Release of dissolved organic carbon and nitrogen by the zooxanthellate coral *Galaxea fascicularis*

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**ABSTRACT**

Corals are known to release large amounts of particulate and dissolved organic carbon (POC and DOC) and nitrogen (PON and DON). Production of POC and PON in the form of mucus has been relatively well studied, but very few data are available on the release of DOC and DON by corals. In order to investigate several aspects of carbon and nutrient cycling in corals, release of DOC and DON by fed and unfed colonies of the zooxanthellate coral *Galaxea fascicularis* (Linnaeus 1767) was measured in the laboratory under controlled conditions. Colonies were either fed with *artemia* or supplied with nitrogen- and phosphorus-enriched seawater. We measured DOC and DON fluxes from corals using the high temperature catalytic oxidation method and DOC release as 14C-photosynthate using a radioisotope technique. Corals released significant amounts of dissolved organic matter (DOM). Two large release peaks were observed in mid-morning and mid-afternoon. DOC concentrations increased from ca 100 \(\mu M\) (background level) to 300–1700 \(\mu M\), depending on the size of the colony and the trophic status. DON concentrations also increased from 15 to 120 \(\mu M\). Release rates varied from 2–3 \(\mu mol\) DOC and 0.5–0.6 \(\mu mol\) DON (mg protein\(^{-1}\)) \(d^{-1}\) for the unfed colonies to 13–25 \(\mu mol\) DOC and 1–3 \(\mu mol\) DON (mg protein\(^{-1}\)) \(d^{-1}\) for the *artemia*-fed colonies to 4–6 \(\mu mol\) DOC and 0.2–1.3 \(\mu mol\) DON (mg protein\(^{-1}\)) \(d^{-1}\) for the nutrient-enriched colonies. Fed corals therefore released more DOC than unfed colonies, but tended to conserve organic nitrogen, suggesting that heterotrophic nutrition may serve corals as a source of new nutrients. Calculations of the carbon balance for the unfed colonies showed that DOC release represents ca 14% of the net daily photosynthetically fixed carbon. Following each peak in release, concentrations of DOM fell back to routine background levels. The role of free-living, epibiotic and/or intracellular bacteria in the uptake of DOM was therefore investigated. Colonies were labelled with 14C-bicarbonate and the subsequent release of 14C-DOM was followed in filtered seawater treated with and without prokaryotic inhibitors. No subsequent uptake of 14C-DOM was observed in the presence of inhibitors, suggesting that bacteria may play an important role in DOM uptake. This process may lead to tight nutrient recycling within coral colonies and may enable corals to thrive in oligotrophic waters.

**KEY WORDS:** Corals · Dissolved organic carbon and nitrogen · Release · Uptake

**INTRODUCTION**

Coral reef environments display a high gross primary production relative to the open ocean (Odum & Odum 1955) and support a large variety of organisms. This high production has been explained by tight nutrient recycling within the reef ecosystem (Smith 1984). Corals are known to release large amounts of nutrients (Crossland 1987, Coffroth 1990) as particulate and dissolved organic carbon (POC and DOC) and nitrogen (PON and DON). The POC and PON are generally referred to collectively as mucus. An important fraction (up to 40%) of the photosynthetically fixed carbon translocated from the zooxanthellae to the coral host is released into the surrounding waters as mucus (Crossland et al. 1980, Edmunds & Davies 1986, Crossland 1987), mucus sheets (Coffroth 1988, 1990) or flocs (Ducklow & Mitchell 1979). Mucus varies greatly in biochemical composition (Ducklow & Mitchell 1979, 1988).
MATERIAL AND METHODS

Coral preparation. Fourteen colonies of *Galaxea fascicularis* were prepared as described by Al-Moghrabi et al. (1993): terminal portions of branches were cut with bone cutters from parent colonies and suspended on nylon threads in aquaria illuminated with metal halide lamps (HQI, 400 W). Constant irradiance of 200 μmol photons m⁻² s⁻¹ was provided on a 12 h photoperiod. Aquaria were supplied with heated (25°C) Mediterranean seawater. This water had low nutrient concentrations (<0.3 μM ammonium, <1 μM nitrate, <0.1 μM phosphorus) and chlorophyll a content (0.2 to 0.3 μg C l⁻¹), an aragonite saturation state of 3.1 to 3.7 (National Bureau of Standards: NBS), a pH of 8.1 to 8.2 and a dissolved inorganic carbon content of 2.3 to 2.4 mmol kg⁻¹. After 1 mo, tissue had grown on the exposed skeleton, and coral fragments were entirely covered with new tissue. Colonies were then transferred to three 5 l tanks and maintained under equivalent conditions of temperature and light.

