

Spatial and temporal variability of benthic primary production in upwelling-influenced Colombian Caribbean coral reefs

In Tayrona National Natural Park (Colombian Caribbean), abiotic factors such as light intensity, water temperature, and nutrient availability are subjected to high temporal variability due to seasonal coastal upwelling. These factors are major drivers controlling coral reef primary production. This offers the opportunity to assess the effects of abiotic factors on key coral reef ecosystem services in terms of productivity. We therefore quantified primary net (P_n) and gross production (P_g) of the dominant local primary producers (scleractinian corals, macroalgae, algal turfs, crustose coralline algae, and microphytobenthos) at a water current/wave-exposed (EXP) and -sheltered (SHE) site in an exemplary bay of Tayrona National Natural Park. A series of short-term incubations was conducted to quantify O_2 fluxes of the different primary producers before and at the end of the upwelling event 2011/2012. At the level of the organism, scleractinian corals showed highest P_n and P_g rates before upwelling (16 and 19 mmol O_2 m⁻² specimen area h⁻¹), and corals and algal turfs dominated the primary production at the end of upwelling (12 and 19 mmol O_2 m⁻² specimen area h⁻¹, respectively). At the ecosystem level, corals contributed most to total P_n (EXP: 81 %; SHE: 65 %) and P_g (EXP: 78 %; SHE: 55 %) before the upwelling, while at the end of the upwelling, corals contributed most to P_n and P_g only at EXP (73 and 75 %) and macroalgae at SHE (52 and 46 %, respectively). Despite the significant spatial and temporal differences in individual productivity of investigated groups and their different contribution to reef productivity, no spatial or temporal differences in daily ecosystem P_n and P_g were detected (194 – 218 and 311 – 409 mmol O_2 m⁻² seafloor area d⁻¹). Our findings therefore indicate that local autotrophic benthic reef communities are well adapted to pronounced fluctuations of environmental key parameters. This might lead to a higher resilience against climate change consequences and anthropogenic disturbances.

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11 **Introduction**

12 The majority of ecosystems depend on primary production. Photoautotrophs convert light energy
13 into chemical energy by photosynthesis, creating the energetic base of most food webs in
14 terrestrial as well as aquatic environments ([Valiela, 1995](#); [Chapin et al., 2011](#)). Among
15 other coastal ecosystems such as mangrove forests, seagrass beds, salt marshes, and kelp
16 forests, coral reefs belong to the most productive ecosystems in the world ([Hatcher, 1988](#);
17 [Gattuso, Frankignoulle & Wollast, 1998](#)). Productivity investigation of coral reefs started in
18 the mid-20th century ([Sargent & Austin, 1949](#); [Odum & Odum, 1955](#)), and today coral reefs
19 are among the best understood marine benthic communities in terms of primary production
20 ([Kinsey, 1985](#); [Hatcher, 1988](#); [Hatcher, 1990](#); [Gattuso, Frankignoulle & Wollast, 1998](#)). It
21 was long assumed that coral reef productivity is relatively balanced as tropical coral reefs
22 typically thrive under relatively stable abiotic conditions ([Hubbard, 1996](#); [Kleypas,](#)
23 [McManus & Menez, 1999](#); [Sheppard, Davy & Pilling, 2009](#)), including light ([Darwin,](#)

24 [1842](#); [Achituv & Dubinsky, 1990](#); [Falkowski, Jokiell & Kinzie III, 1990](#)), water temperature
25 ([Dana, 1843](#); [Coles & Fadlallah, 1991](#); [Veron, 1995](#)), salinity ([Andrews & Pickard, 1990](#);
26 [Coles & Jokiell, 1992](#)), and inorganic nutrient availability ([D'Elia & Wiebe, 1990](#); [Szmant,](#)
27 [1997](#)).

28 Nevertheless, coral reefs also occur in seasonal upwelling-affected regions such as the Arabian
29 Sea off Oman ([Glynn, 1993](#)), the Eastern Tropical Pacific off Panamá and Costa Rica
30 ([Glynn & Stewart, 1973](#); [Cortés & Jiménez, 2003](#)), and the Colombian Caribbean ([Geyer,](#)
31 [1969](#)). Whereas several studies focused on the seasonality of benthic primary production in
32 coral reefs at different latitudes ([Adey & Steneck, 1985](#); [Kinsey, 1985](#); [Falter et al., 2012](#)),
33 variability in primary production of seasonal upwelling-affected coral reefs remains largely
34 underinvestigated.

35 The Tayrona National Natural Park (TNNP) at the Caribbean coast of Colombia offers ideal
36 conditions to assess upwelling-affected primary productivity of coral-dominated benthic
37 communities as it is highly influenced by the Southern Caribbean upwelling system
38 ([Andrade & Barton, 2005](#); [Rueda-Roa & Muller-Karger, 2013](#)) which causes fluctuations in
39 water temperature, light availability, and inorganic nutrient concentrations ([Eidens et al.,](#)
40 [2012](#); [Bayraktarov, Pizarro & Wild, 2014](#)). The upwelling seasonally extends to TNNP
41 ([Andrade & Barton, 2005](#)), where diversely structured coral communities are present
42 ([Werding & Sánchez, 1989](#)). Here, the abundance and community composition of benthic
43 algae were shown to exhibit seasonality related to upwelling events ([Diaz-Pulido &](#)
44 [Garzón-Ferreira, 2002](#); [Eidens et al., 2012](#)). Thereby, the area provides an excellent
45 opportunity to investigate the effects of seasonal coastal upwelling events on the key coral
46 reef ecosystem service productivity under changing *in situ* conditions.

47 The results of a preliminary study conducted by [Eidens et al. \(2012\)](#) indicated that benthic
48 primary production in TNNP differed between the upwelling in 2010/2011 and the consecutive

49 non-upwelling season and the authors suggested a generally positive effect of upwelling
50 conditions on major benthic autotrophs in the area. However, as the region was affected by an
51 unusually strong El Niño-Southern Oscillation (ENSO) event in 2010/2011, which led to a coral
52 bleaching in TNNP before the upwelling in 2010/2011 ([Bayraktarov et al., 2013](#); [Hoyos et al.,](#)
53 [2013](#)), productivity measurements during upwelling in 2010/2011 might not be representative for
54 a typical upwelling event. To test for spatio-temporal patterns in benthic primary production
55 during a typical seasonal cycle, we here quantified benthic primary production before and at the
56 end of the upwelling event in 2011/2012 and further used 3D surface area estimates of dominant
57 primary producers to assess surface area-specific productivity rates of the investigated groups as
58 suggested by [Naumann et al. \(2013\)](#). Accordingly:

- 59 1. We identified dominant functional groups of benthic primary producers and their relative
60 benthic cover at a current/wave-exposed (EXP) and -sheltered (SHE) site in one
61 exemplary bay of TNNP prior to primary production measurements.
- 62 2. We then used incubation experiments to quantify O₂ fluxes of dominant benthic primary
63 producers and applied 3D surface area estimations to allow for comparisons of
64 productivity between investigated groups.
- 65 3. Finally, we combined data on benthic coverage and individual production rates of
66 investigated groups to estimated the specific contribution of each group to total benthic O₂
67 fluxes.

