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

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Abstract

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

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 (Valiela, 1995; Chapin et al., 2011). 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 (Hatcher, 1988; Gattuso, Frankignoulle & Wollast, 1998). Productivity investigation of coral reefs started in the mid-20th century (Sargent & Austin, 1949; Odum & Odum, 1955), and today coral reefs are among the best understood marine benthic communities in terms of primary production (Kinsey, 1985; Hatcher, 1988; Hatcher, 1990; Gattuso, Frankignoulle & Wollast, 1998). 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, McManus & Menez, 1999; Sheppard, Davy & Pilling, 2009), including light (Darwin, 1842; Achituv & Dubinsky, 1990; Falkowski, Jokiel & Kinzie III, 1990), water temperature (Dana, 1843; Coles & Fadlallah, 1991; 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 (Glynn & Stewart, 1973; Cortés & Jiménez, 2003), 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; Kinsey, 1985; Falter et al., 2012), variability in primary production of seasonal upwelling-affected coral reefs remains largely underinvestigated.

The Tayrona National Natural Park (TNNP) at the Caribbean coat of Colombia offers ideal conditions to assess upwelling-affected primary productivity of coral-dominated benthic communities as it is highly influenced by the Southern Caribbean upwelling system (Andrade

& Barton, 2005; Rueda-Roa & Muller-Karger, 2013) which causes fluctuations in water temperature, light availability, and inorganic nutrient concentrations (Eidens et al., 2012; Bayraktarov, Pizarro & Wild, 2014). The upwelling seasonally extends to TNNP (Andrade & Barton, 2005), where diversely structured coral communities are present (Werding & Sánchez, 1989). Here, the abundance and community composition of benthic algae were shown to exhibit seasonality related to upwelling events (Diaz-Pulido & Garzón-Ferreira, 2002; Eidens et al., 2012). Thereby, the area provides an excellent opportunity to investigate the effects of seasonal coastal upwelling events on the key coral reef ecosystem service productivity 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 and the authors suggested a generally positive effect of upwelling conditions on major benthic autotrophs in the area. However, as the region was affected by an unusually strong El Niño-Southern Oscillation (ENSO) event in 2010/2011, which led to a coral bleaching in TNNP before the upwelling in 2010/2011 (Bayraktarov et al., 2013; Hoyos et al., 2013), productivity measurements during upwelling in 2010/2011 might not be representative for a typical upwelling event. To test for spatio-temporal 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 and further used 3D surface area estimates of dominant primary producers to assess surface area-specific productivity rates of the investigated groups as suggested by Naumann et al. (2013). Accordingly:

1. We identified 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 prior to primary production measurements.

2. We then used incubation experiments to quantify O_2 fluxes of dominant benthic primary producers and applied 3D surface area estimations to allow for comparisons of productivity between investigated groups.
3. Finally, we combined data on benthic coverage and individual production rates of investigated groups to estimated the specific contribution of each group to total benthic O_2 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, and only small fringing coral reefs are present in the park due to the proximity to the Sierra Nevada de Santa Marta - the world's highest coastal mountain range (Garzón-Ferreira & Cano, 1991; Garzón-Ferreira, 1998). The region is subjected to strong seasonality caused by the Caribbean Low-Level Jet of northeast (NE) trade winds (Salzwedel & Müller, 1983; Andrade & Barton, 2005), resulting in two major seasons; a dry season from December to April and a rainy season from May to November (Salzwedel & Müller, 1983; Garzón-Ferreira, 1998). 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) that lead to a seasonal coastal upwelling. The upwelling-related changes in key water parameters are well characterized by the comprehensive study of Bayraktarov, Pizarro & Wild (2014). During upwelling, water temperature can decrease to 20 °C while salinity, inorganic nutrient availability, and chlorophyll α increase and characterize the ecosystem which is otherwise close to oligotrophic as mesotrophic (Bayraktarov, Pizarro & Wild, 2014). Water currents triggered by prevailing winds predominantly move from NE, and a clear gradient between the water current- and wave-exposed western (EXP) and -sheltered northeastern (SHE) site of the bay can be observed (Werding & Sánchez, 1989; Bayraktarov, 2013).The study was carried out before the onset of upwelling in 2011/2012 (1st November – 2nd December 2011) and at the end of upwelling in 2011/2012 (20th March – 29th March 2012), allowing for the investigating 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 ± 2 % of the total seafloor coverage at SHE and 90 ± 7 % at EXP and were therefore selected 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 2 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* 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 cm^2), 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 and therefore small bushes of *Dictyota* spp. (surface area 1.86 ± 0.88 cm^2) 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 1) 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 cm^2 and 7.48 ± 3.60 cm^2, respectively). For sand samples, custom-made mini corers with defined surface area (1.20 cm^2) and sediment core depth (1.0 cm) were used.

