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DOC concentrations across a depth gradient on a Caribbean coral reef

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The dissolved organic carbon (DOC) pool on tropical coral reefs is mainly fueled by photosynthates released from benthic primary producers (BPP), such as reef algae and scleractinian corals. DOC concentrations near BPP have repeatedly been observed to be elevated compared to those in the surrounding water column. As the DOC release of BPP increases with increasing light availability, elevated DOC concentrations near them will, in part, also depend on light availability. Consequently, DOC concentrations are likely to be higher on the shallow, well-lit reef terrace than in deeper sections on the fore reef slope. We measured *in situ* DOC concentrations and light intensity in close proximity to the reef alga *Dictyota* sp. and the scleractinian coral *Orbicella faveolata* along a depth gradient from 5 to 20 m depth and compared these to background concentrations in the water column. DOC concentrations near *Dictyota* sp. were significantly higher at 10 m than at 5 and 20 m depth. Furthermore, at 10 m DOC concentrations near *Dictyota* sp. were elevated by 15 µmol C L^{-1} compared to background concentrations in the water column, but not at 5 and 20 m. DOC concentrations near *O. faveolata* and in the water column did not differ between depths and concentrations near *O. faveolata* were not elevated compared to background concentrations at any of the tested depths. Our results indicate that DOC concentrations near *Dictyota* sp. can differ along a depth gradient from 5 to 20 m. However, the occurrence of elevated DOC concentrations did not follow a natural light gradient across depth. Instead, a combination of light availability (including a restriction by photoinhibition) and water movement are proposed to interactively determine the DOC concentrations in the close vicinity of BPP across the reef slope.

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ABSTRACT

The dissolved organic carbon (DOC) pool on tropical coral reefs is mainly fueled by photosynthates released from benthic primary producers (BPP), such as reef algae and scleractinian corals. DOC concentrations near BPP have repeatedly been observed to be elevated compared to those in the surrounding water column. As the DOC release of BPP increases with increasing light availability, elevated DOC concentrations near them will, in part, also depend on light availability. Consequently, DOC concentrations are likely to be higher on the shallow, well-lit reef terrace than in deeper sections on the fore reef slope. We measured *in situ* DOC concentrations and light intensity in close proximity to the reef alga *Dictyota* sp. and the scleractinian coral *Orbicella faveolata* along a depth gradient from 5 to 20 m depth and compared these to background concentrations in the water column. DOC concentrations near *Dictyota* sp. were significantly higher at 10 m than at 5 and 20 m depth. Furthermore, at 10 m DOC concentrations near *Dictyota* sp. were elevated by 15 µmol C L^{-1} compared to background concentrations in the water column, but not at 5 and 20 m. DOC concentrations near *O. faveolata* and in the water column did not differ between depths and concentrations near *O. faveolata* were not elevated compared to background concentrations at any of the tested depths. Our results indicate that DOC concentrations near *Dictyota* sp. can differ along a depth gradient from 5 to 20 m. However, the occurrence of elevated DOC concentrations did not follow a natural light gradient across depth. Instead, a combination of light availability (including a restriction by photoinhibition) and water movement are proposed to interactively determine the DOC concentrations in the close vicinity of BPP across the reef slope.

INTRODUCTION

Dissolved organic carbon (DOC) is the largest pool of reduced carbon on tropical coral reefs (Atkinson & Falter 2003). Typically DOC concentrations are elevated in the reef overlying water compared to the surrounding ocean, suggesting a net production of DOC on coral reefs (Torréton et al. 1997; Van Duyl & Gast 2001). Moreover, the lack of a relationship between particulate organic carbon (POC as proxy for planktonic primary producers) and DOC concentrations (Tanaka et al. 2011), and increased DOC concentrations near the bottom compared to the surface water (Van Duyl & Gast 2001) further indicate that benthic primary producers (BPP) are the main source of DOC on tropical coral reefs. Reef algae and scleractinian corals release a

