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# THE PHYSICAL ENVIRONMENT IN CORAL REEFS OF THE TAYRONA NATIONAL NATURAL PARK (COLOMBIAN CARIBBEAN) IN RESPONSE TO SEASONAL UPWELLING*

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## 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 minimal 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 deep) 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.

*KEYWORDS:* Water current velocity and direction, ADCP, upwelling, coral reefs, Colombian Caribbean.

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# RESUMEN

**El entorno físico en arrecifes coralinos del Parque Nacional Natural Tayrona (Caribe colombiano) en respuesta a la surgencia estacional.** Los arrecifes de coral están sujetos a cambios físicos en su entorno, tales como velocidad del viento, temperatura del agua y corrientes marinas, que pueden llegar a afectar 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 está influenciado por una surgencia estacional que altera todos los factores físicos claves mencionados anteriormente. Con el objetivo de describir las variaciones espacio-temporales en el entorno físico en dos lugares de una bahía típica del PNNT (un lado expuesto y otro protegido del viento y el oleaje), 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. 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 entre ambos lados de la bahía, y 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 este último, el esfuerzo 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 marcadas 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.

*PALABRAS CLAVES:* Velocidad y dirección de corrientes, ADCP, surgencia, arrecifes coralinos, Caribe colombiano.

# 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 for 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, 1993; Brown, 1997;

Hoegh-Guldberg, 1999, 2011; Loya *et al.*, 2001). 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, 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 major rainy season (August-November), the TNNP is influenced by increased precipitations (Salzwedel and Müller, 1983). The consecutive dry season (December-April) 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 studies of Bayraktarov *et al.* (2012, 2013), 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 anchorage 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 Tayrona National Natural Park (TNNP) is located on the northern coast of Colombia, close to the city of Santa Marta, and contains six bays harboring coral communities, seagrass 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; Díaz-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 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 at a water depth of 10 m (Bayraktarov *et al.*, 2014). 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 (Arévalo-Martínez and Franco-Herrera, 2008; Bayraktarov *et al.*, 2014). 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 (Figure 1) at an exposed site on the western side and a sheltered site on the eastern side of the bay (Figure 1c). Study locations were identical to sites from the coral bleaching survey in 2010/2011 in the same bay (see Bayraktarov *et al.*, 2012, 2013). 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, 2013) and a low rugosity of 1.32 ± 0.13 (Corvin Eidens. Justus Liebig University Giessen. Giessen, Germany. 2011. unpubl. data). Here, a high abundance of octocorals was detected (pers. observation and Figure 2a). On the sheltered site, at the same water depth, reef-like frameworks with higher coral diversity, complexity and *M. cavernosa*, *Orbicella faveolata*, *O. franksi* (formerly referred to as *Montastraea faveolata* and *M. franksi*; Budd *et al*., 2012), *D. strigosa*, *C. natans*, and *Porites astreoides* as the predominant species among scleractinian corals were found (Figure 2b). Rugosity at the sheltered site in Gayraca was 1.53 ± 0.12 (Corvin Eidens. Justus Liebig University Giessen. Giessen, Germany. 2011. unpubl. data).

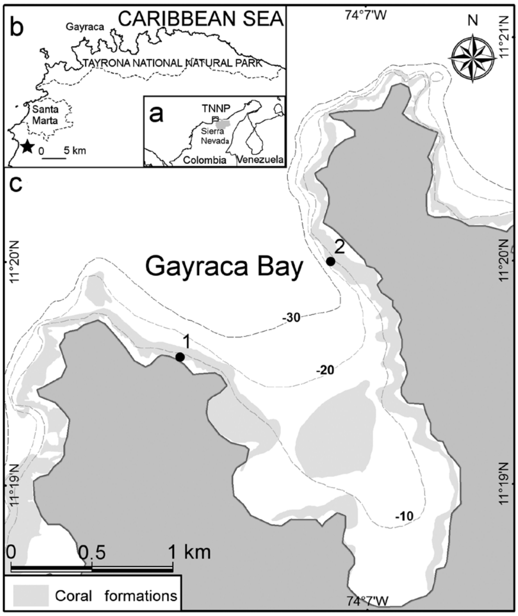

**Figure 1.** Location of Gayraca Bay and Tayrona National Natural Park (TNNP) in the Caribbean Sea. **a.** Location of TNNP in Colombia. **b.** The bays of TNNP and city of Santa Marta. The “star” symbol indicates the location of the meteorological station of the present study. **c.** Sampling locations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

