Seasonal upwelling stimulates primary production of Colombian Caribbean coral reefs

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Abstract. Abiotic factors such as light intensity and water temperature influence coral reef productivity. In Tayrona National Natural Park (Colombian Caribbean), these factors are subject to high temporal variability due to seasonal coastal upwelling events. This offers the opportunity to assess these effects on the key coral reef ecosystem service productivity under *in situ* conditions in space and time. After identifying the dominant functional groups of primary producers (scleractinian corals, macroalgae, algal turfs, microphytobenthos, and crustose coralline algae) at upwelling-exposed and -sheltered sites of Gayraca Bay, we performed incubation experiments to quantify oxygen fluxes induced by the different groups. The experiments were conducted before and at the end of the upwelling event in 2011. The study revealed scleractinian corals to be the most efficient gross primary producers prior to the upwelling, and scleractinian corals and macroalgae at the end of the upwelling event. Overall benthic carbon fixation and respiration values at both sites were higher at the end of the upwelling due to significantly increased gross carbon fixation by corals, macroalgae, and algal turfs as well as elevated respiration by corals and macroalgae. These findings suggest a stimulation of reef primary production caused by seasonal upwelling events and a high temporal plasticity of productivity in the investigated coral communities.

Key words: Primary production, Carbon fluxes, Seasonal upwelling, Colombian Caribbean.

Introduction

In most ecosystems such as coral reefs, primary production through photosynthesis builds the energetic base of communities. Abiotic factors including temperature, light intensity, and nutrient concentration can alter ecosystem primary productivity. Usually coral reefs are found under relatively stable conditions of the above-mentioned factors. However, some coral reefs develop in areas affected by seasonal upwelling, particularly in the Eastern Tropical Pacific (Glynn *et al.* 2001), the Arabian Sea (Glynn 1993), the Indian Ocean (McClanahan *et al.* 2009), and the Southern Caribbean (Werding and Erhardt 1976). Despite several studies about the influences of upwelling on coral dominated benthic ecosystems, so far no investigation attempted to quantify the temporal effects of seasonal upwelling on reef ecosystem productivity.

The waters in Tayrona National Natural Park, located at the Caribbean coast of Colombia, are highly influenced by the Guajira upwelling system (Diaz-Pulido and Garzón-Ferreira 2002, Andrade and Barton 2005). During upwelling season, mean water temperature in the area decreases by several degrees Celsius, whereas light availability increases (Salzwedel and Müller 1983, Andrade and Barton 2005). This seasonality potentially affects scleractinian corals and algal assemblages (Garzón-Ferreira 1998, Diaz-Pulido and Garzón-Ferreira 2002) by changing productivity of functional primary producers, their contribution to ecosystem production, and total reef ecosystem productivity. Therefore, we investigated the response of benthic primary production of dominant functional groups to seasonal upwelling in Tayrona National Natural Park using a series of incubation experiments.

Material and Methods

Study Site

The study was conducted in Gayraca Bay (11.33°N, 74.11°W), situated in Tayrona National Natural Park, (Fig. 1). Strongest upwelling in the park occurs from December to March/April due to the intense Caribbean low-level jet of NE trade winds. During upwelling, mean water temperatures are around 25 °C, but before the onset of upwelling in December, when wind incidence is lowest, mean water temperatures are between 28 and 29 °C (Diaz-Pulido and Garzón-Ferreira 2002). Primary productivity was investigated at the exposed western and sheltered northeastern sides within Gayraca Bay (Fig. 1).

