

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.

1 **Benthic primary production in an upwelling-influenced coral reef,**
2 **Colombian Caribbean**

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15 **Introduction**

16 The majority of ecosystems depend on primary production. Photoautotrophs convert light energy
17 into chemical energy by photosynthesis, creating the energetic base of most food webs in
18 terrestrial as well as aquatic environments ([Valiela, 1995](#); [Chapin et al., 2011](#)). Among other
19 coastal ecosystems such as mangrove forests, seagrass beds, salt marshes, and kelp forests, coral
20 reefs belong to the most productive ecosystems in the world ([Hatcher, 1988](#); [Gattuso,](#)
21 [Frankignoulle & Wollast, 1998](#)). Productivity investigation on coral reefs started in the mid-20th
22 century ([Sargent & Austin, 1949](#); [Odum & Odum, 1955](#)) and nowadays, coral reefs are among
23 the best understood marine benthic communities in terms of primary production ([Kinsey, 1985](#);
24 [Hatcher, 1988](#); [Hatcher, 1990](#); [Gattuso, Frankignoulle & Wollast, 1998](#)).

25 It was long assumed that coral reef productivity is relatively balanced as tropical coral reefs
26 typically thrive under relatively stable abiotic conditions ([Hubbard, 1996](#); [Kleypas, McManus &](#)
27 [Menez, 1999](#); [Sheppard, Davy & Pilling, 2009](#)), including light ([Darwin, 1842](#); [Achituv &](#)
28 [Dubinsky, 1990](#); [Falkowski, Jokiell & Kinzie III, 1990](#)), water temperature ([Dana, 1843](#); [Coles &](#)
29 [Fadlallah, 1991](#); [Veron, 1995](#)), salinity ([Andrews & Pickard, 1990](#); [Coles & Jokiell, 1992](#)), and
30 inorganic nutrient availability ([D'Elia & Wiebe, 1990](#); [Szmant, 1997](#)).

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

37 The Tayrona National Natural Park (TNNP) at the Caribbean coast of Colombia is highly
38 influenced by the Southern Caribbean upwelling system ([Andrade & Barton, 2005](#); [Rueda-Roa &
39 Muller-Karger, 2013](#)), causing seasonal fluctuations in water temperature, salinity, and inorganic
40 nutrient concentrations, among others (Table 1, see also Bayraktarov, Pizarro & Wild (2014)).
41 Here, the abundance and community composition of benthic algae were shown to exhibit
42 upwelling-related seasonality ([Diaz-Pulido & Garzón-Ferreira, 2002](#); [Eidens et al., 2012](#)). The
43 area thereby provides an excellent opportunity to investigate the effects of seasonal coastal
44 upwelling events on the key ecosystem service productivity in coral reefs under changing *in situ*
45 conditions.

46 The results of a preliminary study conducted by [Eidens et al. \(2012\)](#) indicated that benthic
47 primary production in TNNP differed between the upwelling in 2010/2011 and the consecutive
48 non-upwelling season, suggesting a generally positive effect of upwelling conditions on major
49 benthic autotrophs in the area. However, after unusually strong El Niño-Southern Oscillation
50 (ENSO) events in 2010, the area experienced a moderate coral bleaching before the upwelling in
51 2010/2011 ([Bayraktarov et al., 2013](#); [Hoyos et al., 2013](#)), and productivity measurements during
52 upwelling in 2010/2011 may not be representative. To test for patterns in benthic primary
53 production during a typical seasonal cycle, we here quantified benthic primary production before
54 and at the end of the upwelling event in 2011/2012 (hereafter referred to as non-upwelling and
55 upwelling, respectively). To allow for comparisons of productivity between investigated groups,
56 we further estimated surface area-specific productivity rates as suggested by [Naumann et al.
57 \(2013\)](#) and analyzed the data using generalized linear models.
58 Therefore, the goals of the study were to (1) identify dominant functional groups of benthic
59 primary producers and their relative benthic cover at a current/wave-exposed (EXP) and
60 -sheltered (SHE) site in one exemplary bay of TNNP, (2) quantify O₂ fluxes of all dominant

- 61 benthic primary producers and apply 3D surface area estimations, and hence (3) estimate the
- 62 specific contribution of each group to total benthic O₂ fluxes.

63 **Materials and Methods**

64 **Study site and sampling seasons**

65 This study was conducted in Gayraca Bay (11.33°N, 74.11°W), one of several small bays in
66 TNNP, located near the city of Santa Marta (Fig. 1). The continental shelf in the area is relatively
67 narrow due to the proximity to the Sierra Nevada de Santa Marta - the world's highest coastal
68 mountain range. The TNNP contains small fringing coral reefs reaching to a water depth of ~30
69 m ([Garzón-Ferreira & Cano, 1991](#); [Garzón-Ferreira, 1998](#)). The region is subjected to strong
70 seasonality caused by the Caribbean Low-Level Jet of northeast (NE) trade winds ([Salzwedel &](#)
71 [Müller, 1983](#); [Andrade & Barton, 2005](#)), resulting in two major seasons; a dry season from
72 December to April and a rainy season from May to November ([Salzwedel & Müller, 1983](#);
73 [Garzón-Ferreira, 1998](#)). Whereas the rainy season (hereafter referred to as non-upwelling) is
74 characterized by low wind velocities (mean 1.5 m s^{-1}) ([Garzón-Ferreira, 1998](#)) and high
75 precipitation ($> 80 \%$ of the annual rainfall) ([Salzwedel & Müller, 1983](#)), during the dry season
76 (hereafter referred to as upwelling), strong winds prevail (mean $3.5 \text{ m} \cdot \text{s}^{-1}$, max $30 \text{ m} \cdot \text{s}^{-1}$)
77 ([Herrmann, 1970](#); [Salzwedel & Müller, 1983](#)) resulting in a seasonal coastal upwelling. The
78 upwelling-related changes in key water parameters are well characterized by the comprehensive
79 study of [Bayraktarov, Pizarro & Wild \(2014\)](#). During upwelling, water temperature can decrease
80 to $20 \text{ }^{\circ}\text{C}$ while salinity and inorganic nutrient availability increase up to 39 and $3.59 \text{ } \mu\text{mol L}^{-1}$,
81 respectively (Table 1). Water currents triggered by prevailing winds predominantly move from
82 NE to SW, and a clear gradient in wave exposure between the exposed western (EXP) and
83 -sheltered northeastern (SHE) sides of the bay can be observed ([Werding & Sánchez, 1989](#);
84 [Bayraktarov, Bastidas-Salamanca & Wild, in press](#)). The study was carried out during non-
85 upwelling in 2011 (1st November – 2nd December 2011) and during the consecutive upwelling

86 event (20th March – 29th March 2012), allowing for the investigation of the influence of
87 seasonality on benthic primary production.

