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ORIGINAL ARTICLE

Short-Term Spatiotemporal Variability in Seawater Carbonate Chemistry at Two Contrasting Reef Locations in Bocas del Toro, Panama

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Abstract
There is growing concern about the effects of ocean acidification (OA) on coral reefs, with many studies indicating decreasing calcium carbonate production and reef growth. However, to accurately predict how coral reefs will respond to OA, it is necessary to characterize natural carbonate chemistry conditions, including the spatiotemporal mean and variability and the physical and biogeochemical drivers across different environments. In this study, spatial and temporal physiochemical variability was characterized at two contrasting reef locations in Bocas del Toro, Panama, that differed in their benthic community composition, reef morphology, and exposure to open ocean conditions, using a combination of approaches including autonomous sensors and spatial surveys during November 2015. Mean and diurnal temporal variability in both physical and chemical seawater parameters were similar between sites and sampling depths, but with occasional differences in extreme values. The magnitude of spatial variability was different between the two sites, which reflected the cumulative effect from terrestrial runoff and benthic metabolism. Based on graphical vector analysis of TA–DIC data, reef metabolism was dominated by organic over inorganic carbon cycling at both sites, with net heterotrophy and net calcium carbonate dissolution dominating the majority of observations. The results also highlight the potentially strong influence of terrestrial freshwater runoff on surface seawater conditions, and the challenges associated with evaluating and characterizing this influence on benthic habitats. The Bocas del Toro reef is a unique system that deserves attention to better understand the mechanisms that allow corals and coral reefs to persist under increasingly challenging environmental conditions.

Keywords Coral reefs · Carbonate chemistry · Ocean acidification · Spatiotemporal · Freshwater runoff · Bocas del Toro · TA–DIC

Extended author information available on the last page of the article

1 Introduction

As one of the most biologically diverse and economically important marine ecosystems, coral reefs provide numerous ecosystem services including coastal protection, habitat provision, fisheries, building materials, biochemical compounds, and tourism (Moberg and Folke 1999; Pandolfi et al. 2005; Hoegh-Guldberg et al. 2007). Since the onset of the industrial revolution, coral reefs worldwide have experienced drastic changes in function and health, including reductions in coral cover (Hoegh-Guldberg 2005; Wilkinson 2008), calcium carbonate ($CaCO_3$) accretion rates (Perry et al. 2018; Toth et al. 2018), structural complexity (Alvarez-Filip Lorenzo et al. 2009), and biodiversity (Loya et al. 2001; Hughes et al. 2018). The deterioration of coral reefs has been attributed to a number of global and local stressors including climate change, runoff, sedimentation, pollution, disease, and overfishing (Hoegh-Guldberg 1999; Hughes et al. 2003; Bellwood et al. 2004; Wilkinson 2008). In addition to these perturbations, rising atmospheric carbon dioxide (CO_2), as a result of fossil fuel combustion, deforestation, and land-use changes (Orr et al. 2005; Le Quéré et al. 2009), is driving shifts in seawater carbonate chemistry, leading to a decrease in average seawater pH and saturation state with respect to $CaCO_3$ minerals (Ω), commonly referred to as ocean acidification (OA). OA could have direct negative effects on some marine organisms (e.g., pteropods, corals, sea urchins, oysters,) and ecosystems (e.g., pelagic food webs, coral reefs, oyster reefs) (Hoegh-Guldberg et al. 2007; Doney et al. 2009; 2020; Hofmann et al. 2010; Kroeker et al. 2013), and may also alter biogeochemical cycling of C, N, and P (e.g., Doney et al. 2009; Beman et al. 2011).