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 photographs *in situ* and the whole spread out macroalgal thalli were used to obtain covered substrate areas (2D surface) as well as 3D surface areas and further calculate the 2D to 3D conversion factor for macroalgae (4.29 ± 0.82). 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 used mini corer apparatus (1.20 cm^2).

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 1). Temperature and light intensity was continuously monitored during incubations as described above. Light intensities were converted to photosynthetically active radiation (PAR, µmol photons m^{-2} 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 1), whereas water temperatures were higher before the upwelling (t-test, $p < 0.001$; Table 1). 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. All primary producers were incubated in containers that were placed in cooling boxes filled with water to maintain constant *in situ* water temperature (Table 1). 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 filled with seawater only 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). The dissolved O_2 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 O_2 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 O_2 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, Barazanji & Johnson, 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 O_2 fluxes and thereby photosynthesis (Mass et al., 2010a), the results of the field incubations should be regarded as conservative estimates of *in situ* O_2 fluxes and interpreted accordingly.

Data analyses and statistics

To quantify net O_2 production (P_n) and respiration of functional groups, O_2 concentration before incubations was subtracted from concentration after incubations and corrected with blank control values containing only seawater. Individual gross O_2 production (P_g) of investigated functional groups was calculated by adding values of P_n and respiration; individual O_2 fluxes were expressed per mmol O_2 m^{-2} specimen surface area h^{-1}. The relative contribution of each investigated group to total reef production (given as: mmol O_2 m^{-2}

vertically projected seafloor area h^{-1}) was estimated by taking into account the individual production rates and respective mean 2D to 3D conversion factors, the data for benthic coverage as well as the rugosity factor. Estimation of total daily reef productivity was furthermore calculated by 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 as well as total benthic O_2 fluxes were analyzed using two-way ANOVA and Bonferroni's *post hoc* tests to detect possible effects of season (upwelling vs. non-upwelling) and location (EXP vs. SHE) on benthic cover and metabolism. Statistical analysis of metabolic activity within each functional group and the contribution of the functional groups to overall O_2 production were assessed by one-way ANOVA after checking for the assumptions of parametric testing as mentioned above. Spatial differences between the sites during each sampling period as well as seasonal pattern at each site were analyzed by Bonferroni's planned comparison test. If data did not meet the assumptions of parametric testing, data sets were either log transformed or nonparametric Kruskal-Wallis and Dunn's planned comparisons/*post-hoc* tests were used. The analyses were done with STATISTICA (8.0). All values are represented as mean ± standard deviation (SD).

Results

Benthic community composition

At EXP, scleractinian corals dominated the benthic community before (41 ± 12 %) and at the end of the upwelling (39 ± 12 %, Table 3). At SHE, corals, algal turf, and sand cover was similar before upwelling (24 ± 3 %, 26 ± 6 %, and 25 ± 13 %, respectively), while at the end of upwelling, macroalgae exhibited highest benthic cover (47 ± 3 %, Table 3). 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 (ANOVA results Table S1). Macroalgae cover was significantly higher at SHE than at EXP and less abundant at both sites before upwelling than at the end of upwelling (Table S1). CCA cover also differed between the seasons, showing a significant decrease during the upwelling event (Table S1).

O_2 Fluxes of organisms

Highest individual net (P_n) and gross production (P_g) of all investigated functional groups were measured for scleractinian corals at both sites before the upwelling, while corals and algal turfs showed highest individual P_n and P_g rates at the end of the upwelling (Table 2). While significant spatial differences in O_2 production within functional groups were only observed for CCA with higher production at EXP than at SHE before upwelling , temporal differences in O_2 production were detected for corals, macroalgae, and CCA (ANOVA results: Table S2). For scleractinian corals and macroalgae, significant differences in P_n were only present at SHE with lower productivity at the end than before upwelling (Table S2). Primary production of CCA showed opposite pattern at the two sites: P_n and P_g were significantly elevated at EXP before upwelling, while productivity at SHE was significantly higher at the end of the upwelling (Table S2).