88 **Benthic assessment**

89 For the assessment of benthic community structure, the dominant groups of benthic primary
90 producers and the percentage of benthic cover were identified at EXP and SHE prior to primary
91 production measurements using line point intercept transects at a water depth of 10 m (50 m
92 length, $n = 3$), modified from [Hodgson et al. \(2004\)](#). Benthic cover was monitored at 0.5 m
93 intervals directly below the measurement points (101 data points per transect). The dominant
94 benthic autotrophs at the study sites consisted of scleractinian corals, frondose macroalgae, algal
95 turfs (multispecific assemblage of primarily filamentous algae of up to 1 cm height, *sensu*
96 [Steneck \(1988\)](#)), crustose coralline algae (CCA), and sand potentially associated with
97 microphytobenthos. These categories represented 97 ± 1 % of the total seafloor coverage at SHE
98 and 91 ± 2 % at EXP and were therefore selected as representative primary producers for the
99 subsequent incubation experiments. During benthic community assessment, rugosity was
100 determined at both sites using the chain method described by Risk ([1972](#)). Rugosity was
101 quantified along three 10 m sub-transects within each of the 50 m transects and were used to
102 calculate the rugosity factor for each study site as described by [McCormick \(1994\)](#) (SHE: $1.53 \pm$
103 0.12 , EXP: 1.32 ± 0.13).

104 **Sampling of organisms**

105 Specimens of scleractinian corals, macroalgae, algal turfs, and CCA as well as sand samples,
106 from 10 ± 1 m water depth were used for quantification of O₂ fluxes (see Table S1 for number of
107 replicates). All samples were brought to the water surface in Ziploc bags and transported directly
108 to the field lab. Scleractinian corals of the genera *Montastraea* (including the species *M.*

109 *faveolata*, *M. franksi* and *M. annularis*, currently belonging to the genus *Orbicella*; Budd et al.
110 2012) and *Diploria* (including *D. strigosa*, currently belonging to the genus *Pseudodiploria* Budd
111 et al. 2012) accounted for more than 80 % of the total coral cover at the study sites and were
112 therefore used as representative corals in our study. Coral specimens were obtained from the reef
113 using hammer and chisel, fragmented with a multifunction rotary tool (Dremel Corp., 8200-2/45;
114 mean fragment surface area: $13.16 \pm 7.96 \text{ cm}^2$), and fixed on ceramic tiles using epoxy glue
115 (Giesemann GmbH, Aquascape). After fragmentation, specimens were returned to their natural
116 habitat and left to heal for one week prior to the incubation experiments. Algae of the genus
117 *Dictyota* (mainly *D. bartayresiana*) amounted to nearly 100 % of macroalgal cover. Therefore
118 small bushes of *Dictyota* spp. (surface area $1.86 \pm 0.88 \text{ cm}^2$) were used as representatives for
119 macroalgae. Macroalgae were transferred to a storage tank (volume: 500 L in which water was
120 exchanged manually 3-5 times per day and water temperature was within the ranges of incubation
121 experiments; see Table 2) one day before incubation experiments and left to heal. All other
122 functional groups were incubated immediately after sampling. Rubble overgrown by algal turfs
123 and CCA served as samples for the respective functional group (surface area covered by the
124 organisms: $15.63 \pm 10.80 \text{ cm}^2$ and $7.48 \pm 3.60 \text{ cm}^2$, respectively). For sand samples, custom-made
125 mini corers with defined surface area (1.20 cm^2) and sediment core depth (1.0 cm) were used.

126 **Surface area quantification**

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

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

144 **Incubation Experiments**

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

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

182 **Data analyses and statistics**

183 To quantify net O₂ production (P_n) and respiration of functional groups, O₂ concentration before
184 incubations was subtracted from concentration after incubations and corrected with blank control
185 values containing only seawater. Individual gross O₂ production (P_g) of investigated functional
186 groups was calculated by adding values of P_n and respiration; individual O₂ fluxes were
187 expressed as mmol O₂ · m⁻² specimen surface area · h⁻¹.

188 The contribution of each functional group to total reef production (given as: mmol O₂ · m⁻²
189 seafloor area · h⁻¹) was estimated as follows:

$$c_i = p_i s_i b_i r$$

190 taking into account the individual production rates (p_i), the respective mean 2D to 3D surface
191 conversion factor (s_i s_i), group-specific benthic coverage (b_i) as well as the rugosity
192 factor (r r). Estimation of total daily benthic productivity was furthermore calculated by
193 summing up the contribution of the investigated groups and extrapolating the incubation periods
194 to a 12 h light and 12 h dark cycle.

195 After testing for normal distribution (Kolmogorov-Smirnoff test) and homogeneity of variances
196 (Levene test), benthic coverage of functional groups were analyzed using two-way ANOVA and
197 Bonferroni's *post hoc* tests to detect possible effects of season (upwelling vs. non-upwelling) and
198 location (EXP vs. SHE) on benthic cover.

199 We tested the influence of benthic groups, season, wave exposure, and their interactions on O₂
200 productivity by generalized linear models (GLMs) for individual P_n , and P_g of the investigated
201 groups, their contribution to reef metabolism as well as total benthic productivity. Since the
202 experimental design was unbalanced with different number of measurements per benthic group
203 and season, we used Markov-chain Monte Carlo (MCMC) estimations of GLM regression
204 coefficients. In traditional Frequentist statistics, the parameters of interest (i.e. the O₂ productivity
205 describing regression coefficients) are estimated just once (e.g. using Maximum-Likelihood) and
206 their significance is inferred indirectly based on a test-statistic. In contrast, Bayesian methods
207 reallocate the coefficients across a set of possible candidates during each MCMC generation

208 ([Kruschke, 2011](#)). If the bulk of these values, that is the 95 % highest posterior density (HPD), do
209 not include zero, one can directly conclude that the regression coefficient is credible different
210 than zero and an effect on O₂ productivity exists. Moreover, we here performed pair-wise
211 comparisons between benthic groups at different sites and seasons, traditionally being performed
212 by *post-hoc* testing with *P*-value correction for preventing false positive results. A Bayesian GLM
213 does not suffer this drawback because difference of groups can be directly estimated by the
214 posterior ([Kruschke, 2011](#)). Again, there is credible evidence in non-equal group-means, if the
215 posterior-based 95 % HPD interval of the group differences does not include zero. Model
216 performance for all 19 possible combinations of the three independent variables and their
217 interactions was assessed by the deviance information criterion (DIC), a Bayesian measure of
218 model fit that penalizes complexity ([Spiegelhalter et al., 2002](#)). In this information theory based
219 model selection, often there is not a single best model describing the data. Therefore, averaging
220 of regression coefficients for all models within $\Delta\text{DIC} < 2$ of the best one ([Johnson & Omland,](#)
221 [2004](#)) was performed according to DIC weights (i.e. support for the respective regression model).
222 Here, Bayesian GLMs using the MCMCglmm package ([Hadfield, 2010](#)) for the R 3.0.3
223 environment for statistical computing (R Core Team 2014) with a Gaussian error distribution
224 were applied. Prior to the analyses, the mean-variance relationship of measured O₂ flux was
225 stabilized by power transformation ([Yeo & Johnson, 2000](#)). Visual inspection of preliminary
226 GLMs with default weakly informative priors showed high autocorrelation in their posterior
227 distribution. Thus to infer the posterior distribution of the final analyses, we ignored the first
228 50000 estimates as burn-in and sampled every 5th out of 650000 MCMC generations.
229 All values are represented as mean \pm standard deviation (SD) if not noted otherwise.