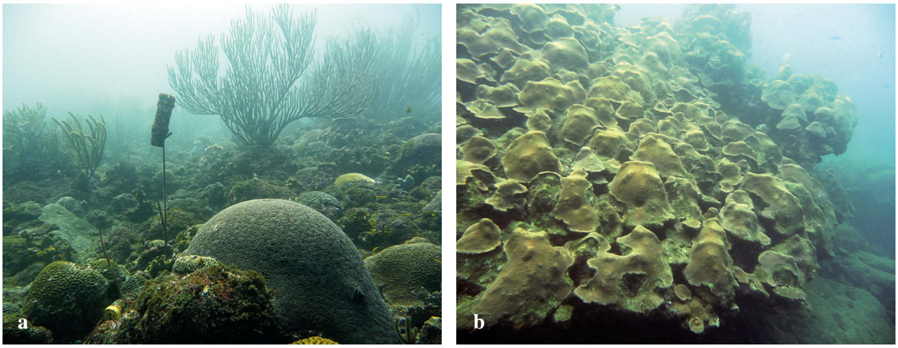

**Figure 2.** Coral communities in Gayraca Bay: **a.** The exposed site, represented by massive to encrusting growth forms of *Montastraea cavernosa*, *Diploria strigosa*, *D. labyrinthiformis*, *Colpophyllia natans*, and high abundance of octocorals. **b.** Sheltered site with reef-like frameworks of higher coral diversity and complexity with *M. cavernosa*, *Orbicella faveolata*, *O. franksi*, *D. strigosa*, *C. natans*, and *Porites astreoides*.

## 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, Santa Marta, 18 km (air-line distance) away from Gayraca Bay for the time period of study (symbol “star” in Figure 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. Quality control of water current data involved a proper installation of the equipment and subsequent data filtering. The ADCP compass was calibrated with its metal frame and installed in an up-facing position with beam No. 3 pointing northward to ensure a correct magnetic orientation of the equipment and avoid errors considering the measurement of directions. The state of sensors indicating an inclination of ADCP was controlled during measurement (pitch, roll) in order to ensure an entirely vertical position of the anchor. 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, 2013). 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), Díaz-Pulido and Garzón-Ferreira (2002), and Paramo *et al.* (2011).

## 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 (Figure 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 (Figure 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 (Figure 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 (Figure 3b).