Contribution of organism-induced O_2 fluxes to total reef O_2 production

Before the upwelling, corals contributed most to benthic O_2 fluxes at EXP and SHE (Table 4). Contribution of corals at EXP to the total benthic O_2 fluxes was significantly higher than for algal turfs and microphytobenthos (ANOVA results: Table S3). At SHE, corals contributed significantly more than macroalgae, microphytobenthos, and CCA (Table S3). At the end of the upwelling season, contribution of corals to total benthic O_2 fluxes were also highest at EXP (Table 4) where corals contributed more to benthic productivity than CCA and microphytobenthos (Table S3). At SHE, macroalgae contributed most to benthic P_n and P_g (Table 4) and significantly more than algal turfs, microphytobenthos, and CCA (Table S3).

Significant spatial differences in contribution to total benthic O_2 production within functional groups were detected for all groups except for microphytobenthos (ANOVA results: Table S4). Coral contribution to total O_2 fluxes was higher at EXP than at SHE before the upwelling and at the end of upwelling (Table 4 and S4). During upwelling, macroalgae contributed more to P_n and P_g at SHE than at EXP, whereas contribution of algal turfs to benthic P_g was higher at SHE than at EXP before the upwelling (Table S4). The share of CCA to total productivity was elevated at EXP before as well as at the end of upwelling (Table S4).

Temporal differences in contribution to total benthic productivity within the investigated groups were also present in all groups except for microphytobenthos (Table S4). Corals at SHE contributed more to total O_2 production before the upwelling than at the end of upwelling (Table 4), while higher rates for macroalgal contribution to total O_2 fluxes were detected for P_n and P_g at the end of the upwelling at the same site (Table S4). For algal turfs, differences in contribution to benthic O_2 fluxes were only present at EXP with elevated P_g rates at the end of the upwelling, whereas higher contribution of CCA to total P_n and P_g was detected before the upwelling at SHE and EXP (Table S4).

Regarding total daily benthic O_2 fluxes (Figure 2), no spatial differences between EXP and SHE were detected, neither before nor at the end of the upwelling (ANOVA results: Table

S5). Furthermore, no significant temporal differences were present between non-upwelling and upwelling (Table S5). Comparing total benthic productivity at the end of the upwelling events in 2010/2011 and 2011/2012, higher P_n and P_g were detected at the end of the upwelling in2010/2011 (ANOVA results: Table S6).

Discussion

O_2 Fluxes of Organisms

Individual mean P_n and P_g were generally highest for corals at both sites during the study periods (10.9 – 16.3 and 17.6 – 20.9 mmol O_2 m^{-2} specimen surface area h^{-1}, respectively). These high productivity rates of corals compared to other investigated primary producers (see Table 2) may be attributed to the mutualistic relationship between zooxanthellae and the coral host, boosting photosynthetic efficiency through high zooxanthellate photosynthesis in coral tissues under high CO_2 and nutrient availability (D'Elia & Wiebe, 1990; Muscatine, 1990). Therefore, corals are among the most productive functional groups in reef systems with several fold higher specific production rates than most reef algae and reef sands (Table 5) (Wanders, 1976b; Kinsey, 1985; Yap, Montebon & Dizon, 1994). Estimated daily gross O_2 production per m^2 vertically projected surface area for both investigated coral genera, *Diploria* and *Montastraea* (492 – 687 and 412 – 518 mmol O_2 m^{-2} seafloor d^{-1}, respectively), are similar to O_2 fluxes of other Caribbean corals, ranging from 67 to 850 mmol O_2 m^{-2} seafloor d^{-1} (Table 5) (Kanwisher & Wainwright, 1967). Generally, O_2 fluxes of all investigated organism groups were within ranges reported in the literature (Table 5).

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

Significant spatial differences were only found for CCA before the upwelling with higher individual O_2 production at EXP compared to SHE. These differences may be explained by the prevailing water current regime in the bay together with high water temperatures of up to 30 °C before the upwelling. An increase in water temperature typically rises metabolic activity in CCA (Littler & Doty, 1975), but decreased water flow at SHE compared to EXP (Bayraktarov, 2013) likely prevented the required gas exchange and nutrient uptake, resulting in lower individual CCA productivity at SHE.

Temporal differences in individual O_2 production within investigated organism groups were most pronounced at SHE with two contrary patterns observed: whereas macroalgae and scleractinian corals produced less O_2 at the end of upwelling, CCA exhibited higher O_2 production rates during this study period. The decreased production rates of macroalgae could be explained by high macroalgal cover High macroalgal cover, as observed at SHE during the upwelling (47 ± 3 %, Table 3), could have resulted in reduced macroalgal O_2 production due to density-dependent intra-specific competition for light and nutrients by the dominant macroalgae *Dictyota* sp. (Edwards & Connell, 2012). The macroalgal die-off together with lower water currents at SHE compared to EXP could further have negatively affected coral productivity as decomposition of macroalgae may result in toxicity towards organisms as stated by Morand & Merceron (2005).