230 **Results**

231 **Benthic community composition**

232 At EXP, scleractinian corals dominated the benthic community during non-upwelling and
233 upwelling (41 ± 12 and 39 ± 12 %, respectively; Table 3). At SHE, corals, algal turf, and sand
234 cover was similar during non-upwelling (24 ± 3 %, 26 ± 6 %, and 25 ± 13 %, respectively), while
235 during upwelling, macroalgae exhibited highest benthic cover (47 ± 3 %, Table 3). During the
236 entire study period, coral and CCA cover was significantly higher at EXP than at SHE, whereas
237 sand showed a contrary pattern with significantly more coverage at SHE (Table 3, see also Table
238 S2 for ANOVA results). Macroalgae cover was significantly higher at SHE than at EXP and less
239 abundant at both sites during non-upwelling than during upwelling (Table 3). CCA cover also
240 differed between the seasons, showing a significant decrease during the upwelling event (Table
241 3).

242 **O₂ fluxes of organisms**

243 More complex Bayesian GLMs, including interactions among the three independent variables
244 season, benthic group, and site, described individual O₂ fluxes better than simple models (For
245 details see Table S3).
246 Of all investigated functional groups, scleractinian corals had highest individual net (P_n) and
247 gross production (P_g), followed by algal turfs, macroalgae, CCA, and microphytobenthos (Fig. 2;
248 see also Table S4 for detailed results of all pair-wise comparisons). Regarding spatial differences
249 in individual productivity, significant differences were detected for algal turfs and CCA. During
250 upwelling, P_n of algal turfs and P_g of CCA was higher at SHE than EXP. On the contrary, during
251 non-upwelling, P_n and P_g of CCA was higher at EXP (Fig. 2).
252 Temporal differences in O₂ production were detected for corals, algal turfs, and CCA (Fig. 2).
253 Whereas P_n of scleractinian corals on both sites and P_g of CCA at EXP were higher during non-

254 upwelling, P_g of CCA at SHE as well as P_n and P_g of algal turfs at both sites showed an opposite
255 pattern with higher productivity rates during upwelling (Fig. 2).

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

257 As in the case of individual O₂ fluxes, contribution and total reef production were better
258 explained by GLMs of higher complexity (Table S3).
259 Contribution of functional groups to benthic productivity exhibited similar pattern than individual
260 productivity with corals contributing generally most to total reef P_n and P_g , but macroalgae
261 contributed most to benthic P_n and P_g at SHE at the end of upwelling (Fig. 3; see also Table S4
262 for detailed results of all pair-wise comparisons).
263 Significant spatial differences in contribution to total benthic P_n within functional groups were
264 detected for corals, algal turf, and macroalgae, and spatial differences for P_g were present in all
265 investigated groups except CCA (Fig. 3). At EXP, Corals contributed more to total P_n and P_g
266 during non-upwelling and upwelling (Fig. 3). At SHE, contributions of macroalgae (P_n and P_g)
267 and microphytobenthos (P_g) were higher only during upwelling, and algal turfs contributed more
268 to P_g at SHE during non-upwelling (Fig. 3).
269 Temporal differences in contribution to total benthic productivity within the investigated groups
270 were present for corals, macroalgae, CCA (for P_n and P_g), and for algal turfs (only P_g) (Fig. 4).
271 During non-upwelling, Corals contributed more to the total productivity at SHE and CCA at EXP,
272 whereas during upwelling, macroalgae contributed more to the total productivity at SHE and
273 algal turf at EXP (Fig. 3).
274 Regarding the total daily benthic O₂ fluxes (Figs. 4), no spatial differences between EXP and
275 SHE were detected, neither during non-upwelling nor during upwelling (see also Table S4 for
276 detailed results of all pair-wise comparisons). During the study, significant temporal differences
277 were only present for P_g at the exposed site with higher O₂ fluxes during the upwelling in
278 2011/2012 compared to non-upwelling (Fig. 4). Comparing total benthic productivity during the

279 upwelling event in 2010/2011 with the subsequent non-upwelling and upwelling, P_n and P_g were
280 significantly higher during the upwelling 2010/2011 for all comparisons (Fig. 4).

281 Discussion

282 O₂ fluxes of organisms

283 Individual mean P_n and P_g were generally highest for corals at both sites during the study periods
284 (P_n : 11.2–16.1 and P_g : 17.4–20.8 mmol O₂ · m⁻² specimen area · h⁻¹). These high productivity rates
285 of corals compared to other investigated primary producers (see Fig. 2) may be attributed to the
286 mutualistic relationship between zooxanthellae and the coral host, enhancing photosynthetic
287 efficiency through high zooxanthellate photosynthesis in coral tissues under high CO₂ and
288 nutrient availability ([D'Elia & Wiebe, 1990](#); [Muscatine, 1990](#)). Therefore, corals are among the
289 most productive functional groups in reef systems with several fold higher specific production
290 rates than most reef algae and reef sands (Table 4) ([Wanders, 1976b](#); [Kinsey, 1985](#); [Yap,](#)
291 [Montebon & Dizon, 1994](#)). Estimated daily P_g per m² seafloor for investigated coral genera, (441
292 – 610 mmol O₂ · m⁻² seafloor · d⁻¹, respectively), is within ranges of other Caribbean corals (67 to
293 850 mmol O₂ · m⁻² seafloor · d⁻¹, Table 4) ([Kanwisher & Wainwright, 1967](#)), and O₂ fluxes of all
294 investigated organism groups were generally within ranges reported in the literature (Table 4).
295 Significant spatial differences during non-upwelling were found for CCA with higher
296 productivity at EXP compared to SHE. These differences may be explained by the prevailing
297 water current regime in the bay together with high water temperatures during non-upwelling
298 (Tables 1 and 2). An increase in water temperature typically rises metabolic activity in CCA
299 ([Littler & Doty, 1975](#); [Hatcher, 1990](#)), but decreased water flow at SHE compared to EXP
300 ([Bayraktarov, Bastidas-Salamanca & Wild, in press](#)) likely prevented the required gas exchange
301 and nutrient uptake, resulting in lower individual CCA productivity at SHE. A possible reason for

302 differences in individual productivity rates of algal turfs and CCA during upwelling with higher
303 rates at SHE may be differences in the composition of these assemblages. Since algal turfs and
304 CCA are multi-specific assemblages and each single species has distinct life histories ([Steneck,
305 1986](#); [Fricke et al., 2011](#)), species composition can vary spatio-temporally, eventually affecting
306 primary productivity of these functional groups ([Littler, 1973](#); [Chisholm, 2003](#); [Copertino,
307 Cheshire & Kildea, 2009](#); [Ferrari et al., 2012](#)).

