

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

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 as one of the key ecosystem services. This offers the opportunity to assess the effects of abiotic factors on reef 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 and -sheltered 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 during non-upwelling and the upwelling event 2011/2012, and generalized linear models were used to analyze group-specific O_2 production, their contribution to benthic O_2 fluxes, and total daily benthic O_2 production. At the organism level, scleractinian corals showed highest P_n and P_g rates during non-upwelling (16 and $19 \text{ mmol } O_2 \cdot \text{m}^{-2} \text{ specimen area} \cdot \text{h}^{-1}$), and corals and algal turfs dominated the primary production during upwelling (12 and $19 \text{ mmol } O_2 \cdot \text{m}^{-2} \text{ specimen area} \cdot \text{h}^{-1}$, respectively). At the ecosystem level, corals contributed most to total P_n and P_g during non-upwelling, while during upwelling, corals contributed most to P_n and P_g only at exposed and macroalgae at sheltered. Despite the significant spatial and temporal differences in individual productivity of the investigated groups and their different contribution to reef productivity, differences for daily ecosystem productivity were only present for P_g at exposed with higher O_2 fluxes during non-upwelling compared to upwelling. Our findings therefore indicate that total benthic primary productivity of local autotrophic reef communities is relatively stable despite pronounced fluctuations of

environmental key parameters. This may result in higher resilience against anthropogenic disturbances and climate change and Tayrona National Natural Park should therefore be considered as a conservation priority area.

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 ([Chapin et al. 2011](#); [Valiela 1995](#)). 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 ([Gattuso et al. 1998](#); [Hatcher 1988](#)).
21 Productivity investigation on coral reefs started in the mid-20th century ([Odum & Odum 1955](#);
22 [Sargent & Austin 1949](#)) and nowadays, coral reefs are among the best understood marine benthic
23 communities in terms of primary production ([Gattuso et al. 1998](#); [Hatcher 1988](#); [Hatcher 1990](#);
24 [Kinsey 1985](#)).
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 et al. 1999](#);
27 [Sheppard et al. 2009](#)), including light ([Achituv & Dubinsky 1990](#); [Darwin 1842](#); [Falkowski et al.](#)
28 [1990](#)), water temperature ([Coles & Fadlallah 1991](#); [Dana 1843](#); [Veron 1995](#)), salinity ([Andrews](#)
29 [& Pickard 1990](#); [Coles & Jokiel 1992](#)), and inorganic nutrient availability ([D'Elia & Wiebe 1990](#);
30 [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 ([Cortés &](#)
33 [Jiménez 2003](#); [Glynn & Stewart 1973](#)), 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](#); [Falter et al. 2012](#); [Kinsey 1985](#)), 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 area
43 thereby provides an excellent opportunity to investigate the effects of seasonal coastal upwelling
44 events on the key ecosystem service productivity in coral reefs under changing *in situ* conditions.
45 The results of a preliminary study conducted by [Eidens et al. \(2012\)](#) indicated that benthic
46 primary production in TNNP differed between the upwelling in 2010/2011 and the consecutive
47 non-upwelling season, suggesting a generally positive effect of upwelling conditions on major
48 benthic autotrophs in the area. However, after unusually strong El Niño-Southern Oscillation
49 (ENSO) events in 2010, the area experienced a moderate coral bleaching before the upwelling in
50 2010/2011 ([Bayraktarov et al. 2013](#); [Hoyos et al. 2013](#)), and productivity measurements during
51 upwelling in 2010/2011 may not be representative. To test for patterns in benthic primary
52 production during a typical seasonal cycle, we here quantified benthic primary production before
53 and at the end of the upwelling event in 2011/2012 (hereafter referred to as non-upwelling and
54 upwelling, respectively). To allow for comparisons of productivity between investigated groups,
55 we further estimated surface area-specific productivity rates as suggested by [Naumann et al.](#)
56 [\(2013\)](#) and analyzed the data using generalized linear models.
57 Therefore, the goals of the study were to (1) identify dominant functional groups of benthic
58 primary producers and their relative benthic cover at a current/wave-exposed (EXP) and
59 -sheltered (SHE) site in one exemplary bay of TNNP, (2) quantify O₂ fluxes of all dominant
60 benthic primary producers and apply 3D surface area estimations, and hence (3) estimate the
61 specific contribution of each group to total benthic O₂ fluxes.

62 **Materials and Methods**

63 **Study site and sampling seasons**

64 This study was conducted in Gayraca Bay (11.33°N, 74.11°W), one of several small bays in
65 TNNP, located near the city of Santa Marta (Fig. 1). The continental shelf in the area is relatively
66 narrow due to the proximity to the Sierra Nevada de Santa Marta - the world's highest coastal
67 mountain range. The TNNP contains small fringing coral reefs reaching to a water depth of ~30
68 m ([Garzón-Ferreira 1998](#); [Garzón-Ferreira & Cano 1991](#)). The region is subjected to strong
69 seasonality caused by the Caribbean Low-Level Jet of northeast (NE) trade winds ([Andrade &](#)
70 [Barton 2005](#); [Salzwedel & Müller 1983](#)), resulting in two major seasons; a dry season from
71 December to April and a rainy season from May to November ([Garzón-Ferreira 1998](#); [Salzwedel](#)
72 [& Müller 1983](#)). Whereas the rainy season (hereafter referred to as non-upwelling) is
73 characterized by low wind velocities (mean 1.5 m s⁻¹) ([Garzón-Ferreira 1998](#)) and high
74 precipitation (> 80 % of the annual rainfall) ([Salzwedel & Müller 1983](#)), during the dry season
75 (hereafter referred to as upwelling), strong winds prevail (mean 3.5 m · s⁻¹, max 30 m · s⁻¹)
76 ([Herrmann 1970](#); [Salzwedel & Müller 1983](#)) resulting in a seasonal coastal upwelling. The
77 upwelling-related changes in key water parameters are well characterized by the comprehensive
78 study of [Bayraktarov et al. \(2014b\)](#). During upwelling, water temperature can decrease to 20 °C
79 while salinity and inorganic nutrient availability increase up to 39 and 3.59 µmol L⁻¹, respectively
80 (Table 1). Water currents triggered by prevailing winds predominantly move from NE to SW, and
81 a clear gradient in wave exposure between the exposed western (EXP) and -sheltered
82 northeastern (SHE) sides of the bay can be observed ([Bayraktarov et al. 2014a](#); [Werdning &](#)
83 [Sánchez 1989](#)). The study was carried out during non-upwelling in 2011 (1st November – 2nd
84 December 2011) and during the consecutive upwelling event (20th March – 29th March 2012),
85 allowing for the investigation of the influence of seasonality on benthic primary production.

86 **Benthic assessment**

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

102 **Sampling of organisms**

103 Specimens of scleractinian corals, macroalgae, algal turfs, and CCA as well as sand samples,
104 from 10 ± 1 m water depth were used for quantification of O_2 fluxes (see Table S1 for number of
105 replicates). All samples were brought to the water surface in Ziploc bags and transported directly
106 to the field lab. Scleractinian corals of the genera *Montastraea* (including the species *M.*
107 *faveolata*, *M. franksi* and *M. annularis*, currently belonging to the genus *Orbicella*; Budd et al.
108 2012) and *Diploria* (including *D. strigosa*, currently belonging to the genus *Pseudodiploria* Budd
109 et al. 2012) accounted for more than 80 % of the total coral cover at the study sites and were

110 therefore used as representative corals in our study. Coral specimens were obtained from the reef
111 using hammer and chisel, fragmented with a multifunction rotary tool (Dremel Corp., 8200-2/45;
112 mean fragment surface area: $13.16 \pm 7.96 \text{ cm}^2$), and fixed on ceramic tiles using epoxy glue
113 (Giesemann GmbH, Aquascape). After fragmentation, specimens were returned to their natural
114 habitat and left to heal for one week prior to the incubation experiments. Algae of the genus
115 *Dictyota* (mainly *D. bartayresiana*) amounted to nearly 100 % of macroalgal cover. Therefore
116 small bushes of *Dictyota* spp. (surface area $1.86 \pm 0.88 \text{ cm}^2$) were used as representatives for
117 macroalgae. Macroalgae were transferred to a storage tank (volume: 500 L in which water was
118 exchanged manually 3-5 times per day and water temperature was within the ranges of incubation
119 experiments; see Table 2) one day before incubation experiments and left to heal. All other
120 functional groups were incubated immediately after sampling. Rubble overgrown by algal turfs
121 and CCA served as samples for the respective functional group (surface area covered by the
122 organisms: $15.63 \pm 10.80 \text{ cm}^2$ and $7.48 \pm 3.60 \text{ cm}^2$, respectively). For sand samples, custom-made
123 mini corers with defined surface area (1.20 cm^2) and sediment core depth (1.0 cm) were used. All
124 necessary permits (DGI-SCI-BEM-00488) were obtained by Instituto de Investigaciones Marinas
125 y Costeras (INVEMAR) in Santa Marta, Colombia which complied with all relevant regulations.