Elevated photosynthetic performance of CCA at SHE at the end of upwelling may be due to higher nutrient concentrations during upwelling compared to non-upwelling (Bayraktarov et al., 2013; Bayraktarov, Pizarro & Wild, 2014). Nutrient limitation of benthic communities in water current-sheltered locations may be more pronounced than in communities exposed to high water flow due to the fact that benthic algal communities are typically nutrient-limited (Hatcher & Larkum, 1983), and nutrient supply of coral reef algae is primarily controlled by water flow (Hatcher, 1990). Elevated nutrient concentration during upwelling may therefore offset the limiting nutrient supply particularly at SHE where water flow was lower than at EXP (Bayraktarov, 2013).

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

Before the upwelling, the share of corals to total benthic P_n and P_g were highest at both EXP (80.6 ± 24.3 and 77.5 ± 19.2 %, respectively) and SHE (64.5 ± 25.5 and 54.9 ± 18.4 %, respectively). At the end of the upwelling, corals only contributed most to P_n and P_g at EXP (72.6 ± 16.7 and 75.4 ± 15.3 %, respectively), whereas macroalgal contribution to benthic primary production was highest at SHE (P_n: 51.6 ± 7.4; P_g: 46.3 ± 12.4 %). The major contribution of corals can be explained by their highest quantified individual O_2 production rates of all investigated organism groups (Table 2) and comparably high benthic coverage of corals, ranging from 24 to 39 % (Table 3). Similar values were estimated for a Southern Caribbean fringing reef by Wanders (1976b), were corals accounted for about two-thirds of total benthic primary production.

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

The identified spatial differences in contribution to total benthic O_2 production for scleractinian corals, macroalgae, and CCA can also be explained by spatial differences in their benthic coverage. Elevated contributions of corals and CCA at EXP compared to SHE (Table 4) not only reflect their spatial abundance patterns (Table 3), but also the higher macroalgal contribution at SHE at the end of the upwelling (Table 4) can be linked to spatial differences in macroalgal coverage with higher abundances at SHE during upwelling (Table 3). The observed pattern in benthic coverage of corals and CCA may be caused by the water current regime in the bay with stronger water currents at EXP compared to SHE (Bayraktarov, 2013), as suggested to be the major driver for differences in local coral communities by Werding & Sánchez (1989). This explanation is supported by the studies of Jokiel (1978) and Fabricius & De'ath (2001), stating that maximum abundance of corals and CCA typically occur in water current-exposed environments. Differences in water current exposure between the study sites could also be the reason for the observed spatial patterns in macroalgae abundance, as the abundance of the dominant macroalgal genus *Dictyota* is highly affected by water current exposure (Renken et al., 2010).

Corals, macroalgae, and CCA also exhibited distinct temporal differences in contribution to total benthic productivity. At SHE, corals contributed more to benthic O_2 production before the upwelling and macroalgae at the end of the upwelling, whereas contribution of CCA at both sites was higher before as compared to at the end of upwelling. Reasons for the observed patterns in coral contribution to total benthic primary production are temporal shifts in individual O_2 productivity of corals with higher production rates before the upwelling event (Table 2) together with slightly higher benthic coverage during this study period (Table 3). The temporal variation in macroalgal contribution to total benthic O_2 fluxes can be explained by the seasonal growth pattern of the dominant macroalgae *Dictyota* sp., most likely caused by variation in nutrient concentrations (Bayraktarov et al., 2013; Bayraktarov, Pizarro & Wild, 2014) and water temperatures, as these factors affect the growth of the dominant macroalgae genus *Dictyota* (Bula-Meyer, 1990; Cronin & Hay, 1996; Diaz-Pulido & Garzón-Ferreira, 2002). The contrary occurrence pattern of macroalgae and CCA especially at SHE with higher CCA cover before compared to the end of upwelling (14 ± 4 vs. 3 ± 2 %, Table 3) suggests that seasonal occurrence of the dominant macroalgae *Dictyota* sp. may also account for the observed temporal variations in CCA abundance at SHE. This assumption is supported by the studies of Lirman & Biber (2000) as well as Belliveau & Paul (2002) that demonstrated that macroalgae can shade CCA, leading to usually negative correlated abundances of these groups. Higher contribution of CCA at EXP before as compared to at the end of upwelling furthermore results from both, elevated CCA production rates (Table 2) and higher abundances before the upwelling (Table 3).