For coral reefs, the paramount concern about OA has been its potential to drive reefs from a state of net $CaCO_3$ accretion to one of net erosion (Kleypas et al. 1999; Bruno and Selig 2007; Fabry et al. 2008; Silverman et al. 2009; Kline et al. 2019) through decreased biogenic calcification rates (Pandolfi et al. 2011; Kennedy et al. 2013; Chan and Connolly 2013), increased rates of $CaCO_3$ dissolution, and bioerosion (Andersson et al. 2009; Wisshak et al. 2012; Andersson and Gledhill 2013; Eyre et al. 2018). Although most laboratory studies have reported decreased rates of calcification by tropical corals and calcifying algae exposed to elevated CO_2, and decreased pH and Ω conditions (Pandolfi et al. 2011; Chan and Connolly 2013; Dove et al. 2013; Kroeker et al. 2013; Johnson et al. 2014), some calcifying organisms have exhibited mixed responses (Ries et al. 2009; Andersson et al. 2011). Thus, the general consensus is that calcifying taxa and species will exhibit differential sensitivity or resilience to distinct OA thresholds (McCulloch et al. 2012; Chan and Connolly 2013) (Fabricius et al. 2011). However, seawater carbonate chemistry can be highly variable between and across different habitats on coral reefs, making it challenging to predict both current and future seawater chemistry conditions. Furthermore, many model projections and experimental treatment scenarios examining the response of reef organisms to OA are based primarily on open ocean trends (e.g., Hoegh-Guldberg et al. 2007; Silverman et al. 2009; Ricke et al. 2013) despite fundamental differences in carbonate chemistry dynamics between the open ocean and coral reefs.

In most coral reef environments, benthic and pelagic metabolism, geomorphology, and hydrodynamics, interact to modify seawater carbonate chemistry over spatial scales ranging from microns to kilometers, and on timescales of seconds to days (Yates et al. 2007; Anthony et al. 2011; Hofmann et al. 2011; Shaw et al. 2012; Duarte et al. 2013; Falter et al. 2013; Page et al. 2018; Cyronak et al. 2020). Biogeochemical processes on coral reefs have the capacity to drive fluctuations in CO_2 parameters (e.g., pCO_2, pH, and Ω_a) over diel and/or seasonal timescales such that the extremes often are equal to or even exceed conditions predicted in the open ocean by the end of the century (Andersson and Mackenzie 2012; Price et al. 2012; Shaw et al. 2012; Bopp et al. 2013; Albright et al. 2015; Kline et al. 2015). Some reefs are also strongly influenced by terrestrial-based runoff and/or riverine inputs that also may significantly modify local seawater chemistry (Drupp et al. 2011; Fagan and Mackenzie 2007). The degree to which seawater carbonate chemistry is modified is linked to water column depth, residence time, biomass and the benthic community composition, with the coral cover and the relative abundances of calcifying to non-calcifying organisms resulting in differential modification of seawater (Anthony et al. 2011; Lowe and Falter 2015; Page et al. 2018). These differences can have consequences for downstream communities, as the dominant biogeochemical processes may exacerbate or alleviate the effects of OA (Anthony et al. 2011; Manzello et al. 2012; Hendriks et al. 2014; Camp et al. 2016; Rivest et al. 2017; Takeshita et al. 2018; Cyronak et al. 2018). Consequently, to understand how OA may affect coral reefs and its inhabitants, it is imperative to first understand the current conditions these systems experience, including the natural range and variability of seawater carbonate chemistry, and the control and the drivers of the natural variability (Andersson and Mackenzie 2012; Page et al. 2016, 2017, 2018).

The recent development of faster and more accurate autonomous sensors for in situ measurements of pH and oxygen (Martz et al. 2010) has advanced the ability to capture high-frequency variability over extended periods of time, providing greater capacity to evaluate the environmental drivers and extremes experienced by reef organisms. Previous studies include evaluating organismal and community functions across natural CO_2 gradients (e.g., Manzello et al. 2008), communities associated with volcanic CO_2 seeps/vents (e.g., Fabricius et al. 2011; Kroeker et al. 2011; Kerrison et al. 2011), highly vegetated areas such as seagrass meadows, kelp forests, and mangroves (e.g., Hendriks et al. 2014; Kapsenberg and Hofmann 2016; Koweek et al. 2017), shallow coral reef flats, fore reefs, and terraces (e.g., Page et al. 2018), and naturally low pH "Ojo" springs (e.g., Crook et al. 2012). Other studies have characterized the natural variability of seawater carbonate chemistry across a range of habitats with differing benthic community composition with the aim to evaluate whether some habitats could serve as refugia from OA (Yates et al. 2014; Camp et al. 2016), while others have attempted to assess the biological impacts of seawater carbonate chemistry variability on calcification rates (Shamberger et al. 2014). Establishing a baseline of contemporary environmental conditions is essential for improving our ability to make robust predictions about the fate of coral reefs. Furthermore, it is a critical aspect in the design of more ecologically relevant manipulation experiments through the incorporation of the natural temporal variability and ranges experienced by these organisms (e.g., Jokiel et al. 2008; Kline et al. 2012, 2019; Dove et al. 2013; Andersson et al. 2015).