68 **Materials and Methods**

69 **Study site and sampling seasons**

70 This study was conducted in Gayraca Bay (11.33°N, 74.11°W), one of several small bays in
71 TNNP, located near the city of Santa Marta (Fig. 1). The continental shelf in the area is relatively
72 narrow, and only small fringing coral reefs are present in the park due to the proximity to the
73 Sierra Nevada de Santa Marta - the world's highest coastal mountain range ([Garzón-Ferreira &](#)
74 [Cano, 1991](#); [Garzón-Ferreira, 1998](#)). The region is subjected to strong seasonality caused by the
75 Caribbean Low-Level Jet of northeast (NE) trade winds ([Salzwedel & Müller, 1983](#); [Andrade &](#)
76 [Barton, 2005](#)), resulting in two major seasons; a dry season from December to April and a rainy
77 season from May to November ([Salzwedel & Müller, 1983](#); [Garzón-Ferreira, 1998](#)). Whereas the
78 rainy season (hereafter referred to as non-upwelling) is characterized by low wind velocities
79 (mean 1.5 m s⁻¹) ([Garzón-Ferreira, 1998](#)) and high precipitation (> 80 % of the annual rainfall)
80 ([Salzwedel & Müller, 1983](#)), during the dry season (hereafter referred to as upwelling), strong
81 winds prevail (mean 3.5 m s⁻¹, max 30 m s⁻¹) ([Herrmann, 1970](#); [Salzwedel & Müller, 1983](#)) that
82 lead to a seasonal coastal upwelling. The upwelling-related changes in key water parameters are
83 well characterized by the comprehensive study of [Bayraktarov, Pizarro & Wild \(2014\)](#). During
84 upwelling, water temperature can decrease to 20 °C while salinity, inorganic nutrient availability,
85 and chlorophyll α increase and characterize the ecosystem which is otherwise close to
86 oligotrophic as mesotrophic ([Bayraktarov, Pizarro & Wild, 2014](#)). Water currents triggered by
87 prevailing winds predominantly move from NE, and a clear gradient between the water current-
88 and wave-exposed western (EXP) and -sheltered northeastern (SHE) site of the bay can be
89 observed ([Werding & Sánchez, 1989](#); [Bayraktarov, 2013](#)). The study was carried out before the
90 onset of upwelling in 2011/2012 (1st November – 2nd December 2011) and at the end of upwelling

91 in 2011/2012 (20th March – 29th March 2012), allowing for the investigating of the influence of
92 seasonality on benthic primary production.

93 **Benthic assessment**

94 For the assessment of benthic community structure, the dominant groups of benthic primary
95 producers and the percentage of benthic cover were identified at EXP and SHE prior to primary
96 production measurements using line point intercept transects at a water depth of 10 m (50 m
97 length, $n = 3$), modified from [Hodgson et al. \(2004\)](#). Benthic cover was monitored at 0.5 m
98 intervals directly below the measurement points (101 data points per transect). The dominant
99 benthic autotrophs at the study sites consisted of scleractinian corals, frondose macroalgae, algal
100 turfs (multispecific assemblage of primarily filamentous algae of up to 1 cm height, *sensu*
101 [Steneck \(1988\)](#)), crustose coralline algae (CCA), and sand potentially associated with
102 microphytobenthos. These categories represented 97 ± 2 % of the total seafloor coverage at SHE
103 and 90 ± 7 % at EXP and were therefore selected for the subsequent incubation experiments.
104 During benthic community assessment, rugosity was determined at both sites using the chain
105 method described by Risk ([1972](#)). Rugosity was quantified along three 10 m sub-transects within
106 each of the 50 m transects and were used to calculate the rugosity factor for each study site as
107 described by [McCormick \(1994\)](#) (SHE: 1.53 ± 0.12 , EXP: 1.32 ± 0.13).

108 **Sampling of organisms**

109 Specimens of scleractinian corals, macroalgae, algal turfs, and CCA as well as sand samples,
110 from 10 ± 1 m water depth were used for quantification of O₂ fluxes (see Table 2 for number of
111 replicates). All samples were brought to the water surface in Ziploc bags and transported directly
112 to the field lab. Scleractinian corals of the genera *Montastraea* (including the species *M.*
113 *faveolata*, *M. franksi* and *M. annularis*, currently belonging to the genus *Orbicella*; Budd et al.

114 2012) and *Diploria* accounted for more than 80 % of the total coral cover at the study sites and
115 were therefore used as representative corals in our study. Coral specimens were obtained from the
116 reef using hammer and chisel, fragmented with a multifunction rotary tool (Dremel Corp., 8200-
117 2/45; mean fragment surface area: $13.16 \pm 7.96 \text{ cm}^2$), and fixed on ceramic tiles using epoxy glue
118 (Giesemann GmbH, Aquascape). After fragmentation, specimens were returned to their natural
119 habitat and left to heal for one week prior to the incubation experiments. Algae of the genus
120 *Dictyota* (mainly *D. bartayresiana*) amounted to nearly 100 % of macroalgal cover and therefore
121 small bushes of *Dictyota* spp. (surface area $1.86 \pm 0.88 \text{ cm}^2$) were used as representatives for
122 macroalgae. Macroalgae were transferred to a storage tank (volume: 500 L in which water was
123 exchanged manually 3 - 5 times per day and water temperature was within the ranges of
124 incubation experiments; see Table 1) one day before incubation experiments and left to heal. All
125 other functional groups were incubated immediately after sampling. Rubble overgrown by algal
126 turfs and CCA served as samples for the respective functional group (surface area covered by the
127 organisms: $15.63 \pm 10.80 \text{ cm}^2$ and $7.48 \pm 3.60 \text{ cm}^2$, respectively). For sand samples, custom-made
128 mini corers with defined surface area (1.20 cm^2) and sediment core depth (1.0 cm) were used.

129 **Surface area quantification**

130 Digital photographs of coral specimens were used to quantify planar projected surface areas of
131 samples by image-processing software (ImageJ, V. 1.46r, National Institute of Health). The 3D
132 surface area of the samples was estimated via multiplication of the planar projected surface areas
133 by the genera-specific 2D to 3D surface area conversion factors derived from computer
134 tomography measurements of *Diploria* and *Montastraea* skeletons (2.28 ± 0.16 and 1.34 ± 0.56 ,
135 respectively), as described by [Naumann et al. \(2009\)](#). Planar leaf area of spread out macroalgal
136 specimens was likewise quantified by digital image analysis and multiplied by the factor 2 to

137 obtain 3D surface area of the samples. Image analysis of photographs *in situ* and the whole
138 spread out macroalgal thalli were used to obtain covered substrate areas (2D surface) as well as
139 3D surface areas and further calculate the 2D to 3D conversion factor for macroalgae ($4.29 \pm$
140 0.82). The 2D surface area of algal turfs samples was determined by image analysis of digital
141 photographs. For CCA, the simple geometry method described by [Naumann et al. \(2009\)](#) was
142 used to estimate the surface area of overgrown pieces of rubble. The obtained surface areas were
143 related to the planar projected surface area of the samples to generate 2D to 3D conversion
144 factors for CCA (2.10 ± 0.89). Specimen surface area for sand samples was defined by the size of
145 the used mini corer apparatus (1.20 cm^2).