Total benthic O_2 fluxes and ecological perspective

Estimated means of total daily benthic O_2 production at both sites before and at the end of the upwelling event in2011/2012 (Figure 2) were within the ranges of other investigated reef slope communities (Table 5). However, it should be taken into account that total shallow reef productivity in earlier studies was quantified using flow respirometry techniques, whereas our experiments were conducted in no-flow incubation chambers. Despite the different methodologies, our results are comparable to the study by Adey & Steneck (1985) where productivity of similar communities from deeper Caribbean fore reefs of St. Croix (mean water depth: 4.5 – 6.3 m) were quantified. Productivity rates reported by Adey & Steneck (1985) were generally similar to O_2 fluxes in Gayraca Bay, although maximal diurnal fluxes were slightly higher than those in our study (Table 5). As light availability decreases with increasing depth, water depths of investigated communities (St. Croix: < 6.3 m, Gayraca Bay: ~10 m) may account for elevated daily productivity in reefs of St. Croix. Another reason could be higher surface to area ratios in reefs of St. Croix compared to Gayraca Bay (rugosity factor: 1.9 – 2.5 and 1.3 – 1.5, respectively), since surface enlargement is a key factor for benthic communities to increase primary production (Wanders, 1976b).

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, neither spatial nor seasonal differences in total benthic O_2 fluxes were detected before and at the end of the upwelling event in 2011/2012. These findings are supported by Hatcher (1990), stating that the relative coverage of benthic photoautotrophs in a reef community may have little effect on its areal production rate. However, the observed lack of seasonality of total benthic productivity stands in contrast to earlier studies (Kinsey, 1977; Smith, 1981; Kinsey, 1985; Eidens et al., 2012) which found an approximately two-fold difference in benthic primary production between seasons. A possible explanation for this finding could come from seasonal changes of abiotic factors, counteracting with each other. On the one hand, decreased water temperatures during upwelling typically mitigate primary production (Crossland, 1984; Carpenter, 1985). On the other hand, abiotic factors that are known to boost primary productivity, namely water currents (Mass et al., 2010a) and nutrient availability (Hatcher, 1990; Chavez, Messie & Pennington, 2011), typically increase during upwelling events, thus promote photosynthesis. In addition, elevated light availability during incubation experiments at the end of the upwelling (Table 1) could have positively affected photosynthesis of benthic autotrophs. The observed similar productivity rates at different seasons and the reestablishment of original benthic community composition after the upwelling events suggest that coral reefs in TNNP are well adapted to the pronounced seasonal variations in light availability, water temperature, and nutrient availability.

Nevertheless, higher total benthic productivity at the end of the upwelling in 2010/2011 compared to the non-upwelling was not only detected during our preliminary study (Eidens et al., 2012) but total benthic O_2 fluxes during the upwelling in 2010/2011 were also higher than at the end of the upwelling in 2011/2012 (see Table S6 for ANOVA results). These findings suggest that interannual influences do affect productivity of the coral reefs in TNNP. Interestingly, water temperature increases and unusual high precipitation occurred in the study area at the end of 2010, related to an ENSO event (Bayraktarov et al., 2013; Hoyos et al., 2013), causing coral bleaching in the region (Bayraktarov et al., 2013). Surprisingly, bleached corals in the bay recovered quickly from the ENSO-triggered disturbances in the course of the following upwelling event (Bayraktarov et al., 2013) and exhibited similar specific O_2 production rates at the end of the upwelling event 2010/2011 compared to subsequent measurements (Table 2) which indicates 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 event, resulting in higher group-specific productivity of macroalgae and particularly algal turfs at the end of the 2010/2011 upwelling event compared to subsequent study periods (Table 2). The elevated production rates of macroalgae and algal turfs together with the fast recovery of corals from bleaching accounted for higher benthic productivity at the end of upwelling in 2011/2011 compared to the non-upwelling (Eidens et al., 2012) as well as to the 2011/2012 upwelling event (Table 5 and S6).

