DOC concentrations across a depth-dependent light gradient on a Caribbean coral reef

Benjamin Mueller [Corresp., 1, 2, 3] , Erik H Meesters [4] , Fleur C van Duyl [1]

[1] Department of Marine Microbiology and Biogeochemistry, NIOZ Royal Netherlands Institute for Sea Research and Utrecht University, Den Burg, The Netherlands

[2] CARMABI Foundation, Willemstad, Curaçao

[3] Department of Freshwater and Marine Ecology, University of Amsterdam, Amsterdam, The Netherlands

[4] Wageningen Marine Research, Den Helder, The Netherlands

Corresponding Author: Benjamin Mueller
Email address: muellerb@ymail.com

Photosynthates released by benthic primary producers (BPP), such as reef algae and scleractinian corals, fuel the dissolved organic carbon (DOC) production on tropical coral reefs. 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-dependent light gradient from 5 to 20 m depth and compared these to background concentrations in the water column. At 10 m (intermediate light), 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 (high and low light, respectively), or near *O. faveolata* at any of the tested depths. DOC concentrations did not differ between depths and thereby light environments for any of the tested water types. However, water type and depth appear to jointly affect *in situ* DOC concentrations across the tested depth-dependent light gradient. Corroborative *ex situ* measurements of excitation pressure on photosystem II suggest that photoinhibition in *Dictyota* sp. is likely to occur at light intensities that are commonly present on Curaçaoan coral reefs under high light levels at 5 m depth during midday. Photoinhibition may have thereby reduced the DOC release of *Dictyota* sp. and DOC concentrations in its close proximity. Our results indicate that the occurrence of elevated DOC concentrations did not follow a natural light gradient across depth. Instead, a combination of multiple factors, such as water type, light availability (including the restriction by photoinhibition), and water movement are proposed to interactively

determine the DOC concentrations in the close vicinity of BPP.

1   **DOC concentrations across a depth-dependent light gradient on a Caribbean coral reef**

2   Mueller B[1,2,3], Meesters EH[4], van Duyl FC[1]

4   [1]NIOZ Royal Netherlands Institute for Sea Research, Department of Marine Microbiology and
5   Biogeochemistry, and Utrecht University, Den Burg, Texel, The Netherlands.

6   [2]Carmabi Foundation, Willemstad, Curaçao.

7   [3]Present address: University of Amsterdam, Department of Freshwater and Marine Ecology,
8   Institute for Biodiversity and Ecosystem Dynamics, Amsterdam, The Netherlands.

9   [4]Wageningen Marine Research, Den Helder, The Netherlands.
10
11   Corresponding author:
12   Benjamin Mueller
13
14   Email address: muellerb@ymail.com

16   **ABSTRACT**

17   Photosynthates released by benthic primary producers (BPP), such as reef algae and scleractinian

18   corals, fuel the dissolved organic carbon (DOC) production on tropical coral reefs. DOC

19   concentrations near BPP have repeatedly been observed to be elevated compared to those in the

20   surrounding water column. As the DOC release of BPP increases with increasing light

21   availability, elevated DOC concentrations near them will, in part, also depend on light

22   availability. Consequently, DOC concentrations are likely to be higher on the shallow, well-lit

23   reef terrace than in deeper sections on the fore reef slope. We measured *in situ* DOC

24   concentrations and light intensity in close proximity to the reef alga *Dictyota* sp. and the

25   scleractinian coral *Orbicella faveolata* along a depth-dependent light gradient from 5 to 20 m

26   depth and compared these to background concentrations in the water column. At 10 m

27   (intermediate light), DOC concentrations near *Dictyota* sp. were elevated by 15 µmol C L^{-1}

28   compared to background concentrations in the water column, but not at 5 and 20 m (high and

29   low light, respectively), or near *O. faveolata* at any of the tested depths. DOC concentrations did

30   not differ between depths and thereby light environments for any of the tested water types.