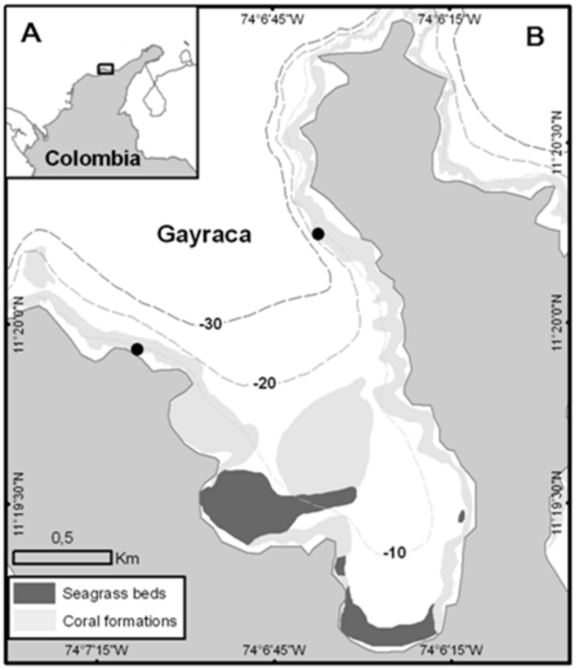

Figure 1: (A) Location of Tayrona National Natural Park at the Caribbean coast of Colombia, (B) detailed map of Gayraca Bay, located within TNNP. The investigation sites at the exposed western part and the sheltered northeastern part are indicated by black dots. Source: INVEMAR-SIAM (2012).

To assess the influence of upwelling on benthic primary production, studies were carried out at the end of the upwelling season in April 2011 and before the next upwelling event in November/December 2011. During the studies, water temperature (°C) and light intensity (lx) were monitored at both sites using light and temperature loggers (HOBO onset Pendant UA-002-64) at 10 m water depth with a temporal solution of 2 minutes (Table 1).

Table 1: Light intensity and water temperature during incubation experiments in Gayraca Bay in April 2011 (upwelling) and November/December 2011 (non-upwelling) at 10 m water depth and in incubation containers.

	Upwelling		Non-upwelling	
	In situ	Incubations	*In situ*	Incubations
Light intensity (PAR µmol photons m^{-2} s^{-1}, Mean ± SD)	234 ±78	248 ±71	146 ±47	154 ±40
Temperature (°C, Mean ± SD)	26.1 ±0.2	26.5 ±0.4	29.1 ±0.2	28.6 ±0.5

Benthic Community Assessment

Prior to primary production measurements, we identified dominant groups of benthic primary producers using line point intercept transects (50 m length, n = 3, modified from Hodgson *et al*. 2004) to obtain percentage of benthic cover at both sites. Scleractinian corals, macroalgae, algal turfs, crustose coralline algae, and sand-inhabiting microphytobenthos, which amounted to 90 ± 5 % of the total seafloor coverage on the sheltered and 92 ± 4 % on the exposed site, were selected for the subsequent incubation experiments.

Sampling

Specimens of the scleractinian corals *Montastraea cavernosa* and *Diploria labyrinthiformis*, macroalgae of the genus *Dictyota*, algal turfs, crustose coralline algae, and sand were used to measure photosynthetic activity (see Table 2 for number of replicates). The water depth of sampling was 9 – 11 m. Corals of the genera *Montastraea* and *Diploria* accounted for more than 80 % of the total coral cover at the investigated sites and were therefore used as representative corals for our study. The samples were fragmented with a multifunction rotary tool and glued on ceramic tiles using coral glue, assuring that no bare skeleton was exposed to incubation waters. After fragmentation, coral samples were returned to their natural habitat to recover for the period of one week. To investigate algal turfs and crustose coralline algae, overgrown rubble was sampled; sand samples were taken using cut-off syringes as mini-corers, and small tissue fragments of macroalgae were used for incubation experiments. The organisms were brought to the surface in Ziploc bags and transported directly to the field lab located at a beach adjacent to the bay. Tissue fragments of macroalgae were transferred to an aquarium one day before incubation experiments to provide recovery after sampling. All other functional groups were incubated immediately after sampling.

