Biogeosciences
Open Access
Discussions

Spatiotemporal variability of sedimentary organic matter supply and recycling processes in coral reefs of Tayrona National Natural Park, Colombian Caribbean

E. Bayraktarov[1] and C. Wild[1,2]

[1]Coral Reef Ecology Group (CORE), Leibniz Center for Tropical Marine Ecology (ZMT), Fahrenheitstraße 6, 28359, Bremen, Germany
[2]Faculty of Biology and Chemistry (FB2), University of Bremen, Bremen, Germany

Correspondence to: E. Bayraktarov (elisa.bayraktarov@zmt-bremen.de)

Discussion Paper | Discussion Paper | Discussion Paper | Discussion Paper

BGD
10, 19895–19933, 2013

Spatiotemporal variability of SOM

E. Bayraktarov and C. Wild

Title Page

Abstract | Introduction
Conclusions | References
Tables | Figures

◄ | ►
◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Abstract

Sediments are fundamental for the functioning of oligotrophic coral reef ecosystems, because they are major places for organic matter recycling. In Tayrona National Natural Park (TNNP), Colombian Caribbean, located between the population center Santa Marta ($> 455\,000$ inhabitants) in the southwest and several river mouths in the east, coral reef sediments experience pronounced changes in environmental conditions due to seasonal coastal upwelling, but knowledge on relevant spatiotemporal effects on organic matter supply to sediments and recycling processes is not available. Therefore, sediment traps were monthly deployed over 14 months complemented by assessment of sedimentary properties and sedimentary O_2 demand (SOD) at water current-exposed and -sheltered sites along distance gradients (12–20 km) to Santa Marta and the eastern river mouths (17–27 km). Findings revealed that seasonal upwelling delivered strong (75–79 % of annual supply) pulses of labile organic matter mainly composed of fresh phytoplankton detritus (C : N ratio 6–8) to the seafloor. Sedimentary chlorophyll contents and SOD increased significantly with decreasing distance to the eastern rivers, but only during upwelling. This suggests sedimentary organic matter supply control by nutrient-enriched upwelling waters and riverine runoff rather than by the countercurrent-located city of Santa Marta. Organic matter pulses caused C turnover rates of 4.4 % h^{-1} that were more than 2-fold higher at water current-exposed compared to -sheltered sites. This indicates intense advective pore water exchange and ensuing rapid recycling of the supplied labile organic matter, particularly in the highly permeable water current-exposed silicate reef sands.

1 Introduction

Marine sediments are the major sites for mineralization and nutrient regeneration of organic matter derived from pelagic primary production. They cover over 70 % of the world's continental shelves (Emery, 1968). Around 83 % of all remineralization in the

ocean bottom takes place in the shelf sediments where 20–50 % of the local net phytoplankton production is deposited (Nixon, 1981; Jørgensen, 1983; Wollast, 1991).

Biogeochemical processes in the oxic surface layer of marine sediments can account for more than half of the total organic carbon mineralization (Jørgensen and Revsbech, 1989) and play a particularly important role for highly permeable, carbonate sediments in coral reefs (Boucher et al., 1994; Alongi et al., 1996; Werner et al., 2006). The efficiency of sedimentary organic matter remineralization largely depends on the properties of sediment e.g. grain-size (Zobell, 1938; Newell, 1965; Meyer-Reil, 1986), permeability (Webb and Theodor, 1968; Precht and Huettel, 2004; Rusch et al., 2006), carbonate content (Capone et al., 1992; Rasheed et al., 2003), sorption capacity (Sansone et al., 1987; Wang and Lee, 1990), and the quality of supplied organic matter. Organic matter quality can be characterized by the lability to degradation and its $C : N$ content close to Redfield ratio 6.6 for fresh phytoplankton detritus, but typically between 6–8 for phytoplankton of the open ocean and intertidal flats (e.g. Canfield et al., 2005). Lability of organic matter usually follows the trend: small soluble molecules > pigments >> lipids > amino acids > carbohydrates (Meyer-Reil, 1986; Henrichs, 1992; Wakeham et al., 1997; Fenchel et al., 1998). Lignin from terrestrial plants belongs to the most refractory organic materials (Hedges et al., 1988; Canfield, 1994). Old and partly degraded organic matter will have a higher $C : N$ ratio as the limiting N is preferentially used up by marine organisms (Canfield et al., 2005).

Reef sediments are typically derived from the calcareous skeletons of corals processed by bio-eroding organisms, but also by other biological, chemical and physical processes (Glynn, 1997; Hallock, 1997). They are usually highly permeable, have large grain-sizes (Huettel et al., 2003; Rasheed et al., 2003), and are associated with many heterotrophic microorganisms (Wild et al., 2006) involved in the recycling of organic matter. Permeable reef sediments function as biocatalytical filters that lead to a very effective processing and regeneration of organic matter (Wild et al., 2004a, 2005a, b, 2008). Consequently, these sediments contribute to the release of the limiting nutrients N and P after remineralization of organic material (Rasheed et al., 2002). Natural

pulses of organic matter (Glud et al., 2008; Wild et al., 2008) that may lead to eutrophication and diseases (Fabricius, 2005), are rapidly degraded and thereby disposed.

Through their contribution to an efficient element cycling (Rasheed et al., 2002; Wild et al., 2004a), reef sediments are crucial for the functioning of coral ecosystems and help to maintain their typically high biomass and primary productivity (Hatcher, 1988; Sorokin, 1993), despite of the surrounding oligotrophic waters (Crossland and Barnes, 1983; Kleypas et al., 1999; Veron, 2000).

The investigation of sedimentary properties and processes in coral reefs is particularly important for regions where agricultural activity, riverine discharge or seasonal upwelling lead to surplus nutrient concentrations which in turn may stimulate phytoplankton blooms and ensuing high supply of organic matter to and accumulation in the sediments (Calvert, 1987). In Tayrona National Natural Park (TNNP), at the northeastern coast of Colombia, phytoplankton primary production is highly influenced by seasonal change through alternating rainy and dry seasons, and a seasonal upwelling (Salzwedel and Müller, 1983; Andrade and Barton, 2005; Paramo et al., 2011). In addition, particularly during rainy season, phytoplankton growth can be stimulated by riverine discharge of several smaller river mouths in the east (Rio Piedras, Mendihuaca, Guachaca, Buritaca, Don Diego, and Palomino) along a distance gradient of 17–27 km from the TNNP bays, while a seasonal upwelling changes the physical parameters (temperature, salinity, and water currents) in the water column and leads to an enrichment of inorganic nutrients for primary production (Franco-Herrera et al., 2006; Arévalo-Martínez and Franco-Herrera, 2008; García-Hoyos et al., 2010; Ramírez-Barón et al., 2010; Paramo et al., 2011; Bayraktarov et al., 2013). Furthermore, due to topographical orientation, the strong winds from the northeast that induce seasonal coastal upwelling, have a stronger impact on all western flanks of the TNNP bays leading to an increased exposition to waves and water currents as compared the eastern, sheltered flanks (Werding and Sánchez, 1989; Bayraktarov et al., 2013). In addition to the river mouths in the east, the TNNP is located at a distance gradient of 12–20 km to the population center Santa Marta with > 455 000 inhabitants (DANE, 2005) and an extensive harbor

area in the southwest that may have effects on organic matter supply and recycling processes in TNNP reef sediments.

Despite these spatiotemporal changes and potential key influences, no studies have addressed their potential effects on sedimentary properties and processes. To our knowledge, studies on the organic matter supplied and recycling processes of coral reef sediments are neither available for the Caribbean nor for any upwelling-influenced coral reefs. Therefore, a comprehensive monthly monitoring of sedimentary status and process variables was performed over 15 months at wind-, wave- and water current-exposed and sheltered sites in the major 4 TNNP bays Chengue, Gayraca, Neguanje, and Cinto. In addition, in one exemplary TNNP bay (Gayraca), the supply of particulate organic carbon and nitrogen (POC and PON) and chlorophyll (chl) *a* from the water column to the seafloor was assessed over 14 months using sediment traps, while grain-size distribution, porosity, carbonate content, concentrations of particulate organic matter (POM) and algal pigments in the sediments, and sedimentary O_2 demand (SOD) were measured at all sampling locations. Through the combined measurement of SOD and POC supply, it was also possible to quantify C turnover rates as a proxy for sedimentary organic matter recycling.

2 Materials and methods

Environmental monitoring of sedimentary processes was accomplished in the TNNP bays Chengue, Gayraca, Neguanje and Cinto, at a water current-exposed site on the western and a -sheltered site on the eastern flank of each bay (Fig. 1).

2.1 Assessment of sedimentary organic matter supply

Organic matter reaching the seafloor was measured monthly between January 2012 and February 2013 at exemplary sites in Gayraca Bay (Fig. 1). Custom-made sediment traps consisting of 40 cm long PVC cylinders with a diameter of 5.7 cm and closed

lower ends were constructed. Traps were deployed in triplicate at each of the two sites in Gayraca at a water depth of 10 m directly in the local coral reefs by attaching them to metal rods which were inserted into the seafloor for the period of study. Traps were always at 5 cm over the sea bottom and at approximately 10 m apart from each other. The deployment time was 48 ± 2 h. After collection, sediment traps were tighly closed in situ and brought upright to the boat where the water with collected suspended material was decanted into 1.8 L clean plastic containers and transported on ice and dark to the laboratory for immediate processing. Aliquotes from the homogenized total trap contents were filtered on pre-combusted glass fiber filters (VWR International; diameter: 25 mm, nominal particle retention: 0.7 µm) for POC (0.1 L), PON (0.1 L), and chl a analyses (0.1 L). Filters with particulate trap material for POM determination were dried for at least 48 h at 40 °C and stored dry and dark until analysis. Dried filters for POC analysis were acidified with sterile 1 N HCl until gas production ceased in order to remove small remaining carbonate grains from the particulate material as decribed by Nieuwenhuize et al. (1994) and subsequently dried for 48 h at 40 °C prior to measurements. Determinations of POC and PON were conducted by an elemental analyzer (EURO EA 3000, EuroVector, Radavalle, Italy). Carbon and nitrogen contents were derived from calculations using elemental standards (Acetanilide: containing 71.05 ± 0.18 % C and 10.42 ± 0.13 % N, HEKAtech GmbH, Wegberg, Germany). Filters for chl a were frozen at -20 °C and kept in the dark until extraction. Each filter was extracted using 6 mL 90 % acetone for 24 h at 4 °C in the dark. Measurements were performed by a fluorometer (excitation filter 436FS10, emmision filter 680FS10; 10AU™ Field Fluorometer, Turner Designs, Sunnyvale, USA) according to the non-acidification methods of Arar and Collins, (1997).