31   However, water type and depth appear to jointly affect *in situ* DOC concentrations across the

32   tested depth-dependent light gradient. Corroborative *ex situ* measurements of excitation pressure

33   on photosystem II suggest that photoinhibition in *Dictyota* sp. is likely to occur at light

34   intensities that are commonly present on Curaçaoan coral reefs under high light levels at 5 m

35   depth during midday. Photoinhibition may have thereby reduced the DOC release of *Dictyota* sp.

36   and DOC concentrations in its close proximity. Our results indicate that the occurrence of

37   elevated DOC concentrations did not follow a natural light gradient across depth. Instead, a

38   combination of multiple factors, such as water type, light availability (including the restriction by

39   photoinhibition), and water movement are proposed to interactively determine the DOC

40   concentrations in the close vicinity of BPP.

41   **INTRODUCTION**

42   Dissolved organic carbon (DOC) is the largest pool of reduced carbon on tropical coral reefs

43   (Atkinson & Falter 2003). A lack of a relationship between particulate organic carbon (POC as

44   proxy for planktonic primary producers) and DOC concentrations (Tanaka et al. 2011), and

45   increased DOC concentrations near the bottom compared to the surface water (Van Duyl & Gast

46   2001) indicate that benthic primary producers (BPP) are an important source of this DOC. Reef

47   algae and scleractinian corals release a substantial portion of their photosynthetically fixed

48   carbon as DOC into the surrounding water; reef algae generally release more DOC than corals

49   (e.g., Haas et al. 2011; Haas et al. 2013b). This algal-derived DOC can promote the growth of

50   opportunistic heterotrophic microbes in the water column as well as in the contact zone between

51   corals and algae (Haas et al. 2013a; Haas et al. 2013b; Nelson et al. 2013). Increased microbial

52   respiration in the coral-algal interface causes anoxia (Gregg et al. 2013; Haas et al. 2013a) in

53   combination with the release of secondary metabolites, and can lead to tissue loss or even coral

54   death (Barott & Rohwer 2012; Morrow et al. 2013). Moreover, while most heterotrophic

55   macroorganisms cannot utilize DOC for their nutrition an increasing number of reef sponges are

56   found to predominantly rely on DOC as carbon source (Yahel et al. 2003; De Goeij et al. 2008;

57   Mueller et al. 2014a). As with microbes, sponges also appear to prefer algal- over coral-derived

58   DOC (Rix et al. 2016). In the so-called sponge loop these sponges utilize the energy stored in

59   DOC and make it available to higher trophic levels via subsequent detritus production

60   (Alexander et al. 2014; De Goeij et al. 2013). Both heterotrophic microbes and DOC-feeding

61   sponges are therefore likely to benefit from elevated DOC concentrations with potential

62   consequences for carbon cycling and overall coral reef functioning (e.g., Rohwer & Youle 2010;

63   Barott & Rohwer 2012; De Goeij et al. 2013; Haas et al. 2016).

64   Elevated DOC concentrations in close proximity to BPP have been repeatedly observed on

65   tropical coral reefs (Van Duyl & Gast 2001; Hauri et al. 2010; Mueller et al. 2014b). However,

66   most studies were conducted in shallow reef areas between 5 and 10 m and little attention was

67   given to deeper reef sections or how DOC concentrations change across depth. Light availability

68   decreases exponentially with depth and is an important environmental parameter that structures

69   benthic communities across the reef slope (e.g. Bak 1974; Veron 2000; Vermeij & Bak 2002).

70   Light availability positively affects the DOC release rates of BPP (Crossland 1987; Haas et al.

71   2010b; Naumann et al. 2010; Barrón et al. 2014 and references therein). The occurrence of

72   elevated DOC concentrations near BPP were found to be positively correlated with the

73   availability of light (Mueller et al. 2014b). We therefore hypothesize that DOC concentrations

74   change with depth and that elevated DOC concentrations near BPP are more likely to occur on

75   the shallow, well-lit reef terrace (5 m) than at the drop off (10 m) or in deeper sections of the fore

76   reef slope (20 m). To test this we measured *in situ* DOC concentrations and light intensity in

77   close proximity to the reef alga *Dictyota* sp. and the scleractinian coral *Orbicella faveolata*

78   (former *Montastraea annularis*) along a depth-dependent light gradient from 5 to 20 m depth and

79   compared these to background concentrations in the water column.