In the first tank ('artemia-fed'), 3 colonies were fed 3 times a week over 6 wk with frozen adult *Artemia* sp. (Al-Moghrabi et al. 1993). Colonies were isolated for 3 h in three 5 l beakers during feeding. In the tank, nutrient concentrations were measured every 3 d with an Alliance I1 autoanalyser following the method of Tréguer & Le Corre (1975). Concentrations remained low during the experiment: <0.2 μM N-NH₄, <0.1 μM P-PO₄, <0.2 μM N-NO₂ and 1 to 1.5 μM N-NO₃.

In the second tank ('NP fed'), 3 colonies were maintained over 6 wk in seawater enriched with inorganic nitrogen and phosphorus. Seawater and stock solutions of NH₄Cl and KH₂PO₄ were continuously pumped into the tank with a peristaltic pump in order to obtain final concentrations of 1 μM N-NH₄ and 0.3 μM P-PO₄. Nutrient concentrations were also measured every 3 to 4 d and were 0.9 to 1.2 μM N-NH₄, 1 to 1.5 μM N-NO₃, 0.3 to 0.5 μM P-PO₄ and <0.2 μM N-NO₂.

In the third tank ('unfed'), 8 colonies were maintained over 6 wk in nutrient-poor Mediterranean seawater (concentrations were comparable to those measured in the 'artemia-fed' tank, t-test, p < 0.05). Three colonies were used in the first experiment to compare their rates of DOM release with those of the fed colonies. The other 5 colonies were used in radioisotope experiments.

Measurements of DOC and DON fluxes using the HTCO method. Three colonies from each tank were incubated in three 2 l beakers containing 0.22 μm filtered seawater (FSW). Colonies were rinsed carefully with FSW to remove bacteria. Beakers were incubated in a thermoregulated bath (26°C) illuminated with a metal halide lamp providing a constant irradiance of 200 μmol m⁻² s⁻¹. The medium was continu-
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Lowry et al. (1951). The standard curve was established using bovine serum albumin as the standard, and absorbance was measured at 750 nm using an Alliance autoanalyzer. Chlorophyll a and c2 were extracted twice into 100 % acetone (24 h at 4°C). The extracts were centrifuged at 11 000 rpm (10 000 x g) for 10 min, and the absorbances were measured at 630, 663 and 750 nm. Chlorophyll concentrations were computed according to the spectrophotometric equations of Jeffrey & Humphrey (1975).

Organic carbon release with 14C-bicarbonate labeling. Radioisotope experiments were performed on 5 colonies of ‘unfed’ Galaxea fascicularis in order to confirm trends observed during the first set of experiments.

Three colonies were incubated over 12 h in 3 beakers containing 100 ml of FSW and 100 µCi (0.37 GBq) of 14C-bicarbonate (total radioactivity: 2 ± 0.1 × 10⁶ dpm). Beakers were maintained at a constant temperature of 26°C and were illuminated with a metal halide lamp providing constant irradiance (200 µmol m⁻² s⁻¹). At the end of the incubation, total radioactivity was measured in the incubation medium (0.7 ± 0.3 × 10⁸ dpm). Colonies were carefully washed with FSW and kept overnight in an open-system aquarium. They were then transferred the next day to 3 beakers containing 100 ml FSW. The release of labelled organic carbon into the incubation medium was investigated from 10:00 to 18:00 h; samples (100 ml) were taken at intervals of 15 to 30 min. The CO₂ released was then measured using a non-dispersive infra-red detector. Standard curves were constructed by injecting known amounts of potassium phthalate or nitrate (DON curves) dissolved in ultra-pure, acidified and air-purged water. Data were corrected for blanks by injection of ultra-pure water. The volume of incubation water decreased during the experiment as samples were regularly taken. The amount of DOC and DON release was therefore calculated by converting the concentrations to total amount of DOC and DON in the experimental beaker.