146 **Incubation Experiments**

147 Prior to incubation experiments, water temperature ($^{\circ}\text{C}$) and light intensity (lx) were monitored at
148 the sampling sites with intervals of 2 min using light and temperature loggers (Onset HOBO
149 Pendant UA-002-64) in order to adjust light and temperature during incubations to *in situ*
150 conditions. The availability of light during light incubations was adjusted to the *in situ* light
151 regimes using net cloth (Table 1). Temperature and light intensity was continuously monitored
152 during incubations as described above. Light intensities were converted to photosynthetically
153 active radiation (PAR, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, 400 to 700 nm) using the approximation of [Valiela](#)
154 [\(1995\)](#). Light availability was generally higher during the upwelling event (t-test, $p < 0.001$;
155 Table 1), whereas water temperatures were higher before the upwelling (t-test, $p < 0.001$; Table
156 1). Quantification of photosynthetic activity for macroalgae, CCA, and microphytobenthos were
157 performed in air-tight glass containers with volumes of 60 mL, whereas for corals and algal turfs,
158 containers with volumes of 600 mL were utilized. For all incubations, we used freshly collected
159 seawater from Gayraca Bay. All primary producers were incubated in containers that were placed

160 in cooling boxes filled with water to maintain constant *in situ* water temperature (Table 1). For
161 dark incubations during daytime, the above mentioned methodology was used, but cooling boxes
162 were closed with opaque lids to prevent light penetration. Comparability among measurements
163 was assured by carrying out all light incubations on cloudless days between 10 am and 2 pm. For
164 each group of primary producers, one light and one dark incubation were performed within each
165 study period. Incubation containers filled with seawater only served as blank controls to quantify
166 photosynthetic activity and respiration of microbes in the water column. Physiological damage of
167 the investigated specimens by hypoxic or hyperoxic conditions were prevented by keeping the
168 incubation times as short as possible (light incubations: 30 to 60 min and dark incubations: 120
169 min as suggested by ([Jantzen et al., 2008](#); [Mass et al., 2010b](#); [Jantzen et al., 2013](#)). The dissolved
170 O₂ concentrations in the incubation water within the glass containers were quantified before
171 incubations and after removing the specimens at the end of each incubation using an optode
172 (Hach Lange, HQ 40). Before O₂ measurements, the incubation medium was gently stirred with
173 the optode sensor allowing a homogenization of the water column. Experiments were conducted
174 in closed, non-mixed incubation chambers in order to avoid additional contamination sources and
175 to provide the most conservative estimates of O₂ production rates of benthic primary producers as
176 suggested by [Haas et al. \(2011\)](#) and [Naumann et al. \(2013\)](#). This also ensured higher
177 measurement accuracy, as water movement during incubations may affect gas transfer velocities
178 across the surface boundary of the incubation chambers ([Wu, Barazanji & Johnson, 1997](#)) and
179 allowed us to compare our results with previous incubation studies (e.g. [Haas et al. 2011](#); [Jantzen](#)
180 [et al. 2013](#); [Naumann et al. 2013](#)). Nevertheless, since it is well known that water flow enhances
181 O₂ fluxes and thereby photosynthesis ([Mass et al., 2010a](#)), the results of the field incubations
182 should be regarded as conservative estimates of *in situ* O₂ fluxes and interpreted accordingly.

183 **Data analyses and statistics**

184 To quantify net O₂ production (P_n) and respiration of functional groups, O₂ concentration before
185 incubations was subtracted from concentration after incubations and corrected with blank control
186 values containing only seawater. Individual gross O₂ production (P_g) of investigated functional
187 groups was calculated by adding values of P_n and respiration; individual O₂ fluxes were
188 expressed per mmol O₂ m⁻² specimen surface area h⁻¹. The relative contribution of each
189 investigated group to total reef production (given as: mmol O₂ m⁻² vertically projected seafloor
190 area h⁻¹) was estimated by taking into account the individual production rates and respective
191 mean 2D to 3D conversion factors, the data for benthic coverage as well as the rugosity factor.
192 Estimation of total daily reef productivity was furthermore calculated by extrapolating the
193 incubation periods to a 12 h light and 12 h dark cycle.

194 After testing for normal distribution (Kolmogorov-Smirnoff test) and homogeneity of variances
195 (Levene test), benthic coverage of functional groups as well as total benthic O₂ fluxes were
196 analyzed using two-way ANOVA and Bonferroni's *post hoc* tests to detect possible effects of
197 season (upwelling vs. non-upwelling) and location (EXP vs. SHE) on benthic cover and
198 metabolism. Statistical analysis of metabolic activity within each functional group and the
199 contribution of the functional groups to overall O₂ production were assessed by one-way ANOVA
200 after checking for the assumptions of parametric testing as mentioned above. Spatial differences
201 between the sites during each sampling period as well as seasonal pattern at each site were
202 analyzed by Bonferroni's planned comparison test. If data did not meet the assumptions of
203 parametric testing, data sets were either log transformed or nonparametric Kruskal-Wallis and
204 Dunn's planned comparisons/*post-hoc* tests were used. The analyses were done with
205 STATISTICA (8.0). All values are represented as mean ± standard deviation (SD).

206 **Results**

207 **Benthic community composition**

208 At EXP, scleractinian corals dominated the benthic community before ($41 \pm 12\%$) and at the end
209 of the upwelling ($39 \pm 12\%$, Table 3). At SHE, corals, algal turf, and sand cover was similar
210 before upwelling ($24 \pm 3\%$, $26 \pm 6\%$, and $25 \pm 13\%$, respectively), while at the end of
211 upwelling, macroalgae exhibited highest benthic cover ($47 \pm 3\%$, Table 3). During the entire
212 study period, coral and CCA cover was significantly higher at EXP than at SHE, whereas sand
213 showed a contrary pattern with significantly more coverage at SHE (ANOVA results Table S1).
214 Macroalgae cover was significantly higher at SHE than at EXP and less abundant at both sites
215 before upwelling than at the end of upwelling (Table S1). CCA cover also differed between the
216 seasons, showing a significant decrease during the upwelling event (Table S1).

217 **O₂ Fluxes of organisms**

218 Highest individual net (P_n) and gross production (P_g) of all investigated functional groups were
219 measured for scleractinian corals at both sites before the upwelling, while corals and algal turfs
220 showed highest individual P_n and P_g rates at the end of the upwelling (Table 2). While significant
221 spatial differences in O₂ production within functional groups were only observed for CCA with
222 higher production at EXP than at SHE before upwelling, temporal differences in O₂ production
223 were detected for corals, macroalgae, and CCA (ANOVA results: Table S2). For scleractinian
224 corals and macroalgae, significant differences in P_n were only present at SHE with lower
225 productivity at the end than before upwelling (Table S2). Primary production of CCA showed
226 opposite pattern at the two sites: P_n and P_g were significantly elevated at EXP before upwelling,
227 while productivity at SHE was significantly higher at the end of the upwelling (Table S2).

