relationship between the DIP efflux from cavities and the water exchange rate coefficient. The regression equation was applied to positive effluxes at exchange rates $< 0.0045\ s^{-1}$ (*contoured black symbols*) (**c**). *CSA* interior cavity surface area. *R* in plot **c** refers to multiple *R*

of DOC by cavity biota could not, however, be established. DOC depletion in cavity water was usually small and close to the confident limits of DOC measurements (Sharp et al. 2002). In spite of this, the relation between DOC depletion in cavity water and the reef concentration suggests a concentration-related removal. Moreover, DOC influxes in cavities BO3 and BO4 agree with preliminary results of DOC removal in closed cavities at BO (J.M. De Goeij and F.C. Van Duyl, unpublished data).

Inorganic nutrient accumulation and fluxes

Light intensities drop linearly in coral cavities from ca 1–5 $\mu E\ m^{-2}\ s^{-1}$ in the front opening to less than 0.1 $\mu E\ m^{-2}\ s^{-1}$ at the rear (Scheffers 2005). This implies that photosynthetic activity of primary producers, such as calcareous algae (ca 19% cover in cavities), cannot be ruled out completely in playing a role in nutrient dynamics in cavity water.

Dissolved inorganic nitrogen ($NH_4 + NO_x$) enhancement in coral cavities was in the form of NO_x and not NH_4. The extent of accumulation of NO_x in cavity water depended on water exchange and cavity concentration of NO_x. This implies that a consistent NO_x generation by mineralization and nitrification occurs in cavities, which apparently exceeds the loss of NO_x to assimilation and denitrification in the reef framework (Tribble et al. 1990). NO_x accumulations in cavity water decreased linearly with increasing water exchange, suggesting conservative mixing. The sandy bottom as well as the biota on the cavity walls are considered to contribute to this NO_x generation.

Net NO_x effluxes from cavities peaked with rates of 4–6 mmol m^{-2} CSA day^{-1} between water exchange rates of 0.0025 and 0.0065 s^{-1}, and are comparable with NO_x fluxes from coral cavities in other reef habitats (e.g., Szmant-Froelich 1983; Rasheed et al. 2002). The overall average efflux is substantially lower (1.9 mmol m^{-2} CSA day^{-1}), but still 30% higher than the average NO_x efflux in closed cavities (Scheffers et al. 2004). The often-reported, enhanced NO_x concentrations in reef overlying waters (e.g., Webb et al. 1975; Andrews and Müller 1983; Hopkinson et al. 1987; Gast et al. 1999) may at least be partly generated by cavity biota. After all, the cryptic interface of well-developed reefs and on reef slopes usually exceeds the exposed surfaces (Richter et al. 2001; Scheffers et al. 2004). NO_x release from cryptic surfaces can theoretically provide in the entire NO_x enhancement in reef overlying waters, assuming an on-reef water residence time of 4–24 h and an average water column depth of 10 m.

Dissolved inorganic nitrogen accumulation in cavity water depends on water exchange as it does for the NO_x. The net NO_x efflux usually exceeded the net DIN efflux (overall average 0.83 mmol m^{-2} CSA day^{-1}). Net influxes of NH_4 from reef water are required to compensate for this difference between DIN and NO_x effluxes. The NH_4 distribution between reef and cavity water was evidently different from that of DIN and NO_x: NH_4 did not accumulate in cavities. This agrees with previous studies of NH_4 in cavity water (Gast et al. 1998; Scheffers et al. 2004). Net influxes of NH_4 were evident at higher water exchange coefficients (>0.025 s^{-1}), possibly because removal or nitrification by cavity biota was enhanced by the increase in through flow. The fate of ammonium may be assimilation by cavity biota, nitrification or absorption (Tribble et al. 1990). For nitrification, NH_4 is oxidized to NO_2 and subsequently to NO_3, which presumably occurs while flowing past the biota on cavity substrata. Nitrification and net release of NO_3 have been reported for reef sediments (Capone et al. 1992; Rasheed et al. 2002) and for reef sponges (Corredor et al. 1988; Diaz and Ward 1997). Together these bottom components cover more than 50% of the interior cavity substratum area at our sites (Fig. 2). Ascribing the average NO_x efflux exclusively to these cover components renders a flux of up to 3.6 mmol NO_x m^{-2} day^{-1}, which falls within the range of fluxes reported for reef sediments and open reef sponges (Corredor et al. 1988; Capone et al. 1992; Diaz and Ward 1997; Rasheed et al. 2002).

Like the DIN and NO_x, DIP accumulated in cavity water, pointing to a net overall release of DIP from the cavity biota. DIP accumulation, however, like the bacterioplankton depletion, did not drop at increasing water exchange in cavities towards the threshold water exchange. Therefore, DIP release from cavity biota may partly reflect the mineralization of bacterioplankton by suspension feeders at water exchange rates below the threshold exchange of 0.0045 s^{-1}. Mineralization of bacterioplankton by suspension feeders contributes to a relative increase of DIP compared with DIN in cavity water, because bacteria are rich in P compared with phytoplankton and metazoans (Sterner and Elser 2002; Kirchman 2000). Moreover, bacterioplankton may be a significant part (more than 30%) of the total particulate organic matter mineralized in cryptic habitats, apart from phytoplankton (Richter and Wunsch 1999; Van Duyl et al. 2002). Therefore, the lower DIN:DIP ratio in cavity (10.9) than in reef water (12.4) was not surprising.

We showed that water exchange in cavities is crucial for optimization of bacterioplankton removal by cryptic biota and the release of inorganic nutrients from cavities. Consumption and mineralization of particulate organic matter peaked in coral cavities at water exchange rates of 0.003–0.005 s^{-1}.

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