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

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Figures

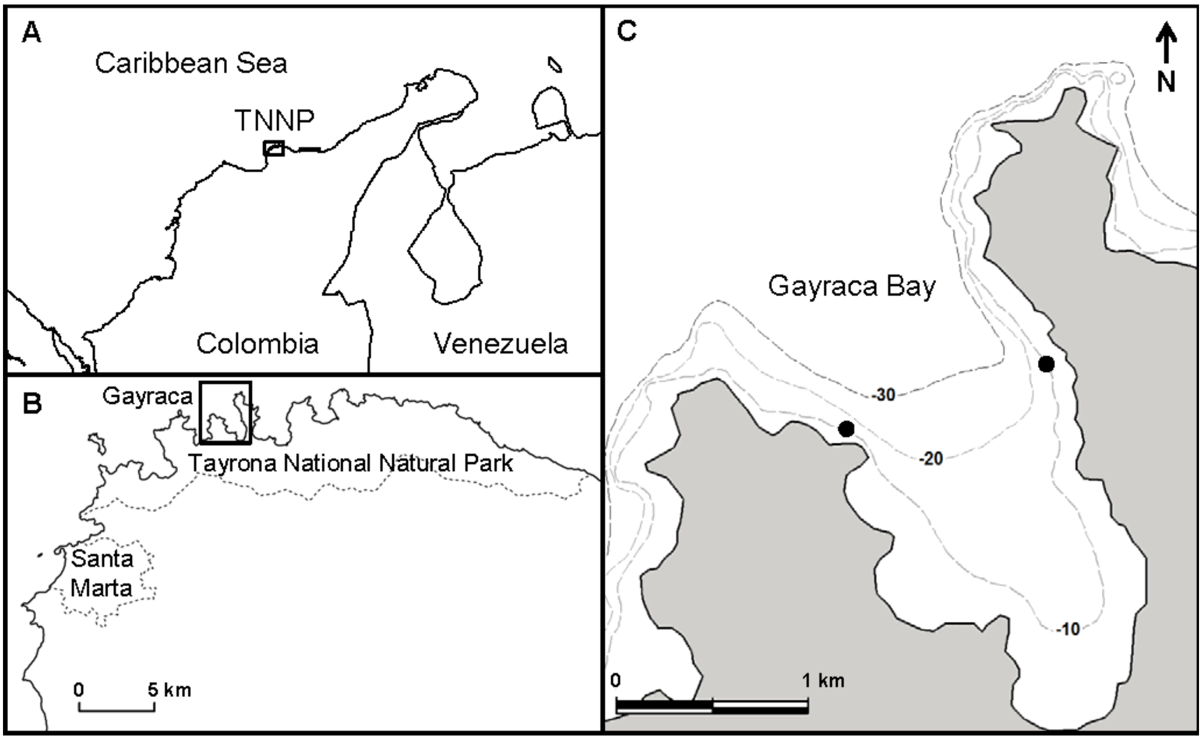

Figure 1. Location of study sites. A) Location of Tayrona National Natural Park (TNNP) at the Caribbean coast of Colombia. B) Location of Gayraca Bay within TNNP (dashed lines – national park border and expansion of the city of Santa Marta. C) Gayraca Bay. The investigation sites at the current-exposed western part and the sheltered north-eastern part are indicated by black dots (dashed lines – isobaths). Source of map: (INVEMAR, 2012).

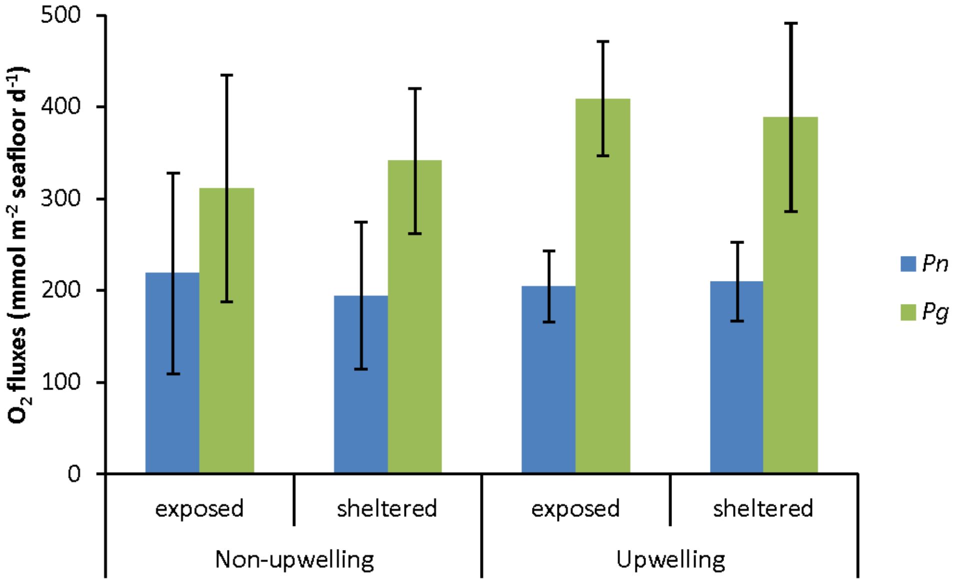

Figure 2. Total benthic O_2 fluxes. Overall benthic O_2 fluxes at the exposed and sheltered site of Gayraca Bay during non-upwelling and upwelling. Values are given as mean ± SD. Abbreviations: P_n = net O_2 fluxes, P_g = gross O_2 fluxes