80   **MATERIALS AND METHODS**

81   Fieldwork was performed under the research permit (#2012/48584) issued by the Curaçaoan

82   Ministry of Health, Environment and Nature (GMN) to the CARMABI foundation.

83   **Study site and general environmental parameters**

84   Sampling was conducted at Snake Bay (12° 8' N, 68° 59' W) on the leeward coast of the Island

85   of Curaçao in the Southern Caribbean. The site consists of an approximately 100 m wide sandy

86   reef terrace with patchy coral communities. The reef terrace gradually slopes towards a drop-off

87   that starts at around 10 m depth. The reef then slopes down under a steep angle (20-30°; Van

88   Duyl (1985) and is characterized by a structurally complex reef topography. The hydrodynamics

89   at the study site are mainly dominated by oceanic currents, which generally flows westwards

90   along the island with approx. 50 cm s^{-1} (Gast et al. 1999). Due to small tidal differences (10-30

91   cm) tidal currents are usually neglectable on the narrow Curaçaoan fringing reefs and water

92   currents over the reef terraces are typically around 10-15 cm s^{-1}.

93   Benthic composition was determined from 20 photo quadrats (1 x 1 m) placed at randomized

94   distances and alternatingly on both sides along a 30 m transect line. On March 24, 2017 the

95   benthic cover following the 5, 10, and 20 m isobaths was recorded in the area where the DOC

96   concentrations were quantified before (see DOC concentrations across a depth-dependent light

97   gradient). Percentage cover of most dominant benthic components was quantified from

98   randomly-generated overlaid points on each photograph using Coral Point Count with Excel

99   Extensions (CPCe) (Kohler & Gill 2006). Two photographs of the 5 m transect and five of the 20

100   m transect had to be excluded from be analysis due to insufficient quality.

101   In June, 2015 water samples to access bacterial concentrations in the water column 2 m off the

102   reef slope (towards the open ocean) were taken at 15 m depth, following the protocol described

103   in Dinsdale et al. (2008) to describe background bacterial abundances. Water samples (n = 5)

104   were transported to the nearby CARMABI research station where they were processed and

105   analyzed (for details see Supplemental Information).

DOC concentrations across a depth-dependent light gradient

To quantify DOC concentrations across a depth-dependent light gradient, water samples were taken *in situ* in close proximity (<5 mm) to the 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. At midday on July 24, 2012 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; high light), 10 (drop-off; intermediate light) and 20 m depth (fore reef slope; low light) (each n = 5). In addition, the water column 2 m off the reef slope (towards the open ocean) 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. At each 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 (each n = 5). The water column was sampled using a similar syringes (n = 5). 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

136 concentrated HCl (38%) to remove inorganic C and stored at 4°C until analysis. DOC

137 concentrations were measured using the high-temperature catalytic oxidation (HTCO) technique

138 in a total organic C analyzer (TOC-VCPN; Shimadzu). The instrument was calibrated with a

139 standard addition curve of Potassium Hydrogen Phthalate (0; 25; 50; 100; 200 µmol C L^{-1}).

140 Consensus Reference Materials (CRM) provided by DA Hansell and W Chen of the University

141 of Miami (Batch 12; 2012; 41-44 µmol C L^{-1}) were used as positive controls for our

142 measurements. Concentrations measured for the batch gave average values (±SD) of 45±3 µmol

143 C L^{-1}. Average analytical variation of the instrument was <3% (5-7 injections per sample).

144 **Maximum excitation pressure over photosystem II in *Dictyota* sp.**

145 To explore the occurrence of photoinhibition as a potential explanation for the lack of elevated

146 DOC concentrations observed near *Dictyota* sp. at 5 m depth , an *ex situ* experiment to determine

147 maximum light-dependent reduction of the effective quantum yield of photosystem II (ΔF/Fm')