The goal of this study was to characterize the high-resolution spatiotemporal variability in seawater carbonate chemistry at two reef environments with different benthic community structure, reef morphology, and exposure to open ocean conditions. Using a combination of autonomous sensors and spatial surveys, we characterized the seawater carbonate chemistry at two coral reef sites in Bocas del Toro, Panama over the month of November 2015. One site, Punta Caracol, is a small lagoonal reef situated within Bahia Almirante and is in close proximity to dense mangroves and seagrass beds, whereas Punta Vieja is a large reef site exposed to the open ocean. We hypothesize that heterogeneity in the benthic community structure and physical environment between the two sites would produce localized differences in seawater carbonate chemistry conditions.

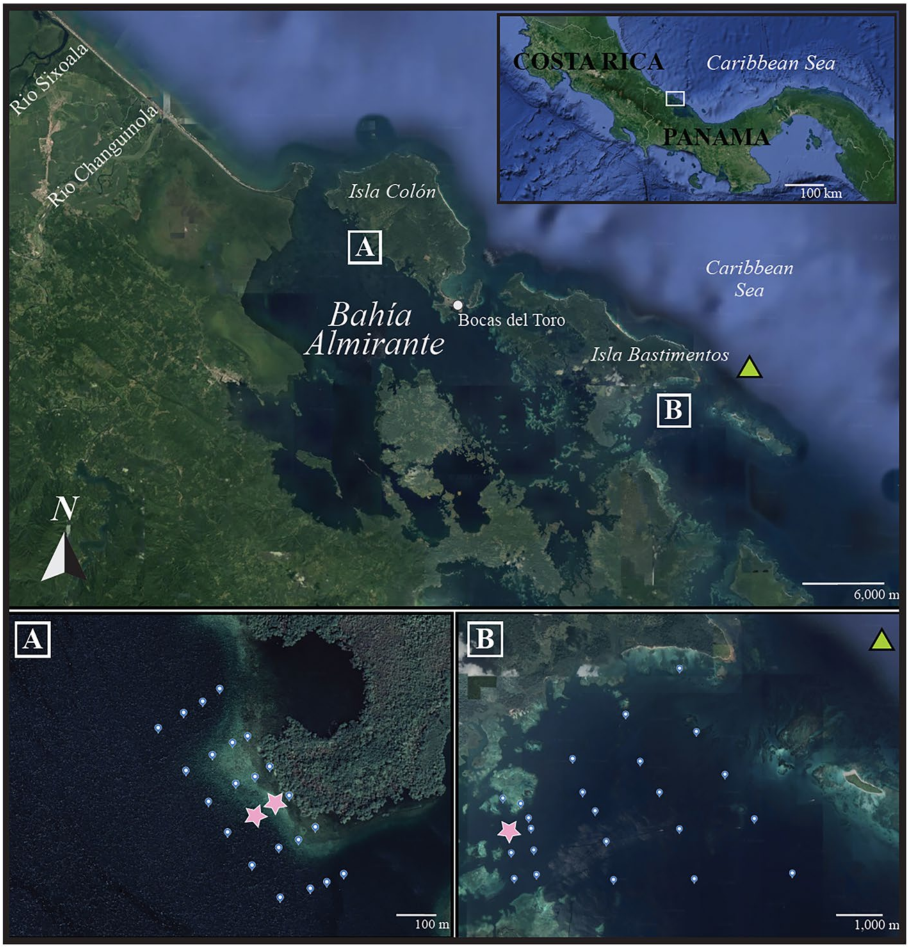

Fig. 1 Location of the two reef survey sites in Bocas del Toro, Panama: Punta Caracol (**A**) and Punta Vieja (**B**), with blue/white dots denoting the location of each discrete water sample collected and pink stars representing the location of autonomous sampling instruments. The offshore reference station is marked with a green triangle. Map imagery from Google