Incubation Experiments

Quantification of photosynthetic activity for macroalgae, crustose coralline algae, and microphytobenthos took place in incubation containers with volumes of 60 mL and for corals and algal turfs in 600 mL containers. Freshly collected seawater from Gayraca Bay was used for incubations. Water oxygen concentrations were measured before and after incubations using an optode (HQ 40, Hach Lange). Samples of functional groups were incubated in containers which were placed in water baths. For light incubations, several layers of screen were used to simulate *in situ* light regimes. Temperature (°C) and light intensity (lx) was monitored during incubations with light and temperature loggers and converted to photosynthetically active radiation (PAR, µmol photons m^{-2} s^{-1}, 400 to 700 nm) using the approximation of Valiela 1984 (Table 1). For dark incubations during daytime, the same methodology was used as mentioned above, but cooling boxes were closed with opaque lids to prevent any light penetration. In order to provide comparability among the measurements, light incubations were carried out on sunny days between 10 am and 2 pm. For each group one light and one dark incubation during upwelling and non-upwelling were performed (see Table 2 for number of replicates). Incubation containers (n = 2 to 5) filled with seawater only served as blank controls to quantify photosynthetic activity in the water column.

Data Analyses And Statistics

To quantify net primary production, oxygen concentration before light incubations was subtracted from concentration after incubations and corrected with blank control values. For respiration measurements, oxygen concentrations after dark incubations were subtracted from the values obtained prior to incubations and also corrected with the values from blank controls. Gross production was calculated by adding values of net production and respiration. These values were converted in weights of carbon using a photosynthetic quotient of one and normalized to surface area covered by the incubated sample and a standardized time unit. Surface area for samples of scleractinian corals, macroalgae, and turfs was determined with the planar projection photography method described by Naumann *et al.* (2009). For crustose coralline algae, the simple geometry method described in Naumann *et al.* (2009) was used. With the obtained data for benthic coverage, the relative daily contribution of each investigated group to overall reef production and respiration (g C m^{-2} d^{-1}) was calculated.

A two-tailed U-test after Wilcoxon, Mann, and Whitney was applied to compare benthic coverage as well as production and respiration rates of dominant primary producers during upwelling and non-upwelling season because data did not meet the assumptions of parametric testing.

Results

The benthic primary producers studied showed no temporal differences in benthic cover over time except for macroalgae, which significantly decreased prior to upwelling at the sheltered site ($p < 0.05$, Fig. 2) and no macroalgae were detected at the exposed site during non-upwelling season.

On the two sites, mean light intensities during incubation experiments in April were higher than in November/December and water temperatures during upwelling were reduced compared to non-upwelling (Table 1) but no spatial differences were detected among the sites at both times.

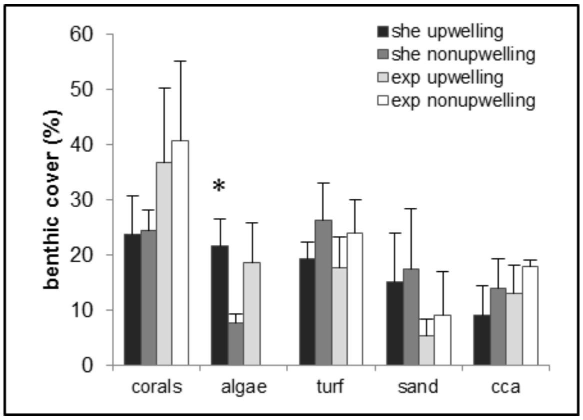

Figure 2: Benthic cover of functional primary producers at sheltered and exposed sites in Gayraca Bay during upwelling and non-upwelling season in 2011 (algae: macroalgae; turf: algal turf; cca: crustose coralline algae; she: sheltered; exp: exposed; boxes: mean; error bars: standard deviation, p-value derived from Wilcoxon-Mann-Whitney-U test, n = 3, * $p < 0.05$).

Primary Production Budget

Benthic gross production as well as respiration at sheltered and exposed sites were higher during the upwelling season compared to non-upwelling conditions (Fig. 3, Table 2). Production to respiration ratios (P:R) ranged from 1.7 at the sheltered site at both times to 2.3 at the exposed site during upwelling and 2.9 during non-upwelling.

