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 \( \text{O}_2 \) 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 \( \text{O}_2 \) production, their contribution to benthic \( \text{O}_2 \) fluxes, and total daily benthic \( \text{O}_2 \) production. At the organism level, scleractinian corals showed highest \( P_n \) and \( P_g \) rates during non-upwelling (16 and 19 mmol \( \text{O}_2 \) • m\(^{-2}\) specimen area • h\(^{-1}\)), and corals and algal turfs dominated the primary production during upwelling (12 and 19 mmol \( \text{O}_2 \) • m\(^{-2}\) specimen area • 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 \( \text{O}_2 \) 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.
Benthic primary production in an upwelling-influenced coral reef, Colombian Caribbean

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Introduction

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

It was long assumed that coral reef productivity is relatively balanced as tropical coral reefs typically thrive under relatively stable abiotic conditions (Hubbard 1996; Kleypas et al. 1999; Sheppard et al. 2009), including light (Achituv & Dubinsky 1990; Darwin 1842; Falkowski et al. 1990), water temperature (Coles & Fadlallah 1991; Dana 1843; Veron 1995), salinity (Andrews & Pickard 1990; Coles & Jokiel 1992), and inorganic nutrient availability (D'Elia & Wiebe 1990; Szmant 1997). Nevertheless, coral reefs also occur in seasonal upwelling-affected regions such as the Arabian Sea off Oman (Glynn 1993), the Eastern Tropical Pacific off Panamá and Costa Rica (Cortés & Jiménez 2003; Glynn & Stewart 1973), and the Colombian Caribbean (Geyer 1969). Whereas several studies focused on the seasonality of benthic primary production in coral reefs at different latitudes (Adey & Steneck 1985; Falter et al. 2012; Kinsey 1985), variability in primary production of seasonal upwelling-affected coral reefs remains largely unknown.

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

The results of a preliminary study conducted by Eidens et al. (2012) indicated that benthic primary production in TNNP differed between the upwelling in 2010/2011 and the consecutive non-upwelling season, suggesting a generally positive effect of upwelling conditions on major benthic autotrophs in the area. However, after unusually strong El Niño-Southern Oscillation (ENSO) events in 2010, the area experienced a moderate coral bleaching before the upwelling in 2010/2011 (Bayraktarov et al. 2013; Hoyos et al. 2013), and productivity measurements during upwelling in 2010/2011 may not be representative. To test for patterns in benthic primary production during a typical seasonal cycle, we here quantified benthic primary production before and at the end of the upwelling event in 2011/2012 (hereafter referred to as non-upwelling and upwelling, respectively). To allow for comparisons of productivity between investigated groups, we further estimated surface area-specific productivity rates as suggested by Naumann et al. (2013) and analyzed the data using generalized linear models.

Therefore, the goals of the study were to (1) identify dominant functional groups of benthic primary producers and their relative benthic cover at a current/wave-exposed (EXP) and sheltered (SHE) site in one exemplary bay of TNNP, (2) quantify O₂ fluxes of all dominant benthic primary producers and apply 3D surface area estimations, and hence (3) estimate the specific contribution of each group to total benthic O₂ fluxes.
Materials and Methods

Study site and sampling seasons

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

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

**Sampling of organisms**

Specimens of scleractinian corals, macroalgae, algal turfs, and CCA as well as sand samples, from 10 ± 1 m water depth were used for quantification of O\(_2\) fluxes (see Table S1 for number of replicates). All samples were brought to the water surface in Ziploc bags and transported directly to the field lab. Scleractinian corals of the genera *Montastraea* (including the species *M. faveolata*, *M. franksi* and *M. annularis*, currently belonging to the genus *Orbicella*; Budd et al. 2012) and *Diploria* (including *D. strigosa*, currently belonging to the genus *Pseudodiploria* Budd et al. 2012) accounted for more than 80 % of the total coral cover at the study sites and were
therefore used as representative corals in our study. Coral specimens were obtained from the reef using hammer and chisel, fragmented with a multifunction rotary tool (Dremel Corp., 8200-2/45; mean fragment surface area: 13.16 ± 7.96 cm²), and fixed on ceramic tiles using epoxy glue (Giesemann GmbH, Aquascape). After fragmentation, specimens were returned to their natural habitat and left to heal for one week prior to the incubation experiments. Algae of the genus Dictyota (mainly D. bartayresiana) amounted to nearly 100% of macroalgal cover. Therefore small bushes of Dictyota spp. (surface area 1.86 ± 0.88 cm²) were used as representatives for macroalgae. Macroalgae were transferred to a storage tank (volume: 500 L in which water was exchanged manually 3-5 times per day and water temperature was within the ranges of incubation experiments; see Table 2) one day before incubation experiments and left to heal. All other functional groups were incubated immediately after sampling. Rubble overgrown by algal turfs and CCA served as samples for the respective functional group (surface area covered by the organisms: 15.63 ± 10.80 cm² and 7.48 ± 3.60 cm², respectively). For sand samples, custom-made mini corers with defined surface area (1.20 cm²) and sediment core depth (1.0 cm) were used. All necessary permits (DGI-SCI-BEM-00488) were obtained by Instituto de Investigaciones Marinas y Costeras (INVEMAR) in Santa Marta, Colombia which complied with all relevant regulations.