228 **Contribution of organism-induced O₂ fluxes to total reef O₂ production**

229 Before the upwelling, corals contributed most to benthic O₂ fluxes at EXP and SHE (Table 4).
230 Contribution of corals at EXP to the total benthic O₂ fluxes was significantly higher than for algal
231 turfs and microphytobenthos (ANOVA results: Table S3). At SHE, corals contributed
232 significantly more than macroalgae, microphytobenthos, and CCA (Table S3). At the end of the
233 upwelling season, contribution of corals to total benthic O₂ fluxes were also highest at EXP
234 (Table 4) where corals contributed more to benthic productivity than CCA and
235 microphytobenthos (Table S3). At SHE, macroalgae contributed most to benthic P_n and P_g (Table
236 4) and significantly more than algal turfs, microphytobenthos, and CCA (Table S3).
237 Significant spatial differences in contribution to total benthic O₂ production within functional
238 groups were detected for all groups except for microphytobenthos (ANOVA results: Table S4).
239 Coral contribution to total O₂ fluxes was higher at EXP than at SHE before the upwelling and at
240 the end of upwelling (Table 4 and S4). During upwelling, macroalgae contributed more to P_n and
241 P_g at SHE than at EXP, whereas contribution of algal turfs to benthic P_g was higher at SHE than
242 at EXP before the upwelling (Table S4). The share of CCA to total productivity was elevated at
243 EXP before as well as at the end of upwelling (Table S4).
244 Temporal differences in contribution to total benthic productivity within the investigated groups
245 were also present in all groups except for microphytobenthos (Table S4). Corals at SHE
246 contributed more to total O₂ production before the upwelling than at the end of upwelling (Table
247 4), while higher rates for macroalgal contribution to total O₂ fluxes were detected for P_n and P_g at
248 the end of the upwelling at the same site (Table S4). For algal turfs, differences in contribution to
249 benthic O₂ fluxes were only present at EXP with elevated P_g rates at the end of the upwelling,
250 whereas higher contribution of CCA to total P_n and P_g was detected before the upwelling at SHE
251 and EXP (Table S4).

252 Regarding total daily benthic O₂ fluxes (Figure 2), no spatial differences between EXP and SHE
253 were detected, neither before nor at the end of the upwelling (ANOVA results: Table S5).
254 Furthermore, no significant temporal differences were present between non-upwelling and
255 upwelling (Table S5). Comparing total benthic productivity at the end of the upwelling events in
256 2010/2011 and 2011/2012, higher P_n and P_g were detected at the end of the upwelling
257 in 2010/2011 (ANOVA results: Table S6).

258 Discussion

259 O₂ Fluxes of Organisms

260 Individual mean P_n and P_g were generally highest for corals at both sites during the study periods
261 (10.9 – 16.3 and 17.6 – 20.9 mmol O₂ m⁻² specimen surface area h⁻¹, respectively). These high
262 productivity rates of corals compared to other investigated primary producers (see Table 2) may
263 be attributed to the mutualistic relationship between zooxanthellae and the coral host, boosting
264 photosynthetic efficiency through high zooxanthellate photosynthesis in coral tissues under high
265 CO₂ and nutrient availability ([D'Elia & Wiebe, 1990](#); [Muscatine, 1990](#)). Therefore, corals are
266 among the most productive functional groups in reef systems with several fold higher specific
267 production rates than most reef algae and reef sands (Table 5) ([Wanders, 1976b](#); [Kinsey, 1985](#);
268 [Yap, Montebon & Dizon, 1994](#)). Estimated daily gross O₂ production per m² vertically projected
269 surface area for both investigated coral genera, *Diploria* and *Montastraea* (492 – 687 and 412 –
270 518 mmol O₂ m⁻² seafloor d⁻¹, respectively), are similar to O₂ fluxes of other Caribbean corals,
271 ranging from 67 to 850 mmol O₂ m⁻² seafloor d⁻¹ (Table 5) ([Kanwisher & Wainwright, 1967](#)).
272 Generally, O₂ fluxes of all investigated organism groups were within ranges reported in the
273 literature (Table 5).

274 In comparison to all other investigated organism groups, coral productivity rates were not only
275 higher, but also exhibited less fluctuation throughout the study (Table 2) despite the high
276 variability in environmental parameters in the area ([Bayraktarov, Pizarro & Wild, 2014](#)). A reason
277 for the observed patterns could be a high plasticity of the coral holobiont, including the coral
278 host, the endosymbiotic zooxanthellae and associated microbes with many symbiotic
279 interrelationships ([Rohwer et al., 2002](#); [Rosenberg et al., 2007](#); [Bellantuono, Hoegh-Guldberg &
280 Rodriguez-Lanetty, 2012](#)). These symbiotic interactions may ensure stable productivity of corals
281 along a wide range of abiotic factors that typically alter metabolic activity. This is well known for
282 variation in light availability ([Porter et al., 1984](#); [Gladfelter, 1985](#)), where acclimation is mainly
283 achieved by the regulation of zooxanthellae density and chlorophyll content within zooxanthellae
284 cells ([Barnes & Chalker, 1990](#); [Stambler, 2011](#)). Our findings are supported by [Kinsey \(1985\)](#)
285 who characterized the productivity of corals as rather stable at low to moderate latitudes (15° to
286 23°; Gayraca Bay: 11° N), while at these latitudes, productivity of other benthic autotrophs such
287 as foliose algae exhibited pronounced seasonality.

288 Significant spatial differences were only found for CCA before the upwelling with higher
289 individual O₂ production at EXP compared to SHE. These differences may be explained by the
290 prevailing water current regime in the bay together with high water temperatures of up to 30 °C
291 before the upwelling. An increase in water temperature typically rises metabolic activity in CCA
292 ([Littler & Doty, 1975](#)), but decreased water flow at SHE compared to EXP ([Bayraktarov, 2013](#))
293 likely prevented the required gas exchange and nutrient uptake, resulting in lower individual
294 CCA productivity at SHE.

295 Temporal differences in individual O₂ production within investigated organism groups were most
296 pronounced at SHE with two contrary patterns observed: whereas macroalgae and scleractinian
297 corals produced less O₂ at the end of upwelling, CCA exhibited higher O₂ production rates during
298 this study period. The decreased production rates of macroalgae could be explained by high

299 macroalgal cover High macroalgal cover, as observed at SHE during the upwelling (47 ± 3 %,
300 Table 3), could have resulted in reduced macroalgal O_2 production due to density-dependent
301 intra-specific competition for light and nutrients by the dominant macroalgae *Dictyota* sp.
302 ([Edwards & Connell, 2012](#)). The macroalgal die-off together with lower water currents at SHE
303 compared to EXP could further have negatively affected coral productivity as decomposition of
304 macroalgae may result in toxicity towards organisms as stated by [Morand & Merceron \(2005\)](#).
305 Elevated photosynthetic performance of CCA at SHE at the end of upwelling may be due to
306 higher nutrient concentrations during upwelling compared to non-upwelling ([Bayraktarov et al.,](#)
307 [2013](#); [Bayraktarov, Pizarro & Wild, 2014](#)). Nutrient limitation of benthic communities in water
308 current-sheltered locations may be more pronounced than in communities exposed to high water
309 flow due to the fact that benthic algal communities are typically nutrient-limited ([Hatcher &](#)
310 [Larkum, 1983](#)), and nutrient supply of coral reef algae is primarily controlled by water flow
311 ([Hatcher, 1990](#)). Elevated nutrient concentration during upwelling may therefore offset the
312 limiting nutrient supply particularly at SHE where water flow was lower than at EXP
313 ([Bayraktarov, 2013](#)).