2 Materials and Methods

2.1 Site Descriptions

2.1.1 Bocas del Toro, Panamá

The Bocas del Toro Archipelago is located along Panama's northwest Caribbean coast. Almirante Bay in the northwest side of the archipelago covers an approximate area of 446 km^2 and is subject to high levels of rainfall, including episodic downpours totaling 3–5 m annually, freshwater discharge, terrestrial inputs, and high sedimentation rates from several rivers, creeks and streams that drain into the bay resulting in high turbidity (Fig. 1)

(Guzmán and Guevara 1998a, b; D'Croz et al. 2005; Carruthers et al. 2005, Guzman et al. 2005). Along the Boca del Drago inlet, a sediment plume is typically present as a result of high sediment runoff from the Changuinola river north of Bocas del Toro and from the Sixaola river in Costa Rica (Seemann et al. 2014). Almirante Bay is a sheltered semi-lagoonal system created by a barrier of islands and shoaling sand cays, which is shielded from the waves and wind outside the archipelago. The bay and adjacent islands are lined by dense mangrove forests dominated by the red mangrove *Rhizophora mangle* (Guzmán and Jiménez 1992; Dominici-Arosemena and Wolff 2005; Collin 2005). Water circulation is predominantly driven by tides in Almirante Bay and occurs through passages between islands and sand cays with one main inlet at Boca del Drago and outlets on either end of Isla Bastimentos (Seemann et al. 2014). The tidal range for the archipelago is small (0.4 m) with complex seasonal variation between diurnal and semidiurnal tides of varying amplitudes (D'Croz et al. 2005). The climate of Bocas del Toro includes frequent and strong rainfall with irregular seasonal patterns (Kaufmann and Thompson 2005; Dominici-Arosemena and Wolff 2005; D'Croz et al. 2005).

2.1.2 Punta Caracol

Punta Caracol is a small, shallow reef site (~ 0.07 km^2) situated along the east coast of Isla Colon on the inside of Almirante Bay (9.377°N, 82.30°W) (Fig. 1). It is characterized by a sequential zonation of varying habitats moving away from the mangrove-dense shoreline to fine-grained sediments and seagrasses (< 1 m depth), sandy sediments and many colonies of *Agaricia*, *Porites, Orbicella*, *Diploria, Montastrea* and *Colpophyllia* (2–4 m), which transition to a mixed community of coral reef organisms and muddy sediments as depth increases from 4 to 12 m (Guzmán and Guevara 1998a, 2005; Loh and Pawlik 2012; Neal et al. 2014). Nestled at the mouth of Big Bright, a large drainage basin, Punta Caracol receives a flux of nutrients and organic material from nearby plantations (Guzmán and Jiménez 1992; Gochfeld et al. 2007). Other factors influencing this site include high fishing pressure, coastal development, and sedimentation from terrestrial runoff (Seemann et al. 2014; Kline 2004).

Punta Caracol is the only reef within the Almirante Bay with documented continuous presence of the staghorn coral *Acropora cervicornis* for the past 800 years (O'Dea et al. 2020). Furthermore, Aronson et al. (2004) documented a phase shift from the dominance of branching *Porites* species to *Agaricia* species within Almirante Bay since the 1970s, most likely due to a decline in water quality. Furthermore, sponges are common and diverse at this reef site and are a critical component of the benthic community (Diaz 2005; Gochfeld et al. 2007; Easson et al 2015).

2.1.3 Punta Vieja

The Punta Vieja reef is situated along the southeast coast of Isla Bastimentos (9.259° N, 82.1081° W) (Fig. 1). In contrast to Punta Caracol, Punta Vieja is outside of Almirante Bay, approximately 10 km from the town of Bocas. Correspondingly, Punta Vieja has greater exposure to the open ocean and is surrounded mostly by uninhabited forest and mangrove crop-ups and keys (Kline 2004; Díaz 2005). The benthic habitat composition differs from Punta Caracol as the reef flat (2–5 m) is dominated mostly by *Acropora cervicornis*, *Acropora palmata,* and *Millepora complanata,* but also contains patches of other massive and branching corals along with gorgonians. Beyond the reef flat, the reef drops off sharply to a depth of ~ 12–14 m where it is dominated by muddy bottom. The coral reefs around Punta Vieja are among the most diverse in Panama, containing 57 of the 64 (89%) scleractinian coral species reported from Caribbean reefs in Panama (Guzman and Guevara 1998b, 1999). These reefs also harbor a high diversity and abundance of sponges which are also a critical component of the benthic community on these reefs (Diaz 2005; Diaz et al 2007).