2.2   Assessment of sedimentary properties

Monitoring of sedimentary parameters took place in monthly intervals between December 2011 and February 2013. Sampling water depths were between 10.0 and 14.5 m depending on sediment availability in the bays. Sediments for porosity determination

and grain-size analysis were collected during major upwelling in 2011/2012 and non-upwelling in 2012 by a custom-made rectangular PVC corer (30 cm × 15 cm × 10 cm) from a sediment depth of 2 cm ($n = 3$ per site and sampling) and transported in plastic zip-lock bags to the laboratory. Sub-samples of sediment (ca. 200 g wet weight) were desalined with destilled water and dried at 80 °C for at least 24 h. Grain-size was determined by sieving dry sediment samples of a known weight through a calibrated sieve stack (mesh sizes of 2000, 1000, 500, 250, 125, 63, and including the < 63 µm fraction) for 10 min by a sieve-shaker (Analysette, Fritsch, Rudolstadt, Germany) and weighted. Porosity was calculated from weight loss of a known volume of wet and desalined sediment after drying at 80 °C for at least 24 h according to Higgins and Thiel (1988). Sediment samples ($n = 3$ for POM and $n = 3$ for algal pigments per site and month) were collected by custom-made cores consisting of cut-off syringes with diameters of 2.9 cm. Sediment cores containing the first 1 cm depth fraction of marine sediment with a surface area of 6.61 cm^2 were sealed by rubber stoppers in situ and transported to the laboratory on ice and dark. For POM analysis, sediment samples were dried for at least 48 h at 40 °C and stored dry and dark until analysis. Prior to analysis, all samples were homogenized by a grinder (Planetary Micro Mill Pulverisette 7, Fritsch, Rudolstadt, Germany) for 3 min. Sub-samples of 15–20 mg of the ultra-fine sediment were pre-weighted in silver cups for POC and aluminium for PON determination. POC samples were acidified several times with 1 N HCl to remove carbonate particles from the sediment according to Nieuwenhuize et al. (1994) and dried at 40 °C for at least one week prior to analysis. Elemental analyses of POC and PON in sediment samples were conducted as described above. Carbonate ($CaCO_3$) content was determined by subtraction of organic carbon content from POC analyses from total carbon determined by PON analyses.

For algal pigment extraction, sediment samples were freeze-dried overnight (Christ Alpha 1-4 LD Freeze dryer, SciQuip Ltd, UK) and homogenized in the dark by pestle and mortar. A sub-sample of 1 g from each homogenized sediment sample was weighted in 10 mL centrifuge tubes and subsequently treated with 7 mL cold 90 % ace-

tone. The samples were thereafter subjected to pulsed ultrasonic treatment (80 % amplitude, 70 W, for 2 min with pulses of 1 s, Bandelin 3100 Ultrasonic Homogenizer with M72 tip, vials on ice). Extraction was completed at 4 °C for 24 h in the dark. Prior to measurements with a UV/VIS spectrometer (Lambda 35 UV/Vis Spectrometer, Perkin Elmer) at wavelenghts 480, 510, 630, 647, 664 and 750 nm, samples containing algal pigments extracts were centrifuged for 10 min at 5000 rmp and 4 °C (Centrifuge 5804R, Eppendorf, USA). Determination of chl a, b, $c_1 + c_2$ and carotenoids was accomplished according to the trichroic equation of Jeffrey and Humphrey (1975) by the non-acidification method method of Arar (1997) in order to differentiate between common phytoplankton (chl a; Millie et al., 1993), green algae and vascular plants (chl b; Lorenzen, 1981; Millie et al., 1993), diatoms, chrysophytes, prymnesiophytes and dinoflagellates (chl $c_1 + c_2$; Millie et al., 1993; Ston et al., 2002).

2.3 Quantification of sedimentary oxygen consumption and carbon turnover

Rates of SOD were measured after a modified incubation method by Wild et al. (2010). Sediment was sampled by the custom-made cores described above and until a maximum of 1 cm sediment depth ($n = 4$ per site and month). Seawater required for incubations was sampled by a clean black neoprene bag of 25 L volume at a water depth of 10 m and sealed under water. Concentrations of dissolved O_2 were measured prior and after incubation by a portable meter (HQ40d, Hach, Loveland, USA) with luminescent dissolved oxygen optode (LDO101-01, Hach, Loveland, USA) immediately after sampling and on the boat. Prior to measurements, the O_2 optode was calibrated in 100 % water-saturated air according to the manufacturer's instructions. Sub-samples of the freshly sampled seawater ($n = 4$ per site and month) were taken by 80 mL glass jars and sediment fractions carefully inserted. Glass jars were closed avoiding any introduction of air and incubations were run in dark cooling boxes filled with ambient seawater for 8 ± 2 h. Incubation temperature was kept constant by a temperature controller with a sensor (STC-1000, SainSonic Inc) and an attached aquarium heater (H-229, HOPAR, Guangdong, China), and never exceeded ±2 °C relative to in situ seawater

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

temperature. Temperature of water during incubation was monitored by a HOBO Pendant temperature/light logger (Onset Computer Corp., Bourne, USA). Net SOD rates were calculated for each glass jar by dividing the difference between initial and end O_2 concentrations by incubation time and subtracting the seawater controls determined in 60 mL Winkler bottles ($n = 4$ per site and month) as described above. Negative rates of sediment O_2 uptake were transformed to absolute numbers and converted into mmol $O_2 \, m^{-2} \, d^{-1}$. Carbon turnover rates in Gayraca Bay were calculated by using the sedimentary POC supply (in mmol $m^{-2} \, h^{-1}$) and mean values of SOD. C turnover values were calculated as % of supplied POC h^{-1} remineralized according to Wild et al. (2004b).

2.4 Statistical data analyses

Seasonal time intervals of the TNNP used for statistical analyses of sedimentary parameters were defined as: major upwelling season (major dry season, December–April), minor non-upwelling season (minor rainy season, May–June), minor upwelling season (minor dry season, July–August), and major non-upwelling season (major rainy season, September–November) in accordance to Salzwedel and Müller (1983); Bula-Meyer (1990); Diaz-Pulido and Garzón-Ferreira (2002); and Andrade and Barton (2005). For analyses of sedimentation of POC, PON and chl *a* along with measurements of porosity and grain-size distributions, the seasonal time intervals were pooled to upwelling (major and minor upwelling) and non-upwelling (major and minor non-upwelling). For analyses of sedimentation rates, only parameteres measured in Gayraca Bay were used.

Seasonality and differences due to exposition to waves and water currents of the sampling locations were examined by a permutation multivariate analysis of variance (PERMANOVA; Anderson, 2001; Anderson et al., 2008). Analyses were performed with seasonal means of sedimentation variables (supply of POC, PON and chl *a* to the

sediment), sedimentary parameters (chl a, chl b, chl $c_1 + c_2$, carotenoids, POC, PON, CaCO$_3$, and SOD), and sediment characterization (grain-size and porosity).

Univariate PERMANOVAS were performed for each sedimentation and sedimentary variable, and sediment characterization, separately in order to identify significant differ-
ences between seasons, bays and exposure (Table 1). For the sedimentary variables chl a, chl b, chl $c_1 + c_2$, carotenoids, POC, PON, CaCO$_3$ and SOD, the fixed factors were seasons with 4 levels (major and minor upwelling, major and minor non-upwelling) and exposure with 2 levels (exposed and sheltered), whereas bays (Chengue, Gayraca, Neguanje, and Cinto) were set as a random factor. For sedimentation variables the
fixed factors were exposure (exposed vs. sheltered site) and season (upwelling vs. non-upwelling), while for sediment characterization parameters, the fixed factors were exposure (exposed vs. sheltered site) and season (upwelling vs. non-upwelling) along with the random factor bay (Chengue, Gayraca, Neguanje, and Cinto). Correlations among sedimentary parameters and along the horizontal distance gradient between
Santa Marta and the TNNP bays were identified by a Spearman's rank correlation (Tables 2 and 3).

Multivariate analyses considered the sedimentary variables grain-size, porosity, carbonate content of sediments, POC, PON, chl a, chl b, chl $c_1 + c_2$, carotenoids, and SOD (Table 4). Prior to analyses, sedimentary variables were normalized by subtract-
ing the mean and dividing by the standard deviation of each variable (z-transformation), thereby enabling a comparison on the same scale where all means equal 0 and the standard deviations are 1 (Quinn and Keough, 2002). Euclidean similarity was used to obtain the resemblance matrix, and a Type III sum of squares (partial, SS) was used in order to calculate the significance levels under a reduced model for all PERMANOVA
analyses. A Principle Coordinates Ordination (PCO; Gower, 1966) was used to visualize the seasonal patterns of sedimentary variables, bays and exposure. The effects and correlations of sedimentary variables with both PCO axes were indicated as vectors.

Statistical analyses were conducted by the software PRIMER[©] (Plymouth Routines in Multivariate Ecological Research; v 6.1.11 PRIMER-E Ltd., UK) and the PRIMER[©]

add on PERMANOVA+ (v 1.0.1 PRIMER-E Ltd., UK). The software SigmaPlot 12.0 (Systat Software, Inc) was used for graphical representation of data.

3 Results

Temporal variations for all data on organic matter supply to sediments and sedimentary parameters of all bays are provided as Supplement (Fig. S1–S6). The seasonal means at the exposed and sheltered sites for the TNNP bays Chengue, Gayraca, Neguanje and Cinto are also available as Supplement (Table S1–S4).

3.1 Sedimentary organic matter supply

Spatial differences. Generally, more POC, PON and chl a were supplied to the seafloor at the exposed site in Gayraca Bay (Figs. 2 and 3), but only sedimentary POC supply had significant difference between sites (Table 1). Mean molar POC : PON ratio was similar between the exposed (7.3) and the sheltered site (7.6) and without significant spatial difference (Table 1). The relative molar chl a fraction of the total trapped POC was higher at the exposed (0.11 %) than at the sheltered site (0.06 %), but without significant difference (Table 1).