substantial portion of their photosynthetically fixed carbon as DOC into the surrounding water, yet reef algae generally release more DOC than corals (e.g., Haas et al. 2011; Haas et al. 2013b). This algal-derived DOC can promote the growth of opportunistic heterotrophic microbes in the water column as well as in the contact zone between corals and algae (Haas et al. 2013a; Haas et al. 2013b; Nelson et al. 2013). Increased microbial respiration in the coral-algal interface causing anoxia (Gregg et al. 2013; Haas et al. 2013a) in combination with the release of secondary metabolites, can lead to tissue loss or even coral death (Barott & Rohwer 2012; Morrow et al. 2013). Moreover, while most heterotrophic organisms cannot utilize DOC for their nutrition an increasing number of reef sponges is found to predominantly rely on DOC as carbon source (Yahel et al. 2003; De Goeij et al. 2008; Mueller et al. 2014a;). And similar to microbes, sponges also appear to prefer algal- over coral-derived DOC (Rix et al. 2016). In the so-called sponge loop these sponges utilize the energy stored in DOC and make it available to higher trophic levels via subsequent detritus production (Alexander et al. 2014; De Goeij et al. 2013). Both heterotrophic microbes and DOC-feeding sponges are therefore likely to benefit from elevated DOC concentrations with potential consequences for carbon cycling and overall coral reef functioning (e.g., Rohwer & Youle 2010; Barott & Rohwer 2012; De Goeij et al. 2013; Haas et al. 2016).

Elevated DOC concentrations in close proximity to BPP have been repeatedly observed on tropical coral reefs (Van Duyl & Gast 2001; Hauri et al. 2010; Mueller et al. 2014b). However, most studies were conducted in shallow reef areas between 5 and 10 m and little attention was given to deeper reef sections or how DOC concentrations change across depth. Light availability decreases exponentially with depth and is an important environmental parameter that structures benthic communities across the reef slope (e.g. Bak 1974; Veron 2000; Vermeij & Bak 2002). Light availability positively affects the DOC release rates of BPP (Crossland 1987; Haas et al. 2010b; Naumann et al. 2010; Barrón et al. 2014 and references therein). Moreover, also the occurrence of elevated DOC concentrations near them were found to be positively correlated with the availability of light (Mueller et al. 2014b). We therefore hypothesize that DOC concentrations change with depth and that elevated DOC concentrations near BPP are more likely to occur on the shallow, well-lit reef terrace (5 m) than at the drop off (10 m) or in deeper sections of the fore reef slope (20 m). To test this we measured *in situ* DOC concentrations and light intensity in close proximity to the reef alga *Dictyota* sp. and the scleractinian coral

Orbicella faveolata (former *Montastraea annularis*) along a depth gradient from 5 to 20 m depth and compared these to background concentrations in the water column.

MATERIALS AND METHODS

Fieldwork was performed under the research permit (#2012/48584) issued by the Curaçaoan Ministry of Health, Environment and Nature (GMN) to the CARMABI foundation.

DOC concentrations and light intensity across depth

To quantify DOC concentrations across depth, water samples were taken *in situ* in close proximity (<5 mm) to the abundant reef alga *Dictyota* sp., the scleractinian coral *O. faveolata* and the water column. Both, *Dictyota* sp. and *O. faveolata* are considered holobionts, including epi- and endophytes and associated microbial communities (sensu Barott et al. 2011), jointly affecting the water properties (e.g., DOC concentration) in their close vicinities. Sampling took place on July 24, 2012 at Snake Bay (12° 8' N, 68° 59' W) on the leeward coast of the Island of Curaçao in the Southern Caribbean. The site consists of an approximately 100 m wide sandy reef terrace with patchy coral communities. The reef terrace gradually slopes towards a drop-off that starts around 10 m depth. The reef then slopes down under a steep angle (20-30°; Van Duyl (1985)) and is characterized by a structurally complex reef topography and high coral cover (>30%; De Goeij and Mueller unpubl. data). At midday between 12:00 hrs and 13:00 hrs (when light intensities are the highest) patches of *Dictyota* sp. and colonies of *O. faveolata* were sampled at 5 (reef flat), 10 (drop-off) and 20 m depth (fore reef slope) (each n = 5). In addition, the water column 2 m off the reef bottom was sampled (n = 5) at the same depths and used to indicate background DOC concentrations (i.e., those not directly affected by DOC release of BPP). Sampling started at 20 m depth and 10 and 5 m were sampled consecutively. Per depth approx. 10 min were spent to collect all samples. The sampling procedure described by van Duyl and Gast (2001) and modified by Mueller et al. (2014b) was followed. In short, water samples were collected using 100 ml acid-washed, polypropylene syringes equipped with a flexible silicon tube attached to their tips. The tube was moved slowly above the surfaces of *Dictyota* sp. and *O. faveolota*, respectively, while collecting water. The water column was sampled using a similar syringe. All water samples were collected facing the water current to avoid potential contamination related to the diver's presence. Ambient light intensity (PAR) was recorded simultaneously while sampling (approx. 10 min; sampling intervals 1 min) using a light meter in