2.2 Sampling Strategy

2.2.1 Autonomous Sampling of Water Column Parameters

To measure short-term variability in seawater biogeochemistry, high-frequency temporal data were collected by deploying stationary autonomous instruments at both Punta Caracol and Punta Vieja from November 3 to 20, 2015 (Fig. 1). Two stations at each site (3 m and 8.4 m at Punta Caracol, and 2.6 m and 7.6 m at Punta Vieja) were equipped with SeapHOx sensors (Martz et al. 2010) that measured temperature (°C), salinity (psu), pressure, dissolved oxygen (DO; ml L^{-1}), and pH every 30 min. SeapHOx pH measurements were determined from the internal Durafet electrode and reported on the total pH scale. The pH was calibrated and validated to discrete seawater samples collected next to the instrument throughout the study (Bresnahan et al. 2014). To characterize the currents at the reef sites, one low-resolution and one high-resolution 1 MHz AquaDopp (Nortek) current profiler were deployed at Punta Caracol and Punta Vieja, respectively. All sensors were secured to the bottom at each station using cinder blocks.

2.2.2 Spatial Sampling of Surface Seawater Carbonate Chemistry

In order to capture the spatial variability in seawater chemistry throughout the diurnal period, surveys were carried out by boat in the morning and afternoon from November 11 to 17, 2015. Surface seawater samples were collected at 24 stations across an area of ~ 0.07 km^2 at Punta Caracol ($n=5$ surveys) and 25 stations across an area of 16 km^2 at Punta Vieja ($n=4$ surveys). In addition to the 25 stations at Punta Vieja, samples were also collected at an offshore station to serve as a reference for open ocean conditions (Fig. 1). Three additional seawater sampling surveys between Punta Caracol and Punta Vieja were carried out to capture the transitional gradient between the sites. At each sampling location, sea surface temperature (± 0.2 °C), salinity (± 0.1 psu) and DO (± 0.2 ml L^{-1}) were measured with a YSI Professional Plus multi-parameter probe. Surface seawater samples were collected with a Niskin bottle from a depth of ~ 0.5 m and immediately transferred to 250-mL Pyrex borosilicate glass bottles and preserved with 100 µL of saturated solution of $HgCl_2$ per standard protocols (Dickson et al. 2007). All samples were sealed with grease coated borosilicate stoppers secured with rubber bands to prevent gas exchange.

The samples were shipped to the Scripps Coastal and Open Ocean Biogeochemistry laboratory for analysis of dissolved inorganic carbon (DIC) and total alkalinity (TA). Concentrations of DIC were measured using an automated infrared inorganic carbon analyzer (AIRICA, Marianda) system with a LI-COR 7000 (Li-COR) infrared CO_2 analyzer as the detector. Total alkalinity was analyzed via an open-cell potentiometric acid titration using an 876 Dosimat (Metrohm) and Electrode Plus pH electrode (Metrohm) (Dickson et al. 2007). Accuracy of the instruments, calculated as the mean offsets (± 1

SD) from Dickson Certified Reference Material (CRM), was − 0.9 ± 2.4 μmol kg^{-1} (n = 51) and − 2.1 ± 2.7 μmol kg^{-1} (n = 136) for TA and DIC, respectively.

2.3 Calculations and Data Analysis

The MATLAB CO2SYS program (Lewis and Wallace 1998) was used to calculate seawater pCO_2, aragonite saturation state (Ω_a) and pH_T (defined on the total H^+ scale) based on in situ seawater temperature, salinity, DIC, and TA. Dissociation constants were adopted from Mehrbach et al. (1973), refit by Dickson and Millero (1987).