Temporal differences. Significantly higher rates of POC and PON sedimentation (Table 1) were measured during major upwelling with $502.5 \pm 201.3\,\mathrm{mg\,POC\,m^{-2}\,d^{-1}}$ (mean $\pm$ SD) and $86.0 \pm 42.6\,\mathrm{mg}$ PON $\mathrm{m^{-2}\,d^{-1}}$ compared to major non-upwelling with $320.4 \pm 98.4\,\mathrm{mg}$ POC and $42.0 \pm 15.1\,\mathrm{mg\,PON\,m^{-2}\,d^{-1}}$, respectively. Rates were also high during minor upwelling with $523.1 \pm 129.6\,\mathrm{mg\,POC\,m^{-2}\,d^{-1}}$ and $82.8 \pm 36.8\,\mathrm{mg\,PON\,m^{-2}\,d^{-1}}$ as compared to minor non-upwelling with $369.0 \pm 138.1\,\mathrm{mg}$ POC and $56.7 \pm 25.1\,\mathrm{mg\,PON\,m^{-2}\,d^{-1}}$, respectively. Chl a supplied to the sediment was generally higher during major ($47.2 \pm 37.8\,\mathrm{mg\,chl}\,a\,\mathrm{m^{-2}\,d^{-1}}$; mean + SD) and minor ($22.4 \pm 15.6\,\mathrm{mg\,chl}\,a\,\mathrm{m^{-2}\,d^{-1}}$) upwelling as compared to major and minor non-upwelling

(4.9 ± 5.1 mg and 7.6 ± 7.8 mg chl a m^{-2} d^{-1}, respectively), and were close to significant seasonal differences (Table 1).

Sedimentation of POC was positively correlated to POC turnover rate and negatively to sedimentary carbonate content and SOD. The sedimentation rate of chl a was positively correlated to sedimentation of POC and PON, and POC turnover. Pulses of organic matter supply were particularly observed during major (December–April) and midyear (July–August) upwelling (Figs. 2 and 3). Annual mean rates of organic matter supplied to the sediments interpolated over 14 months of monitoring were 200 g POC m^{-2} yr^{-1}, 34 g PON m^{-2} yr^{-1}, and 16 g chl a m^{-2} yr^{-1} at the exposed, and 136 g POC m^{-2} yr^{-1}, 21 g PON m^{-2} yr^{-1}, and 7 g chl a m^{-2} yr^{-1} at the sheltered site, respectively.

3.2 Sedimentary status parameters

Spatial differences. Sediments at the exposed sites were largely composed of well-moderately sorted, very coarse sands with a mean grain-size of 973 ± 374 µm (± SD). Poorly-sorted medium-coarse sands with significantly smaller grain-sizes (598 ± 123 µm) were found at the sheltered sites (Table 1). The porosity at the exposed sites (36.5 ± 9.9 % wt/wt; mean ± SD) was generally lower than at the sheltered sites (45.2 ± 4.8 % wt/wt). Carbonate contents were generally low and significantly higher (Table 1) at the sheltered (8.4 ± 2.7 % dry weight; mean ± SD) than at the exposed sites (6.7 ± 2.7 %) and indicated sediments mainly composed of silicate. Significant differences were observed between the bays (Table 1) with highest carbonate content in Chengue (10.1 ± 1.2 %), followed by Neguanje (8.4 ± 1.2 %), Gayraca (7.4 ± 3.4 %), and Cinto (4.4 ± 0.8 %). POC in reef sediments was significantly different between sites of exposure (Table 1) with higher contents at the sheltered (2.40 ± 0.48 mg POC g (dry mass)$^{-1}$) as compared to the exposed (2.14 ± 0.60 mg POC g^{-1}) sites. Highest PON content of 0.38 ± 0.08 mg PON g (dry mass)$^{-1}$ was observed in sediments from Chengue Bay, followed by Gayraca (0.32 ± 0.06 mg PON g^{-1}), Cinto (0.31 ± 0.10 mg PON g^{-1})

and Neguanje ($0.29 \pm 0.06\,\mathrm{mg\,PON\,g^{-1}}$), however with significant difference (Table 1) only between Chengue and Neguanje. No significant differences in sedimentary PON contents were observed between the sites of different water current-exposure (Table 1). The pigments chl a, chl $c_1 + c_2$ and carotenoids exhibited significantly higher concentrations (Table 1) at the sheltered ($6.42 \pm 3.51\,\mathrm{\mu g\,chl}\,a\,\mathrm{g\,(dry\,mass)^{-1}}$, $0.86 \pm 0.45\,\mathrm{\mu g\,chl}\,c_1 + c_2\,\mathrm{g\,(dry\,mass)^{-1}}$ and $2.22 \pm 1.23\,\mathrm{\mu g\,carotenoids\,g\,(dry\,mass)^{-1}}$) than at the exposed sites (4.91 ± 2.49, 0.58 ± 0.31 and $1.49 \pm 0.83\,\mathrm{\mu g\,g^{-1}}$, respectively). For concentrations of chl b, significantly higher concentrations were measured at the exposed ($0.36 \pm 0.25\,\mathrm{\mu g\,chl}\,b\,\mathrm{g\,(dry\,mass)^{-1}}$) than at the sheltered ($0.25 \pm 0.16\,\mathrm{\mu g\,g^{-1}}$) sites. During major upwelling, sedimentary chl a, chl $c_1 + c_2$, and carotenoids increased with decreasing distance to the rivers in the east (Table 2). The significant correlations along the distance gradient disappeared during non-upwelling, except for the positive correlation between distance to Santa Marta and carotenoids during minor non-upwelling (Table 2).

Temporal differences. No seasonal differences were observed for the sedimentary properties grain-size, porosity and carbonate content (Table 1). Sedimentary grain-size was negatively correlated to chl $c_1 + c_2$, carotenoids, SOD, carbonate content and porosity of sediments (Table 3). Carbonate content was positively correlated to PON contents and porosity of sediments (Table 3). Sediment porosity was positively correlated to chl $c_1 + c_2$ and carbonate content of sediment, and highly negatively correlated to sedimentary grain-size (Table 3). POC contents in reef sediments were significantly different between seasons (Table 1). Highest POC was measured during major non-upwelling ($2.54 \pm 0.63\,\mathrm{mg\,POC\,g^{-1}}$; mean $\pm$ SD) and lowest during minor non-upwelling ($2.02 \pm 0.35\,\mathrm{mg\,POC\,g^{-1}}$). Similar POC contents were measured during major ($2.23 \pm 0.54\,\mathrm{mg\,POC\,g^{-1}}$) and minor ($2.31 \pm 0.56\,\mathrm{mg\,POC\,g^{-1}}$) upwelling. Sedimentary POC was highly correlated to PON and was additionally positively correlated to carotenoids and SOD (Table 3). Sedimentary PON contents ranged between $0.31 \pm 0.08\,\mathrm{mg\,PON\,g^{-1}}$ (mean $\pm$ SD) during major upwelling and $0.37 \pm 0.09\,\mathrm{mg\,PON\,g^{-1}}$ during major non-upwelling, but without significant differences between seasons (Table 1).

PON had a highly significant correlation with sediment POC and was positively correlated to carbonate content and sedimentary chl b concentration (Table 3). From all algal pigments, only chl $c_1 + c_2$ and carotenoids showed significant seasonal differences (Table 1) with highest concentrations of $0.82 \pm 0.29\,\mu g\,chl\,c_1 + c_2\,g^{-1}$ (mean $\pm$ SD) and 2.18±0.82 µg carotenoids g^{-1} during major non-upwelling and lowest during minor non-upwelling with 0.50 ± 0.32 and $1.52 \pm 0.70\,\mu g\,g^{-1}$, respectively. Sedimentary contents of chl $c_1 + c_2$ and carotenoids were similar during major ($0.74 \pm 0.47\,\mu g\,chl\,c_1 + c_2\,g^{-1}$ and $1.83 \pm 1.34\,\mu g$ carotenoids g^{-1}) and minor (0.68 ± 0.29 and $1.80 \pm 0.72\,\mu g\,g^{-1}$, respectively) upwelling. Concentrations of chl a in marine sediments were significantly different between seasons (Table 1) with higher values during major ($6.12 \pm 3.99\,\mu g\,chl\,a\,g^{-1}$) upwelling and non-upwelling ($5.59 \pm 1.72\,\mu g\,chl\,a\,g^{-1}$) than compared to minor ($4.90 \pm 1.83\,\mu g\,chl\,a\,g^{-1}$) upwelling and non-upwelling ($4.92 \pm 1.56\,\mu g\,chl\,a\,g^{-1}$). Chl a exhibited positive correlations with chl $c_1 + c_2$, carotenoids and SOD, while chl b was only correlated to sedimentary PON (Table 3). Chl $c_1 + c_2$ had positive correlations with carotenoids, SOD and porosity, and was negatively correlated to grain-size of sediments (Table 3). Carotenoids had positive correlations with POC, SOD and a negative correlation with sedimentary grain-size (Table 3).

3.3 Sedimentary O$_2$ demand and POC turnover

Spatial differences. Sedimentary O_2 uptake was significantly higher (Table 1) at the sheltered ($18.2 \pm 5.9\,mmol\,O_2\,m^{-2}\,d^{-1}$; mean $\pm$ SD) than at the exposed ($12.3 \pm 6.6\,mmol\,O_2\,m^{-2}\,d^{-1}$) sites. SOD had a positive correlation with distance gradient during major upwelling (Table 2). Turnover rates of POC were significantly higher (Table 1) at the exposed ($4.4 \pm 2.1\,\%$ of supplied $POC\,h^{-1}$; $\pm$ SD) than at the sheltered site ($1.6 \pm 0.7\,\%$ of supplied $POC\,h^{-1}$) in Gayraca Bay.

Temporal differences. Seasonal differences had no effects on sedimentary SOD. POC turnover rates were generally higher during major and minor upwelling (3.6 ± 2.5 and $3.1 \pm 1.3\,\%$ of supplied $POC\,h^{-1}$) than during major and minor non-upwelling

(1.8 ± 1.2 and 1.9 ± 1.0 % of supplied $POC h^{-1}$), but without significant seasonal difference (Table 3). SOD was furthermore positively correlated to chl a, chl $c_1 + c_2$, carotenoids, POC and negatively correlated to grain-size of sediments (Table 3). The organic matter pulses during major and minor upwelling stimulated the POC turnover rates at the exposed, but not at the sheltered sites (Fig. 4). Only during midyear upwelling (July–August), POC turnover rates increased from 1.1 to 4.0 % of supplied $POC h^{-1}$ (Fig. 4) at this site. Sedimentation of PON was positively correlated to POC supply and POC turnover, but negatively correlated to SOD.