308 Temporal differences in individual O₂ production within investigated organism groups generally
309 showed two contrary patterns: whereas scleractinian corals on both sites and CCA at EXP
310 produced less O₂ during upwelling, algal turfs and CCA at SHE produced more O₂ during this
311 study period. The decreased productivity rates of corals and CCA at EXP during upwelling
312 indicate that water temperature likely limited productivity of these groups since low water
313 temperatures typically decrease photosynthetic performance of primary producers in coral reefs
314 ([Kinsey, 1985](#); [Hatcher, 1990](#)). In contrast, a two-fold higher photosynthetic performance of algal
315 turfs during upwelling may be due to higher nutrient concentrations together with higher water
316 currents during this season ([Bayraktarov, Pizarro & Wild, 2014](#); [Bayraktarov, Bastidas-
317 Salamanca & Wild, in press](#)), facilitating gas exchange and nutrient uptake and thereby
318 significantly increasing productivity. This assumption is supported by [Carpenter & Williams
319 \(2007\)](#), showing that photosynthesis of algal turfs in coral reefs is limited by nutrient uptake,
320 which in turn depends on nutrient availability and water current speed. Whereas productivity of
321 CCA at EXP seems to be temperature-limited, our findings suggest that productivity of CCA at
322 SHE is rather limited by nutrient availability. Generally, benthic algal communities in coral reefs
323 are nutrient-limited ([Hatcher & Larkum, 1983](#)), and this limitation may be more pronounced in
324 water current-sheltered locations due to the fact that nutrient supply of coral reef algae is
325 primarily controlled by water flow ([Hatcher, 1990](#); [Carpenter & Williams, 2007](#)). Elevated
326 nutrient concentration and water current speed during upwelling ([Bayraktarov, Pizarro & Wild,](#)

327 [2014; Bayraktarov, Bastidas-Salamanca & Wild, in press](#)) may therefore offset the limiting
328 nutrient supply for CCA particularly at SHE where water flow was lower than at EXP
329 ([Bayraktarov, Bastidas-Salamanca & Wild, in press](#)).

330 **Contribution of organism-induced O₂ fluxes to total benthic O₂ production**

331 During non-upwelling, the share of corals in total benthic P_n and P_g were highest at both EXP
332 (80.6 ± 24.3 and 77.5 ± 19.2 %, respectively) and SHE (64.5 ± 25.5 and 54.9 ± 18.4 %, respectively). During the upwelling, corals only contributed most to P_n and P_g at EXP ($72.6 \pm$
333 16.7 and 75.4 ± 15.3 %, respectively), whereas macroalgal contribution to benthic primary
334 production was highest at SHE (P_n : 51.6 ± 7.4 ; P_g : 46.3 ± 12.4 %). The major contribution of
335 corals can be explained by their highest quantified individual O₂ production rates of all
336 investigated organism groups (Fig. 2) and comparably high benthic coverage of corals, ranging
337 from 24 to 39 % (Table 3). Similar values were estimated for a Southern Caribbean fringing reef
338 by [Wanders \(1976b\)](#), where corals accounted for about two-thirds of total benthic primary
339 production.

340
341 Although individual macroalgal production rates were rather low as compared to coral
342 productivity (Fig. 2), the extremely high cover of macroalgae at SHE during upwelling (47 ± 3
343 %) resulted in macroalgae being the main contributor to total benthic production. Reasons for the
344 high macroalgal cover may likely be elevated nutrient concentrations and lower water
345 temperatures throughout the upwelling event (Table 1) ([Bayraktarov, Pizarro & Wild, 2014](#)), as
346 these factors stimulate the growth of the dominant macroalgae genus *Dictyota* ([Bula-Meyer,](#)
347 [1990](#); [Cronin & Hay, 1996](#); [Diaz-Pulido & Garzón-Ferreira, 2002](#)).

348 The identified spatial differences in contribution to total benthic O₂ production for scleractinian
349 corals, macroalgae, CCA, and microphytobenthos can also be explained by spatial differences in

350 their benthic coverage. Elevated contributions of corals and CCA at EXP compared to SHE as
351 well as higher contribution of macroalgae and microphytobenthos at SHE during the upwelling
352 (Fig. 3) reflect their spatial abundance patterns (Table 3). The observed pattern in benthic
353 coverage of corals and CCA may be caused by the water current regime in the bay with stronger
354 water currents at EXP compared to SHE ([Bayraktarov, Bastidas-Salamanca & Wild, in press](#)), as
355 suggested to be the major driver for differences in local coral communities by [Werding &](#)
356 [Sánchez \(1989\)](#). This explanation is supported by the studies of [Jokiel \(1978\)](#) and [Fabricius &](#)
357 [De'ath \(2001\)](#), stating that maximum abundance of corals and CCA typically occur in water
358 current-exposed environments. Differences in water current exposure between the study sites
359 could also be the reason for the observed spatial patterns in macroalgae abundance, as the
360 abundance of the dominant macroalgal genus *Dictyota* is highly affected by water current
361 exposure ([Renken et al., 2010](#)). Likewise, differences in sand abundances between sheltered and
362 exposed sites are likely due to generally higher wave energy and water current velocities at
363 exposed sites ([Bayraktarov, Bastidas-Salamanca & Wild, in press](#)), resuspending sediments and
364 transporting material to sheltered or deeper parts where it accumulates ([Ogston et al., 2004](#)). Our
365 findings are in accordance with former studies, stating that sand abundance is inversely correlated
366 to wave exposure ([Graus & Macintyre, 1989](#); [Roberts, Wilson & Lugo-Fernández, 1992](#)).

367 Corals, macroalgae, algal turfs, and CCA also exhibited distinct temporal differences in
368 contribution to total benthic productivity. At SHE, corals contributed more to benthic O₂
369 production during non-upwelling and macroalgae and algal turfs during upwelling, whereas
370 contribution of CCA at EXP was higher during non-upwelling as compared to upwelling.