a custom-made underwater housing (cosine LI-192SSA underwater quantum sensor connected to LI-1000 data logger; range: PAR 400-700). Water samples were transported (<30 min) to the lab and stored at 4°C until they were processed later that same day.

Processing of DOC samples

Water samples collected were filtered (<20 kPa Hg suction pressure) over a 0.2 µm polycarbonate filter (Whatman, 25 mm). Prior to filtration, filters, glassware and pipette tips were rinsed three times with acid (10 mL 0.4 M HCl) and twice with sample water (10 mL). Afterwards 20 mL of sample water was filtered and the filtrate containing DOC was transferred to pre-combusted (4 h at 450°C) Epa vials (40 mL). Samples were acidified with 6–7 drops of concentrated HCl (38%) to remove inorganic C and stored at 4°C until analysis. DOC concentrations were measured using the high-temperature catalytic oxidation (HTCO) technique in a total organic C analyzer (TOC-VCPN; Shimadzu). The instrument was calibrated with a standard addition curve of Potassium Hydrogen Phthalate (0; 25; 50; 100; 200 µmol C L^{-1}). Consensus Reference Materials (CRM) provided by DA Hansell and W Chen of the University of Miami (Batch 12; 2012; 41-44 µmol C L^{-1}) were used as positive controls for our measurements. Concentrations measured for the batch gave average values (±SD) of 45±3 µmol C L^{-1}. Average analytical variation of the instrument was <3% (5-7 injections per sample).

Data analysis

Differences in DOC concentrations at the substrate-water-interface of *Dictyota* sp., *O. faveolata* and the water column from 5, 10 and 20 m were tested using a Kruskal-Wallis test followed by a Mann-Whitney U test in case of significant differences.

RESULTS

In situ DOC concentration in close proximity to *Dictyota* sp. differed significantly across depths (Kruskal-Wallis, p=0.01) (Figure 1 and Supplemental Information for raw data). The distribution of the data from 10 m was different from that at 5 (Mann-Whitney, p=0.02) and 20 m (Mann-Whitney, p=0.01). Estimated mean DOC concentration at 10 m was 107±5 (±SD) µmol L^{-1} and thus 20 and 25 µmol L^{-1} higher compared to 5 and 20 m, respectively. No differences in DOC concentrations among depths were observed near *O. faveolata* (Kruskal-Wallis, p=0.93) and in the water column (Kruskal-Wallis, p=0.62). At 10 m depth the distribution of the data of

Dictyota sp. differed from that of the water column (Mann-Whitney, p=0.02), with estimated mean DOC concentrations near *Dictyota* sp. being elevated by 15 µmol L^{-1} compared to background concentrations. In contrast, the distribution of the data at 5 m (Mann-Whitney, p=0.81) and 20 m depth (Mann-Whitney, p=0.35) did not differ between *Dictyota* sp. and in the water column. Furthermore, estimated mean DOC concentration near *O. faveolata* did not differ from those in the water column at any of the tested depths. Interestingly, at 20 m estimated mean DOC concentration near *Dictyota* sp. was significantly lower than near *O. faveolata* (Mann-Whitney, p=0.028). The sampling depths of 5, 10 and 20 m corresponded to a light intensity of 1214±285, 702±79 and 374±71 µmol photons m^{-2} s^{-1} (mean±SD) during the sampling (Supplemental Information for raw data).