3.4 Spatiotemporal analysis

Multivariate analyses taking into account the sedimentary parameters grain-size distribution, porosity, carbonate content, sedimentary POC and PON, chl a, chl b, chl $c_1 + c_2$, carotenoids, and SOD as variables showed that spatial differences were more pronounced than seasonal. While no significant seasonal differences were observed among the overall sedimentary parameters, significant spatial differences were present between sites with different exposure and bays (Table 4). Pair-wise comparisons revealed that the measured parameters were only significantly different between the seasons major non-upwelling and minor non-upwelling (Table 4). Differences in sedimentary parameters between bays were significant between Chengue and Neguanje, Chengue and Cinto, and between Neguanje and Cinto (Table 4).

PCO ordination confirmed results of multivariate analyses showing that best separation was obtained by grouping the data in their (dis)similarity according to the degree of exposure between sites (Fig. 5c). Only during major upwelling, the parameters chl a, chl $c_1 + c_2$, carotenoids and SOD were significantly positively correlated to the distance gradient between Santa Marta and the river months in the east indicating that riverine discharge did not affect sedimentary parameters during the other seasons. The countercurrent-located city Santa Marta had no measurable effects on sedimentary properties.

4   Discussion

4.1   Organic matter supply to reef sediments

The organic matter supplied to TNNP reef sediments was generally higher at the wind-, wave- and water current-exposed site and increased significantly during seasonal upwelling. The high contents of organic matter delivered to the sediments at the exposed site are likely the consequence of increased water mixing and transport processes by water currents which may facilitate the accumulation of phytoplankton detritus to heavier, sinking aggregates (Alldredge and Silver, 1988; Kepkay, 1994). The molar C : N ratio of organic matter was above the Redfield ratio of 6.6 for fresh phytoplankton detritus (Redfield, 1958), but generally kept within the range of 6–8 for open ocean and intertidal flat phytoplankton (Canfield et al., 2005). Only during January, C : N ratio of organic matter supplied to the sediments decreased below 6.6 indicating a depletion of organic carbon and a relative enrichment in N. Typically during non-upwelling, C : N ratios exceeded 8 suggesting a relatively less important contribution of phytoplankton to sedimentary organic matter supply.

During major and midyear upwelling, the sedimentation rates of chl a exceeded typical values of $< 15\,\mu g\,m^{-2}\,d^{-1}$ reported for shallow oligotrophic coral reefs (e.g. Gulf of Aqaba, Red Sea; Wild et al., 2009) by 2–3 orders of magnitude. The high amount of chl a delivered to TNNP sediments is unique for coral reefs as it exceeded even sedimentation rates of chlorophyll after natural pulses of large amounts of organic matter e.g. during mass coral spawning events ($< 3.0\,mg\,m^{-2}\,d^{-1}$; Wild et al., 2008). These high rates of chl a sedimentation may potentially be caused by extensive phytoplankton blooms triggered by enrichment of inorganic nutrient availability not only via upwelling (Franco-Herrera et al., 2006; Arévalo-Martínez and Franco-Herrera, 2008; García-Hoyos et al., 2010; Ramírez-Barón et al., 2010; Bayraktarov et al., 2013) but also via discharge of several smaller river mouths in the east of TNNP (Bayraktarov et al., unpublished data).

The supply with organic carbon to the seafloor can range from $50\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in oceanic areas, but may reach 200–$600\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in coastal settings where nutrients are delivered by rivers, upwelling currents or water mixing (Bordenave, 1993). In TNNP, over 75 % of the annual organic matter delivery was supplied during seasonal upwelling (December–April and July–August) to the sediments (79 % at the exposed and 76 % at the sheltered site). Annual POC sedimentation rates in TNNP were close to rates reported for Kaneohe Bay, Hawaii ($179\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$; Taguchi, 1982) and Tuamotu atoll lagoon, French Polynesia ($128\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$; Charpy and Charpy-Roubaud, 1991), higher than rates registered in Davies Reef, Great Barrier Reef, Australia (33–$51\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$; Hansen et al., 1992), but below rates measured in south-west lagoon in New Caledonia ($276\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$; Clavier et al., 1995) or One Tree Island, Great Barrier Reef, Australia ($548\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$; Koop and Larkum, 1987). According to the amount of POC supplied to the sediments, the TNNP can be classified as mesotrophic (100–$300\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$; Nixon, 1995). This is the first dataset on the spatial and temporal dynamics of organic matter supplied to reef sediments in the Caribbean which are influenced by seasonal upwelling.

4.2 Sedimentary properties

Finer sediments with higher porosity and carbonate content were observed at water current-sheltered sites in TNNP as compared to -exposed sites. The sediments at the sheltered sites exhibited higher accumulation of POC and the algal pigments chl a, chl $c_1 + c_2$ and carotenoids. The accessory pigment chl $c_1 + c_2$ indicates that sediments at the sheltered sites were characterized by benthic autotrophs such as diatoms, chrysophytes, prymnesiophytes and/or dinoflagellates (Millie et al., 1993; Ston et al., 2002). A higher concentration of the accessory pigment chl b at the exposed site indicates rather the presence of green algae than vascular plant detritus (Lorenzen, 1981; Millie et al., 1993) due to the observed C : N ratio of 6–8 indicative for phytoplankton (Canfield et al., 2005).

Accumulation of organic matter is facilitated by slow decomposition in low-energy fine-grained sediments (Bordenave, 1993) like at the sheltered sites of TNNP where significantly more organic carbon accumulated. Our findings of higher accumulation of organic material at these sites are supported by several studies showing that fine-grained sediments usually carry high organic matter content and support a higher microbial biomass as compared to coarse sediments (Zobell, 1938; Newell, 1965; Meyer-Reil, 1986). Especially calcareous reef sands are often associated with high numbers of heterotrophic microorganisms (Wild et al., 2006) involved in a rapid remineralization of organic matter (Rasheed et al., 2002; Wild et al., 2004a). However, reef sediments in TNNP had lower carbonate contents ($< 11\%$) than reported for other reef areas (75–85 % for Gulf of Aqaba, Red Sea; Rasheed et al., 2003), and contents of supplied organic material were comparable to organic carbon in reef sediments composed of silicate ($2.4\,\mathrm{mg\,g^{-1}}$; Rasheed et al., 2003). Accumulated organic carbon was below values reported for carbonate coral reefs (e.g. $3.6\,\mathrm{mg\,g^{-1}}$ for the Gulf of Aqaba, Red Sea; Rasheed et al., 2003 or 3.4–$4.7\,\mathrm{mg\,g^{-1}}$ for the Great Barrier Reef; Moriarty, 1982). POC contents in TNNP sediments are in the range of typical values for shallow, oxygenated sediments of the shelf ($< 5\,\mathrm{mg\,g^{-1}}$; Bordenave, 1993; Jørgensen, 1996). The lower content of organic carbon in the coarse, water current-exposed sediments is likely to be the result of an efficient remineralization of organic matter (Webb and Theodor, 1968) through the increased advective transport of solutes within these permeable sediments (Precht and Huettel, 2004; Reimers et al., 2004; Rusch et al., 2006). Dell'Anno et al. (2002) observed that oligotrophic control sites in Mediterranean sediments had mean values of $< 4\,\mathrm{\mu g\,chl\,}a\,\mathrm{g^{-1}}$ and suggested this as a threshold for oligotrophic sediments. As the chl a content in TNNP reef sediments oscillated slightly above this value ($4.9\,\mathrm{\mu g\,chl\,}a\,\mathrm{g^{-1}}$ during non-upwelling and $6.1\,\mathrm{\mu g\,chl\,}a\,\mathrm{g^{-1}}$ during upwelling), they can be characterized as meso-oligotrophic.

4.3 Sedimentary oxygen consumption and organic carbon recycling

Findings of the present study indicate that reef sediments of TNNP are very efficient in the degradation and recycling of organic matter supplied by the water column. The behavior of higher SOD in the finer sediments with higher porosity at sheltered locations in comparison to exposed sites is in agreement with the study of Alongi et al. (1996), who reported SOD of $10.5\,\mathrm{mmol\,m^{-2}\,d^{-1}}$ at sheltered sites compared to $2.1\,\mathrm{mmol\,m^{-2}\,d^{-1}}$ in the carbonate-rich sand of the exposed back-reef lagoon of Ningaloo Reef, Western Australia. The higher oxygen demand at the sheltered sites could be explained by the accumulated detritus which experiences a retention at these sites due to a restricted water circulation as suggested by Alongi et al. (1996). SOD in TNNP was in the range of $10–120\,\mathrm{mmol\,O_2\,m^{-2}\,d^{-1}}$ reported for permeable sediments of the continental shelf (Reimers et al., 2004; Rusch et al., 2006).

At the exposed site in Gayraca Bay, significantly more organic matter was supplied than at the sheltered site. However, values of less accumulated organic matter at the exposed site than at the sheltered site suggest a rapid and efficient remineralization here. Higher sedimentation rates at the exposed site stimulated a 2.8 fold higher POC turnover than at the sheltered site. At the exposed site, highest POC turnover rates $> 5.0\,\%$ of supplied $\mathrm{POC\,h^{-1}}$ were detected during the upwelling months January–March and peaked with $9.5\,\%$ of supplied $\mathrm{POC\,h^{-1}}$ during February, while rates at the sheltered site were $< 2.0\,\%$ of supplied $\mathrm{POC\,h^{-1}}$ with maximum of $4.0\,\%$ of supplied $\mathrm{POC\,h^{-1}}$ in July (midyear upwelling). These results indicate that rapid POC turnover rates were mainly triggered by the surplus of fresh phytoplankton detritus supplied to the sediments during upwelling. Significantly higher turnover rates at the exposed than at the sheltered site with mean values of $4.4\,\%$ of supplied $\mathrm{POC\,h^{-1}}$ (exposed) and $1.6\,\%\,\mathrm{h^{-1}}$ (sheltered) were registered. These rates are higher than those reported for silicate reef sediments supplied by natural organic matter such as eggs of the giant clam *Tridacna* sp., zooxanthellae or coral mucus ($< 1.0\,\%\,\mathrm{POC\,h^{-1}}$; Wild et al., 2005b). Turnover rates of POC in sediments at the exposed site were in the range of carbon-

ate reef sediments supplemented by natural organic substrates (1.4–8.8 % POC h^{-1}; Wild et al., 2004b, 2005b). Turnover rates of 4.4 % POC h^{-1} are exceptionally high for reef sediments under natural conditions. These rates would be expected in carbonate reef sediments which due to their high permeability, filtration rate, and large surface