371 Reasons for the observed patterns in coral contribution to the total benthic primary production are
372 temporal shifts in individual O₂ productivity of corals with higher production rates during non-
373 upwelling event (Fig. 2) together with slightly higher benthic coverage during this study period
374 (Table 3). The temporal variation in macroalgal contribution to total benthic O₂ fluxes can be

375 explained by the seasonal growth pattern of the dominant macroalgae *Dictyota* sp., most likely
376 caused by variation in nutrient concentrations and water temperatures (Table 1), as these factors
377 affect the growth of the dominant macroalgae genus *Dictyota* ([Bula-Meyer, 1990](#); [Cronin & Hay,
378 1996](#); [Diaz-Pulido & Garzón-Ferreira, 2002](#)). Higher contribution of CCA at EXP during non-
379 upwelling as compared to upwelling furthermore results from both, elevated CCA production
380 rates (Fig. 2) and higher abundances during non-upwelling (Table 3). The opposite occurrence
381 pattern of macroalgae and CCA suggests that seasonal shifts in macroalgae abundance may also
382 account for the observed temporal variations in CCA coverage. This assumption is supported by
383 the studies of [Lirman & Biber \(2000\)](#) as well as [Belliveau & Paul \(2002\)](#) demonstrating that
384 macroalgae can shade CCA, leading to usually negative correlated abundances of these groups.

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

386 Estimated means of total daily benthic O₂ production at both sites during non-upwelling and the
387 upwelling event in 2011/2012 (Fig. 4) were within the ranges of other investigated reef slope
388 communities (Table 4). However, it should be taken into account that total shallow reef
389 productivity in earlier studies was quantified using flow respirometry techniques, whereas our
390 experiments were conducted in no-flow incubation chambers and included only the major benthic
391 groups. This might have biased benthic O₂-fluxes due to not-investigated organisms and our data
392 should therefore be interpreted accordingly. Despite the different methodologies, our results are
393 comparable to the study by [Adey & Steneck \(1985\)](#) where productivity of similar communities
394 from deeper Caribbean fore reefs of St. Croix (mean water depth: 4.5–6.3 m) was quantified.
395 Productivity rates reported by [Adey & Steneck \(1985\)](#) were comparable to O₂ fluxes in Gayraca
396 Bay, although maximal diurnal fluxes were twice as high as in our study (Table 4). As light
397 availability decreases with depth, water depths of investigated communities (St. Croix: < 6.3 m,

398 Gayraca Bay: ~10 m) may account for elevated daily productivity in reefs of St. Croix. Another
399 reason could be higher surface to area ratios in reefs of St. Croix compared to Gayraca Bay
400 (rugosity factor: 1.9–2.5 and 1.3–1.5, respectively), since surface enlargement is a key factor for
401 benthic communities to increase primary production ([Wanders, 1976b](#)).

402 Despite the high spatial and temporal differences in benthic coverage and group-specific O₂
403 fluxes of investigated benthic primary producers as well as their contribution to total benthic
404 productivity, no spatial differences in total benthic O₂ fluxes were detected between SHE and
405 EXP, neither during non-upwelling nor upwelling. These findings are supported by [Hatcher](#)
406 [\(1990\)](#), stating that the relative coverage of benthic photoautotrophs in a reef community may
407 have little effect on its areal production rate. Furthermore, seasonal differences were only present
408 for P_g at EXP with higher rates during upwelling compared to non-upwelling. This difference is
409 mainly related to individual productivity of algal turfs, being generally two-fold higher during the
410 upwelling compared to non-upwelling (Fig. 2) and the fact that macroalgae at EXP were only
411 present during upwelling (Table 3), thereby further enhancing total benthic productivity. Our
412 findings are supported by [Kinsey \(1985\)](#) and [Hatcher \(1990\)](#), stating that algae are one the most
413 seasonal component in coral reefs and therefore likely account for seasonal shifts in benthic reef
414 productivity.

415 However, the lack of seasonality of P_n and P_g regarding communities at SHE as well as P_g at EXP
416 stands in contrast to earlier studies ([Kinsey, 1977](#); [Smith, 1981](#); [Kinsey, 1985](#); [Eidens et al.,](#)
417 [2012](#)), which found an approximately two-fold difference in benthic primary production between
418 seasons. A possible explanation for this finding could come from seasonal changes of abiotic
419 factors that compensate each other (Table 1). Whereas decreased water temperatures during
420 upwelling typically decrease primary production ([Crossland, 1984](#); [Carpenter, 1985](#)), abiotic
421 factors that are known to enhance primary productivity, namely water currents ([Mass et al.,](#)
422 [2010a](#)) and nutrient availability ([Hatcher, 1990](#); [Chavez, Messie & Pennington, 2011](#)), typically

423 increase during upwelling events, thus promoting photosynthesis. In addition, elevated light
424 availability during incubation experiments during the upwelling (Table 2) could have positively
425 affected photosynthesis of benthic autotrophs. The observed similar productivity rates during
426 different seasons and the reestablishment of original benthic community composition after the
427 upwelling events suggest that coral reefs in TNNP can cope with the pronounced seasonal
428 variations in light availability, water temperature, and nutrient availability. Nevertheless, total P_n
429 and P_g during the upwelling in 2010/2011 (P_n : 244–272 and P_g : 476–483 mmol O₂ · m⁻² seafloor ·
430 d⁻¹) were not only higher compared to the non-upwelling ([Eidens et al., 2012](#)) but also higher than
431 during the subsequent upwelling in 2011/2012 (Fig. 4). These findings suggest that interannual
432 influences do affect productivity of the coral reefs in TNNP. Interestingly, water temperature
433 increases and unusual high precipitation occurred in the study area at the end of 2010, related to
434 ENSO events ([Bayraktarov et al., 2013](#); [Hoyos et al., 2013](#)), causing coral bleaching in the region
435 ([Bayraktarov et al., 2013](#)). Surprisingly, bleached corals in the bay recovered quickly from the
436 ENSO-triggered disturbances in the course of the following upwelling event ([Bayraktarov et al.,](#)
437 [2013](#)) and exhibited similar specific O₂ production rates during the upwelling in 2010/2011
438 compared to subsequent measurements ([Eidens et al., 2012](#)), indicating a high resilience of TNNP
439 corals. Moreover, macroalgae and algal turf seemed to benefit from the environmental conditions
440 during the upwelling following the ENSO-related disturbance events, resulting in higher group-
441 specific productivity of macroalgae and particularly algal turfs during the 2010/2011 upwelling
442 event compared to subsequent study periods ([Eidens et al., 2012](#)). The elevated production rates
443 of macroalgae and algal turfs together with the fast recovery of corals from bleaching likely
444 accounted for higher benthic productivity during upwelling in 2011/2011 compared to the non-
445 upwelling ([Eidens et al., 2012](#)) as well as to the 2011/2012 upwelling event (Fig. 4). These
446 findings suggest that extreme ENSO-related disturbance events causing interannual variation in

447 primary production do not have long-lasting effects on the functioning of local benthic
448 communities.