148 relative to its maximum at dawn (Fv/Fm) (Iglesias-Prieto et al. 2004; Enríquez and Borowitzka

149 2010) was conducted. On March 16, 2017 30 thalli of *Dictyota* sp. were collected on the reef

150 terrace (5 m depth) at Buoy 0 (12°12′ 35″ N, 68°97′ 10″) and transported in a dark insulated box

151 to the nearby CARMABI Research Station. The algae were allowed to recover and acclimatize in

152 a flow-through seawater aquarium (flow rate: 7 L min^{-1} to ensure stable temperatures throughout

153 the day) until the commencement of the experiment the following day. On March 17, 2017 at 6:00

154 hrs (sun rise time: 6:41 hrs; https://www.timeanddate.com) 10 thalli of *Dictyota* sp. were randomly

155 selected from the aquarium and placed in a plastic dish with sea water. In the lab Fv/Fm was

156 measured in triplicates per thalli with a waterproof PAM fluorometer (Diving PAM, Waltz). After

157 the measurements the thalli were discarded. Light intensity (PAR) and water temperature (°C) were

158 recorded with a light logger (ODYSSEY PAR logger, Dataflow systems; sampling interval 1 min)

159 and a temperature logger (Onset HOBO® Pendant, UA-002-08; sampling intervals 1 min),

160 respectively. After sun set, light intensity gradually increased to approximately 200 µmol photons

161 m^{-2} s^{-1} at 9:00 hrs (see Supplemental Information for light and temperature data). Due to the

162 positioning of the aquarium the light intensity remained stable until 12:00 hrs, when it steeply

163 increased to an average (±SD) of 1237±486 µmol photons m^{-2} s^{-1} for the following three hours. At

164 15:00 hrs 10 new thalli of *Dictyota* sp. were randomly selected, placed in a plastic dish with sea

165   water, and transferred to the lab. After a dark-adaptation period of 30 min to completely relax

166   photochemical quenching, $\Delta F/Fm'$ was measured in triplicates per thalli.

167   **Data analysis**

168   Differences in DOC concentrations at the substrate-water-interface of *Dictyota* sp., *O. faveolata*

169   and the water column from 5, 10 and 20 m were tested using one-way ANOVAs, followed by a

170   Tukey HSD post-hoc test in case of significant differences. DOC concentrations were square root

171   transformed to meet assumptions of the analysis. To further explore the combined effects of

172   water types (*Dictyota* sp. and *O. faveolata* contact water, and water column) and depth, a two-

173   way ANOVA was performed. The maximum excitation pressure over photosystem II (Q_m) was

174   calculated as: $Q_m = 1 - [(\Delta F/Fm'$ at noon)/(Fv/Fm at dawn)] (Iglesias-Prieto et al. 2004). Values

175   that are close to zero indicate that most of the reaction centers of photosystem II remain open,

176   whereas values close to 1.0 indicate that they are closed, suggesting photoinhibition.

177   **RESULTS**

178   **General environmental parameters**

179   Benthic composition differed between the three sampled depths (table 1; see Supplemental

180   Information for benthic composition to higher taxonomic levels). While the reef terrace (5 m;

181   high light) was mainly dominated by the non-biological components sand, coral rubble, and bare

182   coral rock, the percentage cover of scleractinian corals, macroalgae, as well as other living taxa

183   increased at the drop off (10 m; intermediate light) and the fore reef slope (20 m; low light).

184   Similarly, with increasing depth the cover of the study organisms *Dictyota* sp. and *O. faveolata*

185   increased from <1% on the reef terrace to 8.8% and 2.6% at the drop off, and 5.5 % and 3.0% on

186   the fore reef slope, respectively.

187   **Table 1 Community composition (%) of most abundant benthic components at the study**

188   **site at 5, 10, and 20 m depth.** Percentage cover of the studied reef alga *Dictyota* sp. and the

189   scleractinian coral *Orbicella faveolata* are given below.