5 area, support a dense population of benthic phototrophs (Rasheed et al., 2003) and high numbers of heterotrophic microorganisms (Wild et al., 2006) which make them very effective in the remineralization of organic matter (Wild et al., 2004a, 2005a, b, 2008). However, with a carbonate content of < 11 %, the TNNP reef sediments were mainly composed of silicate sands. Silicate sands are less permeable, have a limited

10 specific surface area and consequently, a smaller number of microorganisms as compared to carbonate sands (Rasheed et al., 2003; Wild et al., 2005b). Surprisingly, the C turnover rates of TNNP reef sediments mainly composed by silicate were higher than turnover rates for other silicate reef sands (Wild et al., 2005b). Further studies on carbon turnover rates in silicate reef sands are lacking. Explanations for these

15 high turnover rates may be given by: (1) the sediment properties and/or (2) the quality of supplied organic matter. Sediments at the exposed site are coarse, with lower porosity and continuously flushed by increased water current dynamics. Water currents may augment the advective transport of organic matter through permeable sediments (Huettel et al., 2003; Rasheed et al., 2003; Precht and Huettel, 2004; Reimers et al.,

20 2004), thus transforming them into biocatalytical filter systems in which a rapid and efficient recycling of organic matter is promoted (Wild et al., 2004a, 2005a, 2008; Rusch et al., 2006). At the sheltered site, the finer sediments are not facilitating advective porewater exchange to that extent, so that organic matter is comparably less recycled and rather accumulates (Huettel et al., 2003). In addition to sediment properties, sediments

25 of TNNP received organic matter with extremely high chl *a* contents from phytoplankton detritus of a C : N between 6–8, representing an easily degradable, fresh organic material. Through their sediment properties and the upwelling-triggered supply with fresh organic matter, reef sediments of TNNP appear highly adapted towards processing of organic matter pulses triggered by seasonal upwelling and eutrophication events.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◀ | ▶|

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

4.4 Spatio-temporal influences and ecological perspective

The findings of the present study indicate that the reef sediments in TNNP are rather controlled by location than by season. Water current exposed sediments exhibited higher POC turnover rates after upwelling-induced pulses of organic matter sedimenta-
5 tion than sediments at the sheltered site. The high POC turnover rates at the exposed site suggest a good pelagic-benthic coupling and processing of organic matter pulses during major and midyear upwelling.

Sedimentary chl a and SOD increased significantly with decreasing distance to the eastern rivers during upwelling, while no correlation along this distance gradient was
10 observed during non-upwelling, suggesting an effect of nutrient-enriched upwelling waters and riverine runoff from the east rather than an influence from the countercurrent-located city of Santa Marta in the southwest. Correlations of seawater chl a concentration and biological oxygen demand with this distance gradient were also observed for the water column, however, the correlations were present during non-upwelling and
15 disappeared during upwelling (Bayraktarov et al., unpublished data). Significantly increased chl a concentrations with a mean value of $2.70\,\mu g\,L^{-1}$ were observed during upwelling in TNNP seawater (Bayraktarov et al. unpublished data) which may explain the higher rates of chl a supply to the sediments, where also an accumulation of chl a was registered during this season.

20 Significant seasonal differences were observed for sedimentation rates of POC and PON which were increased during upwelling. Higher organic matter supply to the seafloor during upwelling is consistent with the reported higher phytoplankton growth (Franco-Herrera et al., 2006; Arévalo-Martínez and Franco-Herrera, 2008; García-Hoyos et al., 2010; Ramírez-Barón et al., 2010) as a result of inorganic nutrient en-
25 richment during this season (Salzwedel and Müller, 1983; Bayraktarov et al., 2013). While sedimentation rates of organic matter were higher during upwelling, incorporation of POC, chl $c_1 + c_2$ and carotenoids into the sediments was significantly increased during non-upwelling. In contrast to studies that reported pronounced seasonal effects

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◀ | ▶|

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

on sedimentary properties (Clavier et al., 1995; Rusch et al., 2000), the multivariate analyses in the present study showed that location (exposed vs. sheltered) and the differences between bays had stronger effects on sedimentary parameters than seasonal change.

Turnover rates of POC adjusted to the amount of supplied organic carbon and were always higher at the exposed sites, characterizing them as major places for organic matter recycling in TNNP. These findings suggest fast recycling of organic matter with ensuing release of regenerated nutrients from the reef sediments. This in turn may fuel new benthic primary production. Our results show that the supply of organic matter to the sediments is controlled by phytoplankton production in the water column and is likely triggered by seasonal upwelling and riverine discharge. Rates of sedimentation of organic carbon, sedimentary organic matter, and chl *a* concentrations suggest the marine sediments of TNNP as meso-oligotrophic. The present study thus indicates that the parameters sedimentation rate of organic carbon and sedimentary organic matter including chl *a* contents are cost-effective biophysical indicators that are recommended to be included in regular monitoring activities of TNNP coral reefs.

Supplementary material related to this article is available online at http://www.biogeosciences-discuss.net/10/19895/2013/ bgd-10-19895-2013-supplement.pdf.

References

Alldredge, A. L. and Silver, M. W.: Characteristics, dynamics and significance of marine snow, Prog. Oceanogr., 20, 41–82, 1988.

Alongi, D. M., Tirendi, F., and Goldrick, A.: Organic matter oxidation and sediment chemistry in mixed terrigenous-carbonate sands of Ningaloo Reef, Western Australia, Mar. Chem., 54, 203–219, 1996.

Anderson, M. J.: A new method for non-parametric multivariate analysis of variance, Austral Ecol., 26, 32–46, 2001.

Anderson, M. J., Gorley, R., and Clarke, K: PERMANOVA+ for PRIMER: guide to software and statistical methods, PRIMER-E, Plymouth, UK, 2008.

Andrade, C. A. and Barton, E. D.: The Guajira upwelling system, Cont. Shelf Res., 25, 1003–1022, 2005.

Arar, E. J.: Method 446.0: in vitro determination of chlorophylls a, b, $c_1 + c_2$ and pheopigments in marine and freshwater algae by visible spectrophotometry, Ohio, 26 pp., 1997.

Arar, E. J. and Collins, G. B.: Method 445.0: in vitro determination of chlorophyll a and pheophytin a in marine and freshwater algae by fluorescence, Ohio, 22 p., 1997.

Arévalo-Martínez, D. and Franco-Herrera, A.: Características oceanográficas de la surgencia frente a la Ensenada de Gaira, departamento del Magdalena, época seca menor de 2006. Bol. Invest. Mar. Cost., 37, 131–162, 2008.

Bayraktarov, E., Eidens, C., Pizarro, V., Wilke, T., and Wild, C.: Bleaching susceptibility and recovery of Colombian Caribbean corals in response to water current exposure and seasonal upwelling, PLoS ONE, e80536, 2013.

Bordenave, M. L.: The sedimentation of organic matter, in: Applied Petroleum Geochemistry, 1st Edn., Editions Technip, Paris, 17–20, 1993.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◄ | ►

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Boucher, G., Clavier, J., and Garrigue, C.: Oxygen and carbondioxide fluxes at the water–sediment interface of a tropical lagoon, Mar. Ecol.-Prog. Ser., 107, 185–193, 1994.

Bula-Meyer, G.: 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, 1990.

Calvert, S. E.: Oceanographic controls on the accumulation of organic matter in marine sediments, Geol. Soc., London, Spec. Publ., 26, 137–151, 1987.

Canfield, D. E.: Factors influencing organic carbon preservation in marine sediments, Chem. Geol., 114, 315–329, 1994.

Canfield, D. E., Kristensen, E., and Thamdrup, B.: Heterotrophic carbon metabolism, in: Advances in Marine Biology, Vol. 48, Elsevier Academic Press, San Diego, 129–162, 2005.

Capone, D. G., Dunham, S. E., Horrigan, S. G., and Duguay, L. E.: Microbial nitrogen transformations in unconsolidated coral reef sediments, Mar. Ecol.-Prog. Ser., 80, 75–88, 1992.

Charpy, L. and Charpy-Roubaud, C. J.: Particulate organic matter fluxes in a Tuamotu atoll lagoon (French Polynesia), Mar. Ecol.-Prog. Ser., 71, 53–63, 1991.

Clavier, J., Chardy, P., and Chevillon, C.: Sedimentation of particulate matter in the south-west lagoon of New Caledonia: spatial and temporal patterns, Estuar. Coast. Shelf S., 40, 281–294, 1995.

Crossland, C. J. and Barnes, D. J.: Dissolved nutrients and organic particulates in water flowing over coral reefs at Lizard-Island, Aust. J. Mar. Fresh. Res., 34, 835–844, 1983.

Dell'Anno, A., Mei, M. L., Pusceddu, A., and Danovaro, R.: Assessing the trophic state and eutrophication of coastal marine systems: a new approach based on the biochemical composition of sediment organic matter, Mar. Pollut. Bull., 44, 611–622, 2002.

Departamento Administrativo Nacional de Estadística (DANE): Colombia – Censo General 2005, Nivel Nacional, Bogotá, Colombia, 498 pp., 2005.

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

Emery, K. O.: Relict sediments on continental shelves of world, Am. Assoc. Petr. Geol. B., 52, 445–464, 1968.

Fabricius, K. E.: Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis, Mar. Pollut. Bull., 50, 125–46, 2005.

Fenchel, T., King, G. M., and Blackburn, T. H.: Bacterial biogeochemistry: the ecophysiology of mineral cycling, in: Bacterial Biogeochemistry, Academic Press, San Diego, 307 pp., 1998.

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Franco-Herrera, A., Castro, L., and Tigreros, P. C.: Plankton dynamics in the south-central Caribbean Sea: strong seasonal changes in a coastal tropical system, Caribb. J. Sci., 42, 24–38, 2006.

García-Hoyos, L. M., Franco-Herrera, A., Ramírez-Barón, J. S., and López-Cerón, D. L.: Dinámica océano-atmosfera y su influencia en la biomasa fitoplanctónica, en la zona costera del Departamento del Magdalena, Caribe Colombiano, Bol. Invest. Mar. Cost., 39, 307–335, 2010.

Glud, R. N., Eyre, B. D., and Patten, N.: Biogeochemical responses to mass coral spawning at the Great Barrier Reef: effects on respiration and primary production, Limnol. Oceanogr., 53, 1014–1024, 2008.