449 In conclusion, the present study indicates that although major functional groups of benthic
450 photoautotrophs show considerable variability in primary production, total benthic productivity
451 was relatively constant despite high variations in key environmental parameters. Relatively
452 constant benthic productivity albeit pronounced fluctuations in environmental settings may
453 suggests higher resilience of local benthic communities against environmental changes driven by
454 anthropogenic disturbances and climate change. We therefore suggest that TNNP should be
455 considered as a conservation priority area.

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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).

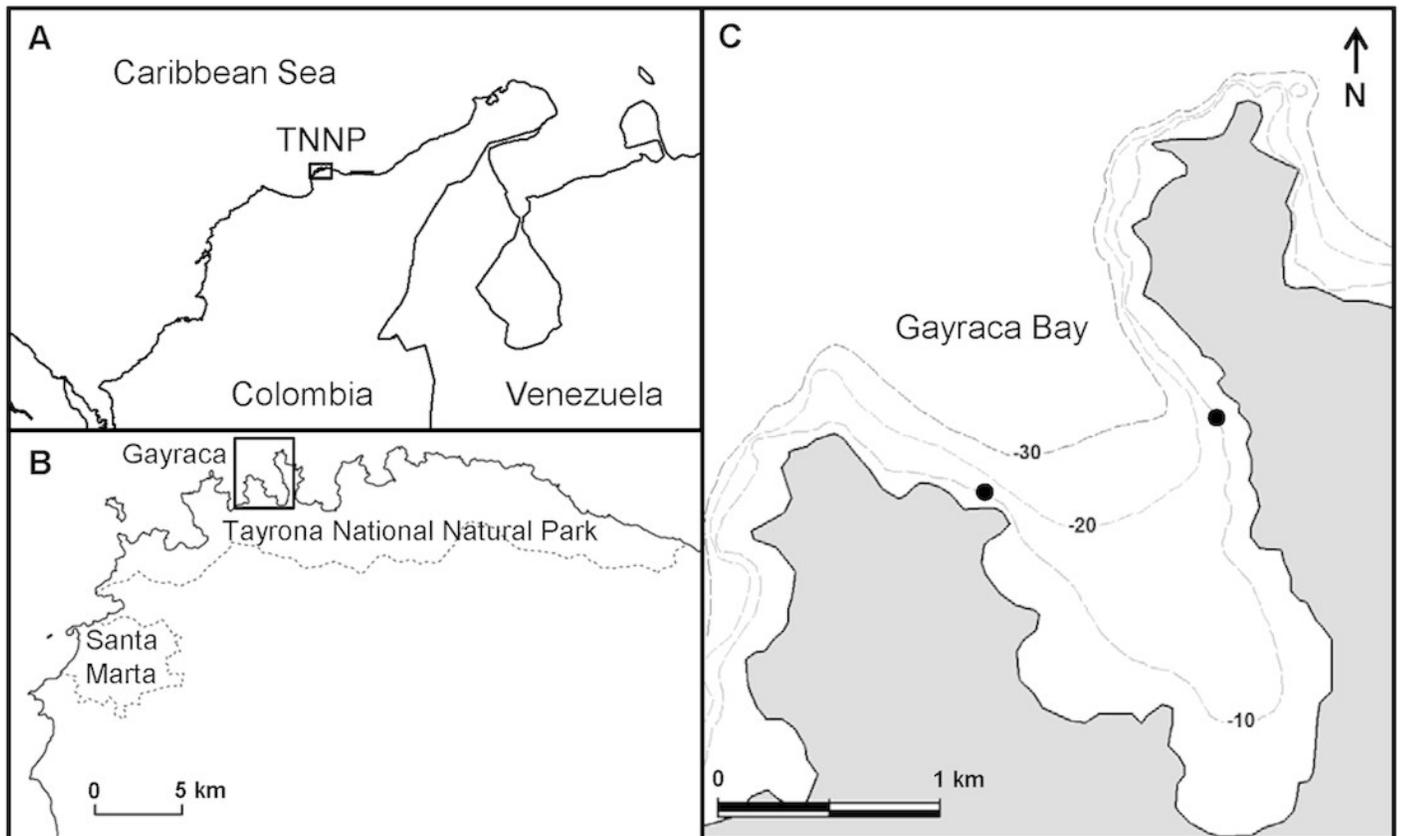


Figure 2

Individual net and gross production of benthic functional groups

Jitter plot of grey dots indicates measured O_2 fluxes. Superimposed black points and error bars represent the mean and 95 % confidence interval according to the Bayesian generalized linear model. Equal lower case letters indicate no differences in mean productivity among benthic groups and brackets display differences within groups. Abbreviations: EXP = exposed, SHE = sheltered, NoUp = non-upwelling, Up = upwelling.