314 **Contribution of organism-induced O_2 fluxes to total benthic O_2 production**

315 Before the upwelling, the share of corals to total benthic P_n and P_g were highest at both EXP
316 (80.6 ± 24.3 and 77.5 ± 19.2 %, respectively) and SHE (64.5 ± 25.5 and 54.9 ± 18.4 %,
317 respectively). At the end of the upwelling, corals only contributed most to P_n and P_g at EXP (72.6
318 ± 16.7 and 75.4 ± 15.3 %, respectively), whereas macroalgal contribution to benthic primary
319 production was highest at SHE (P_n : 51.6 ± 7.4 ; P_g : 46.3 ± 12.4 %). The major contribution of
320 corals can be explained by their highest quantified individual O_2 production rates of all
321 investigated organism groups (Table 2) and comparably high benthic coverage of corals, ranging

322 from 24 to 39 % (Table 3). Similar values were estimated for a Southern Caribbean fringing reef
323 by [Wanders \(1976b\)](#), where corals accounted for about two-thirds of total benthic primary
324 production.

325 Although individual macroalgal production rates were rather low compared to corals (Table 2),
326 the extremely high cover of macroalgae at SHE at the end of upwelling (47 ± 3 %) resulted in
327 macroalgae being the main contributor to total benthic productivity. Reasons for the high
328 macroalgal cover may likely be elevated nutrient concentrations and lower water temperatures
329 throughout the upwelling event ([Bayraktarov et al., 2013](#); [Bayraktarov, Pizarro & Wild, 2014](#)), as
330 these factors stimulate the growth of the dominant macroalgal genus *Dictyota* ([Bula-Meyer,](#)
331 [1990](#); [Cronin & Hay, 1996](#); [Diaz-Pulido & Garzón-Ferreira, 2002](#)).

332 The identified spatial differences in contribution to total benthic O₂ production for scleractinian
333 corals, macroalgae, and CCA can also be explained by spatial differences in their benthic
334 coverage. Elevated contributions of corals and CCA at EXP compared to SHE (Table 4) not only
335 reflect their spatial abundance patterns (Table 3), but also the higher macroalgal contribution at
336 SHE at the end of the upwelling (Table 4) can be linked to spatial differences in macroalgal
337 coverage with higher abundances at SHE during upwelling (Table 3). The observed pattern in
338 benthic coverage of corals and CCA may be caused by the water current regime in the bay with
339 stronger water currents at EXP compared to SHE ([Bayraktarov, 2013](#)), as suggested to be the
340 major driver for differences in local coral communities by [Werding & Sánchez \(1989\)](#). This
341 explanation is supported by the studies of [Jokiel \(1978\)](#) and [Fabricius & De'ath \(2001\)](#), stating
342 that maximum abundance of corals and CCA typically occur in water current-exposed
343 environments. Differences in water current exposure between the study sites could also be the
344 reason for the observed spatial patterns in macroalgal abundance, as the abundance of the
345 dominant macroalgal genus *Dictyota* is highly affected by water current exposure ([Renken et al.,](#)
346 [2010](#)).

347 Corals, macroalgae, and CCA also exhibited distinct temporal differences in contribution to total
348 benthic productivity. At SHE, corals contributed more to benthic O₂ production before the
349 upwelling and macroalgae at the end of the upwelling, whereas contribution of CCA at both sites
350 was higher before as compared to at the end of upwelling. Reasons for the observed patterns in
351 coral contribution to total benthic primary production are temporal shifts in individual O₂
352 productivity of corals with higher production rates before the upwelling event (Table 2) together
353 with slightly higher benthic coverage during this study period (Table 3). The temporal variation
354 in macroalgal contribution to total benthic O₂ fluxes can be explained by the seasonal growth
355 pattern of the dominant macroalgae *Dictyota* sp., most likely caused by variation in nutrient
356 concentrations ([Bayraktarov et al., 2013](#); [Bayraktarov, Pizarro & Wild, 2014](#)) and water
357 temperatures, as these factors affect the growth of the dominant macroalgae genus *Dictyota*
358 ([Bula-Meyer, 1990](#); [Cronin & Hay, 1996](#); [Diaz-Pulido & Garzón-Ferreira, 2002](#)). The contrary
359 occurrence pattern of macroalgae and CCA especially at SHE with higher CCA cover before
360 compared to the end of upwelling (14 ± 4 vs. 3 ± 2 %, Table 3) suggests that seasonal occurrence
361 of the dominant macroalgae *Dictyota* sp. may also account for the observed temporal variations
362 in CCA abundance at SHE. This assumption is supported by the studies of [Lirman & Biber](#)
363 ([2000](#)) as well as [Belliveau & Paul \(2002\)](#) that demonstrated that macroalgae can shade CCA,
364 leading to usually negative correlated abundances of these groups. Higher contribution of CCA at
365 EXP before as compared to at the end of upwelling furthermore results from both, elevated CCA
366 production rates (Table 2) and higher abundances before the upwelling (Table 3).

367 **Total benthic O₂ fluxes and ecological perspective**

368 Estimated means of total daily benthic O₂ production at both sites before and at the end of the
369 upwelling event in 2011/2012 (Figure 2) were within the ranges of other investigated reef slope

370 communities (Table 5). However, it should be taken into account that total shallow reef
371 productivity in earlier studies was quantified using flow respirometry techniques, whereas our
372 experiments were conducted in no-flow incubation chambers. Despite the different
373 methodologies, our results are comparable to the study by [Adey & Steneck \(1985\)](#) where
374 productivity of similar communities from deeper Caribbean fore reefs of St. Croix (mean water
375 depth: 4.5 – 6.3 m) were quantified. Productivity rates reported by [Adey & Steneck \(1985\)](#) were
376 generally similar to O₂ fluxes in Gayraca Bay, although maximal diurnal fluxes were slightly
377 higher than those in our study (Table 5). As light availability decreases with increasing depth,
378 water depths of investigated communities (St. Croix: < 6.3 m, Gayraca Bay: ~10 m) may account
379 for elevated daily productivity in reefs of St. Croix. Another reason could be higher surface to
380 area ratios in reefs of St. Croix compared to Gayraca Bay (rugosity factor: 1.9 – 2.5 and 1.3 – 1.5,
381 respectively), since surface enlargement is a key factor for benthic communities to increase
382 primary production ([Wanders, 1976b](#)).