	Percentage cover (%)		
Benthic component	**5 m**	**10 m**	**20 m**

Macroalgae	0.3	14.0	31.7
Turf algae	0.0	9.3	3.0
Crustose coralline algae	0.0	3.5	6.8
Cyanobacteria	0.0	6.6	5.3
Scleractinian corals	1.9	24.4	32.7
Fire corals	0.0	0.6	0.3
Soft corals/gorgonians	0.0	0.3	0.3
Sponges	0.3	1.5	6.0
Tunicates	0.0	0.1	0.0
Sand	73.5	23.1	6.3
Bare coral rock	11.0	4.3	6.3
Coral rubble	13.1	11.1	1.2
Studied taxa:			
Dictyota sp.	0.1	8.8	5.5
Orbicella faveolata	0.4	2.6	3.0

190

191 Mean bacterial concentration (±SD) in the water column at 15 m depth was $9.6 \pm 1.2 \times 10^5$ cells

192 mL^{-1}.

DOC concentrations across a depth-dependent light gradient

194 At 10 m depth (intermediate light), mean *in situ* DOC concentration in close proximity to the reef

195 alga *Dictyota* sp. was 13 and 11 µmol L^{-1} higher than for the scleractinian coral *O. faveolata*

196 (Tukey HSD, p=0.001) and the water column (Tukey HSD, p=012), respectively (Figure 1 and

197 Supplemental Information for raw data).

198

199
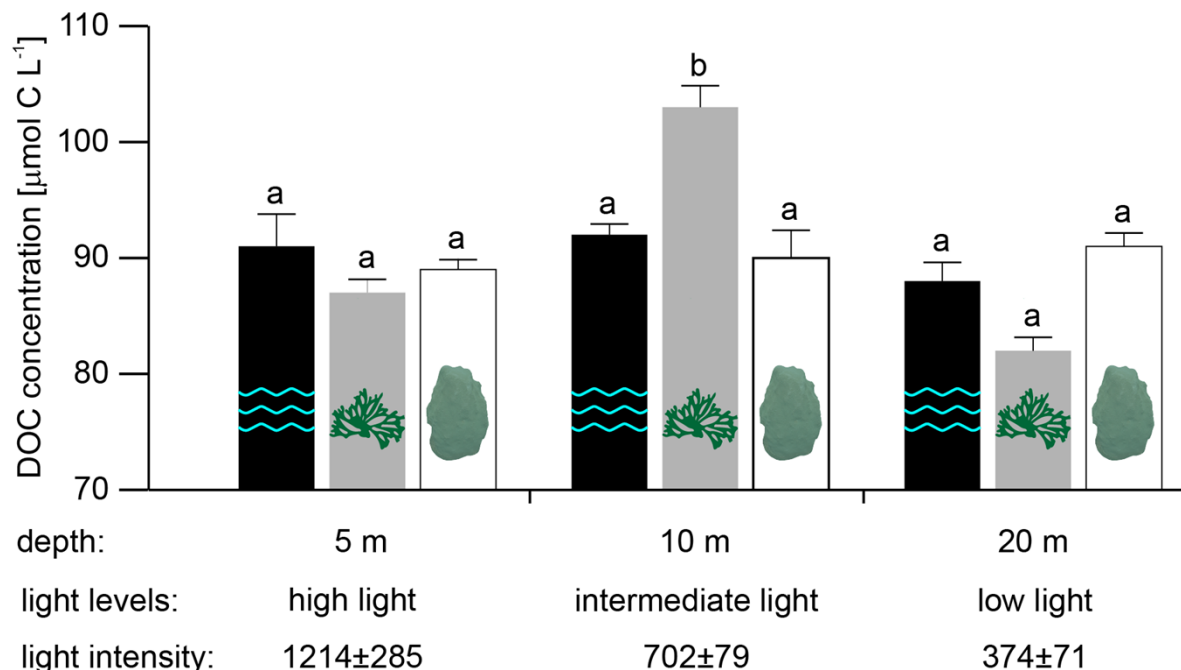
Figure 1 Mean *in situ* DOC concentrations (n = 5, except for water column at 10 m and *Dictyota* sp. at 5 m depth with n = 4) measured in the water column (2 m off the reef slope; black) and at the substrate-water interfaces of the reef algae *Dictyota* sp. (dark grey) and the scleractinain coral *Orbicella faveolata* (white) at 5, 10, and 20 m depth. Error bars indicate SE. Different letters indicate differences between water types for each depth (Tukey HSD, p<0.05). Light intensities (mean±SD) during the sampling are given in μmol photons m^{-2} s^{-1}.