To assess the relative influences of reef metabolic processes on the observed spatial and temporal variability in seawater carbonate chemistry, graphical vector analysis of TA–DIC data was used to evaluate the theoretical effects of net community calcification (NCC) and net community production (NCP) on seawater chemistry (Deffeyes 1965; Suzuki and Kawahata 2003; Cyronak et al. 2018). NCC refers to the balance between gross calcification and gross $CaCO_3$ dissolution and NCP refers to the balance between primary production and total respiration (e.g., Cyronak et al. 2018). The relative balance between NCC and NCP is reflected in the slope of the TA–DIC regressions, such that a slope approaching 2 indicates metabolic modification dominated by inorganic carbon cycling (NCC), whereas a slope approaching 0 represents domination by organic carbon cycling (NCP) (Cyronak et al. 2018). Given the large inputs of freshwater to the system, TA–DIC data were normalized to the average salinity at the offshore reference station (34.4 psu) to remove effects from freshwater dilution and precipitation that occurred in this study. However, traditional salinity normalization using 0 as an end-member could potentially overestimate the nTA and nDIC concentrations (Friis et al. 2003; Richardson et al. 2017) as rivers are known to be a source of alkalinity and inorganic carbon. Therefore, two different freshwater end-members were used to assess the effect of salinity normalization assuming different freshwater TA and DIC concentrations: (1) assuming zero TA and negligible DIC in the freshwater end-member and (2) a nonzero end-member based on observed relationships between TA, DIC, and salinity. Salinity-normalized TA and DIC concentrations were calculated using the equation:

$$C_n = \frac{\left(C_m - C_{fw}\right) \times S_{sw}}{S_m} + C_{fw} \tag{1}$$

where C_m is the measured solute concentration (TA or DIC in μmol kg^{-1}), C_{fw} is the solute concentration of the freshwater being added to the system (μmol kg^{-1}), S_{sw} is the salinity of the seawater in which the data are being normalized to (i.e., 34.4 psu), and S_m is the measured salinity (Friis et al. 2003; Jiang et al. 2014). When we normalize the data using the zero end-member, the equation reduces to:

$$C_n = \frac{\left(C_m \times S_{sw}\right)}{S_m} \tag{2}$$

which is often applied in coral reef biogeochemistry assuming the solute concentration of the freshwater added to the system is zero (e.g., Friis et al. 2003). For the nonzero end-member calculation, freshwater solute concentrations were determined from the relationship of salinity and TA and DIC at each site, where C_{fw} is the y-intercept of the solute-salinity linear regression (Jiang et al. 2014). Type II major axis linear regression analysis was performed on nTA and nDIC data in MATLAB using the lsqfitma.m MODEL-2 least squares fit code (https://www.mbari.org/index-of-downloadable-files/).

3 Results

3.1 Wind, Rain, Tides and Currents

During the deployment period from November 3 to 20, 2015, the weather was predominantly partly cloudy with intermittent rainstorms and an average wind speed of 1.9 ± 1.1 m s^{-1} predominantly from the southeast (Smithsonian Physical Monitoring Program). Total rainfall over the course of the study reached 99.4 mm with the heaviest rainfall occurring on November 11th (Smithsonian Physical Monitoring Program; Fig. 2). Tides in Bocas del Toro were mixed semidiurnal with an average tidal range of 0.31 ± 0.10 m during the study (Fig. 2). Currents at Punta Caracol were predominantly oriented alongshore toward the north–northwest, ranging in speed from 0 to 0.12 m s^{-1} (avg. = 0.03 m $s^{-1} \pm 0.02$ m s^{-1}) while currents at Punta Vieja were generally slower, ranging from 0 to 0.08 m s^{-1} (avg. = 0.02 m $s^{-1} \pm 0.02$ m s^{-1}) with net flow directed from east to west (Fig. 3).