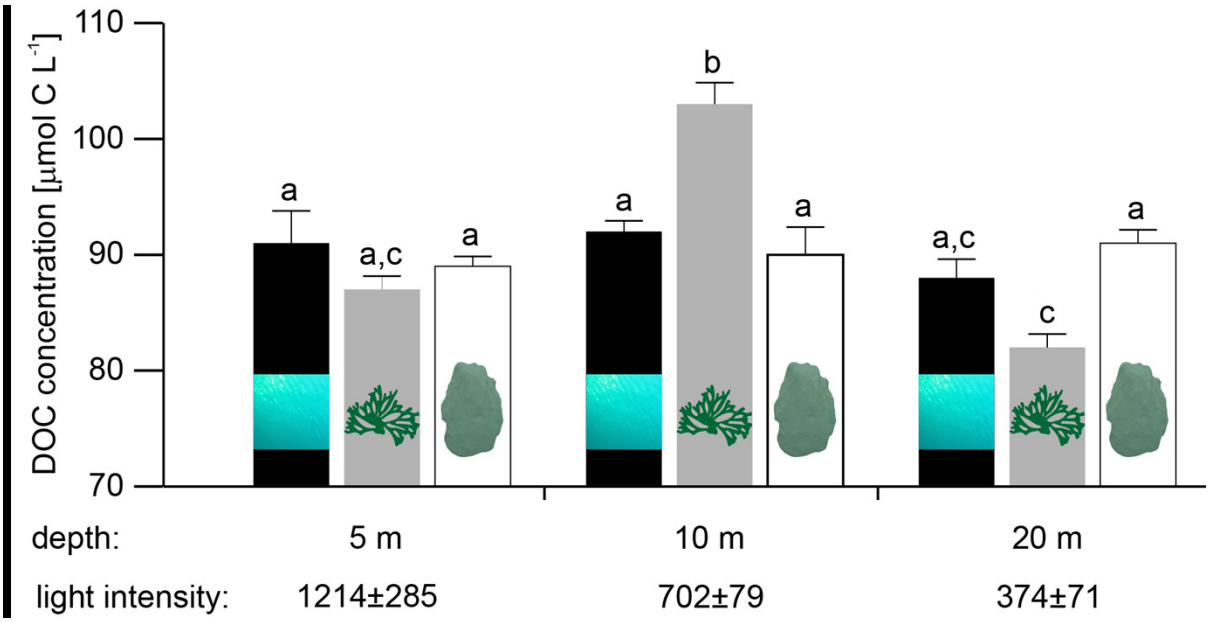
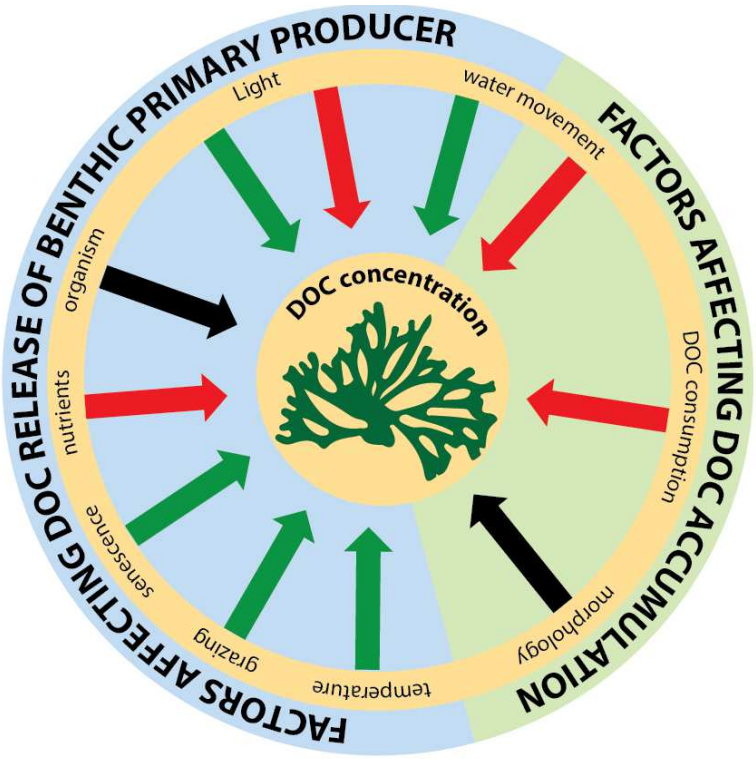