Rates of net photosynthesis and respiration were measured by a single colony in each tank over 24 h. Colonies were incubated in a perspex chamber containing a polarographic oxygen sensor (Ponselle) immersed in a thermoregulated water bath (25°C). The chamber was filled with FSW and stirred continuously with a magnetically coupled stirring bar. Light was provided by a 400 W (Philips, HPIT) metal halide lamp. The oxygen sensor was calibrated before each experiment against air-saturated seawater and a saturated solution of sodium dithionite (zero oxygen). Oxygen was recorded every minute using a Li-Cor LI-1000 datalogger. At the end of the experiments, colonies were frozen pending determination of the protein and chlorophyll a concentrations. Tissues were solubilized in 1 N NaOH at 90°C for 30 min, and the protein content was measured as described by Lowry et al. (1951). The standard curve was established using bovine serum albumin as the standard, and absorbance was measured at 750 nm using an Alliance autoanalyzer. Chlorophyll a and c2 were extracted twice into 100 % acetone (24 h at 4°C). The extracts were centrifuged at 11 000 rpm (10 000 x g) for 10 min, and the absorbances were measured at 630, 663 and 750 nm. Chlorophyll concentrations were computed according to the spectrophotometric equations of Jeffrey & Humphrey (1975).

Role of bacteria in the removal of DOM released by corals. In order to investigate the uptake of DOC by free-living heterotrophic bacteria, 20 ml of incubation medium was sampled from each beaker of the previous radioisotope experiment, following the maximum release of 14C. Samples were incubated separately for 5 h. Sub-samples (3 ml) were taken 3 times during the incubation, Millipore filtered (0.22 µm) and counted for radioactivity. Concentrations of bacteria were determined in each beaker at the beginning and end of each incubation: 2 ml samples were fixed using borax buffered formaldehyde (2% v:v final concentration) and stained with DAPI (4’6 diamidino-2-phenylindole, Porter & Feig 1980). Bacteria were then filtered onto 0.22 µm black Nuclepore™ filters and stored at −20°C.
Organisms were counted at $10^3$ magnification under UV excitation with a Leica epifluorescence microscope. The uptake of labelled organic carbon by epibiotic (Trench 1974) and/or intracellular bacteria was also investigated with 2 colonies of unfed Galaxea fascicularis, prepared as described above. Colonies were transferred the day after labelling to beakers containing 100 ml FSW and 300 $\mu$g ml$^{-1}$ of a mixture of antibiotics (Sigma Co.) containing penicillin (10$^4$ units), streptomycin (10 mg) and amphotericin B (25 $\mu$g). Preliminary experiments were performed on cultures of marine bacteria to determine the concentration of antibiotics needed to obtain a total inhibition of the bacterial growth. Results showed total inhibition of growth at a concentration of 100 $\mu$g ml$^{-1}$. The release of labelled organic carbon in the incubation medium was investigated from 09:00 to 19:00 h. Radioactivity was measured immediately as described above.

Finally, the abundance of epibiotic and intracellular bacteria in the tissues of 2 small colonies of Galaxea fascicularis was investigated. Colonies were thoroughly washed with 0.22 $\mu$m FSW; tissues were removed with a Waterpik and homogenized. Bacterial concentration was determined under epifluorescence microscopy after DAPI staining.