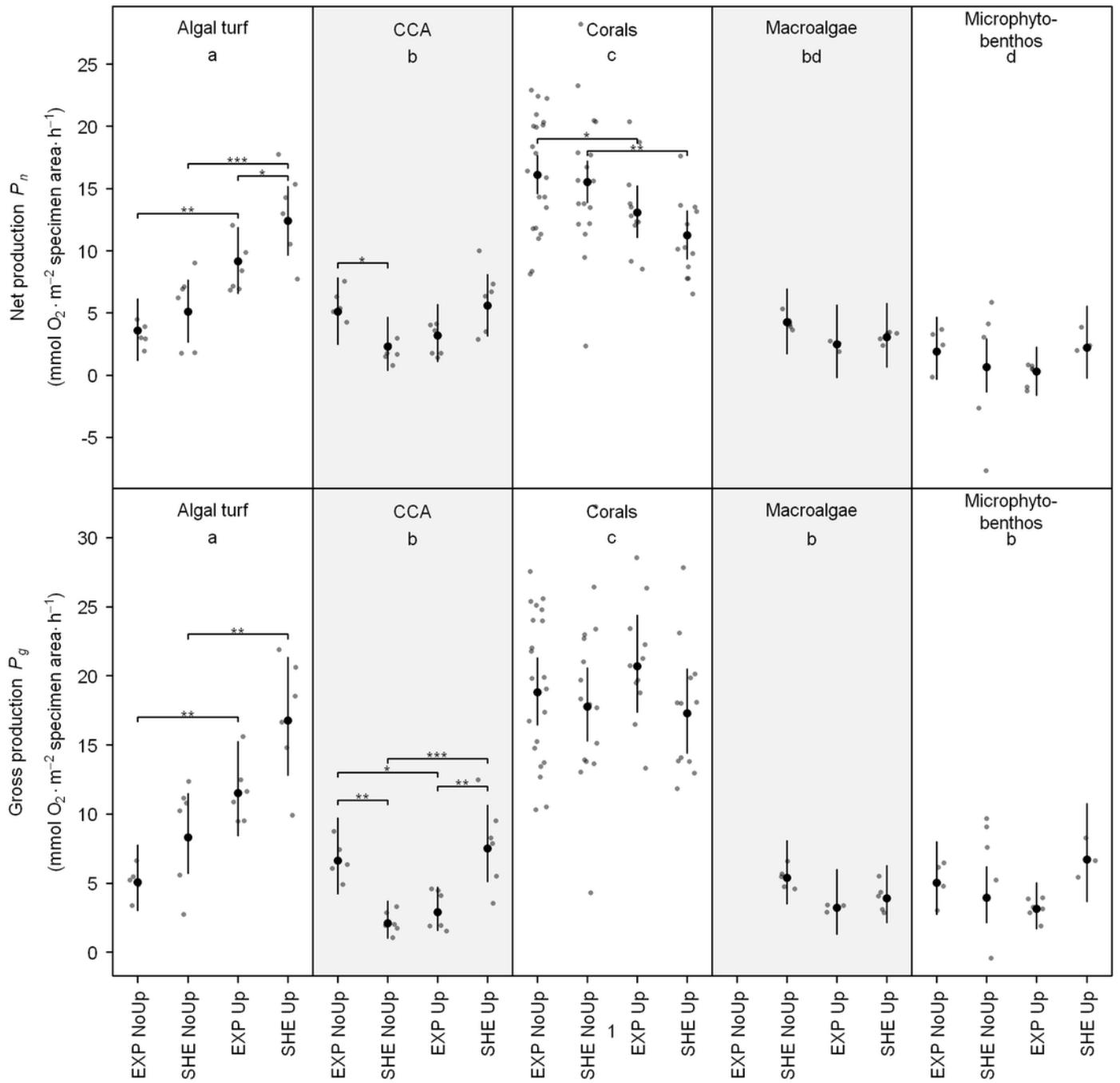


Figure 3

Contribution of functional groups to benthic net and gross prod

Jitter plot of grey dots indicates measured O₂ fluxes. Superimposed black points and error bars represent the mean and 95 % confidence interval according to the Bayesian generalized linear model. Equal lower case letters indicate no differences in mean productivity among benthic groups and brackets display differences within groups. Abbreviations: EXP = exposed, SHE = sheltered, NoUp = non-upwelling, Up = upwelling.

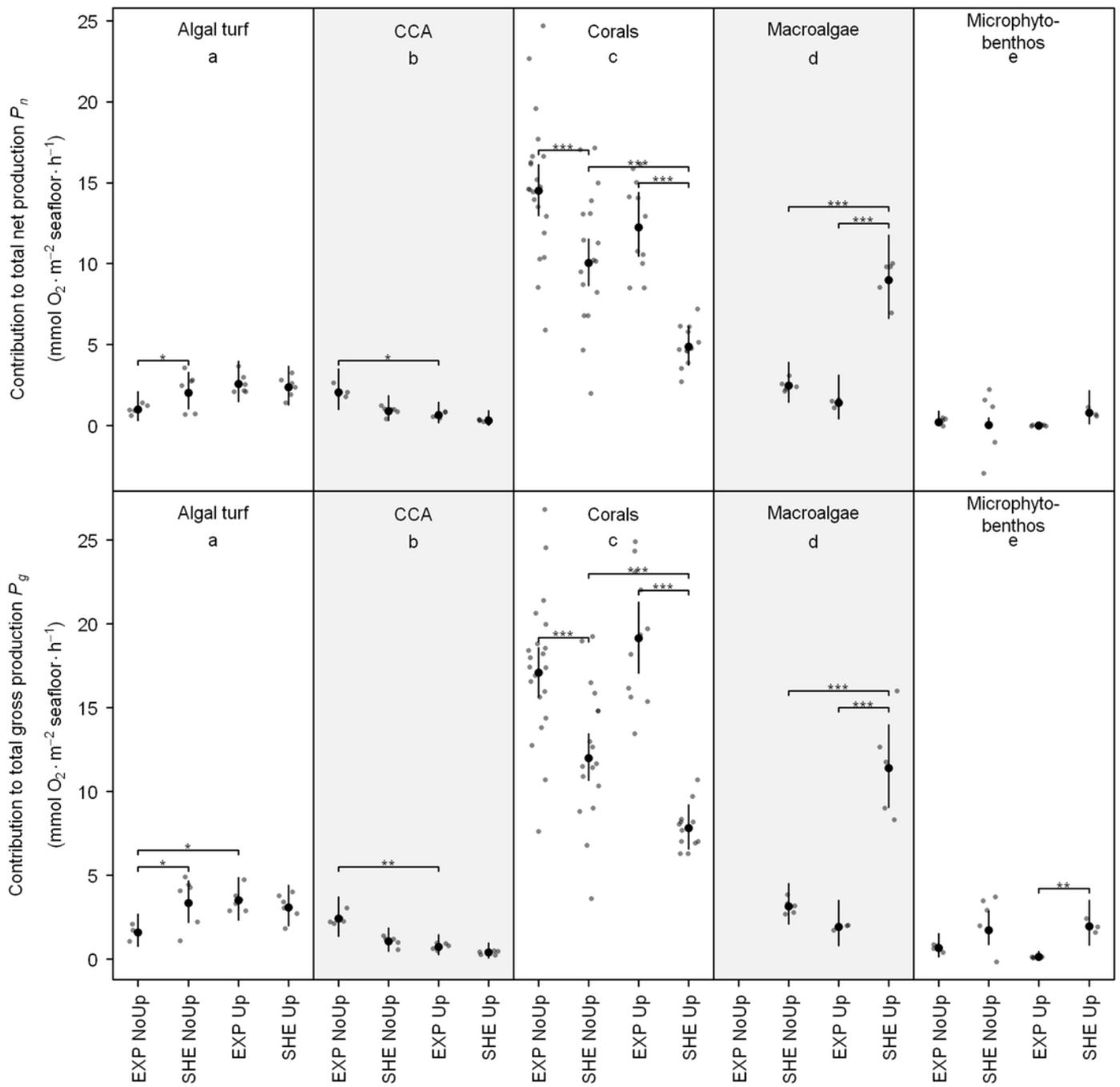


Figure 4

Total benthic net and gross production

Black points and error bars represent the mean and 95 % confidence interval according to the Bayesian generalized linear model. Brackets display differences between seasons.