Glynn, P. W.: Bioerosion and coral-reef growth: a dynamic balance, in: Life and Death of Coral Reefs, edited by: Birkeland, C., Chapman and Hall, New York, 68–94, 1997.

Gower, J. C.: Some distance properties of latent root and vector methods used in multivariate analysis, Biometrika, 53, 325–338, 1966.

Hallock, P.: Reefs and reef limestones in Earth history, in: Life and Death of Coral Reefs, edited by: Birkeland, C., Springer, Berlin, 13–42, 1997.

Hansen, J. A., Klumpp, D. W., Alongi, D. M., Dayton, P. K., and Riddle, M. J.: Detrital pathways in a coral reef lagoon, Mar. Biol., 113, 363–372, 1992.

Hatcher, B. G.: Coral reef primary productivity: a beggar's banquet, Trends Ecol. Evol., 3, 106–111, 1988.

Hedges, J. I., Clark, W. A., and Cowie, G. L.: Organic matter sources to the water column and surficial sediments of a marine bay, Limnol. Oceanogr., 33, 1116–1136, 1988.

Henrichs, S. M.: Early diagenesis of organic matter in marine sediments: progress and perplexity, Mar. Chem., 39, 119–149, 1992.

Higgins, R. P. and Thiel, H.: Introduction to the Study of Meiofauna, Smithsonian Institution Press, Smithsonian, 488 pp., 1988.

Huettel, M., Røy, H., Precht, E., and Ehrenhauss, S.: Hydrodynamical impact on biogeochemical processes in aquatic sediments, Hydrobiologia, 494, 231–236, 2003.

Invemar: Sistema de Información Ambiental Marina de Colombia (SIAM), Invemar, Santa Marta, Colombia, 2012.

Jeffrey, S. W. and Humphrey, G. F.: New spectrophotometric equations for determining chlorophylls a_1, b_1, c_1 and c_2 in higher plants, algae and natural phytoplankton, Biochem. Physiol. Pfl., 167, 191–194, 1975.

Jørgensen, B. B.: Processes at the sediment water interface, in: The Major Biogeochemical Cycles and Their Interactions, edited by: Bolin, B. and Cook, R. B., Wiley, 477–509, 1983.

Jørgensen, B. B.: Material flux in the sediment, in: Eutrophication in Coastal Marine Ecosystems, American Geophysical Union, USA, 115–135, 1996.

Jørgensen, B. B. and Revsbech, N. P.: Oxygen uptake, bacterial distribution, and carbon-nitrogen-sulfur cycling in sediments from the Baltic Sea–North Sea transition, Ophelia, 31, 29–49, 1989.

Kepkay, P. E.: Particle aggregation and the biological reactivity of colloids, Mar. Ecol.-Prog. Ser., 109, 293–304, 1994.

Kleypas, J. A., McManus, J. W., and Meñez, L. A. B.: Environmental limits to coral reef development: where do we draw the line?, Integr. Comp. Biol., 39, 146–159, 1999.

Koop, K. and Larkum, A. W. D.: Deposition of organic material in a coral reef lagoon, One Tree Island, Great Barrier Reef, Estuar. Coast. Shelf S., 25, 1–9, 1987.

Lorenzen, C. J.: Chlorophyll *b* in the eastern North Pacific Ocean, Deep-Sea Res., 28, 1049–1056: 1981.

Meyer-Reil, L. A.: Spatial and temporal distribution of bacterial populations in marine shallow water surface sediments, in: Biogeochemical Processes at the Land-Sea Boundary, Vol. 43, edited by: Lasserre, P. and Martin, J. M., Elsevier, Amsterdam, 141–160, 1986.

Millie, D. F., Paerl, H. W., and Hurley, J. P.: Microalgal pigment assessments using high-performance liquid chromatography: a synopsis of organismal and ecological applications, Can. J. Fish. Aquat. Sci., 50, 2513–2527, 1993.

Moriarty, D. J. W.: Feeding of *Holothuria atra* and *Stichopus chloronotus* on bacteria, organic carbon and organic nitrogen in sediments of the Great Barrier Reef, Aust. J. Mar. Fresh. Res., 33, 255–263, 1982.

Newell, R.: The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*, P. Zool. Soc. Lond., 144, 25–45, 1965.

Nieuwenhuize, J., Maas, Y. E., and Middelburg, J. J.: Rapid analysis of organic carbon and nitrogen in particulate materials, Mar. Chem., 45, 217–224, 1994.

Nixon, S. W.: Remineralization and nutrient cycling in coastal marine ecosystems, in: Nutrients and Estuaries, edited by: Neilson, B. J. and Cronin, L. E., Humana Press, New York, 111–138, 1981.

Nixon, S. W.: Coastal marine eutrophication: a definition, social causes, and future concerns, Ophelia, 41, 199–219, 1995.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◀ | ▶|

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Paramo, J., Correa, M., and Núñez, S.: Evidencias de desacople físico-biológico en el sistema de surgencia en La Guajira, Caribe Colombiano, Rev. Biol. Mar. Oceanog., 46, 421–430, 2011.

Precht, E. and Huettel, M.: Rapid wave-driven advective pore water exchange in a permeable coastal sediment, J. Sea Res., 51, 93–107, 2004.

Quinn, G. P. and Keough, M. J.: Experimental Design and Data Analysis for Biologists, Cambridge University Press, Cambridge, 2002.

Ramírez-Barón, J. S., Franco-Herrera, A., García-Hoyos, L. M., and López, D. A.: La comunidad fitoplanctónica durante eventos de surgencia y no surgencia, en la zona costera del Departamento del Magdalena, Caribe Colombiano, Bol. Invest. Mar. Cost., 39, 233–253, 2010.

Rasheed, M., Badran, M. I., and Huettel, M.: Particulate matter filtration and seasonal nutrient dynamics in permeable carbonate and silicate sands of the Gulf of Aqaba, Red Sea, Coral Reefs, 22, 167–177, 2003.

Rasheed, M., Badran, M. I., Richter, C., and Huettel, M.: Effect of reef framework and bottom sediment on nutrient enrichment in a coral reef of the Gulf of Aqaba, Red Sea, Mar. Ecol.-Prog. Ser., 239, 277–285, 2002.

Redfield, A. C.: The biological control of chemical factors in the environment, Am. Sci., 46, 205–221, 1958.

Reimers, C. E., Stecher, H. A., Taghon, G. L., Fuller, C. M., Huettel, M., Rusch, A., Ryckelynck, N., and Wild, C.: In situ measurements of advective solute transport in permeable shelf sands, Cont. Shelf Res., 24, 183–201, 2004.

Rusch, A., Huettel, M., and Forster, S.: Particulate organic matter in permeable marine sands – dynamics in time and depth, Estuar. Coast. Shelf S., 51, 399–414, 2000.

Rusch, A., Huettel, M., Wild, C., and Reimers, C. E.: Benthic oxygen consumption and organic matter turnover in organic-poor, permeable shelf sands, Aquat. Geochem., 12, 1–19, 2006.

Salzwedel, H. and Müller, K.: A summary of meteorological and hydrological data from the bay of Santa Marta, Colombian Caribbean, An. Inst. Inv. Mar. Punta de Betín, 13, 67–83, 1983.

Sansone, F. J., Andrews, C. C., and Okamoto, M. Y.: Adsorption of short-chain organic acids onto nearshore marine sediments, Geochim. Cosmochim. Ac., 51, 1889–1896, 1987.

Sorokin, Y. I.: Coral Reef Ecology, Springer-Verlag, Berlin, 1993.

Spatiotemporal variability of SOM

E. Bayraktarov and C. Wild

Title Page

Abstract	Introduction
Conclusions	References
Tables	Figures

|◀ ▶|

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Ston, J., Kosakowska, A., Lotocka, M., and Lysiak-Pastuszak, E.: Pigment composition in relation to phytoplankton community structure and nutrient content in the Baltic Sea, Oceanologia, 44, 419–437, 2002.

Taguchi, S.: Sedimentation of newly produced particulate organic matter in a subtropical inlet, Kaneohe Bay, Hawaii, Estuar. Coast. Shelf S., 14, 533–544, 1982.

Veron, J.: Corals of the World, 1st edn., Australian Institute of Marine Science, Townsville, Australia, 463 pp., 2000.

Wakeham, S. G., Lee, C., Hedges, J. I., Hernes, P. J., and Peterson, M. J.: Molecular indicators of diagenetic status in marine organic matter, Geochim. Cosmochim. Ac., 61, 5363–5369, 1997.

Wang, X. and Lee, C.: The distribution and adsorption behavior of aliphatic amines in marine and lacustrine sediments, Geochim. Cosmochim. Ac., 54, 2759–2774, 1990.

Webb, J. E. and Theodor, J.: Irrigation of submerged marine sands through wave action, Nature, 220, 682–683, 1968.

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

Werner, U., Bird, P., Wild, C., Ferdelman, T. G., Polerecky, L., Eickert, G., Jonstone, R., Hoegh-Guldberg, O., de Beer, D.: Spatial patterns of aerobic and anaerobic mineralization rates and oxygen penetration dynamics in coral reef sediments, Mar. Ecol.-Prog. Ser., 309, 93–105, 2006.

Wild, C., Huettel, M., Klueter, A., Kremb, S. G., Rasheed, M. Y. M., and Jørgensen, B. B.: Coral mucus functions as an energy carrier and particle trap in the reef ecosystem, Nature, 428, 66–70, 2004a.

Wild, C., Rasheed, M., Werner, U., Franke, U., Johnstone, R., and Huettel, M.: Degradation and mineralization of coral mucus in reef environments, Mar. Ecol.-Prog. Ser., 267, 159–171, 2004b.

Wild, C., Woyt, H., and Huettel, M.: Influence of coral mucus release on nutrient fluxes in carbonate sands, Mar. Ecol.-Prog. Ser., 287, 87–98, 2005a.

Wild, C., Rasheed, M., Jantzen, C., Cook, P., Struck, U., Huettel, M., and Boetius, A.: Benthic metabolism and degradation of natural particulate organic matter in silicate and carbonate sands of the northern Red Sea, Mar. Ecol.-Prog. Ser., 298, 69–78, 2005b.

Wild, C., Laforsch, C., and Huettel, M.: Detection and enumeration of microbial cells in highly porous carbonate reef sands, Mar. Freshwater Res., 57, 415–420, 2006.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Wild, C., Jantzen, C., Struck, U., Hoegh-Guldberg, O., and Huettel, M.: Biogeochemical responses following coral mass spawning on the Great Barrier Reef: pelagic–benthic coupling, Coral Reefs, 27, 123–132, 2008.