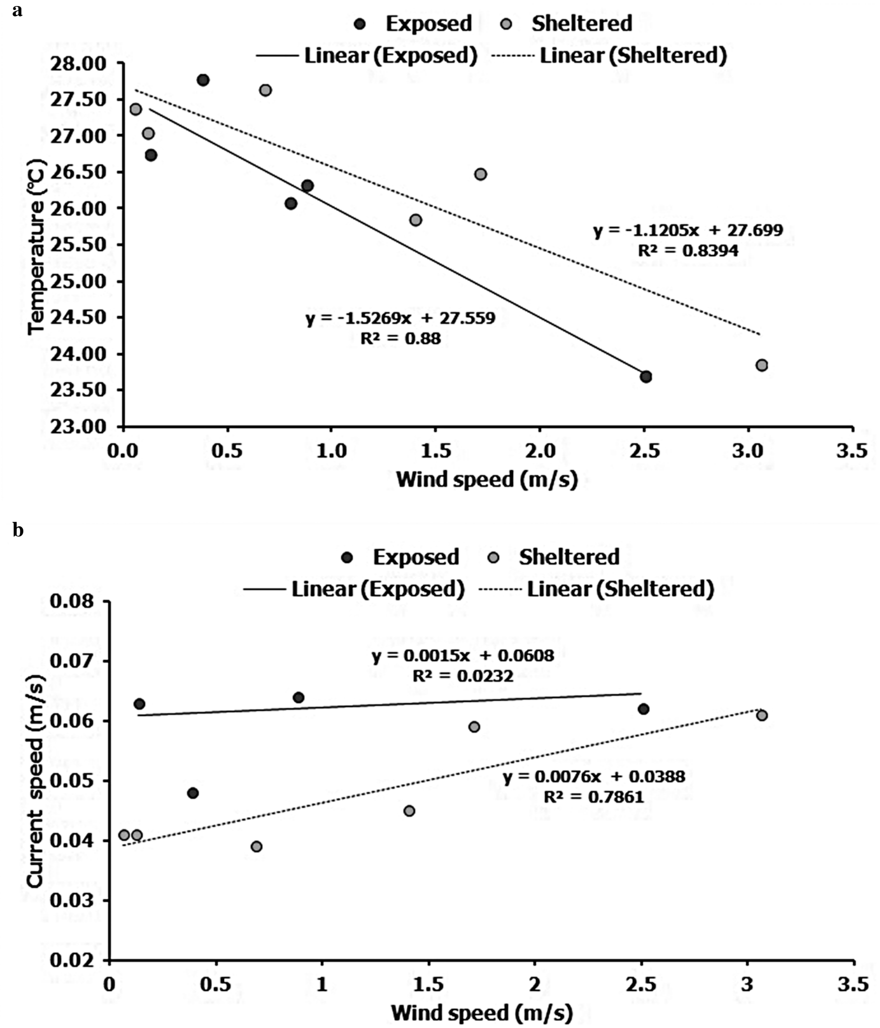

**Figure 3.** Relation between water temperature, wind speed (**a**) and water current velocity and wind speed (**b**) for the exposed and sheltered site in Gayraca Bay.

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 (Figure 4). Mean wind velocities were 0.7 ± 0.6 m $s^{-1}$ for the periods of variable winds (May-July). During non-upwelling, mean wind velocities had only a mean value of 0.4 ± 0.3 m $s^{-1}$.

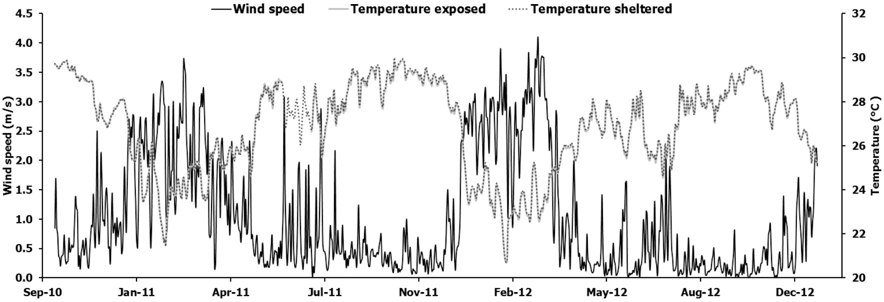

**Figure 4.** Daily mean in situ temperature at a water depth of 10 m for the exposed and sheltered site in Gayraca Bay and daily mean wind speed at a location near to Tayrona National Natural Park. In situ temperature data showed no significant difference between sites.

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 28.7 ± 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 ($r_{Spearman} = -0.69$, $\alpha = 0.05$) 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.

| 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 (Figure 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 (Figure 5). Water current velocities within the water column profile at the sheltered site responded accordingly to the significant positive correlation with wind velocity (Figure 5) calculated for the water current velocities at a water depth of 8-10 m (Figure 3b).