Figure 1 Mean *in situ* DOC concentrations (n=5, except for water column 10 m and Dictyota sp. 5 m with n=4) measured in the water column (2 m off the reef slope; black) and at the substrate-water interfaces of the reef algae *Dictyota* sp. (dark grey) and the scleractinain coral *Orbicella faveolata* (white) at 5, 10 and 20 m depth. Error bars indicate SE. Concentrations with the same letter are not significantly different at α = 0.05. Measured *in situ* light intensity (mean±SD) during the sampling is given in µmol photons m^{-2} s^{-1}.

DISCUSSION

In this study we investigated DOC concentrations in close proximity to the reef alga *Dictyota* sp., the scleractinian coral *O. faveolata,* and in the water column across a depth gradient from 5 to 20 m. DOC concentrations near *Dictyota* sp. differed between depths, whereas those near *O. faveolata* and in the water column remained similar over the tested depth range. Elevated DOC concentrations compared to the background concentrations in the water column were only observed near *Dictyota* sp. at 10 m, but not at 5 and 20 m depth, or near *O. faveolata* at any of the tested depths.

Elevated DOC concentrations in close proximity to BPP occur when DOC release exceeds removal processes. Consequently, environmental parameters that affect the DOC release of BPP (e.g., light availability (Haas et al. 2010b; Barrón et al. 2012), temperature (Gillooly et al. 2001; Haas et al. 2010b), grazing pressure (Berman & Holm-Hansen 1974), senescence (Khailov & Burlakova 1969), nutrient availability (Lopéz-Sandoval et al. 2011; Mueller et al. 2016), hydrodynamic conditions (Wild et al. 2012)), in combination with factors which affect the accumulation of DOC near them (e.g. morphology of the BPP, hydrodynamic conditions (Losee & Wetzel 1993, Escartín & Aubrey 1995), DOC consumption by heterotrophic microbes and sponges (Gast et al. 1999; Yahel et al. 2003; Scheffers et al. 2005; De Goeij et al. 2008)) interactively determine the DOC concentrations in close vicinity to BPP (Figure 2). The lack of elevated DOC concentrations near *Dictyota* sp. at 5 m depth could thus be explained by (1) insufficient DOC release, (2) high DOC removal or (3) a combination of both.



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175 **Figure 2 *In situ* DOC concentrations near benthic primary producers are interactively**
176 **determined by factors that are affecting the DOC release of the benthic primary producers**
177 **and by those affecting the accumulation of DOC.** Green and red arrows indicate positive and
178 negative effects on *in situ* DOC concentrations, respectively. Black arrows indicate the general
179 effect of the organism under consideration and its morphology.

180

181 Light availability is generally considered to have a strong positive effect on DOC release of reef
182 algae. However, Haas et al. (2010b) reported that this positive correlation in the reef alga
183 *Caulerpa* sp. only held until a maximum light intensity was reached. At these light intensities
184 DOC release rates steeply decreased to levels comparable to those in the dark. They explained
185 this decrease with the onset of photoinhibition at a species-specific light intensity, which is a
186 common phenomenon in coral reef BPP (Franklin 1994; Hanelt et al. 1994; Brown et al. 1999;
187 Hoegh-Guldberg & Jones 1999; Iglesias-Prieto et al. 2004). Accordingly, photoinhibition likely
188 reduced the DOC release of *Dictyota* sp. at 5 m depth and therefore contributed to the fact that
189 no elevated DOC concentrations in its close proximity were found at this depth.