In contrast, mean *in situ* DOC concentration at 5 m (high light) and 20 m (low light) did not differ significantly between water types (Table 2A). While mean DOC concentrations in close proximity to *Dictyota* sp. at 20 m appear to be depleted relative to concentrations in the water column and near *O. faveolata*, these differences were not found to be significant (Figure 1). No depth-related differences in mean DOC concentrations were established in any of the tested water types (Table 2B).

212 **Table 2 Results of one-way ANOVAs on the effect of (A) water type (per depth) and (B)**

213 **depth (per water type) on observed mean *in situ* DOC concentrations.** Significant effects are

214 marked with an asterisk.

A. Differences between water types				
Per depth:	**df**	**F**	**p**	
High light (5 m)	2	0.357	0.707	
Intermediate light (10 m)	2	13.378	0.001	*
Low light (20 m)	2	0.129	0.880	
B. Differences between depth:				
Per water type:	**df**	**F**	**p**	
Water column	2	0.148	0.864	
Dictyota sp.	2	3.682	0.06	
Orbicella faveolata	2	2.798	0.101	

215

216 However, both water type and depth appear to jointly affect mean *in situ* DOC concentrations

217 along the tested depth-dependent light gradient (significant interaction: water type x depth,

218 p=0.026; Table 3). The sampling depths 5, 10, and 20 m corresponded to a light intensity of

219 1214±285, 702±79 and 374±71 µmol photons m^{-2} s^{-1} (mean±SD), respectively, during the

220 sampling (between 12:00 and 13:00 hrs).

221

222 **Table 3 Results of a two-way ANOVA on the combined effects of water type and depth on**

223 **observed mean *in situ* DOC concentrations.**

Factor	df	F	p	
Water type	2	4.731	0.015	*

Depth	2	0.054	0.947	
Water type x Depth	4	3.169	0.026	*

224

Maximum excitation pressure over photosystem II in *Dictyota* sp.

226 At dawn, maximum potential quantum yield (Fv/Fm) in *Dictyota* sp. was 0.65±0.04 (mean±SD),

227 which was reduced by 67% to 0.44±0.09 at 15:00 (effective quantum yield; (ΔF/Fm')

228 (Supplemental Information for raw data). The corresponding Q_m value of 0.33 indicates foremost

229 closed reaction centers of photosystem II and thus suggest the occurrence of photoinhibition at

230 light levels of 1237±486 µmol photons m^{-2} s^{-1}, which are comparable to those observed *in situ* on

231 the reef terrace at 5 m depth (high light) during midday (see DOC concentrations across a depth-

232 dependent light gradient).

DISCUSSION

234 In this study we investigated DOC concentrations in close proximity to the reef alga *Dictyota* sp.,

235 the scleractinian coral *O. faveolata,* and in the water column across a depth-dependent light

236 gradient between 5 and 20 m. Due to the positive relationship between light availability and

237 DOC release we hypothesized that DOC concentrations near BPP are highest on the shallow,

238 well-lit reef terrace and decrease along the fore reef slope following a depth-dependent pattern.

239 Elevated DOC concentrations compared to the background concentrations in the water column

240 were only observed near *Dictyota* sp. at an intermediate depths at 10 m, but not at 5 m or 20 m

241 depth, or near *O. faveolata* at any of the tested depth. No depth- and therefore light-related

242 differences in mean DOC concentrations were established in any of the tested water types,

243 however, water type and depth appear to jointly affect *in situ* DOC concentrations across the

244 tested depth-dependent light gradient.