Wild, C., Naumann, M. S., Haas, A., Struck, U., Mayer, F. W., Rasheed, M. Y. M., and Huettel, M.: Coral sand O_2 uptake and pelagic–benthic coupling in a subtropical fringing reef, Aqaba, Red Sea, Aquat. Biol., 6, 133–142, 2009.

Wild, C., Niggl, W., Naumann, M. S., and Haas, A. F.: Organic matter release by Red Sea coral reef organisms: potential effects on microbial activity and in situ O_2 availability, Mar. Ecol.-Prog. Ser., 411, 61–71, 2010.

Wollast, R.: The coastal organic carbon cycle: fluxes, sources, and sinks, in: Ocean Margin Processes in Global Change, edited by: Manroura, R. F. C., Martin, J.-M., and Wollast, R., John Wiley and Sons, Chichester, 365–381, 1991.

Zobell, C. E.: Studies on the bacterial flora of marine bottom sediments, J. Sediment. Res., 8, 10–18, 1938.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Table 1. Seasonal means of sedimentary parameters and univariate analyses. Significant PER-MANOVA results are indicated by asterisks with [a] for significant ($p < 0.05$) and [b] for very significant ($p < 0.01$). Not significant values are displayed in bold face. Abbreviations: exposed site (exp), sheltered site (she), particulate organic nitrogen (PON), particulate organic carbon (POC), chlorophyll a, b, $c_1 + c_2$ (Chl a, b, $c_1 + c_2$), and calcium carbonate ($CaCO_3$).

Variables/Sites	Major upwelling exp	she	Minor upwelling exp	she	Major non-upwelling exp	she	Minor non-upwelling exp	she
POC sedimentation ($mg POC\,m^{-2}\,d^{-1}$)	623 ± 193	382 ± 124	532 ± 95	514 ± 169	399 ± 63	242 ± 48	406 ± 190	338 ± 83
PON sedimentation ($mg PON\,m^{-2}\,d^{-1}$)	110 ± 47	63 ± 19	89 ± 49	77 ± 25	54 ± 12	32 ± 9	66 ± 34	49 ± 12
Chl a sedimentation ($mg chl\,a\,m^{-2}\,d^{-1}$)	66.4 ± 41.2	27.9 ± 21.5	27.6 ± 9.0	17.2 ± 19.9	8.5 ± 5.0	1.2 ± 0.1	12.2 ± 8.8	3.7 ± 4.2
Molar C : N of supplied POM	6.6 ± 2.5	7.3 ± 1.3	8.4 ± 4.0	8.0 ± 2.2	8.7 ± 1.0	8.0 ± 4.5	7.4 ± 0.7	8.1 ± 1.4
Relative proportion of Chl a in supplied POC (%)	0.15 ± 0.11	0.10 ± 0.08	0.07 ± 0.02	0.04 ± 0.04	0.03 ± 0.02	0.01 ± 0.00	0.04 ± 0.02	0.01 ± 0.01
C turnover (% supplied $POC\,h^{-1}$)	5.5 ± 2.1	1.6 ± 0.4	3.8 ± 0.7	2.4 ± 1.5	2.4 ± 1.3	1.0 ± 0.2	2.6 ± 1.0	1.2 ± 0.3
Sedimentary POC ($mg POC\,g^{-1}$)	2.06 ± 0.57	2.38 ± 0.46	2.14 ± 0.38	2.48 ± 0.65	2.51 ± 0.77	2.57 ± 0.45	1.90 ± 0.36	2.13 ± 0.30
Sedimentary PON ($mg PON\,g^{-1}$)	0.31 ± 0.09	0.31 ± 0.06	0.33 ± 0.09	0.34 ± 0.10	0.39 ± 0.10	0.35 ± 0.07	0.31 ± 0.07	0.31 ± 0.06
Sedimentary Chl a ($\mu g chl\,a\,g^{-1}$)	4.60 ± 3.08	7.56 ± 4.23	4.81 ± 1.32	4.99 ± 2.26	5.97 ± 1.68	5.20 ± 1.69	4.58 ± 1.50	5.29 ± 1.56
Sedimentary Chl b ($\mu g chl\,b\,g^{-1}$)	0.33 ± 0.25	0.23 ± 0.14	0.38 ± 0.18	0.26 ± 0.12	0.42 ± 0.27	0.33 ± 0.20	0.32 ± 0.30	0.22 ± 0.17
Sedimentary Chl $c_1 + c_2$ ($\mu g chl\,c\,g^{-1}$)	0.50 ± 0.30	0.98 ± 0.49	0.61 ± 0.19	0.75 ± 0.36	0.82 ± 0.24	0.82 ± 0.33	0.46 ± 0.35	0.54 ± 0.29
Sedimentary Carotenoids ($\mu g carotenoids\,g^{-1}$)	1.18 ± 0.73	2.44 ± 1.50	1.69 ± 0.57	1.91 ± 0.84	2.23 ± 0.84	2.13 ± 0.81	1.25 ± 0.65	1.81 ± 0.65
Sedimentary O_2 uptake ($mmol O_2\,m^{-2}\,d^{-1}$)	10.6 ± 6.1	17.4 ± 5.8	14.3 ± 6.3	18.7 ± 5.6	15.1 ± 6.9	20.5 ± 4.0	12.3 ± 6.1	17.4 ± 7.8
Sedimentary $CaCO_3$ (%)	6.2 ± 2.7	8.5 ± 2.7	7.1 ± 2.5	8.4 ± 2.6	7.3 ± 2.6	8.5 ± 2.6	6.7 ± 2.9	8.3 ± 2.9
Porosity (% wt/wt)	37.5 ± 9.7	43.9 ± 5.3	–	–	35.4 ± 10.4	46.5 ± 4.0	–	–
Grain-size (μm)	1006 ± 352	606 ± 142			940 ± 407	590 ± 105		

Table 1. Continued.

Variables/Sites	Seasons Pseudo-F	(p)	Bays Pseudo-F	(p)	Exposure Pseudo-F	(p)
POC sedimentation ($mg POC\, m^{-2}\, d^{-1}$)	17.410	0.029[a]	–	–	8.916	0.046[a]
PON sedimentation ($mg PON\, m^{-2}\, d^{-1}$)	12.589	0.046[a]	–	–	**6.661**	**0.099**
Chl a sedimentation ($mg chl\, a\, m^{-2}\, d^{-1}$)	**7.853**	**0.057**	–	–	**2.558**	**0.193**
Molar C : N of supplied POM	**0.847**	**0.428**	–	–	**0.003**	**0.945**
Relative proportion of Chl a in supplied POC (%)	**6.892**	**0.159**	–	–	**1.593**	**0.292**
C turnover (% supplied POC h^{-1})	**9.688**	**0.087**	–	–	17.154	0.029[a]
Sedimentary POC ($mg POC\, g^{-1}$)	3.628	0.040[a]	**2.662**	**0.086**	4.625	0.041[a]
Sedimentary PON ($mg PON\, g^{-1}$)	**1.987**	**0.148**	4.041	0.027[a]	**0.034**	**0.845**
Sedimentary Chl a ($\mu g chl\, a\, g^{-1}$)	**1.144**	**0.338**	**0.659**	**0.592**	3.782	0.049[a]
Sedimentary Chl b ($\mu g chl\, b\, g^{-1}$)	**2.635**	**0.081**	16.853	0.001[b]	13.132	0.002[b]
Sedimentary Chl $c_1 + c_2$ ($\mu g chl\, c\, g^{-1}$)	5.566	0.003[b]	**2.307**	**0.114**	9.158	0.009[b]
Sedimentary Carotenoids (μg carotenoids g^{-1})	3.189	0.043[a]	**0.562**	**0.663**	8.723	0.008[b]
Sedimentary O_2 uptake ($mmol O_2\, m^{-2}\, d^{-1}$)	**1.653**	**0.179**	**1.986**	**0.138**	16.676	0.001[b]
Sedimentary $CaCO_3$ (%)	**0.104**	**0.941**	11.122	0.002[b]	4.537	0.047[a]
Porosity (% wt/wt)	**0.003**	**0.956**	**0.666**	**0.603**	**4.404**	**0.052**
Grain-size (μm)	**0.080**	**0.756**	**1.335**	**0.315**	6.715	0.040[a]

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Table 2. Correlation matrix of environmental sedimentary parameters with distance to Santa Marta and seasonal resolution. Significance levels of correlation coefficients (Spearman's rank correlation) among environmental variables with distance to Santa Marta are indicated by asterisks with [a] for significant ($p < 0.05$) and [b] for very significant ($p < 0.01$). Not significant correlations are displayed in bold face. Abbreviations: sedimentary chlorophyll a, b, $c_1 + c_2$ (Chl a, b, c), particulate organic nitrogen (PON), particulate organic carbon (POC), sediment oxygen demand (SOD), and sedimentary carbonate content ($CaCO_3$).

Seasons	Correlations with distance to Santa Marta									
	Chl a	Chl b	Chl c	Carotenoids	POC	PON	SOD	CaCO$_3$	Porosity	Grain-size
Major upwelling	0.76[a]	**−0.44**	0.87[b]	0.87[b]	**0.66**	**0.11**	0.76[a]	**0.44**	**0.33**	**−0.66**
Minor upwelling	**0.22**	**−0.44**	**0.22**	**0.44**	**0.33**	**0.11**	**0.44**	**0.33**	0.33	**−0.66**
Major non-upwelling	**−0.44**	**−0.44**	**−0.11**	**0.00**	**0.11**	**−0.11**	**0.44**	**0.33**	**0.55**	**−0.44**
Minor non-upwelling	**0.22**	**−0.33**	**0.55**	0.87[b]	**0.55**	**0.11**	**0.44**	**0.44**	**0.55**	**−0.44**

Table 3. Correlation matrix of environmental sedimentary parameters. Significance levels of correlation coefficients (Spearman's rank correlation) among sedimentary parameters and distance from Santa Marta are indicated by asterisks with [a] for significant ($p < 0.05$) and [b] for very significant ($p < 0.01$). Not significant correlations are displayed in bold face. Abbreviations: sedimentary chlorophyll a, b, $c_1 + c_2$ (Chl a, b, c), particulate organic nitrogen (PON), particulate organic carbon (POC), sediment oxygen demand (SOD), and sedimentary carbonate content ($CaCO_3$).