3.2 Temporal Variability of Seawater Parameters from Stationary Autonomous Sensors

3.2.1 Punta Caracol

Mean seawater temperature was similar at 3 m and 8 m depth at Punta Caracol, with an average of 30.3 °C (Fig. 2; Table 1). Temperature at both depths decreased by 0.7 °C throughout the study period. Diel trends in temperature were apparent, with the shallower site (3 m) experiencing greater fluctuations than the deeper site (8 m) with an average diel range of 0.7 ± 0.2 °C and 0.4 ± 0.1 °C, respectively. Mean seawater salinity was greater at the deeper site (34.3 ± 0.2 psu) than the shallow site (33.9 ± 0.3 psu). Distinct diel trends in DO and pH were evident at both depths at Punta Caracol (Fig. 2). The mean DO concentration was qualitatively slightly higher at 3 m (169.6 ± 5.9 µmol kg^{-1}) compared to 8 m (160.0 ± 6.5 µmol kg^{-1}) with a mean daily range of 44.4 ± 11.2 µmol kg^{-1} and 38.3 ± 6.9 µmol kg^{-1}, respectively (Table 1). The daily range in DO at 3 m varied from 20.9 to 67.8 µmol kg^{-1} and from 24.8 to 51.2 µmol kg^{-1} at 8 m. The mean pH values for the two depths were comparable (7.96 ± 0.03 (3 m) and 7.97 ± 0.01 (8 m); Table 1) although the shallower site experienced larger variability (Table 1). The range in pH over any given day varied from 0.05 to 0.32 (3 m) and 0.05 to 0.09 (8 m).

3.2.2 Punta Vieja

Mean seawater temperature was similar between the two sampling depths (30.3 °C ± 0.2 °C (3 m) and 30.2 °C ± 0.2 °C (8 m); Table 1), whereas average salinity was slightly higher at 8 m (35.0 ± 0.4 psu; Table 1) compared to 3 m (34.2 ± 0.2 psu; Table 1). DO and pH distinctly followed diel cycles with little apparent influence from tides. Mean DO concentrations were slightly higher for the shallow site (169.1 ± 5.2 µmol kg^{-1}) compared to the deeper site (159.8 ± 8.8 µmol kg^{-1}) with a mean diel range of 44.3 ± 13.2 µmol kg^{-1} and