Surface area quantification

Digital photographs of coral specimens were used to quantify planar projected surface areas of samples by image-processing software (ImageJ, V. 1.46r, National Institute of Health). The 3D surface area of the samples was estimated via multiplication of the planar projected surface areas by the genera-specific 2D to 3D surface area conversion factors derived from computer tomography measurements of Diploria and Montastraea skeletons (2.28 ± 0.16 and 1.34 ± 0.56, respectively), as described by Naumann et al. (2009). Planar leaf area of spread out macroalgal specimens was likewise quantified by digital image analysis and multiplied by the factor 2 to
obtain 3D surface area of the samples. Image analysis of in situ photographs and whole spread out macroalgal thalli were used to obtain covered substrate areas (2D surface) as well as 3D surface areas in order to calculate the 2D to 3D conversion factor for macroalgae (4.29 ± 0.82). This conversion factor was used to correct for the overlap of macroalgal tissue. The 2D surface area of algal turfs samples was determined by image analysis of digital photographs. For CCA, the simple geometry method described by Naumann et al. (2009) was used to estimate the surface area of overgrown pieces of rubble. The obtained surface areas were related to the planar projected surface area of the samples to generate 2D to 3D conversion factors for CCA (2.10 ± 0.89). Specimen surface area for sand samples was defined by the size of the utilized mini corer (1.20 cm²).

Incubation Experiments
Prior to incubation experiments, water temperature (°C) and light intensity (lx) were monitored at the sampling sites with intervals of 2 min using light and temperature loggers (Onset HOBO Pendant UA-002-64) in order to adjust light and temperature during incubations to in situ conditions. The availability of light during light incubations was adjusted to the in situ light regimes using net cloth (Table 2). Temperature and light intensity was continuously monitored during incubations as described above. Light intensities were converted to photosynthetically active radiation (PAR, μmol photons · m² · s⁻¹, 400 to 700 nm) using the approximation of Valiela (1995). Light availability was generally higher during the upwelling event (t-test, p < 0.001; Table 2), whereas water temperatures were higher during non-upwelling (t-test, p < 0.001; Table 2). Quantification of photosynthetic activity for macroalgae, CCA, and microphytobenthos were performed in air-tight glass containers with volumes of 60 mL, whereas for corals and algal turfs, containers with volumes of 600 mL were utilized. For all incubations, we used freshly collected seawater from Gayraca Bay. To ensure independence between the samples, each specimen was
incubated in a distinct container. The containers were placed in cooling boxes filled with seawater to maintain constant in situ water temperature (Table 2). For dark incubations during daytime, the above mentioned methodology was used, but cooling boxes were closed with opaque lids to prevent light penetration. Comparability among measurements was assured by carrying out all light incubations on cloudless days between 10 am and 2 pm. For each group of primary producers, one light and one dark incubation were performed within each study period. Incubation containers containing only seawater served as blank controls to quantify photosynthetic activity and respiration of microbes in the water column. Physiological damage of the investigated specimens by hypoxic or hyperoxic conditions were prevented by keeping the incubation times as short as possible (light incubations: 30 to 60 min and dark incubations: 120 min as suggested by Jantzen et al., 2008; Mass et al., 2010b; Jantzen et al., 2013). Dissolved O₂ concentrations in the incubation water within the glass containers were quantified before incubations and after removing the specimens at the end of each incubation using an optode (Hach Lange, HQ 40). Before O₂ measurements, the incubation medium was gently stirred with the optode sensor allowing a homogenization of the water column. Experiments were conducted in closed, non-mixed incubation chambers in order to avoid additional contamination sources and to provide the most conservative estimates of O₂ production rates of benthic primary producers as suggested by Haas et al. (2011) and Naumann et al. (2013). This also ensured higher measurement accuracy, as water movement during incubations may affect gas transfer velocities across the surface boundary of the incubation chambers (Wu et al. 1997) and allowed us to compare our results with previous incubation studies (e.g. Haas et al., 2011; Jantzen et al., 2013; Naumann et al., 2013). Nevertheless, since it is well known that water flow enhances O₂ fluxes and thereby photosynthesis (Mass et al. 2010a), the results of the field incubations should be regarded as conservative estimates of in situ O₂ fluxes and interpreted accordingly.
Data analyses and statistics

To quantify net O\textsubscript{2} production ($P_n$) and respiration of functional groups, O\textsubscript{2} concentration before incubations was subtracted from concentration after incubations and blank control values were subtracted from the measured O\textsubscript{2} fluxes. Individual gross O\textsubscript{2} production ($P_g$) of investigated functional groups was calculated by adding values of $P_n$ and respiration; individual O\textsubscript{2} fluxes were expressed as mmol O\textsubscript{2} · m\textsuperscript{-2} specimen surface area · h\textsuperscript{-1}.