245 Elevated DOC concentrations in close proximity to BPP occur when DOC release exceeds

246 removal processes. Consequently, environmental parameters, such as light availability (Haas et

247 al. 2010b; Barrón et al. 2012), temperature (Gillooly et al. 2001; Haas et al. 2010b), grazing

248 pressure (Berman & Holm-Hansen 1974), senescence (Khailov & Burlakova 1969), nutrient

249 availability (Lopéz-Sandoval et al. 2011; Mueller et al. 2016), and hydrodynamic conditions

250 (Wild et al. 2012) affect the DOC release of BPP. In combination with factors which affect the

251 accumulation/removal of DOC near them (e.g. morphology of the BPP, hydrodynamic

252 conditions (Losee & Wetzel 1993, Escartín & Aubrey 1995) and DOC consumption by

253 heterotrophic microbes and sponges (Gast et al. 1999; Yahel et al. 2003; Scheffers et al. 2005;

254 De Goeij et al. 2008, Haas et al. 2011, Nelson et al. 2013), these parameters interactively

255 determine the DOC concentrations in close vicinity to BPP. The lack of elevated DOC

256 concentrations near *Dictyota* sp. under high light levels at 5 m depth could thus be explained by

257 (1) reduced DOC release, (2) high DOC removal, or (3) a combination of both.

258 Light availability is generally considered to have a strong positive effect on DOC release of reef

259 algae. However, Haas et al. (2010b) reported that this positive correlation in the reef alga

260 *Caulerpa* sp. only held until a maximum light intensity was reached. At these light intensities

261 DOC release rates steeply decreased to levels comparable to those in the dark. They explained

262 this decrease with the onset of photoinhibition at a species-specific light intensity, which is a

263 common phenomenon in coral reef BPP (Franklin 1994; Hanelt et al. 1994; Brown et al. 1999;

264 Hoegh-Guldberg & Jones 1999; Iglesias-Prieto et al. 2004). While the occurrence of

265 photoinhibition wasn't specifically tested for during the DOC sampling, the corroborative *ex situ*

266 experiment to assess excitation pressure over photosystem II in *Dictyota* sp. suggests that

267 photoinhibition can occur at light levels comparable to those observed *in situ* at 5 m depth on the

268 aforementioned sampling day. Accordingly, photoinhibition may have reduced the DOC release

269 of *Dictyota* sp. on the reef terrace at 5 m depth and therefore contributed to the fact that no

270 elevated DOC concentrations in its close proximity were found.

271 Similar to light availability, hydrodynamic conditions can affect *in situ* DOC concentrations near

272 BPP in two ways. Either positively, when water movement increases the metabolism and DOC

273 release rates of BPP by alleviating the limitation of the diffusive boundary layer around them

274 (Carpenter et al. 1991; Lesser et al. 1994; Wild et al. 2012), or negatively, when water movement

275 and water exchange hamper the accumulation of DOC by dilution (Hauri et al. 2010). Water

276 movement generally decreases exponentially as a function of depth (Shashar et al. 1996) and

277 significantly higher water movement rates are reported at 5 compared to 10 or 20 m depth on the

278 reef slope of Curaçao (Vermeij & Bak 2003). Thus, a reduced DOC release rate of *Dictyota* sp.

279 due to photoinhibition in combination with high water movement and water exchange that

280 hamper the accumulation of DOC, could explain the lack of elevated DOC concentrations near

281   *Dictyota* sp. under high light levels at 5 m depth. It can be further assumed that the negative

282   effect of water movement and water exchange on the accumulation of DOC at 10 m was higher

283   than at 20 m, i.e., a higher DOC release rate was necessary to result in elevated DOC

284   concentrations at 10 m. Yet, despite higher water movement, elevated DOC concentrations near

285   *Dictyota* sp. were only found at 10, but not at 20 m. One explanation for this difference is that

286   DOC release rates were higher at 10 m (intermediate light) than at 20 m (low light), which is in

287   line with the aforementioned positive relation between light availability and DOC release.