**RESULTS**

**DOC and DON release measured using the HTCO method**

Initial concentrations of DOC in the experimental water were low: 100 to 50 $\mu$mol (Figs. 1, 2 & 3). Similar diurnal patterns of DOC flux were observed under the 3 experimental conditions (fed and unfed organisms), with 1 or 2 important release events generally observed in mid-morning and mid-afternoon. The total amount of DOC released during each peak varied according to the experimental conditions and the size of the colony: 100 to 400 $\mu$mol DOC for the 'unfed', 400 to 1700 $\mu$mol DOC for the 'artemia-fed', and 250 to 400 $\mu$mol DOC for the 'NP-fed' organisms (Figs. 1, 2 & 3). The daily net release rates were ca 2.20 to 3.20 $\mu$mol (mg protein)$^{-1}$ d$^{-1}$ for 'unfed', 13 to 25 $\mu$mol DOC (mg protein)$^{-1}$ d$^{-1}$ for 'artemia-fed' and 3.90 to 5.80 $\mu$mol DOC (mg protein)$^{-1}$ d$^{-1}$ for 'NP-fed' organisms (Table 1). These rates were significantly different according to the coral nutritional status (t-test, p < 0.05). Within 2 h following each peak, DOC concentration fell back to routine background levels (Figs. 1 & 2); for the 'NP-fed' colonies, a small quantity (50 to 100 $\mu$mol C) accumulated in the seawater (Fig. 3). No DOC release was observed during the nighttime incubation for fed colonies (Fig. 4).

DON fluxes followed the same pattern as the DOC fluxes. The initial concentration was low: 10 to 15 $\mu$mol. For the 'unfed' and 'artemia-fed' colonies, 1 or 2 release events were observed during the incubation, occurring approximately at the same time as the DOC release (Figs. 1 & 2). Several DON releases occurred in the 'NP-fed' specimens (Fig. 3). The total amount of DON released during each peak varied according to the size of the colony and the experimental conditions: 15 to 70 $\mu$mol for the 'unfed', 50 to 120 $\mu$mol for the 'artemia-fed', and 20 to 40 $\mu$mol for the 'NP-fed' organisms. The daily release rates were 0.50 to 0.60 $\mu$mol DON (mg protein)$^{-1}$ d$^{-1}$ for 'unfed', 1 to 3 $\mu$mol DON (mg protein)$^{-1}$ d$^{-1}$ for 'artemia-fed' and 0.20 to 1.30 $\mu$mol DON (mg protein)$^{-1}$ d$^{-1}$ for 'NP-fed' organisms (Table 1). These rates were not significantly different (t-test, p =
Fig. 2. Changes in total DOC and DON content in seawater during the incubation of 3 'artemia-fed' colonies (referred to as A, B and C). DON determination was not performed with colony A.

Fig. 3. Changes in total DOC and DON content in seawater during the incubation of 3 'NP-fed' colonies (referred to as A, B and C).

0.20 to 0.70). In a fashion similar to that of DOC, following each peak, DON concentration fell back to routine background levels. The C:N ratio of DOM was very low during the peak of release (between 2.5 and 4.5) in the 3 experiments but increased after the peak and varied from 2.5-4.5 to 12-13 during the whole experiment.

Inorganic nitrogen concentrations in the experimental beakers did not change significantly from the beginning to the end of the incubation ($p < 0.05$). Nutrient concentrations varied between 0 and 0.2 μM for nitrite, 0.2 and 0.5 μM for ammonium, and 0.4 and 0.7 μM for nitrate. The rates of net photosynthesis and dark respiration were almost constant (Fig. 5). Net photosynthesis and dark respiration were, respectively, 0.45 to 0.52 μmol O$_2$ h$^{-1}$ (mg protein)$^{-1}$ and 0.26 to 6.30 μmol O$_2$ h$^{-1}$ (mg protein)$^{-1}$. The total amount of carbon fixed varied between 291 and 355 μmol C (equal to 44 and 47 μg C [mg protein$^{-1}$]).

**DOC release measured using $^{14}$HCO$_3$**

One or 2 peaks of $^{14}$C organic matter release were observed during the incubation of the colonies in FSW (Fig. 6). The timing of these peaks was similar to that observed during the HTCO experiments. The total labelled carbon release produced 3-4 × 10$^5$ dpm. After the peak, the concentration decreased over 1 to 2 h. No significant $^{14}$C organic carbon uptake by free-living bacteria was detected (Table 2). However, the concentration of bacteria was low (ca 4 to 7 × 10$^3$ bacteria ml$^{-1}$), due to prior rinsing of corals and filtration of the medium (0.22 μm).