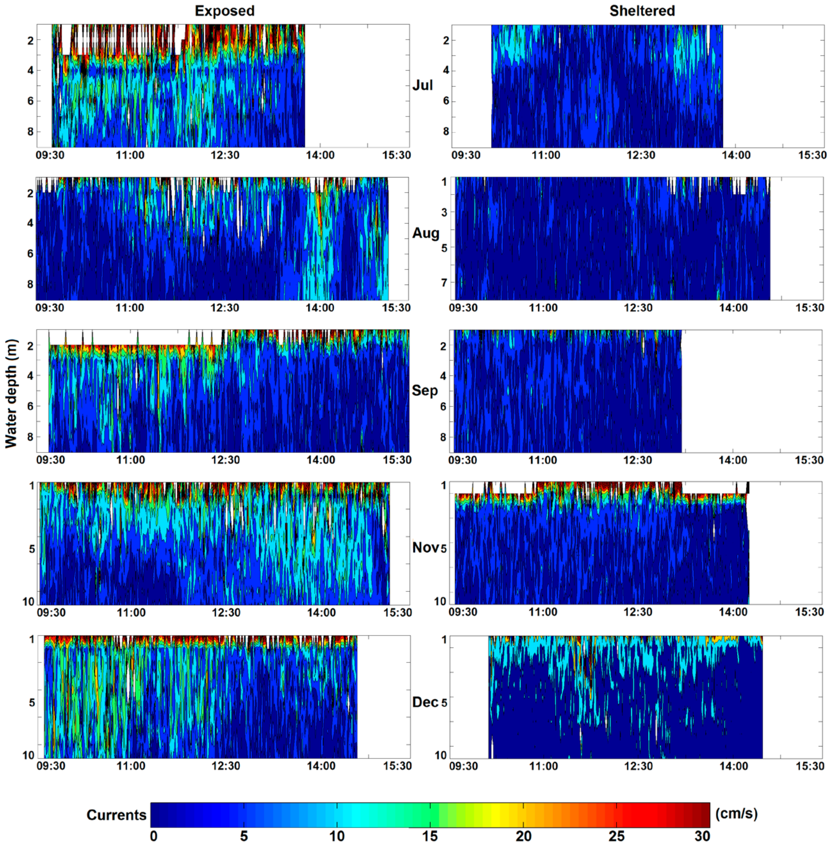

**Figure 5.** Water current velocity profiles of the water column (0-10 m water depth) for the exposed and sheltered site in Gayraca Bay during representative months of 2012. Units of water current velocity are in (cm $s^{-1}$). Abbreviations: July (Jul), August (Aug), September (Sep), November (Nov), and December (Dec).

## 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; Figure 6a). This circulation pattern was repeatedly observed in July (Figure 6b). In August, the circulation pattern changed in a way that water flow entered from the exposed site (ESE) and left the bay through the sheltered site (N; Figure 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 (Figure 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 (Figure 6f).