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 et al. 1997](#)) and allowed us to
178 compare our results with previous incubation studies (e.g. [Haas et al., 2011](#); [Jantzen et al., 2013](#);
179 [Naumann et al., 2013](#)). Nevertheless, since it is well known that water flow enhances O₂ fluxes
180 and thereby photosynthesis ([Mass et al. 2010a](#)), the results of the field incubations should be
181 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 blank control values were
 185 subtracted from the measured O₂ fluxes. Individual gross O₂ production (P_g) of investigated
 186 functional groups was calculated by adding values of P_n and respiration; individual O₂ fluxes
 187 were 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), group-specific benthic coverage (b_i) as well as the rugosity
 192 factor (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 site (EXP vs. SHE) and their interaction 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. We used
 202 Markov-chain Monte Carlo (MCMC) estimations of GLM regression coefficients. In traditional
 203 Frequentist statistics, the parameters of interest (i.e. the O₂ productivity describing regression
 204 coefficients) are estimated just once (e.g. using Maximum-Likelihood) and their significance is
 205 inferred indirectly based on a test-statistic. In contrast, Bayesian methods reallocate the

206 coefficients across a set of possible candidates during each MCMC generation ([Kruschke 2011](#)).

207 If the bulk of these values, that is the 95 % highest posterior density (HPD), do not include zero,

208 one can directly conclude that the regression coefficient is credible different than zero and an

209 effect on O₂ productivity exists. Moreover, we here performed pair-wise comparisons between

210 benthic groups at different sites and seasons, traditionally being performed by *post-hoc* testing

211 with *P*-value correction for preventing false positive results. A Bayesian GLM does not suffer this

212 drawback because difference of groups can be directly estimated by the posterior ([Kruschke](#)

213 [2011](#)). Again, there is credible evidence in non-equal group-means, if the posterior-based 95 %

214 HPD interval of the group differences does not include zero. Model performance for all 19

215 possible combinations of the three independent variables and their interactions was assessed by

216 the deviance information criterion (DIC), a Bayesian measure of model fit that penalizes

217 complexity ([Spiegelhalter et al. 2002](#)). In this information theory based model selection, often

218 there is not a single best model describing the data. Therefore, averaging of regression

219 coefficients for all models within $\Delta\text{DIC} < 2$ of the best one ([Johnson & Omland 2004](#)) was

220 performed according to DIC weights (i.e. support for the respective regression model).

221 Here, Bayesian GLMs using the MCMCglmm package ([Hadfield 2010](#)) for the R 3.0.3

222 environment for statistical computing (R Core Team 2014) with a Gaussian error distribution

223 were applied. Prior to the analyses, the mean-variance relationship of measured O₂ flux was

224 stabilized by power transformation ([Yeo & Johnson 2000](#)). Visual inspection of preliminary

225 GLMs with default weakly informative priors showed high autocorrelation in their posterior

226 distribution. Thus to infer the posterior distribution of the final analyses, we ignored the first

227 50000 estimates as burn-in and sampled every 5th out of 650000 MCMC generations.

228 All values are represented as mean \pm standard deviation (SD) if not noted otherwise.

229 **Results**

230 **Benthic community composition**

231 At EXP, scleractinian corals dominated the benthic community during non-upwelling and
232 upwelling (41 ± 12 and 39 ± 12 %, respectively; Fig. 2). At SHE, corals, algal turf, and sand
233 cover was similar during non-upwelling (24 ± 3 %, 26 ± 6 %, and 25 ± 13 %, respectively), while
234 during upwelling, macroalgae exhibited highest benthic cover (47 ± 3 %, Fig. 2). During the
235 entire study period, coral and CCA cover was significantly higher at EXP than at SHE, whereas
236 sand showed a contrary pattern with significantly more coverage at SHE (Fig. 2). Macroalgae
237 was the only group where interaction between sites and seasons occurred with significantly higher
238 cover at SHE and higher abundances during upwelling at both sites (Fig. 2). CCA cover also
239 differed between the seasons, showing a significant decrease during the upwelling event (Fig. 2).

240 **O₂ fluxes of organisms**

241 More complex Bayesian GLMs, including interactions among the three independent variables
242 season, benthic group, and site, described individual O₂ fluxes better than simple models (For
243 details see Table S2).
244 Of all investigated functional groups, scleractinian corals had highest individual net (P_n) and
245 gross production (P_g), followed by algal turfs, macroalgae, CCA, and microphytobenthos (Fig. 3;
246 see also Table S3 for detailed results of all pair-wise comparisons). Regarding spatial differences
247 in individual productivity, significant differences were detected for algal turfs and CCA. During
248 upwelling, P_n of algal turfs and P_g of CCA was higher at SHE than EXP. On the contrary, during
249 non-upwelling, P_n and P_g of CCA was higher at EXP (Fig. 3).
250 Temporal differences in O₂ production were detected for corals, algal turfs, and CCA (Fig. 3).
251 Whereas P_n of scleractinian corals on both sites and P_g of CCA at EXP were higher during non-
252 upwelling, P_g of CCA at SHE as well as P_n and P_g of algal turfs at both sites showed an opposite
253 pattern with higher productivity rates during upwelling (Fig. 3).

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

255 As in the case of individual O₂ fluxes, contribution and total reef production were better
256 explained by GLMs of higher complexity (Table S2).
257 Contribution of functional groups to benthic productivity exhibited similar pattern than individual
258 productivity with corals contributing generally most to total reef P_n and P_g , but macroalgae
259 contributed most to benthic P_n and P_g at SHE at the end of upwelling (Fig. 4; see also Table S3
260 for detailed results of all pair-wise comparisons).
261 Significant spatial differences in contribution to total benthic P_n within functional groups were
262 detected for corals, algal turf, and macroalgae, and spatial differences for P_g were present in all
263 investigated groups except CCA (Fig. 4). At EXP, Corals contributed more to total P_n and P_g
264 during non-upwelling and upwelling (Fig. 4). At SHE, contributions of macroalgae (P_n and P_g)
265 and microphytobenthos (P_g) were higher only during upwelling, and algal turfs contributed more
266 to P_g at SHE during non-upwelling (Fig. 4).
267 Temporal differences in contribution to total benthic productivity within the investigated groups
268 were present for corals, macroalgae, CCA (for P_n and P_g), and for algal turfs (only P_g) (Fig. 5).
269 During non-upwelling, Corals contributed more to the total productivity at SHE and CCA at EXP,
270 whereas during upwelling, macroalgae contributed more to the total productivity at SHE and
271 algal turf at EXP (Fig. 4).
272 Regarding the total daily benthic O₂ fluxes (Figs. 4), no spatial differences between EXP and
273 SHE were detected, neither during non-upwelling nor during upwelling (see also Table S3 for
274 detailed results of all pair-wise comparisons). During the study, significant temporal differences
275 were only present for P_g at the exposed site with higher O₂ fluxes during the upwelling in
276 2011/2012 compared to non-upwelling (Fig. 5). Comparing total benthic productivity during the
277 upwelling event in 2010/2011 with the subsequent non-upwelling and upwelling, P_n and P_g were
278 significantly higher during the upwelling 2010/2011 for all comparisons (Fig. 5).