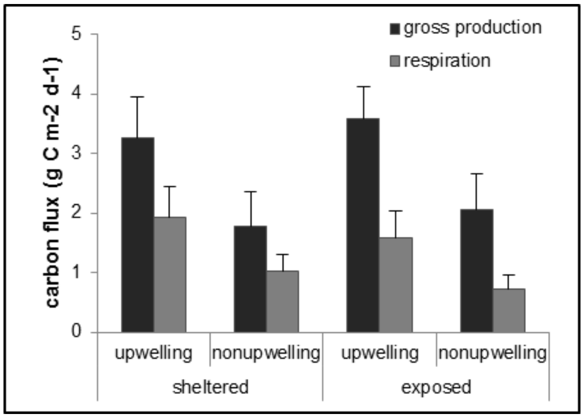

Figure 3: Benthic gross primary production and respiration rates at sheltered and exposed sites of Gayraca Bay during upwelling and non-upwelling season in 2011 (boxes: mean; error bars: standard deviation).

Contributions of scleractinian corals to gross production and respiration rates at both sites were higher than those of the other investigated primary producers, both before and during upwelling (Table 2). On the sheltered site, crustose coralline algae showed the lowest production and respiration rates, whereas on the exposed site microphytobenthos showed the lowest production rates (Table 2).

Together with macroalgae and algal turfs, corals accounted for 85 – 95 % of benthic productivity and

Table 2: Gross carbon fixation and respiration values of dominant benthic primary producers at sheltered and exposed sites of Gayraca Bay during upwelling and non-upwelling season in 2011. N: Number of replicates; GP: gross production in g C related to covered seafloor area per m^2 per day; R: respiration in g C related to covered seafloor area per m^2 per day; SD: standard deviation; LS: level of significance derived from Wilcoxon-Mann-Whitney-U test (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; ns: no significance).

Location	Functional group	N	GP_{day} ($g\ C\ m^{-2}\ d^{-1}$) Mean ± SD		LS	R_{day} ($g\ C\ m^{-2}\ d^{-1}$) Mean ± SD		LS
			Upwelling	Non-upwelling		Upwelling	Non-upwelling	
sheltered	corals	39	1.29 ± 0.29	1.05 ± 0.32	*	0.99 ± 0.24	0.48 ± 0.10	***
	macroalgae	12	0.84 ± 0.10	0.24 ± 0.03	**	0.33 ± 0.09	0.10 ± 0.02	**
	algal turfs	11	0.83 ± 0.13	0.27 ± 0.12	**	0.40 ± 0.16	0.20 ± 0.07	ns
	microphytobenthos	11	0.26 ± 0.15	0.12 ± 0.08	ns	0.19 ± 0.05	0.23 ± 0.08	ns
	crustose coralline algae	11	0.05 ± 0.02	0.11± 0.02	**	0.01 ± 0.00	0.00 ± 0.00	*
	total		3.27 ± 0.68	1.80 ± 0.58		1.92 ± 0.54	1.01 ± 0.27	
exposed	corals	45	1.79 ± 0.28	1.55 ± 0.38	*	0.92 ± 0.21	0.45 ± 0.10	***
	macroalgae	6	0.99 ± 0.09	/	/	0.34 ± 0.03	/	/
	algal turfs	11	0.64 ± 0.12	0.20 ± 0.08	*	0.30 ± 0.19	0.15 ± 0.12	ns
	microphytobenthos	10	0.04 ± 0.01	0.05 ± 0.02	ns	0.02 ± 0.01	0.06 ± 0.01	*
	crustose coralline algae	12	0.13 ± 0.03	0.25 ± 0.08	**	0.01 ± 0.01	0.06 ± 0.01	**
	total		3.59 ± 0.54	2.06 ± 0.62		1.59 ± 0.45	0.70 ± 0.24	

77 – 98 % of respiration. Corals and macroalgae at both sites produced and respired significantly more in the upwelling season compared to non-upwelling conditions (Table 2). For algal turfs, only significant elevated production rates at the end of the upwelling were detected. Microphytobenthos and crustose coralline algae showed opposite changes in photosynthetic performance. Microphytobenthos at the exposed site respired significantly more during non-upwelling measurements compared to upwelling conditions, whereas crustose coralline algae showed significantly higher photosynthetic performance and respiration prior to the upwelling event at both sites (Table 2).