The contribution of each functional group to total reef production (given as: mmol O\textsubscript{2} · m\textsuperscript{-2} seafloor area · h\textsuperscript{-1}) was estimated as follows:

$$c_i = p_i s_i b_i r_i$$

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

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

We tested the influence of benthic groups, season, wave exposure, and their interactions on O\textsubscript{2} productivity by generalized linear models (GLMs) for individual $P_n$, and $P_g$ of the investigated groups, their contribution to reef metabolism as well as total benthic productivity. We used Markov-chain Monte Carlo (MCMC) estimations of GLM regression coefficients. In traditional Frequentist statistics, the parameters of interest (i.e. the O\textsubscript{2} productivity describing regression coefficients) are estimated just once (e.g. using Maximum-Likelihood) and their significance is inferred indirectly based on a test-statistic. In contrast, Bayesian methods reallocate the
coefficients across a set of possible candidates during each MCMC generation (Kruschke 2011). If the bulk of these values, that is the 95% highest posterior density (HPD), do not include zero, one can directly conclude that the regression coefficient is credible different than zero and an effect on O₂ productivity exists. Moreover, we here performed pair-wise comparisons between benthic groups at different sites and seasons, traditionally being performed by post-hoc testing with P-value correction for preventing false positive results. A Bayesian GLM does not suffer this drawback because difference of groups can be directly estimated by the posterior (Kruschke 2011). Again, there is credible evidence in non-equal group-means, if the posterior-based 95% HPD interval of the group differences does not include zero. Model performance for all 19 possible combinations of the three independent variables and their interactions was assessed by the deviance information criterion (DIC), a Bayesian measure of model fit that penalizes complexity (Spiegelhalter et al. 2002). In this information theory based model selection, often there is not a single best model describing the data. Therefore, averaging of regression coefficients for all models within ΔDIC < 2 of the best one (Johnson & Omland 2004) was performed according to DIC weights (i.e. support for the respective regression model). Here, Bayesian GLMs using the MCMCglmm package (Hadfield 2010) for the R 3.0.3 environment for statistical computing (R Core Team 2014) with a Gaussian error distribution were applied. Prior to the analyses, the mean-variance relationship of measured O₂ flux was stabilized by power transformation (Yeo & Johnson 2000). Visual inspection of preliminary GLMs with default weakly informative priors showed high autocorrelation in their posterior distribution. Thus to infer the posterior distribution of the final analyses, we ignored the first 50000 estimates as burn-in and sampled every 5th out of 650000 MCMC generations. All values are represented as mean ± standard deviation (SD) if not noted otherwise.
Results

Benthic community composition

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

O₂ fluxes of organisms

More complex Bayesian GLMs, including interactions among the three independent variables season, benthic group, and site, described individual O₂ fluxes better than simple models (For details see Table S2). Of all investigated functional groups, scleractinian corals had highest individual net ($P_n$) and gross production ($P_g$), followed by algal turfs, macroalgae, CCA, and microphytobenthos (Fig. 3; see also Table S3 for detailed results of all pair-wise comparisons). Regarding spatial differences in individual productivity, significant differences were detected for algal turfs and CCA. During upwelling, $P_n$ of algal turfs and $P_g$ of CCA was higher at SHE than EXP. On the contrary, during non-upwelling, $P_n$ and $P_g$ of CCA was higher at EXP (Fig. 3). Temporal differences in O₂ production were detected for corals, algal turfs, and CCA (Fig. 3). Whereas $P_n$ of scleractinian corals on both sites and $P_g$ of CCA at EXP were higher during non-upwelling, $P_g$ of CCA at SHE as well as $P_n$ and $P_g$ of algal turfs at both sites showed an opposite pattern with higher productivity rates during upwelling (Fig. 3).
Contribution of organism-induced O\(_2\) fluxes to total reef O\(_2\) production

As in the case of individual O\(_2\) fluxes, contribution and total reef production were better explained by GLMs of higher complexity (Table S2). Contribution of functional groups to benthic productivity exhibited similar pattern than individual productivity with corals contributing generally most to total reef \(P_n\) and \(P_g\), but macroalgae contributed most to benthic \(P_n\) and \(P_g\) at SHE at the end of upwelling (Fig. 4; see also Table S3 for detailed results of all pair-wise comparisons).

Significant spatial differences in contribution to total benthic \(P_n\) within functional groups were detected for corals, algal turf, and macroalgae, and spatial differences for \(P_g\) were present in all investigated groups except CCA (Fig. 4). At EXP, Corals contributed more to total \(P_n\) and \(P_g\) during non-upwelling and upwelling (Fig. 4). At SHE, contributions of macroalgae (\(P_n\) and \(P_g\)) and microphytobenthos (\(P_g\)) were higher only during upwelling, and algal turfs contributed more to \(P_g\) at SHE during non-upwelling (Fig. 4).