279 Discussion

280 O₂ fluxes of organisms

281 Individual mean P_n and P_g were generally highest for corals at both sites during the study periods
282 (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
283 of corals compared to other investigated primary producers (see Fig. 3) may be attributed to the
284 mutualistic relationship between zooxanthellae and coral host leading to enhanced photosynthetic
285 efficiency under high CO₂ and nutrient availability ([D'Elia & Wiebe 1990](#); [Muscatine 1990](#)).
286 Estimated daily P_g per m² seafloor for the investigated coral genera, (441-610 mmol O₂ · m⁻²
287 seafloor · d⁻¹), is within the range of other Caribbean corals (67 to 850 mmol O₂ · m⁻² seafloor · d⁻¹,
288 Fig. 2, Kanwisher & Wainwright, 1967), and O₂ fluxes of all investigated organism groups are
289 comparable to values reported in the literature (Fig. 2).

290 Significant spatial differences during non-upwelling were found for CCA with higher
291 productivity at EXP compared to SHE (Fig. 3). These differences may be attributed to the
292 prevailing water current regime in the bay together with high water temperatures during non-
293 upwelling (Tables 1 and 2). An increase in water temperature typically intensifies metabolic
294 activity in CCA ([Hatcher 1990](#); [Littler & Doty 1975](#)). However, the lower water flow at SHE
295 ([Bayraktarov et al. 2014a](#)) may have prevented the required gas exchange and nutrient uptake,
296 resulting in lower individual CCA productivity at this site. In contrast, the higher rates in
297 individual productivity of algal turfs and CCA at SHE during upwelling (Fig. 3) are potentially a
298 result of the differences in species composition (sensu [Littler, 1973](#); [Chisholm, 2003](#); [Copertino,](#)
299 [Cheshire & Kildea, 2009](#); [Ferrari et al., 2012](#)).

300 Temporal differences in individual O₂ production within the investigated organism groups
301 generally showed two contrary patterns: whereas scleractinian corals on both sites and CCA at
302 EXP produced less O₂ during upwelling, algal turfs and CCA at SHE produced more O₂. The

303 decreased productivity rates of corals and CCA at EXP during upwelling indicate that low water
304 temperature has an adverse effect on the productivity of these groups. This argument is supported
305 by studies showing that low water temperatures lead to a decrease in photosynthetic performance
306 of primary producers in coral reefs ([Hatcher 1990](#); [Kinsey 1985](#)). In contrast, the two-fold higher
307 photosynthetic performance of algal turfs during upwelling may be due to higher nutrient
308 concentrations together with higher water currents during this season ([Bayraktarov et al. 2014a](#);
309 [Bayraktarov et al. 2014b](#)), facilitating gas exchange and nutrient uptake. Our findings are
310 supported by [Carpenter & Williams \(2007\)](#), showing that photosynthesis of algal turfs in coral
311 reefs is mainly limited by nutrient uptake, which in turn depends on nutrient availability and
312 water current speed. Whereas productivity of CCA at EXP seems to be temperature-limited, our
313 findings indicate that their productivity at SHE is limited by nutrient availability as previously
314 suggested for benthic algal communities in water current-sheltered coral reef locations ([Carpenter](#)
315 [& Williams 2007](#); [Hatcher 1990](#)).

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

317 Our results indicate that the spatial differences in contribution to total benthic O₂ production for
318 scleractinian corals, macroalgae, CCA, and microphytobenthos are directly linked to spatial
319 differences in their benthic coverage. For instance, the major contribution of corals (Fig. 4) can
320 be explained by their comparably high benthic coverage (ranging from 24 to 39 %; Fig. 2) and
321 highest quantified individual O₂ production rates among all investigated groups (Fig. 3). -This
322 finding is supported by the estimates of [Wanders \(1976\)](#), showing that corals accounted for about
323 two-thirds of the total benthic primary production in a Southern Caribbean fringing reef.

324 Although individual macroalgal production rates were rather low as compared to coral
325 productivity (Fig. 3), the extremely high cover of macroalgae at SHE during upwelling (47 ± 3
326 %) resulted in macroalgae being the main contributors to total benthic production. Macroalgal
327 cover (incl. the dominant genus *Dictyota*) has previously been found to be particularly high
328 during upwelling ([Bula-Meyer 1990](#); [Cronin & Hay 1996](#); [Diaz-Pulido & Garzón-Ferreira](#)
329 [2002](#)). probably due to elevated nutrient concentrations and low water temperatures ([Bayraktarov](#)
330 [et al. 2014b](#)).

331 The elevated contributions of corals and CCA at EXP as well as macroalgae and
332 microphytobenthos at SHE during upwelling (Fig. 4) might be due to site-specific differences in
333 abundances (Fig. 2), which in turn are likely caused by site-specific differences in water current
334 regimes ([Bayraktarov et al. 2014a](#); [Werding & Sánchez 1989](#)).

335 Corals, macroalgae, algal turfs, and CCA also exhibited distinct temporal differences in
336 contribution to total benthic productivity. At SHE, corals contributed more to the benthic O₂
337 production during non-upwelling and macroalgae and algal turfs during upwelling, whereas
338 contribution of CCA at EXP was higher during non-upwelling. These differences can be
339 explained with seasonal growth patterns, temperature-dependent changes in individual O₂
340 productivity and temporal shifts in abundances (Figs. 2 and 3). Opposite abundance patterns of
341 CCA and macroalgae are, for example, in agreement with previous studies of showing that
342 macroalgae can shade CCA, usually leading to negative correlated abundances of these groups
343 ([Belliveau & Paul 2002](#); [Lirman & Biber 2000](#)).

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

345 The estimated total daily benthic O₂ production at both sites during non-upwelling and upwelling
346 (Fig. 5) are, although comparable, on average slightly lower than the values previously reported
347 for other fore reefs communities (Table 3). These differences might be due to a methodological
348 bias. Whereas previous studies utilized flow respirometry techniques, the current study used
349 incubation methodology, which accounts for production values in the target groups only.

350 Despite the high spatial and temporal differences in benthic coverage and group-specific O₂
351 fluxes of investigated benthic primary producers as well as their contribution to total benthic
352 productivity, no spatial differences in total benthic O₂ fluxes were detected between EXP and
353 SHE. These results were consistent during both non-upwelling and upwelling (Fig. 5). Our
354 findings are supported by [Hatcher \(1990\)](#), showing that the relative coverage of benthic
355 photoautotrophs in a reef community may have little effect on its areal production rate. In TNNP,
356 seasonal differences were only present for P_g at EXP with higher rates during upwelling
357 compared to non-upwelling. These differences are mainly related to individual productivity of
358 algal turfs, being generally two-fold higher during upwelling compared to non-upwelling (Fig. 3),
359 and to the absence of macroalgae at EXP during non-upwelling (Fig. 2). This is in agreement with
360 studies by [Kinsey \(1985\)](#) and [Hatcher \(1990\)](#), reporting that algae, as one of the most seasonal
361 component in coral reefs, account for seasonal shifts in benthic reef productivity.