383 Despite the high spatial and temporal differences in benthic coverage and group-specific O₂
384 fluxes of investigated benthic primary producers as well as their contribution to total benthic
385 productivity, neither spatial nor seasonal differences in total benthic O₂ fluxes were detected
386 before and at the end of the upwelling event in 2011/2012. These findings are supported by
387 [Hatcher \(1990\)](#), stating that the relative coverage of benthic photoautotrophs in a reef community
388 may have little effect on its areal production rate. However, the observed lack of seasonality of
389 total benthic productivity stands in contrast to earlier studies ([Kinsey, 1977](#); [Smith, 1981](#); [Kinsey,](#)
390 [1985](#); [Eidens et al., 2012](#)) which found an approximately two-fold difference in benthic primary
391 production between seasons. A possible explanation for this finding could come from seasonal
392 changes of abiotic factors, counteracting with each other. On the one hand, decreased water
393 temperatures during upwelling typically mitigate primary production ([Crossland, 1984](#);
394 [Carpenter, 1985](#)). On the other hand, abiotic factors that are known to boost primary productivity,

395 namely water currents ([Mass et al., 2010a](#)) and nutrient availability ([Hatcher, 1990](#); [Chavez,](#)
396 [Messie & Pennington, 2011](#)), typically increase during upwelling events, thus promote
397 photosynthesis. In addition, elevated light availability during incubation experiments at the end of
398 the upwelling (Table 1) could have positively affected photosynthesis of benthic autotrophs. The
399 observed similar productivity rates at different seasons and the reestablishment of original
400 benthic community composition after the upwelling events suggest that coral reefs in TNNP are
401 well adapted to the pronounced seasonal variations in light availability, water temperature, and
402 nutrient availability.

403 Nevertheless, higher total benthic productivity at the end of the upwelling in 2010/2011
404 compared to the non-upwelling was not only detected during our preliminary study ([Eidens et al.,](#)
405 [2012](#)) but total benthic O₂ fluxes during the upwelling in 2010/2011 were also higher than at the
406 end of the upwelling in 2011/2012 (see Table S6 for ANOVA results). These findings suggest that
407 interannual influences do affect productivity of the coral reefs in TNNP. Interestingly, water
408 temperature increases and unusual high precipitation occurred in the study area at the end of
409 2010, related to an ENSO event ([Bayraktarov et al., 2013](#); [Hoyos et al., 2013](#)), causing coral
410 bleaching in the region ([Bayraktarov et al., 2013](#)). Surprisingly, bleached corals in the bay
411 recovered quickly from the ENSO-triggered disturbances in the course of the following
412 upwelling event ([Bayraktarov et al., 2013](#)) and exhibited similar specific O₂ production rates at
413 the end of the upwelling event 2010/2011 compared to subsequent measurements (Table 2) which
414 indicates a high resilience of TNNP corals. Moreover, macroalgae and algal turf seemed to
415 benefit from the environmental conditions during the upwelling following the ENSO-related
416 disturbance event, resulting in higher group-specific productivity of macroalgae and particularly
417 algal turfs at the end of the 2010/2011 upwelling event compared to subsequent study periods
418 (Table 2). The elevated production rates of macroalgae and algal turfs together with the fast
419 recovery of corals from bleaching accounted for higher benthic productivity at the end of

420 upwelling in 2011/2011 compared to the non-upwelling ([Eidens et al., 2012](#)) as well as to the
421 2011/2012 upwelling event (Table 5 and S6).

422 In conclusion, the present study indicates that coral communities in TNNP are highly adapted to
423 seasonal variations of key environmental parameters, while extreme ENSO-related disturbance
424 events causing interannual variation in primary production furthermore do not have long-lasting
425 effects on the functioning of local benthic communities. These reefs may therefore exhibit high
426 resilience against climate change consequences and anthropogenic disturbances which could have
427 implications for management and conservation priorities.

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Figure 1

Location of study sites.

A) Location of Tayrona National Natural Park (TNNP) at the Caribbean coast of Colombia. B) Location of Gayraca Bay within TNNP (dashed lines – national park border and expansion of the city of Santa Marta). C) Gayraca Bay. The investigation sites at the current-exposed western part and the sheltered north-eastern part are indicated by black dots (dashed lines – isobaths). Source of map: (INVEMAR, 2012).

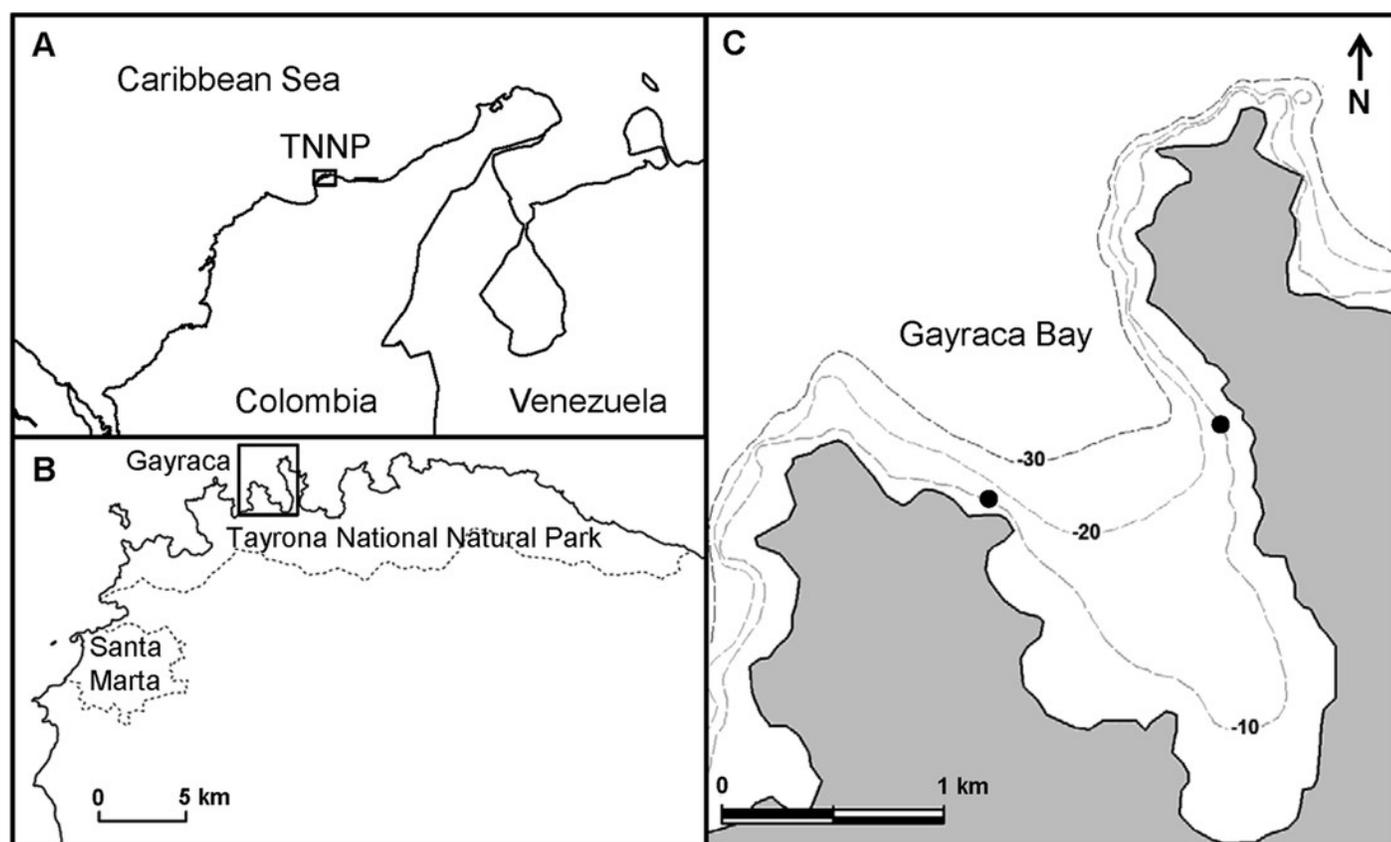


Figure 2

Total benthic O₂ fluxes.