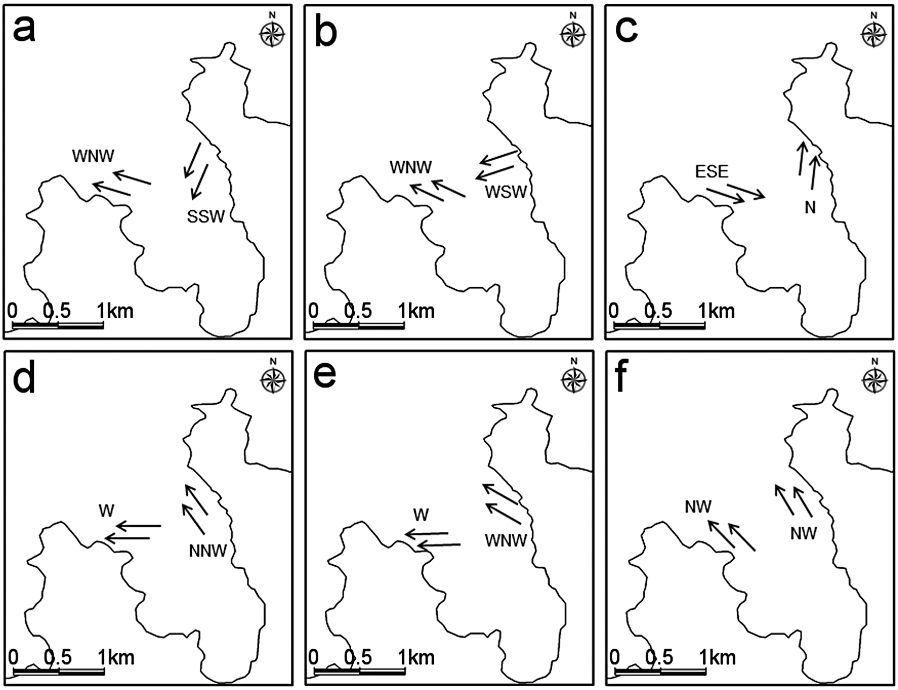

**Figure 6.** Mean current directions for the exposed (western) and sheltered site (eastern flank of the bay) at water depths of 8-10 m in Gayraca Bay for February (**a**), July (b), August (**c**), September (**d**), November (**e**) and December (**f**). Scales indicate 1 km.

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

## DISCUSSION

### The physical environment in Tayrona National Natural Park

In this study, we described the physical environment in a representative bay of Tayrona National Natural Park (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 in 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 eight times higher than the maximal wind intensity registered in the present study. One study using data from the National Centers for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) reanalysis showed that surface winds of an oceanic region within the Colombian Basin in proximity to TNNP presented higher wind velocities (mean of 8.2 m $s^{-1}$) with pronounced oscillations (± 1.7 m / $s^{-1}$) and predominant westward wind direction (Ruiz-Ochoa and Bernal, 2009). The authors however pointed out that reanalysis data is rather suitable for oceanic regions than for coastal zones (Ruiz-Ochoa and Bernal, 2009) as 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. Strong variations in wind velocity during March/April from 3.3 to 0.2 m $s^{-1}$ are consistent with the suggested disruption of Guajira Upwelling pattern during the boreal winter-spring transition (Lonin *et al.*, 2010).

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 upwelling region of Yucatan 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 water current velocities and directions by ADCP anchorage 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 to 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.*, 2013). 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.*, 2013). At the sheltered site, where sedimentation is high due to lower water current velocities, the scleractinian coral *Orbicella* spp. dominated the coral community. This coral species belongs to the most important reef builders in the Caribbean (Goreau, 1959). *Orbicella* 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, 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, 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 *Orbicella* spp. usually takes place during non-upwelling when winds are minimal (0.1 m $s^{-1}$; September, pers. 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 in 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, 1993; Brown, 1997; Hoegh-Guldberg, 1999, 2011; Loya *et al.*, 2001). 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; Bayraktarov *et al.*, 2013). 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, 2013).

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 the 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; Bayraktarov and Wild, 2014). Water currents may also influence the patterns of coral bleaching (Nakamura and van Woesik, 2001; Nakamura *et al.*, 2003; West and Salm, 2003; Bayraktarov *et al.*, 2013) 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 observed mitigation of coral bleaching, particularly at the exposed site (Bayraktarov *et al.*, 2013), before upwelling is ceased 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, 2013). 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 seasonal upwelling, represents an ideal location for studies on the effects of environmental changes on Colombian Caribbean coral ecosystems.

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## LITERATURE CITED

Andrade, C. A. 2000. The circulation and variability of the Colombian Basin in the Caribbean Sea. Ph.D. Thesis, University of Wales, Cardiff. 223 p.

Andrade, C. A. and E. D. Barton. 2005. The Guajira upwelling system. Cont. Shelf Res., 25 (9): 1003-1022.

Andrade, C. A., E. D. Barton and C. N. K. Mooers. 2003. Evidence for an eastward flow along the Central and South American Caribbean Coast. J. Geophys. Res., 108 (C6), 3185. doi:10.1029/2002JC001549.