362 The lack of seasonality of P_n and P_g regarding communities at SHE as well as P_g at EXP stands in
363 contrast to earlier studies ([Eidens et al. 2012](#); [Kinsey 1977](#); [Kinsey 1985](#); [Smith 1981](#)), which
364 found an approximately two-fold difference in benthic primary production between seasons. This
365 lack of seasonality in P_n and partly in P_g in TNNP might be related to seasonal changes of abiotic
366 factors that compensate each other (Table 1). The observed similarity in productivity rates during
367 different seasons suggest that coral reefs in TNNP can cope with pronounced seasonal variations

368 in light availability, water temperature, and nutrient availability. Nevertheless, total P_n and P_g
369 during the upwelling in 2010/2011 (P_n : 244–272 and P_g : 476–483 mmol O₂ · m⁻² seafloor · d⁻¹)
370 were not only higher compared to non-upwelling ([Eidens et al. 2012](#)) but also higher than during
371 the subsequent upwelling in 2011/2012 (Fig. 5). These findings suggest that interannual
372 variations affect the productivity of TNNP coral reefs. Dramatic ENSO-related water temperature
373 increases and high precipitation in the study area ([Bayraktarov et al. 2013](#); [Hoyos et al. 2013](#)) led
374 to coral bleaching at the end of 2010 ([Bayraktarov et al. 2013](#)). Surprisingly, bleached corals in
375 the bay recovered quickly in the course of the following upwelling event ([Bayraktarov et al.](#)
376 [2013](#)) and exhibited similar O₂ production rates during all study periods ([Eidens et al. 2012](#)),
377 indicating a high resilience of TNNP corals. Moreover, macroalgae and algal turf seemed to
378 benefit from the environmental conditions during the upwelling following the ENSO-related
379 disturbance events, resulting in higher group-specific productivity during the upwelling in
380 2010/2011 compared to subsequent study periods ([Eidens et al. 2012](#)). The elevated production
381 rates of macroalgae and algal turfs together with the quick recovery of corals from bleaching
382 likely accounted for a higher benthic productivity during the upwelling in 2011/2011 compared to
383 non-upwelling ([Eidens et al. 2012](#)) and the upwelling in 2011/2012 (Fig. 5). These findings
384 indicate that extreme ENSO-related disturbances do not have long-lasting effects on the
385 functioning of local benthic communities in TNNP.

386 In conclusion, the present study showed that total benthic productivity in TNNP is relatively
387 constant despite high variations in key environmental parameters. This stable benthic
388 productivity suggests a relatively high resilience of local benthic communities against natural
389 environmental fluctuations and anthropogenic disturbances. We therefore recommend that TNNP
390 should be considered as a conservation priority area.

391 **Acknowledgements**

392 We thank J. F. Lazarus-Agudelo, J. C. Vega-Sequeda T. Deuß, M. Kabella, R. Kügler, and J. Rau
393 for assistance during fieldwork and the staff of Instituto de Investigaciones Marinas y Costeras
394 (INVEMAR) for logistic support. We acknowledge the kind collaboration of the administration
395 and staff of the Tayrona National Natural Park. Furthermore, the authors would like to thank Cajo
396 ter Braak and four anonymous reviewers for their useful comments that improved the manuscript
397 significantly. The study was supported by the Center of Excellence in Marine Sciences
398 (CEMarin) in Santa Marta, Colombia.

399 **References**

- 400 Achituv Y, and Dubinsky Z. 1990. Evolution and zoogeography of coral reefs. In: Dubinsky Z,
401 ed. *Coral Reefs Ecosystems of the World*. Amsterdam: Elsevier, 1-9.
- 402 Adey W, and Steneck R. 1985. Highly productive eastern Caribbean reefs: synergistic effects
403 of biological, chemical, physical, and geological factors. In: Reaka M, editor. *The*
404 *ecology of deep and shallow coral reefs*. 2 ed. Rockville. p 163-187.
- 405 Andrade CA, and Barton ED. 2005. The Guajira upwelling system. *Continental Shelf Research*
406 25:1003-1022.
- 407 Andrews JC, and Pickard GL. 1990. The physical oceanography of coral-reef systems. In:
408 Dubinsky Z, ed. *Coral Reefs*. Amsterdam Elsevier, 11-48.
- 409 Bayraktarov E, Bastidas-Salamanca M, and Wild C. 2014a. The physical environment in coral
410 reefs of the Tayrona National Natural Park (Colombian Caribbean) in response to
411 seasonal upwelling. *Boletín de Investigaciones Marinas y Costeras - Invemar* 43:137-
412 157.
- 413 Bayraktarov E, Pizarro V, Eidens C, Wilke T, and Wild C. 2013. Bleaching susceptibility and
414 recovery of Colombian Caribbean corals in response to water current exposure and
415 seasonal upwelling. *PLoS ONE* 8.
- 416 Bayraktarov E, Pizarro V, and Wild C. 2014b. Spatial and temporal variability of water quality
417 in the coral reefs of Tayrona National Natural Park, Colombian Caribbean.
418 *Environmental Monitoring and Assessment*:1-19.
- 419 Belliveau SA, and Paul VJ. 2002. Effects of herbivory and nutrients on the early colonization
420 of crustose coralline and fleshy algae. *Marine Ecology-Progress Series* 232:105-114.
- 421 Budd AF, Fukami H, Smith ND, and Knowlton N. 2012. Taxonomic classification of the reef
422 coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). *Zoological Journal of the*
423 *Linnean Society* 166:465-529.
- 424 Bula-Meyer G. 1990. Altas temperaturas estacionales del agua como condición disturbadora
425 de las macroalgas del Parque Nacional Natural Tairona, Caribe colombiano: una
426 hipótesis. *An Inst Invest Mar Punta de Betín* 19-20:9-21.
- 427 Carpenter RC, and Williams SL. 2007. Mass transfer limitation of photosynthesis of coral reef
428 algal turfs. *Marine Biology* 151:435-450.
- 429 Chapin FS, Matson PA, Vitousek PM, Chapin MC, and SpringerLink (Online service). 2011.
430 Principles of terrestrial ecosystem ecology. 2nd ed. New York: Springer,. p 1 online
431 resource (xv, 529 p.) ill. (some col.).
- 432 Chisholm JRM. 2003. Primary productivity of reef-building crustose coralline algae. *Limnology*
433 *and Oceanography* 48:1376-1387.
- 434 Coles DW, and Jokiel P. 1992. Effects of salinity on coral reefs. In: Connell DW, and Hawker
435 DW, eds. *Pollution in tropical aquatic systems*. Boca Raton: CRC Press, 147-166.

- 436 Coles S, and Fadlallah Y. 1991. Reef coral survival and mortality at low temperatures in the
437 Arabian Gulf: new species-specific lower temperature limits. *Coral Reefs* 9:231-237.
- 438 Copertino MS, Cheshire A, and Kildea T. 2009. Photophysiology of a turf algal community:
439 integrated responses to ambient light and standing biomass. *Journal of Phycology*
440 45:324-336.
- 441 Cortés C, and Jiménez C. 2003. Past, present and future of the coral reefs of the Caribbean
442 coast of Costa Rica. In: Cortés J, ed. *Latin American coral reefs*. 1st ed. Amsterdam
443 Boston: Elsevier, 223-239.
- 444 Cronin G, and Hay ME. 1996. Effects of light and nutrient availability on the growth,
445 secondary chemistry, and resistance to herbivory of two brown seaweeds. *Oikos*
446 77:93-106.
- 447 D'Elia CF, and Wiebe WJ. 1990. Biogeochemical nutrient cycles in coral-reef ecosystems. In:
448 Dubinsky Z, ed. *Coral Reefs*. Amsterdam: Elsevier, 49-74.
- 449 Dana FD. 1843. On the temperature limiting the distribution of corals. *American Journal of*
450 *Science* 45:130-131.
- 451 Darwin C. 1842. *The structure and distribution of coral reefs*: Smith Elder and Co.
- 452 Diaz-Pulido G, and Garzón-Ferreira J. 2002. Seasonality in algal assemblages on upwelling-
453 influenced coral reefs in the Colombian Caribbean. *Botanica Marina* 45:284-292.
- 454 Eidens C, Bayraktarov E, Pizarro V, Wilke T, and Wild C. 2012. Seasonal upwelling stimulates
455 primary production of Colombian Caribbean coral reefs. In: Yellowlees D, and Hughes
456 TP, editors. 12th International Coral Reef Symposium. Cairns, Australia.
- 457 Falkowski PG, Jokiel PL, and Kinzie III RA. 1990. Irradiance and corals. In: Dubinsky Z, ed.
458 *Coral Reefs*. Amsterdam: Elsevier, 89-107.
- 459 Falter JL, Lowe RJ, Atkinson MJ, and Cuet P. 2012. Seasonal coupling and de-coupling of net
460 calcification rates from coral reef metabolism and carbonate chemistry at Ningaloo
461 Reef, Western Australia. *Journal of Geophysical Research-Oceans* 117.
- 462 Ferrari R, Gonzalez-Rivero M, Ortiz JC, and Mumby PJ. 2012. Interaction of herbivory and
463 seasonality on the dynamics of Caribbean macroalgae. *Coral Reefs* 31:683-692.
- 464 Garzón-Ferreira J. 1998. Bahía Chengue, Parque Natural Tayrona, Colombia. In: Kjerfve B, ed.
465 *CARICOMP-Caribbean coral reef, seagrass and mangrove sites Coastal Region and*
466 *Small Islands Papers* 3. Paris: UNESCO, 115-125.
- 467 Garzón-Ferreira J, and Cano M. 1991. Tipos, distribución, extensión y estado de conservación
468 de los ecosistemas marinos costeros del Parque Nacional Natural Tayrona. Final
469 Report. Santa Marta, Colombia. p 82.
- 470 Gattuso J-P, Frankignoulle M, and Wollast R. 1998. Carbon and carbonate metabolism in
471 coastal aquatic ecosystems. *Annual Review of Ecology and Systematics* 29:405-435.
- 472 Geyer O. 1969. Vorläufige Liste der scleractinen Korallen der Bahía de Concha bei Santa
473 Marta, Kolumbien. *Mitt Inst Colombo-Aleman Invest Cient* 3:25-28.
- 474 Glynn PW. 1993. Monsoonal upwelling and episodic *Acanthaster* predation as possible
475 controls of coral reef distribution and community structure in Oman, Indian Ocean.
476 *Atoll Research Bulletin* 379.