Overall benthic O₂ fluxes at the exposed and sheltered site of Gayraca Bay during non-upwelling and upwelling. Values are given as mean \pm SD. Abbreviations: P_n = net O₂ production, P_g = gross O₂ production.

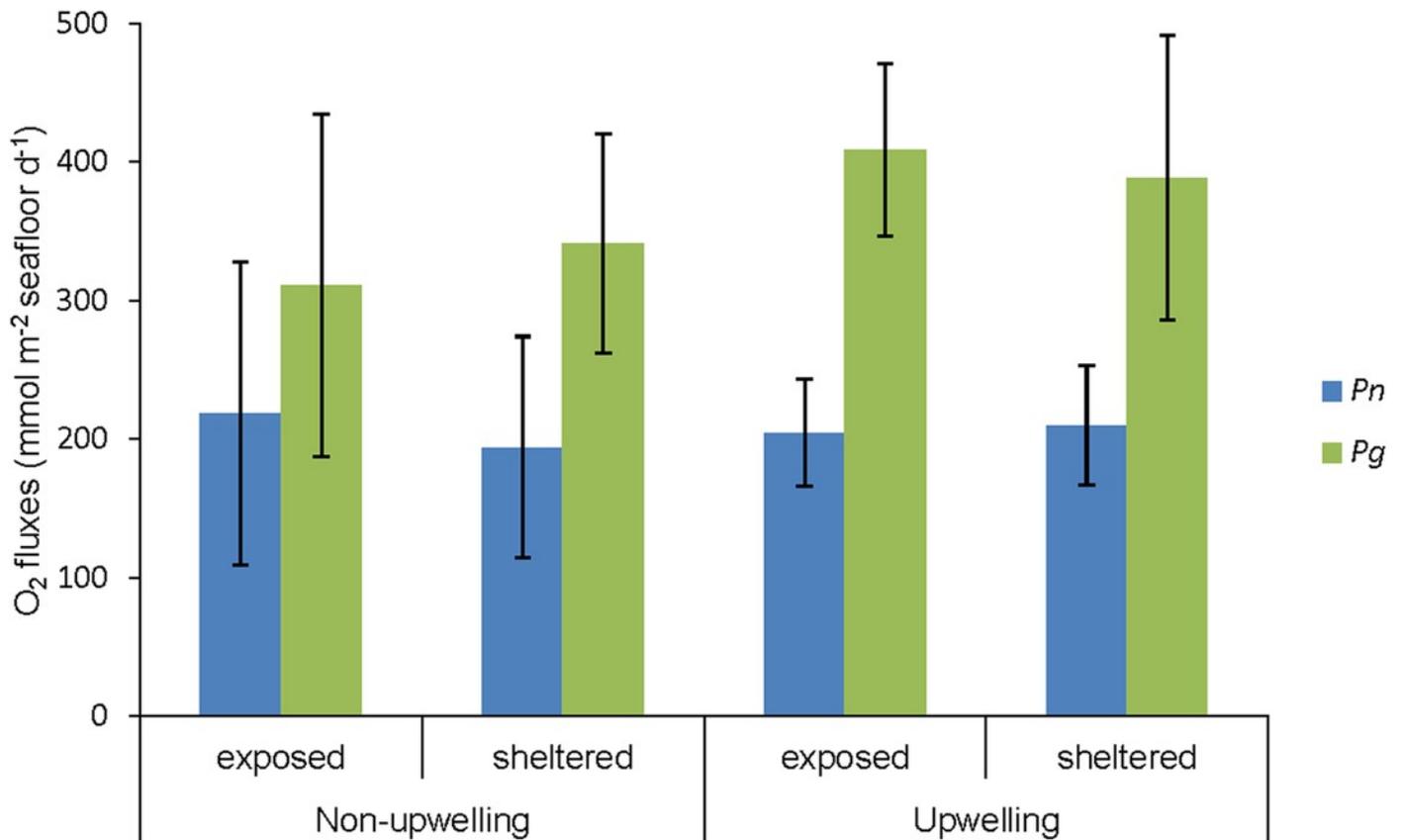


Table 1 (on next page)

Light intensity and water temperature during incubation experiments at sampling sites and in incubation containers.

All values are in mean \pm SD. Data in parenthesis represent light intensity and water temperature at the end of the upwelling event in 2010/2011.

	Non-upwelling		Upwelling	
	<i>In situ</i>	Incubations	<i>In situ</i>	Incubations
Light intensity (PAR $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	146 ± 47	154 ± 40	230 ± 58 (234 ± 78)	257 ± 69 (248 ± 71)
Temperature ($^{\circ}\text{C}$)	29.1 ± 0.2	28.6 ± 0.5	25.3 ± 0.3 (26.1 ± 0.2)	25.4 ± 0.6 (26.5 ± 0.4)

Table 2(on next page)

Table 2. O₂ fluxes of functional benthic groups.

All values in mean ± SD. Data in parenthesis represent O₂ fluxes at the end of the upwelling event in 2010/2011. Missing data are due to the absence of macroalgae at the exposed site during non-upwelling. Abbreviations: n = number of replicates, P_n = net O₂ production, P_g = gross O₂ production.

Location	Functional group	n	P_n (mmol O ₂ m ⁻² specimen surface area h ⁻¹ ± SD)			
			Non-upwelling		Upwelling	
			P_n	P_g	P_n	P_g
Exposed	Corals	11 – 24	16.3 ± 4.7	13.5 ± 3.6 (17.7 ± 4.0)	19.2 ± 5.4	20.9 ± 4.3 (23.4 ± 5.6)
	Macroalgae	3 – 6		2.4 ± 0.5 (8.6 ± 0.9)		3.2 ± 0.3 (10.4 ± 1.0)
	Algal turfs	5 – 6	3.3 ± 1.0	8.5 ± 2.1 (23.1 ± 2.1)	5.1 ± 1.2	11.6 ± 2.3 (30.2 ± 5.6)
	Crustose coralline algae	5 – 6	8.7 ± 1.4	5.4 ± 1.5 (6.1 ± 1.2)	10.2 ± 1.6	6.0 ± 1.7 (6.5 ± 1.4)
	Microphytobenthos	4 – 6	2.3 ± 1.7	0.1 ± 0.9 (4.9 ± 1.5)	5.1 ± 1.6	3.2 ± 0.8 (7.0 ± 1.6)
Sheltered	Corals	12 – 22	15.6 ± 5.8	10.9 ± 3.2 (16.5 ± 4.8)	18.5 ± 6.3	17.6 ± 4.7 (22.6 ± 6.0)
	Macroalgae	5 – 6	4.3 ± 0.6	3.1 ± 0.4 (6.1 ± 0.7)	5.4 ± 0.7	4.0 ± 1.1 (7.6 ± 0.9)
	Algal turfs	5 – 6	5.5 ± 3.0	13.1 ± 3.6 (28.2 ± 8.3)	8.8 ± 3.8	17.1 ± 4.3 (37.2 ± 5.8)
	Crustose coralline algae	5 – 6	3.6 ± 1.5	6.9 ± 2.4 (5.0 ± 1.7)	4.2 ± 1.6	8.7 ± 2.4 (5.5 ± 1.8)
	Microphytobenthos	3 – 6	0.5 ± 5.6	2.7 ± 1.0 (7.3 ± 6.9)	6.2 ± 4.1	6.8 ± 1.4 (11.6 ± 6.6)

Table 3(on next page)

Benthic coverage of functional groups.