Temporal differences in contribution to total benthic productivity within the investigated groups were present for corals, macroalgae, CCA (for \(P_n\) and \(P_g\)), and for algal turfs (only \(P_g\)) (Fig. 5).

During non-upwelling, Corals contributed more to the total productivity at SHE and CCA at EXP, whereas during upwelling, macroalgae contributed more to the total productivity at SHE and algal turf at EXP (Fig. 4).

Regarding the total daily benthic O\(_2\) fluxes (Figs. 4), no spatial differences between EXP and SHE were detected, neither during non-upwelling nor during upwelling (see also Table S3 for detailed results of all pair-wise comparisons). During the study, significant temporal differences were only present for \(P_g\) at the exposed site with higher O\(_2\) fluxes during the upwelling in 2011/2012 compared to non-upwelling (Fig. 5). Comparing total benthic productivity during the upwelling event in 2010/2011 with the subsequent non-upwelling and upwelling, \(P_n\) and \(P_g\) were significantly higher during the upwelling 2010/2011 for all comparisons (Fig. 5).
Discussion

O₂ fluxes of organisms

Individual mean $P_n$ and $P_g$ were generally highest for corals at both sites during the study periods ($P_n$: 11.2–16.1 and $P_g$: 17.4–20.8 mmol O₂ · m⁻² · h⁻¹). These high productivity rates of corals compared to other investigated primary producers (see Fig. 3) may be attributed to the mutualistic relationship between zooxanthellae and coral host leading to enhanced photosynthetic efficiency under high CO₂ and nutrient availability (D'Elia & Wiebe 1990; Muscatine 1990).

Estimated daily $P_g$ per m² seafloor for the investigated coral genera, (441-610 mmol O₂ · m⁻² · d⁻¹), is within the range of other Caribbean corals (67 to 850 mmol O₂ · m⁻² · seafloor · d⁻¹, Fig. 2, Kanwisher & Wainwright, 1967), and O₂ fluxes of all investigated organism groups are comparable to values reported in the literature (Fig. 2).

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

Temporal differences in individual O₂ production within the investigated organism groups generally showed two contrary patterns: whereas scleractinian corals on both sites and CCA at EXP produced less O₂ during upwelling, algal turfs and CCA at SHE produced more O₂. The
decreased productivity rates of corals and CCA at EXP during upwelling indicate that low water temperature has an adverse effect on the productivity of these groups. This argument is supported by studies showing that low water temperatures lead to a decrease in photosynthetic performance of primary producers in coral reefs (Hatcher 1990; Kinsey 1985). In contrast, the two-fold higher photosynthetic performance of algal turfs during upwelling may be due to higher nutrient concentrations together with higher water currents during this season (Bayraktarov et al. 2014a; Bayraktarov et al. 2014b), facilitating gas exchange and nutrient uptake. Our findings are supported by Carpenter & Williams (2007), showing that photosynthesis of algal turfs in coral reefs is mainly limited by nutrient uptake, which in turn depends on nutrient availability and water current speed. Whereas productivity of CCA at EXP seems to be temperature-limited, our findings indicate that their productivity at SHE is limited by nutrient availability as previously suggested for benthic algal communities in water current-sheltered coral reef locations (Carpenter & Williams 2007; Hatcher 1990).

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

Our results indicate that the spatial differences in contribution to total benthic O₂ production for scleractinian corals, macroalgae, CCA, and microphytobenthos are directly linked to spatial differences in their benthic coverage. For instance, the major contribution of corals (Fig. 4) can be explained by their comparably high benthic coverage (ranging from 24 to 39 %; Fig. 2) and highest quantified individual O₂ production rates among all investigated groups (Fig. 3). This finding is supported by the estimates of Wanders (1976), showing that corals accounted for about two-thirds of the total benthic primary production in a Southern Caribbean fringing reef.
Although individual macroalgal production rates were rather low as compared to coral productivity (Fig. 3), the extremely high cover of macroalgae at SHE during upwelling (47 ± 3%) resulted in macroalgae being the main contributors to total benthic production. Macroalgal cover (incl. the dominant genus *Dictyota*) has previously been found to be particularly high during upwelling (*Bula-Meyer* 1990; *Cronin* & *Hay* 1996; *Diaz-Pulido* & *Garzón-Ferreira* 2002), probably due to elevated nutrient concentrations and low water temperatures (*Bayraktarov* et al. 2014b).