- 477 Glynn PW, and Stewart RH. 1973. Distribution of Coral Reefs in Pearl Islands (Gulf of Panama)
478 in Relation to Thermal Conditions. *Limnology and Oceanography* 18:367-379.
- 479 Haas AF, Nelson CE, Kelly LW, Carlson CA, Rohwer F, Leichter JJ, Wyatt A, and Smith JE. 2011.
480 Effects of coral reef benthic primary producers on dissolved organic carbon and
481 microbial activity. *PLoS ONE* 6.
- 482 Hadfield JD. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The
483 MCMCglmm R Package. *Journal of Statistical Software* 33:1-22.
- 484 Hatcher BG. 1988. Coral reef primary productivity: A beggar's banquet. *TREE* 3:106-111.
- 485 Hatcher BG. 1990. Coral reef primary productivity: A hierarchy of pattern and process. *TREE*
486 5:149-155.
- 487 Herrmann R. 1970. Deutungsversuch der Entstehung der "Brisa", eines fohnartigen
488 Fallwindes der nordwestlichen Sierra Nevada de Santa Marta, Kolumbien. *Mitteilungen*
489 *des Instituto Colombo-Alemán de Investigaciones Científicas "Punta de Betin"* 4:83-
490 95.
- 491 Hodgson G, Kiene W, Mihaly J, Liebeler J, Shuman C, and Maun L. 2004. Reef check
492 instruction manual: a guide to reef check coral reef monitoring. Reef Check, Institute
493 of the Environment, University of California at Los Angeles, USA. p 86.
- 494 Hoyos N, Escobar J, Restrepo JC, Arango AM, and Ortiz JC. 2013. Impact of the 2010-2011 La
495 Niña phenomenon in Colombia, South America: The human toll of an extreme weather
496 event. *Applied Geography* 39:16-25.
- 497 Hubbard DK. 1996. Reefs as dynamic systems. In: Birkeland C, ed. *Life and death of coral*
498 *reefs*. New York: Chapman and Hall, 43-67.
- 499 Jantzen C, Schmidt GM, Wild C, Roder C, Khokiattiwong S, and Richter C. 2013. Benthic Reef
500 Primary Production in Response to Large Amplitude Internal Waves at the Similan
501 Islands (Andaman Sea, Thailand). *PLoS ONE* 8.
- 502 Jantzen C, Wild C, El-Zibdah M, Roa-Quiaoit HA, Haacke C, and Richter C. 2008.
503 Photosynthetic performance of giant clams, *Tridacna maxima* and *T-squamosa*, Red
504 Sea. *Marine Biology* 155:211-221.
- 505 Johnson JB, and Omland KS. 2004. Model selection in ecology and evolution. *Trends in*
506 *Ecology & Evolution* 19:101-108.
- 507 Kanwisher JW, and Wainwright SA. 1967. Oxygen balance in some reef corals. *Biol Bull*
508 133:378-390.
- 509 Kinsey DW. 1977. Seasonality and zonation in coral reef productivity and calcification. In:
510 Taylor DL, editor. Proceedings of Third International Coral Reef Symposium. Miami,
511 Florida: Rosenstiel School of Marine and Atmospheric Science. p 383-388.
- 512 Kinsey DW. 1985. Metabolism, calcification and carbon production: 1 systems level studies.
513 In: Gabrie C, and Salvat B, editors. Proceedings Of The Fifth International Coral Reef
514 Congress. Tahiti.
- 515 Kleypas JA, McManus JW, and Menez LAB. 1999. Environmental limits to coral reef
516 development: Where do we draw the line? *American Zoologist* 39:146-159.

- 517 Kruschke JK. 2011. *Doing Bayesian data analysis: a tutorial with R and BUGS*. Burlington, MA:
518 Academic Press.
- 519 Lirman D, and Biber P. 2000. Seasonal dynamics of macroalgal communities of the northern
520 Florida reef tract. *Botanica Marina* 43:305-314.
- 521 Littler MM. 1973. The productivity of Hawaiian fringing-reef crustose Corallinaceae and an
522 experimental evaluation of production methodology. *Limnol Oceanogr* 18:946-952.
- 523 Littler MM, and Doty MS. 1975. Ecological components structuring seaward edges of tropical
524 pacific reefs: Distribution, communities and productivity of *Porolithon*. *Journal of*
525 *Ecology* 63:117-129.
- 526 Mass T, Genin A, Shavit U, Grinstein M, and Tchernov D. 2010a. Flow enhances
527 photosynthesis in marine benthic autotrophs by increasing the efflux of oxygen from
528 the organism to the water. *Proceedings of the National Academy of Sciences of the*
529 *United States of America* 107:2527-2531.
- 530 Mass T, Kline DI, Roopin M, Veal CJ, Cohen S, Iluz D, and Levy O. 2010b. The spectral quality
531 of light is a key driver of photosynthesis and photoadaptation in *Stylophora pistillata*
532 colonies from different depths in the Red Sea. *Journal of Experimental Biology*
533 213:4084-4091.
- 534 McCormick MI. 1994. Comparison of field methods for measuring surface-topography and
535 their associations with a tropical reef fish assemblage. *Marine Ecology-Progress Series*
536 112:87-96.
- 537 Muscatine L. 1990. The role of symbiotic algae in carbon and energy flux in reef corals. In:
538 Dubinsky Z, ed. *Coral Reefs*. Amsterdam: Elsevier, 75-84.
- 539 Naumann MS, Jantzen C, Haas AF, Iglesias-Prieto R, and Wild C. 2013. Benthic Primary
540 Production Budget of a Caribbean Reef Lagoon (Puerto Morelos, Mexico). *PLoS ONE* 8.
- 541 Naumann MS, Niggli W, Laforsch C, Glaser C, and Wild C. 2009. Coral surface area
542 quantification-evaluation of established techniques by comparison with computer
543 tomography. *Coral Reefs* 28:109-117.
- 544 Odum HT, and Odum EP. 1955. Trophic structure and productivity of a windward coral reef
545 community on Eniwetok Atoll. *Ecological Monographs* 25:291-320.
- 546 Risk MJ. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bulletin*
547 152:1-6.
- 548 Rueda-Roa DT, and Muller-Karger FE. 2013. The southern Caribbean upwelling system: Sea
549 surface temperature, wind forcing and chlorophyll concentration patterns. *Deep-Sea*
550 *Research Part I-Oceanographic Research Papers* 78:102-114.
- 551 Salzwedel H, and Müller K. 1983. A summary of meteorological and hydrological data from
552 the Bay of Santa Marta, Colombian Caribbean. *Anales del Instituto de Investigaciones*
553 *Marinas de Punta de Betín* 13:67-83.
- 554 Sargent M, and Austin T. 1949. Organic productivity of an atoll. *Transactions of the American*
555 *Geophysical Union* 30:254-249.
- 556 Sheppard C, Davy SK, and Pilling GM. 2009. *The biology of coral reefs*. Oxford ; New York:
557 Oxford University Press.