Andrews, J. and G. Pickard. 1990. The physical oceanography of coral reef systems. 11-45. In: Dubinsky, Z. (Ed.). Ecosystems of the world: Coral reefs. Elsevier, Amsterdam. 550 p.

Arévalo-Martínez, D. and A. Franco-Herrera. 2008. Características oceanográficas de la surgencia frente a la ensenada de Gaira, departamento del Magdalena, época seca menor de 2006. Bol. Invest. Mar. Cost., 37 (2): 131-162.

Atkinson, M., E. Kotler and P. Newton. 1994. Effects of water velocity on respiration, calcification, and ammonium uptake of a *Porites compressa* community. Pac. Sci., 48 (3): 296-303.

Bayraktarov, E., V. Pizarro, C. Eidens, T. Wilke and C. Wild. 2012. Upwelling mitigates coral bleaching in the Colombian Caribbean. Proc. 12th Int. Coral Reef Symp., Australia: 9A-2.

Bayraktarov, E., V. Pizarro, C. Eidens, T. Wilke and C. Wild. 2013. Bleaching susceptibility and recovery of Colombian Caribbean corals in response to water current exposure and seasonal upwelling. PLoS ONE, 8 (11): e80536. doi:10.1371/journal.pone.0080536.

Bayraktarov, E., V. Pizarro and C. Wild. 2014. Spatial and temporal variability of water quality in the coral reefs of Tayrona National Natural Park, Colombian Caribbean. Environ. Monit. Assess., 186(6): 3641-3659.

Bayraktarov, E. and C. Wild. 2014. Spatiotemporal variability of sedimentary organic matter supply and recycling processes in coral reefs of Tayrona National Natural Park, Colombian Caribbean. Biogeosciences, 11: 2977-2990.

Berens, P. 2009. CircStat: A Matlab Toolbox for circular statistics. J. Stat. Softw., 31 (10): 1-21.

Brown, B. E. 1997. Coral bleaching: causes and consequences. Coral Reefs, 16 (5): 129-138.

Budd, A. F., H. Fukami, N. D. Smith and N. Knowlton. 2012. Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). Zool. J. Linn. Soc., 166: 465-529.

Chollett, I., P. J. Mumby and J. Cortés. 2010. Upwelling areas do not guarantee refuge for coral reefs in a warming ocean. Mar. Ecol. Prog. Ser., 416: 47-56.

Chollett, I., F. E. Müller-Karger, S. F. Heron, W. Skirving and P. J. Mumby. 2012a. Seasonal and spatial heterogeneity of recent sea surface temperature trends in the Caribbean Sea and southeast Gulf of Mexico. Mar. Pollut. Bull., 64 (5): 956-965.

Chollett, I., P. J. Mumby, F. E. Müller-Karger and C. Hu. 2012b. Physical environments of the Caribbean Sea. Limnol. Oceanogr., 57 (4): 1233-1244.

Díaz-Pulido, G. and J. Garzón-Ferreira. 2002. Seasonality in algal assemblages on upwelling-influenced coral reefs in the Colombian Caribbean. Bot. Mar., 45 (3): 284-292.

Done, T. 1983. Coral zonation: its nature and significance. 107-149. In: Barnes, D. (Ed.). Perspectives on coral reefs. Australian Institute of Marine Science, Townsville, Australia. 277 p.

Doty, M. S. 1971. Measurement of water movement in reference to benthic algal growth. Bot. Mar., (14): 32-35.

Fabricius, K. E. and P. Alderslade. 2001. Soft corals and sea fans: a comprehensive guide to the tropical shallow-water genera of the central-west Pacific, the Indian Ocean and the Red Sea. Australian Institute of Marine Science, Townsville, Australia. 264 p.

Fabricius, K. E., Y. Benayahu, and A. Genin. 1995a. Herbivory in asymbiotic soft corals. Science, 268 (5207): 90-92.

Fabricius, K. E., A. Genin and Y. Benayahu. 1995b. Flow-dependent herbivory and growth in zooxanthellae-free soft corals. Limnol. Oceanogr., 40: 1290-1301.