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

Corals, macroalgae, algal turfs, and CCA also exhibited distinct temporal differences in contribution to total benthic productivity. At SHE, corals contributed more to the benthic O$_2$ production during non-upwelling and macroalgae and algal turfs during upwelling, whereas contribution of CCA at EXP was higher during non-upwelling. These differences can be explained with seasonal growth patterns, temperature-dependent changes in individual O$_2$ productivity and temporal shifts in abundances (Figs. 2 and 3). Opposite abundance patterns of CCA and macroalgae are, for example, in agreement with previous studies of showing that macroalgae can shade CCA, usually leading to negative correlated abundances of these groups (*Belliveau* & *Paul* 2002; *Lirman* & *Biber* 2000).
The estimated total daily benthic $O_2$ production at both sites during non-upwelling and upwelling (Fig. 5) are, although comparable, on average slightly lower than the values previously reported for other fore reefs communities (Table 3). These differences might be due to a methodological bias. Whereas previous studies utilized flow respirometry techniques, the current study used incubation methodology, which accounts for production values in the target groups only.

Despite the high spatial and temporal differences in benthic coverage and group-specific $O_2$ fluxes of investigated benthic primary producers as well as their contribution to total benthic productivity, no spatial differences in total benthic $O_2$ fluxes were detected between EXP and SHE. These results were consistent during both non-upwelling and upwelling (Fig. 5). Our findings are supported by Hatcher (1990), showing that the relative coverage of benthic photoautotrophs in a reef community may have little effect on its areal production rate. In TNNP, seasonal differences were only present for $P_g$ at EXP with higher rates during upwelling compared to non-upwelling. These differences are mainly related to individual productivity of algal turfs, being generally two-fold higher during upwelling compared to non-upwelling (Fig. 3), and to the absence of macroalgae at EXP during non-upwelling (Fig. 2). This is in agreement with studies by Kinsey (1985) and Hatcher (1990), reporting that algae, as one of the most seasonal component in coral reefs, account for seasonal shifts in benthic reef productivity.

The lack of seasonality of $P_n$ and $P_g$ regarding communities at SHE as well as $P_s$ at EXP stands in contrast to earlier studies (Eidens et al. 2012; Kinsey 1977; Kinsey 1985; Smith 1981), which found an approximately two-fold difference in benthic primary production between seasons. This lack of seasonality in $P_s$ and partly in $P_g$ in TNNP might be related to seasonal changes of abiotic factors that compensate each other (Table 1). The observed similarity in productivity rates during different seasons suggest that coral reefs in TNNP can cope with pronounced seasonal variations.
in light availability, water temperature, and nutrient availability. Nevertheless, total \( P_n \) and \( P_g \) during the upwelling in 2010/2011 (\( P_n: 244–272 \) and \( P_g: 476–483 \) mmol \( \text{O}_2 \) \( \cdot \text{m}^{-2} \) seafloor \( \cdot \text{d}^{-1} \)) were not only higher compared to non-upwelling (Eidens et al. 2012) but also higher than during the subsequent upwelling in 2011/2012 (Fig. 5). These findings suggest that interannual variations affect the productivity of TNNP coral reefs. Dramatic ENSO-related water temperature increases and high precipitation in the study area (Bayraktarov et al. 2013; Hoyos et al. 2013) led to coral bleaching at the end of 2010 (Bayraktarov et al. 2013). Surprisingly, bleached corals in the bay recovered quickly in the course of the following upwelling event (Bayraktarov et al. 2013) and exhibited similar \( \text{O}_2 \) production rates during all study periods (Eidens et al. 2012), indicating a high resilience of TNNP corals. Moreover, macroalgae and algal turf seemed to benefit from the environmental conditions during the upwelling following the ENSO-related disturbance events, resulting in higher group-specific productivity during the upwelling in 2010/2011 compared to subsequent study periods (Eidens et al. 2012). The elevated production rates of macroalgae and algal turfs together with the quick recovery of corals from bleaching likely accounted for a higher benthic productivity during the upwelling in 2011/2011 compared to non-upwelling (Eidens et al. 2012) and the upwelling in 2011/2012 (Fig. 5). These findings indicate that extreme ENSO-related disturbances do not have long-lasting effects on the functioning of local benthic communities in TNNP.

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

Achituv Y, and Dubinsky Z. 1990. Evolution and zoogeography of coral reefs. In: Dubinsky Z, ed. Coral Reefs Ecosystems of the World. Amsterdam: Elsevier, 1-9.

Adey W, and Steneck R. 1985. Highly productive eastern Caribbean reefs: synergistic effects of biological, chemical, physical, and geological factors. In: Reaka M, editor. The ecology of deep and shallow coral reefs. 2 ed. Rockville. p 163-187.

Andrade CA, and Barton ED. 2005. The Guajira upwelling system. Continental Shelf Research 25:1003-1022.

Andrews JC, and Pickard GL. 1990. The physical oceanography of coral-reef systems. In: Dubinsky Z, ed. Coral Reefs. Amsterdam Elsevier, 11-48.

Bayraktarov E, Bastidas-Salamanca M, and Wild C. 2014a. The physical environment in coral reefs of the Tayrona National Natural Park (Colombian Caribbean) in response to seasonal upwelling. Boletín de Investigaciones Marinas y Costeras - Invemar 43:137-157.