- 558 Smith SV. 1981. The Houtman Abrolhos Islands: carbon metabolism of coral reefs at high-
559 latitude. *Limnology and Oceanography* 26:612-621.
- 560 Spiegelhalter DJ, Best NG, Carlin BP, and Van Der Linde A. 2002. Bayesian measures of model
561 complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical*
562 *Methodology)* 64:583-639.
- 563 Steneck RS. 1988. Herbivory on coral reefs: a synthesis. In: Choat JH, Barnes D, Borowitzka
564 MA, Coll JC, Davies PJ, Flood P, Hatcher BG, Hopley D, Hutchings PA, Kinsey D, Orme
565 GR, Pichon M, Sale PF, Sammarco P, Wallace CC, Wilkinson C, Wolanski E, and
566 Bellwood O, editors. 6th International Coral Reef Symposium. 6 ed. Australia. p 37-49.
- 567 Szmant AM. 1997. Nutrient effects on coral reefs: a hypothesis on the importance of
568 topographic and trophic complexity to reef nutrient dynamics. In: Lessios HA, and
569 Macintyre IG, editors. 8th International Coral Reef Symposium. Panama: Smithsonian
570 Tropical Research Institute, Panama. p 1527-1532.
- 571 Team RC. 2014. R: A Language and Environment for Statistical Computing. Vienna, Austria.
- 572 Valiela I. 1995. *Marine ecological processes*. New York: Springer.
- 573 Veron JEN. 1995. *Corals in space and time: biogeography and evolution of the Scleractinia*.
574 Ithaca: Comstock/Cornell.
- 575 Wanders JBW. 1976. The role of benthic algae in the shallow reef of Curaçao (Netherlands
576 Antilles). I: Primary productivity in the coral reef. *Aquatic Botany* 2:235-270.
- 577 Werding B, and Sánchez H. 1989. The coral formations and their distributional pattern along
578 a wave exposure gradient in the area of Santa Marta, Colombia. *Medio Ambiente*
579 10:61-68.
- 580 Wu EY, Barazanji KW, and Johnson RLJ. 1997. Source of error on A-aDO₂ calculated from
581 blood stored in plastic and glass syringes. *J Appl Physiol* 82:196-202.
- 582 Yeo I-K, and Johnson RA. 2000. A new family of power transformations to improve normality
583 or symmetry. *Biometrika* 87:954-959.

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).

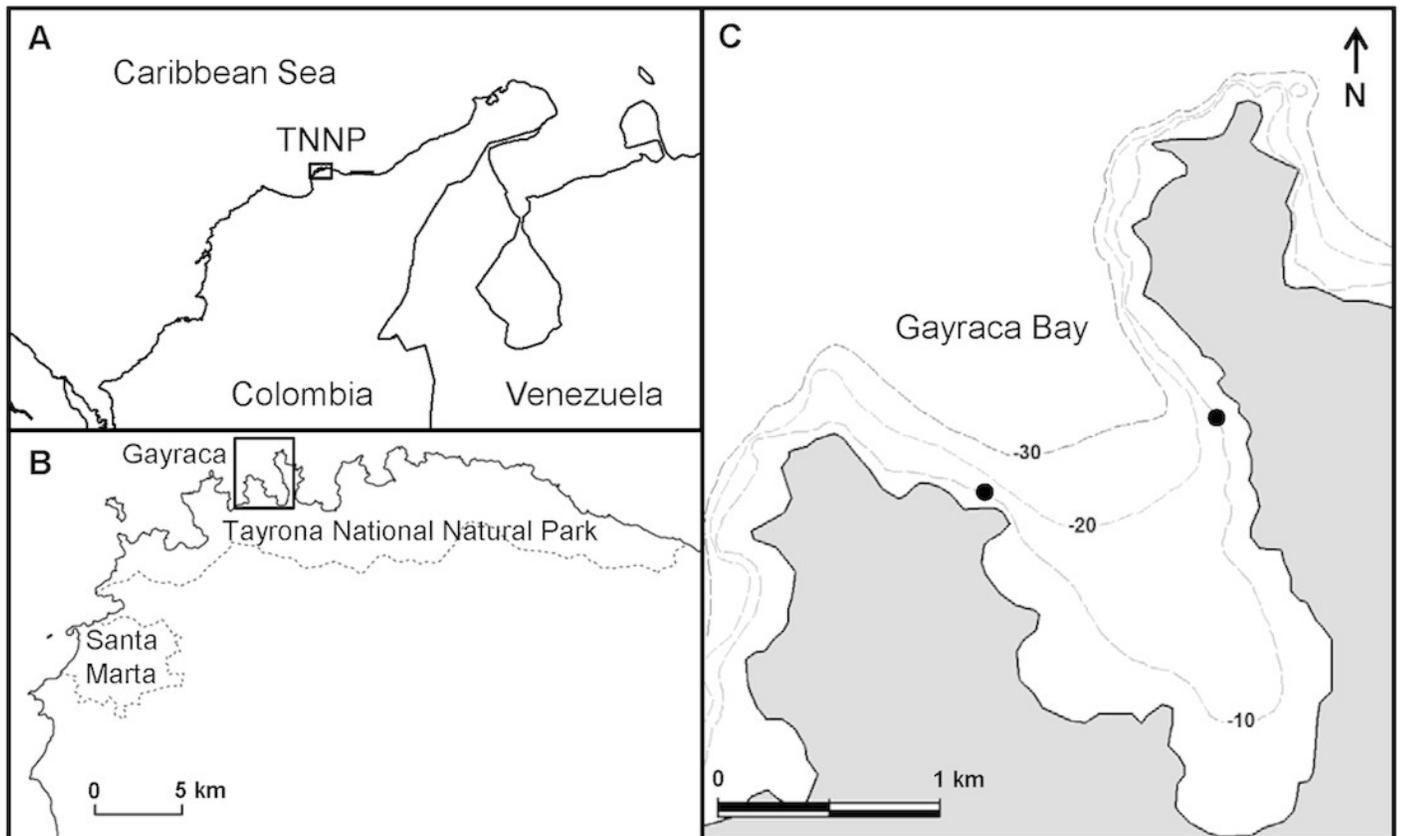


Figure 2

Benthic cover of dominant benthic groups

Jitter plot of grey dots indicates benthic coverage of functional groups quantified by line transects. Superimposed black points and error bars represent the mean \pm standard deviation. F-values refer to the results of two-way analyses of variance with Site and Season as main effects. If interactions between main effects were significant, pair-wise *post-hoc* tests were applied. Significance levels are * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Abbreviations: EXP = exposed, SHE = sheltered, NoUp = non-upwelling, Up = upwelling.