The pattern of $^{14}$C organic carbon release was different for colonies incubated in FSW containing antibiotics (Fig. 7). The organic carbon accumulated in the incubation medium, reached a plateau and remained stable for at least 3 to 5 h. No decrease in the amount of

**Table 1. Galaxea fascicularis. Protein and chlorophyll contents, dissolved organic carbon (DOC) release rates (μmol DOC [mg protein$^{-1}$ d$^{-1}$]) and dissolved organic nitrogen (DON) release rates (μmol DON [mg protein$^{-1}$ d$^{-1}$]) for the studied colonies**

<table>
<thead>
<tr>
<th>Expt</th>
<th>Colony</th>
<th>Protein (mg)</th>
<th>Chlorophyll (mg)</th>
<th>DOC release rates</th>
<th>DON release rates</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Unfed'</td>
<td>A</td>
<td>74.8</td>
<td>2.11</td>
<td>2.20</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>97.2</td>
<td>2.04</td>
<td>3.10</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>58.8</td>
<td>0.68</td>
<td>3.20</td>
<td>0.50</td>
</tr>
<tr>
<td>'Artemia-fed'</td>
<td>A</td>
<td>76.5</td>
<td>2.02</td>
<td>19.50</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>106.9</td>
<td>2.15</td>
<td>24.50</td>
<td>1.20</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>53.8</td>
<td>0.65</td>
<td>12.70</td>
<td>2.80</td>
</tr>
<tr>
<td>'NP-fed'</td>
<td>A</td>
<td>72.2</td>
<td>1.98</td>
<td>5.26</td>
<td>1.30</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>101.5</td>
<td>2.08</td>
<td>5.80</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>56.8</td>
<td>0.65</td>
<td>3.90</td>
<td>0.60</td>
</tr>
</tbody>
</table>
DISCUSSION

Results obtained in this study using 2 different techniques (HTCO and radiolabelling of photosynthates) confirm that scleractinian corals may be important producers of dissolved organic carbon and nitrogen. Production of DOM can be an important contribution to reef trophodynamics as it constitutes a direct input of nutrients (especially nitrogen) to the reef detrital pool.

The release of DOM from 'unfed' corals is likely to be a by-product of phototrophic nutrition (Muscatine et al. 1984) and could be controlled by the host. Muscatine et al. (1972) indeed showed that a host factor stimulates the excretion of organic compounds by zooxanthellae in vitro. We still have no explanation for the timing of DOM release; it does not seem to be due to diurnal changes in zooxanthellar photosynthetic activity, which remained nearly constant during the day (Fig. 5). Similarly, no differences in respiration rate were found at night. Crossland (1987) observed that in situ release of mucus was maximal in the afternoon. He suggested that this pattern could reflect preferential utilization of energy and carbon from photosynthesis in the morning to replenish tissue carbon reserves used during the night. However, this afternoon maximum for mucus production was also observed in corals adapted to shade conditions, even if the daily net photosynthesis was reduced and thus the surplus organic carbon. The relation between light, photosynthesis and mucus/DOC production remains be investigated in future studies.

DOM release appears to be significantly enhanced by heterotrophic feeding as 'artemia-fed' colonies released 2 to 3 times more DOC than the 'unfed' colonies. The first step in digestion in coelenterates is extracellular, whereby particulate food is decomposed in the gastric cavity. According to Schlichter (1982a, b), DOM liberated by this process in the coelenteron is excreted to the external seawater. Although fed corals released more DOC than unfed colonies, they tended to conserve organic nitrogen, which was excreted in the same amount irrespective of the feeding status. This suggests that heterotrophic nutrition may serve corals as a source of new nutrients, supplying nitrogen, phosphorus or vitamins (Dubinsky & Jokiel 1994), while carbon obtained through this pathway is subsequently released. In this case, there could also be a reverse translocation of these new nutrients from coral to algae (D'Elia & Cook 1988). Bythell (1988), who examined the carbon and nitrogen budget of the coral Acropora palmata, suggested that 70% of the nitrogen requirement was met by host particulate feeding, compared to