All values in percent \pm SD. Data in parenthesis represent benthic coverage at the end of the upwelling event in 2010/2011.

Functional group	Non-upwelling		Upwelling	
	Exposed	Sheltered	Exposed	Sheltered
Corals	41 ± 12	24 ± 3	39 ± 12 (37 ± 11)	17 ± 6 (24 ± 6)
Macroalgae	0	8 ± 1	11 ± 7 (19 ± 6)	47 ± 3 (22 ± 4)
Algal turfs	24 ± 5	26 ± 6	23 ± 10 (18 ± 5)	12 ± 5 (19 ± 2)
Crustose coralline algae	18 ± 1	14 ± 4	10 ± 3 (13 ± 4)	3 ± 2 (9 ± 4)
Sand	10 ± 6	25 ± 13	3 ± 3 (6 ± 2)	19 ± 7 (21 ± 10)

Table 4(on next page)

Contribution of functional groups to total benthic O₂ fluxes

All values in mean ± SD. Data in parenthesis represent O₂ fluxes at the end of the upwelling event in 2010/2011. Missing data are due to the absence of macroalgae at the exposed site during non-upwelling. Abbreviations: P_n = net O₂ production, P_g = gross O₂ production.

Location	Functional group	P_n (mmol O ₂ m ⁻² seafloor h ⁻¹ ± SD)		P_g	
		Non-upwelling	Upwelling	Non-upwelling	Upwelling
Exposed	Corals	14.8 ± 4.3	12.4 ± 2.8 (15.0 ± 2.8)	17.4 ± 4.3	19.3 ± 3.9 (19.7 ± 3.1)
	Macroalgae		1.4 ± 0.3 (9.2 ± 1.0)		1.9 ± 0.2 (11.2 ± 1.1)
	Algal turfs	1.0 ± 0.3	2.6 ± 0.6 (5.5 ± 0.5)	1.6 ± 0.4	3.5 ± 0.7 (7.2 ± 1.3)
	Crustose coralline algae	2.1 ± 0.3	0.6 ± 0.2 (1.0 ± 0.2)	2.4 ± 0.4	0.7 ± 0.2 (1.1 ± 0.2)
	Microphytobenthos	0.3 ± 0.2	0.0 ± 0.0 (0.4 ± 0.1)	0.7 ± 0.2	0.1 ± 0.0 (0.6 ± 0.1)
	Total	18.2 ± 4.4	17.1 ± 2.9 (31.2 ± 3.0)	22.1 ± 4.3	25.6 ± 4.0 (39.7 ± 3.6)
Sheltered	Corals	10.5 ± 4.2	4.9 ± 1.3 (10.3 ± 3.0)	12.4 ± 4.1	7.9 ± 1.3 (14.1 ± 3.4)
	Macroalgae	2.5 ± 0.3	9.0 ± 1.3 (8.8 ± 0.9)	3.2 ± 0.4	11.6 ± 3.1 (11.0 ± 1.3)
	Algal turfs	2.2 ± 1.2	2.4 ± 0.7 (8.2 ± 2.4)	3.5 ± 1.5	3.1 ± 0.8 (10.9 ± 1.7)
	Crustose coralline algae	0.8 ± 0.3	0.3 ± 0.1 (0.7 ± 0.2)	0.9 ± 0.3	0.4 ± 0.1 (0.8 ± 0.2)
	Microphytobenthos	0.2 ± 2.1	0.8 ± 0.3 (2.3 ± 2.2)	2.4 ± 1.6	2.0 ± 0.4 (3.7 ± 2.1)
	Total	16.2 ± 4.9	17.5 ± 1.9 (30.4 ± 4.5)	22.3 ± 4.7	24.9 ± 3.5 (40.3 ± 4.5)

Table 5(on next page)

Mean benthic oxygen production of reef slope communities and their dominant functional groups of primary producers.

If necessary, original units were converted to O₂ estimates assuming a C:O₂ metabolic quotient equal to one according to Gattuso et al. (1996) and Carpenter & Williams (2007). Abbreviations: P_n = net O₂ production, P_g = gross O₂ production.

	Location	P_n (mmol O ₂ m ⁻² seafloor d ⁻¹ ± SD)	P_g	Reference
Reef slope communities	Caribbean	194 – 218	311 – 409	This study
	Caribbean	194 – 374	311 – 603	Eidens et al. (2012)
	Various Atlantic/Pacific	-83 – 425	167 – 583	Hatcher (1988)
	Caribbean	113 – 469	313 – 638	Adey & Steneck (1985)
Functional group				
Corals	Caribbean	227 – 344	441 – 610	This study
	Caribbean	328 – 369	441 – 598	Eidens et al. (2012)
	Caribbean	166	447	Wanders (1976b)
	Caribbean		225 – 850	Kanwisher & Wainwright (1967)
Macroalgae	Caribbean	117 – 244	198 – 375	This study
	Caribbean	244 – 444	375 – 624	Eidens et al. (2012)
	Caribbean	142 – 433	250 – 633	(Wanders, 1976a)
	Various Atlantic/Pacific		192 – 3283	Hatcher (1988)
Algal turfs	Caribbean	39 – 157	84 – 253	This study
	Caribbean	39 – 339	84 - 554	Eidens et al. (2012)
	Various Atlantic/Pacific		75 – 1008	Hatcher (1988)
	Various Atlantic/Pacific		83 – 967	Kinsey (1985)
	Caribbean	175 – 433	308 – 617	Wanders (1976b)
Crustose coralline algae	Caribbean	44 – 104	58 – 140	This study
	Caribbean	44 – 104	58 – 140	Eidens et al. (2012)
	Various Atlantic/Pacific		67 – 83	Kinsey (1985)
	Caribbean	58 – 117	192 – 258	Wanders (1976b)
	Great Barrier Reef	50 – 333	75 – 416	Chisholm (2003)
Microphytobenthos	Caribbean	1 – 67	75 – 143	This study
	Caribbean	6 – 87	78 – 191	Eidens et al. (2012)
	SW Pacific	0 – 8	92 – 150	Boucher et al. (1998)
	Various Atlantic/Pacific		50 – 225	Kinsey (1985)