288   Interestingly, whilst not significant, DOC concentrations in close proximity to *Dictyota* sp. at 20

289   m depth tend to be depleted compared to concentrations near *O. faveolata* or in the water

290   column. Reduced water movement and thus a prolonged water residence time combined with a

291   low, but steady release of bio-available algal DOC (Nelson et al. 2013) by *Dictyota* sp., could

292   have stimulated the growth of heterotrophic microbial communities. The bio-available DOC

293   could have further allowed those communities to metabolize otherwise refractory components of

294   the DOC pool and thereby deplete the local DOC stock, as described for the water columns

295   overlying algal-dominated reefs (Dinsdale et al. 2008; Haas et al. 2016).

296   No elevated DOC concentrations were observed near the scleractinian coral *O. faveolata* at any

297   of the sampling depths. In general, the DOC release of scleractinian corals is more variable than

298   that of reef algae and an increasing number of studies suggest that scleractinian corals only

299   contribute marginally to the local DOC pool on tropical coral reefs (e.g., Haas et al. 2010a;

300   Naumann et al. 2010; Haas et al. 2011). Furthermore, the massive morphology of *O. faveolata* is

301   less likely to restrict water exchange than the bushy thalli of *Dictyota* sp. and is thereby less

302   favorable for the accumulation of DOC in its vicinity (Stocking et al. 2016). Given the positive

303   effect of light availability on the DOC release by BPP, we expected to find significantly higher

304   DOC concentrations on the shallow and well-lit reef terrace compared to deeper reef sections,

305   following the natural light gradient across depth. Yet, no significant differences in the mean

306   DOC concentrations between the sampled depths were observed, neither in close vicinity to the

307   BPP *Dictyota* sp. or *O. faveolata*, nor in the water column. Nevertheless, both water type and

308   depth (and thereby light availability) seem to have interactively determined *in situ* DOC

309   concentrations. This is in accordance with previous findings that suggest that DOC release by,

310   and *in situ* DOC concentrations near BPP are at least partly determined by a substrate-specific

311   relationship with light availability (Mueller et al. 2014b). The absence of significant differences

312 in DOC concentrations across the water column was also observed in other studies (Torréton et

313 al. 1997; Nelson et al. 2011). To date only Slattery & Lesser (2015) reported a significant decline

314 in DOC concentration with depth from coral reefs on the Bahamas, albeit this decrease occurred

315 at mesophotic depths below 30 m. This may indicate that at least above mesophotic depths, DOC

316 released by BPP is either quickly mixed and diluted throughout the reef overlying water column

317 and/or taken up by DOC feeding organisms (i.e. heterotrophic bacteria and reef sponges). The

318 abundances of open reef sponges and microbes at our study site, and on Curaçaoan reefs in

319 general, are fairly low (Gast et al. 1999; De Goeij & Van Duyl 2007; Mueller et al. 2014a; De

320 Bakker et al. 2017) compared to abundances at more degraded locations throughout the

321 Caribbean (e.g., Pawlik et al. 2015 and references therein, Haas et al. 2016). However, DOC

322 removal by cryptic sponges living underneath overhangs and in coral cavities, which were not

323 recorded in this study, is estimated to be in the same order of magnitude as gross primary

324 production on these reefs (De Goeij et al. 2013).

325 **CONCLUSION**

326 While light availability has a strong positive effect on the DOC release of BPP, the occurrence of

327 elevated DOC concentrations near them did not follow a natural light gradient across the reef

328 slope in our study system. Instead, a combination of multiple factors, including water type, light

329 availability, which affects the release of DOC (including the restriction by photoinhibition), and

330 water movement, which affects the accumulation/removal of DOC, are proposed to interactively

331 determine the DOC concentrations in the close vicinity of BPP along the reef slope.

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