Fajardo, G. 1979. Surgencia costera en las proximidades de la península colombiana de la Guajira. Bol. Cient. CIOH, 2: 7-19.

García-Hoyos, L. M., A. Franco-Herrera, J. S. Ramírez-Barón and D. L. López-Cerón. 2010. Dinámica océano-atmósfera y su influencia en la biomasa fitoplanctónica, en la zona costera del departamento del Magdalena, Caribe colombiano. Bol. Invest. Mar. Cost., 39 (2): 307-335.

García, F., C. Palacio and U. García. 2011. Constituyentes de la marea en la bahía de Santa Marta (Colombia). Dyna, 78 (167): 142-150.

Garzón-Ferreira, J. 1998. Bahía de Chengue, Parque Natural Tayrona, Colombia. 115-125. In: Kjerfve, B. (Ed.). Caricomp Caribbean coral reef, seagrass and mangrove sites. Coastal Region and Small Islands Papers 3, Unesco, Paris. 82 p.

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

Glynn, P. W. 1973. Ecology of a Caribbean coral reef. The *Porites* reef-flat biotope: Part I. Meteorology and hydrography. Mar. Biol., 20 (4): 297-318.

Glynn, P. W. 1991. Coral reef bleaching in the 1980s and possible connections with global warming. Trends Ecol. Evol., 6 (6): 175-179.

Glynn, P. W. 1993. Coral reef bleaching: ecological perspectives. Coral Reefs, 12: 1-17.

Glynn, P. W. 1996. Coral reef bleaching: facts, hypotheses and implications. Global Change Biol., 2: 495-509.

Gordon, R. 1996. Acoustic Doppler Current Profiler principles of operation: A practical primer. Second edition, RD Instruments, San Diego, USA. 52 p.

Goreau, T. F. 1959. The ecology of Jamaican coral reefs I. Species composition and zonation. Ecology, 40 (1): 67.

Hamner, W. M. and E. Wolanski. 1988. Hydrodynamic forcing functions and biological processes on coral reefs: A status review. Proc. 6th Int. Coral Reef Symp., Australia, 6 (1): 103-113.

Herrmann, R. 1970. Deutungsversuch der Entstehung der "Brisa", eines föhnartigen Fallwindes der nordwestlichen Sierra Nevada de Santa Marta, Kolumbien. Mitt. Inst. Colombo-Alemán Invest. Cient., 4: 83-95.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Mar. Freshw. Res., 50 (8): 839.

Hoegh-Guldberg, O. 2011. The impact of climate change on coral reef ecosystems. 391-403. In: Dubinsky, Z. and N. Stambler (Eds.). Coral reefs: An ecosystem in transition. Springer, Dordrecht, Netherlands. 552 p.

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

Invemar. 2012. Sistema de información ambiental marina de Colombia (SIAM). Instituto de Investigaciones Marinas y Costeras (Invemar), Santa Marta. http://siam.invemar.org.co/siam/index.jsp. 03/09/12.

Jokiel, P. and J. Morrissey. 1993. Water motion on coral reefs: evaluation of the "clod card" technique. Mar. Ecol. Prog. Ser., 93 (1979): 175-181.

Lesser, M. P. 2006. Oxidative stress in marine environments: biochemistry and physiological ecology. Ann. Rev. Physiol., 68: 253-278.

Lonin, S. A., J. L. Hernández and D. M. Palacios. 2010. Atmospheric events disrupting coastal upwelling in the southwestern Caribbean, J. Geophys. Res., 115, C06030, doi:10.1029/2008JC005100.

Loya, Y. 1976. Effects of water turbidity and sedimentation on the community structure of Puerto Rican Corals. Bull. Mar. Sci., 26 (4): 450-466.

Loya, Y., K. Sakai, K. Yamazato, Y. Nakano, H. Sembali and R. van Woesik. 2001. Coral bleaching: the winners and the losers. Ecol. Lett., 4 (2): 122-131.