Bayraktarov E, Pizarro V, Eidsens C, Wilke T, and Wild C. 2013. Bleaching susceptibility and recovery of Colombian Caribbean corals in response to water current exposure and seasonal upwelling. PLoS ONE 8.

Bayraktarov E, Pizarro V, and Wild C. 2014b. Spatial and temporal variability of water quality in the coral reefs of Tayrona National Natural Park, Colombian Caribbean. Environmental Monitoring and Assessment:1-19.

Belliveau SA, and Paul VJ. 2002. Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. Marine Ecology-Progress Series 232:105-114.

Budd AF, Fukami H, Smith ND, and Knowlton N. 2012. Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). Zoological Journal of the Linnean Society 166:465-529.

Bula-Meyer G. 1990. Altas temperaturas estacionales del agua como condición disturbadora de las macroalgas del Parque Nacional Natural Tairona, Caribe colombiano: una hipótesis. An Inst Invest Mar Punta de Betín 19-20:9-21.

Carpenter RC, and Williams SL. 2007. Mass transfer limitation of photosynthesis of coral reef algal turfs. Marine Biology 151:435-450.

Chapin FS, Matson PA, Vitousek PM, Chapin MC, and SpringerLink (Online service). 2011. Principles of terrestrial ecosystem ecology. 2nd ed. New York: Springer,. p 1 online resource (xv, 529 p.) ill. (some col.).

Chisholm JR. 2003. Primary productivity of reef-building crustose coralline algae. Limnology and Oceanography 48:1376-1387.

Coles DW, and Jokiel P. 1992. Effects of salinity on coral reefs. In: Connell DW, and Hawker DW, eds. Pollution in tropical aquatic systems. Boca Raton: CRC Press, 147-166.
Coles S, and Fadlallah Y. 1991. Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species-specific lower temperature limits. *Coral Reefs* 9:231-237.

Copertino MS, Cheshire A, and Kildea T. 2009. Photophysiology of a turf algal community: integrated responses to ambient light and standing biomass. *Journal of Phycology* 45:324-336.

Cortés C, and Jiménez C. 2003. Past, present and future of the coral reefs of the Caribbean coast of Costa Rica. In: Cortés J, ed. *Latin American coral reefs*. 1st ed. Amsterdam Boston: Elsevier, 223-239.

Cronin G, and Hay ME. 1996. Effects of light and nutrient availability on the growth, secondary chemistry, and resistance to herbivory of two brown seaweeds. *Oikos* 77:93-106.

D'Elia CF, and Wiebe WJ. 1990. Biogeochemical nutrient cycles in coral-reef ecosystems. In: Dubinsky Z, ed. *Coral Reefs*. Amsterdam: Elsevier, 49-74.

Dana FD. 1843. On the temperature limiting the distribution of corals. *American Journal of Science* 45:130-131.

Darwin C. 1842. *The structure and distribution of coral reefs*: Smith Elder and Co.

Diaz-Pulido G, and Garzón-Ferreira J. 2002. Seasonality in algal assemblages on upwelling-influenced coral reefs in the Colombian Caribbean. *Botanica Marina* 45:284-292.

Eidens C, Bayraktarog E, Pizarro V, Wilke T, and Wild C. 2012. Seasonal upwelling stimulates primary production of Colombian Caribbean coral reefs. In: Yellowlees D, and Hughes TP, editors. 12th International Coral Reef Symposium. Cairns, Australia.

Falkowski PG, Jokiel PL, and Kinzie III RA. 1990. Irradiance and corals. In: Dubinsky Z, ed. *Coral Reefs*. Amsterdam: Elsevier, 89-107.

Falter JL, Lowe RJ, Atkinson MJ, and Cuet P. 2012. Seasonal coupling and de-coupling of net calcification rates from coral reef metabolism and carbonate chemistry at Ningaloo Reef, Western Australia. *Journal of Geophysical Research-Oceans* 117.

Ferrari R, Gonzalez-Rivero M, Ortiz JC, and Mumby PJ. 2012. Interaction of herbivory and seasonality on the dynamics of Caribbean macroalgae. *Coral Reefs* 31:683-692.

Garzón-Ferreira J. 1998. Bahía Chengue, Parque Natural Tayrona, Colombia. In: Kjerfve B, ed. *CARICOMP-Caribbean coral reef, seagrass and mangrove sites Coastal Region and Small Islands Papers 3*. Paris: UNESCO, 115-125.

Garzón-Ferreira J, and Cano M. 1991. Tipos, distribución, extensión y estado de conservación de los ecosistemas marinos costeros del Parque Nacional Tayrona. Final Report. Santa Marta, Colombia. p 82.

Gattuso J-P, Frankignoulle M, and Wollast R. 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annual Review of Ecology and Systematics* 29:405-435.