Table 2. Amount of 14C organic matter and bacterial concentration in beakers containing the coral incubation medium and the associated bacteria. Data represent mean and standard deviation of 3 samples

<table>
<thead>
<tr>
<th>Concentration</th>
<th>Beaker 1</th>
<th>Beaker 2</th>
<th>Beaker 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amount of radioactivity at the beginning (x10^3 dpm)</td>
<td>475 ± 20</td>
<td>290 ± 11</td>
<td>380 ± 5</td>
</tr>
<tr>
<td>Amount of radioactivity after 2 h incubation (x10^3 dpm)</td>
<td>470 ± 15</td>
<td>290 ± 20</td>
<td>390 ± 10</td>
</tr>
<tr>
<td>Amount of radioactivity after 5 h incubation (x10^3 dpm)</td>
<td>490 ± 10</td>
<td>280 ± 10</td>
<td>390 ± 30</td>
</tr>
<tr>
<td>Concentration of bacteria at the beginning (x10^3 cells ml^-1)</td>
<td>4.0 ± 0.2</td>
<td>7.1 ± 0.3</td>
<td>4.3 ± 0.1</td>
</tr>
<tr>
<td>Concentration of bacteria after 5 h incubation (x10^3 cells ml^-1)</td>
<td>4.1 ± 0.2</td>
<td>7.2 ± 0.2</td>
<td>4.8 ± 0.5</td>
</tr>
</tbody>
</table>
These authors reported, in a study based on 225 observations, that extracellular DOC release was equal to 23% of total carbon fixation.

In this experiment, a decrease in DOM concentrations was observed over a period of 2 h of its release by corals. This decrease could not be attributed to uptake by free-living bacteria, which were present in very low concentrations in the incubation medium. Data on DOC consumption by free-living bacterioplankton have shown removal rates of 0.04 to 0.8 μmol C l⁻¹ h⁻¹ (Carlson & Ducklow 1996, Zweifel et al. 1996). These rates were obtained with high bacterial concentrations (≥10⁶ bacteria ml⁻¹). Therefore, in our experiments, removal of DOM cannot be explained by the activity of the planktonic bacteria since 200 to 500 μmol DOC (or 250 to 600 μM C) or even more disappeared within 2 h (according to the estimated maximal removal rate, only 4 μmol would have been removed by bacteria).

A second hypothesis to explain DOM removal from the incubation medium is the spontaneous assembly of DOC into polymer gels (Chin et al. 1998). This process can start after 30 min of incubation, and the formation of microgels continues for the next 50 h, reaching an equilibrium after this. Therefore, DOM polymers can undergo rapid spontaneous assembly into POM particles. However, this was not the case in our experiments because, in the radioisotope experiments with the antibiotic mixture, there was no subsequent decrease in organic ¹⁴C after its release.

A third and final explanation could be uptake by epibiotic and/or intracellular bacteria. Trench (1974)
demonstrated that these bacteria can interfere with studies on uptake of DOM by corals. According to the results obtained in the incubations with antibiotics, the release of \(^1\)C organic matter was not followed by a subsequent uptake, suggesting that the epibiotic or intracellular bacteria are the main organisms responsible for the disappearance of DOC in our experiments. We can therefore assume that a bacteria-coral association may have existed during our experiments, since a large amount of bacteria was found in the coral tissues. Several symbioses between marine animals and bacteria have been described, especially between bacteria and echinoderms (Kelly & McKenzie 1995), bivalves (Krueger et al. 1996), sponges (Vacelet et al. 1995), clams (Southward 1990), brittle stars (Lesser & Blakemore 1990) and sea anemones (Palincsar et al. 1989).

Few studies have investigated the association between bacteria and corals, and of these most were conducted during diseases (Peters et al. 1983, Ritchie & Smith 1995). However, high bacterial activity has been demonstrated in the coral surface mucopolysaccharide layers (Ducklow & Mitchell 1979, Herndl & Velimirov 1986, Paul et al. 1986).