Tables

Table 1. Light intensity and water temperature during incubation experiments at sampling sites and in incubation containers. All values are in mean ± SD. Data in parenthesis represent light intensity and water temperature at the end of the upwelling event in 2010/2011.

	Non-upwelling		**Upwelling**	
	In situ	Incubations	*In situ*	Incubations
Light intensity (PAR µmol photons m^{-2} s^{-1})	146 ± 47	154 ± 40	230 ± 58 (234 ± 78)	257 ± 69 (248 ± 71)
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)

Table 2. O_2 fluxes of functional benthic groups. All values in mean ± SD. Data in parenthesis represent O_2 fluxes at the end of the upwelling event in 2010/2011. Missing data are due to the absence of macroalgae at the exposed site during non-upwelling. Abbreviations: n = number of replicates, P_n = net O_2 production, P_g = gross O_2 production.

Location	**Functional group**	**n**	**P_n**		**P_g**	
			(mmol O_2 m^{-2} specimen surface area h^{-1} ± SD)			
			Non-upwelling	Upwelling	Non-upwelling	Upwelling
Exposed	Corals	11 – 24	16.3 ± 4.7	13.5 ± 3.6 (17.7 ± 4.0)	19.2 ± 5.4	20.9 ± 4.3 (23.4 ± 5.6)
	Macroalgae	3 – 6		2.4 ± 0.5 (8.6 ± 0.9)		3.2 ± 0.3 (10.4 ± 1.0)
	Algal turfs	5 – 6	3.3 ± 1.0	8.5 ± 2.1 (23.1 ± 2.1)	5.1 ± 1.2	11.6 ± 2.3 (30.2 ± 5.6)
	Crustose coralline algae	5 – 6	8.7 ± 1.4	5.4 ± 1.5 (6.1 ± 1.2)	10.2 ± 1.6	6.0 ± 1.7 (6.5 ± 1.4)
	Microphytobenthos	4 – 6	2.3 ± 1.7	0.1 ± 0.9 (4.9 ± 1.5)	5.1 ± 1.6	3.2 ± 0.8(7.0 ± 1.6)
Sheltered	Corals	12 – 22	15.6 ± 5.8	10.9 ± 3.2 (16.5 ± 4.8)	18.5 ± 6.3	17.6 ± 4.7 (22.6 ± 6.0)
	Macroalgae	5 – 6	4.3 ± 0.6	3.1 ± 0.4 (6.1 ± 0.7)	5.4 ± 0.7	4.0 ± 1.1 (7.6 ± 0.9)
	Algal turfs	5 – 6	5.5 ± 3.0	13.1 ± 3.6 (28.2 ± 8.3)	8.8 ± 3.8	17.1 ± 4.3 (37.2 ± 5.8)
	Crustose coralline algae	5 – 6	3.6 ± 1.5	6.9 ± 2.4 (5.0 ± 1.7)	4.2 ± 1.6	8.7 ± 2.4 (5.5 ± 1.8)
	Microphytobenthos	3 – 6	0.5 ± 5.6	2.7 ± 1.0 (7.3 ± 6.9)	6.2 ± 4.1	6.8 ± 1.4 (11.6 ± 6.6)

Table 3. Benthic coverage of functional groups. All values in percent ± SD. Data in parenthesis represent benthic coverage at the end of the upwelling event in 2010/2011.

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

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Table 4. Contribution of functional groups to total benthic O_2 fluxes. All values in mean ± SD. Data in parenthesis represent O_2 fluxes at the end of the upwelling event in 2010/2011. Missing data are due to the absence of macroalgae at the exposed site during non-upwelling. Abbreviations: P_n = net O_2 production, P_g = gross O_2 production.