Similar to light availability also hydrodynamic conditions can affect *in situ* DOC concentrations near BPP in two ways. Either positively, when water movement increases the metabolism and DOC release rates of BPP by alleviating the limitation of the diffusive boundary layer around them (Carpenter et al. 1991; Lesser et al. 1994; Wild et al. 2012), or negatively, when water movement and water exchange hamper the accumulation of DOC by dilution (Hauri et al. 2010). Water movement generally decreases exponentially as a function of depth (Shashar et al. 1996) and significantly higher water movement rates are reported at 5 compared to 10 or 20 m depth on the reef slope of Curaçao (Vermeij & Bak 2003). Thus, a reduced DOC release rate of *Dictyota* sp. due to photoinhibition in combination with high water movement and water exchange that hamper the accumulation of DOC, could explain the lack of elevated DOC concentrations near *Dictyota* sp. at 5 m depth. It can be further assumed that the negative effect of water movement and water exchange on the accumulation of DOC at 10 m was higher than at 20 m, i.e., a higher DOC release rate was necessary to result in elevated DOC concentrations at 10 m. Yet, despite higher water movement, elevated DOC concentrations near *Dictyota* sp. were only found at 10, but not at 20 m. This suggests that DOC release rates were higher at 10 m than at 20 m, which is in line with the aforementioned positive relation between light availability and DOC release. Interestingly, at 20 m depth DOC concentrations in close proximity to *Dictyota* sp. were depleted compared to concentrations near *O. faveolata* (and lower relative to, but not significantly different from those in the water column). Reduced water movement and thus a prolonged water residence time combined with a low, but steady release of bio-available DOC by *Dictyota* sp., could have stimulated the growth of heterotrophic microbial communities. The bio-available DOC could have further allowed those communities to metabolize otherwise refractory components of the DOC pool and thereby deplete the local DOC stock, as described for the water columns overlying algal-dominated reefs (Dinsdale et al. 2008; Haas et al. 2016).

No elevated DOC concentrations were observed near the scleractinian coral *O. faveolata* at any of the sampling depths. In general, the DOC release of scleractinian corals is more variable than that of reef algae and an increasing number of studies suggest that scleractinian corals only contribute marginally to the local DOC on tropical coral reefs (e.g., Haas et al. 2010a; Naumann et al. 2010; Haas et al. 2011). Furthermore, the massive morphology of *O. faveolata* is less likely to restrict water exchange than the bushy thalli of *Dictyota* sp. and is thereby less favorable for the accumulation of DOC in its vicinity (Stocking et al. 2016). Given the positive effect of light

availability on the DOC release by BPP, we expected to find significantly higher DOC concentrations on the shallow and well-lit reef terrace compared to deeper reef sections, following the natural light gradient across depth. Surprisingly, significant differences in the mean DOC concentrations between the sampled depths were only observed in *Dictyota* sp., but not in *O. faveolata* or the water column. The absence of significant differences in DOC concentrations across the water column was also observed in other studies (Torréton et al. 1997; Nelson et al. 2011). To date only Slattery & Lesser (2015) reported a significant decline in DOC concentration with depth from coral reefs on the Bahamas, albeit this decrease occurred at mesophotic depths below 30 m. This may indicate that at least above mesophotic depths, DOC released by BPP is either quickly taken up by DOC feeding organisms (i.e. heterotrophic bacteria and reef sponges) and/or mixed and diluted throughout the reef overlying water column.

CONCLUSION

While light availability has a strong positive effect on the DOC release of BPP, the occurrence of elevated DOC concentrations near them did not follow a natural light gradient across the reef slope in our study system. Instead, a combination of light availability, which affects the release of DOC (including the restriction by photoinhibition) and water movement, which affects the accumulation of DOC, are proposed to interactively determine the DOC concentrations in the close vicinity of BPP.

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