This study demonstrates the apparently important role of bacteria in the regulation of DOM fluxes in corals. They are able to quickly take up DOM previously released and to transform it into bacterial biomass. These bacteria can be in turn a food source for corals (Sorokin 1993) or can use DOM for their own nutritional requirements and transfer other essential nutrients such as amino acids to their host. Schlichter (1982a, b) demonstrated in the soft coral *Heteroxenia lucrescens* that photosynthates produced by zooxanthellae in the gastrodermis are released to the coelenteron, washed out from the coelenteron into the surrounding seawater and 'recaptured' by the epidermis. Therefore, photosynthates potentially lost from the symbiotic system can be re-absorbed quickly by the epidermal parts of the colony. This release-uptake described by Schlichter (1982a, b) could have been due to epibiotic bacteria. In our experiments, after each release event, DOM concentrations fell back to routine background levels (ca 100 \(\mu\)M), with no further bacterial uptake at this concentration. This may be explained by a different composition between DOM released by corals, which may be mostly 'labile', and DOM present in the incubation medium, of a more 'refractory' nature. One of the next steps in this study will be to characterize the composition of the newly released DOM.

The amounts of DOM measured in this experiment are likely to be underestimated since DOM can be used by bacteria as soon as it is released. Comparison of the results of Figs. 6 & 7 shows that DOM concentration increased regularly during the whole experiment with antibiotics whereas only 1 or 2 peaks could be measured under normal conditions. Corals could therefore release small amounts of DOM at all times, which would be taken up immediately by bacteria, except during massive release. In this case, bacteria seem to be saturated and to require more time to process all the DOM. In the field, a large fraction of the released DOM may not remain available to corals due to the high flow rates over the reef flat which remove mucus and DOM from the waters adjacent to corals (Patterson et al. 1991). Therefore, DOM can be transferred to other reef organisms (Ducklow & Mitchell 1979, Gottfried & Roman 1983, Herndl & Velimirov 1986) and may constitute an important source of organic matter export from the reef bottom organisms to the water column. Bacteria, for instance, are known to efficiently use the organic material released by corals. Colony-forming bacteria are usually found in coral mucus and may play an important role in the mobilization of this mucus for consumption by other organisms (Ducklow & Mitchell 1979). Moriarty & Hansen (1990) demonstrated that heterotrophic bacteria present on hard calcareous substrates utilize DOM released during photosynthesis by corals. During the peak of DON excretion, the C:N ratio of the DOM was very low (5:2) compared to the Redfield ratio for marine plankton (106:16). DOM is therefore a high quality food at that time and may sustain the high bacterial growth and production rates often reported in coral reef waters (Moriarty et al. 1985, Ducklow 1990, Sorokin 1993). The range of C:N ratios obtained in this study (2.5 to 13) is close to that reported for mucous aggregates excreted by other coral colonies (7.4 to 44; Krupp 1984, Cowroth 1990). The rapid uptake of freshly excreted DOM may explain the low and relatively constant concentrations that have been measured in natural reef environments (Pagès et al. 1997) and the low DOM concentrations measured in reef waters relative to the open ocean (Suzuki et al. 1995).

Dissolved organic carbon in the oceans is one of the largest pools of reduced carbon on earth, yet little is known about its composition (Williams & Druffel 1987), transformation, fluxes, or absolute concentration (Sharp 1993). There is also a general lack of quantitative information on both the production and the fate of the DON pool (Hopkinson 1993). Our results confirm previous observations that scleractinian corals can release a significant proportion of their photosynthetically fixed carbon as DOC. DON is also excreted, albeit at a lower rate than DOC. This is one of the first studies estimating the amount of DOM that corals are able to release in seawater in relation to their nutritional status. High rates of DOM release occur at specific times of the day. The mechanisms responsible for this timing are unknown and thus it is impossible to extrap-
olate these results to the field. Finally, this study shows the important role of epibiotic and/or intracellular bacteria in the uptake of the released DOM. This can lead to a tight recycling of inorganic nutrients inside coral colonies, which is often described as a key process enabling coral reef ecosystems to thrive in oligotrophic waters (Smith 1984).

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