Geyer O. 1969. Vorläufige Liste der scleractinen Korallen der Bahía de Concha bei Santa Marta, Kolumbien. *Mitt Inst Colombo-Aleman Invest Cient* 3:25-28.

Glynn PW. 1993. Monsoonal upwelling and episodic *Acanthaster* predation as possible controls of coral reef distribution and community structure in Oman, Indian Ocean. *Atoll Research Bulletin* 379.
Glynn PW, and Stewart RH. 1973. Distribution of Coral Reefs in Pearl Islands (Gulf of Panama) in Relation to Thermal Conditions. *Limnology and Oceanography* 18:367-379.

Haas AF, Nelson CE, Kelly LW, Carlson CA, Rohwer F, Leichter JJ, Wyatt A, and Smith JE. 2011. Effects of coral reef benthic primary producers on dissolved organic carbon and microbial activity. *PLoS ONE* 6.

Hadfield JD. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software* 33:1-22.

Hatcher BG. 1988. Coral reef primary productivity: A beggar's banquet. *TREE* 3:106-111.

Hatcher BG. 1990. Coral reef primary productivity: A hierarchy of pattern and process. *TREE* 5:149-155.

Herrmann R. 1970. Deutungsversuch der Entstehung der "Brisa", eines fohnartigen Fallwindes der nordwestlichen Sierra Nevada de Santa Marta, Kolumbien. *Mitteilungen des Instituto Colombo-Alemán de Investigaciones Científicas "Punta de Betín"* 4:83-95.

Hodgson G, Kiene W, Mihaly J, Liebeler J, Shuman C, and Maun L. 2004. Reef check instruction manual: a guide to reef check coral reef monitoring. Reef Check, Institute of the Environment, University of California at Los Angeles, USA. p 86.

Hoyos N, Escobar J, Restrepo JC, Arango AM, and Ortiz JC. 2013. Impact of the 2010–2011 La Niña phenomenon in Colombia, South America: The human toll of an extreme weather event. *Applied Geography* 39:16-25.

Hubbard DK. 1996. Reefs as dynamic systems. In: Birkeland C, ed. *Life and death of coral reefs*. New York: Chapman and Hall, 43-67.

Jantzen C, Schmidt GM, Wild C, Roder C, Khokhlatiwong S, and Richter C. 2013. Benthic Reef Primary Production in Response to Large Amplitude Internal Waves at the Similan Islands (Andaman Sea, Thailand). *PLoS ONE* 8.

Jantzen C, Wild C, El-Zibdah M, Roa-Quiaoit HA, Haacke C, and Richter C. 2008. Photosynthetic performance of giant clams, *Tridacna maxima* and *T-squamosa*, Red Sea. *Marine Biology* 155:211-221.

Johnson JB, and Omland KS. 2004. Model selection in ecology and evolution. *Trends in Ecology & Evolution* 19:101-108.

Kanwisher JW, and Wainwright SA. 1967. Oxygen balance in some reef corals. *Biol Bull* 133:378-390.

Kinsey DW. 1977. Seasonality and zonation in coral reef productivity and calcification. In: Taylor DL, editor. Proceedings of Third International Coral Reef Symposium. Miami, Florida: Rosenstiel School of Marine and Atmospheric Science. p 383-388.

Kinsey DW. 1985. Metabolism, calcification and carbon production: 1 systems level studies. In: Gabrie C, and Salvat B, editors. Proceedings Of The Fifth International Coral Reef Congress. Tahiti.

Kleypas JA, McManus JW, and Menez LAB. 1999. Environmental limits to coral reef development: Where do we draw the line? *American Zoologist* 39:146-159.
Kruschke JK. 2011. *Doing Bayesian data analysis: a tutorial with R and BUGS*. Burlington, MA: Academic Press.

Lirman D, and Biber P. 2000. Seasonal dynamics of macroalgal communities of the northern Florida reef tract. *Botanica Marina* 43:305-314.

Littler MM. 1973. The productivity of Hawaiian fringing-reef crustose Corallinaceae and an experimental evaluation of production methodology. *Limnol Oceanogr* 18:946-952.

Littler MM, and Doty MS. 1975. Ecological components structuring seaward edges of tropical pacific reefs: Distribution, communities and productivity of *Porolithon*. *Journal of Ecology* 63:117-129.

Mass T, Genin A, Shavit U, Grinstein M, and Tchernov D. 2010a. Flow enhances photosynthesis in marine benthic autotrophs by increasing the efflux of oxygen from the organism to the water. *Proceedings of the National Academy of Sciences of the United States of America* 107:2527-2531.

Mass T, Kline DI, Roopin M, Veal CJ, Cohen S, Iluz D, and Levy O. 2010b. The spectral quality of light is a key driver of photosynthesis and photoadaptation in *Stylophora pistillata* colonies from different depths in the Red Sea. *Journal of Experimental Biology* 213:4084-4091.

McCormick MI. 1994. Comparison of field methods for measuring surface-topography and their associations with a tropical reef fish assemblage. *Marine Ecology-Progress Series* 112:87-96.