Mass, T., A. Genin, U. Shavit, M. Grinstein and D. Tchernov. 2010. Flow enhances photosynthesis in marine benthic autotrophs by increasing the efflux of oxygen from the organism to the water. Proc. Nat. Acad. Sci. USA, 107 (6): 2527-2531.

Mesa, O. J., G. Poveda and L. F. Carvajal. 1997. Introducción al clima de Colombia. Universidad Nacional de Colombia, Medellín. 390 p.

Molares, R. J. 2004. Clasificación e identificación de las componentes de marea del Caribe colombiano. Bol. Cient. CIOH, (22): 105-114.

Monismith, S. G. 2007. Hydrodynamics of coral reefs. Ann. Rev. Fluid Mech., 39 (1): 37-55.

Nakamura, T. and R. van Woesik. 2001. Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar. Ecol. Prog. Ser., 212 (2): 301-304.

Nakamura, T., H. Yamasaki and R. van Woesik. 2003. Water flow facilitates recovery from bleaching in the coral *Stylophora pistillata*. Mar. Ecol. Prog. Ser., 256: 287-291.

Paramo, J., M. Correa and S. Núñez. 2011. Evidencias de desacople físico-biológico en el sistema de surgencia en La Guajira, Caribe colombiano. Rev. Biol. Mar. Oceanogr., 46 (3): 421-430.

Petùs, C., C. García-Valencia, F. Thomas and M. Cessaraccio. 2007. Caracterización preliminar del proceso de surgencia costera de La Guajira a partir de observación satelital. Informe final, Instituto de Investigaciones Marinas y Costeras (Invemar) y Corporación Autónoma Regional de La Guajira (Corpoguajira), Santa Marta. 53 p.

Riegl, B. and W. E. Piller. 2003. Possible refugia for reefs in times of environmental stress. Int. J. Earth Sci., 92 (4): 520-531.

Rodríguez-Ramírez, A., J. Garzón-Ferreira, A. Batista-Morales, D. L. Gil, D. I. Gómez-López, K. Gómez-Campo, T. López-Londoño, R. Navas-Camacho, M. C. Reyes-Nivia and J. Vega-Sequeda. 2010. Temporal patterns in coral reef, seagrass and mangrove communities from Chengue bay Caricomp site (Colombia): 1993-2008. Rev. Biol. Trop., 58 (Suppl. 3): 45-62.

Ruiz-Ochoa. M. and G. Bernal. 2009. Variabilidad estacional e interanual del viento en los datos del reanálisis NCEP/NCAR en la cuenca Colombia, mar Caribe. Av. Rec. Hidrául., 20: 7-20.

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

Sebens, K. and T. Done. 1992. Water flow, growth form and distribution of scleractinian corals: Davies Reef (GBR), Australia. Proc. 7th Int. Coral Reef Symp., Guam, 1: 557-568.

van Woesik, R. 2010. Calm before the spawn: global coral spawning patterns are explained by regional wind fields. Proc. R. Soc. Biol. Sci. Ser. B, 277 (1682): 715-722. doi: 10.1098/rspb.2009.1524.

Veron, J. E. N. 2000. Corals of the world. First edition, Austr. Inst. Mar. Sci., Townsville, Australia. 463 p.

Weis, V. M. 2008. Cellular mechanisms of Cnidarian bleaching: stress causes the collapse of symbiosis. J. Exp. Biol., 211 (Pt 19): 3059-3066.

Werding, B. and H. Sánchez. 1989. The coral formations and their distributional pattern along a wave exposure gradient in the area of Santa Marta, Colombia. Medio Ambiente, 10 (2): 61-68.

West, J. M. and R. V. Salm. 2003. Resistance and resilience to coral bleaching: Implications for coral reef conservation and management. Conserv. Biol., 17 (4): 956-967.

Wild, C., C. Laforsch, C. Mayr, R. Fuß and W. Niggl. 2012. Effect of water currents on organic matter release by two scleractinian corals. Aquat. Ecol., 46 (3): 335-341.

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