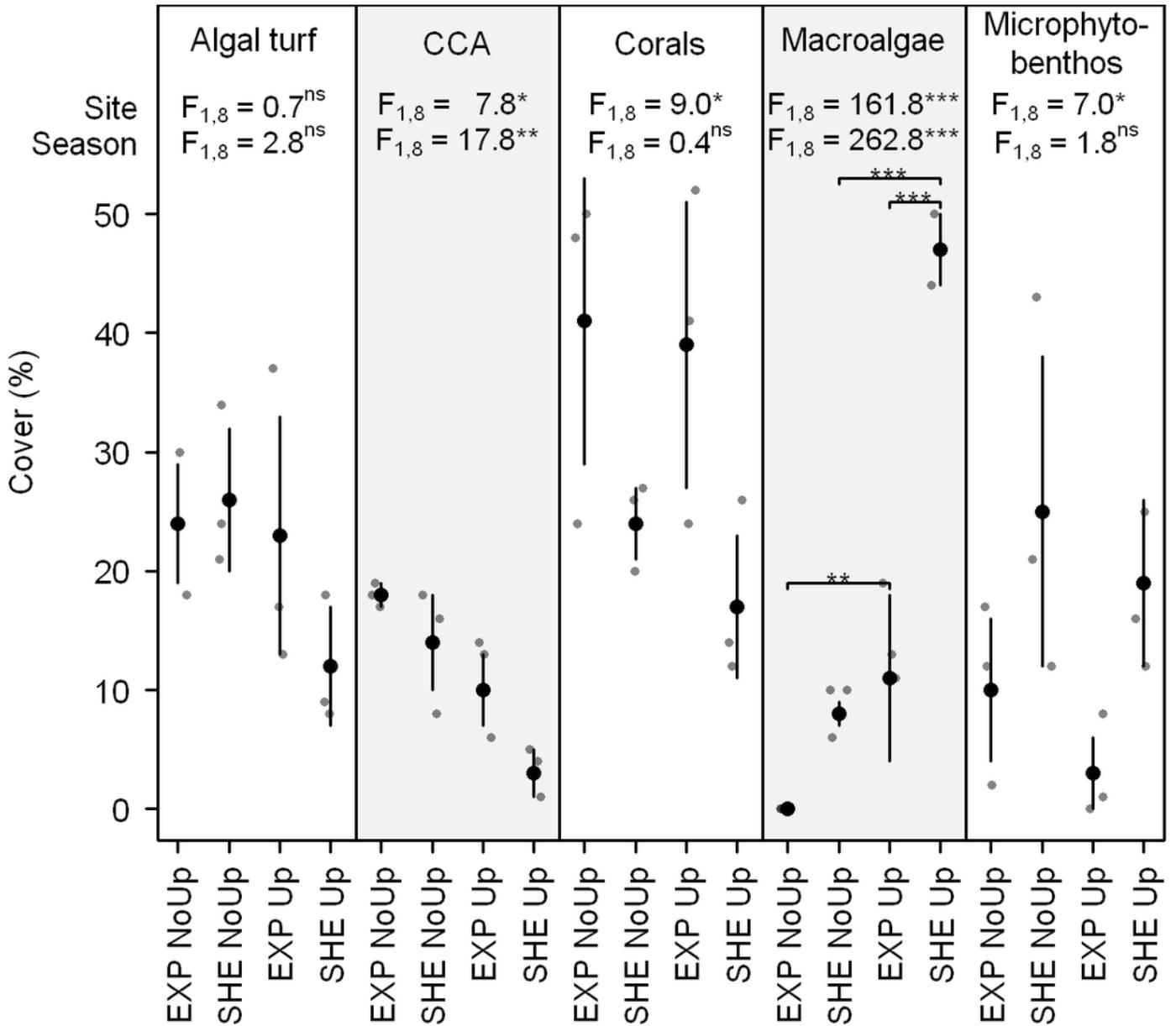


Figure 3

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. Significance levels are * $pMCMC < 0.05$, ** $pMCMC < 0.01$, *** $pMCMC < 0.001$. Abbreviations: EXP = exposed, SHE = sheltered, NoUp = non-upwelling, Up = upwelling.

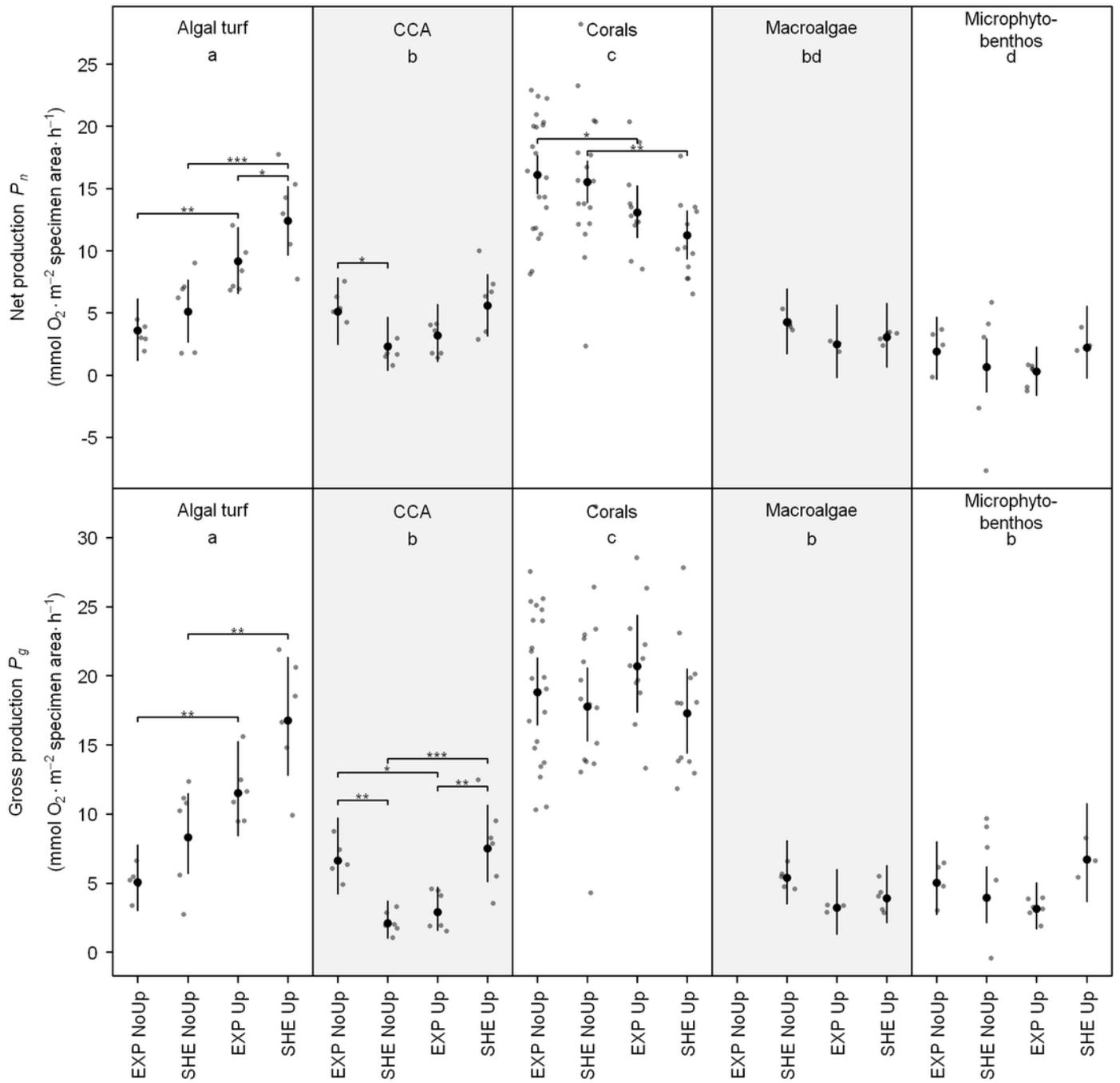


Figure 4

Contribution of functional groups to benthic net and gross production

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. Significance levels are * $pMCMC < 0.05$, ** $pMCMC < 0.01$, *** $pMCMC < 0.001$. Abbreviations: EXP = exposed, SHE = sheltered, NoUp = non-upwelling, Up = upwelling.