Discussion

Carbon fluxes and production to respiration ratios of coral-dominated benthic communities in Gayraca Bay during the two periods study were within ranges of primary productivity measurements in coral reefs at fore reefs reported in the literature (gross fixation 2.0 to 7.0 g C m^{-2} d^{-1}, P:R 0.5 to 5.5, Hatcher 1990). Production was as high as in other highly productive benthic communities such as seagrass beds (1.5 to 3.0 g C m^{-2} d^{-1}) and kelp forests (1.7 to 4.9 g C m^{-2} d^{-1}, Castro and Huber 2010) but obtained values may be overestimated because respiration measurements were only conducted during daytime when respiration is usually higher than at night (Titlyanov 1991, Anthony & Hoegh-Guldberg 2003). Furthermore, carbon fixation and respiration values at both sites were higher during upwelling when compared to non-upwelling conditions, but no spatial differences among the sites were detected during both study periods, suggesting higher temporal than spatial changes of community metabolism in this area.

Except for microphytobenthos, temporal variability in primary production was detected for all groups studied, though no temporal shifts in benthic coverage among most functional groups could be identified, indicating seasonal metabolic shifts within these groups. Only in macroalgae cover, high seasonal variability was found as previously reported by Diaz-Pulido and Garzón-Ferreira (2002). Together with the seasonal occurrence of macroalgae, elevated carbon fixation and respiration rates of scleractinian corals and algal turfs during the upwelling event largely accounted for the observed temporal patterns in primary productivity.

For scleractinian corals, macroalgae and algal turfs that account for most of benthic carbon fixation, light regimes during incubations experiments were lower than saturating light intensities (Chalker *et al*. 1983, Kanwisher and Wainwright 1967, Wanders 1976, Titlyanov 1991), suggesting that elevated light intensities during the upwelling event enhanced photosynthetic activity of these groups. Despite the fact that respiration is sensitive to temperature changes (Lopéz-Urrutia *et al*. 2006) and lower water temperature should decrease the photosynthetic performance of the investigated organisms (Hatcher 1990, Kinsey 1985), this effect was not detected for corals and macroalgae. We assume that light-enhanced productivity led to elevated cell activity and thereby accounted for the increased respiration rates observed for coral and macroalgae during upwelling. Furthermore, not only decreased light availability, but also elevated temperatures may have also negatively affected primary production during the non-upwelling season.

The upwelling system in this area is considered as oligotrophic (Petús et al. 2007) and our own monthly nutrient concentration measurements in Gayraca Bay indicate nutrient-poor conditions throughout the year, yet at the same time revealed low, but significant increases in concentrations of nitrate and nitrite at the study sites during the upwelling season (Bayraktarov et al. unpublished data). The slightly elevated nutrient availability during the upwelling might account to some extent for the elevated benthic production rates and the seasonal occurrence of macroalgae.

We conclude that light availability, water temperature, and nutrient concentrations, all affected by seasonal upwelling in this area, appear to be particularly important for the dominant primary producers which show temporal patterns in carbon fluxes, namely corals, macroalgae, and algal turfs. In previous studies, seasonal algal blooms accounted for most of the seasonality in coral reefs at lower latitudes (Kinsey 1977, 1985), whereas corals seem to show seasonal pattern in productivity at higher latitudes (Atkinson and Grigg 1984). This study showed that both seasonal macroalgal blooms as well as the seasonality in photosynthetic performance of corals and algal turfs account for temporal shifts in community metabolism of lower latitude reefs subjected to seasonal upwelling events.

The observed upwelling-controlled temporal variability in primary production not only affects primary producers, but may also influence higher trophic levels of benthic and pelagic communities within coral reef ecosystems. Future studies should therefore identify the effects of temporal variability in primary production on higher trophic levels within coral reefs and adjacent ecosystems as well as the key factors controlling community metabolism and ecosystem functioning in these areas.

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