Location	**Functional group**	**P_n**		**P_g**	
		(mmol O_2 m^{-2} seafloor h^{-1} ± SD)			
		Non-upwelling	Upwelling	Non-upwelling	Upwelling
Exposed	Corals	14.8 ± 4.3	12.4 ± 2.8 (15.0 ± 2.8)	17.4 ± 4.3	19.3 ± 3.9 (19.7 ± 3.1)
	Macroalgae		1.4 ± 0.3 (9.2 ± 1.0)		1.9 ± 0.2 (11.2 ± 1.1)
	Algal turfs	1.0 ± 0.3	2.6 ± 0.6 (5.5 ± 0.5)	1.6 ± 0.4	3.5 ± 0.7 (7.2 ± 1.3)
	Crustose coralline algae	2.1 ± 0.3	0.6 ± 0.2 (1.0 ± 0.2)	2.4 ± 0.4	0.7 ± 0.2 (1.1 ± 0.2)
	Microphytobenthos	0.3 ± 0.2	0.0 ± 0.0 (0.4 ± 0.1)	0.7 ± 0.2	0.1 ± 0.0 (0.6 ± 0.1)
	Total	**18.2 ± 4.4**	**17.1 ± 2.9 (31.2 ± 3.0)**	**22.1 ± 4.3**	**25.6 ± 4.0 (39.7 ± 3.6)**
Sheltered	Corals	10.5 ± 4.2	4.9 ± 1.3 (10.3 ± 3.0)	12.4 ± 4.1	7.9 ± 1.3 (14.1 ± 3.4)
	Macroalgae	2.5 ± 0.3	9.0 ± 1.3 (8.8 ± 0.9)	3.2 ± 0.4	11.6 ± 3.1 (11.0 ± 1.3)
	Algal turfs	2.2 ± 1.2	2.4 ± 0.7 (8.2 ± 2.4)	3.5 ± 1.5	3.1 ± 0.8 (10.9 ± 1.7)
	Crustose coralline algae	0.8 ± 0.3	0.3 ± 0.1 (0.7 ± 0.2)	0.9 ± 0.3	0.4 ± 0.1 (0.8 ± 0.2)
	Microphytobenthos	0.2 ± 2.1	0.8 ± 0.3 (2.3 ± 2.2)	2.4 ± 1.6	2.0 ± 0.4 (3.7 ± 2.1)
	Total	**16.2 ± 4.9**	**17.5 ± 1.9 (30.4 ± 4.5)**	**22.3 ± 4.7**	**24.9 ± 3.5 (40.3 ± 4.5)**

Table 5. Mean benthic oxygen production of reef slope 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**	**P_g**	**Reference**
		(mmol O_2 m^{-2} seafloor d^{-1} ± SD)		
Reef slope communities	Caribbean	194 – 218	311 – 409	This study
	Caribbean	194 – 374	311 – 603	Eidens et al. (2012)
	Various Atlantic/Pacific	-83 – 425	167 – 583	Hatcher (1988)
	Caribbean	113 – 469	313 – 638	Adey & Steneck (1985)
Functional group				
Corals	Caribbean	227 – 344	441 – 610	This study
	Caribbean	328 – 369	441 – 598	Eidens et al. (2012)
	Caribbean	166	447	Wanders (1976b)
	Caribbean		225 – 850	Kanwisher & Wainwright (1967)
Macroalgae	Caribbean	117 – 244	198 – 375	This study
	Caribbean	244 – 444	375 – 624	Eidens et al. (2012)
	Caribbean	142 – 433	250 – 633	(Wanders, 1976a)
	Various Atlantic/Pacific		192 – 3283	Hatcher (1988)
Algal turfs	Caribbean	39 – 157	84 – 253	This study
	Caribbean	39 – 339	84 - 554	Eidens et al. (2012)
	Various Atlantic/Pacific		75 – 1008	Hatcher (1988)
	Various Atlantic/Pacific		83 – 967	Kinsey (1985)
	Caribbean	175 – 433	308 – 617	Wanders (1976b)
Crustose coralline algae	Caribbean	44 – 104	58 – 140	This study
	Caribbean	44 – 104	58 – 140	Eidens et al. (2012)
	Various Atlantic/Pacific		67 – 83	Kinsey (1985)
	Caribbean	58 – 117	192 – 258	Wanders (1976b)
	Great Barrier Reef	50 – 333	75 – 416	Chisholm (2003)
Microphytobenthos	Caribbean	1 – 67	75 – 143	This study
	Caribbean	6 – 87	78 – 191	Eidens et al. (2012)
	SW Pacific	0 – 8	92 – 150	Boucher et al. (1998)
	Various Atlantic/Pacific		50 – 225	Kinsey (1985)