Muscatine L. 1990. The role of symbiotic algae in carbon and energy flux in reef corals. In: Dubinsky Z, ed. *Coral Reefs*. Amsterdam: Elsevier, 75-84.

Naumann MS, Jantzen C, Haas AF, Iglesias-Prieto R, and Wild C. 2013. Benthic Primary Production Budget of a Caribbean Reef Lagoon (Puerto Morelos, Mexico). *PLoS ONE* 8.

Naumann MS, Niggl W, Laforsch C, Glaser C, and Wild C. 2009. Coral surface area quantification-evaluation of established techniques by comparison with computer tomography. *Coral Reefs* 28:109-117.

Odum HT, and Odum EP. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecological Monographs* 25:291-320.

Risk MJ. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bulletin* 152:1-6.

Rueda-Roa DT, and Muller-Karger FE. 2013. The southern Caribbean upwelling system: Sea surface temperature, wind forcing and chlorophyll concentration patterns. *Deep-Sea Research Part I-Oceanographic Research Papers* 78:102-114.

Salzwedel H, and Müller K. 1983. A summary of meteorological and hydrological data from the Bay of Santa Marta, Colombian Caribbean. *Anales del Instituto de Investigaciones Marinas de Punta de Betín* 13:67-83.

Sargent M, and Austin T. 1949. Organic productivity of an atoll. *Transactions of the American Geophysical Union* 30:254-249.

Sheppard C, Davy SK, and Pilling GM. 2009. *The biology of coral reefs*. Oxford ; New York: Oxford University Press.
Smith SV. 1981. The Houtman Abrolhos Islands: carbon metabolism of coral reefs at high-latitude. *Limnology and Oceanography* 26:612-621.

Spiegelhalter DJ, Best NG, Carlin BP, and Van Der Linde A. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 64:583-639.

Steneck RS. 1988. Herbivory on coral reefs: a synthesis. In: Choat JH, Barnes D, Borowitzka MA, Coll JC, Davies PJ, Flood P, Hatcher BG, Hopley D, Hutchings PA, Kinsey D, Orme GR, Pichon M, Sale PF, Sammarco P, Wallace CC, Wilkinson C, Wolanski E, and Bellwood O, editors. 6th International Coral Reef Symposium. 6 ed. Australia. p 37-49.

Szmant AM. 1997. Nutrient effects on coral reefs: a hypothesis on the importance of topographic and trophic complexity to reef nutrient dynamics. In: Lessios HA, and Macintyre IG, editors. 8th International Coral Reef Symposium. Panama: Smithsonian Tropical Research Institute, Panama. p 1527-1532.

Team RC. 2014. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Valiela I. 1995. *Marine ecological processes*. New York: Springer.

Veron JEN. 1995. *Corals in space and time: biogeography and evolution of the Scleractinia*. Ithaca: Comstock/Cornell.

Wanders JBW. 1976. The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles). I: Primary productivity in the coral reef. *Aquatic Botany* 2:235-270.

Werding B, and Sánchez H. 1989. The coral formations and their distributional pattern along a wave exposure gradient in the area of Santa Marta, Colombia. *Medio Ambiente* 10:61-68.

Wu EY, Barazanji KW, and Johnson RJ. 1997. Source of error on A-aDO2 calculated from blood stored in plastic and glass syringes. *J Appl Physiol* 82:196-202.

Yeo I-K, and Johnson RA. 2000. A new family of power transformations to improve normality 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 ± 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 * pMCMC < 0.05, ** pMCMC < 0.01, *** pMCMC < 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 (± 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 ± SD. Data in parenthesis represent water temperature and light intensity and at the end of the upwelling event in 2010/2011.
|                      | Non-upwelling |           | Upwelling |           |
|----------------------|---------------|-----------|-----------|-----------|
|                      | *In situ*     | Incubations | *In situ* | Incubations |
| Temperature (°C)     | 29.1 ± 0.2    | 28.6 ± 0.5 | 25.3 ± 0.3 | 25.4 ± 0.6 |
| (26.1 ± 0.2)         |               |           | (26.5 ± 0.4) |           |
| Light intensity      | 146 ± 47      | 154 ± 40  | 230 ± 58  | 257 ± 69  |
| (PAR µmol photons m⁻² s⁻¹) |            |           | (234 ± 78) | (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$^{-1}$) | $P_g$ (mmol O$_2$ m$^{-2}$ seafloor d$^{-1}$) | 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                            |                                               |                                               | This study                    |
| 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                           |                                               |                                               | This study                    |
| Caribbean                             | 39–157                                        | 84–253                                        | This study                    |
| Various Atlantic/Pacific              | 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              |                                               |                                               | This study                    |
| Caribbean                             | 44–104                                        | 58–140                                        | This study                    |
| Various Atlantic/Pacific              | 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                     |                                               |                                               | This study                    |
| 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)                 |