Abbreviations: EXP = exposed, SHE = sheltered, NoUp = non-upwelling, Up10 = upwelling 2010/2011, Up11 = upwelling 2011/2012.

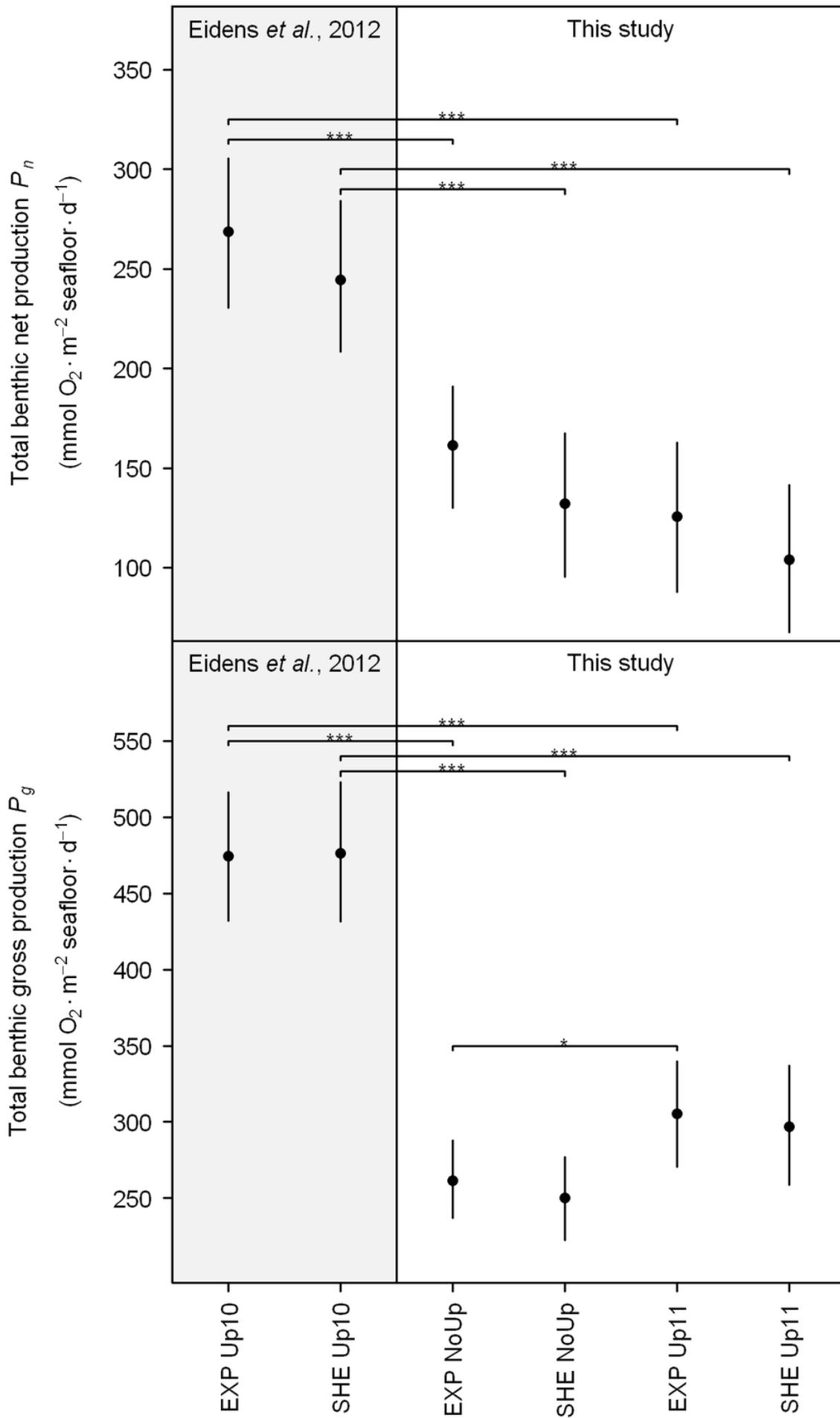


Table 1 (on next page)

Seasonality in water temperature, salinity and nitrate availability in Gayraca Bay

Mean values (\pm SD) at the exposed and sheltered sites and a water depth of 10 m for upwelling (December – April) and non-upwelling (May - November) periods from 2010-2013.

nd = below detection level.

Variables	Non-upwelling		Upwelling		Range
	Exposed	Sheltered	Exposed	Sheltered	
Temperature (°C)	28.5 ± 1.7	28.7 ± 1.7	25.7 ± 2.6	25.7 ± 2.5	20.5–30.0
Salinity	35.3 ± 1.5	35.3 ± 1.2	37.1 ± 1.1	37.0 ± 0.8	32.6–38.5
Nitrate (μmol L ⁻¹)	0.26 ± 0.20	0.32 ± 0.16	1.31 ± 0.95	1.34 ± 0.99	nd–3.59

Table 2(on next page)

Water temperature and light intensity during incubation experiments at sampling sites and in incubation containers

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

	Non-upwelling		Upwelling	
	<i>In situ</i>	Incubations	<i>In situ</i>	Incubations
Temperature (°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)
Light intensity (PAR μmol photons m ⁻² s ⁻¹)	146 ± 47	154 ± 40	230 ± 58 (234 ± 78)	257 ± 69 (248 ± 71)

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. Superscript letters indicate significant differences (p -value $<$ 0.05).

Functional group	Non-upwelling		Upwelling	
	Exposed	Sheltered	Exposed	Sheltered
Corals	41 ± 12 ^a	24 ± 3 ^b	39 ± 12 ^a (37 ± 11)	17 ± 6 ^b (24 ± 6)
Macroalgae	0 ^{c,e}	8 ± 1 ^{d,e}	11 ± 7 ^{c,f} (19 ± 6)	47 ± 3 ^{d,f} (22 ± 4)
Algal turfs	24 ± 5	26 ± 6	23 ± 10 (18 ± 5)	12 ± 5 (19 ± 2)
Crustose coralline algae	18 ± 1 ^{g,i}	14 ± 4 ^{h,i}	10 ± 3 ^{g,j} (13 ± 4)	3 ± 2 ^{h,j} (9 ± 4)
Sand	10 ± 6 ^k	25 ± 13 ^l	3 ± 3 ^k (6 ± 2)	19 ± 7 ^l (21 ± 10)

Table 4(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)	P_g	Reference
Reef slope communities	Caribbean	103–169	250–305	This study
	Caribbean	125–272	250–483	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)