	Chl a	Chl b	Chl c	Carotenoids	PON	POC	SOD	CaCO$_3$	Porosity	Grain-size
Chl a		**−0.05**	0.69[b]	0.83[b]	**−0.16**	**0.11**	0.39[a]	**0.05**	**0.09**	**−0.34**
Chl b			**−0.14**	**−0.14**	0.36[a]	**−0.06**	**−0.05**	**0.31**	**−0.12**	**0.21**
Chl c				0.80[b]	**−0.03**	**0.31**	0.40[a]	**0.33**	0.40[a]	−0.51[b]
Carotenoids					**0.12**	0.40[a]	0.62[b]	**0.29**	**0.22**	−0.41[a]
PON						0.80[b]	**0.21**	0.36[a]	**−0.03**	**0.11**
POC							0.42[a]	**0.32**	**0.20**	**−0.16**
SOD								**0.31**	**0.31**	−0.37[a]
CaCO$_3$									0.69[b]	−0.61[b]
Porosity										−0.90[b]

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◄ | ►►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Table 4. Multivariate analyses: significant differences among environmental sedimentary parameters in Tayrona National Natural Park and multiple comparisons between seasons and bays. Main effects of multivariate analyses and the multiple comparisons between seasons (major upwelling, minor upwelling, major non-upwelling, and minor non-upwelling) and bays (Chengue, Gayraca, Neguanje, and Gayraca) are shown for the parameters sedimentary chl a, b, $c_1 + c_2$, carotenoids, POC, PON, SOD, and $CaCO_3$. Significant PERMANOVA results are indicated by asterisks with [a] for significant ($p < 0.05$) and [b] for very significant ($p < 0.01$). Not significant values are displayed in bold face. Abbreviations: particulate organic carbon (POC), particulate organic nitrogen (PON), chlorophyll a, b, $c_1 + c_2$ (chl a, b, c), and sediment oxygen demand (SOD).

| Factors	DF	Pseudo-F	(p)
Seasons (fixed)	3	**1.835**	**0.059**
Bays (random)	1	3.651	0.001[b]
Exposure (fixed)	3	8.299	0.001[b]
Exposure [a]Season	3	**1.157**	**0.311**
Multiple comparisons between seasons		t	(p)
Major upwelling – minor upwelling		**0.715**	**0.731**
Major upwelling – major non-upwelling		**1.412**	**0.128**
Major upwelling – minor non-upwelling		**1.085**	**0.325**
Minor upwelling – major non-upwelling		**0.999**	**0.416**
Minor upwelling – minor non-upwelling		**1.053**	**0.364**
Major non-upwelling – minor non-upwelling		2.067	0.014[a]
Multiple comparisons between bays		t	(p)
Chengue – Gayraca		**1.474**	**0.154**
Chengue – Neguanje		2.665	0.007[b]
Chengue – Cinto		2.441	0.006[b]
Gayraca – Neguanje		**1.614**	**0.102**
Gayraca – Cinto		**1.478**	**0.102**
Neguanje – Cinto		1.841	0.043[a]
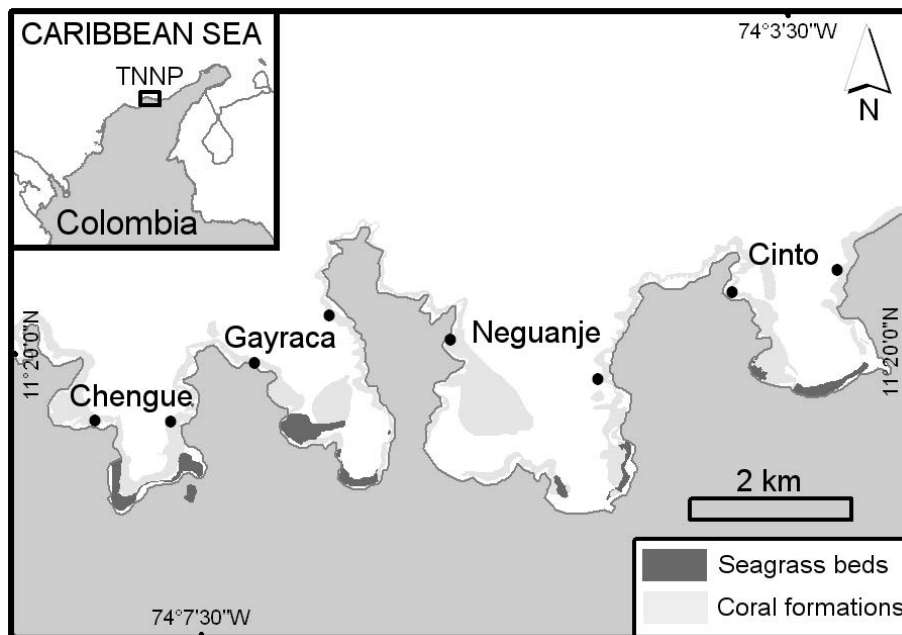
Fig. 1. Bays of Tayrona National Natural Park (TNNP). Displayed are Chengue, Gayraca, Neguanje and Cinto and the sampling locations at the western (water current-exposed sites) and the eastern (water current-sheltered sites) flanks of each bay. Source: Invemar (2012).
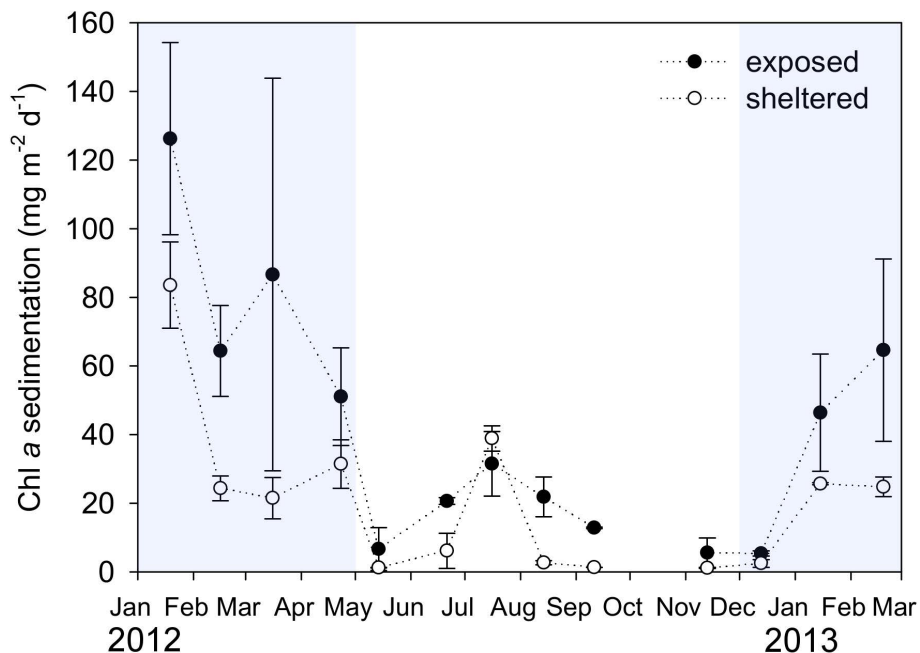
Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◀ | ▶|

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Fig. 2. Sedimentary supply of particulate organic matter (POM) to the seafloor. **(a)** Sedimentary particulate organic carbon (POC) supply; **(b)** sedimentary particulate organic nitrogen (PON) supply to the seafloor at an exposed and sheltered site in one exemplary bay in Tayrona National Natural Park (TNNP; Gayraca).

Fig. 3. Sedimentary supply of chlorophyll *a* to the seafloor at an exposed and sheltered site in one exemplary bay in Tayrona National Natural Park (TNNP; Gayraca).

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Fig. 4. Rates of C turnover at an exposed and sheltered site in Gayraca Bay.
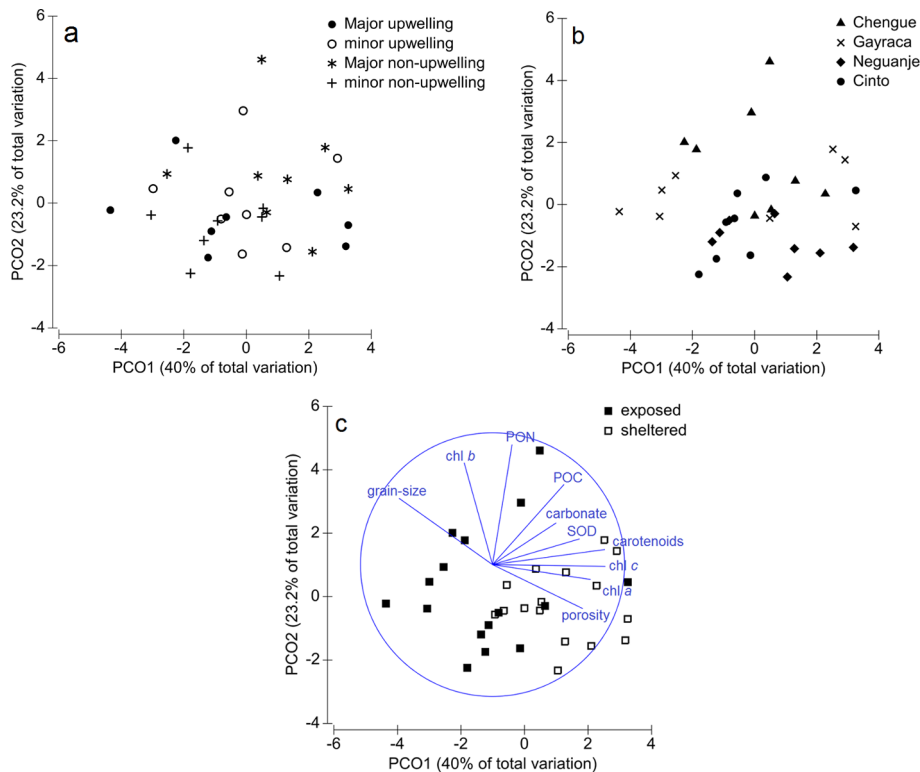
Fig. 5. Graphical representation of multivariate analyses results by Principle Coordinates Ordination (PCO). PCO of environmental sedimentary parameters was grouped by seasons **(a)**, bays **(b)**, and exposure to wave and water-currents of the sampling locations **(c)**. Effects and directions of environmental variables in **(c)** are displayed as vectors with the abbreviations: particulate organic carbon (POC), particulate organic nitrogen (PON), chlorophyll a, b, $c_1 + c_2$ (chl a, b, c), and sediment oxygen demand (SOD).

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◄ | ►

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion