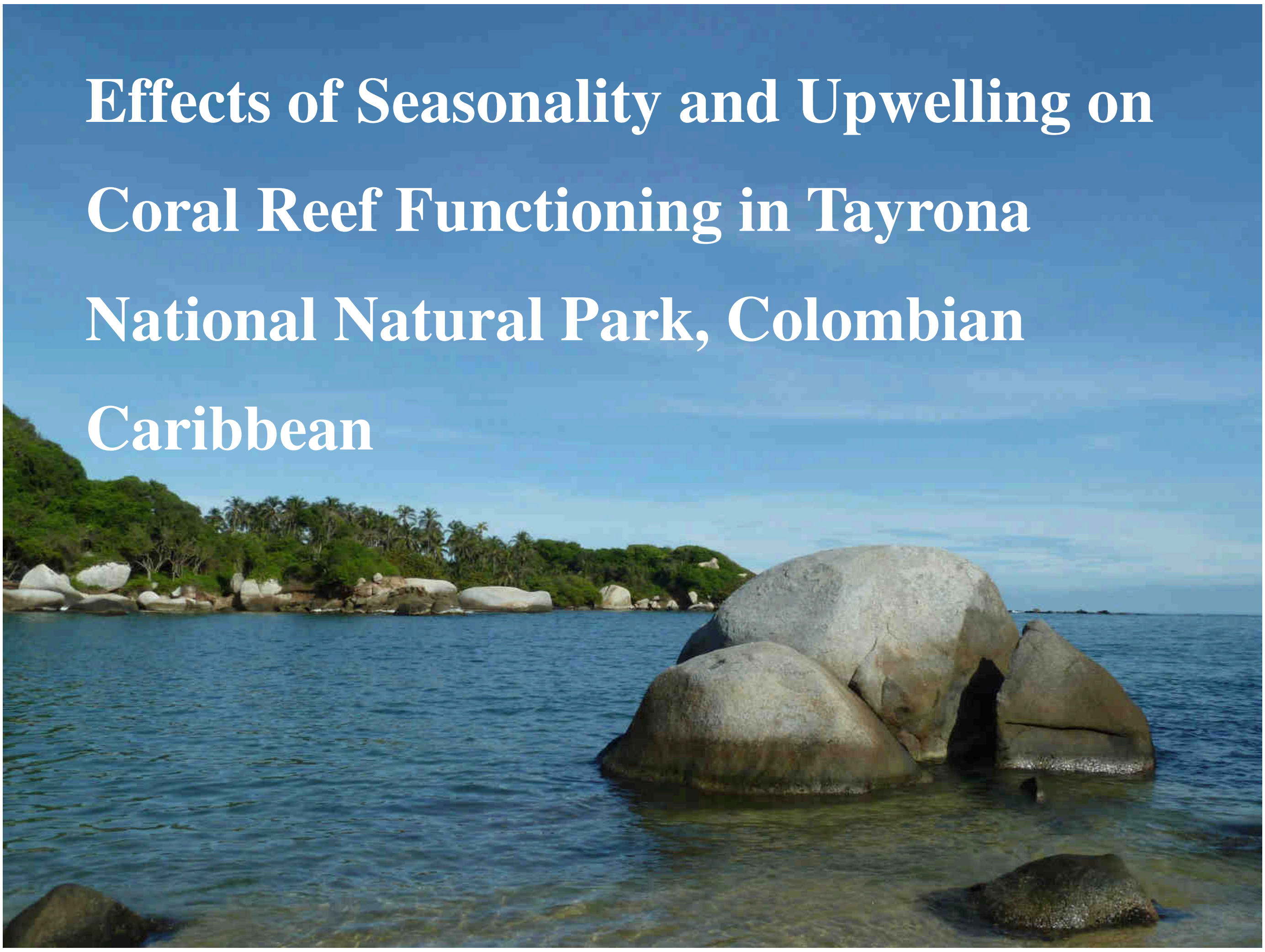
Effects of Seasonality and Upwelling on Coral Reef Functioning in Tayrona National Natural Park, Colombian Caribbean



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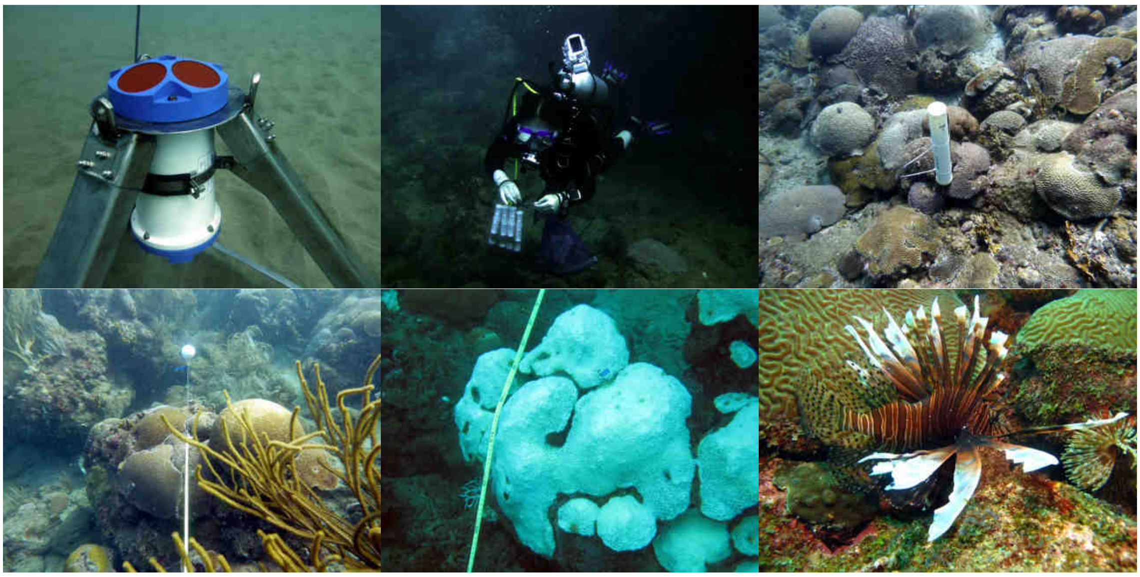

Pictures of diver and lionfish were kindly provided by J. F. Lazarus-Agudélo.

The present study has been realized between February 2011 and November 2013 at the Leibniz Center for Tropical Marine Ecology (ZMT) in Bremen, Germany, the Center of Excellence in Marine Sciences (CEMarin) in Rodadeo - Santa Marta, Colombia and the Instituto de Investigaciones Marinas y Costeras (Invemar) in Rodadero - Santa Marta, Colombia.

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Dedicated to my family (my own and my “borrowed”) and Luis Alonso

Destruyendo las reservas naturales, todas se están agotando. El "hermano menor" tiene que cambiar su forma de actuar. Todavía hay tiempo, nosotros podemos ayudar para que sigan existiendo animales, plantas, naturaleza y agua.

The natural reserves are being destroyed and depleted. The "little brother" has to change his way of behaving. There is still time; we can help that animals, plants, nature and water keep existing.

- The *Kogui*, descendants of the *Tayrona* who once lived in the region of Sierra Nevada de Santa Marta, Colombia about us as "little brother"

Picture: *Mamo-Kogui* Luis

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Kogui children. Picture kindly provided by Diocesis de Riohacha.

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Thesis Abstract

The Tayrona National Natural Park (TNNP) is located at the Northeast coast of Colombia and belongs to the biodiversity hotspots in the Colombian Caribbean. Despite its relatively pristine coral communities as compared to other Caribbean locations, coral reef performance remains largely under-investigated. Especially the effects of alternating rainy and dry seasons, going along with seasonal upwelling on the reef ecosystem are unknown. This thesis therefore deals with the seasonal effects on local coral reefs by answering three key questions, each of which addresses a different component of the coral reef ecosystem. (I) Water column: How are the coral reefs-surrounding water currents and water quality affected by seasonal change? (II) Reef sediments: What regulates the supply of organic matter to the seafloor and the processes of remineralization and regeneration of essential nutrients for benthic primary production? (III) Benthic communities: How is the benthic primary production, the condition of corals, and the distribution of invasive lionfish affected by seasonal change and upwelling? These questions are answered within the seven chapters of this thesis. The chapters are embraced by a general introduction and a synopsis in a nutshell. The approach for answering the key questions consisted of (1) the deployment of an Acoustic Doppler Current Profiler (ADCP) tracking water current velocity and direction, (2) a monthly monitoring (25 months) of key water quality parameters, (3) the study of organic matter supply to the sediments and initiation of sedimentary processes, (4) an estimate of the primary production of benthic phototrophs, (5) a coral bleaching and recovery monitoring in dependence to water current exposition, and (6) the assessment of lionfish abundances over a total area of 6000 m^2 in TNNP.

Major findings showed that:

a) Higher water currents predominated at a Western, wind- and wave-exposed location during non-upwelling as compared to an Eastern, sheltered site in a representative bay. Wind-stress at the exposed site affected water currents throughout the entire water column during both seasons, but reached only up to 3 – 4 m water depth at the sheltered site during non-upwelling and down to 10 m during upwelling (Chapter 1). Differences in exposition to water currents had implications for the distribution of organisms and were considered as major local control for the patterns of coral bleaching and recovery (Chapter 6).

b) Water quality in TNNP was close to oligotrophic conditions adequate for coral reef growth during non-upwelling, but exceeded critical threshold values for inorganic nutrient concentrations and phytoplankton blooms during upwelling and also in relation to riverine discharge along a distance gradient towards several smaller river mounths (Chapter 2).

c) Reef sediments in TNNP are highly dynamic and receptive to upwelling-triggered pulses of labile organic matter supplied to the seafloor and have very high rates of carbon turnover as compared to other silicate sands. Reef sediments can be classified as meso-oligotrophic according to their annual organic carbon supply and the contents of accumulated organic matter (Chapter 3). The nutrients released by the sediments maintain a high benthic primary productivity (Chapter 4).

d) Local autotrophic reef communities are well adapted to fluctuations of environmental key parameters; no spatial or temporal differences in the net and gross primary production at the ecosystem level were observed (Chapter 4).

e) Scleractinian corals at a water current-sheltered site were more susceptible to coral bleaching than corals at an -exposed site in TNNP. The coral communities of limited complexity at the exposed site recovered more efficiently than the reef-building and more diverse corals at the sheltered site. The results suggest the existence of local resilience patterns (mainly driven by water currents; Chapter 1) of these Caribbean reefs against coral bleaching (Chapter 6).

f) Lionfish populations of mostly adult *Pterois volitans* individuals have established in all TNNP bays. Invasive lionfish disturb local coral reefs via fast and uncontrolled consumption of small herbivorous fish due to the lack of natural predators. Abundances of *P. volitans* are similar to those at Indo-Pacific reef locations where this invasive species formerly originated from. The presence of *P. volitans* highlights that immediate management actions for the control of this species are crucial in order to preserve the integrity of TNNP coral reefs (Chapter 7).

The chapters of the present thesis deal with global (e.g. temperature-induced coral bleaching) and local threats (e.g. water quality decline and lionfish invasion) for TNNP coral reefs. The results suggest that while threats of global warming may be counteracted

by the presence of seasonal upwelling coinciding with highest heat stress, the effects of local threats may only be avoided by improved management actions and conservation. The thesis highlights that TNNP is a unique environment in which coral reefs, naturally exposed to harsh seasonal changes, likely have developed an increased local resilience to climate change and anthropogenic disturbances. The comprehensive monitoring dataset represents the first holistic approach to describe the condition and functioning of TNNP coral reefs influenced by strong seasonal changes. Thereby, the work constitutes a solid baseline on several levels (water column, sediments, and benthic communities) for future research of this relatively undisturbed ecosystem.

Zusammenfassung

Der Tayrona National Natural Park (TNNP) an der nordöstlichen Küste von Kolumbien gilt als einer der Biodiversitäts-Hotspots der kolumbianischen Karibik. Trotz seiner vergleichsweise unberührten Korallengemeinschaften, sind der Einfluss von alternierenden Regen- und Trockenzeiten, welche mit einem saisonalen Tiefenwasserauftrieb einhergehen, auf die lokalen benthischen Riffsysteme weitgehend unerforscht. Um die saisonalen Effekte auf die lokalen Korallenriffe zu untersuchen, werden im Rahmen dieser Arbeit drei Kernfragen beantwortet, welche sich auf verschiedene Komponenten des Korallenriffökosystems beziehen: (I) Wassersäule: Wie verändern sich riffnahe Wasserströmungen und Wasserqualität zu unterschiedlichen Jahreszeiten? (II) Riffsedimente: Was kontrolliert die Zufuhr von organischem Material zum Meeresboden, sowie die Prozesse der Remineralisierung und Regenerierung von essentiellen Nährstoffen für benthische Primärproduktion? (III) Benthische Gemeinschaten: Inwieweit werden benthische Primärproduktion, Korallenzustand, sowie das Auftreten des invasiven Rotfeuerfisches durch saisonalen Veränderungen und Auftriebphänomene beeinflusst? Diese Fragen werden nach einer allgemeinen Einleitung im Rahmen der sieben Kapitel dieser Arbeit beantwortet und die Hauptergebnisse in einer Synopsis zusammengefasst. Um die Fragestellungen zu beantworten wurden (1) durch den Einsatz eines Ultraschall-Doppler-Profil-Strömungsmessers (Acoustic Doppler Current Profiler, ADCP) Wasserstömungsgeschwindigkeiten und –richtungen bestimmt, (2) über einen Zeitraum von 25 Monaten Schlüsselparameter der Wasserqualität monatlich quantifiziert, (3) der Eintrag organischen Materials in Riffsedimente und damit verbundene Sedimentprozesse erforscht, (4) Korallenbleiche und Erholung davon in Abhängigkeit zur Strömungsexposition untersucht, (5) die Photosyntheseleistung benthischer Primärproduzenten und deren Beitrag zur gesamten benthischen Primärproduktion erfasst, sowie (6) die Häufigkeiten des Rotfeuerfisches über eine Gesamtfläche von 6000 m² im TNNP ermittelt.

Die Untersuchungen lieferten folgende Hauptergebnisse:

a) An der westlichen, wind- und strömungsexponierten Seite einer repräsentativen Bucht im TNNP herrschten während der Jahreszeit ohne Tiefenwasserauftrieb höhere Wasserströmungsgeschwindigkeiten als an der geschützten, östlichen Seite. Die Wasserströmung an der exponierten Seite wurde zu jeder Jahreszeit in

der gesamten Wassersäule durch den Wind beeinflusst, wohingegen Wind an der geschützten Seite nur während des saisonalen Auftriebs einen Effekt auf Wasserströmungen bis in einer Tiefe von 10 m hatte und sonst Strömungen nur bis ca. 3 – 4 m Wassertiefe einwirkten (Kapitel 1). Die unterschiedlichen Wasserströmungsgeschwindigkeiten zwischen den exponierten und geschützten Buchtseiten sind von großer Bedeutung für die benthische Gemeinschaftsstruktur als auch der Hauptfaktor für die auftretende räumliche Muster von Korallenbleiche und anschliessende Erholung davon (Kapitel 6).

b) Die gemessene Wasserqualität des TNNP während der Saison ohne Auftrieb erfüllte generell die Anforderungen, welche für das Wachstum von Korallenriffen notwendig sind. Die kritischen Schwellenwerte für Nährstoffkonzentrationen und Algenblüten wurden aufgrund von terrestrischem Eintrag über Flussmündungen, sowie während des saisonalen Auftriebs, überschritten (Kapitel 2).

c) Riffsedimente des TNNP reagierten sehr dynamisch auf schubweise Einträge von frischem organischen Material durch den Auftrieb und wiesen sehr hohe Kohlenstoffumsatzraten im Vergleich zu anderen Silikatsanden auf. Aufgrund des hohen jährlichen Eintrags organischem Materials, sowie des akkumulierten Kohlenstoffs innerhalb des Sedimentes (Kapitel 3), können die Riffsande des TNNP als meso-oligotroph eingestuft werden. Die durch die Sedimente freigesetzten Nährstoffe ermöglichen eine hohe benthische Primärproduktion (Kapitel 4).

d) Die lokalen autotrophen Riffgemeinschaften sind gut an saisonale Schwankungen wichtiger Umweltparameter angepasst; es konnten keine räumlichen oder zeitlichen Unterschiede in der Netto- und Brutto-Primärproduktion auf der Ökosystemebene beobachtet wurden (Kapitel 4).

e) Steinkorallen an einem strömungsgeschützten Ort im TNNP waren anfälliger für Korallenbleiche als Korallen an einer exponierten Stelle. Die generell flacheren Korallengemeinschaften an der exponierten Stelle erholten sich besser von der Korallenbleiche als die riffbildenden und vielfältigeren Gemeinschaften an der geschützen Stelle. Die Ergebnisse deuten auf die Existenz einer lokalen, strömungsbedingten (Kapitel 1) Widerstandsfähigkeit dieser karibischen Riffe gegen Korallenbleiche (Kapitel 6) hin.

f) Populationen des invasiven Rotfeuerfisches *Pterois volitans* haben sich in den letzten Jahren in den Buchten des TNNP etabliert. Es handelt sich dabei größtenteils um erwachsene Individuen, welche das Funktionieren der Riffe durch einen schnellen und unkontrollierten Konsum von kleinen herbivoren Fischen gefährden, da es im Gebiet an natürlichen Feinden mangelt. Die im TNNP erfassten Häufigkeiten entsprechen jenen des Ursprungsgebietes von *P. volitans* im Indopazifik. Das Auftreten von *P. volitans* zeigt, dass sofortige Maßnahmen zur Bekämpfung des Rotfeuerfisches notwendig sind, um die Integrität der Korallenriffe im TNNP zu bewahren (Kapitel 7).

Die vorliegende Arbeit beschäftigt sich mit den Auswirkungen globaler (z.B. Temperatur-induzierte Korallenbleiche) als auch lokaler Bedrohungen (z.B. Verschlechterung der Wasserqualität und Rotfeuerfischinvasion) auf Korallenriffe des TNNP. Die erhobenen Daten deuten darauf hin, dass zeitgleiches Auftreten von saisonalem Tiefenwasser-auftriebs beim höchstem Hitzestress den Bedrohungen der globalen Erwärmung auf Korallengemeinschaften im TNNP entgegenwirken könnte. Allerdings können nur verbessertes Management- sowie umfassende Umweltschutzmaßnahmen die Auswirkungen lokaler Bedrohungen minimieren. Die Ergebnisse der Studien zeigen auf, dass der TNNP aufgrund seiner natürlich vorkommenden, rauen, jahreszeitlichen Veränderungen eine einzigartige Umgebung für Korallenriffen darstellt. Diese speziellen Bedingungen könnten die Korallenriffe des TNNP widerstandsfähig gegenüber den Folgen des Klimawandels als auch lokaler anthropogenen Störungen gemacht haben. Diese Arbeit beinhaltet den ersten umfassenden Datensatz einer ganzheitlichen Herangehensweise, um den durch starke saisonale Umweltveränderungen beeinflussten Zustand und das Funktionieren der Korallenriffe im TNNP zu beschreiben. Gleichzeitig bieten die Studien eine Reihe von Schlüsselindikatoren für ein effizientes Umweltmonitoring. Somit bildet die Arbeit eine solide Basis auf mehreren Ebenen (Wassersäule, Sedimente und benthische Lebensgemeinschaften) für die zukünftige Erforschung dieses relativ ungestörten Ökosystems.

Resumen

El Parque Nacional Natural Tayrona (PNNT) se encuentra en la costa noreste de Colombia y constituye uno de los puntos de mayor biodiversidad del Caribe colombiano. A pesar que sus comunidades coralinas están relativamente en buen estado, en comparación con otros lugares del Caribe, el funcionamiento de estas comunidades ha sido poco estudiada, en especial los efectos que tienen los cambios estacionales y la surgencia anual que ocurre con la llegada de los vientos Alisios. Por lo anterior, esta tesis expone los efectos estacionales en los arrecifes de coral del PNNT para responder a tres preguntas claves, cada una de las cuales aborda un componente diferente del ecosistema arrecifal. (I) Columna del agua: ¿Cómo cambian las corrientes y la calidad del agua que rodea los arrecifes de coral con las estaciones? (II) Sedimentos arrecifales: ¿Qué regula el suministro de materia orgánica al fondo marino y los procesos de remineralización y regeneración de los nutrientes esenciales para la producción primaria bentónica? (III) Comunidades bentónicas: ¿Cómo es afectada la producción primaria bentónica, la condición de los corales, y la distribución del pez león invasor, por el cambio estacional y la surgencia? Estas preguntas se responden en los siete capítulos del presente documento. Los capítulos están enmarcados por una introducción general y un breve resumen. El enfoque para responder a estas preguntas consistió en (1) el anclaje de un Acoustic Doppler Current Profiler (ADCP) para registrar la velocidad y dirección de las corrientes marinas, (2) un monitoreo mensual (25 meses en total) de los principales parámetros de calidad de agua, (3) el estudio del suministro de materia orgánica a los sedimentos y el inicio de los procesos sedimentarios, (4) la estimación de la producción primaria de los organismos bentónicos autótrofos, (5) un monitoreo del blanqueamiento de corales y recuperación en relación con la exposición a corrientes marinas, y (6) la evaluación de la abundancia del pez león en un área total de 6.000 m^2 en el PNNT.

Los principales resultados muestran que:

a) Durante la temporada en que no hay surgencia, las corrientes marinas son más intensas en el costado occidental de la bahía, el cual está expuesto al viento y oleaje en comparación con el lado oriental que es más protegido. Además, en el costado expuesto la fricción del viento afecta toda la columna del agua en ambas temporadas, mientras que en el sitio protegido llega sólo hasta 3 - 4 m de profundidad cuando no hay surgencia y hasta 10 m cuando hay surgencia

(Capítulo 1). Las diferencias en el grado de exposición a las corrientes marinas determinan la distribución de los organismos y además son consideradas como los principales controles locales de los patrones del blanqueamiento coralino y la subsecuente recuperación (Capítulo 6).

b) La calidad del agua en el PNNT es similar a las condiciones oligotróficas adecuadas para el crecimiento de los corales durante la época de no surgencia, pero superó los valores críticos de concentración de nutrientes inorgánicos y de afloraciones fitoplanctónicas durante la surgencia y en relación a las descargas fluviales (Capítulo 2).

c) Los sedimentos arrecifales en el PNNT son muy dinámicos con relación a los pulsos de materia orgánica lábil influenciados por la surgencia. La materia orgánica que llega al fondo marino provoca tasas muy altas del procesamiento del carbono en comparación con arenas arrecifales dominadas por silicato. Los sedimentos arrecifales en el PNNT se pueden clasificar como meso-oligotróficos de acuerdo al suministro anual de carbono orgánico y al contenido de materia orgánica acumulada en el fondo (Capítulo 3). Los nutrientes liberados por los sedimentos mantienen una alta productividad primaria bentónica (Capítulo 4).

d) Las comunidades arrecifales autótrofas locales están bien adaptadas a las fluctuaciones en los parámetros ambientales claves. Lo anterior se concluye ya que no se observaron diferencias espaciales ni temporales en la producción primaria (bruta y neta) a nivel ecosistémico (Capítulo 4).

e) Los corales escleractíneos presentes en el costado protegido a corrientes marinas en las bahías del PNNT, son más susceptibles al blanqueamiento que los corales que se encuentran en el costado expuesto. La comunidad de corales del costado expuesto que se caracterizan por tener una baja complejidad, se recupera más eficientemente que la comunidad más diversa y estructuralmente más compleja del costado protegido. Los resultados sugieren la existencia de patrones de resiliencia local (principalmente debido a las corrientes marinas; Capítulo 1) de estos arrecifes del Caribe contra el blanqueamiento coralino (Capítulo 6).

f) El pez león, *Pterois volitans*, se ha establecido efectivamente en las bahías del PNNT. Los individuos registrados fueron en su mayoría adultos. El pez león es una especie invasora que debido a la falta de depredadores naturales, afecta los arrecifes coralinos locales a través del consumo rápido e incontrolado de pequeños peces herbívoros. Las abundancias de *P. volitans* son muy similares a lugares del Indo-Pacífico de donde esta especie proviene. La presencia de *P. volitans* es alarmante por lo que medidas de control inmediatas son fundamentales para preservar la integridad de los arrecifes de coral en el PNNT (Capítulo 7).

Los capítulos de la presente tesis doctoral abarcan fenómenos globales (p. ej. el blanqueamiento coralino inducido por aumentos en la temperatura) y amenazas locales (p. ej. el deterioro de la calidad del agua y la invasión del pez león) para arrecifes coralinos en el PNNT. Los resultados sugieren que mientras que las amenazas del calentamiento global puedan ser contrarrestadas por la presencia de la surgencia estacional coincidiendo con el mayor estrés térmico, los efectos de las amenazas locales sólo se pueden evitar mediante la mejora de las medidas de manejo y conservación. La tesis destaca que el PNNT es un ambiente único en el que los arrecifes de coral, naturalmente expuestos a cambios estacionales fuertes, probablemente han desarrollado una mayor capacidad de adaptación a las condiciones locales del cambio climático y las perturbaciones antropogénicas. El conjunto de datos del monitoreo representa el primer enfoque holístico para describir la condición y el funcionamiento de los arrecifes de coral en PNNT, influidos por fuertes cambios estacionales. De esta manera, el trabajo constituye una línea base sólida de varios niveles (columna de agua, sedimentos y las comunidades bentónicas) para la futura investigación de este ecosistema relativamente poco deteriorado.

General Introduction

Tayrona National Natural Park

The Tayrona National Natural Park (TNNP) is located at the Northeastern Colombian coast between 11°17' – 11°22' N and 73°53' – 74°12' W. Despite of its relatively small coastline of only ca. 40 km, TNNP belongs to the most biodiverse areas of the tropical and subtropical Atlantic (Garzón-Ferreira and Cano 1991; Diaz Pulido and Díaz Ruiz 2003). Along its rocky coastline with capes, inlets and bays (Fig. 1), the TNNP is home to a variety of seagrass beds, mangroves and coral communities (Garzón-Ferreira and Cano 1991; Garzón-Ferreira and Díaz 2003). A record diversity was reported especially for macroalgae (Bula-Meyer and Norris 2001; Diaz-Pulido and Garzón-Ferreira 2002) but also for other marine organisms (e.g. mollusks; Díaz 1995; Diaz-Pulido 1998) in TNNP. However, coral reefs in TNNP belong to the least studied ecosystems as compared to other worldwide reef locations (Fig. 2).

Figure 1. Gayraca Bay in Tayrona National Natural Park.

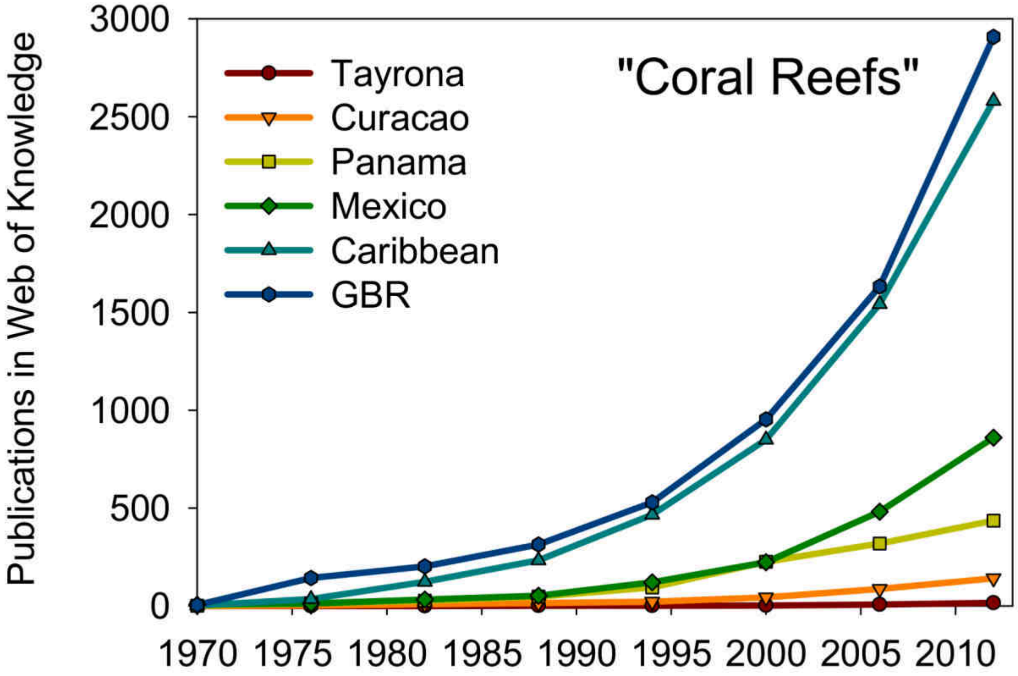

Figure 2. Cumulative number of Web of Knowledge listed publications through time for the topic "Coral Reefs" and the regions: Tayrona Park (dark red line, circles), Curaçao (orange line, triangles facing down), Panama (yellow line, squares), Mexico (green line, diamonds), the Caribbean (light blue line, triangles facing up) and the Great Barrier Reef (GBR, dark blue line, circles). Source: apps.webofknowledge.com/.

Seasonality and upwelling events in TNNP

The climate of TNNP is subtropical with air temperature ranging between 25 and 30 °C (mean of 28 °C) and an annual rainfall of 350 mm (Salzwedel and Müller 1983; Martínez and Acosta 2005). The TNNP region experiences strong seasonal variations through the alternation of rainy and dry seasons mainly triggered by the North-South displacement of the Intertropical Convergence Zone and strong Trade Winds from the North and Northeast (Salzwedel and Müller 1983; Mesa et al. 1997). The rainfall probability is highest for the months September – November (> 52 % of the annual rainfall; Salzwedel and Müller 1983) which hence represent the major rainy season. During major dry season (December – April), strong winds from the Caribbean Low-Level Jet of Northeast Trade Winds parallel to the coastline displace humidity and trigger an Ekman transport of surface waters off the coast of TNNP and an upwelling of sub-surface waters from a depth of 110 – 120 m (Andrade et al. 2003; Andrade and Barton 2005; Paramo et al. 2011; Rueda-Roa and Muller-Karger 2013). Typically, the major dry season is followed by a short period of variable rainfall (May – June, minor rainy season) followed by a relatively dry period of variable winds also termed "Veranillo de San Juan" (July – August, minor dry season; Salzwedel and Müller 1983; Bula-Meyer 1990; Diaz-Pulido and

Garzón-Ferreira 2002; Andrade and Barton 2005). Some studies simplify the climatic conditions of TNNP as rainy season (May – November; > 80 % of the annual rainfall) and dry season (December – April, seasonal upwelling; Salzwedel and Müller 1983; Diaz-Pulido and Garzón-Ferreira 2002). The seasonal upwelling during dry season changes the physical parameters (e.g. seawater temperature decreases, increases of water current velocities; Chapter 1), the water quality (e.g. increases in inorganic nutrient and chlorophyll concentrations, decreases of salinity and water clarity; Chapter 2), increases the input of organic matter delivered from the water column to the sediments (Chapter 3), and makes the TNNP a unique environment for coral reefs. The drastically changing environmental seawater and sedimentary parameters make the TNNP a perfect natural laboratory to study adaptation potential of corals (Chapter 6) and other benthic primary producers (Chapter 4) to climate change and anthropogenic disturbances. The seasonal influences on the distribution of recent lionfish invasion in the TNNP bays were addressed in Chapter 7.

Key environmental status and process variables

Water currents: enhance transport processes through advection which would be otherwise subjected to the slow exchange by molecular diffusion (Huettel et al. 2003). Studies showed that water currents can alter the physiology of marine organisms (e.g. enhance photosynthesis, organic matter release by corals or increase ammonium uptake rates of organisms; Atkinson et al. 1994; Mass et al. 2010; Wild et al. 2012). They were suggested to also affect the characteristic distribution of organisms in the TNNP bays (Werding and Sánchez 1989) and to have implications for coral bleaching (Chapter 6). Water currents were shown to alleviate coral bleaching and increase recovery (Nakamura and van Woesik 2001; Nakamura et al. 2003; West and Salm 2003; Chapter 6). Water current dynamics in TNNP during representative months were elucidated in Chapter 1 by the deployment of an Acoustic Doppler Current Profiler (ADCP).

Water quality: The ideal habitats for coral reefs are warm, shallow, sunlit, and oligotrophic, but carbonate-supersaturated environments with a high degree of stability in order to allow for optimal calcification and growth (Hoegh-Guldberg 1999; Kleypas et al. 1999). Coral reef water quality can decline upon increased inorganic nutrients, enrichment with organic particulate matter, light reduction from turbidity and increased sedimentation which were shown to have detrimental effects on coral reef functioning

(Fabricius 2005). In this thesis, the water quality parameters inorganic nutrient, chlorophyll *a*, and particulate organic carbon and nitrogen concentrations along with biological O_2 demand, pH and water clarity were monitored directly above local coral reefs. Water quality in TNNP can either have spatial changes according to its location between the population center Santa Marta in the Southwest and several smaller river mouths in the East, or seasonal, due to the transition from rainy to dry seasons going along with coastal upwelling (Chapter 2).

Sedimentary processes: Highly permeable reef sands (Huettel et al. 2003; Rasheed et al. 2003), often composed by biogenic carbonates (Hallock 1997) and rich in heterotrophic microorganisms (Wild et al. 2006) are indispensable for recycling of organic matter and the release of essential nutrients for benthic primary production to the reef (Rasheed et al. 2002; Wild et al. 2004). As a consequence, reef sands are crucial for the functioning of coral ecosystems and help to maintain a high biomass and primary productivity (Hatcher 1988; Sorokin 1993) despite of the surrounding oligotrophic waters (Kleypas et al. 1999; Veron 2000). In Chapter 3, the spatial and temporal differences of organic matter delivered by the water column to the sediment floor, its composition and accumulation within the sediments were investigated by means of a monthly monitoring over 14 months in one representative bay. Thereby, the organic matter supplied to the sediment was measured by sediment traps which collected samples for the measurement of particulate organic carbon and nitrogen, and chlorophyll *a*. In parallel, the sediment properties grain-size, porosity, carbonate content, the amount of particulate organic carbon and nitrogen, the algal pigments chlorophyll *a*, *b*, c_1+c_2 and carotenoids were addressed by the sampling of sediments in four bays of TNNP.

Coral reefs in TNNP

Highly diverse coral assemblages develop up to depths of 25 – 30 m in the bays of TNNP despite the limited available substrate for reef settlement (Werding and Sánchez 1989). A decline in live coral cover by 4 % (from 34 to 30 %) was registered for the period 1998 – 2010 in TNNP (Vega-Sequeda et al. 2011) which was extensively attributed to the moderate coral bleaching event during 2010 (Chapter 6). However, coral reefs in TNNP are less degraded than other Caribbean locations (Burke et al. 2011); the rare genus *Acropora* spp. can be still observed in every TNNP bay (Werding and Sánchez 1989; Garzón-Ferreira and Cano 1991; Rodríguez-Ramírez et al. 2010).

Some authors suggested that an optimal reef development in TNNP is hindered by the decline in water quality, increased sedimentation and drastic changes of temperature and salinity during seasonal upwelling (Antonius 1972; Werding and Sánchez 1989). These factors were addressed in Chapter 1, 2 and 3.

Due to their topographical orientation, the Western (windward) flanks of the bays are stronger impacted by wind from the Northeast than the Eastern, (leeward) flanks. The wind impact creates an exposure to higher wave- and water currents at the Western sides of the bays. Werding and Sánchez (1989) first observed that a characteristic zonation of encrusting coral assemblages with high octocorals abundance were found at sites exposed to stronger wave impact than at the opposite, sheltered side of one bay where true reefs and reef-building species with higher complexity were registered. Therefore, the spatial differences in environmental parameters (Chapter 1, 2 and 3), the primary production budgets of benthic phototrophs (Chapter 4), and susceptibility of corals to coral bleaching and recovery (Chapter 6) were addressed by surveys at two opposing sites within the bays.

Primary production of benthic phototrophs

All marine life depends on the primary production of organisms that convert light into chemical energy and consequently, the production of organic matter by photosynthesis (e.g. Duarte and Cebrian 1996). Corals reefs belong to the most productive ecosystems (Sorokin 1993). Reefs in TNNP harbor besides scleractinian corals, a large variety of benthic phototrophs such as macroalgae, algal turfs, crustose coralline algae, and microphytobenthos that inhabit the permeable reef sands (Chapter 4). Primary production is classified by gross and net primary production. Gross primary production is the total amount of energy fixed to organic matter per unit time through photosynthesis. Whereas, net primary production is energy fixed in photosynthesis minus energy lost during respiration and thereby characterizes the amount of energy that is available for the growth of organisms through organic matter production (Hallock and Schlager 1986). The spatial and temporal variations of the primary production budget in one TNNP bay are addressed in Chapter 4.

The lionfish problem of Caribbean coral reefs

Invasive species can alter the biogeochemical cycles and trophic net structures of marine ecosystems (Mack et al. 2000) resulting in changed functioning and services provided by the ecosystem with strong implications for coastal human populations (Schüttler and Karez 2008). The Indo-Pacific lionfish *Pterois volitans* is an invasive marine fish that got introduced in the Western Atlantic. Local lionfish populations may disturb functioning of coral reefs through high consumption of small herbivorous fishes, including parrotfishes (Albins and Hixon 2008; Morris and Akins 2009), thus indirectly promote the outcompeting of corals by naturally uncontrolled growth of seaweeds (Mumby et al. 2006; Mumby and Steneck 2008). Lionfish invaded from North Carolina/USA to the Lesser Antilles through the Caribbean (Schofield 2009; Schofield 2010). In Colombia, it arrived to the oceanic islands of San Andrés and Providencia in 2008 and invaded the entire continental coast of the country in the following year (Betancur-R. et al. 2011). In the middle of 2009, *P. volitans* was first sighted in a TNNP bay (González et al. 2009). Since then, its distribution and abundance remained unknown. In Chapter 7, the current distribution and abundances of invasive lionfish are presented. Potential seasonal effects on lionfish distribution and suggestions for future management actions are further discussed.

Objectives

The aim of this thesis was to monitor seasonal and upwelling-induced effects on water quality and sedimentary status and process parameters, and to understand their implications for the reef ecosystem in terms of its benthic primary production and coral condition during a bleaching event (Fig. 3). Further seasonal effects on the distribution of invasive lionfish that may have detrimental consequences for the coral reef functioning in TNNP were studied. This thesis investigated the local resilience of coral reefs subjected to natural seasonal change, coastal upwelling and riverine discharge (Fig. 3).

The specific objectives were:

1. To describe the seasonal change of water current dynamics in one exemplary bay in TNNP.
2. To monitor the spatial and temporal changes in water quality over 25 months and address the trophic condition of TNNP reefs.

3. To assess the supply with organic matter from the water column to the reef sediments and estimate their rate of remineralization and regeneration of essential nutrients.
4. To estimate the seasonal effects on the net and gross primary production of benthic reef organisms.
5. To report the first moderate coral bleaching event for decades in TNNP, describe the bleaching extent and recovery in one TNNP bay and address local spatio-temporal resilience patterns.
6. To record spatial and temporal distribution and abundances of invasive lionfish in the bays of TNNP and recommend future management actions.

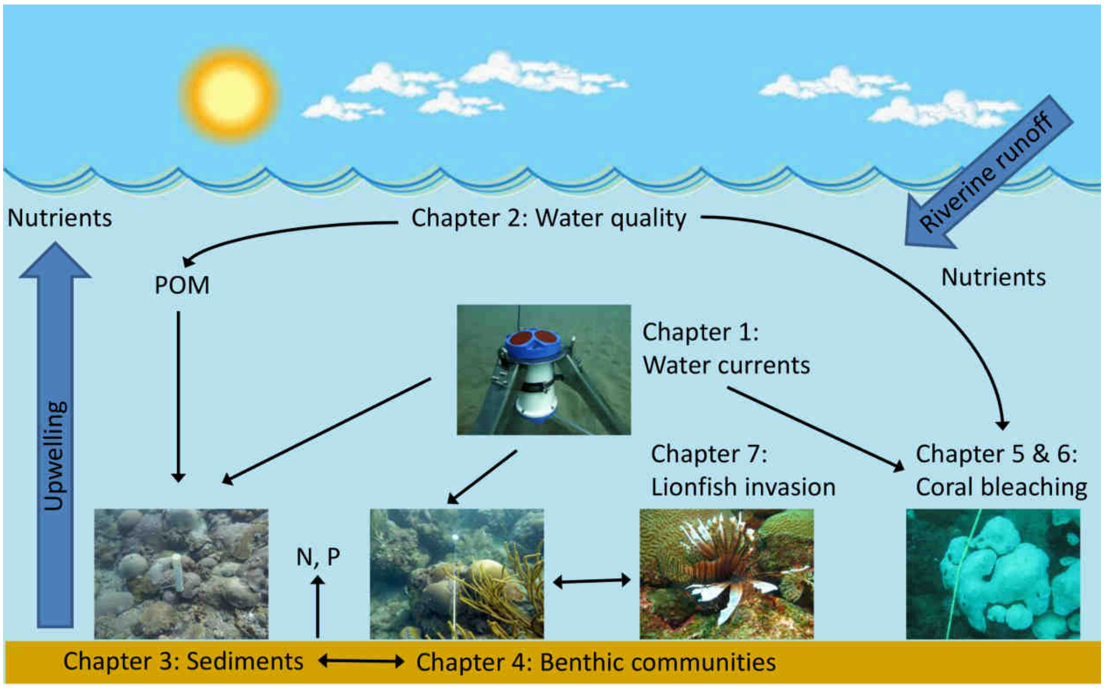

Figure 3. Schematic overview of thesis design and interconnectivity of chapters. Water currents (Chapter 1) have effects on the supply of organic matter to the sediments (Chapter 3), the distribution of benthic organisms (Chapter 4), and patterns of coral bleaching and recovery (Chapter 5 & 6). Seasonal upwelling and riverine runoff deliver inorganic nutrients for primary production of phytoplankton and consequently alter water quality (Chapter 2). The water quality affects coral condition and induces coral bleaching (Chapter 5 & 6). Particulate organic matter (POM) of fresh phytoplankton detritus from the water column is supplied to the sediments where it is remineralized and recycled (Chapter 3). Essential nutrients, particularly nitrogen (N) and phosphorus (P), are released by the sediments and stimulate benthic primary production (Chapter 4). The invasive lionfish influences the functioning of benthic reef communities through the consumption of small herbivorous fish and thereby promoting algal growth (Chapter 7). Picture adapted from Arrigo 2005.

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Publication outline

This thesis includes seven articles, thereof two are accepted for publication and five are submitted for review to international peer-reviewed journals. Each article represents one chapter. The first chapter deals with the underlying water current dynamics and their seasonal change in one representative bay. The second chapter reveals the seasonal and upwelling-induced changes of water quality parameters in the TNNP. Chapter 3 describes the seasonal change of organic matter supplied to the sediments and the sedimentary processes of TNNP reefs. Chapter 4 deals with the effects of seasonality and upwelling on the benthic primary production budget. Chapter 5 is a book chapter on coral bleaching and serves as an introduction to the topic of Chapter 6. This chapter is a case study of the first reported significant coral bleaching event in TNNP and reveals how coral bleaching patterns depended upon different exposure to water currents described in Chapter 1. The last Chapter 7 introduces the issue of recent lionfish invasion of TNNP bays, observes spatiotemporal dynamics of distribution and abundances, and discusses necessary management actions. The specific contribution of each author with regard to study idea and design, data acquisition, analysis and writing the manuscripts are outlined for each publication below:

Publication 1

Bayraktarov E., Bastidas-Salamanca M. L., Wild C.

The physical environment in coral reefs of the Colombian Caribbean in response to seasonal upwelling

The idea for this study was developed by E. Bayraktarov and M. L. Bastidas-Salamanca with advice by C. Wild. Collection of data was carried out by E. Bayraktarov and L. M. Bastidas-Salamanca. Data analysis and writing of the manuscript were accomplished by E. Bayraktarov and L. M. Bastidas-Salamanca with improvements by C. Wild. This article has been submitted to Boletín de Investigaciones Marinas y Costeras – Invemar.

Publication 2

Bayraktarov E., Pizarro V., Wild C.

Spatial and temporal variability of water quality in coral reefs of Tayrona National Natural Park, Colombian Caribbean

The concept for this study was developed by E. Bayraktarov and C. Wild. Data acquisition was performed by E. Bayraktarov and V. Pizarro. Data analysis and writing of the manuscript were conducted by E. Bayraktarov with improvements by V. Pizarro and C. Wild. This article has been submitted to Environmental Monitoring and Assessment.

Publication 3

Bayraktarov E., Wild C.

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

The concept for this study was developed by E. Bayraktarov and C. Wild. Sampling was carried out by E. Bayraktarov. Data analysis and writing was conducted by E. Bayraktarov with support by C. Wild. This article has been submitted to Biogeosciences.

Publication 4

Eidens C., Bayraktarov E., Pizarro V., Wilke T., Wild C.

Primary production in upwelling-influenced Colombian Caribbean coral reefs

This publication was initiated by C. Eidens and C. Wild. Sampling was carried out by C. Eidens with help by E. Bayraktarov and V. Pizarro. Data analysis and writing were accomplished by C. Eidens with improvements by E. Bayraktarov, V. Pizarro, T. Wilke and C. Wild. This article has been submitted to PLoS ONE.

Publication 5

Plass-Johnson J. G., Cardini U., van Hoytema N., Bayraktarov E., Burghardt I., Naumann M. S., Wild C

Coral bleaching

This chapter has been initiated by C. Wild. The outline and structure have been designed by J. G. Plass-Johnson and C. Wild. Writing of the manuscript was conducted by J. G. Plass-Johnson, U. Cardini, N. van Hoytema, E. Bayraktarov, I. Burghardt, M. S. Naumann, and C. Wild. This article has been accepted as chapter for the upcoming Springer book entitled Environmental Indicators edited by R. Armon and H. Osmonen.

Publication 6

Bayraktarov E., Pizarro V., Eidens C., Wilke T., Wild C.

Bleaching susceptibility and recovery of Colombian Caribbean corals in response to water current exposure and seasonal upwelling

This publication was initiated by E. Bayraktarov and V. Pizarro with advice by C. Wild. Data collection was conducted by E. Bayraktarov and V. Pizarro. Analysis of data and writing were performed by E. Bayraktarov with improvements by V. Pizarro, C. Eidens, T. Wilke and C. Wild. This article has been accepted for publication by PLoS ONE and is currently in press.

Publication 7

Bayraktarov E., Alarcón-Moscoso J., Polanco-F. A., Wild C.

Spatial and temporal distribution of the invasive lionfish *Pterois volitans* in coral reefs of Tayrona National Natural Park, Colombian Caribbean

This publication was initiated by C. Wild and E. Bayraktarov. Data sampling was carried out by J. Alarcón-Moscoso and E. Bayraktarov. Data analysis and writing were conducted by E. Bayraktarov with improvements by J. Alarcón-Moscoso, A. Polanco-F. and C. Wild. This article has been submitted to Aquatic Invasions.

1

The Physical Environment in Coral Reefs of the Colombian Caribbean in Response to Seasonal Upwelling

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This article has been submitted to Boletín de Investigaciones Marinas y Costeras – Invemar.

Resumen

El ambiente físico en arrecifes coralinos del Caribe Colombiano en respuesta a la surgencia estacional. Los arrecifes de coral están sujetos a cambios físicos en su entorno, incluyendo la velocidad del viento, temperatura del agua y las corrientes marinas, las cuales pueden llegar a afectar a los procesos ecológicos en diferentes escalas espaciales y temporales; sin embargo, es poco lo que se conoce sobre la dinámica de las variables físicas en los ecosistemas de arrecifes de coral. En este contexto, el Parque Nacional Natural Tayrona (PNNT) en el Caribe Colombiano, es un sitio ideal de estudio, ya que contiene arrecifes coralinos y es influenciado por una surgencia estacional que altera todos los factores físicos claves mencionados anteriormente. En este estudio se midieron la velocidad del viento con una estación meteorológica y la temperatura del agua con loggers durante más de dos años, así como la velocidad y dirección de las corrientes marinas con un *Acoustic Doppler Current Profiler* (ADCP) durante meses representativos para cada estación en un sitio de arrecife coralino expuesto y protegido a viento y oleaje en una bahía representativa del PNNT con el objetivo de describir las variaciones espacio-temporales en el ambiente físico. Los resultados revelaron que la temperatura del agua (28,7 ± 0,8 °C y máxima de 30.3 °C durante la época de no surgencia; 25,1 ± 1,7 °C y mínima 20,3 °C durante la surgencia) no presentó diferencias significativas entre ambos lados de la bahía, no obstante exhibió una correlación negativa con la velocidad del viento (0,4 ± 0,3 m s^{-1} durante la no surgencia y 1,8 ± 1,0 m s^{-1}; máximo: 4,1 m s^{-1}

durante la surgencia) para los dos sitios observados. Las velocidades de las corrientes resultaron estadísticamente mayores en el lado expuesto comparado con el protegido durante períodos de no surgencia a una profundidad entre 8 a 10 m. Durante la surgencia, las velocidades de las corrientes también fueron más altas en el lado expuesto (6,4 cm s^{-1} expuesto y 5,9 cm s^{-1} protegido), pero cuando la velocidad del viento superó 1,7 m s^{-1}, no se encontraron diferencias entre ambos lados de la bahía. Las corrientes marinas mostraron una circulación anticiclónica al interior de la bahía durante la surgencia siguiendo el patrón de vientos, pero ningún patrón claro durante la no surgencia. Se encontró una correlación positiva entre la magnitud del viento y la velocidad de la corriente en el lado protegido, pero no ocurrió así en el lado expuesto. En el sitio expuesto, el estrés del viento afectó la magnitud de las corrientes en toda la columna de agua (hasta los 10 m de profundidad) durante ambas temporadas, pero su influencia llegó sólo hasta 3 – 4 m de profundidad en el sitio protegido durante la época de no surgencia y hasta 10 m durante la surgencia. Estos resultados indican que los organismos que viven en el lado expuesto experimentan una exposición constante a mayores corrientes marinas a lo largo del año con respecto a los organismos del lado protegido. Esto puede explicar las fuertes diferencias en la composición de las comunidades arrecifales entre ambos lados de la bahía, ya que la magnitud de las corrientes y la circulación local controlan la distribución de larvas de invertebrados así como la disponibilidad de plancton y nutrientes esenciales.

Abstract

Coral reefs are subjected to physical changes in their surroundings including wind velocity, water temperature and water currents that can affect ecological processes on different spatial and temporal scales. However, the dynamics of these physical variables in coral reef ecosystems are poorly understood. In this context, Tayrona National Natural Park (TNNP) in the Colombian Caribbean is an ideal study location, because it contains coral reefs and is exposed to seasonal upwelling that strongly changes all key physical factors mentioned above. This study therefore investigated wind velocity and water temperature over two years, as well as water current velocity and direction for representative months of each season at a wind- and wave-exposed and a -sheltered coral reef site in one exemplary bay of TNNP using meteorological data, temperature loggers, and an Acoustic Doppler Current Profiler (ADCP) in order to describe the spatiotemporal variations of the physical environment. Findings revealed that water temperatures (28.7 ± 0.8 °C and maximal 30.3 °C during non-upwelling; 25.1 ± 1.7 °C and minimum 20.3 °C during upwelling) exhibited no significant differences between sites and were negatively correlated with wind velocities (0.4 ± 0.3 m s^{-1} during non-upwelling and 1.8 ± 1.0 m s^{-1} with a maximum of 4.1 m s^{-1} during upwelling). Water current velocity was significantly higher at the exposed compared to the sheltered site during non-upwelling periods at a water depth of 8 – 10 m. During upwelling, water current velocities were also higher at the exposed site (6.4 cm s^{-1} exposed and 5.9 cm s^{-1} sheltered), but when wind speed surpassed 1.7 m s^{-1}, no spatial differences occurred. Water currents showed a clockwise circulation during upwelling following the wind fields, but no clear circulation pattern during non-upwelling. Significant positive correlation between wind and water current velocity was detected at the sheltered, but not at the exposed site. Wind-stress at the exposed site affected water currents throughout the entire water column (at least 10 m water depth) during both seasons, but reached only until 3 – 4 m water depth at the sheltered site during non-upwelling and down to 10 m during upwelling. Consequently, organisms at the exposed site experience constantly high water current exposure throughout the year. This may explain the pronounced site-specific reef community composition differences as water current velocity and circulation control distribution of invertebrate larvae and supply with plankton and essential nutrients.

Introduction

The physical variables surface wind, water temperature and water currents have different ecologic effects on coral reef ecosystems. A recent study showed that wind fields are an essential factor for coral spawning and thereby determine the success of coral reproduction (van Woesik 2010). But winds are also important in triggering of water currents through creation of pressure gradients through wind stress at the water surface (Andrews and Pickard 1990). Increased water temperature as a consequence of climate change plays a major role in coral bleaching events (Glynn 1991; Glynn 1993; Brown 1997; Hoegh-Guldberg 1999; Loya et al. 2001; Hoegh-Guldberg 2011). However, probably the most important physical forcing in coral reefs are water currents and changes in local hydrodynamics. Water currents control many ecological aspects of coral reefs such as water quality, sedimentation patterns, nutrient uptake, recruitment and larval dispersal, coral bleaching patterns and disturbances through storms (Hamner and Wolanski 1988; Andrews and Pickard 1990; Nakamura and van Woesik 2001; Nakamura et al. 2003; Monismith 2007). The hydrodynamics in coral reefs entail a wide range of scales, starting from eddies produced by island wakes to changes in the hydrographic micro-environment of single coral polyps (Andrews and Pickard 1990; Monismith 2007). So far, the spatial and temporal dynamics of the key physical variables wind velocity, water temperature and water currents in coral reef ecosystems are generally poorly understood.

In Tayrona National Natural Park (TNNP), on the Northern coast of Colombia, the physical environment of coral reefs is subjected to seasonal changes between a rainy and dry season (Salzwedel and Müller 1983; Garzón-Ferreira 1998; Petùs et al. 2007). During rainy season, the TNNP is influenced by increased precipitations (Salzwedel and Müller 1983). The consecutive dry season is characterized by strong winds from the Northeast and coastal upwelling (Andrade and Barton 2005; Paramo et al. 2011). The seasonal change between non-upwelling and upwelling periods makes the region highly interesting for studies on the dynamics of physical variables in coral reef ecosystems, especially in response to environmental change. Despite the ecological importance of the region and seasonally changing impact of wind, water temperature and water currents, studies on the dynamics of these physical variables in the TNNP coral ecosystem are lacking. So far, no study has addressed the seasonal changes of *in situ* water current dynamics in TNNP coral reefs.

The aim of the present study therefore was to relate wind velocity to water temperature and currents over time and to describe how the spatiotemporal dynamics of these physical variables change between a non-upwelling and upwelling season at a wind- and wave-exposed and a -sheltered site in one representative bay of TNNP. As exposed, we characterize locations that due to orientation of the TNNP bays, experience increased wave action and turbulence as compared to sheltered sites. In the pilot study of Bayraktarov et al. (2012), it was observed that during a coral bleaching event, the extent of bleached corals was three times lower at an exposed as at a sheltered site. This indicates that a key factor controlling coral reef ecosystem functioning in TNNP may reside in the water currents that act on different temporal and spatial scales. Therefore, a monthly measurement of water currents was carried out during representative months of the upwelling and non-upwelling periods and also during the transition time between both periods in 2012, at an exposed and sheltered site by deployment of a high-accuracy Acoustic Doppler Current Profiler (ADCP) in close proximity to the coral ecosystem. The study was complemented by measurement of *in situ* temperature at both sites of the bay and analysis of meteorological data on wind intensity over a total study period of 27 months.

Study area

The TNNP is located on the Northern coast of Colombia, close to the city of Santa Marta, and contains six bays harboring coral communities, sea grass beds and mangrove ecosystems; it represents a hotspot of biodiversity in the Colombian Caribbean (Garzón-Ferreira and Cano 1991; Garzón-Ferreira 1998). Due to their topographic orientation, all bays of TNNP are exposed to strong winds from the Caribbean Low-Level Jet of Northeast (NE) Trade Winds (Andrade and Barton 2005) during the dry season (Salzwedel and Müller 1983; Diaz-Pulido and Garzón-Ferreira 2002; Paramo et al. 2011). Winds parallel to the coast displace humidity and trigger an Ekman transport of surface waters off the coast of TNNP and an upwelling of subsurface waters (Andrade et al. 2003; Andrade and Barton 2005; Paramo et al. 2011) which leads to a strong decrease in seawater temperature (from 30 °C in November to below 21 °C in February; this study) and an increase in salinity (from 33 to 38; Salzwedel and Müller 1983; Petùs et al. 2007; Bayraktarov et al. 2012). The climate is governed by a major dry season (December – April) with strong winds from North (N) and NE when the Intertropical Convergence Zone (ITCZ) is located South (S), a time period of variable winds (May – July) termed "Veranillo de San Juan" and a major rainy season (August – November) when the ITCZ is located N (Mesa et al. 1997) going along with more than 80 % of the annual rainfall (Salzwedel and Müller 1983). Highest seawater temperatures usually occur between October and November and can reach up to 30 °C (Bayraktarov et al. 2012). During the first months of each year, the prevailing wind direction in the Caribbean is from East (E) to West (W) which is the direction responsible for seasonal upwelling reported by several authors for the NE coast of Colombia and Venezuela (Fajardo 1979; Andrade 2000; Andrade et al. 2003; Andrade and Barton 2005; Paramo et al. 2011). The TNNP constitutes one of three major upwelling nuclei of the Guajira Upwelling System (Paramo et al. 2011), extending from the Guajira Peninsula to the city of Santa Marta (Andrade and Barton 2005). Specifically for the Santa Marta region, studies showed that continental winds create a wind stress of 1.2 dyn cm^{-2} triggering an Ekman transport off the coast which was able to increase concentrations of inorganic nutrients and chlorophyll *a*, characterizing the oligotrophic region during non-upwelling as mesotrophic in periods of upwelling (Franco-Herrera et al. 2007; Arévalo-Martínez and Franco-Herrera 2008). Tidal amplitudes for the TNNP area are small: García et al. (2011) reported for Santa Marta Bay a tide amplitude of 48 cm which was further classified as mixed, mainly diurnal, and was in accordance with other Colombian Caribbean regions such as Cartagena and Islas del Rosario (Molares 2004).

The study was carried out in Gayraca Bay, located at 11.33 °N, 74.11 °W (Fig. 1) at an exposed site on the Western side and a sheltered site on the Eastern side of the bay (Fig. 1C). Study locations were identical to sites from the coral bleaching survey in 2010/2011 in the same bay (see Bayraktarov et al. 2012; Chapter 6). Coral community composition and appearance are different between opposing sides of the TNNP bays (Werding and Sánchez 1989). Corals at the exposed site and a water depth of 10 m exhibited mainly massive to encrusting growth forms with colonies of *Montastraea cavernosa*, *Diploria strigosa*, *D. labyrinthiformis* and *Colpophyllia natans* dominating the coral community (Bayraktarov et al. 2012) and a low rugosity of 1.32 ± 0.13 (Chapter 4). Here, a high abundance of octocorals was detected (personal observation and Fig. 2A). On the sheltered site, at the same water depth, reef-like frameworks with higher coral diversity, complexity and *M. cavernosa*, *M. faveolata*, *M. franksi*, *D. strigosa*, *C. natans* and *Porites astreoides* as the predominant species among scleractinian corals were found (Fig. 2B). Rugosity at the sheltered site in Gayraca was 1.53 ± 0.12 (Chapter 4).

Materials and methods

Data collection

Continuous physical measurements were carried out between the years 2010 and 2012. Meteorological data of daily mean wind velocity was kindly provided by the meteorological station COMARTA of the University Jorge Tadeo Lozano in El Rodadero de Santa Marta, 18 km (air-line distance) away from Gayraca Bay for the time period of study (symbol "star" in Fig. 1B). Wind velocity was registered by an anemometer (Davis Instruments, Hayward, CA, USA) installed to a weather station (Weather Wizard III station, Davis Instruments, Hayward, CA, USA) which was placed

10 m above sea level. Continuous water temperature was measured *in situ* by HOBO TidBit v2 temperature loggers (Onset Computer Corp., Bourne, MA, USA) with temporal intervals of 5 min and accuracy of ± 0.2 °C. The loggers were attached to the reef structure at the exposed and sheltered sites at a water depth of 10 m between October 2010 and December 2012. During February 2012, water current velocity and direction were registered by a single point Aquadopp Current Meter (Nortek, Rud, Norway) with an acoustic frequency of 2 MHz at a water depth of 10 m. Underwater currents during the months July, August, September, November and December of 2012 were measured by a Workhorse Sentinel Acoustic Doppler Current Profiler (ADCP; Teledyne RD Instruments, Poway, CA, USA) with an acoustic frequency of 300 KHz at a water depth of 8 – 10 m. This water depth was of particular interest for this study as it corresponded to major occurrence of coral colonies and ecosystem (Bayraktarov et al. 2012). The Workhorse ADCP additionally measured water current profiles from the bottom to the sea surface in 1 m intervals. The current meters were monthly deployed at the exposed and two days later for the same daily and tidal phase at the sheltered site (approximately 6 h at each site). The anchorage location was within a radius of 20 m to the first bleaching monitoring transect at the exposed and sheltered site in the study of Bayraktarov et al. (2012). Measurements of water currents were performed for 2012 during upwelling/dry season (December – April), the period of variable winds between upwelling and non-upwelling season (May – July), and non-upwelling/rainy season (August – November).

Data analyses

A Spearman's correlation was applied in order to identify relations between wind velocity vs. water temperature and wind velocity vs. water current velocities for the exposed and sheltered site. Circular statistics by means of the MatLab ® toolbox CircStat (Berens, 2009) were applied to analyze the mean current direction and dispersion. A preliminary analysis (Q-Q plots for testing multinormality) revealed that the data series ($n = 6$ for exposed and $n = 6$ for the sheltered site) in scaled intervals and units (cm s^{-1}) were imbalanced as data length for the different days of measurement was not equal. A z-transformation was applied in order to calculate the standardized anomalies and identify outliers and extreme values (excluded when $-2.58 > z > 2.58$). As the data did not meet the requirements for parametric testing, a Kruskal-Wallis test was applied to identify differences in current velocities between sites (exposed vs. sheltered) and seasons (non-upwelling vs. upwelling) at a water depth of 8 – 10 m. For the investigation of water currents, February and December represented the upwelling/dry season, July the transition period of variable winds "Veranillo de San Juan", and August – November the major non-upwelling/rainy season according to Salzwedel and Müller (1983); Diaz-Pulido and Garzón-Ferreira (2002) and Paramo et al. (2011).

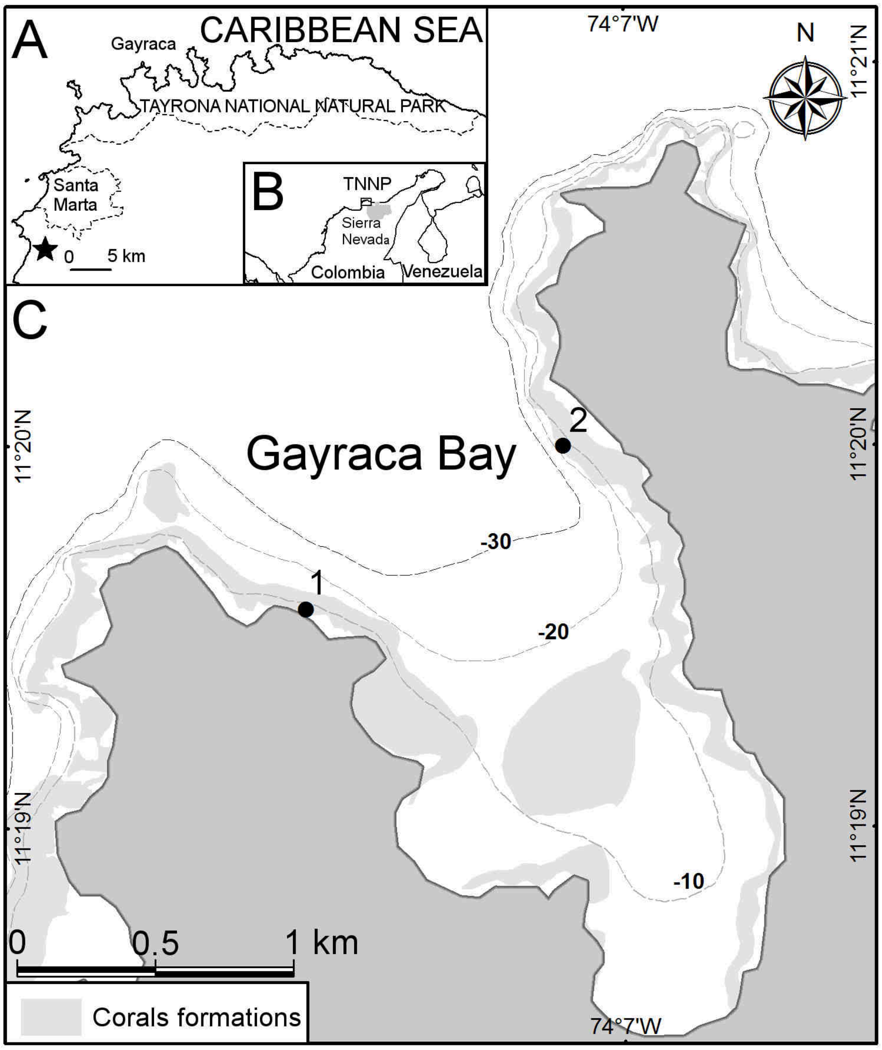

Figure 1. Location of Gayraca Bay and Tayrona National Natural Park (TNNP) in the Caribbean Sea. (A) Location of TNNP in Colombia. (B) The bays of TNNP and city of Santa Marta. The "star" symbol indicates the location of the meteorological station of the present study. (C) Sampling locations in Gayraca Bay. Circles indicate (1) exposed and (2) sheltered site. Depth contours are depicted with dashed lines. Source: Invemar 2012.

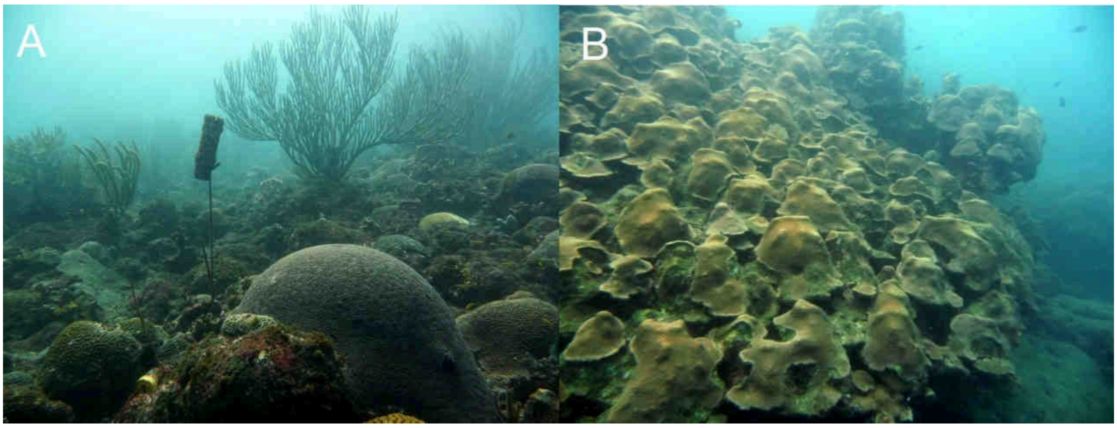

Figure 2. Coral communities at (A) the exposed site, represented by massive to encrusting growth forms of *Montastraea cavernosa*, *Diploria strigosa*, *D. labyrinthiformis*, *Colpophyllia natans*, and high abundance of octocorals and (B) sheltered site with reef-like frameworks of higher coral diversity and complexity with *M. cavernosa*, *M. faveolata*, *M. franksi*, *D. strigosa*, *C. natans* and *Porites astreoides* in Gayraca Bay.

Results

Spatiotemporal variability of the physical environment in Gayraca Bay

Significant negative correlation between water temperature and wind velocity was present for both sites of the bay (Fig. 3A). No correlation was found between water current velocities at a water depth of 8 – 10 m and wind velocity for the exposed site, while a significant positive correlation was observed for the sheltered site (Fig. 3B), showing that here current dynamics were controlled by the increase of winds. At this water depth, mean water current velocities at the exposed site (4.8 - 7.4 cm s^{-1}) were higher than at the sheltered site (3.9 - 6.1 cm s^{-1}) and were not affected by changing winds between seasons (Fig. 3B). We observed that water current velocities at the sheltered site reached the current velocity regime present at the exposed site above a threshold value of 1.7 m s^{-1} wind velocity (Fig. 3B).

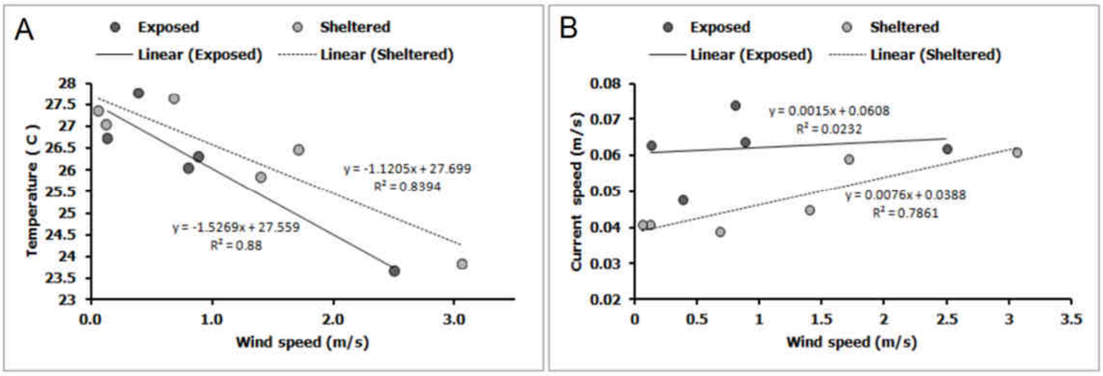

Figure 3. Relation between water temperature and wind speed (A) and water current velocity and wind speed (B) for the exposed and sheltered site in Gayraca Bay.

Calculated from the values registered between 2010 and 2012 and respective seasons, mean wind velocity for the upwelling periods was 1.8 ± 1.0 m s^{-1} (mean ± SD), but reached maximal values of 4.1 m s^{-1} in March (Fig. 4). For the periods of variable winds between upwelling and non-upwelling, mean wind velocities were 0.7 ± 0.6 m s^{-1} and 0.4 ± 0.3 m s^{-1} for non-upwelling, respectively.

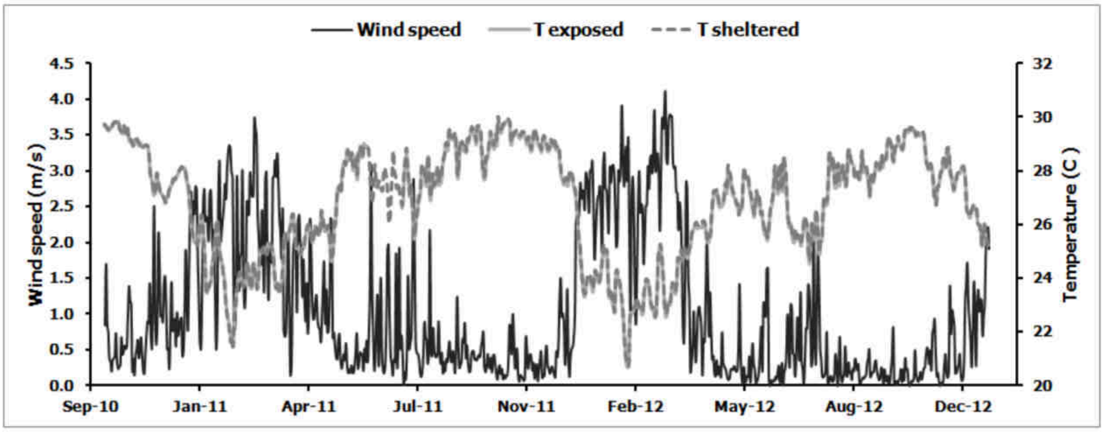

Figure 4. Daily mean *in situ* temperature at the exposed and sheltered site in Gayraca Bay and daily mean wind speed at a location near to Tayrona National Natural Park.

Water temperature was lowest during upwelling with 25.1 ± 1.7 °C (mean ± SD) for both sites, reaching minimal values of 20.3 °C for the exposed and 20.4 °C for the sheltered site in February. Intermediate mean temperature was detected for the periods of variable winds with 26.9 ± 1.2 °C for the exposed and 27.0 ± 1.1 °C for the sheltered site. The temperature was highest for the non-upwelling period with 27.7 ± 0.8 °C for both sites, but with maximal values of 30.3 °C detected in November (Table 1). *In situ* water temperature showed no significant differences between the exposed and the sheltered site (Kruskal-Wallis, $\alpha = 0.05$, $p < 0.05$). Consequently, a significant negative correlation ($r_{\text{Spearman}} = -0.69$, $\alpha = 0.05$) was observed between water temperature and wind velocity for both sites.

Table 1. *In situ* water temperature during upwelling (December – April), period of variable winds (May – July) and non-upwelling (August – November) for the exposed (exp) and sheltered (she) site in Gayraca Bay. Mean, maximum (Max) and minimal (Min) seawater temperatures are displayed.

Seasons 2010 – 2012	Mean Temp ± SD (°C)		Max Temp (°C)		Min Temp (°C)	
	exp	she	exp	she	exp	she
Upwelling	25.1 ± 1.7	25.1 ± 1.7	28.9	29.1	20.3	20.4
Variable winds	26.9 ± 1.2	27.0 ± 1.1	29.6	29.6	23.9	24.2
Non-upwelling	28.7 ± 0.8	28.7 ± 0.8	30.3	30.3	25.1	25.2

Mean water current velocities at a water depth of 8 – 10 m were always higher at the exposed compared to the sheltered site (Table 2), however no significant differences occurred during the upwelling months February and December (Table 3). At the observed water depth, water current velocities were significantly higher at the exposed than at the sheltered site for the non-upwelling months August, September, November and the month of variable winds, July (Kruskal-Wallis, $\alpha = 0.05$, $p < 0.05$).

Table 2. Water current velocities and directions (mean ± SD) for the exposed (exp) and sheltered (she) site at water depths of 8 – 10 m in Gayraca Bay. Upwelling months are indicated in italics.

	Mean Velocity. (cm s^{-1})		Mean Direction (°)	
	exp	she	exp	she
February	6.2 ± 2.0	6.1 ± 2.7	291 ± 27	208 ± 70
July	7.4 ± 3.3	4.5 ± 2.2	295 ± 42	257 ± 77
August	5.1 ± 2.9	3.9 ± 2.0	100 ± 68	7 ± 71
September	4.8 ± 2.7	4.1 ± 2.1	267 ± 66	330 ± 52
November	6.3 ± 2.8	4.1 ± 2.1	259 ± 62	299 ± 56
December	6.4 ± 4.0	5.9 ± 2.5	314 ± 75	330 ± 39

Table 3. Comparisons of water current velocities between the exposed (exp) and sheltered (she) site at depth of 8 – 10 m for Gayraca Bay (Kruskal-Wallis, $\alpha = 0.05$, $p < 0.05$).

	February	July	August	September	November	December
H_{cal}	0.0667	114.988	18.696	5.823	109.689	0.0043
H_{crit}	3.8415	3.8415	3.8415	3.8415	3.8415	3.8415
Result	exp = she	exp > she	exp > she	exp > she	exp > she	exp = she

For all months during which ADCP measurements were performed, water current velocities through the water column profile were higher at the exposed than at the sheltered site (Fig. 5). Minimal current velocities were observed during non-upwelling (August, September) for the water column at the sheltered site. Here, noticeable water currents were only present for the first 3 m water depth during non-upwelling (November) and for the first 4 m during period of variable winds (July). Highest water current velocities at the sheltered site were observed during upwelling (December), however below the current velocities at the exposed site (Fig. 5). Water current velocities within the water column profile at the sheltered site responded accordingly to the significant positive correlation with wind velocity (Fig. 5) calculated for the water current velocities at a water depth of 8 – 10 m (Fig. 3B).

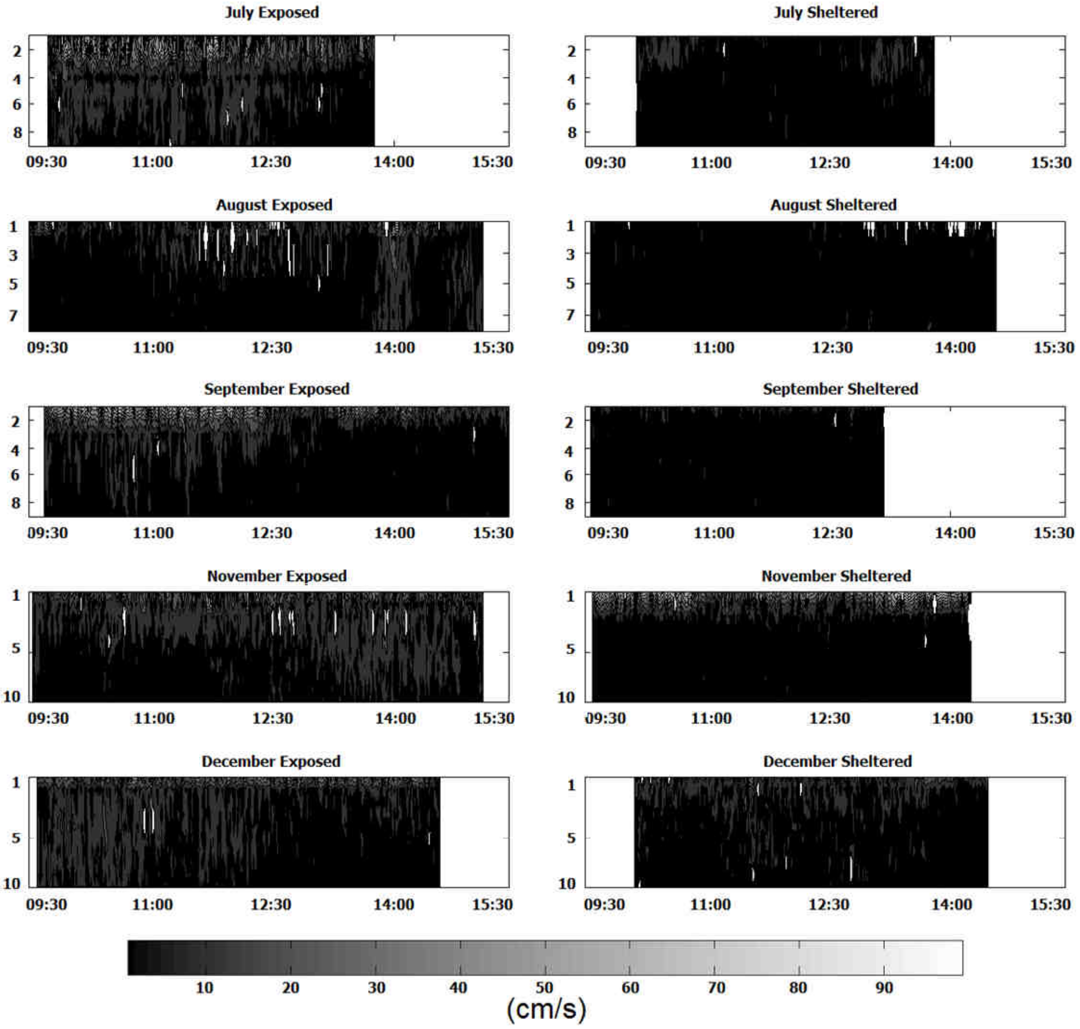

Figure 5. Water current velocity profiles of the water column (0 – 10 m water depth) for the exposed and sheltered site in Gayraca Bay. Units are in (cm s^{-1}).

Circulation of water currents in Gayraca Bay

In February, water current directions at a water depth of 8 – 10 m indicated that the clockwise circulation into the bay followed the coast-line into the bay's interior, entering from the sheltered site (SSW) and leaving the bay through the exposed site (WNW; Fig. 6A). This circulation pattern was repeatedly observed in July (Fig. 6B). In August, the circulation pattern of currents changed in a way that water flow entered from the exposed site (ESE) and left the bay through the sheltered site (N; Fig. 6C). During September and November, water currents at the exposed site were present in every direction, but predominated in W, while the dominant direction at the sheltered site was NW (Fig. 6D-E). A clear circulation pattern could not be deduced from these non-upwelling months. In December, the predominant direction was NW for both sites which did not allow a clear interpretation of circulation patterns (Fig. 6F).

Water currents at the exposed site were more homogeneous and had minor dispersion over time as compared to the sheltered site throughout the period of study. Highest dispersion in water current directions was registered during the months February, July, August and December (Table 2).

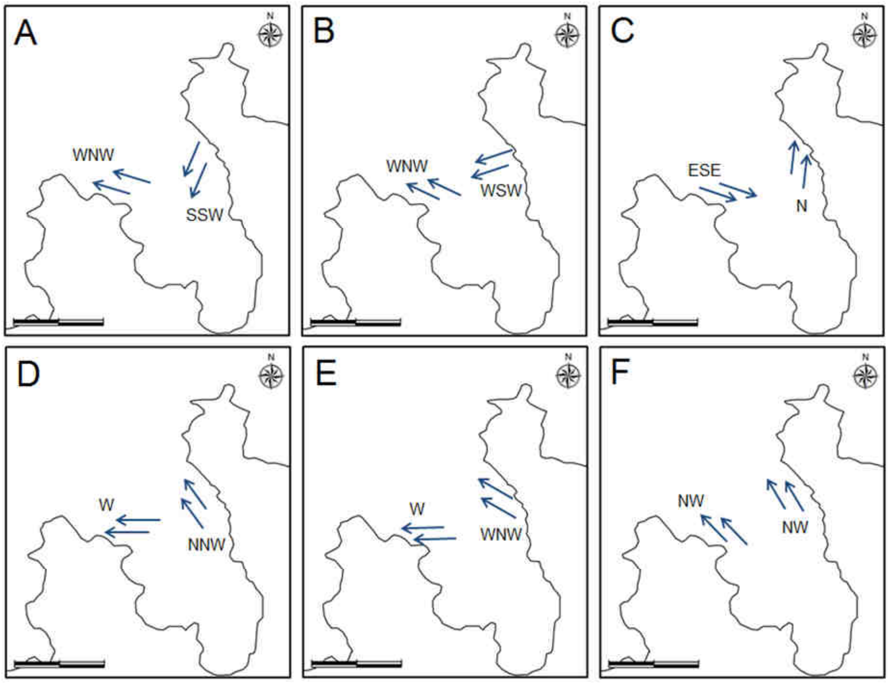

Figure 6. Mean current directions for the exposed (Western) and sheltered site (Eastern flank of the bay) at water depths of 8 – 10 m in Gayraca Bay for A) February, B) July, C) August, D) September, E) November and F) December. Scale indicates 1 km.

Discussion

The physical environment in Tayrona National Natural Park

In this study, we described the physical environment in a representative bay of TNNP by the variables wind velocity, water temperature, and water current velocity and direction. Wind velocity and *in situ* water temperature strongly differed between periods of upwelling (25.1 °C mean water temperature and 1.8 m s^{-1} wind speed) and non-upwelling (28.7 °C and 0.4 m s^{-1}, respectively). Water currents at a depth of 8 – 10 m exhibited spatial (exposed vs. sheltered site) and temporal differences (upwelling vs. non-upwelling) for Gayraca Bay with mean velocities of 6.7 cm s^{-1} at the exposed and 5.4 cm s^{-1} at the sheltered site during upwelling, and 5.4 and 4.0 cm s^{-1} during non-upwelling, respectively. Our data thereby indicate clear seasonal differences of the physical environment in TNNP.

Wind velocity during upwelling periods of the present study was below the mean monthly velocity range of 2.1 – 5.6 m s^{-1} registered for the years 1981 – 1982 by anemometric measurements in Santa Marta (Salzwedel and Müller 1983). Wind velocities were also below the range recorded for non-upwelling with 0.8 – 1.8 m s^{-1} (Salzwedel and Müller 1983). Reported maximal values of 30 m s^{-1} for 1967 –1968 (Herrmann 1970) and 22 m s^{-1} for 1981 –1982 (Salzwedel and Müller 1983) were up to 8 times higher than the maximal wind intensity registered in the present study. The apparent discrepancy in wind velocity between our results and typical values reported for the region may be due to the wind-sheltered location of the meteorological station of the present study located at a distance of 18 km to TNNP. However, our results clearly show the increase in winds from non-upwelling to upwelling season.

Our results on mean water temperature at 10 m water depth lie within the range reported for surface seawater temperature of 24.8 – 26.4 °C during upwelling periods and 27.4 – 28.6 °C during non-upwelling registered between 1966 and 1983 for the bay of Santa Marta, 14 km away from TNNP (Salzwedel and Müller 1983). Studies on mean water temperature in a water depth of between 0 and 60 m in a bay, 11 km away from our study sites, revealed typical values of 25.2 ± 0.8 °C during upwelling (December – April) and 27.5 ± 1.6 °C during non-upwelling (May – June) for 2007 – 2008 (García-Hoyos et al. 2010). The latter study did not consider the warmest months of the non-upwelling period, i.e. October and November, which may be the reason why the reported water temperature mean was below the value of the present study. Here, our research provides the most comprehensive data on continuous *in situ* water temperature with a high resolution and a water depth of 10 m over a time period of over two years for a TNNP bay. According to a mean surface seawater temperature of 26.1 °C, a minimal monthly mean of 24.3 °C and maximal monthly mean of 27.9 °C reported by Chollett et al. (2012a), the region of TNNP was classified to represent a physicochemical province characterized by lowest seasonal temperature maximum, generally cold temperature average and minimum surface seawater temperatures influenced by upwelling among the regions in the Caribbean Sea (Chollett et al. 2012a). For the wider Caribbean, similar physicochemical characteristics were only present for the region of Yucatan upwelling in Mexico, the Southern Caribbean upwelling including Colombia (TNNP and Guajira Peninsula) and the Northeastern coast of Venezuela (Chollett et al. 2012a). These physicochemical provinces are highly interesting with regard to global increases in surface seawater temperature as a consequence of climate change. Here, no significant summer warming was observed, while the wider Caribbean Sea experienced a trend in increasing surface seawater temperature of 0.33 °C decade^{-1} as calculated from satellite data for 1985 –2009 (Chollett et al. 2012b).

So far, no study has investigated *in situ* current velocities and directions by ADCP deployment in the Colombian Caribbean coral reef ecosystems. We identified not only that significant water currents were present, but also that their velocities were significantly higher during upwelling compared to non-upwelling for both investigated sites in Gayraca Bay. Water current velocities at a water depth of 8 – 10 m and throughout the water column profile were always higher at the exposed than at the sheltered site. Mean water current velocities between 8 – 10 m ranged between 3.9 and 7.4 cm s^{-1}; however measurements through the water column profile indicated water current velocities between 3.0 and 90.0 cm s^{-1} in dependence of water depth.

The water current velocities measured for the TNNP at a water depth of 8 – 10 m of the present study were below most values reported by other studies. Surface water current velocities of between 8.3 cm s^{-1} and 13.0 cm s^{-1} were recorded for the reef flat in Puerto Rico (Glynn 1973). Water current velocities of between 10 to 50 cm s^{-1} were registered in Florida patch reefs (1 – 2 m water depth), 23 cm s^{-1} in Bahamas reefs (surface), 35 cm s^{-1} in the southwest Caribbean (5 – 18 m water depth), 22 to 24 cm s^{-1} in a Hawaiian fringing reef and between 10 and 144 cm s^{-1} in various Pacific atoll reefs (water depths of 0.5 – 1.5 m; Andrews and Pickard 1990). Our results for water current velocities at 8 – 10 m water depth are in accordance with Sebens and Done (1992), who measured water current velocities below 5 cm s^{-1} at a water depth of 10 m for Davies Reef/Great Barrier Reef, Australia. Differences between our data and typical reported water current velocities may be due to the fact that most studies addressed surface currents which due to increased wind forcing are typically higher than bottom water currents. Deviations are also likely a result of the different geographic environments (e.g. bays, island wakes, fringing reefs, atolls) and the different methods of water current measurements. Methods for recording of water current velocities such as through the dissolution of calibrated gypsum clods (Doty 1971; Jokiel and Morrissey 1993) or the insertion and tracking of water-soluble, fluorescein marker (Glynn 1973) may over- or underestimate real current velocities. Highest accuracy in the detection of water current flow patterns at a certain depth and through the water column is currently provided by measurements with ADCP (Gordon 1996) as used in the present study.

Spatiotemporal dynamics of physical variables and reef zonation

We observed spatial differences between the velocities of water currents which were higher at an exposed than at a sheltered site in Gayraca Bay. For a water depth of 8 – 10 m, characterized by a high abundance of coral communities at both sites, but octocorals exclusively at the exposed site, mean water current velocities at the exposed were significantly higher than currents measured at the sheltered site for the months of non-upwelling and variable winds. Surprisingly, above a threshold wind level of 1.7 m s^{-1}, current velocities at the sheltered site and this water depth reached the water current regime at the exposed site indicating a strong control of water currents at this site by changes in winds. However, profiles of water current velocities showed generally higher water current velocities through the water column at the exposed site. These results suggest that while at the exposed site strong currents prevail over the year, water currents at the sheltered site are governed by the strength of wind fields. This may have important implications for the coral ecosystem and explain the site-specific reef community composition of massive to encrusting coral species with low complexity and high abundance of octocorals at the exposed site and reef-building corals with more complex framework at the sheltered site (Werding and Sánchez 1989; Bayraktarov et al. 2012). Our results are in agreement with the study of Werding and Sánchez (1989), who suggested that the bays of TNNP experience a typical relative wave exposure pattern: Here, the strong NE winds during upwelling period can drive waves from the NE to SW with an increasing wave gradient from the Eastern to the Western flank of the bays (Werding and Sánchez 1989). This wave exposure gradient may be an important factor for the distribution of scleractinian corals with rudimentary reef structures, but favoring other groups such as octocorals and sponges at the exposed site as compared to highly complex coral communities at the sheltered site of the bay (Werding and Sánchez 1989; Bayraktarov et al. 2012). At the sheltered site, where sedimentation is high due to low water current velocities, the scleractinian coral *Montastraea* spp. dominated the coral community. This coral species belongs to the most important reef builders in the Caribbean (Goreau 1959). *Montastraea* grows under environmental conditions of high sedimentation rates due to its efficiency in sediment removal through secretion of mucus, movement of its cilia and extension of polyps (Loya 1976). Exclusively at the exposed site, where water current velocities were high, octocorals such as gorgonians were observed. Octocorals are suspension feeders that rely on water currents to provide them with phytoplankton and other small (< 20 µm) organic particles (Fabricius et al. 1995a; Fabricius et al. 1995b). Their specific zonation at the exposed site in Gayraca Bay is in agreement with their requirements of intermediate water flows (8 – 15 cm s^{-1}; Fabricius et al. 1995a; Fabricius et al. 1995b; Fabricius and Alderslade 2001) available at this site of Gayraca Bay in the present study.

Ecological implications of wind, water temperature and currents

The observed spatiotemporal dynamics of the physical environment between an upwelling and a non-upwelling season and two opposing sites of one bay in TNNP described by the variables wind velocity, water temperature and water currents may have strong ecological implications for the investigated reef ecosystem.

Wind velocity was significantly lower during non-upwelling and higher during upwelling. A significant negative correlation between winds and *in situ* water temperature for both, the exposed and the sheltered site pointed out the link between upwelling-triggered decrease in water temperature and increasing winds during the months of dry season (December to April) as described by several authors (Andrade et al. 2003; Andrade and Barton 2005; Paramo et al. 2011). Changes in wind intensity did not affect water current velocities at the exposed site which were high throughout the year. However, a significant positive correlation between winds and current velocities at the sheltered site indicated that here water movement was governed by winds.

Wind driven currents and circulation control the distribution of invertebrate larvae and supply with plankton and nutrients (Andrews and Pickard 1990) and are therefore crucial for the coral ecosystem of TNNP. Spawning of the scleractinian coral *Montastraea* spp. usually takes place during non-upwelling when winds are minimal (0.1 m s^{-1}; September, personal observation) which is supported by the hypothesis by van Woesik (2010) that low wind fields are necessary for coral spawning and consequently the successful reproduction of corals to occur. In absence of regional precipitation, winds and wind stress control the salinity, heating and cooling of surface seawater and additionally influence currents by the establishment of pressure gradients (Andrews and Pickard 1990).

We observed upwelling-triggered decrease in water temperature which was positively correlated with increases in wind intensity at both sites of the bay. The insignificant differences in absolute water temperatures between the exposed and sheltered site of Gayraca indicated that the whole bay experienced a similar temperature regime. Water temperature is a crucial factor for reef functioning and zonation of coral reefs (Done 1983; Veron 2000). Increases in surface seawater temperature as a consequence of climate change have detrimental effects for corals as they can induce coral bleaching (Glynn 1991; Glynn 1993; Brown 1997; Hoegh-Guldberg 1999; Loya et al. 2001; Hoegh-Guldberg 2011). Upwelling-induced decrease of water temperature during time of highest heat stress can mitigate coral bleaching (Glynn 1996, Riegl and Piller 2003, Chollett et al. 2010). Such mitigation of coral bleaching by a seasonal upwelling through a decrease in water temperature was also identified for TNNP (Rodríguez-Ramírez et al. 2010; Bayraktarov et al. 2012).

Our results suggest that water current velocities at a water depth of 8 – 10 m at the exposed site were significantly higher than those at the sheltered site for non-upwelling and period of variable winds. During upwelling, the mean water current velocities were still higher at the exposed than at the sheltered site, but differences were not significant anymore at this water depth. However, water current velocities throughout the water column profile were always higher at the exposed than at the sheltered site. Water currents constitute an important control factor for complex reef ecosystems as water flow-induced mass exchange and transport processes are orders of magnitude faster than through molecular diffusion in still water (Huettel et al. 2003). This can have important physiological consequences for corals represented by e.g. an increase in particulate organic matter release (Wild et al. 2012), enhanced photosynthesis (Mass et al. 2010) or higher ammonium uptake rates (Atkinson et al. 1994) under a high water flow regime. Besides, water currents control many important processes related to water quality e.g. distribution of nutrients, recruitment and larval dispersal, but also sedimentary dynamics e.g. sedimentation of fine sediment in locations with low hydrodynamics and turbidity (Andrews and Pickard 1990). Water currents may also influence the patterns of coral bleaching (Nakamura and van Woesik 2001; Nakamura et al. 2003; West and Salm 2003) and thus coral resilience to stressful condition. For Gayraca Bay, October and November were the months during which highest water temperature was detected and thus represent the time of the year with highest probability for heat stress accumulation in scleractinian corals. The significantly higher water currents at the exposed than at the sheltered site during these months may contribute to the mitigation of coral bleaching, particularly at the exposed site, before upwelling starts and induces an alleviation of the stressful conditions at both sites of the bay by a natural reduction of seawater temperature. This is further supported by a study where three times less bleaching occurrence and faster recovery was observed for corals at an exposed than at a sheltered site in Gayraca Bay (Bayraktarov et al. 2012; Chapter 6). Water currents may mitigate coral bleaching by rapid removal of toxic reactive oxygen species which are produced before and during the process of coral bleaching (Nakamura and van Woesik 2001; Lesser 2006; Weis 2008).

The present study revealed spatiotemporal changes of the physical variables wind, water temperature and currents in a highly biodiverse, unique environment which, due to a seasonal upwelling, represents an ideal location for studies on the effects of environmental changes in Colombian Caribbean coral ecosystems.

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2

Spatial and Temporal Variability of Water Quality in Coral Reefs of Tayrona National Natural Park, Colombian Caribbean

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Abstract

Tayrona National Natural Park (TNNP) is a hotspot of coral reef biodiversity in the Colombian Caribbean, located between Santa Marta city (> 455,000 inhabitants) and several smaller river mouths (Rio Piedras, Mendihuaca, Guachaca). The region also experiences strong seasonal variation in physical parameters (temperature, salinity, wind, water currents) due to alternating dry seasons with coastal upwelling and rainy seasons. However, the spatial and temporal effects on water quality parameters relevant for coral reef functioning have not been investigated. Therefore, inorganic nutrient, chlorophyll *a*, and particulate organic carbon (POC) concentrations along with biological O_2 demand (BOD), pH and water clarity directly above local coral reefs (~ 10 m water depth) were monitored for 25 months in 4 bays along a distance gradient (12 - 20 km) to Santa Marta in the Southwest and to the first river mouth (17 - 27 km) in the East. This is by far the most comprehensive coral reefs water quality dataset for the region. Findings revealed that particularly during non-upwelling, chlorophyll *a* and POC concentrations along with BOD significantly increased with decreasing distance to the rivers in the East, suggesting that the observed spatial water quality decline was triggered by riverine runoff and not by the countercurrent-located Santa Marta. Nitrate, nitrite, and chlorophyll *a* concentrations significantly increased during upwelling, while pH and water clarity decreased. Generally, water quality in TNNP was close to oligotrophic conditions adequate for coral reef growth during non-upwelling, but exceeded critical threshold values during upwelling and in relation to riverine discharge.

Introduction

Additionally to climate change, coastal coral reefs are threatened by local anthropogenic stressors e.g. agricultural and riverine runoff, sewage discharge, and fossil fuel combustion leading to eutrophication and water quality decline (Selman et al. 2008). It is well known that intact corals require warm, shallow, sunlit, and oligotrophic, but carbonate-supersaturated conditions with a high degree of stability in order to allow for optimal calcification and growth (Hoegh-Guldberg 1999; Kleypas et al. 1999) and thereby maintain the functional integrity of the reef. Reef degradation is often the consequence of water quality decline by terrestrial runoff from urban development, agriculture and deforestation (Fabricius 2005). Especially low water quality by increased inorganic nutrients, enrichment with organic particulate matter, light reduction from turbidity and increased sedimentation has shown to have detrimental effects on coral reef functioning (Fabricius 2005). However, adaptation potential of coral reefs to environmental change is still under debate (Berkelmans and van Oppen 2006; Hoegh-Guldberg 2011) as these ecosystems have highly dynamic ecological time scales, and the effects of change can be substantially different among regions and habitats (Birkeland 1988; Done 1999).

In the Colombian Caribbean, coral reefs are subjected to anthropogenic sedimentation, eutrophication, chemical pollution, overfishing, dynamite fishing, nautical activities and coral mining in addition to natural threats e.g. hurricanes, algae proliferation, diseases and coral bleaching (Rodríguez-Ramírez et al. 2010). The Tayrona National Natural Park (TNNP), located between 11°17' – 11°22' N and 73°53' – 74°12' W at the Northeast coast of Colombia, is a region of the Colombian Caribbean where coral reefs develop. The TNNP is adjacent to the population center Santa Marta (> 455,000 inhabitants; DANE 2005) in the Southwest (at 12 – 20 km) and to several smaller river mouths (Rio Piedras, Mendihuaca, Guachaca, Buritaca, Don Diego, and Palomino; Restrepo and Kjerfve 2004) in the East (17 – 27 km). Surrounded by the World's highest coastal mountain range, Sierra Nevada de Santa Marta, the TNNP represents a biodiversity hotspot in the Colombian Caribbean (Garzón-Ferreira and Cano 1991; Garzón-Ferreira 1998), harboring a variety of coral communities, sea grass beds and mangrove ecosystems along the rocky coastline with capes, inlets and bays (Garzón-Ferreira and Díaz 2003).

In addition to anthropogenic impact, coral reefs in TNNP experience drastic changes in environmental conditions due to seasonality and the presence of coastal upwelling (Salzwedel and Müller 1983), but still exhibit similar health conditions in comparison to other relatively pristine Caribbean coral reef locations (Garzón-Ferreira and Díaz 2003; Rodríguez-Ramírez et al. 2010). During major dry season, from December to April, strong winds from the Caribbean Low-Level Jet of Northeast (NE) Trade Winds displace humidity and induce an Ekman transport of surface water off the coast of the TNNP bays resulting in an upwelling of Subtropical Underwater (Corredor 1979) from water depths of between 110 – 120 m (Garzón-Ferreira 1998; Rueda-Roa and Muller-Karger 2013). This phenomenon represents a seasonal coastal upwelling which is one focal center of the Southern Caribbean Upwelling System extending from 61 to 75.51° W and 10 to 12.51° N (Andrade 2000; Castellanos et al. 2002; Andrade and Barton 2005; Paramo et al. 2011; Rueda-Roa and Muller-Karger 2013). Seasonal upwelling in TNNP is particularly interesting due to its unique low-level inorganic nutrient enrichment (Corredor 1979; Diaz-Pulido and Garzón-Ferreira 2002) as compared to other upwelling systems such as the Peru Upwelling (Zuta and Guillén 1970) or the Northwest African Upwelling System (Jones 1972) for which 6 to 10 times higher nitrate concentrations were reported. The strong winds from NE also particularly affect the Western (windward) flanks of the TNNP bays resulting in increased waves and water currents as compared to the Eastern (leeward), sheltered counterparts (Werding and Sánchez 1989). A short period of low wind fields and increased precipitation were reported for the months May and June, representing a minor rainy season, which is followed by a period of variable winds between July and August, also termed "Veranillo de San Juan" or minor dry season (Salzwedel and Müller 1983; Bula-Meyer 1990; Diaz-Pulido and Garzón-Ferreira 2002). During major rainy season, from September to November, > 52 % of the annual rainfall occurs (Salzwedel and Müller 1983) and intensifies riverine discharge.

A decline in live coral cover by 4 % (from 34 to 30 %) was registered for the period 1998 – 2010 in TNNP (Vega-Sequeda et al. 2011), which was extensively attributed to the moderate coral bleaching event during 2010 (Vega-Sequeda et al. 2011; Bayraktarov et al. 2012). However, coral reefs in TNNP are less degraded than other Caribbean locations (Burke et al. 2011); the rare genus *Acropora* spp. can be still observed in every TNNP bay (Werding and Sánchez 1989; Garzón-Ferreira and Cano 1991; Rodríguez-Ramírez et al. 2010).

So far, it is known that the TNNP region experiences strong seasonal variations in physical parameters e.g. seawater temperature (decrease from 28 – 21 °C; Salzwedel and Müller 1983; Bayraktarov et al. 2012), salinity (increase from 33 – 38; Salzwedel and Müller 1983; Bayraktarov et al. 2012), higher wind (Salzwedel and Müller 1983) and water current velocity (from 3.9 to 7.4 cm s^{-1} at 10 m water depth; Chapter 1) going along with increased inorganic nutrient and chlorophyll *a* concentrations (Arévalo-Martínez and Franco-Herrera 2008; Paramo et al. 2011; Rueda-Roa and Muller-Karger 2013). However, spatial and temporal effects on water quality parameters relevant for coral reef functioning in the TNNP region remain under-investigated. Most studies have no spatial and only limited temporal resolution, lack recent data, concentrated on limited sets of environmental parameters, used indirect (satellite) methods for data acquisition or covered regions without direct proximity to TNNP (Salzwedel and Müller 1983; 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). Reef water quality in TNNP can be characterized by the key environmental status variables temperature, salinity, inorganic nutrients, chlorophyll *a*, particulate organic matter, oxygen availability, water clarity and the process variable biological oxygen demand. This study therefore investigated the spatial and temporal variability of these key environmental status and process variables characterizing water quality of upwelling-influenced coral reefs in TNNP. Thus, monthly monitoring assessing the water quality was performed at water-current exposed and – sheltered sites in four bays in TNNP over a time period of 25 months. Monitoring was complemented by meteorological data on wind velocity and daily precipitation. Multivariate analyses were used to identify changes in key environmental factors triggered by the consecutive periods of high precipitation and coastal upwelling that may control coral reef functioning in TNNP.

Material and methods

Sample collection

Monitoring of several water column status and process variables in the TNNP bays Chengue, Gayraca, Neguanje and Cinto (Fig. 1) took place monthly between October 2010 and February 2013 (summarized in Table S1, supplementary material). Study sites were located at a water current-exposed site on the Western flank and a water current-sheltered site on the Eastern flank of each bay (Fig. 1). Samplings were conducted under comparable weather conditions for the respective season and between the second and third week of each month, from 8:00 am to 3:00 pm. On the first sampling day, the bays Neguanje and Cinto were monitored, whereas Chengue and Gayraca were surveyed one day later, which was required for measurements and consecutive sample processing in the laboratory. All water samplings and *in situ* measurements (except water clarity) were performed at a water depth of 10 m, and 1 m above the sea bottom. Meteorological data of daily mean wind velocity and precipitation was kindly provided by the meteorological station COMARTA of the University Jorge Tadeo Lozano located in El Rodadero, Santa Marta, 18 km away from TNNP. Seasonal mean values were calculated for the time period October 2010 to February 2013.

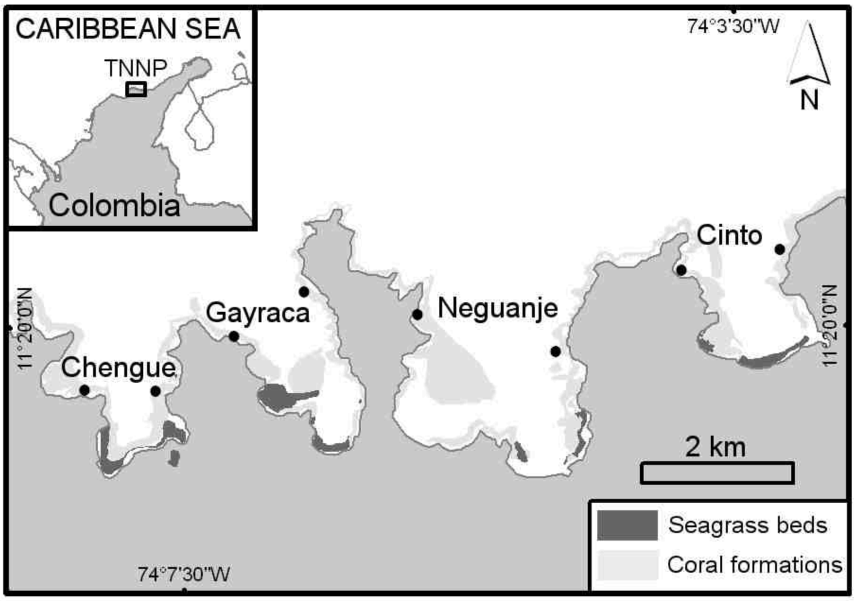

Figure 1. The bays of Tayrona National Natural Park (TNNP). Displayed are Chengue, Gayraca, Neguanje and Cinto and the sampling locations at the Western (water current-exposed sites) and the Eastern (water current-sheltered sites) flanks of each bay. Source: Invemar 2012.

Water clarity, as an indirect measure for turbidity, was evaluated monthly by Secchi disc with a replication of 4 deployments at each site in TNNP. Measurements were always conducted at the shady side of the boat. Water temperature was continuously measured *in situ* by calibrated HOBO TidBit v2 temperature loggers or HOBO Pendant temperature/light loggers (Onset Computer Corp., Bourne, USA) with temporal intervals of 5 min. Temperature loggers were attached to the reef structure. Readouts were performed monthly *in situ* by a HOBO Waterproof Shuttle Data Transporter (Onset Computer Corp., Bourne, USA). Water samples were collected by clean 3.8 L plastic containers (n = 3 per site and month) and one black 25 L neoprene bag, and were sealed under water. Plastic container samples were transported on ice and in the dark to the laboratory and processed immediately. Thereof, subsamples were taken for further determination of salinity (0.7 L), inorganic nutrient (0.1 L) and chlorophyll *a* (chl *a*; 1 L) concentrations, and particulate organic matter (POM; 1 L for particulate organic nitrogen, PON, and 1 L for particulate organic carbon, POC) in seawater. Salinity was measured with a portable meter (HQ40d, Hach, Loveland, USA) equipped with a 4-pole conductivity probe (CDC401, Hach, Loveland, USA). For inorganic nutrients, chl *a* and POM, subsamples were filtered on pre-combusted glass micro fiber filters (VWR International; diameter: 25 mm, nominal particle retention: 0.7 µm). For determination of POC and PON, filters containing POM were dried for at least 48 h at 40 °C and stored dry and dark until analysis. Filters for POC were acidified with sterile HCl until gas production ceased in order to remove small remaining carbonate grains from the particulate material. After acid addition, samples were dried for 48 h at 40 °C prior to measurements. Elemental analyses of PON and POC were conducted by a EuroVector 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). Filtered water subsamples for inorganic nutrient concentrations and filters containing particulate material for chl *a* extraction were frozen at -20 °C until analysis. The inorganic nutrients nitrate (NO_3^-), nitrite (NO_2^-) and soluble reactive phosphorus (SRP) mostly present in the form orthophosphate (PO_4^{3-}) were measured spectophotometrically by a Perkin Elmer UV/VIS Spectrometer Lambda 12 (PerkinElmer, Massachusetts, USA) according to Garay et al. (2003). For chl *a* determination, each filter was extracted by 6 mL 90 % acetone for 24 h at 4 °C and dark. Measurements were performed by a fluorometer (10AU™ Field Fluorometer, Turner Designs, Sunnyvale, USA).

Seawater sampled by neoprene bag was used for measurements of O_2, biological oxygen demand (BOD) and pH. Measurements of O_2 were carried out by a portable meter (HQ40d, Hach, Loveland, USA) and luminescent dissolved oxygen optode (LDO101-01, Hach, Loveland, USA) immediately after sampling and on the boat. Prior to measurements, O_2 optode was calibrated in 100 % water-saturated air according to the manufacturer's instructions. Rates of BOD in seawater were measured after a modified method by Wild et al. (2010). Sub-samples of freshly sampled seawater (n = 4 per site and month) were taken by 60 mL Winkler bottles and incubations were run in dark cooling boxes filled with ambient seawater for 24 ± 2 h. Concentrations of dissolved O_2 were measured prior and after incubation by a luminescent dissolved oxygen electrode (LDO101-01, Hach, Loveland, USA). 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 *in situ* seawater temperature. Temperature of water during incubation was monitored by a HOBO Pendant temperature/light logger (Onset Computer Corp., Bourne, USA). Net BOD rates were calculated for each Winkler bottle by dividing the difference between initial and end O_2 concentrations by incubation time. Negative rates of O_2 consumption were converted to absolute numbers. Values of pH (n = 4 per site and month) were measured by a portable meter (HQ40d, Hach, Loveland, USA) and a calibrated pH electrode (PHC301-01, Hach, Loveland, USA).

Statistical data analyses

Time intervals of seasons in TNNP can vary from year to year and as a consequence, references on seasonality for the region can be confounding (Salzwedel and Müller 1983). For simplification, in this study the following seasonal time intervals are defined and were thereafter used for further analyses of environmental data: 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).

Analyses were performed with seasonal means of environmental variables resulting in N = 32 independent samples (4 levels of seasons, 4 levels of bays, and 2 levels of exposure) for each of the 12 variables during period of study (Table S1, supplementary material). Correlations among environmental variables, meteorological data and along the distance gradient were identified by a Spearman's rank correlation. 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). Multivariate analyses considered the environmental variables temperature, salinity, inorganic nutrients (NO_3^-, NO_2^- and SRP), chl *a*, POM (POC and

PON), and dissolved O_2 concentration along with BOD, pH, water clarity, wind velocity, and precipitation. 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. Prior to analyses, environmental variables were normalized by subtracting the mean and dividing by the standard deviation of each variable (z-transformation), thereby enabling the analyses on a comparable 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. The horizontal distance between each sampling location and the harbor of the nearby city Santa Marta was included as continuous predictor (covariate). A Type I sum of squares (sequential, SS) was used in order to calculate the significance of each of the factors independently from the covariate. A distance-based test for homogeneity of multivariate dispersions (PERMDISP) was applied to prove if the multivariate dispersion was homogeneous among the levels of the factors. Pair-wise comparisons among all pairs of factor levels were obtained for significant results by additional *post hoc* PERMANOVA routines. Univariate PERMANOVAS were performed for each environmental variable separately in order to identify significant differences between seasons, bays and exposure. A Principle Coordinates Ordination (PCO; Gower 1966) was used to visualize the seasonal patterns of environmental variables, bays and exposure. The effects and correlations with PCO axes of environmental variables were indicated as vectors.

Results

Environmental variables characterizing water quality are represented as seasonal means for the TNNP bays Chengue, Gayraca, Neguanje and Cinto. Discrimination between the water current exposed and – sheltered sites in the bays during the seasons for each environmental variable is provided as supplementary material (Table S2 – S5). As mentioned above, the transition between non-upwelling (rainy season) and upwelling (dry season) is not well-defined, and seasonal periods may vary between the years (Salzwedel and Müller 1983). Therefore, in this study we defined a major upwelling season and a major non-upwelling season, and two transition periods that have a mixed seasonal character. Seasonal discrimination is based on wind, precipitation, salinity and seawater temperature patterns of the TNNP region.

Spatial variability of water quality in TNNP coral reefs

Within the measured variables, significant differences between the water current-exposed and -sheltered sites of the bays were only found for dissolved oxygen concentrations (O_2; Table 1). Oxygen availability was higher at the exposed sites (6.42 ± 0.36 mg L^{-1}, mean ± SD) as compared to the sheltered counterparts (6.31 ± 0.37 mg L^{-1}). For all other water quality variables, no significant differences were observed between exposed and sheltered sites. However, data from sheltered sites exhibited much higher variability than data from exposed sites (Table S2 – S5, supplementary material).

Concentrations of chl *a* along with POC, O_2 and BOD increased significantly with decreasing distance to the rivers in the East, while nitrite and pH decreased. While chl *a* showed a dependence on the distance during major upwelling and non-upwelling, the correlations of POC, O_2 and BOD along this gradient were only significant during rainy season, but not during dry season. Here, also SRP had a positive correlation with increasing distance to Santa Marta. During transition period (minor rainy season), SRP and POC were positively correlated with distance to Santa Marta. During the second transition period (minor dry season), significantly negative correlations between nitrate and pH along the distance gradient were detected (Table 2).

Temporal variability of water quality in TNNP coral reefs

Seasonal environmental change was observed in the water quality variables temperature, salinity, inorganic nutrient (nitrate, nitrite, and SRP), chl *a* concentrations, POM (POC and PON), and O_2 concentrations along with BOD, pH, and water clarity during period of study (Gayraca bay as exemplary bay, Fig. 2). Environmental change was induced by series of dry seasons going along with strong winds and seasonal upwelling, transition periods (minor upwelling and non-upwelling) and rainy seasons (non-upwelling).

Table 1. Univariate analyses: significant differences among environmental variables in Tayrona National Natural Park. Significant PERMANOVA results are indicated by asterisks with * for significant ($p < 0.05$) and ** for very significant ($p < 0.01$). Not significant values are displayed in gray. Values in brackets indicate that the assumption of homogeneity of dispersions could not be met. Abbreviations: nitrate (NO_3^-), nitrite (NO_2^-), soluble reactive phosphorus (SRP), chlorophyll *a* (Chl *a*), particulate organic nitrogen (PON), particulate organic carbon (POC), dissolved oxygen availability (O_2), and biological oxygen demand (BOD).

	Seasons		Bays		Exposure		Distance	
Variables	Pseudo-*F*	(*p*)	Pseudo-*F*	(*p*)	Pseudo-*F*	(*p*)	Pseudo-*F*	(*p*)
Temperature	3345.5	0.001**	1.924	0.14	0.210	0.679	0.229	0.9
Salinity	(213.79)	(0.001**)	0.402	0.764	0.012	0.914	3.020	0.185
NO_3^-	181.04	0.001**	0.925	0.448	3.384	0.084	0.355	0.79
NO_2^-	13.689	0.001**	5.525	0.005**	2.432	0.13	0.072	0.998
SRP	(1.688)	(0.198)	0.876	0.487	0.219	0.668	2.408	0.236
Chl *a*	4.121	0.022*	0.582	0.669	0.043	0.839	8.561	0.046*
PON	4.562	0.014*	2.513	0.085	0.128	0.726	3.013	0.197
POC	2.582	0.083	2.646	0.073	(0.010)	(0.902)	4.800	0.129
O_2	13.249	0.001**	5.657	0.005**	7.908	0.015*	0.700	0.587
BOD	1.428	0.230	3.182	0.038*	(2.043)	(0.172)	1.353	0.354
pH	(13.459)	(0.001**)	(0.450)	(0.73)	0.075	0.781	11.742	0.039*
Water clarity	26.757	0.001**	12.055	0.001**	1.281	0.263	0.861	0.514

Table 2. Correlation matrix of environmental variables with distance to Santa Marta in seasonal resolution. Significance levels of correlation coefficients (Spearman's rank correlation) among environmental variables with distance to Santa Marta are represented. Levels of significance are indicated by asterisks with * for significant ($p < 0.05$) and ** for very significant ($p < 0.01$). Not significant correlations are displayed in gray. Abbreviations: nitrate (NO_3^-), nitrite (NO_2^-), soluble reactive phosphorus (SRP), chlorophyll *a* (Chl *a*), particulate organic nitrogen (PON), particulate organic carbon (POC), dissolved oxygen availability (O_2), and biological oxygen demand (BOD).

Seasons	Correlations with distance to Santa Marta									
	NO_3^-	NO_2^-	SRP	Chl *a*	PON	POC	O_2	BOD	pH	Water clarity
Major upwelling	-0.43	0.02	0.88**	0.76*	0.33	0.43	0.10	0.17	0.46	-0.60
Minor upwelling	-0.79*	-0.17	-0.02	0.02	0.31	0.31	0.60	0.38	-0.76*	-0.57
Major non-upwelling	-0.33	-0.69*	0.36	0.88**	0.52	0.71*	0.76*	0.79*	-0.83**	-0.60
Minor non-upwelling	0.60	0.64	0.71*	0.52	0.57	0.86**	-0.45	-0.12	-0.34	-0.19

Meteorological data showed highest wind velocity during major upwelling (1.88 ± 0.97 m sec^{-1}; mean ± SD) and lowest during major non-upwelling (0.40 ± 0.36 m sec^{-1}). Highest daily precipitation was recorded during major non-upwelling (3.21 ± 7.67 mm d^{-1}; mean ± SD) and lowest during major upwelling (0.35 ± 2.49 mm d^{-1}), (Table S6, supplementary material). Wind velocity and daily precipitation had a highly significant negative correlation (Table 3). Multivariate analyses showed that a significant difference was present between seasons and bays in the measured environmental variables (Table 4). The model explained 73.4 % of environmental data variation. Multiple comparison analyses showed that the environmental variables were different between all seasonal periods (major and minor upwelling as well as major and minor non-upwelling; Table 4). Significant differences in environmental variables were present between Chengue and Neguanje, Gayraca and Cinto and between Neguanje and Cinto (Table 4).

Univariate analyses showed that seawater temperature was significantly different between seasons (Table 1). Temperature had mean values of 25.0 ± 1.6 °C during major (mean ± SD) and 27.3 ± 1.2 °C during minor upwelling, as well as 28.9 ± 0.7 °C during major and 27.3 ± 1.0 °C during minor non-upwelling. Maximum registered temperature was 30.6 °C during non-upwelling and minimal with 20.0 °C during upwelling (Fig. 2a). Temperature had significant negative correlations with salinity, NO_3^-, NO_2^-, SRP, chl *a*, and was positively correlated to pH (Table 3). Highly significant negative correlation was found between temperature, wind velocity and daily mean precipitation (Table 3).

Salinity was highest during major (36.9 ± 0.9; mean ± SD) and minor upwelling (35.7 ± 0.9), and lowest during major (34.9 ± 1.6) and minor non-upwelling (35.4 ± 1.6). Significant differences between all investigated seasons were present (Table 1). However, it cannot be excluded that seasonal differences in salinity are also a result of the different dispersion of data between seasons as the assumption of homogeneity of dispersions among groups could not be met. Salinity ranged between a maximum of 39.0 during upwelling and 32.3 during non-upwelling (Fig. 2a). Significant positive correlations were registered for salinity with NO_3^-, NO_2^-, and wind velocity (Table 3). Salinity was highly negatively correlated to precipitation (Table 3).

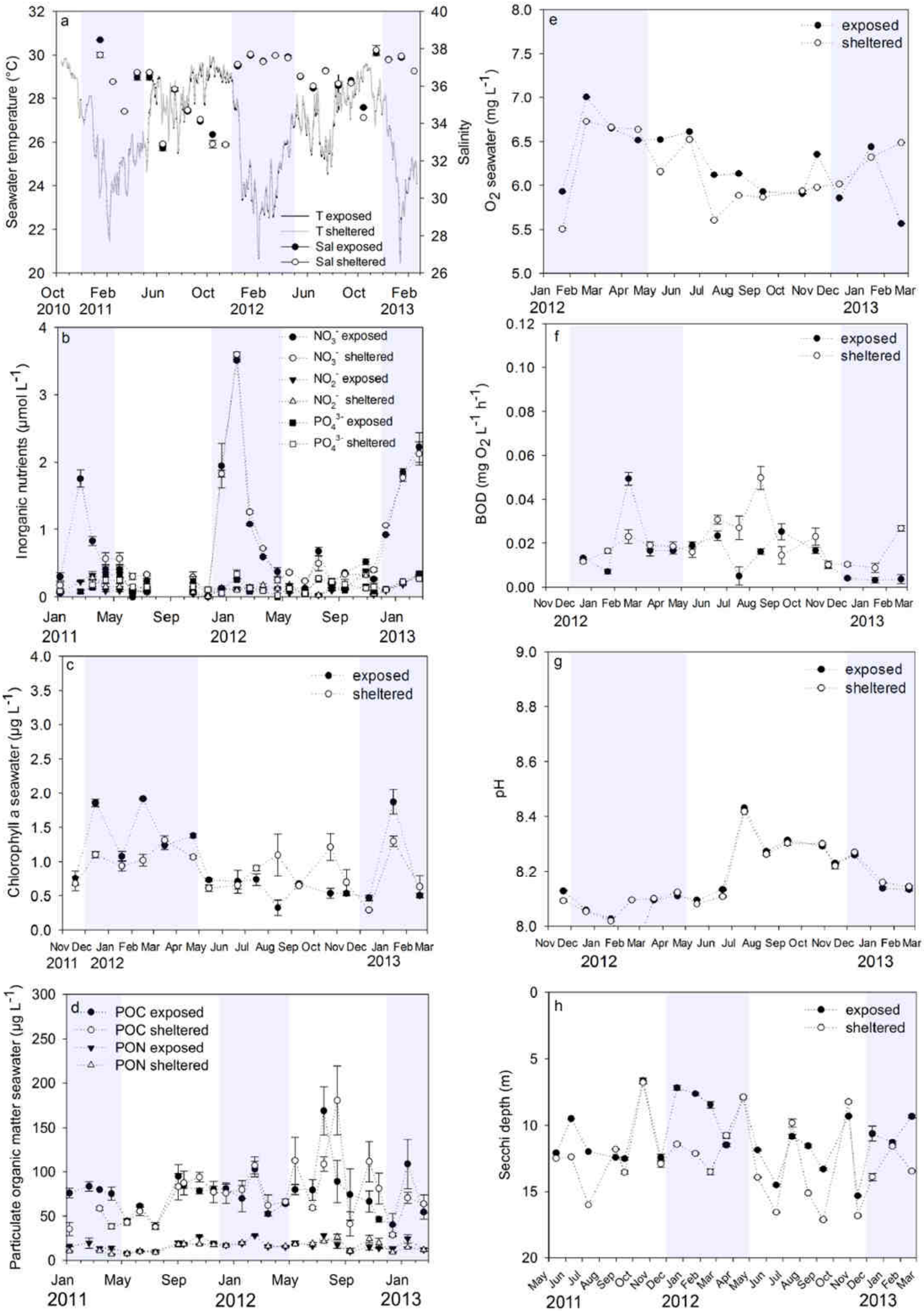

Figure 2. Graphical representation of environmental monitoring data at a water current-exposed and -sheltered site in Gayraca as exemplary bay. (a) Seawater temperature (T) and salinity (Sal); (b) inorganic nutrient concentrations for nitrate (NO_3^-), nitrite (NO_2^-) and soluble reactive phosphorus (PO_4^{3-}); (c) concentration of chlorophyll *a*; (d) particulate organic material with particulate organic carbon (POC) and particulate nitrogen (PON); (e) availability of dissolved oxygen (O_2); (f) biological oxygen demand (BOD); (g) pH value and (h) water clarity measured by Secchi depth. Error bars indicate ± SD. Major upwelling periods are highlighted in blue.

The inorganic nutrient concentrations of nitrate and nitrite were significantly different between seasons (Table 1) with 1.23 ± 0.87 µmol L^{-1} NO_3^- (mean ± SD) and 0.15 ± 0.07 µmol L^{-1} NO_2^- during major and 0.35 ± 0.21 µmol L^{-1} NO_3^- and 0.08 ± 0.12 µmol L^{-1} NO^{2-} during minor upwelling, as compared to 0.27 ± 0.19 µmol L^{-1} NO_3^- and 0.08 ± 0.09 µmol L^{-1} NO_2^- during major and 0.32 ± 0.30 µmol L^{-1} NO_3^- and 0.09 ± 0.05 µmol L^{-1} NO_2^- during minor non-upwelling, respectively. No seasonal differences were observed for SRP which kept stable mean concentrations between 0.14 – 0.17 µmol L^{-1} throughout the years and seasons (Fig. 2b). Nitrate and nitrite were positively correlated to SRP, chl *a*, wind velocity and had a negative correlation with precipitation. SRP had a significant positive correlation with POC, wind velocity and a negative correlation with precipitation (Table 3). Content of SRP increased with distance to Santa Marta indicating eastward sources of phosphate (Table 2, 3).

Concentrations of chl *a* were significantly different between seasons (Table 1) with higher concentrations of 2.70 ± 4.14 µg L^{-1} (mean ± SD) during major upwelling and 1.69 ± 3.47 µg L^{-1} during major non-upwelling as compared to 1.36 ± 2.64 µg L^{-1} during minor upwelling and 0.89 ± 1.39 µg L^{-1} during minor non-upwelling periods. However, results of multiple comparisons among seasons showed that chl *a* had only a statistically significant difference between major upwelling and non-upwelling, and between major upwelling and minor non-upwelling. Concentrations of chl *a* were positively correlated to PON, POC, wind velocity and negatively correlated to water clarity and precipitation (Table 3).

Table 3. Correlation matrix of environmental variables. Significance levels of correlation coefficients (Spearman's rank correlation) among environmental variables and distance from Santa Marta are represented. Levels of significance are indicated by asterisks with * for significant ($p < 0.05$) and ** for very significant ($p < 0.01$). Not significant correlations are displayed in gray. Abbreviations: temperature (T), salinity (S), nitrate (NO_3^-), nitrite (NO_2^-), soluble reactive phosphorus (SRP), chlorophyll *a* (Chl *a*), water clarity based on Secchi depth (Secchi), particulate organic nitrogen (PON), particulate organic carbon (POC), biological oxygen demand (BOD), dissolved oxygen availability (O_2).

	T	S	NO_3^-	NO_2^-	SRP	Chl *a*	Secchi	PON	POC	BOD	O_2	pH	Wind	Rain
Distance	-0.03	-0.10	-0.03	-0.01	0.36*	0.40*	-0.27	0.34	0.54*	0.35*	0.22	-0.17	-	-
T		-0.84**	-0.67**	-0.54**	-0.39*	-0.18	0.15	0.24	0.10	0.12	-0.34	0.46**	-0.86**	0.86**
S			0.79**	0.39*	0.32	0.29	-0.18	-0.21	-0.06	-0.16	0.20	-0.28	0.94**	-0.94**
NO_3^-				0.66**	0.35*	0.42*	-0.31	-0.12	-0.03	-0.32	0.04	-0.24	0.75**	-0.75**
NO_2^-					0.39*	0.42*	-0.24	0.09	-0.07	-0.10	0.08	-0.30	0.48**	-0.48**
SRP						0.23	-0.08	0.30	0.42*	0.03	0.07	0.02	0.41*	-0.41*
Chl *a*							-0.61**	0.47**	0.41*	0.06	0.05	0.08	0.32	-0.32
Secchi								-0.36*	-0.24	0.15	-0.17	-0.01	-0.21	0.21
PON									0.83**	0.13	-0.34	0.37*	-0.14	0.14
POC										0.21	-0.18	0.29	0.00	0.00
BOD											0.33	-0.20	-0.19	0.19
O_2												-0.69**	0.23	-0.23
pH													-0.25	0.25
Wind														-1.00**

Table 4. Multivariate analyses: significant differences among environmental variables in Tayrona National Natural Park and multiple comparisons between seasons and bays. The main effects of multivariate analyses and the multiple comparisons between seasons (major upwelling, minor non-upwelling, minor upwelling, and major non-upwelling) and bays (Chengue, Gayraca, Neguanje, and Gayraca) are shown. Significant PERMANOVA results are indicated by asterisks with * for significant ($p < 0.05$) and ** for very significant ($p < 0.01$). Not significant values are displayed in gray.

Factors	DF	Pseudo-*F*	(*p*)
Distance to Santa Marta (covariate)	1	1.992	0.072
Seasons (fixed)	3	16.366	0.001**
Bays (random)	1	2.619	0.002**
Exposure (fixed)	3	1.162	0.345
Multiple comparisons between seasons		*t*	(*p*)
Major upwelling - minor upwelling		3.758	0.001**
Major upwelling - major non-upwelling		6.676	0.001**
Major upwelling - minor non-upwelling		6.189	0.001**
Minor upwelling - major non-upwelling		2.464	0.001**
Minor upwelling - minor non-upwelling		2.544	0.007**
Major non-upwelling - minor non-upwelling		3.265	0.002**
Multiple comparisons between bays		*t*	(*p*)
Chengue - Gayraca		0.949	0.473
Chengue - Neguanje		1.480	0.111
Chengue - Cinto		1.361	0.128
Gayraca - Neguanje		1.544	0.104
Gayraca - Cinto		1.664	0.043*
Neguanje - Cinto		1.779	0.024*

Particulate organic matter showed seasonal differences only in PON (Table 1). PON had highest values during major non-upwelling period with 18.7 ± 7.8 μg L^{-1} (mean ± SD) followed by 17.5 ± 6.8 μg L^{-1} during major upwelling, 16.7 ± 6.1 μg L^{-1} during minor upwelling and lowest with 15.3 ± 6.4 μg L^{-1} during minor non-upwelling. Multiple comparisons detected significant seasonal differences between minor upwelling and major non-upwelling and between major non-upwelling and minor non-upwelling. POC varied between 81.1 ± 31.5 μg L^{-1} during major and 89.7 ± 47.2 μg L^{-1} during minor upwelling as compared to 85.7 ± 41.0 μg L^{-1} during major and 74.8 ± 28.0 μg L^{-1} during minor non-upwelling. A highly significant correlation was found between PON and POC during period of study. Furthermore, PON was positively correlated with pH (Table 3).

Oxygen availability was highest during minor non-upwelling (6.54 ± 0.13 mg L^{-1}; mean ± SD) and major upwelling season 6.44 ± 0.40 mg L^{-1} as compared to major non-upwelling 6.22 ± 0.36 and minor upwelling season (6.19 ± 0.26 mg L^{-1}) and had significant differences (Table 1) between seasons (major upwelling and minor upwelling, major upwelling and major non-upwelling, minor upwelling and minor non-upwelling, and between major non-upwelling and minor non-upwelling). Highest O_2 concentrations were measured in Cinto (6.47 ± 0.37 mg L^{-1}), followed by Chengue (6.40 ± 0.39 mg L^{-1}) and Neguanje (6.39 ± 0.30 mg L^{-1}) and lowest in Gayraca (6.21 ± 0.36 mg L^{-1}; Tables 5 – 8). However, significant difference between bays (Table 1) could be only verified between Gayraca and Neguanje by multiple comparison tests. A significant negative correlation was present between O_2 and pH values for the period of study (Table 3).

Highest rates of BOD were recorded during minor non-upwelling (0.021 ± 0.011 mg O_2 L^{-1} h^{-1}; mean ± SD) and lowest during major upwelling (0.016 ± 0.011 mg O_2 L^{-1} h^{-1}). Rates between major non-upwelling (0.020 ± 0.019 mg O_2 L^{-1} h^{-1}) and minor non-upwelling (0.020 ± 0.006 mg O_2 L^{-1} h^{-1}) were similar. No significant seasonal differences were detected for BOD (Table 1). Significant difference in BOD among bays (Table 1) could not be verified by pair-wise comparisons. However, highest BOD was recorded for Cinto (0.021 ± 0.017 mg O_2 L^{-1} h^{-1}), followed by Gayraca (0.018 ± 0.012 mg O_2 L^{-1} h^{-1}), Neguanje (0.017 ± 0.012 mg O_2 L^{-1} h^{-1}) and Chengue (0.016 ± 0.008 mg O_2 L^{-1} h^{-1}; Tables 5 – 8).

Highest mean pH values were registered during minor upwelling (8.24 ± 0.12; mean ± SD) and major non-upwelling (8.23 ± 0.08) as compared to major upwelling (8.12 ± 0.07) and minor non-upwelling (8.11 ± 0.02). Differences of pair-wise comparisons were significant between major upwelling and minor upwelling, major upwelling and major non-upwelling, minor upwelling and minor non-upwelling, and between major non-upwelling and minor non-upwelling. However, it cannot be excluded that seasonal differences in pH are also a result of the inhomogeneous dispersion of compared data groups (Table 1).

Water clarity had significant differences between seasons (Table 1) with highest values during minor non-upwelling (12.1 ± 2.7 m Secchi depth, mean ± SD), followed by minor upwelling (11.8 ± 1.6 m) and lowest during major non-upwelling (10.3 ± 3.5 m) and major upwelling (9.1 ± 2.7 m). Significant differences could be detected between all seasonal periods except for between minor upwelling and minor non-upwelling. Among bays, significant differences were present between Chengue (10.8 ± 2.7 m) and Cinto (9.7 ± 3.1 m), Gayraca (11.3 ± 2.7 m) and Neguanje (10.0 ± 2.9 m), Gayraca and Cinto, and between Neguanje and Cinto. Gayraca was the bay with highest water clarity (Tables 5 – 8). Water clarity had a significant negative correlation with chl *a* and PON (Table 3).

Seasonal patterns and key control environmental factors

Ordination (PCO) showed coherent seasonal pattern among all environmental variables for TNNP (Fig. 3) which are consistent with results from multivariate PERMANOVA analysis (Table 4). PCO ordination could explain 41.1 % of the total data variation by the first axis and 20.1 % by the orthogonal second axis. Data during major upwelling and major non-upwelling were clearly separated from each other according to their (dis)similarity in Euclidean distance of environmental variables (Fig. 3a), whereas minor upwelling and non-upwelling overlapped between the dominant upwelling and non-upwelling seasons. However, minor upwelling and non-upwelling seasons were closer related to major non-upwelling than to upwelling season (Fig. 3a). A highly significant correlation (correlation coefficient > 0.80) was found between the first PCO axis and salinity, NO_3^- and wind velocity, whereas temperature was negatively correlated. The second PCO axis had a highly significant positive correlation with PON and POC. Further significant correlations (correlation coefficient > 0.40) for the first PCO axis were found for NO_2^- and chl *a*, whereas water clarity, pH and precipitation were negatively correlated. The second PCO axis was positively correlated with SRP, chl *a*, BOD and pH. The environmental variables temperature, salinity, nitrate, PON, POC and wind velocity had strongest effect on the seasonal grouping of data and can be considered as key control factors in TNNP coral reefs.

Grouping the similarity of samples by the factor bay showed that Cinto had higher dispersion of data and was less similar to the other bays Chengue, Gayraca and Neguanje (Fig. 3b). The vertical axis correlating with PON and POC separated Cinto from grouping with other bays. A higher dispersion was also present for samples collected at the sheltered sites of the bays as compared to the exposed sites (Fig. 3c). Separation between similarities of data collected at exposed and sheltered sites was mainly due to differences along the second PCO axis which mainly correlated with PON and POC.

Discussion

Generally, results of the present study show that water quality in TNNP coral reefs is mainly influenced by seasonality and riverine discharge, particularly during rainy season. A direct effect of the countercurrent-located population center, Santa Marta, was not observed. Seasonal effects were stronger than changes in water quality along the distance gradient between Santa Marta in the Southwest and several river mouths in the East. Water quality in TNNP coral reefs can be considered close to oligotrophic during minor non-upwelling, whereas critical thresholds were exceeded during upwelling and in relation to riverine discharge. Whereas chl *a*, POC and BOD changed along the distance gradient, the variables inorganic nutrient, chl *a*, and O_2 concentrations along with water clarity were especially sensitive towards seasonal change.

Spatial variability of water quality in TNNP coral reefs

On a small spatial scale (< 2 km), our findings showed that only mean O_2 concentrations were significantly higher at water-current exposed than -sheltered locations indicating wave and water current-induced transport of O_2 to the coral reefs. Differences in wave and water current velocities can exist between the sites in TNNP (Werding and Sánchez 1989; Chapter 1). More O_2 transported to the exposed as compared to the sheltered sites can be explained as water current-induced transport processes are orders of magnitude higher than mass exchange through molecular diffusion in still water (Huettel et al. 2003). Water current velocity did not significantly affect other measured environmental variables, however samples at the sheltered sites had a higher variability which could be a consequence of longer residence times and heterogeneous accumulation through a reduced mixing at these sites (Andrews and Pickard 1990). Drastic decreases in O_2 concentrations leading to hypoxia were reported to impair calcification rates in corals (Colombo-Pallotta et al. 2010; Wijgerde et al. 2012), however these effects are unlikely to occur between the exposed and sheltered sites as the mean difference in dissolved oxygen (6.42 mg L^{-1} at exposed; 6.31 mg L^{-1} at sheltered) was clearly above levels of hypoxia (2 mg L^{-1} O_2).

Table 5. Mean environmental variables (± SD) in Chengue Bay and a water depth of 10 m during major upwelling (December – April), minor upwelling (July - August), major non-upwelling (September - November) and minor non-upwelling (May - June) periods. Abbreviation: soluble reactive phosphorus (SRP).

Water column Chengue	Major non-upwelling	Major upwelling	Minor non-upwelling	Minor upwelling
Temperature (°C)	28.85 ± 0.70	25.08 ± 1.63	27.34 ± 0.94	27.35 ± 1.17
Salinity	34.7 ± 1.7	37.0 ± 0.9	35.5 ± 1.5	35.7 ± 0.9
Nitrate (µmol L^{-1})	0.28 ± 0.16	1.22 ± 0.75	0.26 ± 0.13	0.46 ± 0.30
Nitrite (µmol L^{-1})	0.11 ± 0.10	0.15 ± 0.06	0.07 ± 0.04	0.08 ± 0.03
SRP (µmol L^{-1})	0.14 ± 0.08	0.15 ± 0.11	0.10 ± 0.06	0.17 ± 0.13
Chlorophyll *a* (µg L^{-1})	0.79 ± 0.38	1.60 ± 2.48	0.69 ± 0.19	2.31 ± 4.69
Particulate N (µg L^{-1})	17.9 ± 7.1	17.2 ± 5.6	15.4 ± 7.5	15.3 ± 6.4
Particulate organic C (µg L^{-1})	74.8 ± 30.5	81.9 ± 25.8	68.7 ± 23.1	78.3 ± 38.8
Dissolved O$_2$ (mg L^{-1})	6.15 ± 0.17	6.51 ± 0.45	6.63 ± 0.14	6.14 ± 0.21
Biological O$_2$ demand (mg O$_2$ L^{-1} h^{-1})	0.016 ± 0.008	0.016 ± 0.009	0.019 ± 0.003	0.015 ± 0.006
pH	8.27 ± 0.03	8.12 ± 0.06	8.11 ± 0.01	8.34 ± 0.10
Water clarity (Secchi depth in m)	10.3 ± 3.3	10.1 ± 2.1	11.5 ± 2.8	12.5 ± 1.6

On a larger spatial scale (< 50 km), we could show that during rainy (non-upwelling) season, chl *a* along with POC concentrations and BOD increased with decreasing distance to the rivers in the East, while no correlation along this distance gradient was observed during upwelling. This relationship was still present for chl *a* concentration during upwelling. Fabricius (2005) reviewed that the effects of riverine runoff e.g. increased inorganic nutrient concentrations, enrichment with particulate organic matter, and light reduction due to turbidity and sedimentation are detrimental for coral reef development and can finally lead to reef degradation. In our study, the eastward increase in chl *a*, POC and BOD during rainy season can be explained by intensified riverine discharge from several smaller river mouths in the East which is likely transported by the westward Caribbean Current (Wüst 1964; Gordon 1967) to the TNNP bays. This argument is supported by our data showing that the Western bays Chengue and Gayraca exhibited better water quality (higher water clarity, lower chl *a*, and BOD) than the Eastern bays Neguanje and Cinto. In the study of Franco-Herrera et al. (2006), high chl *a* concentrations during rainy season in TNNP were attributed to riverine discharge of the Magdalena River – the principal river in Colombia, located at more than 80 km to the Southwest from TNNP. However, the latter study did not consider a horizontal distance gradient in TNNP for the sampling of water parameters like in the present study. Consequently, in our study, chl *a* concentrations increased with distance to the countercurrent-located Magdalena River, suggesting a more likely effect of the smaller river mouths (Rio Piedras, Mendihuaca, Guachaca, Buritaca, Don Diego, and Palomino) in the East on water quality decline.

Table 6. Mean environmental variables (± SD) in Gayraca Bay and a water depth of 10 m during major upwelling (December – April), minor upwelling (July - August), major non-upwelling (September - November) and minor non-upwelling (May - June) periods. Abbreviation: soluble reactive phosphorus (SRP).

Water column Gayraca	Major non-upwelling	Major upwelling	Minor non-upwelling	Minor upwelling
Temperature (°C)	28.85 ± 0.73	24.95 ± 1.69	27.27 ± 1.04	27.25 ± 1.26
Salinity	34.8 ± 1.8	37.0 ± 0.9	35.5 ± 1.6	35.8 ± 0.8
Nitrate (µmol L^{-1})	0.27 ± 0.17	1.33 ± 0.96	0.27 ± 0.18	0.36 ± 0.19
Nitrite (µmol L^{-1})	0.12 ± 0.13	0.16 ± 0.08	0.09 ± 0.05	0.08 ± 0.05
SRP (µmol L^{-1})	0.14 ± 0.08	0.16 ± 0.12	0.15 ± 0.12	0.19 ± 0.08
Chlorophyll *a* (µg L^{-1})	0.87 ± 0.53	1.71 ± 1.38	0.65 ± 0.12	0.86 ± 0.52
Particulate N (µg L^{-1})	17.5 ± 6.0	15.3 ± 5.3	13.5 ± 5.0	17.7 ± 6.9
Particulate organic C (µg L^{-1})	76.3 ± 27.6	67.8 ± 25.7	66.9 ± 26.9	97.1 ± 56.4
Dissolved O_2 (mg L^{-1})	6.02 ± 0.17	6.30 ± 0.42	6.45 ± 0.18	5.94 ± 0.22
Biological O_2 demand (mg O_2 L^{-1} h^{-1})	0.017 ± 0.008	0.015 ± 0.012	0.022 ± 0.007	0.028 ± 0.016
pH	8.23 ± 0.08	8.10 ± 0.09	8.10 ± 0.02	8.35 ± 0.08
Water clarity (Secchi depth in m)	12.1 ± 3.5	10.6 ± 2.2	13.7 ± 2.0	12.1 ± 1.8

The city of Santa Marta with a population of nearly half a million (DANE 2005) is located Southwest to TNNP and belongs to one of the most important touristic locations of Colombia (with ca. 1 million of tourists in December – January p.a., Moscarella et al. 2010). Unfortunately, Santa Marta is also known for its coastal water contamination by fecal and total coliforms, as well as by drastic increased nitrogen and phosphorus runoff due to a submarine outfall discharge of 900 – 1200 L s^{-1} untreated sewage water (Moscarella et al. 2010). However, the present study only observed water quality in the neighboring TNNP in relation to the river mouths in the East with no noticeable effect of the population center Santa Marta. Our results thereby suggest that the observed water quality decline was mainly triggered by riverine runoff and not by the countercurrent-located Santa Marta. Thus, the unilateral direction of water currents obviously plays a key role in controlling spatial variability of water quality in TNNP.

Table 7. Mean environmental variables (± SD) in Neguanje Bay and a water depth of 10 m during major upwelling (December – April), minor upwelling (July - August), major non-upwelling (September - November) and minor non-upwelling (May - June) periods. Abbreviation: soluble reactive phosphorus (SRP).

Water column Neguanje	Major non-upwelling	Major upwelling	Minor non-upwelling	Minor upwelling
Temperature (°C)	28.87 ± 0.69	25.09 ± 1.59	27.37 ± 0.93	27.26 ± 1.14
Salinity	35.2 ± 1.4	36.8 ± 0.8	35.4 ± 1.7	35.6 ± 1.0
Nitrate (µmol L^{-1})	0.24 ± 0.20	1.17 ± 0.88	0.25 ± 0.23	0.30 ± 0.11
Nitrite (µmol L^{-1})	0.04 ± 0.03	0.12 ± 0.06	0.07 ± 0.04	0.05 ± 0.04
SRP (µmol L^{-1})	0.12 ± 0.09	0.16 ± 0.11	0.17 ± 0.11	0.14 ± 0.06
Chlorophyll *a* (µg L^{-1})	2.18 ± 4.72	3.69 ± 4.89	0.73 ± 0.26	0.76 ± 0.24
Particulate N (µg L^{-1})	18.8 ± 8.4	19.1 ± 6.9	15.4 ± 4.5	15.7 ± 4.2
Particulate organic C (µg L^{-1})	89.4 ± 47.1	90.6 ± 31.7	75.2 ± 22.7	81.0 ± 24.6
Dissolved O_2 (mg L^{-1})	6.24 ± 0.22	6.47 ± 0.35	6.54 ± 0.05	6.31 ± 0.19
Biological O_2 demand (mg O_2 L^{-1} h^{-1})	0.018 ± 0.015	0.016 ± 0.014	0.017 ± 0.006	0.016 ± 0.003
pH	8.21 ± 0.08	8.14 ± 0.06	8.11 ± 0.02	8.14 ± 0.02
Water clarity (Secchi depth in m)	9.1 ± 3.1	7.7 ± 2.4	12.0 ± 2.1	11.8 ± 1.5

Temporal variability of water quality in TNNP coral reefs

Significant seasonal differences in TNNP were found for the variables temperature, salinity, nitrate, nitrite, chl *a*, PON, O_2, and water clarity. However, the general seasonal pattern in TNNP bays represented by PCO ordination could be largely attributed to temperature, salinity, nitrate, PON, POC and wind velocity followed by nitrite, SRP, chl *a*, BOD, water clarity, pH and precipitation. Thus, seasonality had a stronger effect on change in environmental variables than location as deduced from significant differences between seasons of PERMANOVA analyses and seasonal grouping of environmental data by PCO.

Table 8. Mean environmental variables (± SD) in Cinto Bay and a water depth of 10 m during major upwelling (December – April), minor upwelling (July - August), major non-upwelling (September - November) and minor non-upwelling (May - June) periods. Abbreviation: soluble reactive phosphorus (SRP).

Water column Cinto	Major non-upwelling	Major upwelling	Minor non-upwelling	Minor upwelling
Temperature (°C)	28.93 ± 0.71	24.89 ± 1.64	27.28 ± 1.03	27.34 ± 1.24
Salinity	35.0 ± 1.4	36.7 ± 0.9	35.4 ± 1.6	35.5 ± 0.9
Nitrate (µmol L^{-1})	0.27 ± 0.21	1.19 ± 0.89	0.49 ± 0.46	0.29 ± 0.14
Nitrite (µmol L^{-1})	0.06 ± 0.04	0.15 ± 0.06	0.13 ± 0.06	0.11 ± 0.23
SRP (µmol L^{-1})	0.16 ± 0.13	0.17 ± 0.10	0.16 ± 0.11	0.17 ± 0.07
Chlorophyll *a* (µg L^{-1})	2.90 ± 4.83	3.91 ± 5.82	1.50 ± 2.72	1.50 ± 2.21
Particulate N (µg L^{-1})	20.6 ± 9.1	18.1 ± 8.5	16.9 ± 7.8	18.4 ± 6.4
Particulate organic C (µg L^{-1})	102.5 ± 49.5	84.8 ± 37.4	88.6 ± 34.2	102.2 ± 59.5
Dissolved O_2 (mg L^{-1})	6.45 ± 0.56	6.49 ± 0.34	6.54 ± 0.03	6.38 ± 0.16
Biological O_2 demand (mg O_2 L^{-1} h^{-1})	0.027 ± 0.030	0.018 ± 0.009	0.020 ± 0.006	0.026 ± 0.008
pH	8.22 ± 0.08	8.13 ± 0.06	8.11 ± 0.02	8.13 ± 0.01
Water clarity (Secchi depth in m)	9.6 ± 3.4	8.2 ± 2.7	11.2 ± 3.0	11.0 ± 1.2

Low seawater temperature coinciding with high salinity is often used as indicator for seasonal coastal upwelling (Corredor 1979; Fajardo 1979; Corredor 1981). Our *in situ* temperature data over two years indicate that the TNNP seasonal upwelling consists of one primary cooling period between December and April, followed by an increase in water temperature between May and June and a secondary cooling between July and August due to a midyear upwelling. Upwelling relaxation, or a non-upwelling phase, was observed between September and November. Our results on a semiannual upwelling cycle in TNNP are consistent with patterns of surface seawater temperature (SST) measured for the upwelling centers of the Southern Caribbean Upwelling System (Rueda-Roa and Muller-Karger 2013).

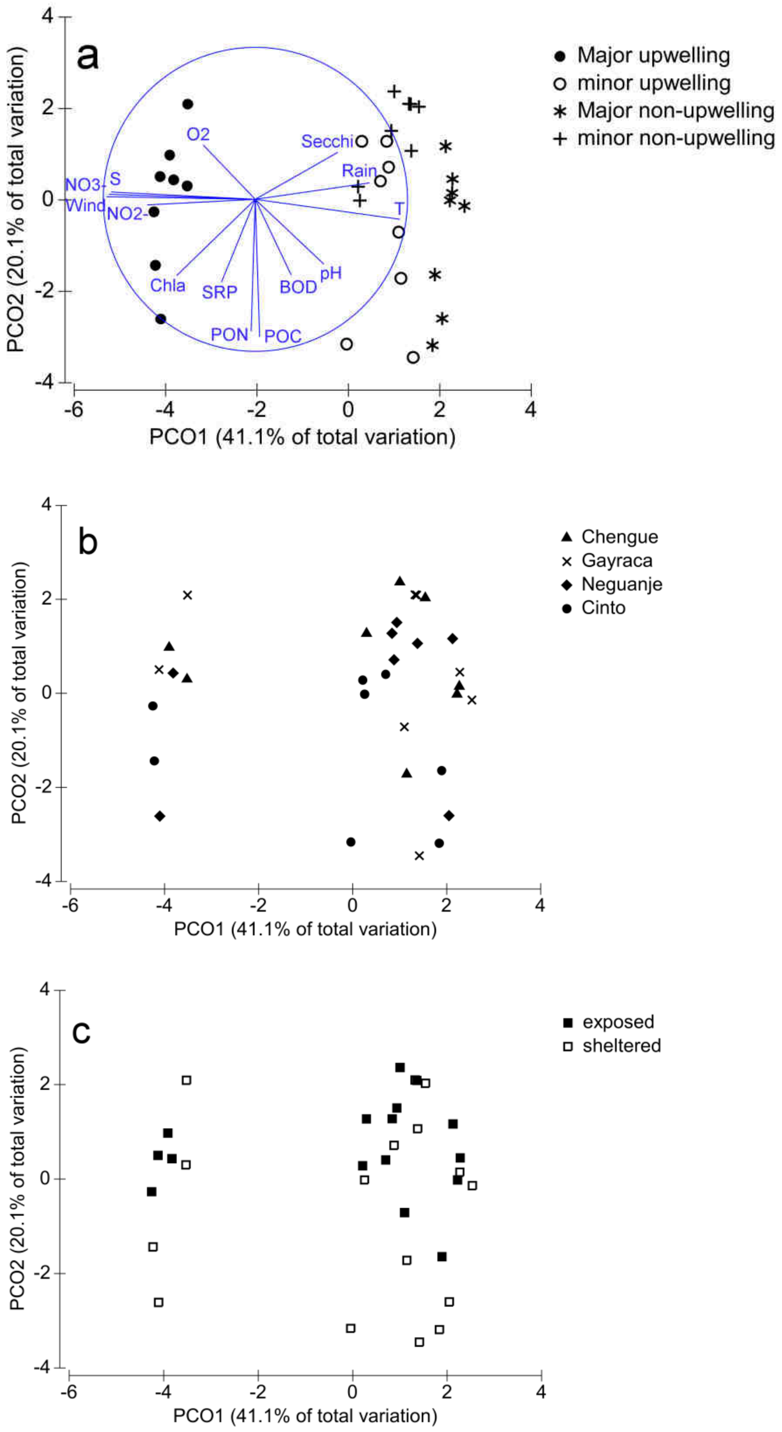

Figure 3. Graphical representation of multivariate analyses results by Principle Coordinates Ordination (PCO). PCO of environmental variables was grouped by seasons (a); bays (b), and exposure to wave and water-currents of the sampling locations (c). Effects and directions of environmental variables in (a) are displayed as vectors with the abbreviations: temperature (T), salinity (S), nitrate (NO_3^-), nitrite (NO_2^-), soluble reactive phosphorus (SRP), particulate organic nitrogen (PON), particulate organic carbon (POC), chlorophyll *a* (Chl*a*), availability of dissolved oxygen (O_2), biological oxygen demand (BOD), pH, water clarity (Secchi), wind velocity (Wind) and precipitation (Rain).

The principal source of inorganic nutrients, particularly nitrate, for new primary production is the upwelling from deeper water into the euphotic zone (Dugdale and Goering 1967; Eppley and Peterson 1979). Concentrations of up to 35 µmol L^{-1} nitrate and 1 – 2 µmol L^{-1} phosphate have been reported for subsurface waters representing the source of upwelling (Anderson and Lucas 2009). However, the inorganic nutrient concentrations of nitrate during upwelling in TNNP were 4 times below the upwelling in Peru (Zuta and Guillén 1970), 6 times below concentration in north-west Africa (Jones 1972) and 12 time lower than concentrations reported for the upwelling in the Gulf of Panama (D'Croz and O'Dea 2007). This low-level inorganic nutrient enrichment is unique among seasonal coastal upwelling settings (Corredor 1979; Diaz-Pulido and Garzón-Ferreira 2002) and is an inherent property of the largely nutrients-depleted Subtropical Underwater – the major upwelling source in TNNP (Corredor 1979). Inorganic nutrient concentrations during non-upwelling are within concentration ranges typical for coral reefs with < 0.6 µmol L^{-1} nitrate and < 0.2 µmol L^{-1} phosphate (Kleypas et al. 1999), but only slightly above the threshold levels displaying eutrophic conditions during upwelling (dissolved inorganic nitrogen ~ 1 µmol L^{-1} and phosphate ~ 0.1 – 0.2 µmol L^{-1}; Bell 1992; Lapointe 1997). This confirms that inorganic nutrient concentration are not hindering the development of coral reefs in TNNP as reported for other upwelling regions e.g. the Gulf of Panama in the Pacific (D'Croz and O'Dea 2007).

Chlorophyll *a* was significantly higher during upwelling as compared to non-upwelling periods. This relationship is consistent with previous studies carried out in the area (Franco-Herrera et al. 2006; Franco-Herrera et al. 2007; Arévalo-Martínez and Franco-Herrera 2008; García-Hoyos et al. 2010; Ramírez-Barón et al. 2010). However, values above the suggested eutrophication threshold of 0.45 – 0.50 µg L^{-1} (Bell 1992; De'ath and Fabricius 2010) during both seasons indicate that seasonal upwelling was not the only stimulation of phytoplankton growth. Chlorophyll *a* concentrations increased with eastward distance to the city of Santa Marta indicating an influence of riverine discharge by rivers leading to water quality decline.

The presence of POM showed no clear seasonal patterns for POC and PON. Although both, PON and POC were correlated to chl *a*, only PON was significantly higher during non-upwelling – in contrast to chlorophyll *a* which had higher concentration during upwelling. This behavior of PON could be either explained by additional sources of POM stimulated during rainy season and riverine discharge or by an uncoupling between the upwelling pulse in surplus inorganic nutrients and new primary production as reported by Paramo et al. (2011).

Water clarity seasonally ranging between mean values of 9.1 and 12.1 m Secchi depth were close to the suggested threshold value of 10 m indicating good quality of inshore waters of the Great Barrier Reef (Great Barrier Reef Marine Park Authority 2009; De'ath and Fabricius 2010). Lower water clarity during upwelling is likely related to increases in chl *a* concentrations and higher turbidity due to stronger water currents (Chapter 1). Our results showing a good correlation between water clarity, chl *a* and particulate nitrogen concentrations are confirmed by Fabricius and De'ath (2004) and suggest that water clarity is an excellent and cost-effective water quality indicator for coastal management in TNNP.

Wind velocity registered during the period of study was significantly higher during major upwelling as compared to non-upwelling. No differences in mean wind velocity were found between the minor upwelling and non-upwelling seasons. Winds were highly negatively correlated to precipitation and temperature, and positively correlated to salinity, inorganic nutrients and chlorophyll *a* concentrations, which is a characteristic relationship for the wind-driven coastal upwelling system (Salzwedel and Müller 1983; Andrade and Barton 2005; García-Hoyos et al. 2010; Rueda-Roa and Muller-Karger 2013). However, wind velocities of the present study were below the reported values for the region (2.1 – 5.6 m s^{-1}, but up to 22 m s^{-1} registered during upwelling for the years 1981 – 1982 in Santa Marta (Salzwedel and Müller 1983), with maximum values of 30 m s^{-1} for 1967 –1968 (Herrmann 1970) during upwelling) which could be a consequence of the wind-sheltered location of meteorological station located at a distance of 18 km to TNNP.

Ecological consequences for reef functioning

Major environmental control can be attributed to seawater temperature, salinity, nitrate, PON, POC and wind velocity in TNNP as these factors determined the environmental change in water quality between consecutive seasons (correlation of > 0.8 with PCO axes).

Coral reefs in TNNP growing at seawater temperatures between 20.0 and 30.6 °C experience annually the whole range of temperature (21 - 29.5 °C; Kleypas et al. 1999) allowing for coral development. Seawater temperature plays a crucial role in the process of coral bleaching, the reversible loss of endosymbiotic algae which can lead to weakening, disease or mortality of corals in case of prolonged thermal stress (Hoegh-Guldberg 1999). Absence of coral bleaching in TNNP was attributed to the natural decrease in seawater temperature by upwelling during or after the period of highest heat stress (Rodríguez-Ramírez et al. 2010; Bayraktarov et al. 2012) constituting the region a "refuge" for corals against global warming-induced seawater temperature increase (Chollett et al. 2010).

Coral reefs in TNNP experience strong changes in salinity (32.5 – 39.0) driven by the alteration of rainy and dry seasons, but were still within the environmental limits for coral reefs (23.3 – 40.0; Kleypas et al. 1999). Drastic changes in salinity were identified as a factor inducing coral bleaching, often in combination with high seawater temperature (Hoegh-Guldberg and Smith 1989; del Mónaco et al. 2012) and could have been one of triggers for coral bleaching end of 2010 in TNNP which was a year with anomalously high precipitation (Chapter 6).

Seasonal upwelling increased inorganic nutrient concentrations from oligotrophic ($<$ 0.6 µmol L^{-1} nitrate and $<$ 0.2 µmol L^{-1} phosphate; Kleypas et al. 1999) to levels high enough to sustain macroalgal blooms in Caribbean reefs (dissolved inorganic nitrogen ~ 1 µmol L^{-1} and phosphate ~ 0.2 µmol L^{-1}; Lapointe 1997). Eutrophication may shift reef communities from corals to macroalgae or heterotrophic filter feeders (Birkeland 1988; Bellwood et al. 2004; Fabricius and De'ath 2004) and consequently lead to a loss of species biodiversity (De'ath and Fabricius 2010). Indeed, for the TNNP region, an upwelling-triggered macroalgal bloom was first hypothesized by Bula-Meyer (1977; 1985; 1990) and later confirmed by the comprehensive monitoring study of Diaz-Pulido and Garzón-Ferreira (2002). The authors showed that during upwelling, the algal assemblage in TNNP was dominated by the brown macroalgae *Dictyota* spp., whereas during non-upwelling (rainy season), mainly turf algae were present (Diaz-Pulido and Garzón-Ferreira 2002). Abundance of macroalgae in TNNP reefs was mainly correlated to cold seawater temperature during upwelling, but the authors speculated that there may be an effect of increased inorganic nutrient concentrations (Diaz-Pulido and Garzón-Ferreira 2002). This can be confirmed by the present study as nitrate and phosphate concentrations during upwelling exceeded the threshold level defined for macroalgal bloom in the Caribbean.

POM concentrations in the water column showed no clear seasonal patterns in TNNP. Only PON was increased during non-upwelling. POM consists of organic carbon and nitrogen particles (> 1 µm; Eppley and Peterson 1979; Druffel et al. 1992) that contribute to the nutrient availability of coastal regions (Fabricius 2005). Most scleractinian corals continuously release POM (Wild et al. 2004; Wild et al. 2005; Naumann et al. 2010) and thereby contribute as active reef ecosystem engineers to the recycling of nutrients (Wild et al. 2011). POM can be used as an energy source by a variety of benthic organisms including corals (Lewis 1976; Anthony 1999). However, not all coral species are able to utilize POM (Veron 2000). In contrast to dissolved inorganic nutrients which are preferentially taken up by coral symbionts, POM can stimulate growth in both, corals and their symbionts (Dubinsky and Jokiel 1994), representing a better source of energy for the coral holobiont. So far, no explicit eutrophication threshold values for POM are reported. Most studies considered the effects of suspended particulate matter on coral reefs (Lewis 1976; Anthony 1999; Fabricius 2005) of which POM constitutes a significant part.

Conclusions and future monitoring recommendations

This study comprises the most comprehensive monitoring of coral reefs water quality with a high seasonal and spatial resolution in the Tayrona National Natural Park bays. The data represent an actual baseline for future studies and management assessments. The present study is comparable to other environmental monitoring studies e.g. Schaffelke et al. (2012) for the Great Barrier Reef, however on a smaller spatial and temporal scale, and provides environmental data for correlative analyses of coral reef status in TNNP. We showed that the status variables chl *a* and water clarity, along with the process variable BOD, are good and cost-effective indicators for the assessment of water quality changes due to their significant correlations with other important environmental parameters which cannot always be addressed in monitoring studies. These environmental indicators suggest that the Western bays Chengue and Gayraca had better environmental conditions as compared to the Eastern bays Neguanje and Cinto in TNNP. Overall, water quality in TNNP was close to oligotrophic condition during non-upwelling, but exceeded critical threshold values during upwelling and in relation to riverine discharge. Future work should include investigation on the physiological response of coral reef organisms to upwelling- and riverine runoff-induced environmental change in water quality which, as suggested by Cooper et al. (2009), first invoke a response at the genetic and colony level such as symbiont photophysiology and coral brightness.

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Appendix 1

Table S1. Environmental variables measured throughout the period of study. Replication indicates total number of collected or measured samples. Abbreviations: Nitrate (NO_3^-), nitrite (NO_2^-), soluble reactive phosphorus (SRP), chlorophyll *a* (chl *a*), particulate organic matter (POM), particulate organic nitrogen (PON), particulate organic carbon (POC), biological oxygen demand (BOD) and dissolved oxygen availability (O_2).

Variable	Method	Start	End	N
Temperature	*in situ* loggers	Oct 2010	Feb 2013	288 per day and site
Salinity	conductimeter	Jan 2011	Feb 2013	624
Inorganic nutrients (NO_3^-, NO_2^-, SRP)	spectro-photometry	Jan 2011	Feb 2013	624
chl *a*	fluorometry	Jan 2011	Feb 2013	624
Water clarity	Secchi depth	May 2011	Feb 2013	640
POM (PON + POC)	elemental analyzer	Jan 2011	Feb 2013	624
BOD	incubations	Nov 2011	Feb 2013	512
O_2	luminescent dissolved oxygen electrode	Nov 2011	Feb 2013	512
pH	pH electrode	Nov 2011	Feb 2013	512

Table S2. Mean environmental variables (± SD) at the exposed (exp) and sheltered (she) sites and a water depth of 10 m in Chengue Bay for the major upwelling (December – April), minor upwelling (July - August), major non-upwelling (September - November) and minor non-upwelling (May - June) periods. Abbreviation: soluble reactive phosphous (SRP).

Water column Chengue	Major upwelling		Minor upwelling		Major non-upwelling		Minor non-upwelling	
	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site
Temperature (°C)	25.1 ± 1.6	25.1 ± 1.6	27.4 ± 1.2	27.4 ± 1.2	28.9 ± 0.7	28.8 ± 0.7	27.4 ± 0.9	27.3 ± 1.0
Salinity	37.0 ± 1.0	37.0 ± 0.8	35.7 ± 0.9	35.7 ± 0.9	34.7 ± 1.7	34.7 ± 1.7	35.5 ± 1.6	35.4 ± 1.5
Nitrate (µmol L^{-1})	1.30 ± 0.74	1.15 ± 0.77	0.56 ± 0.36	0.36 ± 0.21	0.30 ± 0.18	0.27 ± 0.15	0.28 ± 0.11	0.23 ± 0.15
Nitrite (µmol L^{-1})	0.15 ± 0.06	0.15 ± 0.06	0.09 ± 0.03	0.07 ± 0.03	0.12 ± 0.12	0.11 ± 0.09	0.07 ± 0.04	0.06 ± 0.03
SRP (µmol L^{-1})	0.16 ± 0.12	0.15 ± 0.10	0.11 ± 0.06	0.23 ± 0.16	0.12 ± 0.07	0.15 ± 0.08	0.09 ± 0.06	0.11 ± 0.06
Chlorophyll *a* (µg L^{-1})	1.21 ± 0.85	1.91 ± 3.26	3.89 ± 6.36	0.74 ± 0.07	0.72 ± 0.22	0.86 ± 0.49	0.67 ± 0.21	0.70 ± 0.19
Particulate N (µg L^{-1})	16.4 ± 5.3	17.7 ± 5.8	12.5 ± 3.4	18.1 ± 7.6	18.0 ± 8.1	17.8 ± 6.2	15.6 ± 9.4	15.1 ± 5.3
Particulate organic C (µg L^{-1})	78.2 ± 21.4	84.8 ± 28.7	58.8 ± 16.3	97.8 ± 45.4	81.7 ± 33.3	68.0 ± 26.7	63.5 ± 19.6	73.9 ± 25.9
Dissolved O_2 (mg L^{-1})	6.81 ± 0.37	6.28 ± 0.37	6.28 ± 0.19	6.00 ± 0.13	6.15 ± 0.20	6.14 ± 0.13	6.69 ± 0.17	6.57 ± 0.02
Biological O_2 demand (mg O_2 L^{-1} h^{-1})	0.019 ± 0.009	0.013 ± 0.008	0.018 ± 0.006	0.013 ± 0.006	0.014 ± 0.008	0.017 ± 0.008	0.019 ± 0.002	0.019 ± 0.004
pH	8.11 ± 0.05	8.12 ± 0.07	8.33 ± 0.10	8.35 ± 0.11	8.28 ± 0.03	8.26 ± 0.03	8.11 ± 0.01	8.11 ± 0.02
Water clarity (Secchi depth in m)	9.8 ± 1.7	10.3 ± 2.4	12.0 ± 1.9	13.0 ± 1.0	10.2 ± 3.7	10.4 ± 2.9	10.3 ± 2.0	12.7 ± 3.0

Table S3. Mean environmental variables (± SD) at the exposed (exp) and sheltered (she) sites and a water depth of 10 m in Gayraca Bay for the major upwelling (December – April), minor upwelling (July - August), major non-upwelling (September - November) and minor non-upwelling (May - June) periods. Abbreviation: soluble reactive phosphous (SRP).

Water column Gayraca	Major upwelling		Minor upwelling		Major non-upwelling		Minor non-upwelling	
	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site
Temperature (°C)	24.9 ± 1.7	25.0 ± 1.7	27.2 ± 1.3	27.3 ± 1.2	28.8 ± 0.7	28.9 ± 0.7	27.2 ± 1.1	27.3 ± 1.0
Salinity	37.1 ± 0.9	37.0 ± 0.9	35.8 ± 0.8	35.9 ± 0.8	34.9 ± 1.7	34.7 ± 1.9	35.4 ± 1.7	35.5 ± 1.6
Nitrate (μmol L^{-1})	1.31 ± 0.95	1.34 ± 0.99	0.37 ± 0.23	0.34 ± 0.16	0.26 ± 0.19	0.27 ± 0.16	0.17 ± 0.16	0.37 ± 0.15
Nitrite (μmol L^{-1})	0.16 ± 0.09	0.16 ± 0.07	0.06 ± 0.03	0.09 ± 0.05	0.12 ± 0.15	0.11 ± 0.11	0.08 ± 0.03	0.11 ± 0.06
SRP (μmol L^{-1})	0.16 ± 0.13	0.16 ± 0.11	0.16 ± 0.08	0.22 ± 0.07	0.14 ± 0.09	0.14 ± 0.08	0.15 ± 0.16	0.14 ± 0.09
Chlorophyll *a* (μg L^{-1})	2.25 ± 1.59	1.12 ± 0.77	0.69 ± 0.27	1.03 ± 0.66	0.82 ± 0.34	0.92 ± 0.67	0.66 ± 0.16	0.64 ± 0.06
Particulate N (μg L^{-1})	17.1 ± 5.7	13.3 ± 3.9	16.8 ± 6.6	18.5 ± 7.3	17.1 ± 5.8	17.9 ± 6.4	13.5 ± 4.9	13.5 ± 5.3
Particulate organic C (μg L^{-1})	73.3 ± 25.8	62.3 ± 24.6	91.3 ± 51.5	102.4 ± 62.4	71.6 ± 23.0	81.2 ± 31.6	66.2 ± 18.2	67.5 ± 34.4
Dissolved O_2 (mg L^{-1})	6.27 ± 0.45	6.34 ± 0.39	6.13 ± 0.01	5.75 ± 0.15	6.10 ± 0.20	5.94 ± 0.05	6.57 ± 0.05	6.34 ± 0.20
Biological O_2 demand (mg O_2 L^{-1} h^{-1})	0.014 ± 0.015	0.017 ± 0.007	0.017 ± 0.007	0.038 ± 0.016	0.017 ± 0.008	0.016 ± 0.008	0.021 ± 0.004	0.023 ± 0.009
pH	8.09 ± 0.10	8.12 ± 0.07	8.35 ± 0.08	8.34 ± 0.08	8.24 ± 0.07	8.23 ± 0.09	8.11 ± 0.02	8.09 ± 0.02
Water clarity (Secchi depth in m)	9.3 ± 1.7	11.8 ± 1.9	11.6 ± 0.7	12.5 ± 2.4	11.6 ± 2.9	12.6 ± 4.0	12.7 ± 1.7	14.7 ± 1.7

Table S4. Mean environmental variables (± SD) at the exposed (exp) and sheltered (she) sites and a water depth of 10 m in Neguanje Bay for the major upwelling (December – April), minor upwelling (July - August), major non-upwelling (September - November) and minor non-upwelling (May - June) periods. Abbreviation: soluble reactive phosphous (SRP).

Water column Neguanje	Major upwelling		Minor upwelling		Major non-upwelling		Minor non-upwelling	
	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site
Temperature (°C)	25.1 ± 1.5	25.1 ± 1.7	27.1 ±1.1	27.3 ± 1.2	28.8 ± 0.7	28.9 ± 0.7	27.4 ± 0.9	27.3 ± 0.9
Salinity	36.8 ± 0.9	36.9 ± 0.8	35.5 ± 1.0	35.6 ± 1.0	35.2 ± 1.2	35.1 ± 1.5	35.4 ± 1.8	35.4 ± 1.7
Nitrate (µmol L^{-1})	1.20 ± 0.99	1.15 ± 0.79	0.24 ± 0.11	0.36 ± 0.07	0.33 ± 0.23	0.15 ± 0.09	0.30 ± 0.20	0.20 ± 0.25
Nitrite (µmol L^{-1})	0.11 ± 0.06	0.13 ± 0.06	0.05 ± 0.04	0.06 ± 0.05	0.05 ± 0.03	0.04 ± 0.03	0.08 ± 0.03	0.06 ± 0.04
SRP (µmol L^{-1})	0.17 ± 0.12	0.16 ± 0.09	0.16 ± 0.06	0.12 ± 0.06	0.10 ± 0.05	0.13 ± 0.12	0.20 ± 0.13	0.14 ± 0.09
Chlorophyll *a* (µg L^{-1})	2.45 ± 3.39	4.82 ± 5.75	0.61 ± 0.20	0.91 ± 0.18	0.87 ± 0.69	3.50 ± 6.46	0.62 ± 0.22	0.84 ± 0.26
Particulate N (µg L^{-1})	16.3 ± 6.4	21.6 ± 6.5	14.6 ± 3.5	16.8 ± 4.7	15.0 ± 5.7	22.5 ± 9.1	14.2 ± 3.9	16.8 ± 4.8
Particulate organic C (µg L^{-1})	76.2 ± 29.0	103.6 ± 28.6	74.1 ± 19.5	87.9 ± 28.0	76.8 ± 38.9	102.8 ± 52.2	69.0 ± 16.5	81.4 ± 26.9
Dissolved O_2 (mg L^{-1})	6.60 ± 0.36	6.33 ± 0.30	6.37 ± 0.15	6.26 ± 0.22	6.24 ± 0.26	6.25 ± 0.18	6.51 ± 0.05	6.58 ± 0.02
Biological O_2 demand (mg O_2 L^{-1} h^{-1})	0.014 ± 0.007	0.018 ± 0.017	0.017 ± 0.003	0.015 ± 0.004	0.017 ± 0.009	0.020 ± 0.019	0.014 ± 0.004	0.019 ± 0.007
pH	8.14 ± 0.06	8.14 ± 0.06	8.15 ± 0.01	8.13 ± 0.03	8.19 ± 0.08	8.23 ± 0.08	8.11 ± 0.02	8.11 ± 0.02
Water clarity (Secchi depth in m)	7.4 ± 2.4	7.9 ± 2.4	11.4 ± 1.8	12.2 ± 0.7	9.3 ± 3.1	8.9 ± 3.1	11.7 ± 2.5	12.3 ± 1.8

Table S5. Mean environmental variables (± SD) at the exposed (exp) and sheltered (she) sites and a water depth of 10 m in Cinto Bay for the major upwelling (December – April), minor upwelling (July - August), major non-upwelling (September - November) and minor non-upwelling (May - June) periods. Abbreviation: soluble reactive phosphous (SRP).

Water column Cinto	Major upwelling		Minor upwelling		Major non-upwelling		Minor non-upwelling	
	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site
Temperature (°C)	24.8 ± 1.6	25.0 ± 1.7	27.4 ± 1.2	27.3 ± 1.3	28.9 ± 0.7	28.9 ± 0.7	27.3 ± 1.0	27.3 ± 1.0
Salinity	36.6 ± 1.0	36.8 ± 0.8	35.6 ± 1.0	35.3 ± 0.9	34.9 ± 1.5	35.1 ± 1.4	35.5 ± 1.6	35.4 ± 1.8
Nitrate (µmol L^{-1})	1.13 ± 0.85	1.25 ± 0.94	0.30 ± 0.11	0.28 ± 0.18	0.29 ± 0.25	0.25 ± 0.17	0.37 ± 0.40	0.62 ± 0.50
Nitrite (µmol L^{-1})	0.15 ± 0.06	0.15 ± 0.06	0.06 ± 0.04	0.15 ± 0.32	0.06 ± 0.05	0.06 ± 0.04	0.12 ± 0.06	0.14 ± 0.06
SRP (µmol L^{-1})	0.16 ± 0.10	0.18 ± 0.11	0.14 ± 0.05	0.19 ± 0.08	0.14 ± 0.09	0.18 ± 0.17	0.16 ± 0.12	0.16 ± 0.10
Chlorophyll *a* (µg L^{-1})	4.20 ± 6.39	3.62 ± 5.27	0.76 ± 0.21	2.23 ± 2.99	2.84 ± 4.90	2.95 ± 4.89	2.03 ± 3.74	0.96 ± 0.94
Particulate N (µg L^{-1})	16.7 ± 7.4	19.7 ± 9.4	16.5 ± 4.3	20.4 ± 7.9	20.4 ± 10.5	20.7 ± 8.0	16.0 ± 6.0	17.8 ± 9.4
Particulate organic C (µg L^{-1})	79.0 ± 36.4	90.7 ± 37.9	80.3 ± 22.1	126.1 ± 77.8	92.5 ± 48.7	112.0 ± 49.8	87.5 ± 25.2	89.7 ± 42.6
Dissolved O$_2$ (mg L^{-1})	6.53 ± 0.37	6.45 ± 0.30	6.36 ± 0.02	6.41 ± 0.23	6.25 ± 0.16	6.64 ± 0.73	6.56 ± 0.01	6.52 ± 0.03
Biological O$_2$ demand (mg O$_2$ L^{-1} h^{-1})	0.016 ± 0.008	0.019 ± 0.011	0.023 ± 0.004	0.029 ± 0.009	0.018 ± 0.012	0.036 ± 0.038	0.018 ± 0.004	0.022 ± 0.007
pH	8.13 ± 0.06	8.12 ± 0.06	8.14 ± 0.01	8.13 ± 0.00	8.23 ± 0.08	8.21 ± 0.08	8.10 ± 0.02	8.11 ± 0.02
Water clarity (Secchi depth in m)	8.0 ± 3.0	8.5 ± 2.4	10.5 ± 1.4	11.5 ± 0.7	9.3 ± 2.9	9.9 ± 4.0	10.6 ± 3.2	11.7 ± 3.0

Table S6. Meteorological data on wind velocity and daily precipitation. Data was provided by the meteorological station COMARTA, Universidad Jorge Tadeo Lozano, Santa Marta, Colombia. Mean ± SD, maximum (Max) and minimal (Min) seasonal values are displayed.

	Wind velocity (m sec^{-1})			Daily precipitation (mm d^{-1})		
Seasons	Mean	Max	Min	Mean	Max	Min
Major upwelling	1.88 ± 0.97	4.08	0.07	0.35 ± 2.49	34.04	0.00
Minor upwelling	0.54 ± 0.51	2.88	0.00	0.68 ± 2.24	16.26	0.00
Major non-upwelling	0.40 ± 0.36	2.50	0.00	3.21 ± 7.67	55.36	0.00
Minor non-upwelling	0.53 ± 0.54	3.08	0.00	2.61 ± 8.95	62.47	0.00

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Spatiotemporal Variability of Sedimentary Organic Matter Supply and Recycling Processes in Coral Reefs of Tayrona National Natural Park, Colombian Caribbean

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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.

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; 2005b; 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; Chapter 1) 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; Chapter 2, 4). 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 to the Eastern, sheltered flanks (Werding and Sánchez 1989; Bayraktarov et al. 2013; Chapter 1). 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.

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).

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

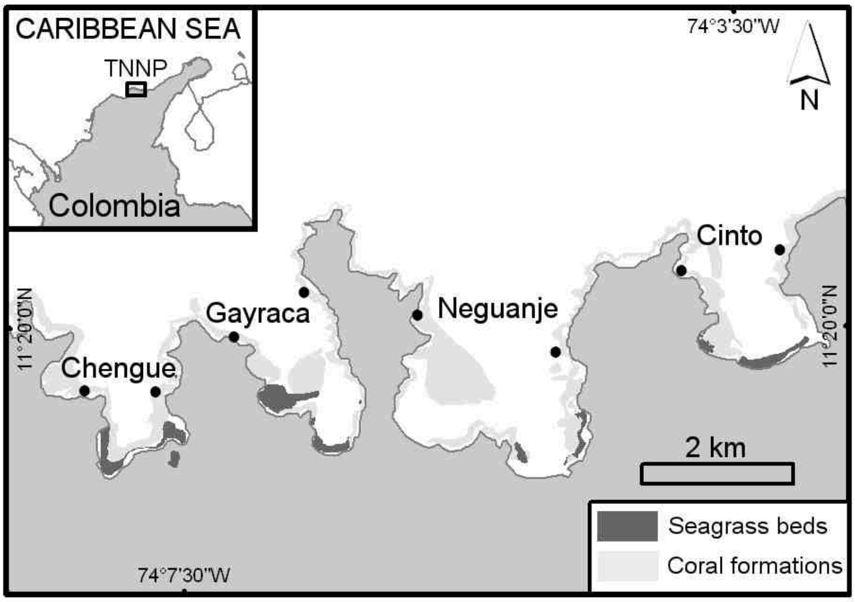

Figure 1. Bays of Tayrona National Natural Park (TNNP). Displayed are Chengue, Gayraca, Neguanje and Cinto and the sampling locations at the Western (water current-exposed sites) and the Eastern (water current-sheltered sites) flanks of each bay. Source: Invemar (2012).

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 dryed 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).

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 x 15 x 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 < 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 % acetone. 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 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).

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 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).

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 parameters 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 differences 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 (Table 2; Table 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 subtracting 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.

Results

Temporal variations for all data on organic matter supply to sediments and sedimentary parameters of all bays are provided as supplementary material (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 supplementary material (Table S1 – S4).

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 (Fig. 2 and Fig. 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).

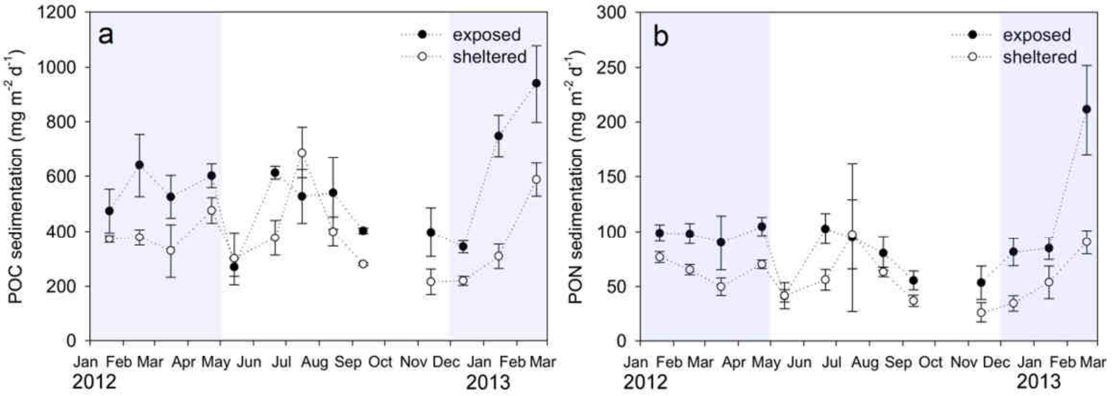

Figure 2. Sedimentary supply of particulate organic matter (POM) to the seafloor. (a) Sedimentary particulate organic carbon (POC) supply; (b) sedimentary particulate organic nitrogen (PON) supply to the seafloor at an exposed and sheltered site in one exemplary bay in Tayrona National Natural Park (TNNP; Gayraca). Major upwelling (December – April) is highlighted in blue.

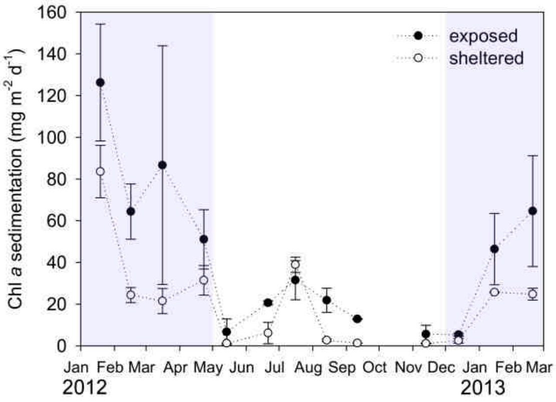

Figure 3. Sedimentary supply of chlorophyll (Chl) *a* to the seafloor at an exposed and sheltered site in one exemplary bay in Tayrona National Natural Park (TNNP; Gayraca). Major upwelling (December – April) is highlighted in blue.

Temporal differences. Significantly higher rates of POC and PON sedimentation (Table 1) were measured during major upwelling with 502.5 ± 201.3 mg POC m^{-2} d^{-1} (mean ± SD) and 86.0 ± 42.6 mg PON m^{-2} d^{-1} compared to major non-upwelling with 320.4 ± 98.4 mg POC and 42.0 ± 15.1 mg PON m^{-2} d^{-1}, respectively. Rates were also high during minor upwelling with 523.1 ± 129.6 mg POC m^{-2} d^{-1} and 82.8 ± 36.8 mg PON m^{-2} d^{-1} as compared to minor non-upwelling with 369.0 ± 138.1 mg POC and 56.7 ± 25.1 mg PON m^{-2} d^{-1}, respectively. Chl *a* supplied to the sediment was generally higher during major (47.2 ± 37.8 mg chl *a* m^{-2} d^{-1}; mean ± SD) and minor (22.4 ± 15.6 mg chl *a* m^{-2} d^{-1}) upwelling as compared to major and minor non-upwelling (4.9 ± 5.1 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 (Fig. 2 and Fig. 3). Annual mean rates of organic matter supplied to the sediments interpolated over 14 months of monitoring were 200 g POC m^{-2} y^{-1}, 34 g PON m^{-2} y^{-1}, and 16 g chl *a* m^{-2} y^{-1} at the exposed, and 136 g POC m^{-2} y^{-1}, 21 g PON m^{-2} y^{-1}, and 7 g chl *a* m^{-2} y^{-1} at the sheltered site, respectively.

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 ± 0.06 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 ± 3.51 µg chl *a* g (dry mass)$^{-1}$, 0.86 ± 0.45 µg chl c_1+c_2 g (dry mass)$^{-1}$ and 2.22 ± 1.23 µg carotenoids g (dry mass)$^{-1}$) than at the exposed sites (4.91 ± 2.49, 0.58 ± 0.31 and 1.49 ± 0.83 µg g^{-1}, respectively). For concentrations of chl *b*, significantly higher concentrations were measured at the exposed (0.36 ± 0.25 µg chl *b* g (dry mass)$^{-1}$) than at the sheltered (0.25 ± 0.16 µg g^{-1}) sites.

Table 1. Seasonal means of sedimentary parameters and univariate analyses. Significant PERMANOVA results are indicated by asterisks with * for significant ($p < 0.05$) and ** for very significant ($p < 0.01$). Not significant values are displayed in gray. 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 ($CaCO_3$).

	Major upwelling		Minor upwelling		Major non-upwelling		Minor non-upwelling		Seasons		Bays		Exposure	
Variables/Sites	exp	she	exp	she	exp	she	exp	she	Pseudo-*F*	(*p*)	Pseudo-*F*	(*p*)	Pseudo-*F*	(*p*)
POC sedimentation (mg POC m^{-2} d^{-1})	623 ± 193	382 ± 124	532 ± 95	514 ± 169	399 ± 63	242 ± 48	406 ± 190	338 ± 83	17.410	0.029*	-	-	8.916	0.046*
PON sedimentation (mg PON m^{-2} d^{-1})	110 ± 47	63 ± 19	89 ± 49	77 ± 25	54 ± 12	32 ± 9	66 ± 34	49 ± 12	12.589	0.046*	-	-	6.661	0.099
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	7.853	0.057	-	-	2.558	0.193
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	0.847	0.428	-	-	0.003	0.945
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	6.892	0.159	-	-	1.593	0.292
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	9.688	0.087	-	-	17.154	0.029*
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	3.628	0.040*	2.662	0.086	4.625	0.041*
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	1.987	0.148	4.041	0.027*	0.034	0.845
Sedimentary Chl *a* (µg 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	1.144	0.338	0.659	0.592	3.782	0.049*
Sedimentary Chl *b* (µg 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	2.635	0.081	16.853	0.001**	13.132	0.002**
Sedimentary Chl c_1+c_2 (µg 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	5.566	0.003**	2.307	0.114	9.158	0.009**
Sedimentary Carotenoids (µg 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	3.189	0.043*	0.562	0.663	8.723	0.008**
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	1.653	0.179	1.986	0.138	16.676	0.001**
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	0.104	0.941	11.122	0.002**	4.537	0.047*
Porosity (% wt/wt)	37.5 ± 9.7	43.9 ± 5.3	-	-	35.4 ± 10.4	46.5 ± 4.0	-	-	0.003	0.956	0.666	0.603	4.404	0.052
Grain-size (µm)	1006 ± 352	606 ± 142			940 ± 407	590 ± 105			0.080	0.756	1.335	0.315	6.715	0.040*

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).

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 * for significant ($p < 0.05$) and ** for very significant ($p < 0.01$). Not significant correlations are displayed in gray. 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 ($CaCO_3$).

	Correlations with distance to Santa Marta									
Seasons	Chl *a*	Chl *b*	Chl *c*	Carotenoids	POC	PON	SOD	$CaCO_3$	Porosity	Grain-size
Major upwelling	**0.76***	-0.44	**0.87****	**0.87****	0.66	0.11	**0.76***	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****	0.55	0.11	0.44	0.44	0.55	-0.44

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 ± 0.63 mg POC g^{-1}; mean ± SD) and lowest during minor non-upwelling (2.02 ± 0.35 mg POC g^{-1}). Similar POC contents were measured during major (2.23 ± 0.54 mg POC g^{-1}) and minor (2.31 ± 0.56 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 ± 0.08 mg PON g^{-1} (mean ± SD) during major upwelling and 0.37 ± 0.09 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 ± 0.29 μg chl c_1+c_2 g^{-1} (mean ± 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 ± 0.70 µg g^{-1}, respectively. Sedimentary contents of chl c_1+c_2 and carotenoids were similar during major (0.74 ± 0.47 µg chl c_1+c_2 g^{-1} and 1.83 ± 1.34 µg carotenoids g^{-1}) and minor (0.68 ± 0.29 and 1.80 ± 0.72 µg 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 ± 3.99 µg chl *a* g^{-1}) upwelling and non-upwelling (5.59 ± 1.72 µg chl *a* g^{-1}) than compared to minor (4.90 ± 1.83 µg chl *a* g^{-1}) upwelling and non-upwelling (4.92 ± 1.56 µg 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).

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 * for significant ($p < 0.05$) and ** for very significant ($p < 0.01$). Not significant correlations are displayed in gray. 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****	**0.83****	-0.16	0.11	**0.39***	0.05	0.09	-0.34
Chl *b*			-0.14	-0.14	**0.36***	-0.06	-0.05	0.31	-0.12	0.21
Chl *c*				**0.80****	-0.03	0.31	**0.40***	0.33	**0.40***	**-0.51****
Carotenoids					0.12	**0.40***	**0.62****	0.29	0.22	**-0.41***
PON						**0.80****	0.21	**0.36***	-0.03	0.11
POC							**0.42***	0.32	0.20	-0.16
SOD								0.31	0.31	**-0.37***
$CaCO_3$									**0.69****	**-0.61****
Porosity										**-0.90****

Sedimentary O_2 demand and POC turnover

Spatial differences. Sedimentary O_2 uptake was significantly higher (Table 1) at the sheltered (18.2 ± 5.9 mmol O_2 m^{-2} d^{-1}; mean ± SD) than at the exposed (12.3 ± 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 ± 2.1 % of supplied POC h^{-1}; ± SD) than at the sheltered site (1.6 ± 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 ± 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.

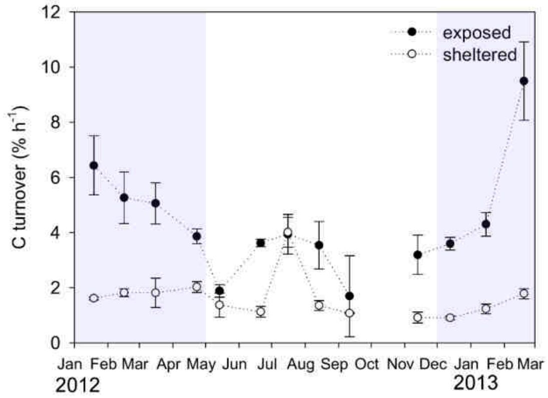

Figure 4. Rates of C turnover at an exposed and sheltered site in Gayraca Bay. Major upwelling (December – April) is highlighted in blue.

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).

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 Cinto) are shown for the parameters sedimentary chlorophyll *a*, *b*, c_1+c_2, carotenoids, particulate organic carbon, particulate organic nitrogen, sediment oxygen demand and carbonate content. Significant PERMANOVA results are indicated by asterisks with * for significant ($p< 0.05$) and ** for very significant ($p< 0.01$). Not significant values are displayed in gray.

Factors	DF	Pseudo-*F*	(*p*)
Seasons (fixed)	3	1.835	0.059
Bays (random)	1	**3.651**	**0.001****
Exposure (fixed)	3	**8.299**	**0.001****
Exposure *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***
Multiple comparisons between bays		*t*	(*p*)
Chengue - Gayraca		1.474	0.154
Chengue - Neguanje		**2.665**	**0.007****
Chengue - Cinto		**2.441**	**0.006****
Gayraca - Neguanje		1.614	0.102
Gayraca - Cinto		1.478	0.102
Neguanje - Cinto		**1.841**	**0.043***

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.

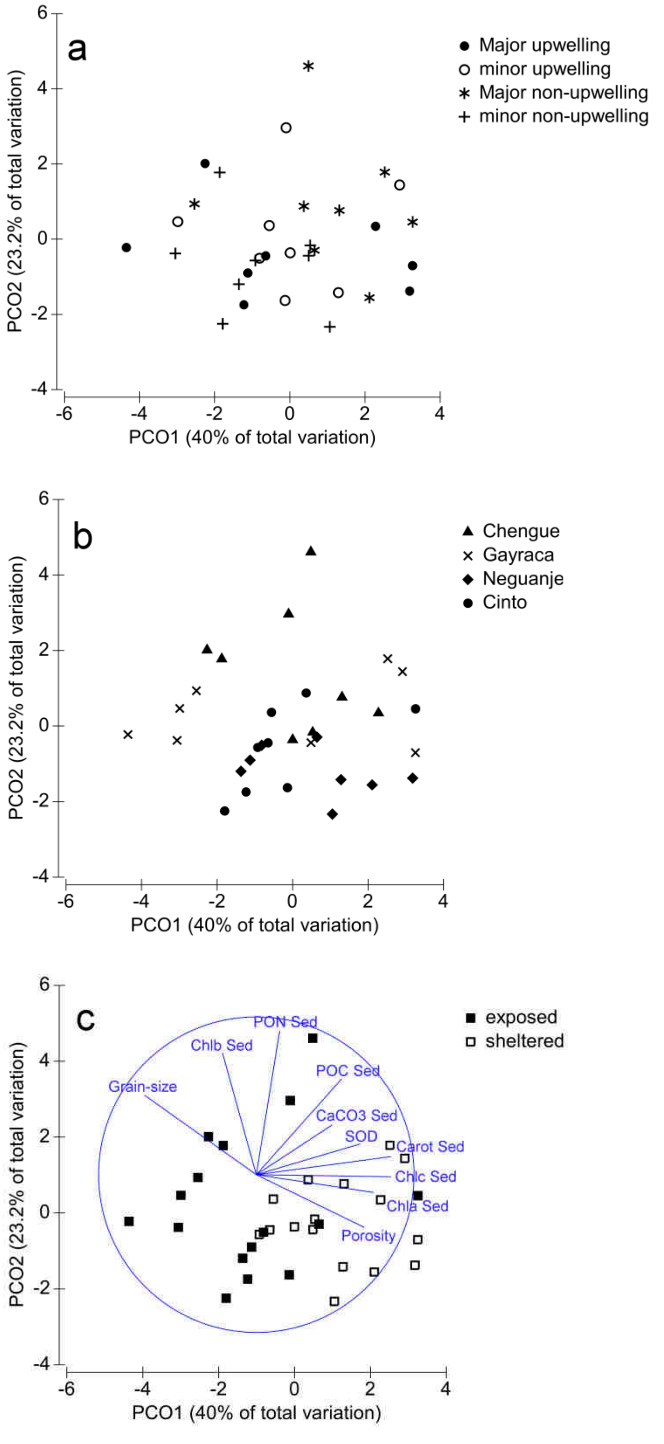

Figure 5. Graphical representation of multivariate analyses results by Principle Coordinates Ordination (PCO). PCO of environmental sedimentary parameters was grouped by seasons (a), bays (b), and exposure to wave and water-currents of the sampling locations (c). Effects and directions of environmental 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*), carotenoids (carot), and sediment oxygen demand (SOD).

Discussion

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 µg 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; Chapter 2) but also via discharge of several smaller river mouths in the East of TNNP (Chapter 2).

The supply with organic carbon to the seafloor can range from 50 g C m^{-2} y^{-1} in oceanic areas, but may reach 200 – 600 g C m^{-2} y^{-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 g C m^{-2} y^{-1}; Taguchi 1982) and Tuamotu atoll lagoon, French Polynesia (128 g C m^{-2} y^{-1}; Charpy and Charpy-Roubaud 1991), higher than rates registered in Davies Reef, Great Barrier Reef, Australia (33 – 51 g C m^{-2} y^{-1}; Hansen et al. 1992), but below rates measured in South-West lagoon in New Caledonia (276 g C m^{-2} y^{-1}; Clavier et al. 1995) or One Tree Island, Great Barrier Reef, Australia (548 g C m^{-2} y^{-1}; Koop and Larkum 1987). According to the amount of POC supplied to the sediments, the TNNP can be classified as mesotrophic (100 – 300 g C m^{-2} y^{-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.

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 pigments chl c_1+c_2 indicate 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 mg g^{-1}; Rasheed et al. 2003). Accumulated organic carbon was below values reported for carbonate coral reefs (e.g. 3.6 mg g^{-1} for the Gulf of Aqaba, Red Sea; Rasheed et al. 2003 or 3.4 – 4.7 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 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 μg chl *a* 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 μg chl *a* g^{-1} during non-upwelling and 6.1 μg chl *a* g^{-1} during upwelling), they can be characterized as meso-oligotrophic.

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 mmol $m^{-2}d^{-1}$ at sheltered sites compared to 2.1 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 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 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 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 % of supplied POC h^{-1} were detected during the upwelling months January – March and peaked with 9.5 % of supplied POC h^{-1} during February, while rates at the sheltered site were < 2 % of supplied POC h^{-1} with maximum of 4.0 % of supplied 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 POC h^{-1} (exposed) and 1.6 % 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 % POC h^{-1}; Wild et al. 2005b). Turnover rates of POC in sediments at the exposed site were in the range of carbonate 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 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; 2005b; 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 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 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. 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; Rusch et al. 2006; Wild et al. 2008). At the sheltered site, the finer sediments are not facilitating advective porewater exchange and matter to that extent, so that organic matter is comparably less recycled and rather accumulates (Huettel et al. 2003). In addition to sediment properties, sediments 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.

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 sedimentation 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 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 disappeared during upwelling (Chapter 2). Significantly increased chl *a* concentrations with a mean value of 2.70 $\mu g\ L^{-1}$ were observed during upwelling in TNNP seawater (Chapter 2) 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.

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 enrichment during this season (Salzwedel and Müller 1983; Chapter 2). 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 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.

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Appendix 2

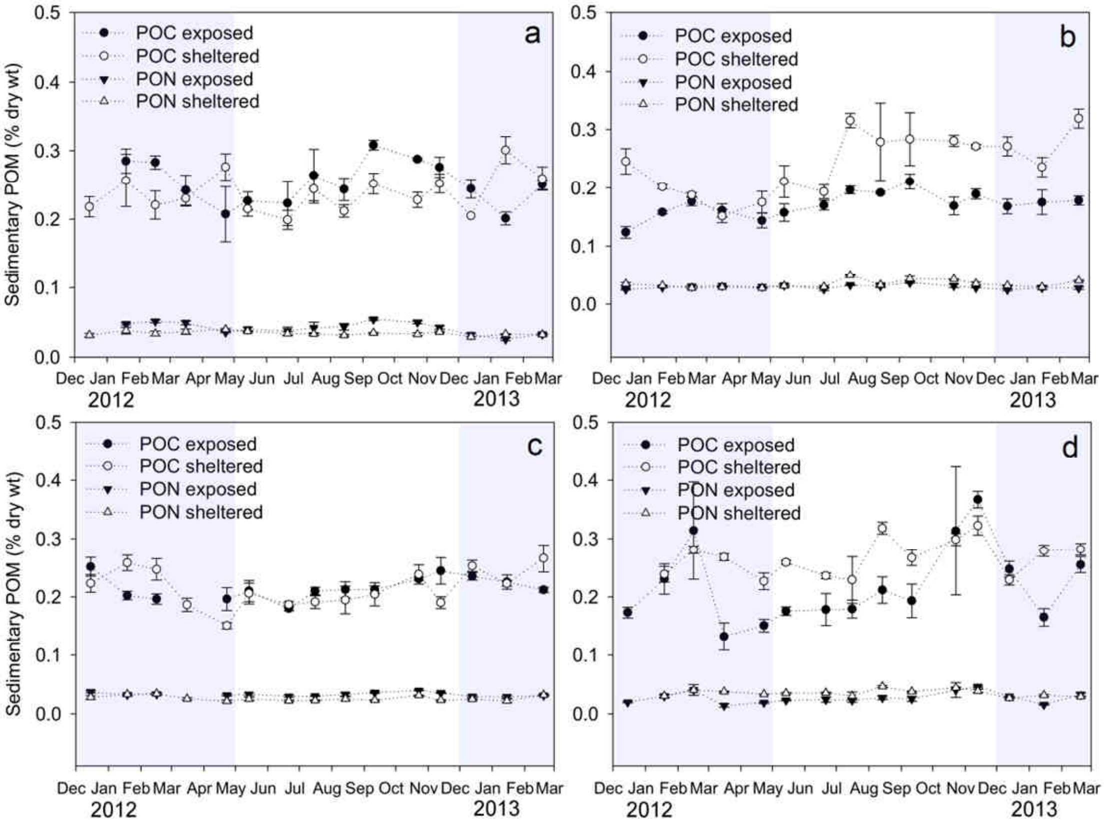

Figure S1: Sedimentary particulate organic matter (POM) in Tayrona National Natural Park. Displayed are contents of particulate organic carbon (POC) and nitrogen (PON) at an exposed and sheltered site in the bays (a) Chengue; (b) Gayraca; (c) Neguanje; and (d) Cinto. Major upwelling (December – April) is highlighted in blue.

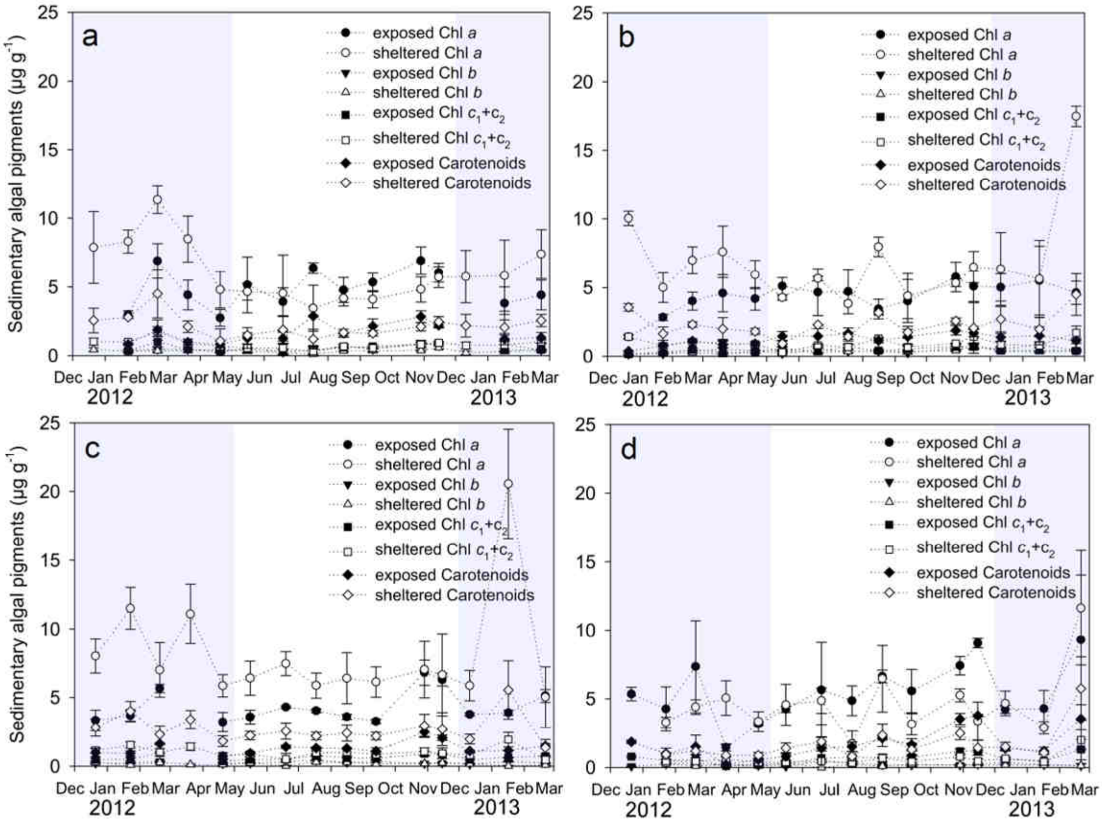

Figure S2. Sedimentary algal pigments in Tayrona National Natural Park. Displayed are contents of the algal pigments chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), chlorophyll c_1+c_2 (Chl c_1+c_2) and carotenoids at the exposed and sheltered sites of the bays (a) Chengue; (b) Gayraca; (c) Neguanje; and (d) Cinto. Major upwelling (December – April) is highlighted in blue.

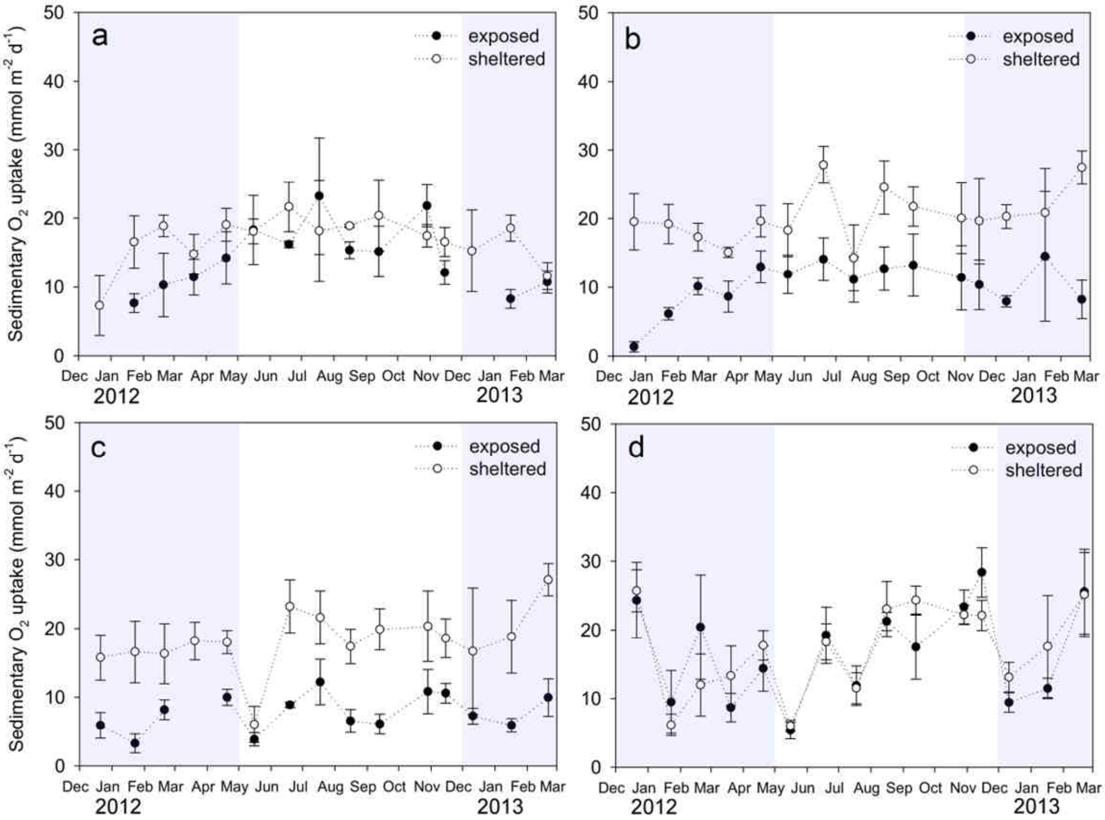

Figure S3. Sedimentary O_2 uptake in Tayrona National Natural Park. Displayed are sedimentary O_2 uptake rates at an exposed and sheltered site in the bays (a) Chengue; (b) Gayraca; (c) Neguanje; and (c) Cinto. Major upwelling (December – April) is highlighted in blue.

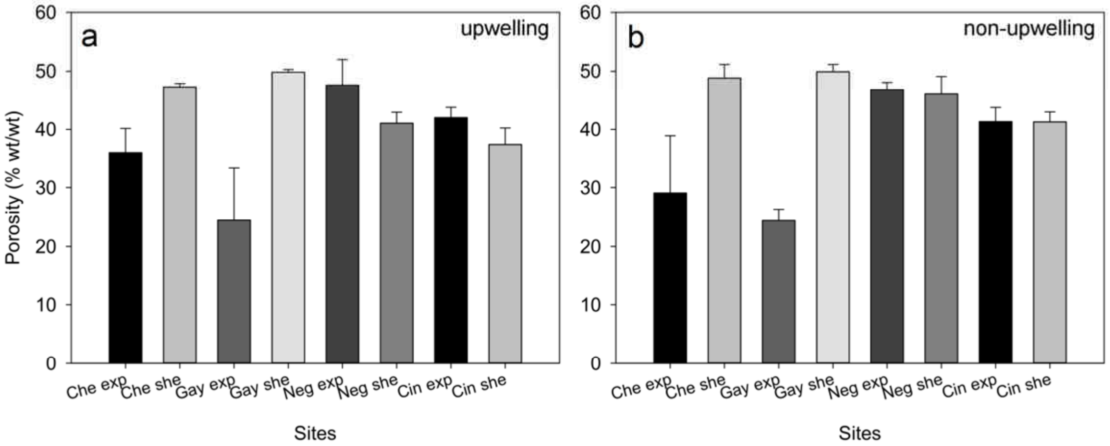

Figure S4. Porosity of Tayrona National Natural Park sediments. Displayed are porosities during (a) upwelling and (b) non-upwelling period. Abbreviations: Chengue exposed (Che exp), Chengue sheltered (Che she), Gayraca exposed (Gay exp), Gayraca sheltered (Gay she), Neguanje exposed (Neg exp), Neguanje sheltered (Neg she), Cinto exposed (Cin exp), Cinto sheltered (Cin she).

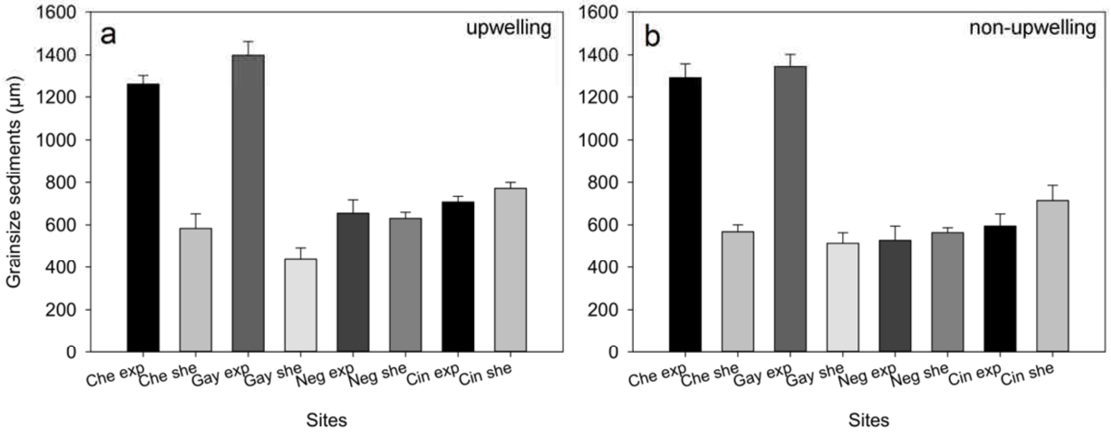

Figure S5. Grain-size of Tayrona National Natural Park sediments. Displayed are grain-sizes during (a) upwelling and (b) non-upwelling period. Abbreviations: Chengue exposed (Che exp), Chengue sheltered (Che she), Gayraca exposed (Gay exp), Gayraca sheltered (Gay she), Neguanje exposed (Neg exp), Neguanje sheltered (Neg she), Cinto exposed (Cin exp), Cinto sheltered (Cin she).

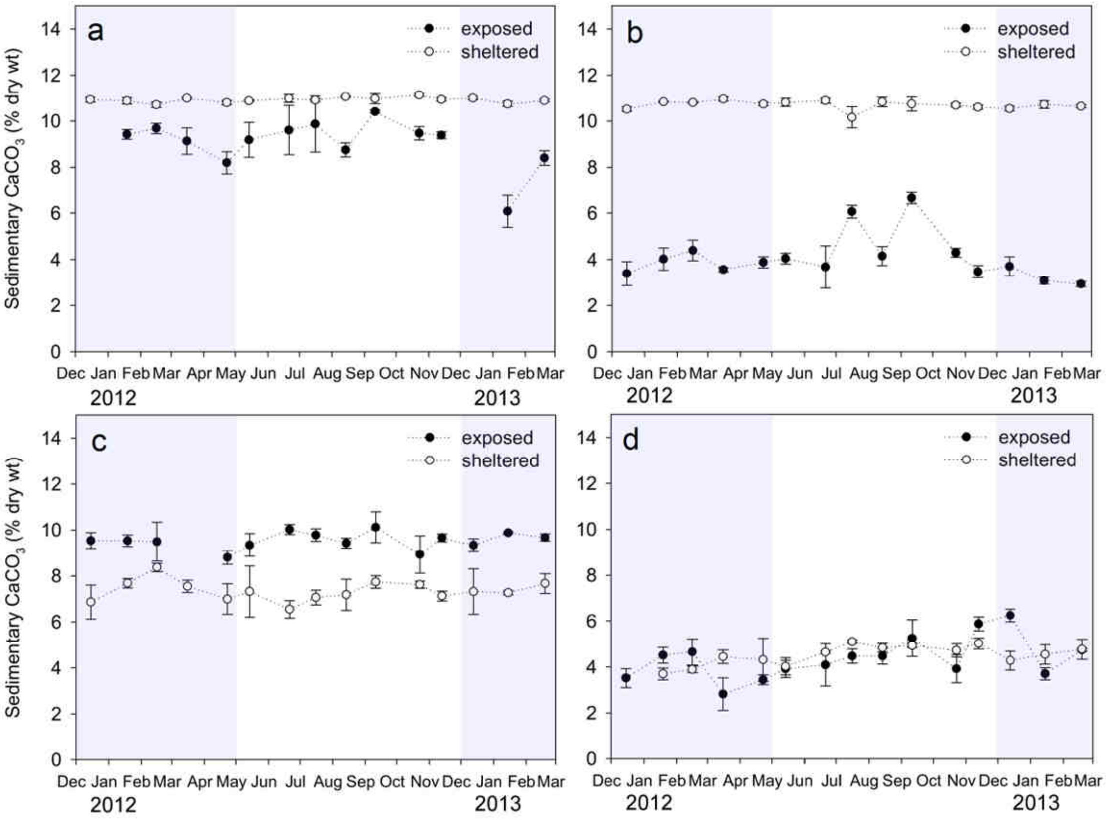

Figure S6. Carbonate content of marine sediments in Tayrona National Natural Park. Displayed are sedimentary carbonate (CaCO$_3$) contents at exposed and sheltered sites in the bays (a) Chengue; (b) Gayraca; (c) Neguanje; and (d) Cinto. Major upwelling (December – April) is highlighted in blue.

Table S1. Mean sediment parameters (± SD) at the exposed (at 12 m water depth) and sheltered (at 11 m water depth) sites in Chengue Bay for the major upwelling (December – April), minor upwelling (July - August), major non-upwelling (September - November) and minor non-upwelling (May - June) periods. Abbreviations: particulate organic nitrogen (PON), particulate organic carbon (POC), chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), chlorophyll c_1+c_2 (Chl *c*), and sedimentary carbonate content ($CaCO_3$).

Sediments Chengue	Major upwelling		Minor upwelling		Major non-upwelling		Minor non-upwelling	
	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site
Sedimentary PON (mg PON g^{-1})	0.40 ± 0.10	0.35 ± 0.05	0.43 ± 0.10	0.32 ± 0.03	0.49 ± 0.06	0.35 ± 0.03	0.39 ± 0.07	0.36 ± 0.04
Sedimentary POC (mg POC g^{-1})	2.45 ± 0.45	2.49 ± 0.41	2.54 ± 0.47	2.28 ± 0.31	2.91 ± 0.20	2.44 ± 0.24	2.25 ± 0.39	2.07 ± 0.21
Sedimentary Chl *a* (µg chl *a* g^{-1})	4.05 ± 1.49	7.26 ± 2.43	5.58 ± 1.08	3.81 ± 1.18	6.10 ± 0.97	4.88 ± 0.97	4.53 ± 1.58	4.60 ± 1.81
Sedimentary Chl *b* (µg chl *b* g^{-1})	0.48 ± 0.31	0.36 ± 0.12	0.54 ± 0.29	0.23 ± 0.13	0.69 ± 0.24	0.45 ± 0.14	0.39 ± 0.28	0.27 ± 0.14
Sedimentary Chl *c* (µg chl *c* g^{-1})	0.44 ± 0.21	0.93 ± 0.29	0.48 ± 0.24	0.50 ± 0.28	0.82 ± 0.18	0.77 ± 0.19	0.41 ± 0.26	0.55 ± 0.33
Sedimentary Carotenoids (µg carotenoid g^{-1})	1.08 ± 0.33	2.28 ± 0.86	2.25 ± 0.71	1.44 ± 0.54	2.39 ± 0.49	2.06 ± 0.45	1.27 ± 0.55	1.68 ± 0.66
Sedimentary O_2 uptake (mmol O_2 m^{-2} d^{-1})	10.4 ± 3.4	15.2 ± 4.9	19.9 ± 7.4	18.5 ± 5.2	16.4 ± 5.0	18.1 ± 3.5	17.4 ± 3.4	19.9 ± 3.2
Porosity (% wt/wt)	36.1 ± 4.1	47.3 ± 0.6	-	-	29.1 ± 9.9	48.8 ± 2.3	-	-
Grain-size (µm)	1263.1 ± 40.5	583.1 ± 69.0	-	-	1293.3 ± 64.5	567.9 ± 32.3	-	-
Sedimentary $CaCO_3$ (% dry wt)	8.5 ± 1.3	10.9 ± 0.1	9.3 ± 1.0	11.0 ± 0.1	9.8 ± 0.5	11.0 ± 0.2	9.4 ± 0.9	10.9 ± 0.1

Table S2. Mean sediment parameters (± SD) at the exposed and sheltered sites and a water depth of 10 m in Gayraca Bay for the major upwelling (December – April), minor upwelling (July - August), major non-upwelling (September - November) and minor non-upwelling (May - June) periods. Abbreviations: particulate organic nitrogen (PON), particulate organic carbon (POC), chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), chlorophyll c_1+c_2 (Chl *c*), and sedimentary carbonate content ($CaCO_3$).

Sediments Gayraca	Major upwelling		Minor upwelling		Major non-upwelling		Minor non-upwelling	
	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site
PON sedimentation (mg PON m^{-2} d^{-1})	110.3 ± 47.4	62.9 ± 18.8	88.7 ± 48.6	76.8 ± 24.7	54.2 ± 11.5	31.8 ± 8.9	65.9 ± 34.4	49.0 ± 12.2
POC sedimentation (mg POC m^{-2} d^{-1})	623.2 ± 192.5	381.9 ± 124.4	532.0 ± 95.2	514.3 ± 168.9	399.3 ± 62.8	241.5 ± 47.5	406.1 ± 189.5	338.2 ± 83.1
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 organic matter	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 (% 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 PON (mg PON g^{-1})	0.28 ± 0.04	0.31 ± 0.04	0.32 ± 0.03	0.41 ± 0.10	0.32 ± 0.05	0.40 ± 0.06	0.29 ± 0.05	0.30 ± 0.04
Sedimentary POC (mg POC g^{-1})	1.61 ± 0.25	2.23 ± 0.57	1.94 ± 0.08	2.97 ± 0.76	1.89 ± 0.25	2.79 ± 0.40	1.64 ± 0.20	2.02 ± 0.34
Sedimentary Chl *a* (µg chl *a* g^{-1})	4.02 ± 1.59	7.72 ± 3.63	4.08 ± 1.31	5.90 ± 2.36	4.96 ± 1.34	5.41 ± 1.36	4.88 ± 1.18	4.83 ± 0.78
Sedimentary Chl *b* (µg chl *b* g^{-1})	0.43 ± 0.28	0.26 ± 0.12	0.36 ± 0.07	0.37 ± 0.07	0.54 ± 0.27	0.50 ± 0.20	0.34 ± 0.21	0.36 ± 0.11
Sedimentary Chl *c* (µg chl *c* g^{-1})	0.35 ± 0.12	1.05 ± 0.38	0.55 ± 0.19	0.98 ± 0.37	0.65 ± 0.16	1.01 ± 0.43	0.48 ± 0.20	0.50 ± 0.29
Sedimentary Carotenoids (µg carotenoids g^{-1})	1.01 ± 0.42	2.56 ± 1.15	1.40 ± 0.39	2.30 ± 0.97	1.68 ± 0.40	2.13 ± 1.02	1.46± 0.41	1.47 ± 0.77
Sedimentary O_2 uptake (mmol O_2 m^{-2} d^{-1})	8.8 ± 5.1	19.9 ± 4.4	11.9 ± 3.1	19.4 ± 6.8	11.7 ± 4.1	21.3 ± 5.1	13.0 ± 3.0	23.1 ± 5.9
Porosity (% wt/wt)	24.5 ± 9.0	49.8 ± 0.5	-	-	24.4 ± 1.8	49.9 ± 1.2	-	-
Grain-size (µm)	1398.0 ± 64.4	440.1 ± 52.4	-	-	1345.5 ± 56.3	514.0 ± 49.6	-	-
Sedimentary $CaCO_3$ (% dry wt)	3.6 ± 0.6	10.7 ± 0.2	5.1 ± 1.1	10.5 ± 0.5	4.6 ± 1.4	10.7 ± 0.2	3.9 ± 0.6	10.9 ± 0.1

Table S3. Mean sediment parameters (± SD) at the exposed (at 14.5 m water depth) and sheltered (at 10 m water depth) sites in Neguanje Bay for the major upwelling (December – April), minor upwelling (July - August), major non-upwelling (September - November) and minor non-upwelling (May - June) periods. Abbreviations: particulate organic nitrogen (PON), particulate organic carbon (POC), chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), chlorophyll c_1+c_2 (Chl *c*), and sedimentary carbonate content ($CaCO_3$).

Sediments Neguanje	Major upwelling		Minor upwelling		Major non-upwelling		Minor non-upwelling	
	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site
Sedimentary PON (mg PON g^{-1})	0.32 ± 0.03	0.28 ± 0.06	0.31 ± 0.03	0.24 ± 0.04	0.37 ± 0.03	0.26 ± 0.04	0.31 ± 0.03	0.24 ± 0.04
Sedimentary POC (mg POC g^{-1})	2.17 ± 0.26	2.26 ± 0.43	2.11 ± 0.17	1.93 ± 0.28	2.29 ± 0.25	2.11 ± 0.32	1.95 ± 0.26	1.97 ± 0.23
Sedimentary Chl *a* (µg chl *a* g^{-1})	4.02 ± 0.92	8.98 ± 4.61	3.82 ± 0.29	6.14 ± 1.34	5.46 ± 1.74	6.61 ± 1.94	3.94 ± 0.51	6.94 ± 1.12
Sedimentary Chl *b* (µg chl *b* g^{-1})	0.24 ± 0.09	0.13 ± 0.09	0.35 ± 0.10	0.28 ± 0.05	0.25 ± 0.09	0.19 ± 0.07	0.26 ± 0.07	0.13 ± 0.13
Sedimentary Chl *c* (µg chl *c* g^{-1})	0.57 ± 0.19	1.14 ± 0.52	0.68 ± 0.08	0.99 ± 0.20	0.78 ± 0.19	0.96 ± 0.26	0.49 ± 0.03	0.68 ± 0.36
Sedimentary Carotenoids (µg carotenoid g^{-1})	1.12 ± 0.32	2.92 ± 1.55	1.30 ± 0.05	2.30 ± 0.43	1.88 ± 0.66	2.61 ± 0.82	1.17 ± 0.27	2.39 ± 0.46
Sedimentary O_2 uptake (mmol O_2 m^{-2} d^{-1})	7.2 ± 2.7	18.4 ± 5.4	9.4 ± 3.9	19.5 ± 3.8	9.2 ± 3.0	19.6 ± 3.5	6.4 ± 2.8	14.6 ± 9.7
Porosity (% wt/wt)	47.6 ± 4.4	41.1 ± 1.9	-	-	46.8 ± 1.3	46.0 ± 3.1	-	-
Grain-size (µm)	654.6 ± 63.0	630.2 ± 28.8	-	-	527.6 ± 67.0	563.7 ± 23.2	-	-
Sedimentary $CaCO_3$ (% dry wt)	9.5 ± 0.5	7.5 ± 0.6	9.6 ± 0.3	7.1 ± 0.5	9.6 ± 0.7	7.5 ± 0.3	9.7 ± 0.5	6.9 ± 0.9

Table S4. Mean sediment parameters (± SD) at the exposed and sheltered sites and a water depth of 10 m in Cinto Bay for the major upwelling (December – April), minor upwelling (July - August), major non-upwelling (September - November) and minor non-upwelling (May - June) periods. Abbreviations: particulate organic nitrogen (PON), particulate organic carbon (POC), chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), chlorophyll c_1+c_2 (Chl *c*), and sedimentary carbonate content ($CaCO_3$).

Sediments Cinto	Major upwelling		Minor upwelling		Major non-upwelling		Minor non-upwelling	
	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site	exposed site	sheltered site
Sedimentary PON (mg PON g^{-1})	0.25 ± 0.10	0.33 ± 0.05	0.25 ± 0.05	0.38 ± 0.12	0.37 ± 0.15	0.40 ± 0.04	0.24 ± 0.05	0.35 ± 0.02
Sedimentary POC (mg POC g^{-1})	2.09 ± 0.77	2.58 ± 0.28	1.96 ± 0.35	2.74 ± 0.66	2.91 ± 1.25	2.96 ± 0.32	1.77 ± 0.31	2.47 ± 0.14
Sedimentary Chl *a* (µg chl *a* g^{-1})	4.74 ± 2.69	4.71 ± 2.74	5.75 ± 1.22	4.09 ± 3.07	7.35 ± 1.75	3.93 ± 1.30	4.95 ± 2.32	4.71 ± 1.12
Sedimentary Chl *b* (µg chl *b* g^{-1})	0.21 ± 0.15	0.17 ± 0.09	0.26 ± 0.08	0.16 ± 0.09	0.20 ± 0.06	0.18 ± 0.08	0.27 ± 0.52	0.16 ± 0.22
Sedimentary Chl *c* (µg chl *c* g^{-1})	0.52 ± 0.28	0.61 ± 0.37	0.72 ± 0.09	0.51 ± 0.27	1.04 ± 0.26	0.56 ± 0.22	0.46 ± 0.68	0.42 ± 0.10
Sedimentary Carotenoids (µg carotenoid g^{-1})	1.22 ± 0.73	1.43 ± 1.16	1.82 ± 0.41	1.58 ± 1.01	2.99 ± 1.06	1.74 ± 0.71	1.10 ± 1.15	1.64 ± 0.42
Sedimentary O_2 uptake (mmol O_2 m^{-2} d^{-1})	15.5 ± 7.7	16.1 ± 7.3	16.6 ± 5.4	17.3 ± 6.9	23.1 ± 5.7	22.9 ± 2.0	12.3 ± 7.9	12.1 ± 6.8
Porosity (% wt/wt)	42.0 ± 1.8	37.4 ± 2.8	-	-	41.3 ± 2.4	41.3± 1.7	-	-
Grain-size (µm)	707.0 ± 26.9	770.9 ± 28.4	-	-	594.6 ± 56.9	713.7 ± 71.7	-	-
Sedimentary $CaCO_3$ (% dry wt)	4.2 ± 1.1	4.3 ± 0.5	4.5 ± 0.3	5.0 ± 0.2	5.0 ± 1.0	4.9 ± 0.2	4.0 ± 0.6	4.3 ± 0.4

4

Spatial and Temporal Variability of Benthic Primary Production in Upwelling-Influenced Colombian Caribbean Coral Reefs

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Abstract

In Tayrona National Natural Park, Colombian Caribbean, abiotic factors controlling coral reef primary production, namely light intensity, water temperature, and nutrient availability, are subject to high temporal variability due to seasonal coastal upwelling. This offers the opportunity to assess the effects of abiotic factors on the key coral reef ecosystem service productivity. We therefore quantified primary net (*Pn*) and gross production (*Pg*) of the dominant local primary producers (scleractinian corals, macroalgae, algal turfs, crustose coralline algae, and microphytobenthos) at a current/wave-exposed (EXP) and -sheltered (SHE) site in an exemplary bay in Tayrona National Natural Park. A series of short-term incubations was conducted to quantify O_2 fluxes of the different primary producers before and at the end of the upwelling event 2011/2012. On the organism level, scleractinian corals showed highest individual productivity before upwelling, and corals and algal turfs at the end of upwelling. On the ecosystem level, corals contributed most to total *Pn* (EXP: 84 %; SHE: 86 %) and *Pg* (EXP: 78 %; SHE: 55 %) before the upwelling, while at the end of the upwelling, corals contributed most to *Pn* and *Pg* at EXP (64 and 75 %, respectively) and macroalgae at SHE (65 and 46 %, respectively). Despite the significant spatial and temporal differences in individual productivity of investigated groups and their different contribution to reef productivity, no spatial or temporal differences in ecosystem *Pn* and *Pg* were detected. Our findings therefore indicate that local autotrophic benthic reef communities are well adapted to pronounced fluctuations of environmental key parameters. This may therefore hint to local resilience patterns against climate change consequences and anthropogenic disturbances.

Introduction

The majority of all ecosystems depend on primary production. Photoautotrophs convert light energy into chemical energy by photosynthesis, creating the energetic base of most food webs in terrestrial as well as aquatic environments. Among other coastal ecosystems such as mangrove forests, seagrass beds, salt marshes, and kelp forests, coral reefs belong to the most productive ecosystems in the world and therefore serve as a significant food source for over one billion people worldwide (UNEP 2004). Given the importance of coral reefs for mankind, productivity investigation started as early as the mid-20th century (Sargent and Austin 1949; Odum and Odum 1955), and today coral reefs are among the best understood marine benthic communities in terms of primary production (Kinsey 1985; Hatcher 1988; 1990; Gattuso et al. 1998). It was long assumed that coral reef productivity is relatively balanced due to the fact that tropical coral reefs typically thrive under relatively stable abiotic conditions (Hubbard 1996; Kleypas et al. 1999; Sheppard et al. 2009), including light (Darwin 1842; Achituv and Dubinsky 1990; Falkowski et al. 1990), water temperature (Dana 1843; Coles and Fadlallah 1991; Veron 1995), salinity (Andrews and Pickard 1990; Coles and Jokiel 1992), and nutrient availability (D'Elia and Wiebe 1990; Szmant 1997).

Nevertheless, coral-dominated benthic systems occur in some regions under highly unstable conditions that can affect benthic community structure and productivity. At high-latitudinal settings (e.g. the Arabian Sea, the Red Sea, Bahamas, Japan, Hawaii, Southern Australia, South Africa), coral reefs exhibit a wide range of seasonal fluctuations such as day length, irradiance, and water temperature (Crossland 1988). Other factors for temporal perturbation are wind-driven seasonal coastal upwelling events, leading to a replacement of surface water by deeper water (Mann and Lazier 2005). This generally causes changes in water temperatures, nutrient concentrations, and light availability, among others (Kämpf et al. 2004; Andrade and Barton 2005).

Coral reefs also occur in seasonal upwelling-affected waters such as the Arabian Sea off Oman (Glynn 1993), the Eastern Tropical Pacific off Panamá and Costa Rica (Glynn et al. 2001; Cortés and Jiménez 2003), and the Colombian Caribbean (Geyer 1969). Whereas several studies focused on the seasonality of benthic primary production in coral reefs (Adey and Steneck 1985; Kinsey 1985; Falter et al. 2012), no attempt has been made so far to assess temporal variability in primary production of seasonal upwelling-affected coral reefs.

The Tayrona National Natural Park (TNNP) at the Northern Caribbean coast of Colombia offers ideal conditions to investigate primary productivity of coral-dominated benthic communities affected by seasonal upwelling, because it is highly influenced by the Guajira Upwelling System (Andrade and Barton 2005), altering water temperature, light availability, and inorganic nutrient concentrations (Bayraktarov et al. 2012; Eidens et al. 2012; Chapter 2). The upwelling seasonally extends into the waters of TNNP (Andrade and Barton 2005), where rich and diversely structured coral communities are present (Werding and Sánchez 1989). Here, the abundance and community composition of benthic algae can exhibit high seasonality (Diaz-Pulido and Garzón-Ferreira 2002; Eidens et al. 2012), partly due to prevailing current and wave regimes (Werding and Sánchez 1989; Chapter 1). Given these settings, the area provides the opportunity to test the effect of seasonal coastal upwelling events on the key coral reef ecosystem service productivity under changing *in situ* conditions.

To quantify O_2 fluxes of the major functional groups and furthermore estimate their specific contribution to total benthic O_2 fluxes at a current/wave-exposed (EXP) and sheltered (SHE) site before and at the end of an upwelling season in one exemplary bay of TNNP, we used benthic survey techniques along with short-term incubation experiments.

Materials and methods

Ethics statement

All required permits for the study were obtained by Instituto de Investigaciones Marinas y Costeras (Invemar), Santa Marta, Colombia, which complied with all relevant regulations.

Study site

This study was conducted in Gayraca Bay (11.33°N, 74.11°W), one of several small bays in TNNP, located near the city of Santa Marta (Fig. 1). Due to the proximity to the Sierra Nevada de Santa Marta, the world's highest coastal mountain range, the continental shelf in the area is narrow, and only small fringing coral reefs are present in the park. The study area is subjected to high seasonality caused by the Trade Winds as well as the latitudinal displacement of the Intertropical Convergence Zone. Two main seasons are distinguishable; a dry season from December to April and a rainy season from May to November (Salzwedel and Müller 1983; Garzón-Ferreira 1998). Whereas the rainy season (hereafter referred to as non-upwelling) is characterized by low wind velocities (mean 1.5 m s^{-1}) (Garzón-Ferreira 1998) and high precipitation (> 80 % of the annual rainfall) (Salzwedel and Müller 1983), in the dry season (hereafter referred to as upwelling), strong winds prevail (mean 3.5 m s^{-1}, max 30 m s^{-1}; Herrmann 1970; Salzwedel and Müller 1983). During the upwelling, mean water temperatures are usually around 25 °C, but can drop below 21 °C (Salzwedel and Müller 1983; Bayraktarov et al. 2012; Chapter 1, 2), whereas during the non-upwelling mean water temperatures are around 28 °C and can rise above 30 °C (Table 1) (Salzwedel and Müller 1983; Bayraktarov et al. 2012; Chapter 1, 2). Due to prevailing winds, surf predominantly moves in from NE and a clear gradient between the current- and wave-exposed Western (EXP) and -sheltered Northeastern (SHE) site of the bay can be observed (Werding and Sánchez 1989; Bayraktarov et al. 2012; Chapter 1).

Note that we originally planned to conduct the study during the 2010/2011 upwelling event. However, the unusually strong El Niño-Southern Oscillation (ENSO) event in 2010/2011 (Hoyos et al. 2013) caused anomalous high precipitation and water temperatures in the study area (Bayraktarov et al. 2012; del Mónaco et al. 2012; Chapter 6), resulting in the first moderate coral bleaching in TNNP for decades at the end of 2010 (Bayraktarov et al. 2012; Chapter 6). This, in turn, strongly affected productivity of benthic communities as observed at the end of the upwelling season 2010/2011. Therefore, our study had to be repeated for the consecutive upwelling season 2011/2012. Nonetheless, though the 2010/2011 data are not representative and are thus not considered for achieving the primary objectives of this paper, they constitute a rare and fine opportunity for assessing intra-upwelling differences caused by extreme ENSO-related conditions. We therefore include these data as secondary results in our paper and refer to them within the context of a comparative discussion.

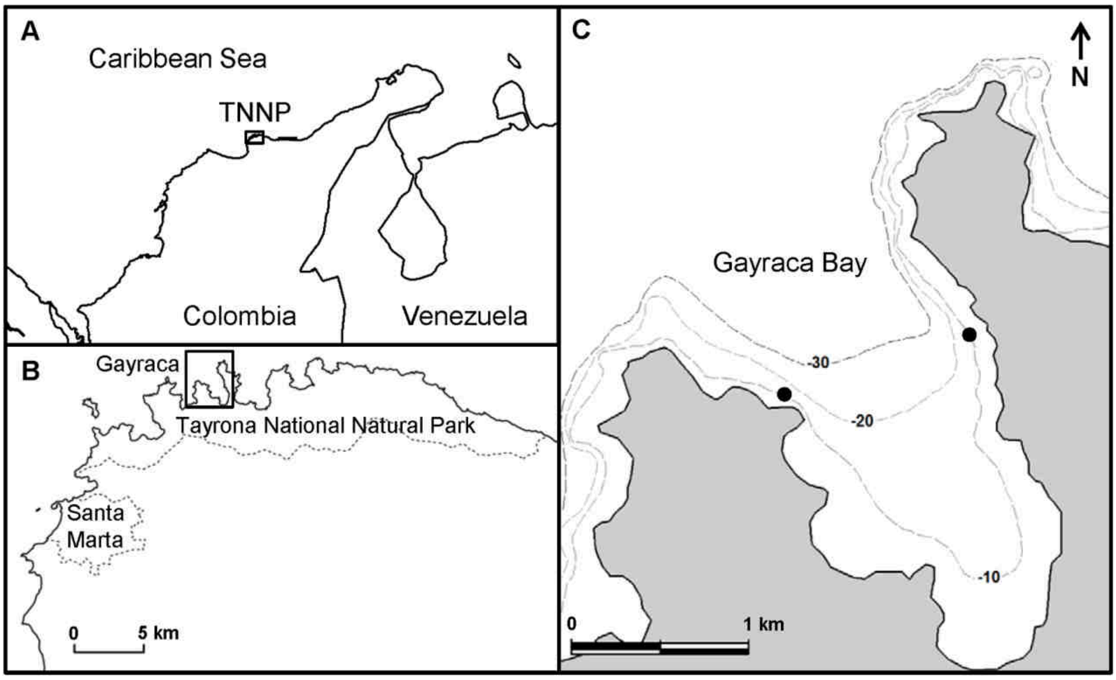

Figure 1. Location of study sites. A) Location of Tayrona National Natural Park (TNNP) at the Caribbean coast of Colombia. B) Location of Gayraca Bay within TNNP (dashed lines – national park border and expansion of the city of Santa Marta. C) Gayraca Bay. The investigation sites at the current-exposed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

To identify dominant groups of benthic primary producers and obtain the percentage of benthic cover, we assessed benthic community structure at EXP and SHE prior to primary production measurements using line point intercept transects at the 10 m isobath (50 m length, n = 3), modified from Hodgson et al. (2004). Dominant benthic autotrophs at the study sites were scleractinian corals, macroalgae, algal turfs (*sensu* Steneck (1988)), crustose coralline algae (CCA), and sand potentially associated with microphytobenthos. These categories amounted to 97 ± 2 % of the total seafloor coverage at SHE and 90 ± 7 % at EXP and were therefore selected for the subsequent incubation experiments. During benthic community assessment, rugosity at both sites was determined using the chain method described by Risk (1972). Rugosity was quantified along three 10 m sub-transects in each of the 50 m transects (n = 3) and used to calculate the rugosity factor for each study site as described by McCormick (1994) (SHE: 1.53 ± 0.12, EXP: 1.32 ± 0.13).

Sampling of organisms

Specimens of scleractinian corals, macroalgae, algal turfs, and CCA as well as sand samples, from 10 ± 1 m water depth were used for quantification of O_2 fluxes (see Table 2 for number of replicates). All samples were brought to the water surface in Ziploc bags and transported directly to the field lab. Scleractinian corals of the genera *Montastraea* and *Diploria* accounted for more than 80 % of the total coral cover at the study sites and were therefore used as representative corals in our study. Coral specimens were obtained from the reef using hammer and chisel, fragmented with a multifunction rotary tool (Dremel Corp., 8200-2/45; mean fragment surface area: 13.16 ± 7.96 cm^2), and fixed on ceramic tiles using epoxy glue (Giesemann GmbH, Aquascape). After fragmentation, specimens were returned to their natural habitat and left to heal for one week prior to the incubation experiments. Since algae of the genus *Dictyota* amounted to nearly 100 % of macroalgal cover, small bushes of *Dictyota* spp. (surface area 1.86 ± 0.88 cm^2) were used as representatives for macroalgae. Macroalgae were transferred to a storage tank (volume: 500 L, water exchange manually 3 - 5 times a day, water temperature within ranges of incubation experiments; see Table 1) one day before incubation experiments and left to heal. All other functional groups were incubated immediately after sampling. Rubble overgrown by algal turfs and CCA served as samples for the respective functional group (surface area covered by the organisms: 15.63 ± 10.80 cm^2 and 7.48 ± 3.60 cm^2, respectively). For sand samples, custom-made mini corers with defined surface area (1.20 cm^2) and sediment core depth (1.0 cm) were used.

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

	Non-upwelling		Upwelling	
	In situ	Incubations	*In situ*	Incubations
Light intensity (PAR µmol photons m^{-2} s^{-1})	146 ± 47	154 ± 40	230 ± 58 (234 ± 78)	257 ± 69 (248 ± 71)
Temperature (°C)	29.1 ± 0.2	28.6 ± 0.5	25.3 ± 0.3 (26.1 ± 0.2)	25.4 ± 0.6 (26.5 ± 0.4)

Surface area quantification

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

Incubation experiments

Quantification of photosynthetic activity for macroalgae, CCA, and microphytobenthos took place in air-tight glass containers with volumes of 60 mL, whereas for corals and algal turfs, containers with volumes of 600 mL were used. For all incubations, we used freshly collected seawater from Gayraca Bay. All primary producers were incubated in containers that were placed in cooling boxes filled with water to maintain constant *in situ* water temperature (Table 1). For light incubations, several layers of net cloth were used to simulate *in situ* light regimes (Table 1). Temperature (°C) and light intensity (lx) was monitored during incubations with light and temperature loggers (Onset HOBO Pendant UA-002-64) with a temporal resolution of 2 minutes. Light intensities were converted to photosynthetically active radiation (PAR, μmol photons m^{-2} s^{-1}, 400 to 700 nm) using the approximation of Valiela (1995). During incubation experiments, water temperature (°C) and light intensity (lx) were also continuously monitored at EXP and SHE with above mentioned light and temperature loggers. *In situ* water temperatures were higher before the upwelling ($p < 0.001$; Table 1), whereas light availability was higher at the end of the upwelling event ($p < 0.001$; Table 1). Water temperature and light availability during incubation experiments were furthermore similar to *in situ* light and temperature regimes (Table 1). For dark incubations during daytime, the above mentioned methodology was used, but cooling boxes were closed with opaque lids to prevent light penetration. To assure comparability among measurements, light incubations were carried out on cloudless days between 10 am and 2 pm. For each group of primary producers, one light and one dark incubation were performed within each study period. Incubation containers filled with seawater only served as blank controls to quantify photosynthetic activity and respiration of microbes in the water column. To prevent the investigated specimens from physiological damage by hypoxic or hyperoxic conditions, all light incubations lasted for only 30 to 60 min and dark incubations for 120 min. Dissolved O_2 concentrations in the incubation water were quantified in the beakers before incubations and after removing the specimens at the end of incubations using an optode (Hach Lange, HQ 40). Before O_2 measurements, the incubation medium was gently stirred with the optode sensor to homogenise the water column. In order to avoid additional contamination sources and to provide the most conservative estimates of O_2 production rates of benthic primary producers, experiments were conducted in closed, non-mixed incubation chambers. This also ensured higher measurement accuracy, as water movement during incubations may affect gas transfer velocities across the surface boundary of the incubation chambers (Murphy and Gardner 1975; Wu et al. 1997) and allows for comparability with previous incubation studies (e.g. Haas et al. 2011; 2013). Nevertheless, since it is well known that water flow enhances O_2 fluxes and thereby photosynthesis (Mass et al. 2010), the results of the field incubations are only conservative estimates of *in situ* O_2 fluxes and should be interpreted accordingly.

Data analyses and statistics

To quantify net O_2 production (*Pn*) and respiration (*R*) of functional groups, O_2 concentration before incubations was subtracted from concentration after incubations and corrected with blank control values. Individual gross O_2 production (*Pg*) of investigated functional groups was calculated by adding values of *Pn* and *R*; individual O_2 fluxes are expressed per mmol O_2 m^{-2} specimen surface area h^{-1}. The relative contribution of each investigated group to total reef production (given as: mmol O_2 m^{-2} vertically projected seafloor area h^{-1}) was estimated by taking into account the individual production rates and respective mean 2D to 3D conversion factors, the data for benthic coverage as well as the rugosity factor. Estimation of total daily reef productivity was furthermore calculated by extrapolation of incubation periods to a 12 h light and 12 h dark period.

After testing for normal distribution (Kolmogorov-Smirnoff test) and homogeneity of variances (Levene test), benthic coverage of functional groups as well as total benthic O_2 fluxes were analysed using two-way ANOVA and Bonferroni's *post hoc* test to detect possible effects of season (upwelling vs. non-upwelling) and location (EXP vs. SHE) on benthic cover and metabolism. Rugosity as well as *in situ* light and temperature data were analysed using unpaired two tailed t-test. Statistical analysis of metabolic activity within each functional group and the contribution of the functional groups to overall O_2 production were assessed by one-way ANOVA after checking for the assumptions of parametric testing as mentioned above. Spatial differences between the sites during each sampling period as well as seasonal pattern at each site were analysed by Bonferroni's planned comparison test, whereas differences between the various groups of primary producers were identified using Tukey-Kramer *post hoc* tests. If data did not meet the assumptions of parametric testing, data sets were either log transformed or nonparametric Kruskal-Wallis and Dunn's planned comparisons/*post hoc* tests were used. The analyses were done with STATISTICA (8.0) for Windows. All values are represented as mean ± standard deviation (SD).

Results

Benthic community composition

At the exposed site (EXP), scleractinian corals dominated the benthic community both before (41 ± 12 %) and at the end of the upwelling (39 ± 12 %, Table 2). At the sheltered site (SHE), corals, algal turf, and sand cover was similar before upwelling (24 ± 3 %, 26 ± 6 %, and 25 ± 13 %, respectively), while at the end of the upwelling, macroalgae exhibited highest benthic cover (47 ± 3 %, Table 2). During the entire study duration, CCA cover was generally higher at EXP than at SHE (both $p < 0.01$), whereas sand showed a contrary pattern with more coverage at SHE ($p < 0.01$). At the end of the upwelling, macroalgal cover was significantly higher at SHE than at EXP ($p < 0.001$).

Whereas macroalgae were less abundant on both sites before upwelling than at the end of upwelling (EXP: $p < 0.05$; SHE: $p < 0.001$), CCA cover at SHE was higher before than at the end of upwelling ($p < 0.05$).

Table 2. Benthic coverage of functional groups. All values in percent ± SD. Data in parenthesis represent benthic coverage at the end of the upwelling event 2010/2011.

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

O_2 fluxes of organisms

Highest individual net (*Pn*) and gross production (*Pg*) of all investigated functional groups were measured for scleractinian corals at both sites before the upwelling, while corals and algal turfs showed highest individual *Pn* and *Pg* rates at the end of the upwelling (Table 3). While spatial differences in O_2 production within functional groups were only observed for CCA with higher production at EXP than at SHE before upwelling ($p < 0.001$ for *Pn* and *Pg*), temporal differences in O_2 production were detected for all functional groups except microphytobenthos (Table 3). For scleractinian corals, differences in *Pn* were only present at SHE with lower productivity at the end than before upwelling ($p < 0.01$). *Pn* and *Pg* of macroalgae exhibited the same pattern ($p < 0.05$ for both). Algal turfs, on the other hand, exhibited higher *Pg* rates at SHE at the end than before upwelling ($p < 0.01$). Primary production of CCA showed opposite pattern at the two sites: *Pn* and *Pg* were elevated at EXP before upwelling ($p < 0.05$ and $p < 0.01$, respectively), while productivity at SHE was higher at the end of the upwelling (*Pn*: $p < 0.01$, *Pg*: $p < 0.001$).

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

Before the upwelling, corals contributed most to benthic O_2 fluxes at EXP ($p < 0.001$ for all comparisons with other benthic groups) and at SHE more to total benthic *Pn* and *Pg* than algal turfs ($p < 0.05$, only for *Pn*), macroalgae ($p < 0.05$, only for *Pg*), microphytobenthos ($p < 0.001$ for *Pn* and $p < 0.01$ for *Pn*), and CCA ($p < 0.001$ for *Pn* and *Pg*). At the end of the upwelling season, contribution of corals to total benthic O_2

fluxes were highest at EXP ($p < 0.001$ for all comparisons with other benthic groups) whereas at SHE, macroalgae contributed significantly more than all other groups with respect to *Pn* and *Pg* ($p < 0.001$ for all comparisons) followed by corals ($p < 0.001$ for comparisons with algal turfs, CCA, and microphytobenthos) and algal turfs ($p < 0.05$ for comparisons with CCA and $p < 0.001$ for microphytobenthos, Table 4).

Table 3. O_2 fluxes of functional benthic groups. All values in mean ± SD. Data in parenthesis represent O_2 fluxes at the end of the upwelling event 2010/2011. Missing data are due to the absence of macroalgae at the exposed site during non-upwelling. Abbreviations: *Pn* = net O_2 production, *R* = respiration, *Pg* = gross O_2 production.

Location	Functional group	N	P_n		R		P_g	
			(mmol O_2 m^{-2} specimen surface area h^{-1} ± SD)					
			Non-upwelling	Upwelling	Non-upwelling	Upwelling	Non-upwelling	Upwelling
Exposed	Corals	56	16.3 ± 4.7	13.5 ± 3.6 (17.7 ± 4.0)	2.9 ± 1.2	7.4 ± 1.2 (5.7 ± 2.1)	19.2 ± 5.4	20.9 ± 4.3 (23.4 ± 5.6)
	Macroalgae	9		2.4 ± 0.5 (8.6 ± 0.9)		0.8 ± 0.2 (1.8 ± 0.2)		3.2 ± 0.3 (10.4 ± 1.0)
	Algal turfs	16	3.3 ± 1.0	8.5 ± 2.1 (23.1 ± 2.1)	1.9 ± 0.5	3.1 ± 0.6 (7.1 ± 4.5)	5.1 ± 1.2	11.6 ± 2.3 (30.2 ± 5.6)
	Crustose coralline algae	17	8.7 ± 1.4	5.4 ± 1.5 (6.1 ± 1.2)	1.5 ± 0.2	0.6 ± 0.3 (0.4 ± 0.2)	10.2 ± 1.6	6.0 ± 1.7 (6.5 ± 1.4)
	Microphytobenthos	16	2.3 ± 1.7	0.1 ± 0.9 (4.9 ± 1.5)	2.8 ± 0.3	3.1 ± 0.5 (2.1 ± 1.0)	5.1 ± 1.6	3.2 ± 0.8 (7.0 ± 1.6)
Sheltered	Corals	51	15.6 ± 5.8	10.9 ± 3.2 (16.5 ± 4.8)	2.9 ± 1.3	6.7 ± 2.6 (6.2 ± 2.1)	18.5 ± 6.3	17.6 ± 4.7 (22.6 ± 6.0)
	Macroalgae	17	4.3 ± 0.6	3.1 ± 0.4 (6.1 ± 0.7)	1.2 ± 0.2	0.9 ± 0.7 (1.5 ± 0.4)	5.4 ± 0.7	4.0 ± 1.1 (7.6 ± 0.9)
	Algal turfs	17	5.5 ± 3.0	13.1 ± 3.6 (28.2 ± 8.3)	3.3 ± 1.2	4.0 ± 1.0 (9.0 ± 3.5)	8.8 ± 3.8	17.1 ± 4.3 (37.2 ± 5.8)
	Crustose coralline algae	17	3.6 ± 1.5	6.9 ± 2.4 (5.0 ± 1.7)	0.6 ± 0.2	1.9 ± 0.7 (0.4 ± 0.3)	4.2 ± 1.6	8.7 ± 2.4 (5.5 ± 1.8)
	Microphytobenthos	14	0.5 ± 5.6	2.7 ± 1.0 (7.3 ± 6.9)	5.7 ± 1.9	4.0 ± 0.9 (4.3 ± 1.2)	6.2 ± 4.1	6.8 ± 1.4 (11.6 ± 6.6)

Spatial differences in contribution to total benthic O_2 production within functional groups were detected for all groups except microphytobenthos. Coral contribution to total *Pn* and *Pg* was higher at EXP than at SHE before the upwelling ($p < 0.05$ and $p < 0.001$, respectively) and at the end of the upwelling ($p < 0.001$ for both). During upwelling, macroalgae contributed more to *Pn* and *Pg* at SHE than at EXP ($p < 0.001$ for both), whereas contribution of algal turfs to benthic *Pg* at the same site was higher before the upwelling ($p < 0.05$). The share of CCA to total productivity was elevated at EXP before ($p < 0.001$ for *Pn* and *Pg*) as well as at the end of the upwelling ($p < 0.01$ for *Pn* and $p < 0.05$ for *Pg*).

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

Location	Functional group	P_n		R		P_g	
		(mmol O_2 m^{-2} seafloor h^{-1} ± SD)					
		Non-upwelling	Upwelling	Non-upwelling	Upwelling	Non-upwelling	Upwelling
Exposed	Corals	14.8 ± 4.3	12.4 ± 2.8 (15.0 ± 2.8)	2.5 ± 0.6	6.9 ± 1.5 (4.7 ± 1.1)	17.4 ± 4.3	19.3 ± 3.9 (19.7 ± 3.1)
	Macroalgae		1.4 ± 0.3 (9.2 ± 1.0)		0.5 ± 0.1 (1.9 ± 0.2)		1.9 ± 0.2 (11.2 ± 1.1)
	Algal turfs	1.0 ± 0.3	2.6 ± 0.6 (5.5 ± 0.5)	0.6 ± 0.2	0.9 ± 0.2 (1.7 ± 1.1)	1.6 ± 0.4	3.5 ± 0.7 (7.2 ± 1.3)
	Crustose coralline algae	2.1 ± 0.3	0.6 ± 0.2 (1.0 ± 0.2)	0.4 ± 0.1	0.1 ± 0.0 (0.1 ± 0.0)	2.4 ± 0.4	0.7 ± 0.2 (1.1 ± 0.2)
	Microphytobenthos	0.3 ± 0.2	0.0 ± 0.0 (0.4 ± 0.1)	0.4 ± 0.1	0.1 ± 0.0 (0.2 ± 0.1)	0.7 ± 0.2	0.1 ± 0.0 (0.6 ± 0.1)
	Total	18.2 ± 4.4	17.1 ± 2.9 (31.2 ± 3.0)	3.8 ± 0.6	8.5 ± 1.5 (8.5 ± 1.5)	22.1 ± 4.3	25.6 ± 4.0 (39.7 ± 3.6)
Sheltered	Corals	10.5 ± 4.2	4.9 ± 1.3 (10.3 ± 3.0)	1.8 ± 0.4	2.9 ± 0.7 (3.8 ± 0.9)	12.4 ± 4.1	7.9 ± 1.3 (14.1 ± 3.4)
	Macroalgae	2.5 ± 0.3	9.0 ± 1.3 (8.8 ± 0.9)	0.7 ± 0.1	2.5 ± 2.1 (2.1 ± 0.6)	3.2 ± 0.4	11.6 ± 3.1 (11.0 ± 1.3)
	Algal turfs	2.2 ± 1.2	2.4 ± 0.7 (8.2 ± 2.4)	1.3 ± 0.5	07 ± 0.2 (2.6 ± 1.0)	3.5 ± 1.5	3.1 ± 0.8 (10.9 ± 1.7)
	Crustose coralline algae	0.8 ± 0.3	0.3 ± 0.1 (0.7 ± 0.2)	0.1 ± 0.0	0.1 ± 0.0 (0.1 ± 0.0)	0.9 ± 0.3	0.4 ± 0.1 (0.8 ± 0.2)
	Microphytobenthos	0.2 ± 2.1	0.8 ± 0.3 (2.3 ± 2.2)	2.2 ± 0.7	1.2 ± 0.3 (1.4 ± 0.4)	2.4 ± 1.6	2.0 ± 0.4 (3.7 ± 2.1)
	Total	16.2 ± 4.9	17.5 ± 1.9 (30.4 ± 4.5)	6.1 ± 1.0	7.5 ± 2.3 (10.0 ± 1.5)	22.3 ± 4.7	24.9 ± 3.5 (40.3 ± 4.5)

Temporal differences in contribution to total benthic productivity within the investigated groups were also present in all groups except microphytobenthos. Corals at SHE contributed more to total O_2 production before the upwelling than at the end of the upwelling ($p < 0.01$ for *Pn* and $p < 0.001$ for *Pg*), while at the same site higher rates for macroalgal contribution to total O_2 fluxes were detected for *Pn* and *Pg* at the end of the upwelling (both $p < 0.001$). For algal turfs, differences in contribution to benthic O_2 fluxes were only present at EXP with elevated *Pg* rates at the end of the upwelling ($p < 0.05$), whereas higher contribution of CCA to total *Pn* and *Pg* was detected before the upwelling at SHE (both $p < 0.01$) and EXP (both $p < 0.001$).

Regarding total benthic O_2 fluxes (Table 4), no spatial differences between EXP and SHE were detected, neither before nor at the end of the upwelling. Furthermore, no significant temporal differences were present between non-upwelling and the upwelling. Comparing total benthic productivity at the end of the upwelling events in 2010/2011 and 2011/2012, higher *Pn* ($p < 0.001$) and *Pg* ($p < 0.01$) were detected during the upwelling 2010/2011.

Discussion

O_2 fluxes of organisms

Individual mean *Pn* and *Pg* were generally highest for corals at both sites during the study periods (10.9 – 16.3 and 17.6 – 20.9 mmol O_2 m^{-2} specimen surface area h^{-1}, respectively). These high productivity rates of corals compared to other investigated primary producers (see Table 3) may be attributed to the mutualistic relationship between zooxanthellae and the coral host, boosting photosynthetic efficiency through high zooxanthellate photosynthesis in coral tissues under high CO_2 and nutrient availability (D'Elia and Wiebe 1990; Muscatine 1990). Therefore, corals are among the most productive functional groups in reef systems with several fold higher specific production rates than most reef algae and reef sands (Table 5) (Wanders 1976b; Kinsey 1985; Yap et al. 1994). Estimated daily gross O_2 production per m^2 vertically projected surface area of both investigated coral genera, *Diploria* and *Montastraea* (492 – 687 and 412 – 518 mmol O_2 m^{-2} seafloor d^{-1}, respectively), are in accordance with O_2 fluxes of other Caribbean corals, ranging from 67 to 850 mmol O_2 m^{-2} seafloor d^{-1} (Table 5) (Kanwisher and Wainwright 1967). Generally, O_2 fluxes of all investigated organism groups were within ranges reported in the literature (Table 5).

In comparison to all other investigated organism groups, coral productivity rates were not only higher, but also exhibited less fluctuation throughout the study (Table 3). A reason for the observed patterns could be high plasticity of the coral holobiont, including the coral host, the endosymbiotic zooxanthellae and associated microbes with many symbiotic interrelationships (Rohwer et al. 2002; Rosenberg et al. 2007; Bellantuono et al. 2012). These symbiotic interactions may ensure stable productivity of corals along a wide range of abiotic factors that typically alter metabolic activity. This is well known for variation in light availability (Porter et al. 1984; Gladfelter 1985), where acclimation is mainly achieved by the regulation of zooxanthellae density and chlorophyll content within zooxanthellae cells (Barnes and Chalker 1990; Stambler 2011). Our findings are supported by Kinsey (1985) who characterised productivity of corals as rather stable at low to moderate latitudes (15° to 23°; Gayraca Bay: 11° N), while at these latitudes, productivity of other benthic autotrophs such as foliose algae exhibited pronounced seasonality.

Table 5. Mean benthic oxygen production of reef slope communities and their dominant functional groups of primary producers. If necessary, original units were converted to O_2 estimates assuming a C:O_2 metabolic quotient equal to one according to Gattuso et al. (1996) and Carpenter and Williams (2007). Data in parenthesis represent O_2 fluxes at the end of the upwelling event 2010/2011. Abbreviations: *Pn* = net O_2 production, R = respiration, *Pg* = gross O_2 production.

	Location	P_n	R	P_g	$P_g:R$	Reference
		(mmol O_2 m^{-2} seafloor d^{-1} ± SD)				
Reef slope communities	Caribbean	194 – 218 (364 – 374)	92 – 204 (203 – 239)	311 – 409 (578 – 603)	2.0 – 3.4 (2.5 – 2.6)	This study
	Various Atlantic/Pacific	-83 – 425		167 – 583	0.5 – 5.5	Hatcher 1988
	Caribbean	113 – 469	72 – 437	313 – 638		Adey and Steneck 1985
Functional group						
Corals	Caribbean	227 – 344 (337 – 369)	119 – 321 (230 – 246)	441 – 610 (583 – 598)	1.9 – 3.9 (2.4 – 2.7)	This study
	Caribbean	166	281	447	1.6	Wanders 1976a
	Caribbean			225 – 850	1.9 – 5.0	Kanwisher and Wainwright 1967
Macroalgae	Caribbean	117 – 244 (315 – 444)	81 – 181 (152 – 131)	198 – 375 (466 – 624)	2.4 – 2.9 (3.1 – 3.5)	This study
	Caribbean	142 – 433	42 – 200	250 – 633	2.2 – 5.7	Wanders 1976b
	Various Atlantic/Pacific			192 – 3283	1.2 – 6.3	Hatcher 1988
Algal turfs	Caribbean	39 – 157 (277 – 339)	45 – 83 (171 – 215)	84 – 253 (447 – 554)	1.8 – 2.6 (2.1 – 2.6)	This study
	Various Atlantic/Pacific			75 – 1008	1.2 – 6.7	Hatcher 1988
	Various Atlantic/Pacific		17 – 500	83 – 967	1.0 – 4.6	Kinsey 1985
	Caribbean	175 – 433	133 – 188	308 – 617	1.4 – 1.8	Wanders 1976a
Crustose coralline algae	Caribbean	44 – 104 (60 – 73)	14 – 44 (10 – 11)	58 – 140 (71 – 82)	2.9 – 5.6 (6.7 – 8.7)	This study
	Various Atlantic/Pacific		50 – 67	67 – 83	1.3 – 1.4	Kinsey 1985
	Caribbean	58 – 117	133 – 167	192 – 258	2.5 – 3.0	Wanders 1976b
	Great Barrier Reef	50 – 333		75 – 416	3.2 – 7.0	Chisholm 2003
Microphytobenthos	Caribbean	1 – 67 (59 – 87)	67 – 137 (51 – 104)	75 – 143 (110 – 191)	1.0 – 1.4 (1.8 – 2.2)	This study
	SW Pacific	0 – 8	83 – 150	92 – 150	1.0 – 1.1	Boucher et al. 1998
	Various Atlantic/Pacific		117 – 200	50 – 225	0.6 – 1.1	Kinsey 1985

Significant spatial differences were only found for CCA before the upwelling with higher individual O_2 production at EXP compared to SHE. Since major factors controlling CCA productivity, namely water temperature and light availability (Littler and Doty 1975), did not differ between sites, differences in CCA productivity may be explained by the prevailing current regime in the bay together with high water temperatures of up to 30 °C before the upwelling. An increase in water temperature typically rises metabolic activity in CCA (Littler and Doty 1975), but decreased water flow at SHE compared to EXP (Chapter 1, 6) likely prevented the required gas exchange and nutrient uptake, resulting in lower individual CCA productivity at SHE.

Temporal differences in individual O_2 production within investigated organism groups were most pronounced at SHE with two contrary patterns observed: whereas macroalgae and scleractinian corals produced less O_2 at the end of upwelling, algal turfs and CCA exhibited higher O_2 production rates during this study period. The decreased production rates of corals and macroalgae could be explained by high macroalgal cover together with the observed macroalgal die-off at the end of upwelling. High macroalgal cover, as observed at SHE during the upwelling (47 ± 3 %, Table 2), could have resulted in reduced macroalgal O_2 production due to density-dependent intra-specific competition for light and nutrients by the dominant macroalgae *Dictyota* sp. (Edwards and Connell 2012).

The macroalgal die-off together with lower water currents at SHE compared to EXP could also have negatively affected coral productivity as decomposition of macroalgae may result in toxicity towards organisms as stated by Morand and Merceron (2005). Elevated photosynthetic performance of algal turfs and CCA at SHE at the end of upwelling may be due to higher nutrient concentrations during upwelling compared to non-upwelling (Chapter 2). Nutrient limitation of benthic communities at current-sheltered locations may be more pronounced than for communities exposed to high water flow, given the fact that benthic algal communities are typically nutrient-limited (Hatcher and Larkum 1983), and nutrient supply of coral reef algae is primarily controlled by water flow (Hatcher 1990). Elevated nutrient concentration during upwelling may therefore offset limited nutrient supply particularly at SHE where water flow is lower than at EXP (Chapter 1, 6). Another reason for the significantly increased O_2 production rate of turf algae at the end compared to before upwelling may be the higher light availability, because particularly turf algae benefit at high light conditions (Carpenter 1985). Observed shifts in O_2 production of algal turfs and CCA could furthermore be attributed to shifts in species composition of investigated algae assemblages resulting from spatiotemporal variation of abiotic factors.

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

Before the upwelling, the share of corals to total benthic *Pn* and *Pg* were highest at both EXP (83.6 ± 30.1 and 77.5 ± 19.2 %, respectively) and SHE (85.7 ± 41.6 and 54.9 ± 18.4 %, respectively). At the end of the upwelling, corals only contributed most to *Pn* and *Pg* at EXP (64.4 ± 27.2 and 75.4 ± 15.3 %, respectively), whereas macroalgal contribution to benthic primary production was highest at SHE (*Pn*: 64.8 ± 16.7; *Pg*: 46.3 ± 12.4 %). The major contribution of corals can be explained by the highest quantified individual O_2 production rates of all investigated organism groups during our study (Table 3), together with comparably high benthic coverage of corals, ranging from 24 to 39 % (Table 2). Similar values were estimated for a Southern Caribbean fringing reef by Wanders (1976b), were corals accounted for about two-thirds of total benthic primary production.

Given the fact that individual macroalgal production rates were rather low compared to corals (Table 3), the extremely high cover of macroalgae at SHE at the end of upwelling (47 ± 3 %) accounted for the major contribution of macroalgae to total benthic productivity. Reasons for the high macroalgal cover may likely be elevated nitrate concentrations (Chapter 2) and lower water temperatures throughout the upwelling event, as these factors stimulate the growth of the dominant macroalgae genus *Dictyota* (Bula-Meyer 1990; Cronin and Hay 1996; Diaz-Pulido and Garzón-Ferreira 2002).

The identified spatial differences in contribution to total benthic O_2 production for scleractinian corals, macroalgae, and CCA can also be explained by spatial differences in their benthic coverage. Elevated contributions of corals and CCA at EXP compared to SHE (Table 4) not only correlate with their spatial abundance patterns (Table 2), but likewise higher macroalgal contribution at SHE at the end of the upwelling (Table 4) can clearly be linked to spatial differences in macroalgal coverage with higher abundances at SHE during the upwelling (Table 2). The observed pattern in benthic coverage of corals and CCA may likely be caused by the water current regime in the bay with elevated water currents at EXP compared to SHE (Chapter 1, 6), as suggested for differences in local coral communities by Werding and Sánchez (1989). This explanation is supported by the studies of Jokiel (1978) and Fabricius and De'ath (2001), stating that maximum abundance of corals and CCA typically occur in water current-exposed environments. Differences in water current exposure between the study sites could also be the reason for the observed spatial patterns in macroalgae abundance, as the abundance of the dominant macroalgal genus *Dictyota* is highly affected by water current exposure (Renken et al. 2010).

Corals, macroalgae, and CCA also exhibited distinct temporal differences in contribution to total benthic productivity. At SHE, corals contributed more to benthic O_2 production before the upwelling and macroalgae at the end of the upwelling, while the share of CCA was elevated before compared to the end of upwelling at both sites. Reasons for the observed patterns in coral contribution to total benthic primary production are temporal shifts in individual O_2 productivity of corals with higher production rates before the upwelling event (Table 3) together with slightly higher benthic coverage during this study period (Table 2). The temporal variation in macroalgal contribution to total benthic O_2 fluxes can be explained by the seasonal growth pattern of the dominant macroalgae *Dictyota* sp., most likely caused by variation in nutrient concentrations (Chapter 2) and water temperatures (Chapter 1, 2), as these factors affect the growth of the dominant macroalgae genus *Dictyota* (Bula-Meyer 1990; Cronin and Hay 1996; Diaz-Pulido and Garzón-Ferreira 2002). Given the contrary occurrence pattern of macroalgae and CCA especially at SHE with higher CCA cover before compared to the end of upwelling (14 ± 4 vs. 3 ± 2 %, Table 2), seasonal occurrence of the dominant macroalgae *Dictyota* sp. may also account for the observed temporal variations in CCA abundance at SHE. This assumption is supported by the study of Lirman and Biber (2000) as well as Belliveau and Paul (2002) demonstrating that macroalgae can shade CCA, leading to usually negative correlated abundances of these groups. Higher contribution of CCA at EXP before compared to the end of upwelling furthermore results from both, elevated CCA production rates (Table 3) and higher abundances before the upwelling (Table 2).

Total benthic O_2 fluxes and ecological perspective

Estimated means of total daily benthic O_2 production at both sites before and at the end of the upwelling event 2011/2012 were within the ranges of other investigated reef slope communities (Table 5; Hatcher 1988), although total reef productivity in earlier studies was quantified in shallower reef compartments using flow respirometry techniques and our experiments were conducted in no-flow incubation chambers. Despite different methodologies, our results are most comparable to the study by Adey and Steneck (1985), as they quantified productivity of similar communities in rather deep Caribbean fore reefs of St. Croix (mean water depth: 4.5 – 6.3 m). Productivity rates reported by Adey and Steneck (1985) were generally similar to O_2 fluxes in Gayraca Bay, although maximal diurnal fluxes were slightly higher than in our study (Table 5). Given that light availability decreases with increasing depth, water depths of investigated communities (St. Croix: < 6.3 m, Gayraca Bay: ~10 m) may account for elevated daily productivity in reefs of St.

Croix. Another reason could be higher surface to area ratios in reefs of St. Croix compared to Gayraca Bay (rugosity factor: 1.9 – 2.5 and 1.3 – 1.5, respectively), since surface enlargement is a key factor for benthic communities to increase primary production (Wanders 1976b).

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

Nevertheless, significant differences in total benthic productivity at the end of the upwelling events in 2010/2011 and 2011/2012 (see Table 5) suggest that interannual influences do affect productivity of the coral reefs in TNNP. Interestingly, water temperature increases and unusual high precipitation occurred in the study area at the end of 2010, related to an El ENSO event (Bayraktarov et al. 2012; Hoyos et al. 2013), causing coral bleaching in the region (Bayraktarov et al. 2012; del Mónaco et al. 2012; Chapter 6). Surprisingly, bleached corals in the bay recovered quickly from the ENSO-triggered disturbances in the course of the following upwelling event (Bayraktarov et al.

2012; Chapter 6) and exhibited similar specific O_2 production rates at the end of the upwelling event 2010/2011 compared to subsequent measurements. Moreover, macroalgae and algal turf seemed to benefit from the environmental conditions during the upwelling following the ENSO-related disturbance event, resulting in significantly higher group-specific productivity of macroalgae and particularly algal turfs at the end of the 2010/2011 upwelling event compared to subsequent study periods (Table 3). The elevated production rates of macroalgae and algal turfs together with the fast recovery of corals from bleaching account for higher benthic productivity at the end of upwelling 2011/2011 compared to the 2011/2012 upwelling event (Table 5).

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

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5

Coral bleaching

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Abstract

Bleaching of corals (reversible loss of endosymbiotic zooxanthellae) is an unspecific indicator for a range of environmental stressors including too high or too low water temperatures, sedimentation, high irradiance or turbidity, mechanical disturbance, or infection by microbial pathogens. Coral bleaching may result in the death of affected corals depending on the severity and duration of the environmental stressor that induced bleaching. We know that the frequency and extent of high temperature-induced coral bleaching increased over the last century with recent large-scale events and resulting mass coral mortality in the Indian Ocean (1998), the Pacific Ocean (2002), the Caribbean (2005), and even all the world oceans (1998 and 2010). This may lead to major changes in the benthic community composition (i.e. phase shifts) of coral reefs and pronounced modifications of biogeochemical cycles that support coral reef functioning.

Introduction

Coral bleaching is a dynamic process that includes multiple levels of systemic causes and effects. Interactions of the environment at multiple spatial and temporal scales affect coral reef systems. Coral bleaching can be effective as an indicator of large-scale, exogenous environmental processes, or alternatively, there can be indicators of bleaching at the level of the organism up to the ecosystem indicating endogenous processes. Likewise, there can be temporal processes at the scale of the organism or ecosystem that allow differing indications of bleaching cause and effect. Because of the multiple spatial and temporal scales that interact with the processes of bleaching, we try to identify (1) early warning indicators of bleaching and/or bleaching as an early warning indicator, (2) indicators of direct impacts on corals, and finally, (3) indicators of long-term changes under specific conditions within and among communities. To clarify these ideas, below are examples of each group of indicators.

1) Early warning indicators of bleaching can be species or environmental parameters that can be highly susceptible to environmental changes, providing insight into developing issues before they affect the system as whole. For example, many corals are highly susceptible to changing water conditions, specifically changes in temperature. These changes in water conditions may be used as indicators of possible wide-scale, coral reef bleaching (see sections 1.2 and 1.5). Likewise, coral reefs are seen as indicators for global environmental change because they are found in environments at their physiological thresholds (see section 1.2). Therefore, coral bleaching can be seen as an indicator of global processes (see section 1.1).
2) Indicators of direct impacts are used to ascertain a process that is currently taking effect. For example, corals may release their symbiotic zooxanthellae prior to and during bleaching events. These changes in zooxanthellae numbers can work as indicators of direct effects (see section 1.3).
3) Finally, indicators of long-term changes provide evidence of an event that has already taken place. There is a range of susceptibility to bleaching in coral reef organisms with some species being highly robust. Post-bleaching examination of coral reef species composition can provide insight into bleaching that has not been directly witnessed (see section 1.5)

We start this chapter by exploring the definition and historical knowledge of coral bleaching. The following three sections provide information about the causes of bleaching and the physiological processes. The final three sections cover the ecological consequences of bleaching, including some brief ideas on conservation and management strategies. The processes that induce bleaching in corals and the response of these organisms are closely linked, and an indication of the bleaching processes at any level of organisation may help us to understand patterns and processes of local and global coral reef systems.

1.1 Definition and occurrence of coral bleaching

The most conspicuous, rapid and destructive impact of global climate change on coral reef ecosystems is reflected by a physiological stress response of reef corals, a phenomenon called coral bleaching. The term coral bleaching is derived from the whitening of the tissue of reef corals that host endosymbiotic *Symbiodinium* microalgae (i.e. zooxanthellae) (Fig. 1a). This whitening results from the expulsion of the zooxanthellae and/or the loss of photosynthetic, algal pigments, allowing the white aragonite skeleton to become visible through the transparent coral tissue (Fig. 1b). Coral bleaching disrupts the symbiosis between zooxanthellae and their cnidarian host, entailing the loss of an essential, internal photosynthetic energy transfer from the algal symbionts to the coral (Hoegh-Guldberg and Smith 1989)(section 1.3). At times, bleaching may be reversible, but rapid mortality of weakened and/or diseased corals is common with repetitive or intense events. In extreme instances, consequences for the functioning of coral reefs can be severely negative, as bleaching can lead to systemic failures and serious ecosystem degradation caused by usually irreversible phase shifts of benthic reef communities (Douglas 2003; Wild et al. 2011).

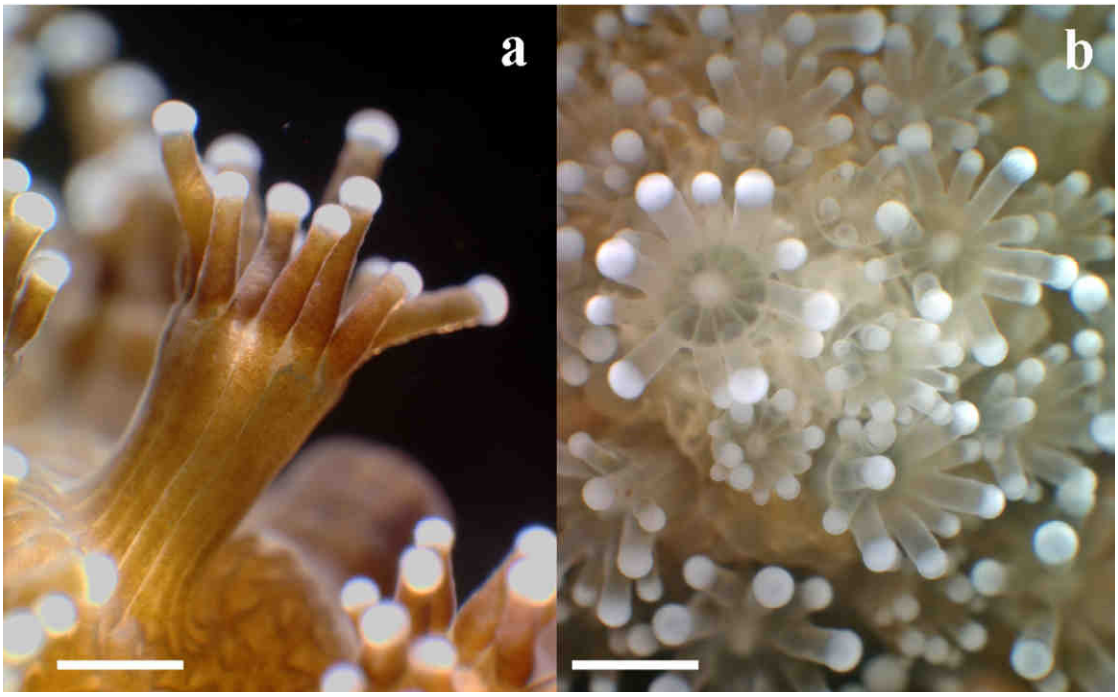

Figure 1. Macro photographs showing unbleached and bleached polyp tissue of the scleractinian coral *Stylophora pistillata*. Panel a: lateral view of protruded unbleached polyps with visible zooxanthellae population, panel b: overhead view of protruded bleached polyps with nearly transparent tissue; scale bars: 0.25 mm (a) and 0.5 mm (b) Photography: E. Tambutté (Centre Scientifique de Monaco).

The primary environmental factor triggering coral bleaching is elevated water temperatures, which cause physiological thermal stress (Hoegh-Guldberg 1999). Extreme levels of solar irradiance, including visible (Hoegh-Guldberg and Smith 1989; Banaszak and Lesser 2009) and ultraviolet radiation (Lesser et al. 1990; Shick et al. 1996), can create additional physiological stress to increase the deleterious impact of thermal bleaching. Furthermore, coral bleaching can result from a range of abiotic and biotic stressors as a product of their typical coastal, shallow water distribution (section 1.2). Often, many stressors act in concert to increase susceptibility of corals to thermal bleaching further by lowering their temperature threshold and, subsequently, exacerbating the degree of coral mortality (Lesser 2004; 2006).

Considering the main environmental factors that induce reef corals to bleach (temperature and light), the stability of the coral-zooxanthellae symbiosis can serve as a sensitive environmental indicator, in particular, for temperature anomalies, which are included in climate change projections (Hoegh-Guldberg et al. 2007). Because corals often live in environments where temperatures are close to their physiological thermal threshold, they are highly vulnerable to bleach at temperatures 1 °C above the historical mean summer maximum in many regions (e.g. Toscano et al. 2000)(section 1.2). Satellite sea surface temperature data have shown that bleaching of variable severity can be expected if this warming persists for several weeks or increases, and this correlation is now used to forecast the global spatiotemporal distribution and intensity of coral bleaching events (Strong et al. 2006). Given the low thermal tolerance of many reef coral taxa, temperature anomalies can trigger widespread bleaching events posing serious threat to coral reefs world-wide (Hoegh-Guldberg 1999; Pandolfi et al. 2003; Pandolfi et al. 2011).

The phenomenon of coral bleaching has been known for more than 100 years; however, the first comprehensive report on a temperature-induced bleaching event originates from 1929 when Yonge and Nichols (1931) recorded widespread coral bleaching and mortality on reef flats within the Great Barrier Reef. Thereafter, regular reports on bleaching observations can be found in the literature. The first Caribbean thermal "mass bleaching" event of the early 1980s had a widespread impact and led to increased awareness of other bleaching events induced by elevated water temperatures and high solar irradiance (Glynn 1983; Lessios et al. 1983; Glynn and D'Croz 1990; Glynn 1996). Region-wide mass coral bleaching can affect thousands of square kilometres of reef-covered seafloor over relatively small time scales (i.e., within weeks) and thus, constitute a major cause for large-scale coral mortality and the simultaneous decline of coral reef ecosystems (Hoegh-Guldberg et al. 2007).

On a global scale, mass bleaching events can be associated with extended periods of elevated water temperatures generally associated with anomalies in the Southern Pacific Oscillation (i.e. El Niño or La Niña events), which can affect multiple oceanic regions (Hoegh-Guldberg 1999). In 1998, the first, and to date most severe, of four global bleaching events (Fig. 2a) affected reefs in all tropical and subtropical latitudes causing a loss of 16 % of corals world-wide (Wilkinson 2008). During this event, 80 % of all corals in the Western Indian Ocean bleached and nearly 50 % died, with up to 95 % mortality at some sites (Lindén and Sporrong 1999; Souter et al. 2000). Another global event occurred in 2002, where the Great Barrier Reef represented the major bleaching hotspot (Fig. 2b; e.g. Berkelmans et al. 2004). In 2005, the Caribbean was most severely affected resulting in more than 80 % of corals bleached and over 40 % mortality (Fig. 2c; Eakin et al. 2010). The most recent global bleaching event in 2010 (Fig. 2d) significantly impacted many regions throughout the Indo-Pacific (Burke et al. 2011; Krishnan et al. 2011; Guest et al. 2012; Furby et al. 2013), including Western Australia, which experienced up to 95 % bleaching and 84 % mortality in certain reef areas (Moore et al. 2012).

Intensity and frequency of world-wide coral bleaching events may be recognised as biological indicators for consequences of global climate change on coral reefs (Hughes 2000). If current rates of CO_2 emission and ocean warming persist, model predictions for the coming decades project the intensity and frequency of bleaching events may increase with possible annual occurrences (Hoegh-Guldberg 1999; Sheppard 2003; Donner et al. 2007; Hoegh-Guldberg et al. 2007; Lesser 2007; Eakin et al. 2009; Hoegh-Guldberg 2011). One of the latest models predicts that preserving >10 % of coral reefs world-wide would require limiting warming to <1.5 °C relative to pre-industrial levels, a figure considerably less than the globally agreed 2 °C (Frieler et al. 2013). This prospect clearly constitutes a massive threat to the existence of present-day coral reef ecosystems. Due to the lack of human observers and limited reporting effort in remote locations, the analysis of global bleaching observation databases (e.g. ReefBase) is limited in spatial and temporal terms (Burke et al. 2011). As a consequence, many bleaching events remain unobserved and unreported, masking their actual global frequency and intensity.

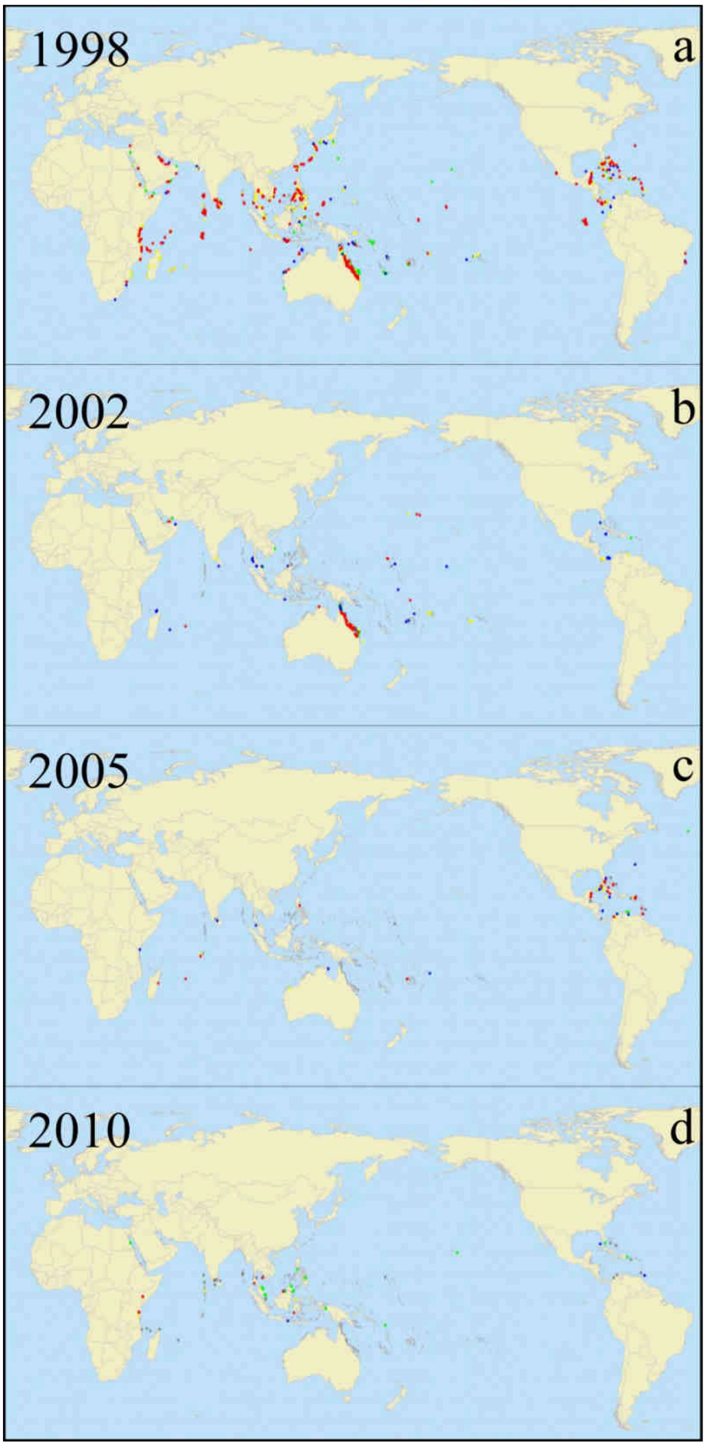

Figure 2. Overview of bleaching reports covering the four global mass bleaching events since 1998. Panels a-d: 1998, 2002, 2005 and 2010, respectively. Bleaching severity indicated by colour coding: red = high, yellow = medium, blue = low, grey = severity unknown, green = no bleaching. Maps adopted and modified from ReefGIS online services (http://reefgis.reefbase.org/) based on the comprehensive ReefBase database (2013) compiled by contributions of UNEP-WCMC, The WorldFish Center, National Oceanographic and Atmospheric Administration (NOAA), Great Barrier Reef Marine Park Authority, Australian Institute of Marine Science and coral-list (coral.aoml.noaa.gov/mailman/listinfo/coral-list/) maintained by NOAA.

These contrasting results have stimulated further research, which has suggested differing levels of thermal stress tolerance and acclimatisation of particular coral taxa, or possibly entire reef communities, acquired from past stress exposures and/or local mitigating environmental, abiotic factors (e.g. shading, current speed, upwelling zones or depth; Maynard et al. 2008; Brown and Cossins 2011)(section 1.6). Nevertheless, the capacity for stress resistance and bleaching resilience appears highly variable and limited, as evidenced by recent mass bleaching events that affected much of the occurring coral taxa, and a subsequent, marginal recovery of these systems (Grimsditch et al. 2006; Baird and Maynard 2008; Baker et al. 2008; Sheppard et al. 2008; Somerfield et al. 2008; Veron et al. 2009). Finally, the physiological capacity for stress acclimatisation may also be closely related to the actual type of active stressors, which will be addressed in more detail in the following sections.

1.2 Causes of coral bleaching

Although the mechanisms of coral bleaching are still not completely understood, various factors that may trigger this process have been the subject of intense research (Brown 1997; Lesser 2011). Corals undergo bleaching if the environmental conditions that contribute to the stability of the relationship between *Symbiodinium* and the coral host fail (section 1.3). Many field and laboratory studies found increased seawater temperature to be the major factor for the breaking down of the symbionts-host environment, leading to the subsequent occurrence of bleaching events (e.g. Hoegh-Guldberg and Smith 1989, Jokiel and Coles 1990; Lesser et al. 1990; Glynn 1993; Fitt et al. 1993). Temperature increases of 1-2 ° C above the mean summer maximum, persisting for several consecutive weeks, can lead to coral bleaching (Jokiel and Coles 1990; Bruno et al. 2001) indicating that many coral species are living close to their upper thermal limits (Jokiel and Coles 1990). Therefore, thermal thresholds have been studied as early warning indicators of potential bleaching events. Rankings of susceptibility of different taxa to thermal stress have been published (Fitt et al. 2001; Loya et al. 2001; Marshall and Baird 2000; Okamoto et al. 2005) (section 1.5). However, thermal thresholds vary among areas and it is not clear how these limits apply *in situ* where several processes (e.g. wind, wave action, and upwelling) can work synergistically to alter the effects of thermal stress (Berkelmans and Willis 1999; Abdo et al. 2012).

While thermal stress is viewed as the principal cause of coral bleaching, several other biotic and abiotic factors have been found to impact the stability of the symbiosis, including: reduced seawater temperatures (Muscatine et al. 1991; Gates et al. 1992; Kobluk and Lysenko 1994; Saxby et al. 2003); supra-optimal levels of visible or ultraviolet radiation (Gleason and Wellington 1993; Lesser and Farrell 2004; Brown and Dunne 2008); ocean acidification (Anthony et al. 2008); salinity fluctuations (Meehan and Ostrander 1997; Kerswell and Jones 2003); bacterial infection (Rosenberg et al. 2009); and cyanide exposure (Jones and Hoegh-Guldberg 1999). Hoegh-Guldberg (1999) added copper ions and pesticides, while Glynn (1996) included sub-aerial exposure, sedimentation, and oil as contributory factors.

However, of critical importance is that mass coral bleaching events, such as those recorded in 1998, 2002, 2005, and 2010 (Goreau et al. 2000; Berkelmans et al. 2004; Guest et al. 2012) (section 1.1), have been associated with the effects of anthropogenic global warming (Hughes et al. 2003; Donner et al. 2005), which has resulted in a steady rise of marine baseline temperatures. Consequently, forecasts of warming events on a global scale such as the occurrence of El Niño events serve as early warning indicators of potential bleaching of wide areas of coral reefs. Likewise, a sudden drop in seawater temperature induced by either atmospheric chilling or intense upwelling may also result in coral bleaching across wide areas (Hoegh-Guldberg et al. 2005) and should be monitored and used as an early warning indicator. Finally, ocean acidification and changes in solar radiation have the potential to cause mass bleaching across large spatial scales as climate change occurs (Anthony et al 2008; Lesser 2011). These are indicators of long-term changes in coral reef communities and may be monitored with the use of time series data. All the large scale stressors mentioned above and their combined effects may have dramatic consequences on the geographic extent, increasing frequency, and regional severity of future mass bleaching events.

Local stressors such as pollutants, nutrient loading or sedimentation result in localised bleaching events (tens to hundreds of kilometres) because of the constrained nature of the stress source. However, these can act synergistically by effectively lowering the threshold temperature at which coral bleaching occurs, thereby reducing coral resistance and resilience to global climate change (Lesser 2004; 2006; Wooldridge 2009; Carilli et al. 2012). Consequently, these local stressors should also be monitored as they can act as indicators of subsequent bleaching events, especially if they occur simultaneously with high summer water temperatures.

While there is consensus in identifying the above described environmental drivers (e.g. temperature, light) as (direct or indirect) causes of coral bleaching, the scientific community is not in agreement on the role of bacteria as potential causative agents of bleaching. Most coral biologists contend that changes in the microbial community of bleached corals are a mere result of the process. Indeed, during a bleaching event, coral-associated microbial communities show major shifts in their composition and metabolism (Bourne et al. 2007), with an increase in microorganisms capable of pathogenesis (Littman et al. 2011). This has been confirmed by reports that found a positive link between coral bleaching events and subsequent coral disease epizootics (Miller et al. 2006; Muller et al. 2008; Brandt and McManus 2009; Cróquer and Weil 2009; McClanahan et al. 2009). Consequently, the occurrence of coral diseases might be an indicator of an effect of coral bleaching on both the organism and the ecosystem level, or otherwise bleaching can be used as early warning indicator of subsequent susceptibility of the coral community to disease outbreaks.

However, bleaching has also been found to occur as a direct result of bacterial infection in the coral tissue, particularly by gram-negative bacteria of the genus *Vibrio*. Kushmaro et al. (1996) found that bleaching of the Mediterranean coral *Oculina patagonica* was caused by *Vibrio shiloi*, which produces extracellular proline-rich peptides referred to as Toxin P, which blocks photosynthesis and bleaches and lyses zooxanthellae. However, the mere presence of the *Vibrio* bacterium is not sufficient to cause coral bleaching: virulence factors for adhesion and ingress into the coral and Toxin P are produced by the bacterium only at elevated seawater temperatures (Kushmaro et al. 1998; Toren et al. 1998; Banin et al. 2000). Similarly, *V. coralliilyticus* in combination with elevated temperature caused bleaching in the coral *Pocillopora damicornis* (Ben-Haim and Rosenberg 2002; Ben-Haim et al. 2003). These observations led to the 'Bacterial Bleaching Hypothesis' (Rosenberg and Falkovitz 2004; Rosenberg et al. 2009), which proposes a microbial infection as the primary trigger of coral bleaching. Conversely, Ainsworth et al. (2007) found no evidence to support this hypothesis and argued against its generalisation, suggesting that the bacterial infection is opportunistic rather than a primary pathogenic cause of bleaching and that non-microbial environmental stressors trigger coral bleaching in *O. patagonica*. Nevertheless, a recent experiment with the coral *Montipora digitata* demonstrated that corals exposed to thermal stress in synergy with external bacterial challenge (by different inoculated strains of *V. coralliilyticus*, *V. harveyi*, *Paracoccus carotinifaciens*, *Pseudoalteromonas* sp., and *Sulfitobacter* sp.) undergo more severe bleaching than colonies exposed to thermal stress alone (Higuchi et al. 2013). Conversely, a 'healthy' microbial community (i.e. the microbial community found in healthy colonies) increases the thermal tolerance of the holobiont compared to that of coral colonies whose bacterial community was treated with antibiotics (Gilbert et al. 2012).

From these findings, it appears likely that environmental drivers act on the coral microorganisms as well as the coral host, causing a change in the microbial community that in some cases contributes directly or indirectly to bleaching (Rosenberg et al. 2009). Finally, these studies stress the importance of the interaction between abiotic and biotic factors and of the stability of the coral microbiota for the resilience of the holobiont to bleaching, calling attention to a more careful consideration of bacteria as fundamental players in the bleaching process. Because of the present development of molecular techniques (e.g., qPCR, CARD-FISH), which are becoming accessible to more researchers every day, monitoring of the bacterial community or of a particular bacterial bioindicator (such as *Vibrio*) may serve as an early warning indicator of bleaching events or as an indicator of direct impact on corals once the bleaching process occurs.

As we come to understand the causes of bleaching and the interaction between different biotic and abiotic stressors across spatial and temporal scales, on both the organism and the ecosystem level, it is fundamental to develop environmental indicators that help in managing and protecting coral reef ecosystems from degradation. Finally, monitoring of these indicators, on both a global and local scale should be implemented and response protocols need to be developed if we are to save these ecosystems in the coming decades.

1.3 Mechanisms of coral bleaching

Coral bleaching is primarily induced by two factors: photoinhibition and oxidative stress. A clear indicator for coral bleaching is that the coral's zooxanthellae are experiencing either one or both of these stressors. Photoinhibition is the process in which a constantly high absorption of excitation energy and a decrease in photosynthetic electron transport combine to cause damage to the photosystem II reaction centre of photosynthetic organisms (Hoogenboom et al. 2012). Photoinhibition can be caused by exposure to thermal stress and increased ultraviolet radiation (UVR). It leads to a reduced yield from photosynthesis and energy expenditure on the repair of damaged tissues (Long et al. 1994). Oxidative stress occurs within an organism when the production and accumulation of Reactive Oxygen Species (ROS) exceed the organism's capacity to control their levels (Fridovich 1998). ROS are a group of compounds (superoxide radicals, hydrogen peroxide, hydroxyl radicals, and ions) that, when they accumulate in the cells, can damage lipids, DNA, and proteins. They are normally controlled by anti-oxidants produced by the organism (section 1.2). ROS production can increase rapidly in photosynthetic organisms such as zooxanthellae when they are exposed to increased temperature and UVR (Lesser and Farrell 2004; Suggett et al. 2008). As these two factors increase, the production of ROS overwhelms the antioxidant defences and causes extensive damage (Martindale and Holbrook 2002). Besides being transferred to the host from the zooxanthellae (Suggett et al. 2008), ROS are also produced by the cnidarian hosts as a response to thermal stress (Dykens et al. 1992). A build-up of ROS in coral tissues might be monitored as an indicator for a potential future bleaching event. As the host cells are exposed to, and damaged by, the built up ROS, there are several ways in which the symbiosis can be uncoupled. In apoptosis, a programmed cell death pathway is initiated due to exposure to ROS or extensive damage to the DNA or other cell components. In necrosis, the cell's functioning is disrupted to a degree where it disintegrates without a controlling pathway (Martindale and Holbrook 2002). Additionally, zooxanthellae can be expelled from the host tissue by exocytosis into the gastrovascular cavity, or the cell can be detached from the endoderm as a whole (Gates et al. 1992). For an extensive review of coral bleaching mechanisms, the authors refer the reader to Lesser (2011).

Photosynthesis by zooxanthellae can provide the coral host with a significant proportion of its energy demand (Tremblay et al. 2012). A loss of this contribution due to bleaching severely impacts coral fitness, reducing reproductive output and growth (Cantin et al. 2010; Manzello 2010; Brown 2012). Calcification can be "light enhanced" during the day (Gattuso et al. 1999; Schutter et al. 2012), and although the precise physiological mechanism behind this process is still under debate, a loss of zooxanthellae has a clear adverse effect on calcification (Moya et al. 2008). Coral bleaching can also increase the occurrence of growth anomalies, disturbing the normal development of coral colonies (McClanahan et al. 2009). The reproductive capability of the coral is influenced in the period following a bleaching event, with a reduced number of gametes being produced by bleached coral tissue (Armoza-Zvuloni et al. 2011). Coral reproduction is further impacted by increased water temperatures through reduced fertilisation success (Albright and Mason 2013), and reduced larvae survivorship and settlement (Randall and Szmant 2009a; Randall and Szmant 2009b). There are, however, factors that seem to reduce the impact of thermal stress on coral reproduction. Cox (2007) found no change in reproductive parameters after a bleaching in *Montipora capitata* and hypothesized that this was due to the coral's capacity to increase its heterotrophic feeding. Along with carbon fixation by the zooxanthellae, heterotrophic feeding is an important source of energy for corals, and Grottoli et al. (2006) found that some corals are able to meet 100 % of their daily metabolic requirements through heterotrophic feeding. Corals of the species *M. capitata* were able to replenish their energy reserves within six weeks after a bleaching event when exposed to naturally available zooplankton. Plasticity in heterotrophic feeding has been found to help corals in both resistance to thermal stress (Borell et al. 2008) and recovery from a bleaching events (Connolly et al. 2012)(section 1.6). The status of a reef's coral energy reserves in the time following a bleaching event would be a useful indicator of the chance of full recovery.

1.4 What can we learn from bleaching of other symbiont-bearing organisms?

Research and literature addressing the symbiosis with *Symbiodinium* and bleaching has primarily focused on hard corals as indicators of bleaching, as these are the main builders of tropical coral reefs. However, symbioses between organisms other than corals and *Symbiodinium* remain poorly understood despite the fact that these relationships may help to provide clarity on processes within scleractinian corals and act as indicators for bleaching of various levels. Such symbioses are widespread within various ecologically relevant taxa of marine invertebrates and protists: Cnidaria (Hexa- and Octocorallia, some Scyphozoa such as *Cassiopea*), Mollusca (e.g., Bivalvia of the genera *Tridacna* and *Hippopus*: Hernawan 2008; Nudibranchia: Burghardt et al. 2008), Acoelomorpha (the genus *Waminoa*: Barneah et al. 2007), Porifera (Steindler et al. 2002), and Foraminifera (Lee et al. 1979). Similar to scleractinian corals, symbiosis with *Symbiodinium* in other organisms has evolved as a strategy to complement nutrition; these relationships can be either facultative or obligatory.

Despite many similarities (such as the cultivation of photosynthetically active and proliferating *Symbiodinium* in specific organs, specialised cell structures of host and symbiont, exchange of certain metabolites/chemicals), there are still important differences between corals and other symbiotic systems, particularly on the host side. In most symbioses, *Symbiodinium* lives intracellular as endosymbionts; in Cnidaria, *Symbiodinium* are found within the cells of the endoderm, and in Nudibranchia, they reside within the digestive gland. In contrast, *Symbiodinium* in many bivalves (e.g., *Tridacna* spp.) are harboured extracellularly in specialised structures (Norton et al. 1992). Within the Acoelomorpha, they occur in parenchyma cells (intracellular) or in the lumen (extracellular; Barneah et al. 2007). In the unicellular Foraminifera, they reside in the endo- and ectoplasma (Köhler-Rink and Kühl 2000).

There is an abundance of literature on the impacts of a changing environment and the effects on scleractinian corals leading to their bleaching (e.g. Fitt et al. 2000; Berkelmans and van Oppen 2006). Throughout various non-coral taxa, investigations of other symbioses and bleaching susceptibility are, nevertheless, unfortunately scarce. Only a few studies have demonstrated that a large variety of *Symbiodinium* symbioses can suffer, and therefore indicate bleaching (octocorals: Strychar et al. 2005; Goulet et al. 2008; Prada et al. 2010; *Tridacna*: Norton et al. 1995; Buck et al. 2002; Porifera: Vicente 1990; Fromont and Garson 1999; Foraminifera: Talge and Hallock 2003). Bleaching mechanisms in these symbioses seem similar to coral systems and are mainly triggered by factors such as high water temperature and irradiance. Thus far, non-coral symbiotic systems have rarely been used as indicators for bleaching, although they have an important ecological role and their proportion in coral reef ecosystems is large. It would be crucial to include these symbioses in bleaching studies, since they reflect various host-symbiont-assemblages that might react differently from corals to bleaching conditions. Therefore, they represent an ideal array of indicators to monitor bleaching.

Many previous studies on corals highlight the importance of symbiont genotype in bleaching susceptibility, and the high diversity in *Symbiodinium* may be the key to the survival of coral reefs in times of coral bleaching. Diversity of *Symbiodinium* differs in various invertebrate hosts. Most scleractinian corals house clades A-D of *Symbiodinium*, but other symbiotic invertebrates and protozoans potentially house an even wider range of types. For example, in Foraminifera six different clades can be detected (A, C, F-I; Carlos et al. 1999; Pawlowski et al. 2001; Pochon and Gates 2010). Acoelomorph flatworms house clades A and C (Barneah et al. 2007), the jellyfish *Cassiopea* spp. houses clades A, B and D (LaJeunesse 2001; Santos et al. 2002 Lampert et al. 2011), sponges contain clades A, C and G (Hill et al. 2011), and various solar-powered nudibranchs cultivate clades A-D (Wägele and Johnsen 2001; Loh et al. 2006; Fitzpatrick et al. 2012). Symbiont acquisition is either vertical, which is the transfer of symbionts through oocytes or clonal cell division as seen in a few scleractinian corals, one species of *Waminoa* and foraminferans, or more commonly, they are acquired horizontally where every generation needs to acquire new symbionts. Vertical transmission of symbionts offers a reliable pool of certain zooxanthellae suited for stable environmental conditions. Alternatively, this acquisition mode offers less flexibility. In contrast, horizontal transmission offers flexibility such that each new generation takes up suitable *Symbiodinium* types. Depending on the specificity of the symbiosis, this could be a disadvantage, since needed *Symbiodinium* types might not always be available in the environment. Since most symbioses practice horizontal symbiont transmission, they depend on pools of *Symbiodinium* available in the environment (free-living stages in the water column and sediment) and in other symbiotic organisms (connected by expulsion of living symbionts).

Both *Symbiodinium* diversity and symbiont acquisition seem to be important for bleaching susceptibility of the holobiont. Bleaching susceptibility has most often been attributed to the thermal tolerance of the algal symbiont (Ulstrup et al. 2006). *Symbiodinium* display significant differences in physiological performance both: within and among clades (Savage et al. 2002; Baker 2003; Robison and Warner 2006; Hennige et al. 2009). These dissimilarities obviously affect host performance (Berkelmans and van Oppen 2006) and influence the holobiont's ability to handle environmental stresses such as increased temperature (D'Croz and Mate 2004; Goulet et al. 2005). It has been suggested that the high diversity in *Symbiodinium* might be the key to survival of coral reefs in times of coral bleaching. Most research has focused on whether or not corals are able to associate flexibly with diverse symbionts whose different physiologies impart greater resistance to environmental extremes (Baker 2003; Berkelmans and van Oppen 2006). This model has been called the 'Adaptive Bleaching Hypothesis' (ABH: Buddemeier and Fautin 1993). According to the ABH, zooxanthellae may enter the host from exogenous sources (symbiont 'switching') or, if multiple zooxanthellae already concurrently exist within the host, a shift in symbiont dominance may occur (symbiont 'shuffling'; Baker 2003). The ABH has been controversially discussed in the previous literature. Unfortunately, the results of various studies testing the ABH are ambiguous, and the studies focused mainly on reef-building corals. Nevertheless, the high diversity of *Symbiodinium* in various invertebrate taxa might be important in times of bleaching, since they offer pools of potentially resistant *Symbiodinium* genotypes to bleached corals. Additionally, many non-coral symbioses are mobile and could act as vectors for spreading other genotypes that are better adapted to alternative environmental conditions. For instance, a study by Stat and Gates (2008) demonstrated that symbionts can be introduced to new geographic locations vectored by mobile symbiotic invertebrate hosts. They showed that new *Symbiodinium* genotypes were introduced into Hawaiian waters by *Cassiopea* sp.

In contrast to the many studies that focus on and emphasise the responsibility of the symbiont in bleaching, divergences in host tolerance or, particular host-symbiont-assemblages, have been examined far less frequently as possible causes of bleaching (Brown et al. 2002; D'Croz and Mate 2004; Goulet et al. 2005). Studies have demonstrated that holobionts consisting of identical *Symbiodinium* types but differing in coral hosts react differently to environmental stressors and could, therefore, be used as indicators for bleaching with different sensibility (Bhagooli and Hidaka 2004; Baird et al. 2009; Barshis et al. 2010; Bellantuono et al. 2012). Another recent study by Oliver and Palumbi (2011) indicated that only the combination of heat-resistant symbionts with heat-acclimatised/adapted hosts resulted in thermal tolerant holobionts. Thus, the interplay of both partners seems to determine bleaching susceptibility (Ralph et al. 2001; Bhagooli and Hidaka 2004; Bhagooli et al. 2008; Fitt et al. 2009).

Concerning bleaching tolerance, generally, the relative role of the host is better understood when compared to the symbiont (Abrego et al. 2008; Baird et al. 2009). Due to the diverse phylogenetic origins of different invertebrate hosts, microenvironments offered to symbionts can vary (Jiménez et al. 2011). Factors such as host tissue thickness appear crucial in holobiont susceptibility to bleaching (Loya et al. 2001; Stimson et al. 2002; Ainsworth 2008), and furthermore, host-driven protective mechanisms that could contribute to the regulation of the holobiont's bleaching response include the production of anti-oxidant enzymes (Lesser et al. 1990; Baird et al. 2009), fluorescent pigments (Salih et al. 2000), and mycosporine-like amino acids (MAAs; Dunlap and Shick 1998).

In summary, there are four main reasons to focus more on non-coral symbioses with *Symbiodinium* as indicators for bleaching in the future. (1) The wide variety of *Symbiodinium* genotypes (with significant differences in physiological performance and thus thermal tolerance) in various invertebrate symbiotic systems might act as potential *Symbiodinium* pools by offering symbiont types that are better suited for post-bleaching conditions. (2) Many non-coral symbiotic systems are (in contrast to corals) mobile. Mobile symbiotic systems are of particular interest since they can potentially adapt to changed environmental conditions by escaping to areas with more suitable environmental conditions (vertically and horizontally). They can potentially function as mobile Symbiodinium vectors by spreading symbiont types that are better suited for post-bleaching conditions by means of expulsion. (3) Since the relative contribution of the host in terms of bleaching tolerance is still unclear (Abrego et al. 2008; Baird et al. 2009), it is crucial to perform comparative studies investigating different symbiotic systems that share Symbiodinium as a symbiont. How do various host/symbiont-assemblages react to environmental stressors? (4) Non-coral symbiotic systems can be used as indicators to trace bleaching conditions early. Some of these systems are already used as bio-indicators for other purpose, for instance foraminiferans (subfamily Soritinae) are important in mineral and calcium cycles (Murray 1991; Fujita et al. 2000) and are used as bio-indicators in reef monitoring programs (Hallock et al. 2003). Another example is the jellyfish genus *Cassiopea*: Niggl et al. (2010) demonstrated that organic matter derived from the jellyfish *Cassiopea* sp. may function as a newly discovered pathway for organic matter from the benthic environment to pelagic food chains in coral reefs. Thus, a combination of organism traits and ecosystem processes could be combined to act as indicators for bleaching.

1.5 Ecological and biogeochemical consequences of coral bleaching

The impact of coral bleaching on fundamental physiological processes, such as coral growth, calcification, and reproduction, results in broad-scale consequences for the ecosystem functions and services provided by this ecosystem engineer (Wild et al. 2011). Reduced growth and reproduction may thereby result in reduced resilience of coral-dominated reef communities. Similarly, reduction the abilities of corals to compete with other invertebrates or reef algae (Reed et al. 2010) can lead to fundamental changes in the community structure of tropical benthic assemblages. Branching, framework-building corals, including the genera *Acropora*, *Seriatopora*, *Pocillopora*, and *Stylopora*, are morphologies that are more sensitive to thermal stress and bleach more often than massive and encrusting growth forms (Marshall and Baird 2000; Loya et al. 2001; McClanahan et al. 2002). In addition, larger branching colonies are more susceptible to thermal stress than their smaller counterparts (Nakamura and van Woesik 2001; Mumby et al. 2001a; Bena and van Woesik 2004). Consequently, mass coral bleaching events will likely change the coral reef landscape from one supporting a diversity of coral colony morphologies and species to a landscape dominated by fewer species with robust, small, massive, and encrusting coral forms. Therefore, coral morphology and species composition across the benthic reef community are potential proxies for the ecological effects of bleaching events.

Coral-generated production of inorganic materials (i.e. framework structures and calcareous sands) will decrease substantially with increasing bleaching frequency and extent because of the bleaching-induced inhibition of calcification (section 1.3). Parameters such as reef rugosity may therefore also act as potential indicators reflecting the reef ecosystem consequences of coral bleaching. The calcifying activities of reef-building corals ultimately result in a three-dimensional matrix that provides space, shelter, and food for many reef associated organisms (Sale et al. 2005). Coral reefs are therefore associated with high abundances of fishes (McClanahan and Shafir 1990) and other animals. Coral bleaching may reduce the framework building and habitat generation capacity of reef corals. The resulting reduction in structural complexity also reduces the availability of habitat space at a variety of scales and leads to a considerable reduction in coral reef fish diversity (McClanahan and Shafir 1990). This highlights fish abundance and diversity as good indicators for coral bleaching consequences on the associated organisms.

Scleractinian corals continuously release particulate and dissolved organic matter (POM and DOM) (e.g. Wild et al. 2004). During thermal-induced bleaching, two different kinds of organic matter are increasingly released: (1) POM as zooxanthellae, and (2) POM derived from the coral host (Niggl et al. 2009). Degradation of these two POM sources by reef microbes is much lower for the released zooxanthellae ($< 1\ \%\ h^{-1}$) than for the coral-derived POM ($> 5\ \%\ h^{-1}$) (Wild et al. 2005). The very low microbial degradation rates for the cellulose-containing zooxanthellae indicates that most of the suspended zooxanthellae released during coral bleaching are not degraded and recycled by the reef microbes fast enough to allow recycling to take place in the reef. Alternatively, zooxanthellae are exported from the reef via the prevailing water currents. Thus, from a biogeochemical point of view, coral bleaching most likely involves a considerable loss of energy and essential nutrients from the reef ecosystem. In contrast, coral-derived POM may function as an energy carrier and particle trap (Wild et al. 2004; Huettel et al. 2006). This material, because of its fast microbial degradation rates, potentially stays within the reef system and is recycled, particularly by the benthic community (Wild et al. 2004). Histological analyses (Fitt et al. 2009) indicate that internal mucus production in the coral tissue is depleted during bleaching so that mucus-POM release by corals is most likely stimulated only during the early phase of bleaching, but drops to lower levels the longer the bleaching event lasts. This dynamic flux of POM was confirmed by the study of Piggot et al. (2009), who demonstrated that the number of mucus-producing cells (i.e., mucocytes) in coral tissue is potentially a good indicator for bleaching because they decline after an initial bleaching response. Coral bleaching thereby largely reduces the metabolic exchange between corals and all reef organisms that feed on coral-derived organic matter (e.g. microbes, filter feeders, fish) while also reducing the capacity of corals to trap organic matter. This may lead to further loss of POM from the reef system with subsequent important biogeochemical consequences.

Corals can recover from bleaching (section 1.3), which also allows the reoccurrence of organic matter release by this key ecosystem engineer. The respective recovery time scales range from weeks to months (Gates 1990; Jokiel and Coles 1990), so that short- to mid-term effects on organic matter cycles driven by the corals can be expected from a brief impedance of the coral engineer during reversible bleaching. However, this may include long-term changes in the reefs nutrient recycling capacity. The initiation of carbon and nutrient cycles by coral-derived organic matter will, therefore, likely be reduced by coral bleaching.

Bleaching-induced mortality of the coral polyp also results in the exposure of bare skeletons. These structures are particularly sensitive to physical, chemical, and biological erosion processes (Stoddart 2008). In addition, colonisation of these stable surfaces by microbial biofilms, algae, or other invertebrates may not only reduce coral recruitment success (e.g. Webster et al. 2004), but also change important biogeochemical processes in the reef, such as nitrogen fixation (Davey et al. 2008).

1.6 Coral susceptibility and resilience to bleaching and subsequent reef degradation

1.6.1 Susceptibility and resilience

In corals, photosynthesis of endosymbiotic zooxanthellae is significantly affected by light availability and water temperature. These environmental factors can affect coral susceptibility and resilience to bleaching, and because of this, considerable work has gone into understanding the parameters that influence light and temperature conditions in coral reef ecosystems (reviewed in: Brown 1997; Hoegh-Guldberg 1999; Loya et al. 2001; Baker et al. 2008; van Woesik and Jordán-Garva 2011). Given the spatial and temporal heterogeneity in marine environments and in climatic processes, and their dynamic interactions that are potentially confounding, it has not been easy to unequivocally discern all environmental processes affecting coral reef systems.

Ecological resilience is the potential of an ecosystem to absorb repeating disturbances and adapt to change while keeping its function and structure (Holling 1973; Nyström et al. 2000; Scheffer et al. 2001; Nyström et al. 2008). Resilience of corals against coral bleaching encompasses the processes of resistance and recovery (Pimm 1984; West and Salm 2001), which represent two important environmental indicators of how corals cope with climate change and direct anthropogenic and natural disturbances. Resistance describes the capability of corals to withstand or to survive bleaching and bears an extrinsic (function of environmental factors) and an intrinsic, species-specific component (West and Salm 2003). Recovery is the process of regeneration after a severe bleaching event that resulted in significant mortality, and is directly associated with the growth and the replenishment of communities via coral recruitment (Marshall and Schuttenberg 2006; Diaz-Pulido et al. 2009).

At the ecosystem level, there is a degree of overlap in resilience and susceptibility, because those factors that make a coral reef susceptible can also increase systemic resilience depending on temporal and spatial occurrence of impacting factors. Research addressing the environmental factors that can mitigate coral bleaching and enhance recovery potential and resilience has identified several environmental indicators. Factors that mitigate thermally induced coral bleaching (Brown 1997; Hoegh-Guldberg 1999; Hughes et al. 2003; van Oppen and Lough 2009) include decreased temperature stress during warm periods through either local seasonal upwelling (Glynn 1996; Riegl and Piller 2003; Chollett et al. 2010) or long amplitude internal wave pulses (Wall et al. 2012). Currently, upwelling-induced mitigation of coral bleaching, and consequently resilient reefs were observed in the western coast of Mexico (Glynn and Leyte-Morales 1997; Reyes-Bonilla 2001; Reyes-Bonilla et al. 2002), the Gulf of Panama (Podestá and Glynn 1997; Glynn et al. 2001), the Gulf of Papagayo/Costa Rica (Jiménez et al. 2001), the Bahamas (Riegl and Piller 2003), South Africa (Riegl 2003), Northern Madagascar (McClanahan et al. 2007), and the Colombian Caribbean (Rodríguez-Ramírez et al. 2008; Bayraktarov et al. 2012; Chapter 6). In addition, Wall et al. (2012) observed that corals of the Andaman Sea/Thailand at sites exposed to deep-water intrusions by long amplitude internal waves were less susceptible to coral bleaching than corals at sheltered sites. Less coral bleaching and faster recovery was also observed in regions with exposure to a naturally high water flow (Nakamura and van Woesik 2001; Nakamura et al. 2003; West and Salm 2003). Hydrodynamics enhance water flow-induced mass exchange (e.g., respiration or uptake of nutrients) and molecular transport processes (Huettel et al. 2003), and have considerable consequences for coral physiology (Atkinson et al. 1994; Mass et al. 2010; Wild et al. 2012). They play a role in the removal of toxic Reactive Oxygen Species (ROS) and its derivatives, which are produced during bleaching (Nakamura and van Woesik 2001; Lesser 2006) (section 1.3).

Bleaching can also be influenced by the amount and type of irradiance that arrives at the corals through the atmosphere and water. An increase in particle concentrations within either environment results in the scattering of light and the lessening of its intensity. This has been demonstrated in the Tuamotu Islands, where the absence of bleaching was attributed to high cloud cover (Mumby et al. 2001b). Likewise, coastal reefs with high levels of suspended terrigenous material display less bleaching than reefs further from shore (West and Salm 2003). Similarly, coral bleaching was less in areas that received shading, such as reefs near tall cliffs in the Pacific (Salm et al 2001). However, it is not just the quantity of light that reaches the corals, but also the quality of light can have strong impacts. Increases in ultraviolet radiation can cause photoinhibition (section 1.3) and this can be a concern for corals in shallow water or in geographical areas with a damaged atmospheric layer (Shick et al. 1996). Bleaching has also been attributed to other factors including reduced salinity (Kerswell and Jones 2003) and exposure to toxins (Jones et al. 1999) (section 1.2), and although these can present localised confounding factors, most managers assessing bleaching susceptibility consider the mediation of high water temperatures of most importance due to its widespread implications (section 1.7). Faster recovery from bleaching and thereby higher resilience in the long term was attributed to corals that increased their heterotrophically acquired carbon budget (Grottoli et al. 2006) (section 1.3).

Understanding the effect of varying environmental conditions on corals is becoming increasingly important, because climate change is likely to increase the spatial and temporal variability of these factors, some of which are directly related to coral bleaching. When high temperature anomalies are severe and prolonged, as can be experienced during El Niño years, regional-scale bleaching can be pronounced (Glynn 1993) (section 1.2). In some regions, the frequency and intensity of tropical storms may also increase (Hughes et al. 2003), although, there are indications that storms may provide a net benefit to coral reefs because they mix warming surface layers with deeper waters (Riegl 2007). Changes in global weather patterns will lead to more extreme rainfall in some areas (Hoegh-Guldberg et al. 2007). This, combined with increasing coastal populations, may increase pollution and eutrophication on near-shore reefs (Glynn 1996), reducing overall coral fitness and making them more susceptible to bleaching. Moreover, thermal expansion of the oceans indicates that sea levels will continue to rise, and further redistribution of heat in the oceans may lead to changes in the dominant currents known as the "global conveyor belt" (Hoegh-Guldberg and Bruno 2010). Although not a direct factor of coral bleaching, ocean acidification may lead to a reduction in carbonate accretion and density, resulting in a decrease in overall coral fitness (Hoegh-Guldberg et al. 2007). The synergistic effects of these factors, and the changes on spatial and temporal scales, indicate that reefs will experience increasingly variable environmental conditions, and thus, increasing stress that promotes the likelihood of coral bleaching events. This is particularly true for reefs with pre-existing environmental factors, such as land-based pollution of areas with limited cold water exchange, which may increase their susceptibility and make them less resilient to bleaching events.

1.6.2 Reef degradation

In worst case scenarios, combined stressors will interact before, during and after bleaching events leading to increased degradation of reefs. Within coral reef communities, there is taxonomic variation in susceptibility to bleaching (van Woesik et al.

2011) (section 1.5). Coral reefs are generally resilient to localised disturbances because depleted populations can be repopulated by unaffected populations (Sale 1991). However, the extent of coral bleaching can vary depending on population composition and susceptibility (section 1.5), and community effects can vary based on the extent of bleaching events. Immediate ecological responses to bleaching events are less studied than longer-term responses, but studies have shown that other (non-coral) species are affected by their degree of specialisation to corals and their ability to shift resources during alternative ecological states (Pratchett et al. 2009). Specifically, species that rely on corals for food or habitat, such as fish, show the quickest changes in populations, while reduction in coral populations may have sub-lethal effects on coral-specific organisms because later generations are not able to find habitat for recruitment. For example, butterfly fish and certain damselfish populations that experienced losses after extreme bleaching events were able to shift to bleached coral for habitat, but declined because the impacted reef was not suited for larval recruitment (Wilson et al. 2006). Therefore, it may be possible to use species that react strongly to changes in coral communities as pre-bleaching indicators of potential, post-bleaching, coral reef health.

Bleaching-induced changes in habitat can lead to the long-term loss of species and function and overall degradation of reefs. On the community level, continuing function depends on the pre- and post-condition of the reef. In the Caribbean, reefs that existed in equilibrium state between corals and algae became algae-dominated after a relatively minor bleaching event due to an already reduced herbivore community (Ostrander et al. 2000), indicating that the pre-bleaching status of the ecosystem leads to higher levels of susceptibility. Sub-lethal effects on coral reef species, or inter-generational effects, depend on the recovery of the current system.

Although the susceptibility of coral reefs to degradation in relation to coral bleaching events is not easy to understand fully, many indications of possible effects can depend on the environment (changes in light attenuation and water temperature) and the community composition (present groups of organisms). It may be possible to use these conditions as an indication of susceptibility and the possible effects on these vulnerable ecosystems.

1.7 Management strategies against coral bleaching

Coral survival and recovery prospects can be promoted through appropriate marine protected area (MPA) design (Salm et al. 2001). Conservation priority is often focused on areas of high-biodiversity (hotspots) that are currently exposed to local anthropogenic stressors (Myers et al. 2000). The disadvantage of this conservation strategy is that the influence of climate change is hardly manageable because local processes such as overfishing or pollution reduce reef resilience prior to climate change driven impacts. Therefore, West and Salm (2003) suggested identifying areas with low exposure to climate threats and reducing human impact on these particular regions (section 1.6). This would assure the potential for corals to persist in "refugia" and resist bleaching in times of changing climate (Glynn 2000; Riegl and Piller 2003). Current conservation strategies take into account reef resilience assessments during climate change in order to define management priorities (Obura and Grimsditch 2009; Maynard et al. 2010). McClanahan et al. (2012) recently proposed an evidence-based framework for the identification of climate change resilience of coral reefs to define conservation priorities. This novel framework includes the measurement of 11 key factors selected by perceived importance, empirical evidence, and feasibility of measurement (McClanahan et al. 2012). Rau et al. (2012) go one step further and encourage marine science and management communities to evaluate actively all marine management strategies, including unconventional ones such as shading of local reefs from solar radiation during increased thermal stress (Jones et al. 1998; Hoegh-Guldberg 1999; Jones et al. 2008), low-voltage direct current, which has been proposed to stimulate coral growth (Sabater and Yap 2002; Goreau et al. 2004; Sabater and Yap 2004), and wave- or tidal powered artificial upwelling (Kirke 2003; Hollier et al. 2011). In times of dramatic climate change, our hope lies in the most resilient reefs and the increase of reef resilience through management actions, which should, therefore, be considered as essential conservation priorities.

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6

Bleaching Susceptibility and Recovery of Colombian Caribbean Corals in Response to Water Current Exposure and Seasonal Upwelling

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Abstract

Coral bleaching events are globally occurring more frequently and with higher intensity, mainly caused by increases in seawater temperature. In Tayrona National Natural Park (TNNP) in the Colombian Caribbean, local coral communities are subjected to seasonal wind-triggered upwelling events coinciding with stronger water currents depending on location. This natural phenomenon offers the unique opportunity to study potential water current-induced mitigation mechanisms of coral bleaching in an upwelling influenced region. Therefore, coral bleaching susceptibility and recovery patterns were compared during a moderate and a mild bleaching event in December 2010 and 2011, and at the end of the subsequent upwelling periods at a water current-exposed and -sheltered site of an exemplary bay using permanent transect and labeling tools. This was accompanied by parallel monitoring of key environmental variables. Findings revealed that in 2010 overall coral bleaching before upwelling was significantly higher at the sheltered (34 %) compared to the exposed site (8 %). Whereas 97 % of all previously bleached corals at the water current-exposed site had recovered from bleaching by April 2011, only 77 % recovered at the sheltered site, but 12 % had died there. In December 2011, only mild bleaching (< 10 % at both sites) was observed, but corals recovered significantly at both sites in the course of upwelling. No differences in water temperatures between sites occurred, but water current exposure and turbidity were significantly higher at the exposed site, suggesting that these variables may be responsible for the observed site-

specific mitigation of coral bleaching. This indicates the existence of local resilience patterns against coral bleaching in Caribbean reefs.

Introduction

Climate change can impede scleractinian corals in their role as reef ecosystem engineers (Gutiérrez et al. 2011; Wild et al. 2011) mainly because mass coral bleaching, one of the main consequences of climate change-induced ocean warming, negatively impacts growth and health of affected corals (Hoegh-Guldberg et al. 2011).

In 2005, such a mass coral bleaching event affected 80 % of all Caribbean reef corals, after which 40 % died, when thermal stress exceeded any recorded data on seawater temperature of the last 20 years (Wilkinson and Souter 2008). This particular mass coral bleaching event was later termed the “Caribbean Crisis” (Eakin et al. 2010). However, local differences were considerable. In the Colombian Caribbean, up to 80 % of all hard corals showed signs of bleaching in locations such as Islas del Rosario (Cartagena) or Islas San Bernardo (Rodríguez-Ramírez et al. 2008). In contrast, no severe bleaching occurred for coral communities in the bays of the Tayrona National Natural Park (TNNP) near the city of Santa Marta before 2010 (Rodríguez-Ramírez et al. 2008; Rodríguez-Ramírez et al. 2010). During the “Caribbean Crisis” in 2005, only 1 – 5 % of the coral cover in TNNP was affected by bleaching with a negligible mortality of below 1 % (Rodríguez-Ramírez et al. 2008).

It remains uncertain why hard corals in the TNNP were not affected by the “Caribbean Crisis”. This area is of high interest and suitable for studies on adaptation potential of corals as it is influenced by pronounced changes of environmental variables between a rainy season with high precipitation and riverine discharge and a dry season that goes along with seasonal coastal upwelling (Salzwedel and Müller 1983; Andrade and Barton 2005; Bayraktarov et al. 2012). The major rainy season (May-November) is represented by low winds, more than 80 % of the annual rainfall, low salinity and increased seawater temperature (Salzwedel and Müller 1983; Paramo et al. 2011). Highest seawater temperatures usually occur between October and November and can reach up to 30 °C (Bayraktarov et al. 2012).

The TNNP constitutes one of three major upwelling nuclei of the Guajira Upwelling System (Paramo et al. 2011) extending from the Guajira Peninsula, near the border with

Venezuela, to the city of Santa Marta in the Colombian Caribbean (Andrade and Barton, 2005). The Guajira Upwelling is part of the Southern Caribbean Upwelling System (Rueda-Roa and Muller-Karger 2013). Upwelling coincides with the major dry season (December-April), during which the bays of TNNP are exposed to strong winds from the Caribbean low-level jet of north-east trade winds (Andrade and Barton 2005). Increased winds parallel to the coast displace humidity and trigger an Ekman transport off the coast and an upwelling of sub-surface waters in the coastal zone (Andrade et al. 2003; Andrade and Barton 2005). This seasonal upwelling thereby leads to changes in physicochemical variables such as temperature decrease (from 28 °C to 21 °C) (Salzwedel and Müller 1983; Paramo et al. 2011; Bayraktarov et al. 2012; Chapter 1, 2) and salinity increase (from 33 to 38) (Salzwedel and Müller 1983; Bayraktarov et al. 2012; Chapter 2). Increased concentrations of inorganic nutrients and chlorophyll *a* characterize the usually oligotrophic region during non-upwelling as mesotrophic in periods of upwelling (Franco-Herrera et al. 2007; Chapter 2). The wind pattern triggering upwelling may lead to a different exposition of higher wave- and water current-impact at all western sides of the TNNP bays as compared to the sheltered eastern sides due to their topographical orientation.

It was first hypothesized by Glynn (Glynn 1996) and later supported by several other studies (Riegl and Piller 2003; West and Salm 2003; Chollett et al. 2010) that upwelling centers can serve as refuge areas for corals by counteracting seawater temperature increases that may provoke coral bleaching. Further studies provide evidence for reduced coral bleaching in other upwelling-affected regions such as on the western coast of Mexico (Glynn and Leyte-Morales 1997; Reyes-Bonilla 2001; Reyes-Bonilla et al. 2002), the Gulf of Panama (Podestá and Glynn 1997; Glynn et al. 2001), the Gulf of Papagayo/Costa Rica (Jiménez et al. 2001), the Bahamas (Riegl and Piller 2003), South Africa (Riegl 2003), Northern Madagascar (McClanahan et al. 2007) and TNNP (Rodríguez-Ramírez et al. 2008). Chollett et al. (2010) suggested the TNNP region as potential refuge area against coral bleaching as seasonal upwelling events may coincide with severe warming events and consequently offset bleaching impact due to upwelling-induced seawater temperature decrease.

However, so far no studies have addressed the effects of water-current exposition on coral communities in a region influenced by seasonal upwelling. We hypothesize that local differences of coral bleaching mitigation through water current exposure are present in TNNP which make corals at water current-exposed sites less susceptible to bleaching than their water current-sheltered counterparts.

The goal of the present study was therefore to observe coral bleaching susceptibility and recovery patterns between water current-exposed and -sheltered sites of one exemplary bay in TNNP by a detailed monitoring, to compare bleaching incidence over a study period of two years (2010 – 2012) and to understand possible mechanisms of water current-mediated coral bleaching mitigation in a region with seasonal upwelling. For this purpose, coral bleaching monitoring campaigns (line-transect methods and labeling tools) and measurements of key environmental variables (water temperature, salinity, water currents, inorganic nutrient concentrations, chlorophyll *a*, and water clarity as indirect measure for turbidity) were combined.

Materials and methods

Ethics statement

All necessary permits were obtained for the described study by Instituto de Investigaciones Marinas y Costeras (Invemar) in Santa Marta, Colombia which complied with all relevant regulations.

Description of study site

The TNNP is located at the northern coast of Colombia (Fig. 1A) and represents a biodiversity hotspot in the Colombian Caribbean (Garzón-Ferreira and Cano 1991). The region is affected by a distinct seasonality including a rainy and a dry season during which coastal upwelling occurs. In this study, the months December, January, February, March and April were categorized as upwelling (dry season) and the months May, June, July, August, September, October and November, as non-upwelling (rainy season) according to (Salzwedel and Müller 1983; Diaz-Pulido and Garzón-Ferreira 2002; Paramo et al. 2011).

The study was carried out in Gayraca Bay, located at 11.33 °N, 74.11 °W (Fig. 1B). Here, moderate coral bleaching was observed at the beginning of this study in November 2010. Therefore, monitoring of coral communities was initiated in December 2010 and proceeded until April 2012. A water current-exposed site on the western side of the bay with strong impact of winds, waves and water currents, and a water current-sheltered site on the eastern side of the bay were selected for investigation. The sites had a hard coral cover of 41 ± 9 % at the exposed and 24 ± 1 % at the sheltered site (determined in December 2011), and were located ca. 1 km away from each other (Fig. 1C).

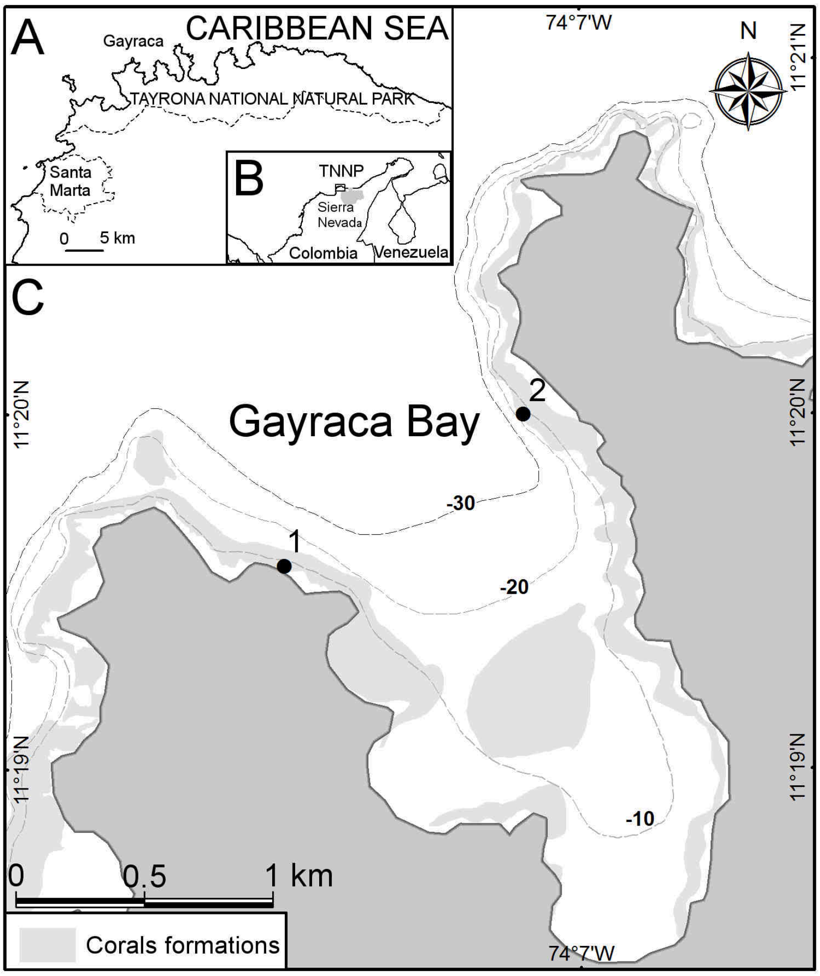

Figure 1. Location of Gayraca Bay and Tayrona National Natural Park (TNNP) in the Caribbean Sea. (A) Location of TNNP. (B) The bays of TNNP and city of Santa Marta. (C) Sampling locations in Gayraca Bay. Circles indicate (1) water current-exposed and (2) -sheltered site. Depth contours are depicted with dashed lines. Source of map: Invemar 2012.

Coral bleaching monitoring

Scleractinian corals were monitored by SCUBA along permanent line-transects at the water current-exposed and -sheltered site (Fig. 1C) in a water depth of 10 ± 1 m. Surveys on coral bleaching were performed in two campaigns and at both sites. Therefore, one campaign consisted in monitoring of coral bleaching before onset of upwelling in December and a repeated monitoring during coral recovery phase end of upwelling in March/April the following year. During the first campaign, monitoring was performed on 5 transects of 10 m length and during the second on 3 transects of 50 m length.

Transect replicates were arranged at 1 – 3 m from each other. Coral bleaching was observed after seawater temperature increased (associated with El Niño in 2010) and unusually strong rainfalls (NOAA´s Climate Prediction Center, www.cpc.ncep.noaa.gov). Permanent transects were labeled using buoys at beginning and end of each transect as well as by equally spaced marks (every ~3 m) fixed on the ground throughout each transect. A measuring tape was attached to the buoys and marks during monitoring. Corals were identified at the species level. All surveyed corals were marked by labeling tools (nails with plastic marks indicating colony numbers) during the first campaign and by underwater maps containing exact coral position and species identification during the second campaign in order to survey same coral colonies over time. Coral bleaching and recovery were monitored for each coral colony along the line transects according to BLAGRRA (http://www.agrra.org/BLAGRRA). Coral condition was categorized and scored as normal (0), pale (1), bleached (2) and recently dead/overgrown (3). A lower score denominated a better condition during coral bleaching event or more efficient regeneration during recovery phase.

Site-specific bleaching and mortality indexes (BMI) were calculated according to (McClanahan 2004) for each site and coral bleaching monitoring campaign according to the formula:

$$BMI = \frac{(0 \cdot c1 + 1 \cdot c2 + 2 \cdot c3 + 3 \cdot c4)}{3}$$

in which the % coral cover of each coral condition category (c_1 = normal, c_2 = pale, c_3 = bleached and c_4 = recently dead/overgrown) was weighted by their score 0 – 3.

The community bleaching susceptibility index (CBSI) was calculated in analogy to BMI (McClanahan 2004; Wall et al. 2012) as an index for bleaching response of coral communities at each site taking their specific susceptibility to bleaching into account. Calculations involved 5 species for the exposed and 8 for the sheltered site. Mean benthic cover data of each of these species along 3 transects of 50 m from the second coral bleaching monitoring campaign was used due a more comprehensive representation of the coral community at both sites. The surveyed coral species were ranked according to their reported bleaching susceptibility (CARICOMP 1997; McField 1999; Manzello et al. 2007) into 4 bleaching susceptibility groups (0 – 3). Therefore, *Montastraea cavernosa* (s_1) accounted for less susceptible corals with no weight (0); *Colpophyllia natans* (s_2), *Diploria* *strigosa* (s_3) and *D. labyrinthiformis* (s_4) were addressed as moderate susceptible with a score of (1); *Porites astreoides* (s_5) and *Siderastrea siderea* (s_6) were susceptible with (2), and *Orbicella faveolata* (s_7) and *O. franksi* (s_8) (formerly referred to as *Montastraea faveolata* and *Montastraea franksi*; Budd et al. 2012) belonged to corals characterized as highly susceptible with (3) (CARICOMP 1997; Manzello et al. 2007). The following formula for CBSI was modified from Wall et al. (2012) where s_1 to s_8 represent the live coral cover of each species in %:

$$CBSI = \frac{(0 \cdot s1 + 1 \cdot (s2 + s3 + s4) + 2 \cdot (s5 + s6) + 3 \cdot (s7 + s8))}{3}$$

Monitoring of environmental variables

All measurements (water currents) and water samplings (for salinity, inorganic nutrients and chlorophyll *a* concentration) were performed monthly at a water depth of 10 m and in direct vicinity (within a radius of 20 m) to the first coral monitoring transects at both study sites (Fig. 1C). Water temperature was measured continuously in situ using calibrated HOBO TidBit v2 temperature loggers (Onset Computer Corp., Bourne, USA) with temporal intervals of 5 min and accuracy of ± 0.2 °C between October 2010 and May 2012. Therefore, loggers were attached to the reef structure and 10 m water depth at both study sites.

Water current exposure was determined by the clod card technique (Doty 1971; Jokiel and Morrissey 1993) using gypsum clods (type "stone", Class III, Dentales America Ldta, Bogotá, Colombia) attached to acrylic plates by water-proof contact cement (Líder Epoxi SinteSolda, Sinteco S. A., Bogotá, Colombia) between February 2012 and February 2013. Time of deployment on the reef structure was 48 ± 2 h (n = 4 per site and month). Still water controls were obtained by inserting clod cards into a closed 35 L bucket with predrilled holes avoiding a saturation of gypsum (n = 4 per month, sheltered site), as described elsewhere (Jokiel and Morrissey 1993). Diffusion factor index (DF) was used as an indirect measure of water current velocity and was obtained by dividing the weight loss of water current exposed gypsum clods by their calm water controls (Doty 1971; Watson 1976; Jokiel and Morrissey 1993).

Water samples for determination of salinity, inorganic nutrient concentrations (nitrate, nitrite and soluble reactive phosphorus (SRP) mainly present in the form of orthophosphate) and chlorophyll *a* were collected using 3.8 L plastic containers (n = 3 per site and month) from the water column 1 m above the bottom and between January

2011 and February 2013 and 8 - 11 am. Salinity was measured with a portable meter (HQ40d, Hach, Loveland, USA) equipped with a 4-pole conductivity probe (CDC401, Hach, Loveland, USA) with accuracy of ± 0.1. Samples were transported on ice and dark to the laboratory, filtered immediately (glass fiber filters, 0.7 µm particle retention, VWR International) and frozen at -20 °C until analysis. Inorganic nutrient concentrations from seawater samples were measured spectrophotometrically according to (Garay et al. 2003). Chlorophyll *a* from filters was extracted by 6 mL 90 % acetone per sample for 24 h at 4 °C and dark. Measurements were performed by a fluorometer (10AU™ Field Fluorometer, Turner Designs, Sunnyvale, USA) with a detection limit of 0.025 µg L^{-1}.

Measurements of water clarity as an indirect measure of turbidity were performed monthly by Secchi disc with a replication of n = 4 at each site in Gayraca Bay between May 2011 and February 2013. Measurements were conducted at the shady side of the boat at 8 - 11 am.

Data analyses

Permutation multivariate analysis of variance (PERMANOVA; Anderson et al. 2008) was applied for multivariate data of the coral bleaching monitoring and univariate data on monthly monitored environmental variables. Tests were performed using type III sums of squares and 999 permutations under a reduced model. For analysis of coral bleaching, relative proportions of corals characterized as normal, pale, bleached and recently dead/overgrown per transect (variables) were evaluated while each transect represented an independent sample. Site (2 levels: exposed vs. sheltered) and monitoring time (2 levels: before upwelling vs. end of upwelling) were set as fixed factors for analysis. Euclidean similarity distance was applied to create the resemblance matrix for all analyses. For analyses of environmental monitoring variables, univariate PERMANOVA routines were applied after resemblance of monthly means for each variable (temperature, degree-heating days, salinity, water current velocity, nitrate, nitrite, SRP, chlorophyll *a*, and water clarity) and the fixed factors site (2 levels: exposed vs. sheltered) and season (2 levels: upwelling vs. non-upwelling).

Temperature indices (mean, maximum and minimal water temperature) were calculated from *in situ* continuous temperature measurements (every 5 min) and are represented as monthly and seasonal means for both sites during the study period. Degree-heating days were calculated from daily mean temperature data according to

(Podestá and Glynn 1997), in analogy to degree-heating weeks (Gleeson 1994; Gleeson and Strong 1995). Seawater temperature above the locally-calculated coral bleaching threshold of 29.4 °C (Tošić and Navas-Camacho 2012) was considered as thermal stress.

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-ELtd., UK). The software SigmaPlot12.0 (Systat Software, Inc) was used for graphical representation of data.

Results

Coral bleaching monitoring

Coral bleaching occurred at the end of 2010 and 2011 in the TNNP region. The bleaching extent was higher in December 2010 (8 – 34 %) than in December 2011 (4 – 6 %; Fig. 2). During the first coral bleaching monitoring campaign, significant differences were found between sites (Table 1) indicating that the proportion of overall bleached corals was significantly smaller at the exposed compared to the sheltered site (8 % vs. 34 %, respectively; Fig. 2). Sites had a different community composition with *O. faveolata* and *O. franksi* only occurring at the sheltered site (Fig. 3). Here, in December 2010, 100 % of all *O. faveolata* and 88 % of *O. franksi* were bleached (Fig. 3A). The content of 19 % pale corals were distributed over 29 % of all *M. cavernosa*, 13 % of *O. franksi*, 14 % of *D. strigosa* and 33 % of *P. astreoides* (Fig. 3A). At the exposed site, 17 % of all *M. cavernosa* and 33 % of all *D. labyrinthiformis* were bleached (Fig. 3B). These corals were not observed to bleach at the sheltered site. The remaining 16 % pale corals at the exposed site were distributed over 16 % of all *M. cavernosa* and 22 % *D. strigosa* (Fig. 3B).

During the second coral bleaching monitoring campaign, 6 % of the corals bleached at the exposed and 4 % at the sheltered site, whereas same coral species were affected at both sites (Fig. 4). Here, no significant difference in relative proportion of overall bleached corals was observed between sites (Table 1). Bleaching was mainly represented by the species *D. strigosa* (3 % bleached) at the sheltered site, *M. cavernosa* (15 %) at the exposed site and *S. siderea* at both sites (14 % at sheltered and 40 % at exposed, Fig. 4).

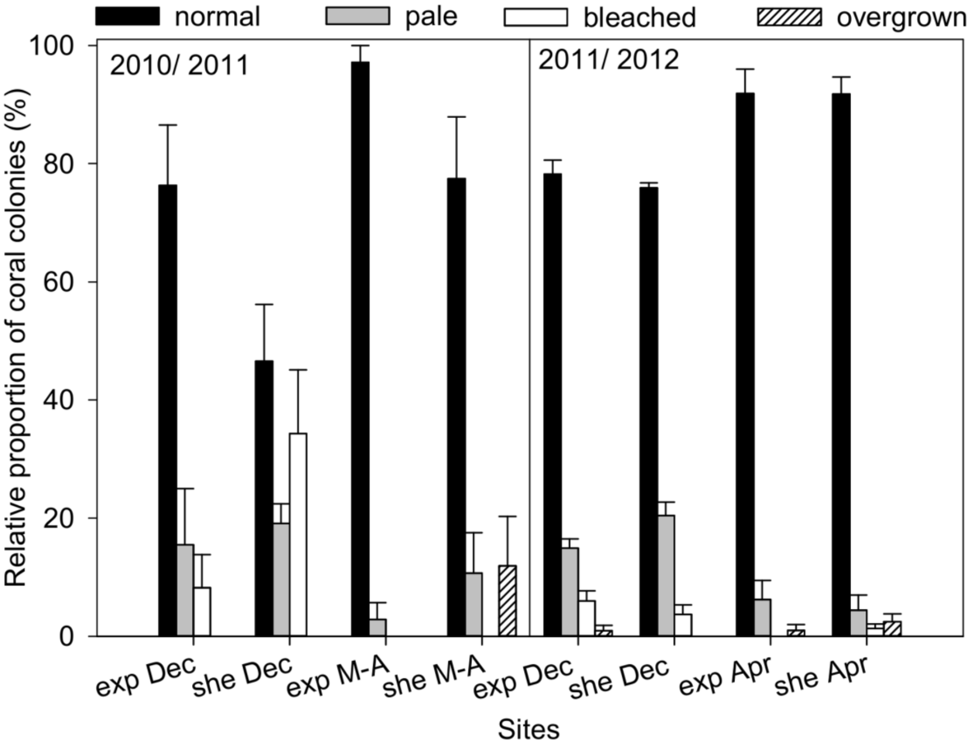

Figure 2. Relative proportion of normal, pale, bleached and overgrown coral colonies. Coral conditions during two coral bleaching monitoring campaigns (December (Dec) 2010-March/April (M-A) 2011 and December 2011-April (Apr) 2012) for the water current-exposed (exp) and -sheltered (she) site in Gayraca Bay along line transects and a water depth of 10 m are illustrated. Replication during first monitoring campaign (2010/2011) accounted for 5 transects of 10 m length and during second monitoring campaign (2011/2012) for 3 transects of 50 m length, respectively. Mean values of transect replicates + SE are displayed.

During the first coral bleaching monitoring campaign, significant differences in monitoring time (Table 1) indicated a recovery of corals from bleaching. Whereas 20.8 % of the relative coral proportion (pale and bleached; Fig. 2) recovered after upwelling with a rate of 7.0 % month^{-1} at the water current-exposed site, a higher pale and bleached coral proportion of 30.8 % recovered at the sheltered site resulting in a recovery rate of 6.3 % month^{-1} (Fig. 2). An overall better recovery was observed at the exposed site where 97 % normal corals were found, whereas only 72 % could be identified as normal at the sheltered site and 12 % coral cover died here by April 2011.

During the second coral bleaching monitoring campaign, a significant difference between monitoring times (Table 1) indicated that corals recovered from bleaching by the end of upwelling. Here, rates of recovery between sites were similar for the mild bleaching resulting in 3.4 % month^{-1} at the exposed and 3.5 % month^{-1} at the sheltered site.

Table 1. PERMANOVA results for two campaigns of coral bleaching monitoring. Levels of significance are indicated by asterisks with * for significant ($p < 0.05$) and ** for very significant ($p < 0.01$). Abbreviations: degrees of freedom (df), sum of squares (SS, type III), mean sum of squares (MS).

	First coral bleaching monitoring (2010/2011)					Second coral bleaching monitoring (2011/2012)				
	df	*SS*	*MS*	Pseudo-*F*	*p*	*df*	*SS*	*MS*	Pseudo-*F*	*p*
Site	1	0.424	0.424	4.917	0.013*	1	0.002	0.002	0.389	0.663
Time	1	0.633	0.633	7.339	0.004**	1	0.120	0.120	24.700	0.003**
Site * time	1	0.117	0.117	1.360	0.271	1	0.006	0.006	1.172	0.296
Residuals	16	1.381	0.086			8	0.039	0.005		
Total	19	2.555				11	0.167			

The BMI as a measure of coral bleaching response was 0.28 in December 2010 and 0.30 in December 2011 for the exposed site, whereas at the sheltered site, a higher BMI of 0.88 and a similar BMI of 0.28 were registered, respectively. During recovery phases of both years, BMI was lower for the exposed site with 0.03 in March/April 2011 and 0.09 in April 2012 as compared to 0.46 and 0.15, respectively. The CBSI characterizing the specific bleaching susceptibility of the coral community was 8.8 for the exposed and 13.2 for the sheltered site indicating higher susceptibility of coral community to bleaching here.

Water column variables

A seasonality for the TNNP region was deduced from in situ seawater temperature of 28.5 ± 1.1 °C (mean ± SD) and salinity of 35.3 ± 1.6 during non-upwelling (rainy season) as compared to 25.0 ± 1.7 °C and 37.0 ± 0.9, during upwelling (dry season), respectively. Water temperature ranged from 20.3 °C (February 2012) to 30.3 °C (October 2011) and salinity from 32.5 (October, June) to 38.5 (January; Fig. 5). Water temperature and salinity were significantly different between seasons (Table 2).

A locally-calculated coral bleaching threshold of 29.4 °C (Tošić and Navas-Camacho 2012) was used to define degree-heating days as described above. From this calculation, temperature anomalies of 21 degree-heating days at the exposed and 22 at the sheltered site were detected for October-November 2010 (Table 2). Continuous temperature monitoring in high temporal resolution did not reveal any statistical differences between sites. However, in 2011 the temperature anomaly for October-November accounted for 15 degree-heating days at the exposed and 23 at the sheltered site (Table 2). The total temperature anomaly during the rainy season in 2011 was represented by 23 degree-heating days at the exposed and 34 at the sheltered site (Table 3).

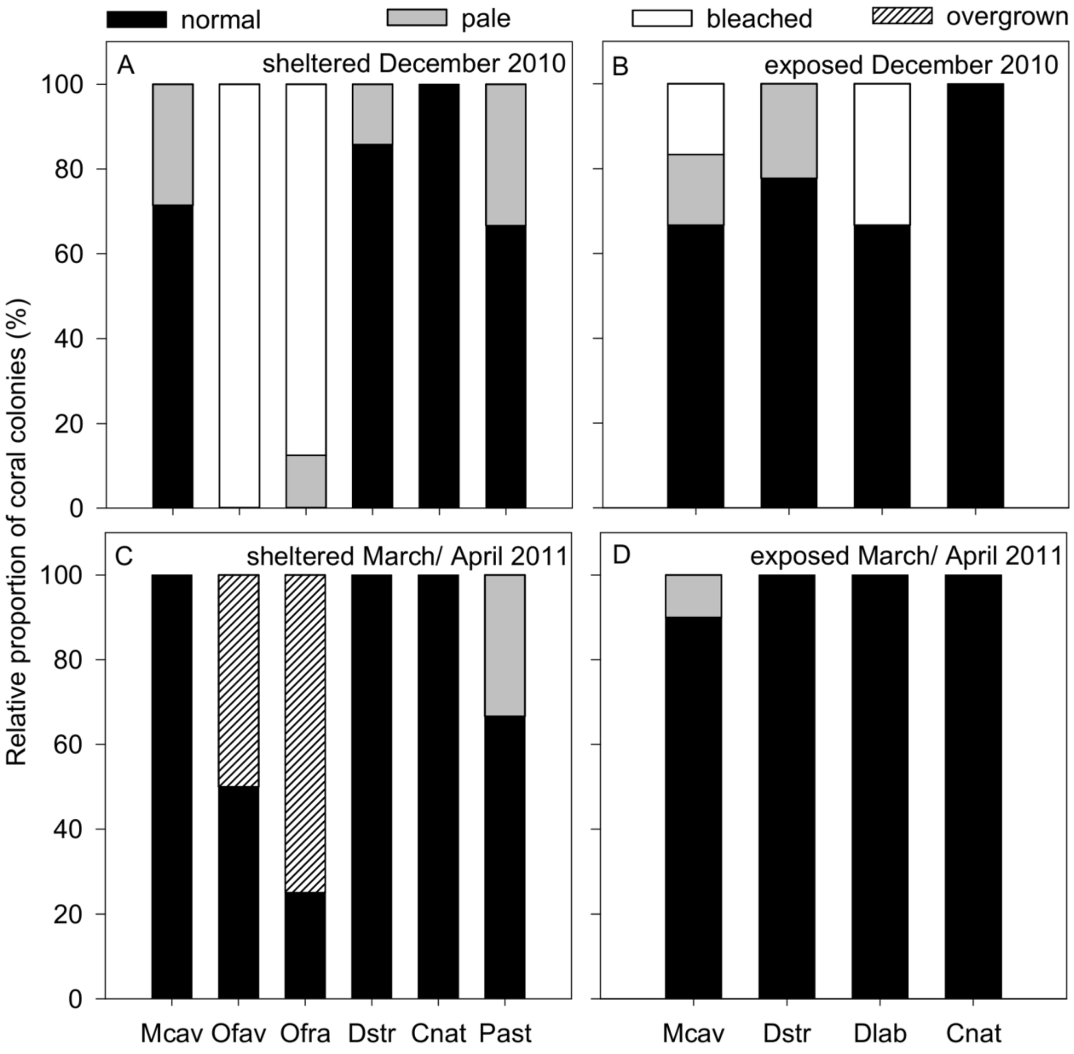

Figure 3. Relative proportion of coral species conditions during the first coral bleaching monitoring campaign. Condition of coral colonies (normal, pale, bleached, overgrown) along line-transects at the water current-exposed and -sheltered site in December 2010 and March/April 2011 in Gayraca Bay and a water depth of 10 m. Coral condition at the sheltered (A) and the exposed (B) site in December 2010 are displayed in the upper panels and (C) and (D) represent the sheltered and exposed site in March/April 2011. Abbreviations: *Montastraea cavernosa* (Mcav), *Orbicella faveolata* (Ofav), *O. franksi* (Ofra), *Diploria strigosa* (Dstr), *D. labyrinthiformis* (Dlab), *Colpophylla natans* (Cnat), *Porites astreoides* (Past).

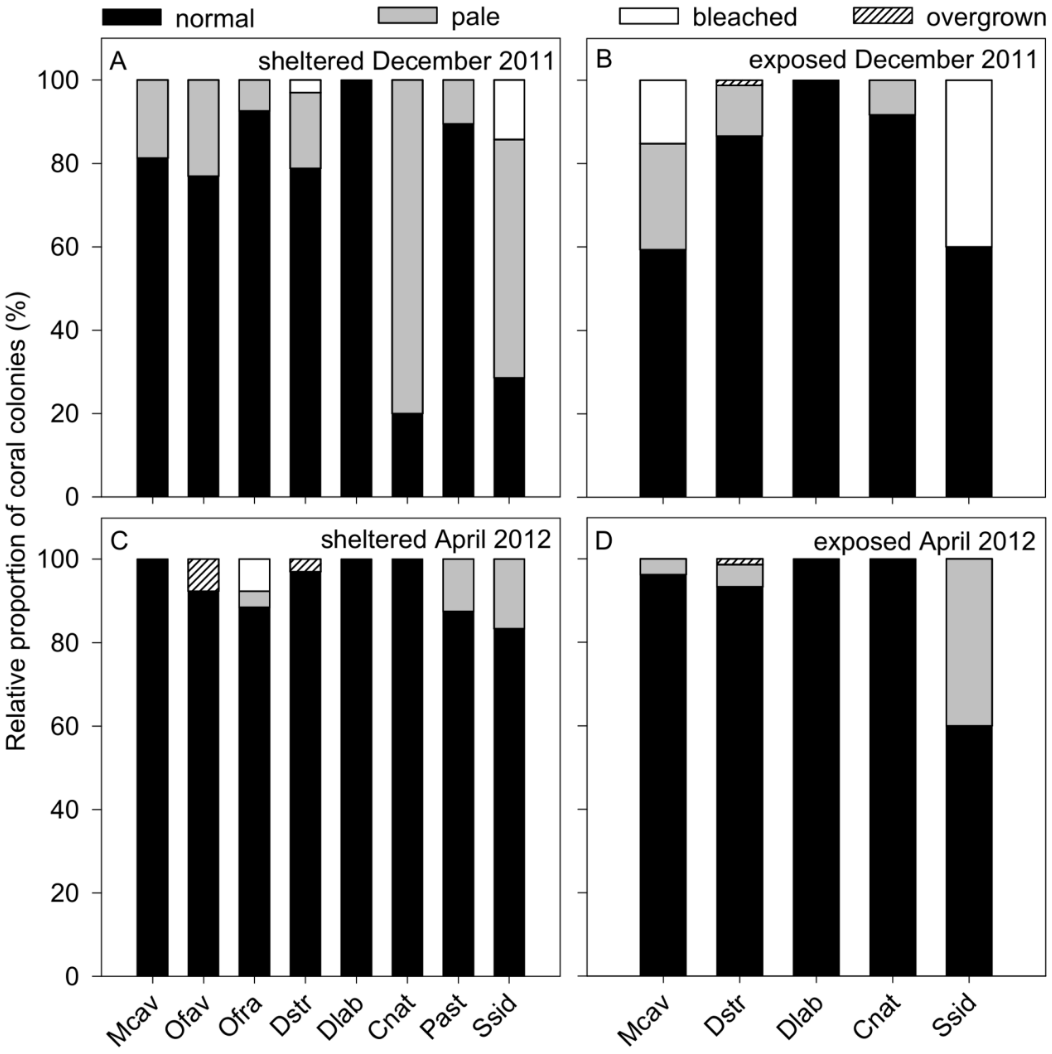

Figure 4. Relative proportion of coral species conditions during the second coral bleaching monitoring campaign. Condition of coral colonies (normal, pale, bleached, overgrown) along line-transects at the water current-exposed and -sheltered site in December 2011 and April 2012 in Gayraca Bay and a water depth of 10 m. Coral condition at the sheltered (A) and the exposed (B) site in December 2011 are displayed in the upper panels and (C) and (D) represent the sheltered and exposed site in April 2012. Abbreviations: *Montastraea cavernosa* (Mcav), *Orbicella faveolata* (Ofav), *O. franksi* (Ofra), *Diploria strigosa* (Dstr), *D. labyrinthiformis* (Dlab), *Colpopyllia natans* (Cnat), *Porites astreoides* (Past), *Siderastrea siderea* (Ssid).

Water currents measured by clod cards were significantly higher at the exposed as compared to the sheltered site according to still water control-normalized clod cards (Table 2).

Nitrate concentrations were significantly increased during upwelling when compared to non-upwelling (Table 2) with 1.20 ± 1.03 μmol L^{-1} at the exposed and 1.16 ± 1.12 μmol L^{-1} at the sheltered site as compared 0.15 ± 0.15 μmol L^{-1} and 0.31 ± 0.19 μmol L^{-1} during non-upwelling. However, no significant differences were found between sites (Table 2).

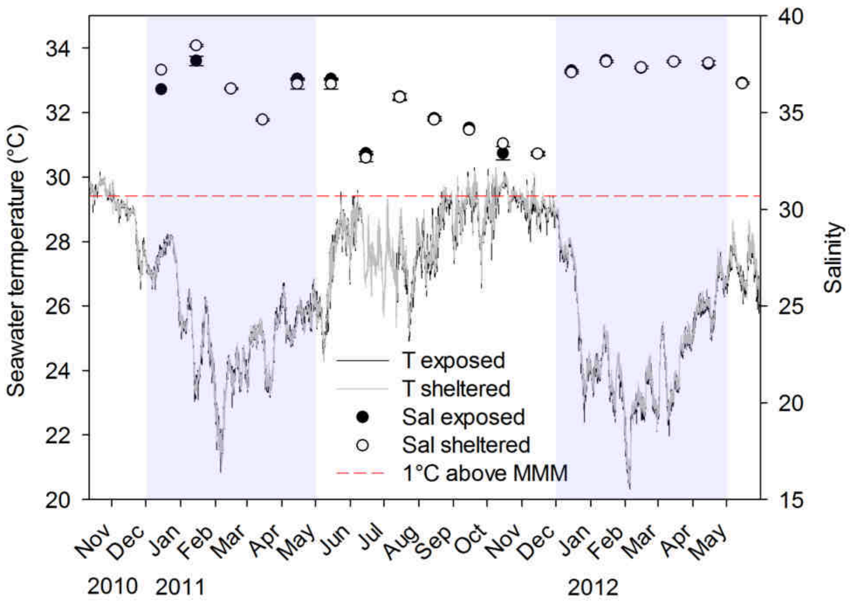

Figure 5. High resolution *in situ* seawater temperature and mean monthly salinity. Seawater temperature with a resolution of 5 min, accuracy of ± 0.2 °C and salinity as monthly means for the water current-exposed and -sheltered site of Gayraca Bay and a water depth of 10 m are displayed. The coral bleaching threshold of 1 °C above maximum monthly mean (MMM) (Tošić and Navas-Camacho 2012) is depicted as a red dashed line. Upwelling months December-April are highlighted in blue.

Chlorophyll *a* concentrations had mean concentrations of 2.25 ± 1.59 µg L^{-1} (mean ± SD) for the exposed and 1.02 ± 0.80 µg L^{-1} for the sheltered site during upwelling and 0.74 ± 0.28 µg L^{-1} and 0.87 ± 0.58 µg L^{-1}, respectively. Significant difference was observed between seasons but not between sites (Table 2).

Water clarity was significantly different between the exposed and sheltered site with more turbid water at the exposed site (Table 2). Significant differences between seasons revealed that seawater was more transparent during non-upwelling (Table 2).

Discussion

Bleaching susceptibility and recovery patterns of TNNP corals

In this study, we observed over a time period of two years that hard corals at a water current-sheltered site were more susceptible to coral bleaching than corals at an -exposed site in the upwelling influenced TNNP. Riegl and Piller (2003) observed that coral health and recovery from the mass bleaching event in 1998 for the Bahamas was better at sites where a small-scale upwelling was present (70 % healthy corals) as compared to nearby located sites governed by down-welling of heated surface water (44 % healthy corals). Jiménez et al. (2001) showed that corals at locations exposed to oceanic conditions and seasonal upwelling in Costa Rica experienced a reduced warming and consequently less coral bleaching than locations where upwelling was absent. Riegl (2003) reported that corals in South Africa were protected against coral bleaching by a seasonal upwelling whenever upwelling and warming coincided. Whereas the mentioned studies correlate a reduced coral bleaching during warming events to seawater temperature decrease, the present study is the first one to show that differences in susceptibility of corals were potentially driven by the degree of exposure to water currents as no temperature differences were detected between the sites in the same upwelling-influenced bay.

Table 2. Environmental variables and PERMANOVA results. Environmental variables are displayed as mean ± SD. Levels of significance for differences between sites (exposed vs. sheltered) and seasons (upwelling vs. non-upwelling) are indicated by asterisks with * for significant ($p < 0.05$) and ** for very significant ($p < 0.01$). Abbreviations: exposed site (exp), sheltered site (she), soluble reactive phosphorus (SRP), and diffusion factor index (DF).

	Non-upwelling (mean ± SD)		Upwelling (mean ± SD)		Sites		Seasons	
	exp	she	exp	she	Pseudo-*F*	*p*	Pseudo-*F*	*p*
Temperature (°C)	28.5 ± 1.1	28.4 ± 1.1	25.0±1.7	25.0 ± 1.7	0.000	0.994	79.157	0.001**
Degree-heating days	44	56	0	0	0.153	0.694	10.639	0.001**
Salinity	35.29 ± 1.53	35.29 ± 1.61	37.07 ± 0.94	37.03 ± 0.86	0.002	0.958	24.791	0.001**
Water currents (DF)	13.16 ± 7.66	7.81 ± 4.08	17.03 ± 6.93	9.93 ± 3.94	5.926	0.024*	1.359	0.275
Nitrate (µmol L^{-1})	0.15 ± 0.15	0.31 ± 0.19	1.20 ± 1.03	1.16 ± 1.12	0.022	0.899	19.393	0.001**
Nitrite (µmol L^{-1})	0.06 ± 0.04	0.09 ± 0.06	0.14 ± 0.08	0.14 ± 0.06	0.051	0.814	2.107	0.147
SRP (µmol L^{-1})	0.16 ± 0.14	0.15 ± 0.07	0.14 ± 0.13	0.14 ± 0.12	0.077	0.774	0.005	0.940
Chlorophyll *a* (µg L^{-1})	0.74 ± 0.28	0.87 ± 0.58	2.25 ± 1.59	1.02 ± 0.80	3.314	0.069	8.574	0.004**
Water clarity (m)	11.6 ± 2.1	12.7 ± 2.9	8.5 ± 1.7	11.1 ± 1.9	6.278	0.015*	4.274	0.044*

The results of our study are further supported by observations of Wall et al. (2012) where corals at the Similan Islands in the Andaman Sea (Thailand) at sites sheltered from deep-water intrusions by long amplitude internal waves (LAIW) were more susceptible to bleaching in 2010 (above 50 % bleached and recently dead corals) than corals at exposed sites (39 – 45 %) characterized by stronger currents and mixing of water masses (Roder et al. 2010). Similar to our study, Wall et al. (2012) found a difference in community composition of more susceptible coral species at the sheltered sites (*Acropora* spp. and massive *Porites* spp.), whereas the more resistant *Diploastrea* spp. were predominant at the exposed locations. Some of the susceptible coral species represented at both sites (e.g. *Pocillopora* spp. and branching *Porites* spp.) vanished from the sheltered sites and only remained in reduced numbers at the exposed sites (Wall et al. 2012). For TNNP, the observed spatial differences in bleaching susceptibility of scleractinian corals during the first coral bleaching monitoring campaign can be partly attributed to the differences in coral community composition as the mainly bleached coral species *O. faveolata* and *O. franksi* only occurred at the sheltered site. Bleaching at the exposed site was represented by *M. cavernosa* and *D. labyrinthiformis*. Multivariate regression analyses of coral communities at sheltered Eastern and exposed Western sites in four consecutively located bays in TNNP (including Gayraca Bay) revealed that the specific community composition between sites depended mainly on exposure characterized by strong Northeast winds, waves and resulting water currents among the tested factors (exposure, bay, season during monitoring, water temperature, temperature variance, and salinity; Eidens C, unpublished data). Indicator species analyses furthermore implied that the reef-building but bleaching-susceptible *Orbicella* spp. almost exclusively occurred at the sheltered sites within all bays, while the exposed sites were dominated by encrusting forms of *Diploria* spp. and *S. siderea* (Eidens C, unpublished data). In Gayraca Bay, *Orbicella* spp. accounted for 41 % of the overall coral community at the sheltered site. This characteristic coral community pattern was also observed by Werding and Sánchez (1989) who suggested a difference in wave exposure gradient between two opposing sites of one TNNP bay to be the causal factor for the specific coral community composition between sites. The results of the present study suggest that differences in water currents exposure shape the specific coral community distribution and have thereby an indirect effect on the different coral bleaching responses between the exposed and sheltered site.

The massive *O. faveolata* and *O. franksi* that were severely affected by coral bleaching in 2010 are particularly bleaching-susceptible species in the Caribbean and TNNP (CARICOMP 1997; Manzello et al. 2007). However, bleaching of the latter species was largely absent during the second coral bleaching monitoring campaign of the present study. Here, the affected corals were *D. strigosa* and *S. siderea* for the sheltered and *M. cavernosa* and *S. siderea* at the exposed site, but differences in bleaching of overall coral cover between sites were insignificant.

Corals of the genus *Orbicella* (formerly known as *Montastraea*; Budd et al. 2012) play a crucial role in reef accretion, thereby providing a framework to a vast variety of organisms in the wider Caribbean (Goreau 1959). The complete absence of bleaching in 2011 for *Orbicella* that survived bleaching in 2010 may be a result of rapid acclimatization e.g. via a shift to a more resistant symbiotic community of the coral host (Baker 2001; Toller et al. 2001; LaJeunesse 2002; Baker 2003; Baker et al. 2004), through the expression of heat shock proteins which repair denatured cellular components (Black et al. 1995), antioxidant enzymes inactivating harmful oxygen radicals (Lesser et al. 1990; Lesser 2006; Baird et al. 2009), photoprotective fluorescent proteins that reflect and dissipate excess light (Salih et al. 2000), ultraviolet radiation-absorbing mycosporine-like amino acids (Dunlap and Shick 1998), and increase of host tissue thickness (Ainsworth et al. 2008) that play an important role in the regulation of coral bleaching response.

Table 3. Indices of water temperature. Water temperature indices are displayed with seasonal (upwelling vs. non-upwelling) and spatial (exposed vs. sheltered site) resolution. Upwelling months are indicated by italics. Degree-heating days were calculated from mean daily temperature above local coral bleaching threshold of 29.4 °C (Tošić and Navas-Camacho 2012). Abbreviations: exposed site (exp), sheltered site (she), mean temperature (mean temp), maximum temperature (max temp), and minimal temperature (min temp).

	Mean temp (°C)		Max temp (°C)		Min temp (°C)		Degree-heating days (> 29.4°C) (d)	
Months vs. sites	exp	she	exp	she	exp	she	exp	she
Oct 10	29.63	29.63	30.17	30.04	28.89	29.17	19	20
Nov 10	28.65	28.65	29.84	29.92	26.52	26.77	2	2
Dec 10	27.43	27.42	28.25	28.25	25.36	25.38	0	0
Jan 11	24.94	24.92	26.52	26.50	22.92	22.82	0	0
Feb 11	23.44	23.40	24.75	24.87	20.84	21.08	0	0
Mar 11	24.73	24.71	26.26	25.94	23.16	23.23	0	0
Apr 11	25.65	25.63	26.84	26.82	24.73	24.77	0	0
May 11	27.10	27.07	29.54	29.27	24.32	24.29	0	0
Jun 11	28.69	27.91	29.59	29.52	26.67	25.62	0	0
Jul 11	27.16	27.43	28.94	29.34	24.90	25.33	0	0
Aug 11	28.27	28.34	29.67	29.74	26.30	26.48	1	3
Sep 11	28.88	28.96	30.29	30.19	26.55	26.72	7	8
Oct 11	29.41	29.49	30.27	30.29	27.43	27.95	14	20
Nov 11	29.03	29.12	30.02	30.12	28.00	28.35	1	3
Dec 11	26.44	26.51	28.94	29.07	22.39	22.99	0	0
Jan 12	23.88	23.94	25.36	25.43	21.80	21.89	0	0
Feb 12	22.69	22.75	24.22	24.48	20.32	20.39	0	0
Mar 12	24.07	24.13	25.40	25.55	21.96	22.39	0	0
Apr 12	26.13	26.19	27.78	27.78	24.92	24.97	0	0
Non-upwelling (rainy season) 2010	29.04	29.04	30.17	30.04	26.52	26.77	21	22
Upwelling (dry season) 2010/11	25.27	25.25	28.25	28.25	20.84	21.08	0	0
Non-upwelling (rainy season) 2011	28.39	28.31	30.29	30.29	24.32	24.29	23	34
Upwelling (dry season) 2011/12	24.66	24.72	28.94	29.07	20.32	20.39	0	0

Corals recovered by March/April, 5 – 6 months after the moderate coral bleaching end of 2010 and mild bleaching event in 2011. During time of recovery, seawater temperature decreased below 21 °C during both years of study. Coral recovery in TNNP was faster than the recovery time of 6 – 8 months characterized as a good recovery after the 1998 severe bleaching event of the Great Barrier Reef (Berkelmans 2001). Longest recovery periods after severe coral bleaching events can take up to 13 years (Connell 1997). In contrast to the study of Wall et al. (2012), where no differences in coral recovery were observed between LAIW-exposed and –sheltered sites of the Similan Islands/Andaman Sea, we observed a faster and more efficient coral recovery at the water current-exposed site as compared to the -sheltered counterpart where a coral mortality of 12 % occurred. However, data on coral bleaching and recovery cannot be compared to recent previous coral bleaching events in the TNNP so far, as the extent of bleaching during the last decade was negligible (Rodríguez-Ramírez et al. 2008; Vega-Sequeda et al. 2008; Navas-Camacho et al. 2010).

Potential reasons for the observed bleaching patterns

Our findings suggest that the overall coral community bleaching was mitigated at a water current exposed as compared to a sheltered site of the same upwelling influenced bay in TNNP. The following possible explanatory factors were examined in detail: (1) decrease of seawater temperature after or during time of highest heat stress; (2) reduced temperature anomalies above bleaching threshold; (3) increased water current exposure through stronger winds during upwelling; and (4) increased turbidity that may reduce light/UV stress.

Several studies have discussed the coral bleaching mitigation effect of upwelling-induced decrease of water temperature during time of highest heat stress (Glynn 1996; Riegl and Piller 2003; Chollett et al. 2010). However, in our study the differences in absolute water temperatures between the exposed and sheltered site of Gayraca Bay were insignificant and the calculated temperature anomalies between sites were comparable. Consequently, our data indicate that water temperature decreases were not mainly responsible for the observed coral bleaching and recovery dynamics between the investigated sites.

The key reason for the observed coral bleaching and recovery patterns is likely the difference in exposure to water currents at the investigated locations. This is supported by the study of Nakamura and van Woesik (2001) in which bleaching of staghorn corals during the 1998 bleaching event was more pronounced at water current exposure-sheltered compared to -exposed locations close to Ryukyu Island (Japan). The observed findings in the present study are also in accordance with Nakamura et al. (2003), demonstrating that a recovery was facilitated for the artificially bleached hard coral *Stylophora pistillata* through high water current exposure. Water currents can generally influence coral physiology and performance (Nakamura and van Woesik 2001; Nakamura et al. 2003; West and Salm 2003). Possible reasons are that water current-induced mass exchange and transport processes are orders of magnitude faster than the exchange via molecular diffusion in still water (Huettel et al. 2003) leading to increase in particulate organic matter release (Wild et al. 2012), enhanced photosynthesis (Mass et al. 2010) and ammonium uptake rates in corals (Atkinson et al. 1994). Water currents may mitigate coral bleaching by rapid removal of toxic reactive oxygen species (ROS), nitric oxides, and their permeable derivatives (Lesser 2006; Weis 2008) from the host's and symbionts' cells (Nakamura and van Woesik 2001). This may explain the reduced overall coral community bleaching and increased recovery detected at the water current-exposed site in Gayraca Bay. Some studies suggested that the difference in water currents and wave-exposition may mediate the reef community structure (Werding and Sánchez 1989; Garzón-Ferreira 1998) which in turn defines the community susceptibility to coral bleaching. This may explain the higher community bleaching susceptibility index observed at the water current-sheltered as compared to the -exposed site. In accordance with Werding and Sánchez (1989), the present study suggests that water current exposure influences the specific coral community composition between the exposed and sheltered sites in TNNP and thereby has also an indirect effect on differences in coral bleaching response between sites.

A further explanation for the observed findings may be the increased turbidity at the water current-exposed site, likely due to resuspension of fine sediments. Regions with increased turbidity (Goreau et al. 2000; Meesters et al. 2002) and high cloud cover (Mumby et al. 2001) exhibit low bleaching susceptibility, which consequently supports our observations of more resilient corals at the water current-exposed site with higher turbidity as compared to the -sheltered site.

The described extrinsic environmental factors and the intrinsic, species- or colony-specific factors can be emphasized as mechanisms to promote coral resistance and resilience (West and Salm 2003). We consider the differences in water currents as major local control for the coral ecosystem in TNNP and suggest that they potentially determine the characteristic species distribution between the exposed and the sheltered sites of the bays, reported by various studies (Werding and Sánchez 1989; Garzón-Ferreira and Cano 1991; Bayraktarov et al. 2012).

The potential role of seasonal upwelling in coral bleaching mitigation

Before 2010, significant coral bleaching events were absent for decades in TNNP (Rodríguez-Ramírez et al. 2008; Rodríguez-Ramírez et al. 2010). During the same time in 2010 that we observed a moderate coral bleaching for the upwelling influenced TNNP, massive coral bleaching events were detected in Puerto Cabello (del Mónaco et al. 2012) and Los Roques National Park in Venezuela (Bastidas et al. 2012) which experience no seasonal upwelling (Rueda-Roa and Muller-Karger 2013). Here, up to 63 % bleached corals were reported for Puerto Cabello (del Mónaco et al. 2012) and 72 % bleached and pale coral colonies for Los Roques National Park (Bastidas et al. 2012). Bleaching extent in these non-upwelling regions was more than twice as much as at the water current-sheltered and 7 – 9 times more than at the -exposed site in our study. These findings, along with the absence of coral bleaching in the past, suggest that seasonal upwelling potentially plays a role in coral bleaching mitigation in TNNP. Coral bleaching in Puerto Cabello was correlated to increased seawater temperature to 31 °C due to El Niño forcing and a subsequent La Niña phase of the El Niño Southern Oscillation which drastically decreased salinity in the reef seawater by strong rainfalls (del Mónaco et al. 2012), also present in the TNNP region. In Los Roques National Park, high coral bleaching extent which accounted for the first mass bleaching event in 20 years for the region, was explained by unusually high thermal anomalies of more than 16 degree-heating weeks (DHW) (Bastidas et al. 2012). The authors (Bastidas et al. 2012) suggested that Los Roques was massively impacted in 2010 because the region was lacking significant coral bleaching events in the past. So far, there is some evidence that susceptibility of corals to bleaching depends on the thermal history (Brown et al. 2002; Thompson and van Woesik 2009; Donner 2011) of coral reefs and consequently on former bleaching events (Hoegh-Guldberg 1999). Coral bleaching extent and/or frequency of bleaching events may be higher for regions without coral bleaching history when seawater temperatures rise above coral bleaching thresholds (Hoegh-Guldberg 1999). This partly explains the moderate coral bleaching in Gayraca Bay observed in the present study.

During the Caribbean Crisis in 2005, Rodríguez-Ramírez et al. (2010) attributed the minimal coral bleaching occurrence of 1 – 5 % coral cover in TNNP to seasonal upwelling. Later, Chollett et al. (2010) suggested the TNNP region as potential refuge for corals against future coral bleaching events as typically heating and upwelling-induced cooling of seawater are in synchrony. However, during the El Niño impacted year 2010, heating started anomalously earlier than expected with the consequence that coral bleaching threshold of 4 DHW was already exceeded during September as compared to previous years or the second coral bleaching monitoring where accumulation of thermic stress for scleractinian corals started in November-December. In addition, during 2010, a record heat accumulation of 12 DHW was reported during November as compared to previous years (maximum 7 DHW; http://coralreefwatch.noaa.gov/). A typical pattern of upwelling-influenced coral bleaching mitigation may have been present during the second coral bleaching monitoring campaign where a maximum experienced heat stress of 4 DHW coincided with onset of seasonal upwelling. Thereby, the present study also supports the hypothesis formulated by Glynn (1996) that upwelling areas could act as possible refuge habitats in which corals are protected from temperature-induced coral bleaching.

Ecological implications

In our study, we identified direct and indirect water current-induced coral bleaching mitigation for an exemplary bay in the upwelling influenced TNNP. This study thereby indicates the existence of local resilience patterns against coral bleaching for reefs in TNNP. Compared to other nearby non-upwelling locations in the Caribbean such as Islas del Rosario, Islas de San Bernardo (Colombia; Rodríguez-Ramírez et al. 2008) or Puerto Cabello and Los Roques National Park (Venezuela; Bastidas et al. 2012; del Mónaco et al. 2012), where coral bleaching was more severe, the bays of the TNNP may act as refugia for corals from bleaching in times of ocean warming due to global climate change.

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7

Spatial and Temporal Distribution of the Invasive Lionfish *Pterois volitans* in Coral Reefs of Tayrona National Natural Park, Colombian Caribbean.

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Abstract

The lionfish *Pterois volitans* is an invasive species throughout the Western Atlantic that disturbs functioning of local ecosystems such as coral reefs via fast and intense consumption of small herbivorous fish. In 2009, lionfish populated the bays of Tayrona National Natural Park (TNNP), a biodiversity hotspot in the Colombian Caribbean that is strongly influenced by changing environmental conditions due to a rainy and dry season. So far, the spatial and temporal distribution of *P. volitans* in the bays of TNNP is unknown. Therefore, this study assessed the abundance and size classes of *P. volitans* during monthly surveys throughout the year 2012 in four bays (thereof two bays where lionfish extractions were undertaken) of TNNP at 10 m water depth in coral reefs using transect tools. Findings revealed lionfish abundances of 2.9 ± 0.9 individuals ha^{-1} with lengths of 20 – 25 cm for TNNP, hinting to an established, mostly adult local population. Actual TNNP lionfish abundances are thereby very similar to those at Indo-Pacific reef locations where the invasive lionfish formerly originated from. Significant spatial differences for lionfish abundances and lengths between different bays in TNNP suggest habitat preferences of *P. volitans* depending on age. Lionfish abundances were highly variable over time, but without significant differences between seasons. Extraction measures reduced lionfish abundances by 22 – 71 % compared to uncontrolled locations, but with a strong location specificity. This study therefore recommends improved management actions in order to control the already established invasive lionfish population in TNNP.

Introduction

Invasive species can alter the biogeochemical cycles and trophic net structures of marine ecosystems (Mack et al. 2000) resulting in changed functioning and services provided by the ecosystem with strong implications for coastal human populations (Schüttler and Karez 2008). After a successful dispersion, reproduction and survival, the invader may generate losses of the endemic populations and thus modify ecosystem processes (Albins and Hixon 2011). The Indo-Pacific lionfish *Pterois volitans* belongs to the family Scorpaenidae and is an invasive marine fish that got introduced in the Western Atlantic (Whitfield et al. 2002; Schofield 2010; Albins and Hixon 2011; Arias-González et al. 2011). It is assumed that the vectors of introduction were releases or escapes from marine aquaria (Hare and Whitfield 2003; Semmens et al. 2004; Ruiz-Carus et al. 2006). First sightings date from the 80's in Florida coastal waters (Morris and Whitfield 2009) and later with higher numbers off the coast of North Carolina (Whitfield et al. 2002). Its fast and successful expansion throughout the warm and temperate waters of the North Atlantic and Caribbean (Betancur-R. et al. 2011) are attributed to the planktonic dispersion of its eggs which usually attach to floating structures (Whitfield et al. 2002). Scorpaenidae larvae have characteristic long cranial thorns that reduce the possibility of being preyed (Morris and Whitfield 2009). Mature lionfish females were reported to have an approximate body length of 17 cm (Morris 2009). Lionfish in invaded areas have many advantages over native fauna e.g. due to their high fecundity of over two-million eggs per year and female through spawning every 4 days (Morris 2009; Morris and Whitfield 2009), generalist diet on a variety of smaller fishes, including juveniles of larger species, shrimps and small mobile invertebrates (Morris and Akins 2009), effective larval dispersal mechanisms (Morris and Whitfield 2009), defensive venomous spines (Morris and Whitfield 2009; Albins and Hixon 2011), efficient predation (Albins and Hixon 2008; 2011; Côté and Maljković 2010), rapid growth (Albins and Hixon 2011), low parasite load (Morris 2009), and habitat generality (Barbour et al. 2010; Albins and Hixon 2011). These characteristics make lionfish succeed over native fishes and/or dramatically decrease local populations in invaded areas (Albins and Hixon 2008; Arias-González et al. 2011).

So far, the effects that lionfish could have on the endemic biota are difficult to estimate (Schofield 2009). However, studies reported negative effects from its role as predator on the trophic net (Albins and Hixon 2011). Synergetic effects with other factors of environmental stress such as climate change, overfishing and pollution should be taken into account (Albins and Hixon 2008; 2011).

Lionfish invaded from North Carolina/USA to the Lesser Antilles through the Caribbean. In Colombia, it arrived to the oceanic islands of San Andrés and Providencia in 2008 and invaded the entire continental coast of the country in the following year. The presence of *P. volitans* was first recorded for the Tayrona National Natural Park (TNNP) in the Northeast Colombian coast in May - July 2009 at water depths between 12 – 20 m over coral patches (González et al. 2009). In 2010, juvenile *P. volitans* (3 – 10 cm lengths) were observed in the mangrove ecosystem of Chengue Bay in TNNP (Arbeláez and Acero P. 2011). The ecological consequences of lionfish are of particular interest for TNNP as it is an area of major coastal biodiversity within the Colombian Caribbean (Garzón-Ferreira and Cano 1991). Increasing numbers of lionfish sightings in the TNNP are alarming as in contrast to many native fishes, they have few natural predators owing to their venomous spines (Whitfield et al. 2007) and not recognition by potential native predators due to crypsis and mimicry (Morris 2009; Skelhorn et al. 2010; Albins and Hixon 2011).

So far, little is known about the spatial and temporal distribution of lionfish in the TNNP area. Therefore, the aim of the present study was to assess monthly *P. volitans* abundances and body lengths throughout one year for four bays in TNNP. The first objective was to compare TNNP data on lionfish with other invaded locations and also with its native locations in the Indo-Pacific. The second objective was to determine whether lionfish abundances change over time and if differences between a rainy and dry season exist. The third objective addressed the efficiency of management actions that started in May 2012 in two bays of TNNP by comparing bays in which lionfish numbers were controlled by extraction methods to pristine bays. The present study provides recent and comprehensive lionfish distribution data and establishes an actual baseline with high temporal and spatial resolution for TNNP reefs in the Colombian Caribbean. Further needs of management actions to control the already established invasive lionfish population in TNNP are discussed.

Materials and methods

Study site

The Tayrona National Natural Park (TNNP) is located at the Northeastern coast of Colombia, between 11° 17' - 11° 22' N and 73° 53' - 74° 12' W (Fig. 1). The region contains a rocky coastline with capes, inlets and bays with sandy beaches covering a total of 85 km (Garzón-Ferreira and Cano 1991; Díaz et al. 2000; Martínez and Acosta 2005). The area of survey included the main TNNP bays Chengue, Gayraca, Neguanje and Cinto (Fig. 1). TNNP is influenced by the North-South displacement of the Intertropical Convergence Zone (ITCZ) resulting in a major dry season (December - April) and transition season (May - July) with strong influence of Northeast (NE) Trade Winds and a major rainy season (August - November; Salzwedel and Müller 1983; Mesa et al. 1997). During dry season, a seasonal upwelling occurs that is triggered by the continental winds along the NE coast of Colombia and Venezuela (Andrade and Barton 2005; Paramo et al. 2011). Seasonal upwelling leads to strong environmental changes such as temperature decrease (from 28 °C in December to 21 °C in February; Bayraktarov et al. 2012; Chapter 1, 2) and increase in salinity (from 33 to 38; Salzwedel and Müller 1983; Bayraktarov et al. 2012). Reports on the increased concentrations of inorganic nutrients and chlorophyll *a* characterize the oligotrophic region during non-upwelling as mesotrophic in periods of upwelling (Franco-Herrera et al. 2007; Arévalo-Martínez and Franco-Herrera 2008; Chapter 2). During rainy season, more than 80 % of annual rainfall occurs (Salzwedel and Müller 1983; Mesa et al. 1997) and seawater temperature is increased (28 – 30 °C; Bayraktarov et al. 2012; Chapter 1, 2).

Coral reef formations are growing on both sides of each bay between water depths of 5 to 20 m (Werding and Erhardt 1976; Werding and Sánchez 1989; Garzón-Ferreira and Cano 1991) and represent a habitat for over 180 reef fish species (Olaya-Restrepo et al. 2008). The Western coast of each bay is exposed to wind, waves and water currents that are enhanced during upwelling, while the Eastern side is characterized by usually calm water conditions, high sedimentation rates and shelter from NE swell due to topographical orientation (Werding and Sánchez 1989). Additionally to coral reefs, the bays harbor mangrove ecosystems, seagrass beds and reef fish assemblages (Garzón-Ferreira and Cano 1991; Olaya-Restrepo et al. 2008).

Lionfish assessment in space and time

In order to address the goals of the study, *P. volitans* abundances were monitored monthly in four bays of TNNP. Surveys comprised monitoring along line transects of 50 m length and 5 m width in triplicates that were located at the Western and another triplicate set of transects at the Eastern flank of each bay (Fig. 1) in order to encompass a representative area for lionfish distribution. Transects were located at water depths between 9 and 11 m, parallel to the coastline. The investigated area covered 1500 m^2 per bay and a total area of 6000 m² for the TNNP. The method of visual census was applied by SCUBA (English et al. 1997; Lang et al. 2010), while counting the total number of *P. volitans* (Fig. 2a) observed during a time of 25 min per triplicate (Morris 2009). Places where lionfish may hide such as holes and cavities between rocks and coral framework were carefully examined. Estimated total body lengths of lionfish were recorded *in situ* for each localized individual (Fig. 2b) from the tip of the snout to the tip of the caudal fin and were categorized in size classes of 5 – 10, 10 – 15, 15 – 20, 20 – 25, 25 – 30, 30 – 35, and 35 – 40 cm. The surveys were performed between the second and the third week of each month, always at a time between 8:00 am. and 3:00 pm.

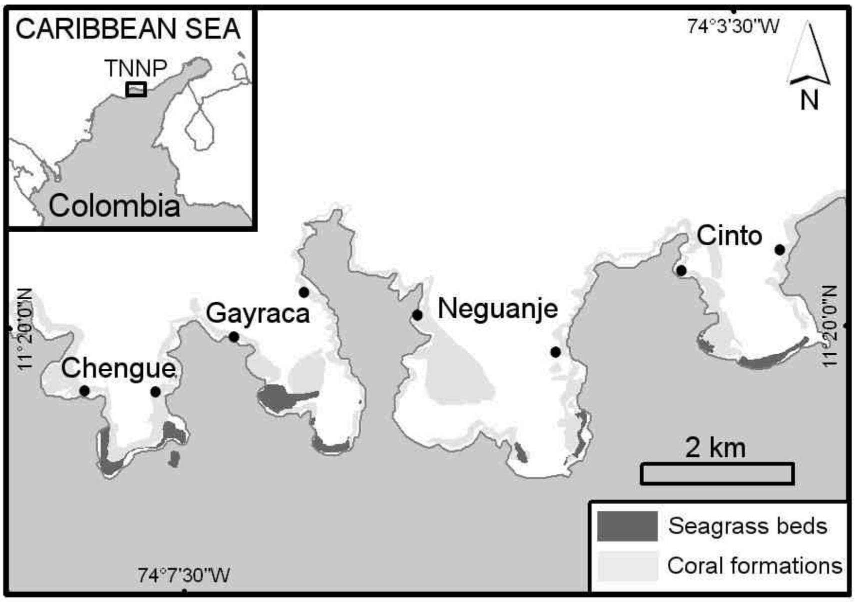

Figure 1. Area of survey in the Tayrona National Natural Park (TNNP). The points indicate the sampling locations at the western and eastern flank of each bay. Source: Invemar 2012

Lionfish extractions started in May 2012 as a joint project between Universidad Nacional de Colombia, Universidad Jorge Tadeo Lozano, Universidad del Magdalena, Instituto de Investigaciones Marinas y Costeras 'José Benito Vives de Andréis' (Invemar) and the

National Natural Parks of Colombia. Extractions were performed monthly by spearing and nets at variable depths by SCUBA diving in the TNNP bays Chengue and Cinto. Unregistered additional extractions of lionfish by dive centers could not be included in the present survey.

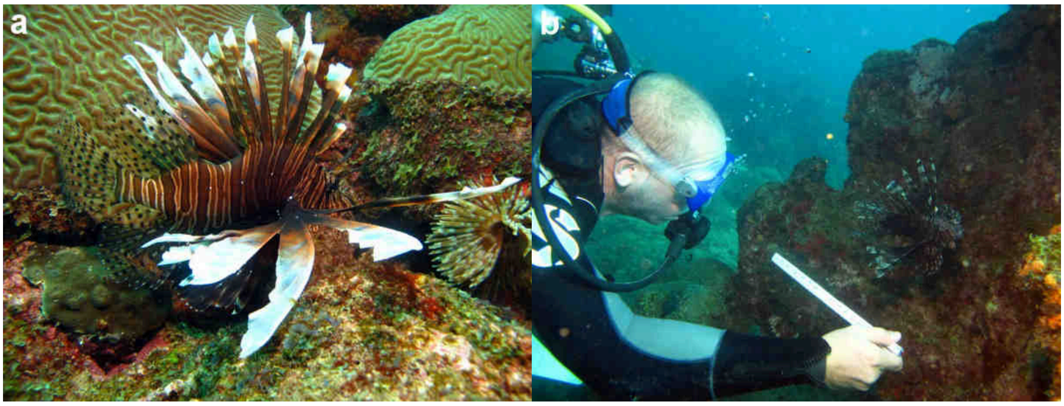

Figure 2. Lionfish *Pterois volitans* in its invaded coral reef environment in Tayrona National Natural Park (a) and *in situ* estimation of total body length (b). Pictures were kindly provided by J. F. Lazarus-Agudélo

Data analysis

Mean annual abundance of *P. volitans* for the TNNP bays Chengue, Gayraca, Neguanje and Cinto (Fig. 3) were calculated from monthly collected data (12 months) and 6 transects per bay, resulting in an annual transects replication of n = 69 for Chengue and Neguanje and n = 72 for Gayraca and Cinto. Mean monthly abundance of lionfish for the TNNP bays had a replication of n = 6 transects per bay (Fig. 4). For calculation of the monthly abundance of lionfish in TNNP (Fig. 5), data from 6 transects per bay were pooled resulting in a replication of n = 24 per month. Replication for the months March and December was only n = 21 as monitoring could not be performed in two of the sampling locations. Mean estimated sizes of lionfish (Fig. 6) were calculated from total estimated body lengths of fishes observed along the transects in the respective bay.

Differences in *P. volitans* abundances between bays and months were tested by a Generalized Linear Model (GLM) for Poisson-distributed data and the software R (R Development Core Team 2008). Multiple comparisons between bays (Chengue, Gayraca, Neguanje and Cinto) and months (January – December) were performed by a Tukey's Honestly Significant Difference (HSD) *post hoc* test. Differences in size classes between bays were analyzed by a One Way ANOVA after testing for normality of data by Shapiro Wilk test and homogeneity of variances by an Equal Variance Test. Here, a Holm-Sidak *post hoc* test was applied for multiple comparisons of size classes within the four bays.

ANOVA and the graphical representation of data were performed by the software SigmaPlot 12.0 (Systat Software, Inc).

Results

Spatial distribution of lionfish in TNNP

Throughout the year 2012, a total number of 123 *Pterois volitans* were observed during 12 months in 4 bays over a total monitored area of 6000 m². Lowest lionfish abundance was found in Chengue Bay with 1.4 ± 0.6 individuals ha^{-1} (annual mean ± SE), followed by Neguanje with 1.8 ± 0.6, and Cinto with 3.4 ± 0.8 individuals ha^{-1}. Highest numbers of lionfish were present in Gayraca with 4.9 ± 1.3 individuals ha^{-1} (Fig. 3). Significant differences in lionfish abundances were present between the bays Chengue and Cinto (GLM, Tukey's HSD *post hoc*, $p = 0.02$), Chengue and Gayraca ($p < 0.001$), and Gayraca and Neguanje ($p = 0.001$).

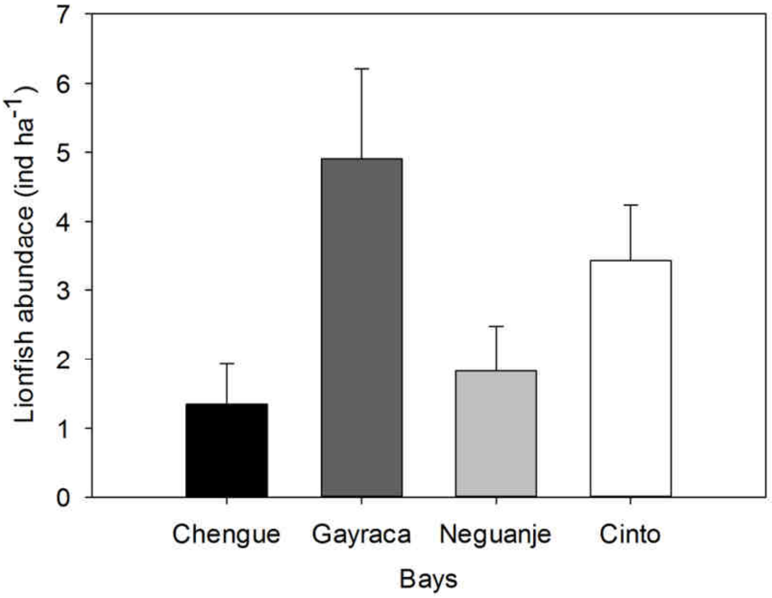

Figure 3. Abundances (annual mean ± SE) of *Pterois volitans* in the Tayrona National Natural Park bays Chengue, Gayraca, Neguanje and Cinto.

Fluctuations of lionfish abundances in the TNNP bays Chengue, Gayraca, Neguanje and Cinto with a monthly resolution throughout 2012 are depicted in Fig. 4. In Chengue, lionfish abundances were below 5 individuals ha^{-1} until July and disappeared thereafter completely until December, where 1.1 ± 1.1 individuals ha^{-1} were registered. Highest abundances were observed in Gayraca during January with 16.7 ± 10.3 individuals ha^{-1} (monthly mean ± SE) and August with 12.2 ± 4.6 individuals ha^{-1}, while intermediate abundances were present during September with 10.0 ± 5.6 individuals ha^{-1} and December with 7.8 ± 6.5 individuals ha^{-1} in this bay. In Neguanje, highest lionfish abundances were recorded for January with 5.6 ± 5.6 individuals ha^{-1} and February with 5.6 ± 3.6 individuals ha^{-1}. Here, no lionfish was observed between July and December, except for September where 2.2 ± 2.2 individuals ha^{-1} were registered. In Cinto, lionfish abundances peaked during September with 16.7 ± 5.6 individuals ha^{-1} and June with 6.7 ± 2.4 individuals ha^{-1}, but were otherwise below 5 individuals ha^{-1}.

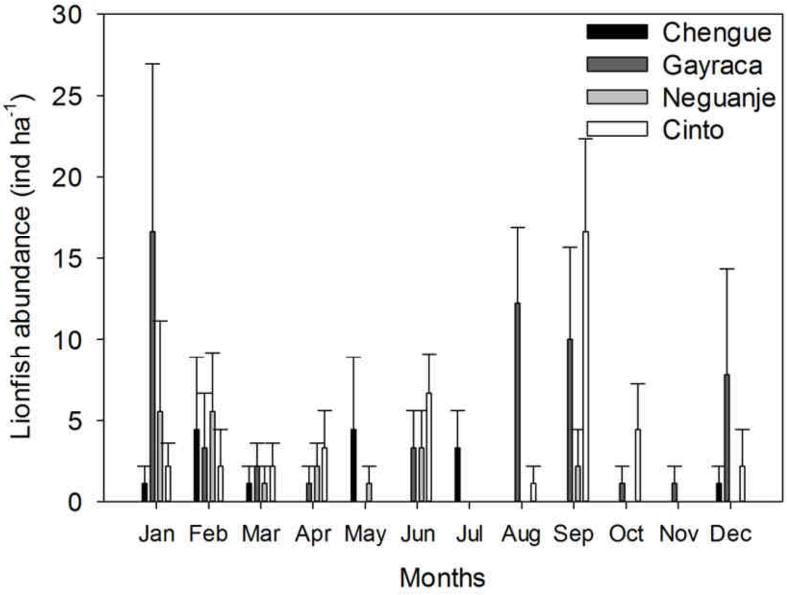

Figure 4. Abundances (monthly mean ± SE) of *Pterois volitans* in the Tayrona National Natural Park bays Chengue, Gayraca, Neguanje and Cinto throughout the months of 2012.

Temporal distribution of lionfish in TNNP

On the temporal scale, highest abundance of lionfish was observed in September with 7.2 ± 2.4 individuals ha^{-1} (monthly mean ± SE) and January with 6.4 ± 3.0 individuals ha^{-1}; lowest during November with 0.3 ± 0.3 individuals ha^{-1} and July with 0.8 ± 0.6 individuals ha^{-1} (Fig. 5). Significant differences between months were present between September and April (GLM, Tukey's HSD *post hoc*, p = 0.05), July and January (p = 0.04), September and July (p = 0.02), September and May (p = 0.03), and between September and October (p = 0.03). However, lionfish abundances were not significantly different between rainy (August – November) and dry season (December – April) in TNNP.

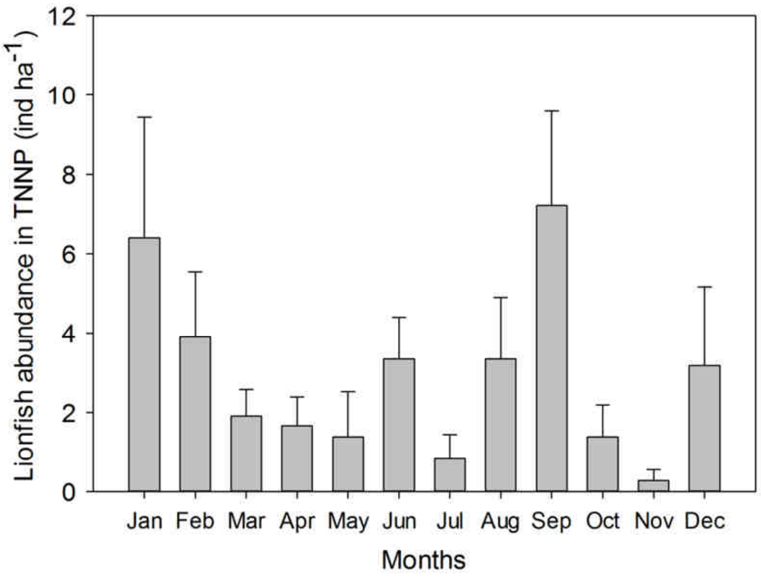

Figure 5. Monthly abundance of *Pterois volitans* (monthly mean ± SE) in Tayrona National Natural Park.

The average of pooled data from 12 months of monitoring and 4 bays with a total of n = 69 transect replicates revealed a mean of 2.9 ± 0.9 individuals ha^{-1} (annual mean ± SE) for the TNNP region.

Largest estimated lionfish body lengths of 40 cm were registered for Cinto in January and August, and Neguanje in September (Fig. 6). Significant differences in lionfish body lengths were observed between Chengue (mean of 10 – 15 cm) and Gayraca (20 – 25 cm; ANOVA, Holm-Sidak *post hoc*, $p < 0.001$), Chengue and Cinto (20 – 25 cm; $p = 0.025$), and Gayraca and Neguanje (15 – 20 cm; $p = 0.025$) represented by Fig. 6. A total of 75 % of all registered lionfish individuals had a body length larger than 17 cm representing the size of a mature female (Morris 2009). The total percentage of adults was distributed as 6 % in Chengue, 37 % in Gayraca, 10 % in Neguanje and 22 % in Cinto.

The effect of fish extraction measures

Extraction of lionfish in Chengue (1.4 ± 0.6 individuals ha^{-1}) resulted in significantly lower abundances as compared to Gayraca (4.9 ± 1.3 individuals ha^{-1}) but was also lower than abundances in Cinto (3.4 ± 0.8 individuals ha^{-1}), where extractions were also performed. For Chengue, no significant lionfish individuals were registered after July 2012 until the end of the study. However, lionfish abundances in the controlled Cinto Bay with 3.4 ± 0.8 individuals ha^{-1} was on the one hand lower than abundances in the uncontrolled Gayraca (20 %), but higher than numbers present in Neguanje.

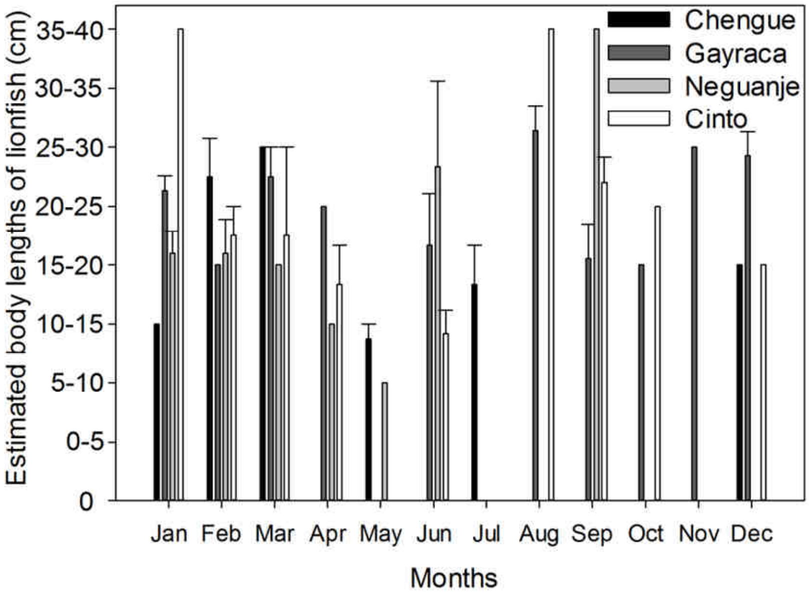

Figure 6. Estimated size of lionfish in the bays Chengue, Gayraca, Neguanje and Cinto. Missing error bars represent sample sizes which did not allow the calculation of mean and SE at some locations and months.

Discussion

Spatial and temporal distribution of *P. volitans*

Our data on *P. volitans* distribution in the Tayrona National Natural Park (TNNP) in the Colombian Caribbean show that a local population with mean body length of 20 – 25 cm has developed in the bays Chengue, Gayraca, Neguanje and Cinto. The lionfish lengths observed in TNNP hint to a population mostly dominated by adult fishes that are able to recruit sexually. This assumption is confirmed by the study of Morris (2009) who reported average sizes of mature females of 17 cm.

With an annual mean of 2.9 individuals ha^{-1}, lionfish abundance in TNNP was similar to some locations in the Indo-Pacific where it originated from, e.g. Palau Archipelago with 2.2 individuals ha^{-1} (Grubich et al. 2009), but below ~ 80 individuals ha^{-1} reported for the Gulf of Aqaba/ Red Sea (Fishelson 1997). Table 1 shows a comparison of lionfish abundance in TNNP to other invaded and native habitats worldwide. Lionfish abundances in TNNP were below the values reported for other invaded areas of the Western Atlantic such as the Bahamas with 393 (Green and Côté 2009) or the coast off North Carolina/ USA with 150 individuals ha^{-1} (Morris and Whitfield 2009) which may be due to the relatively recent invasion of TNNP in 2009 (González et al. 2009) vs. an invasion by the species in the Bahamas since 2004 (Schofield 2009). High abundances of lionfishes in invaded areas are likely the result of unlimited growth and reproduction due to the availability of food sources and lack of natural predators. Some predators obviously learned to target lionfish as potential prey (Bernadsky and Goulet 1991; Maljković et al. 2008). So far, two Caribbean large-bodied grouper species, *Epinephelus striatus* and *Mycteroperca tigris*, were observed to successfully ingest lionfish (Maljković et al. 2008). However, *E. striatus* is one of the species categorized as endangered in the Colombian Caribbean red list of marine fishes (Mejía and Acero P. 2002). Mumby et al. (2011) presented data on the reduction of lionfish biomass by groupers which may thus serve as natural biocontrol of growing lionfish populations. However, the lack of these natural lionfish predators in TNNP (Olaya-Restrepo et al. 2008) and the wider Caribbean (Sadovy 2005) is alarming. In contrast to Mumby et al. (2011), the study of Hackerott et al. (2013) concluded that the success of lionfish population was not influenced by interaction with native predators in 71 reefs and different biogeographic regions in the Caribbean. These confounding results once more stress the necessity of immediate management actions to control further lionfish reproduction and invasion.

Our monthly data on *P. volitans* distribution over four bays in TNNP showed no seasonal patterns between a rainy season, during which 80 % of the annual rainfall occurs, and a dry season, going along with seasonal upwelling and drastic decrease in seawater temperature from 28 °C to 21 °C (Salzwedel and Müller 1983; Bayraktarov et al. 2012; Chapter 2). Seasonal upwelling did not affect the established lionfish population as the critical temperature at which lionfish ceases feeding was reported to be 16 °C with lethal consequences at 10 °C (Kimball et al. 2004) which lie below the lowest seawater temperature that can be expected for the TNNP region. However, we observed high temporal variability in lionfish abundance throughout the year with highest occurrence during September and January and lowest during July and November, encompassing both, the rainy and dry season. Temporal variability in lionfish abundance is most likely a consequence of the extraction measures within the bays. Here, further data on the extractions of lionfish within the TNNP bays are necessary.

Effect of lionfish extraction measures

Abundances and body lengths of *P. volitans* for Chengue Bay, in which extractions were performed, were smaller than for the uncontrolled Gayraca and Neguanje. However, extractions could not effectively reduce lionfish abundances in Cinto which were lower than abundances in Gayraca but higher than in Neguanje. Body lengths found in Cinto corresponded to those in Gayraca. The smallest body lengths observed in Chengue indicate that a mostly juvenile population may have developed in this bay. This is likely to be a consequence of extraction during management actions targeting predominantly larger adult individuals which are easier to observe and catch. Smaller juveniles may hide between the roots of mangroves (Arbeláez and Acero-P. 2011) or in crevices and holes of the reef framework. Additionally, Chengue Bay comprises a highly developed mangrove ecosystem (Garzón-Ferreira and Cano 1991) which may serve as nursery for lionfish larvae and juveniles. This is further supported by the study of Arbeláez and Acero-P. (2011), who found lionfish juveniles of 3 – 10 cm lengths at the submerged roots of the mangroves bordering the entrance to the southern lagoon in Chengue Bay.

Table 1. Comparison of *P. volitans* abundance in TNNP with worldwide reports on invaded and native habitats.

Region and Year	Habitat for lionfish	Reported abundance (ind ha^{-1})	Source
Chengue Bay (TNNP, Colombian Caribbean), 2012	invasive	1.4 ± 0.6	this study
Gayraca Bay (TNNP, Colombian Caribbean), 2012	invasive	4.9 ± 1.3	this study
Neguanje Bay (TNNP, Colombian Caribbean), 2012	invasive	1.8 ± 0.6	this study
Cinto Bay (TNNP, Colombian Caribbean), 2012	invasive	3.4 ± 0.8	this study
TNNP, Colombian Caribbean, 2012	invasive	2.9 ± 0.9	this study
New Providence, Bahamas, Western Atlantic, 2008	invasive	393.3 ± 144.4	Green and Côté (2009)
Coast off North Carolina, USA, Western Atlantic, 2004	invasive	21.2 ± 5.1	Whitfield et al. (2007)
Coast off North Carolina, USA, Western Atlantic, 2008	invasive	150	Morris and Whitfield (2009)
Palau Archipelago, Western Pacific, 2008	native	2.2	Grubich et al. (2009)
Gulf of Aqaba, Red Sea, 1997	native	~ 80	Fishelson (1997)

The present study shows that extraction strategies which started in May were successful for Chengue Bay where lionfish abundances and body lengths were significantly reduced in comparison to other bays. Here, lionfish numbers ceased after

July and no further individuals were observed until December. However, no significant lionfish reductions were observed for Cinto, the second bay in which extractions were performed. Factors affecting fish populations that cannot be excluded are the differences in coral reef complexity between the bays and the potential food sources for lionfish. These important points need to be addressed in further studies.

Our study suggests that management actions for the TNNP require further improvement in terms of extraction frequencies and a larger control area in order to significantly reduce the established lionfish population. The implementation and improvement of management actions in order to preserve the condition of Caribbean coral reef ecosystems during *P. volitans* invasion are crucially essential. The national plan to control and manage lionfish invasion in Colombia is focused on three focal strategy points: (1) realization of fundamental research, (2) implementation of management actions and (3) focus on education and control (MADS et al. 2013). Whereas the first two points are encompassed by research groups of universities and research institutes, the third point is coordinated by the National Natural Parks of Colombia dealing with all territories of marine parks and reserves. The extraction of lionfish outside the marine parks territories lies in the hands of regional environmental officers.

Considering the national plan to control and manage lionfish invasion, potential management actions required for the Colombian Caribbean region may further focus on raising the community's awareness by introducing the lionfish problem and the consequences of its invasion. Extractions on a wider scale can be promoted by consumption of lionfish on a local and commercial scale as suggested by Morris et al. (2011). Lionfish meat proved to be a good candidate for human nutrition due to its relatively high content of fillet yield (30.5 %) comparable to groupers, graysbys, and coneys (Morris et al. 2011). Lionfish meat had higher content of essential n-3 fatty acids and a relatively low amount of saturated fatty acids as compared to other marine reef fish species (red snapper, dolphinfish, blue fin tuna, triggerfish, grouper and tilapia; Morris et al. 2011). The authors suggested that public outreach should especially focus on education about lionfish invasion, handling and cleaning of *P. volitans* in order to minimize risks for envenomation of fishers and processors (Morris et al. 2011).

The establishment of marine reserves can effectively protect larger fishes (Halpern 2003) that could prey on lionfish. Further controlled fishing restrictions especially on native apex predator populations will become imperative in the course of controlling a spreading lionfish invasion.

The invasion of *P. volitans* in the Western Atlantic and the Caribbean is considered as one of the top global threats to conservation of biodiversity (Sutherland et al. 2010). Local lionfish population may disturb functioning of coral reefs through high consumption of small herbivorous fishes, including parrotfishes (Albins and Hixon 2008; Morris and Akins 2009), thus indirectly promote the outcompeting of corals by naturally uncontrolled growth of seaweeds (Mumby et al. 2006; Mumby and Steneck 2008). Combined with decrease in live coral cover due to overfishing of herbivores by humans and lionfish (Albins and Hixon 2011), consequences of global climate change (Hoegh-Guldberg et al. 2011), and environmental degradations, the future of coral ecosystems is severely endangered (Jackson 2010) in the Western Atlantic and Caribbean.

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Synopsis

This thesis provides first comprehensive long-term monitoring data-sets describing the condition and functioning of coral reefs in Tayrona National Natural Park (TNNP) in the Colombian Caribbean by a holistic approach. The investigations encompassed a monitoring of the physical environment in terms of water current velocity and direction (Chapter 1) and water quality of coral reef-surrounding water body (Chapter 2). The study followed the supply and fate of organic matter from the water column to the reef sediments and evaluated the sedimentary properties such as carbon turnover rate and organic matter accumulation (Chapter 3). Spatial and temporal implications of the different water current regimes on reef condition were studied through the assessment of primary production of the dominant autotrophic reef organisms (Chapter 4) and by monitoring of the first coral bleaching event for the region in 2010 (Chapter 6). Finally, the last Chapter 7 introduces the recent threat of lionfish invasion in TNNP coral reefs and provides first distribution data.

Spatial effects on reef functioning

Spatial effects in TNNP arise from a distance gradient between the population center Santa Marta in the Southwest (> 455,000 inhabitants) and several smaller rivers in the East on a scale of < 50 km. Due to the topographical orientation of TNNP bays, a second scale for spatial effects is given by the differences in exposition to winds-, waves- and water currents between two opposing bay flanks. This second, within-bay scale is much smaller (< 2 km).

Findings in Chapter 1 revealed that wind-stress at the Western, exposed site affected water currents throughout the entire water column (at least 10 m water depth) during all seasons, but reached only until 3 – 4 m water depth at the sheltered site during non-upwelling and down to 10 m during upwelling in one representative bay. Consequently, organisms at the exposed site experience constantly high water current exposure throughout the year. These results are in agreement with the study of Werding and Sánchez (1989) who showed that coral communities at the Western flank of one TNNP bay were exposed to higher wave impact than organisms at the Eastern, sheltered side. The authors suggested that a characteristic *Gorgonia-Diploria* community developed at the exposed side of the bay while the sheltered side was represented by deep and shallow coral communities of high diversity and structural complexity (Werding and Sánchez

1989). The characteristic coral communities in the TNNP bays and the implications of water currents during a coral bleaching event were further discussed in Chapter 6.

Results of Chapter 2 showed that particularly during non-upwelling, seawater chlorophyll (chl) *a* and particulate organic carbon (POC) concentrations along with biological O_2 demand (BOD) in the water column significantly increased with decreasing distance to the rivers in the East. This suggested that the observed spatial water quality decline was triggered by riverine runoff and not by the countercurrent-located Santa Marta. The effect of water quality decline through riverine discharge was also suggested by (Franco-Herrera et al. 2006), however as a consequence of runoff from Magdalena River – one of Colombia´s principal rivers located at more than 80 km in the Southwest from TNNP. On the contrary, the results of this thesis showed that water quality parameters declined with decreasing distance to the river mouths in the East which are much closer located to TNNP than Magdalena River. Riverine discharge from the rivers in the East was likely transported by the westward Caribbean Current (Wüst 1964; Gordon 1967) to TNNP where it had a greater impact on the Eastern bays Neguanje and Cinto, than on the Western bays Chengue and Gayraca. The latter two bays had better water quality conditions (higher water clarity, lower chl *a* and BOD).

Chapter 3 dealing with sedimentary properties and processes showed that chlorophyll contents and sedimentary O_2 demand (SOD) increased significantly with decreasing distance to the Eastern rivers, but only during upwelling. This suggests sedimentary organic matter supply controlled by nutrient-enriched upwelling waters and riverine runoff rather than by the countercurrent-located city of Santa Marta. Pulses of organic matter caused carbon turnover rates of 4.4 % supplied POC h^{-1} that were more than 2-fold higher at water current-exposed compared to the -sheltered site. The carbon turnover rates in TNNP sediments exceeded typical turnover rates in other silicate reef sands (< 1 % supplied POC h^{-1}; Wild et al. 2005) and represent a unique feature of TNNP for the rapid remineralization of upwelling-fueled organic matter. Higher rates of carbon turnover at the water current-exposed site indicated that a rapid recycling of the supplied labile organic matter was possibly the result of an intense advective pore water exchange (Huettel et al. 2003) of the highly permeable silicate sands in TNNP.

In Chapter 4, it could be shown that despite the significant spatial differences in individual productivity of the investigated primary producers (scleractinian corals, macroalgae, algal turfs, crustose coralline algae, and microphytobenthos), no spatial differences in ecosystem net and gross primary production were detected. This suggests that well adapted, local autotrophic benthic reef communities were present at both sites of the representative bay. A high benthic primary productivity on the ecosystem level was maintained by nutrients released after a rapid remineralization and recycling of organic matter by TNNP reef sediments (Chapter 3).

Chapter 5 gave an introduction to the topic of Chapter 6: coral bleaching. In Chapter 6, the first moderate coral bleaching event was reported for the TNNP region. Findings revealed that the overall coral bleaching was significantly higher at the sheltered (34 %) compared to the exposed site (8 %) in December 2010. Whereas 97 % of all previously bleached corals at the water current-exposed site had recovered from bleaching by April 2011, only 77 % recovered at the sheltered site, but 12 % had died. The results suggested that water current exposure and turbidity, which were significantly higher at the exposed site, were responsible for the observed site-specific mitigation of coral bleaching and are in agreement with other studies (Mumby et al. 2001; Nakamura and van Woesik 2001; Nakamura et al. 2003). It was shown that organisms at the exposed site experience higher water currents velocities throughout the year than the benthic community at the sheltered site (Chapter 1).

Significant spatial differences of lionfish abundances and body lengths between the different bays in TNNP were reported in Chapter 7. These findings suggested habitat preferences of *P. volitans* depending on age. Over 75 % of the total registered lionfish had a body length larger than 17 cm representing the size of a mature female (Morris 2009) highlighting the need of immediate improvements of the management actions for control of invasive *P. volitans* in TNNP.

Temporal effects on reef functioning

Chapter 2 showed that seawater nitrate, nitrite, and chlorophyll *a* concentrations significantly increased during upwelling, while pH and water clarity decreased. Increases in inorganic nutrients which promote enhanced phytoplankton growth are typical for the upwelling influenced TNNP (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). The present study showed that water quality in TNNP was close to oligotrophic conditions adequate for coral reef growth during non-upwelling, but exceeded critical threshold values during upwelling and in relation to riverine discharge. Exceeded threshold levels of inorganic nutrient concentrations induced macroalgal blooms but sustained them only during seasonal upwelling (Diaz-Pulido and Garzón-Ferreira 2002; Chapter 4). However, nutrient levels of the largely nutrient-depleted Subtropical Underwater (Corredor 1979) were below levels of other upwelling systems and did not hinder the development of coral reefs in TNNP as reported for other upwelling regions e.g. the Gulf of Panama in the Pacific (D'Croz and O'Dea 2007).

Chapter 3 showed that strong (75 – 79 % of annual supply) pulses of labile organic matter mainly composed of fresh phytoplankton detritus (C:N ratio 6 – 8) were delivered to the seafloor during seasonal upwelling. This suggested that the sedimentary organic matter supply was controlled by nutrient-enriched upwelling waters and riverine runoff rather than by the countercurrent-located city of Santa Marta, in accordance to findings for the water quality in Chapter 2. Significantly increased chlorophyll *a* in the water column reached mean values of 2.70 μg L^{-1} during seasonal upwelling (Chapter 2). The high POC turnover rates measured in TNNP silicate reef sediments suggest a good pelagic-benthic coupling and processing of organic matter during major and midyear upwelling comparable to the recycling of other natural pulses of organic matter by coral reef sediments (Wild et al. 2008).

Chapter 4 showed that scleractinian corals had highest primary productivity before upwelling. At the end of upwelling, corals and algal turfs were mainly contributing to the benthic primary production. On the ecosystem level, corals contributed most to the total net primary production (84 % at the exposed and 86 % at the sheltered site) and gross primary production (78 % and 55 %, respectively) before the upwelling, while at the end of upwelling, corals contributed most to the net and gross production only at the exposed site (64 and 75 %). During this time, at the sheltered site, macroalgae had highest contribution to net and gross production (65 and 46 %, respectively). Despite the significant spatial and temporal differences in productivity of individual organisms and their different contribution to reef productivity, no spatial or temporal differences in ecosystem net and gross primary production were detected. These findings indicate that local autotrophic benthic reef communities are well adapted to pronounced fluctuations of environmental key parameters and may possess local resilience against climate change and anthropogenic disturbances

Corals recovered significantly from coral bleaching in 2010 and 2011 in the course of seasonal upwelling (Chapter 6). During the same time, corals in other Caribbean regions such as Puerto Cabello or Los Roques National Park in Venezuela, that are not influenced by seasonal upwelling, suffered massive coral bleaching events (Bastidas et al. 2012; del Mónaco et al. 2012). Bleaching extent in these non-upwelling regions was more than twice as much as at the water current-sheltered and 7 – 9 times more than at the - exposed site in the present study. These findings, along with the absence of coral bleaching in the past, suggest that seasonal upwelling potentially plays a role in coral bleaching mitigation in TNNP. As typically highest seawater heat stress and seasonal upwelling coincide (Chollett et al. 2010), the TNNP may represent a refuge habitat in which corals are protected from temperature-induced coral bleaching of future global warming (Glynn 1996; Riegl and Piller 2003; West and Salm 2003; Chapter 6).

The monthly data on *P. volitans* distributions over one year in four TNNP bays (Chapter 7) showed no seasonal patterns between a rainy season, during which 80 % of the annual rainfall occurs, and a dry season, going along with seasonal upwelling and drastic decreases in seawater temperature from 28 to 21 °C (Salzwedel and Müller 1983; Chapter 1, 2). Seasonal upwelling did not affect the established lionfish population as the critical temperature at which lionfish ceases feeding was reported to be 16 °C with lethal consequences at 10 °C (Kimball et al. 2004) which lie below the lowest seawater temperature that can be expected for the TNNP region.

Ecological implications

The TNNP constitutes a unique environment for coral reefs where seasonal changes in water quality parameters (Chapter 1, 2) and sedimentary processes (Chapter 3) are driven by coastal upwelling and riverine discharge. Regions of coral reefs influenced by seasonal upwelling are rare: e.g. on the western coast of Mexico (Glynn and Leyte-Morales 1997; Reyes-Bonilla 2001; Reyes-Bonilla et al. 2002), the Gulf of Panama (Podestá and Glynn 1997; Glynn et al. 2001), the Gulf of Papagayo/Costa Rica (Jiménez et al. 2001), the Bahamas (Riegl and Piller 2003), South Africa (Riegl 2003), and Northern Madagascar (McClanahan et al. 2007). Facing the threat of global climate change and its implications for world-wide coral reefs, regions influenced by seasonal upwelling may become important refugia against global warming-induced coral bleaching (Glynn 1996; Chollett et al. 2010; Riegl and Piller 2003; West and Salm 2003; Chapter 6). However, most of the upwelling influenced coral reefs experience conditions that are beyond the threshold values for coral reef development due to extensive enrichment in inorganic nutrients and phytoplankton blooms (D'Croz and O'Dea 2007). The special features of seasonal upwelling in TNNP are that onset of upwelling is typically synchronized with time of highest heat accumulation in the seawater counteracting coral bleaching (Chollett et al. 2010; Chapter 6) and that the upwelled waters are relatively nutrient depleted (Corredor 1979) as compared to other upwelling regions and thereby not exceeding meso-oligotrophic conditions for coral growth (Chapter 2, 3). The results of this thesis indicate the existence of local resilience patterns of TNNP coral reefs and suggest that while threats of global warming may be counteracted by the presence of seasonal upwelling coinciding with highest heat stress, the effects of local threats (eutrophication due to riverine discharge) can only be avoided by improved management actions and conservation.

Recommendation of effective indicators for future monitoring

In this thesis, it was shown that the status variables chl *a* and water clarity, along with the process variable BOD, are good and cost-effective indicators for the assessment of water quality due to their significant correlations with other important environmental parameters which cannot always be addressed in monitoring studies. The parameters sedimentation rate of organic carbon and sedimentary organic matter, including chl *a* contents, are reliable biophysical indicators that are recommended to be included in regular monitoring activities of TNNP coral reefs. Future work should include investigation on the physiological response of coral reef organisms to upwelling- and riverine runoff-induced environmental change in water quality which, as suggested by Cooper et al. (2009), first invoke a response at the genetic and colony level such as symbiont photophysiology and coral brightness.

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Erklärung

Gemäß §6 der Promotionsordnung der Universität Bremen für die mathematischen, natur- und ingenieurwissenschaftlichen Fachbereiche vom 14. März 2007 versichere ich, dass die Arbeit mit dem Titel

„Effects of seasonality and upwelling on coral reef functioning in Tayrona National Natural Park, Colombian Caribbean"

1. ohne unerlaubte fremde Hilfe selbstständig verfasst und geschrieben wurde
2. keine anderen als die angegebenen Quellen und Hilfsmittel benutzt wurden
3. die den benutzten Werken wörtlich oder inhaltlich entnommenden Stellen als solche kenntlich gemacht wurden
4. es sich bei den von mir abgegebenen Arbeiten um 3 identische Exemplare handelt.

Brisbane, 11ten November 2013

Elisa Bayraktarov