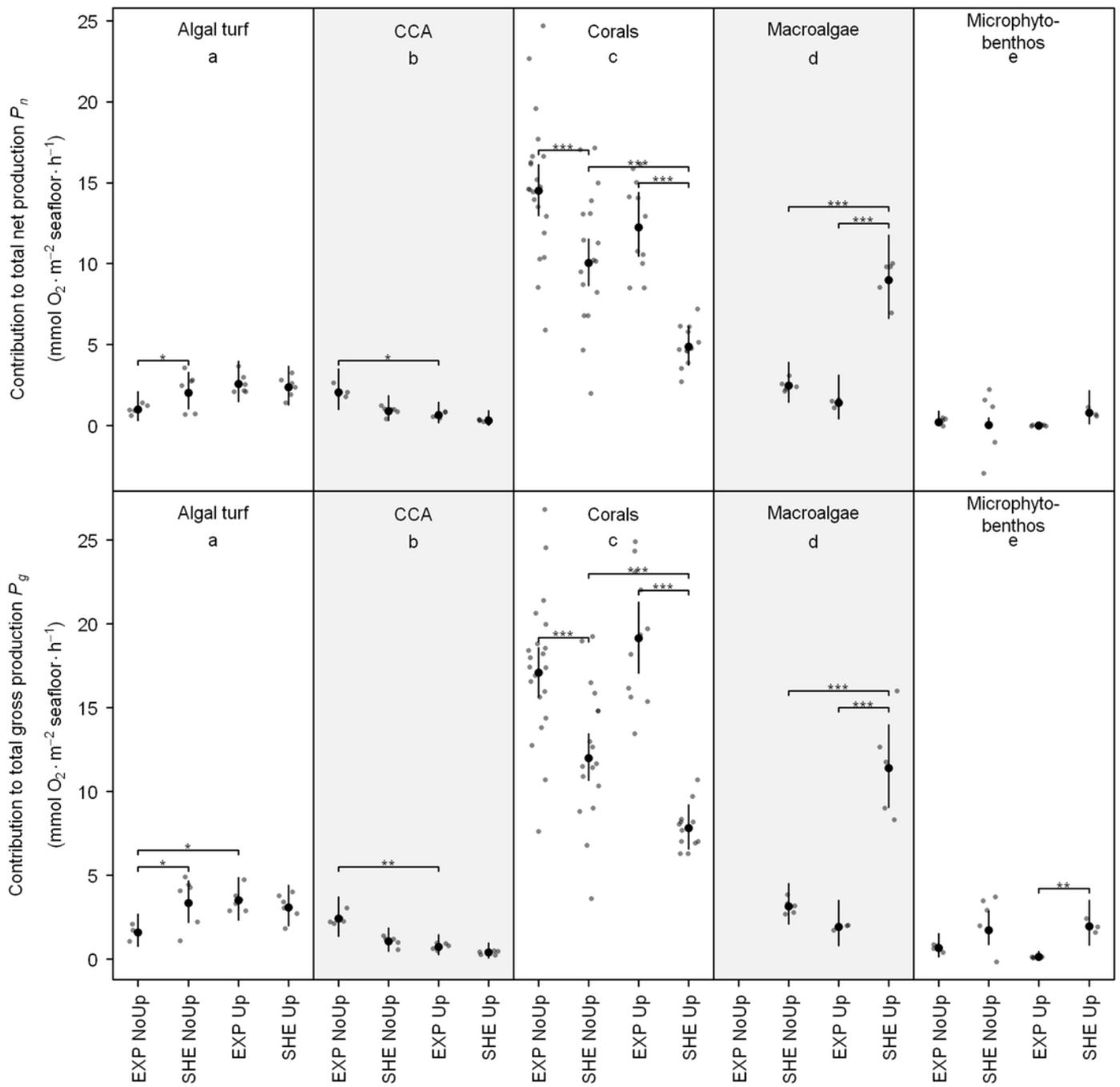


Figure 5

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.

Significance levels are * $p_{MCMC} < 0.05$, ** $p_{MCMC} < 0.01$, *** $p_{MCMC} < 0.001$.

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

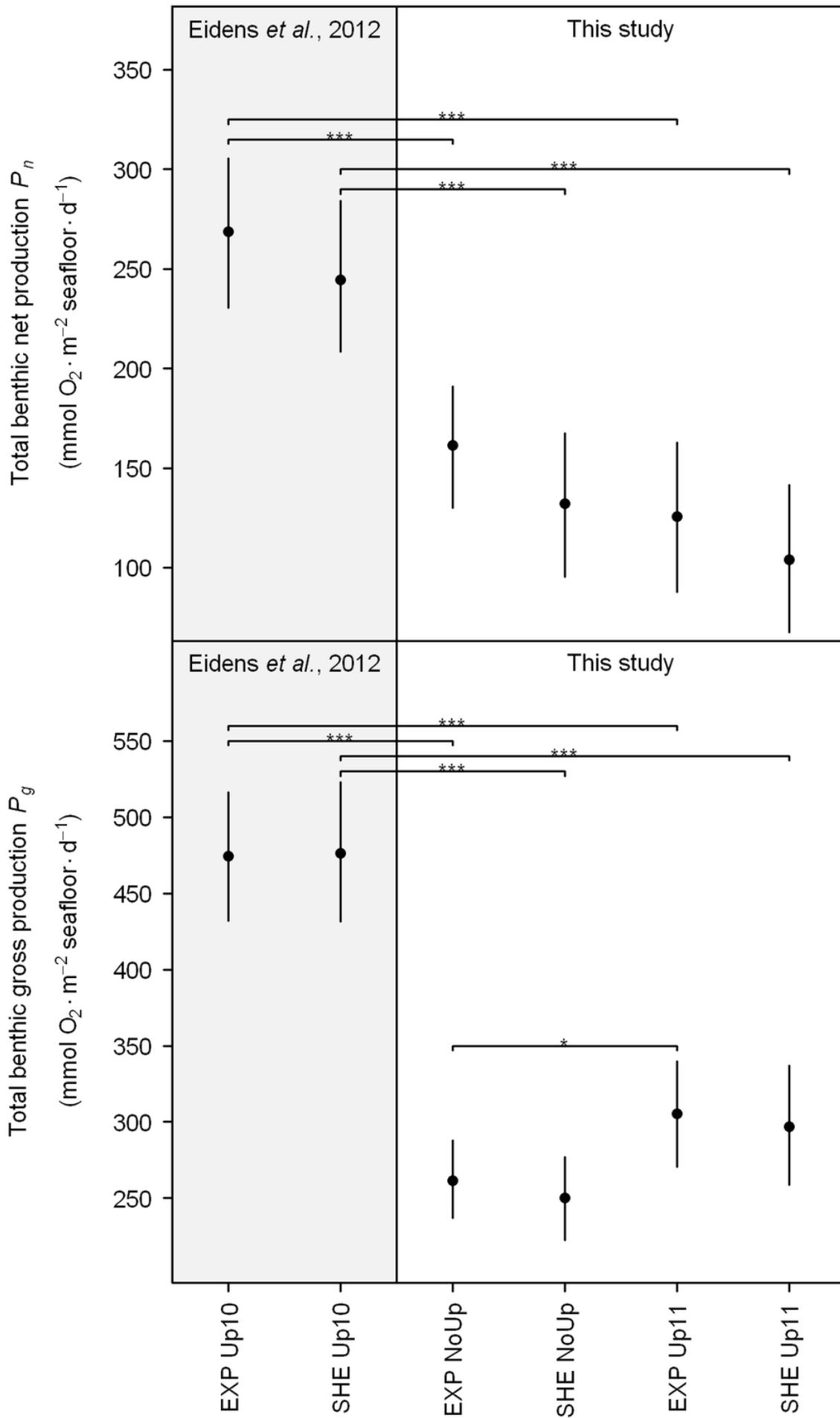


Table 1 (on next page)

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)

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

If necessary, original units were converted to O_2 estimates assuming a C: O_2 metabolic quotient equal to one according to Gattuso et al. (1996) and Carpenter & Williams (2007). Abbreviations: P_n = net O_2 production, P_g = gross O_2 production.

	Location	P_n (mmol O ₂ m ⁻² seafloor d ⁻¹)	P_g	Reference
Reef slope/fore reef 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)