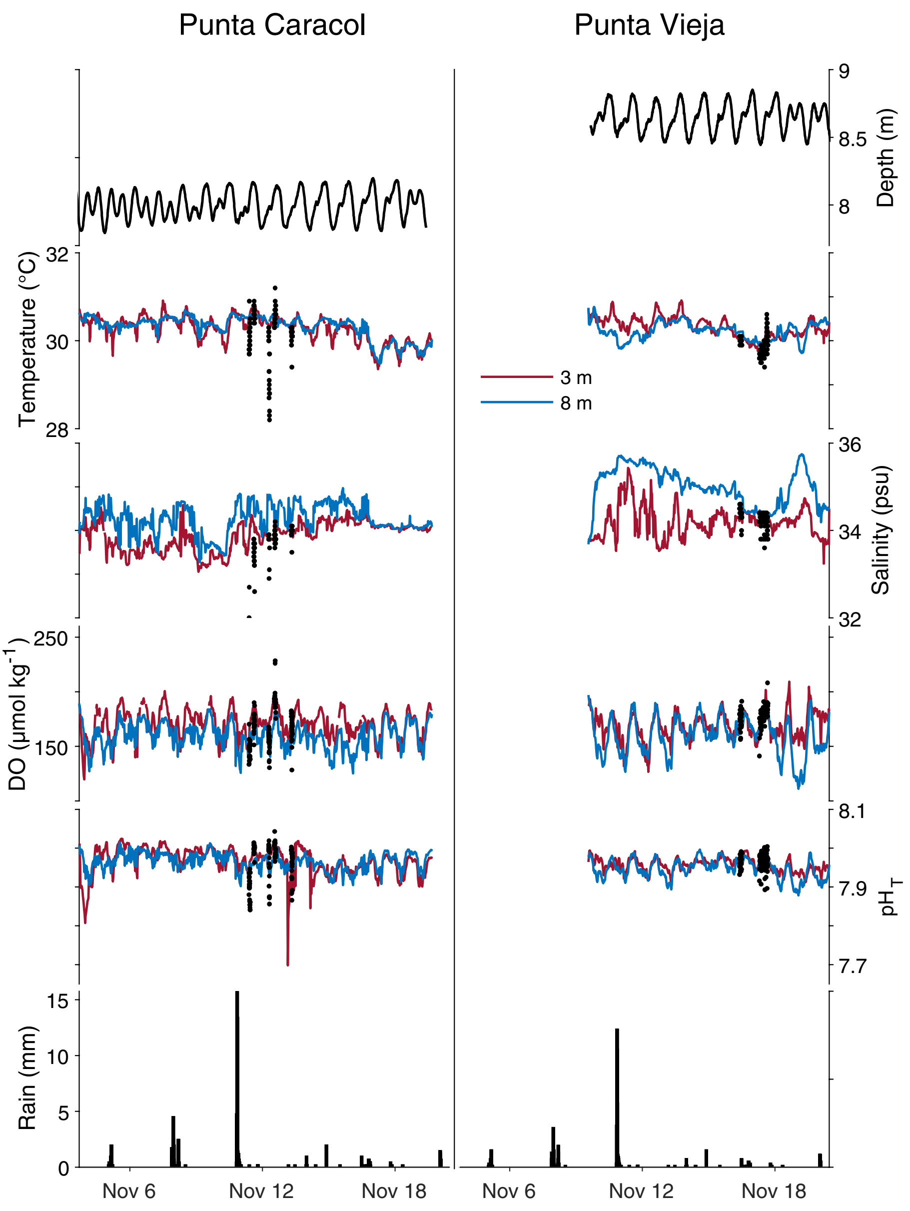

Fig. 2 Time series profiles for Punta Caracol (left) and Punta Vieja (right) between Nov 3 to Nov 20 showing the depth at the deeper sites, temperature, salinity, DO, and pH_T measured with four stationary autonomous sensors. The red line indicates the 3 m sampling depth and the blue represents the 8 m sampling depth. Black dots are the surface discrete samples from the spatial surveys. Rainfall data was collected at the Smithsonian Tropical Research Institute's Bocas del Toro field station

49.6 ± 14.7 μmol kg^{-1}, respectively (Table 1). The diel range in DO varied from 28.9 to 62.1 μmol kg^{-1} at 3 m and 32.4 to 80.7 μmol kg^{-1} at 8 m. Mean pH was similar between the two depths (7.96 ± 0.01 (3 m) and 7.95 ± 0.02 (8 m)), with little difference in the mean

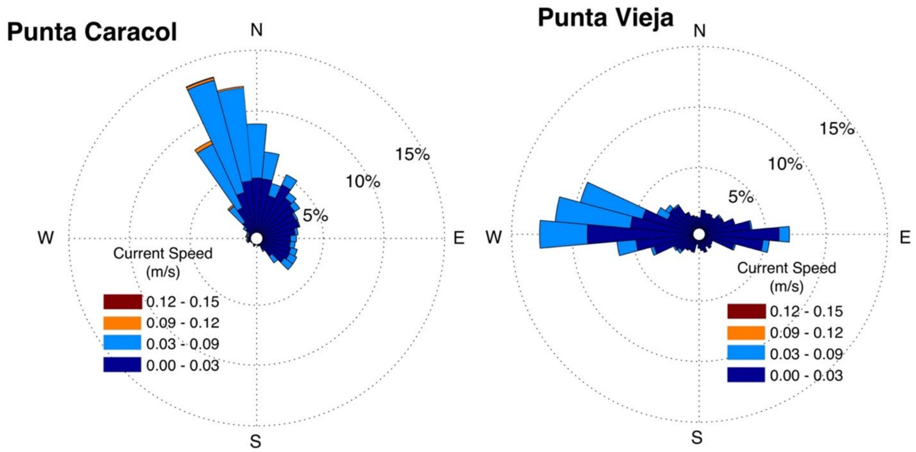

Fig. 3 Current profile data from Punta Caracol and Punta Vieja showing the dominant current directions and speeds. The ranges in current speed are represented by the different colors, and the dotted circles indicate the percentage of time during which the currents measured fell in each speed and direction bin

Table 1 Summary table of the average (±SD) and average range (±SD) of measured biogeochemical parameters from the spatial and temporal studies at both sites

	Punta Caracol			Punta Vieja		
	Spatial	Temporal		Spatial	Temporal	
		3 m	8 m		3 m	8 m
Average						
Temperature (°C)	30.2 ± 0.5	30.3 ± 0.2	30.3 ± 0.3	29.9 ± 0.2	30.3 ± 0.2	30.2 ± 0.2
Salinity	32.8 ± 1.6	33.9 ± 0.3	34.3 ± 0.2	34.2 ± 0.1	34.2 ± 0.2	35.0 ± 0.4
DO (µmol/kg)	166.8 ± 18.0	169.6 ± 5.9	160.0 ± 6.5	177.6 ± 6.2	169.1 ± 5.2	159.8 ± 8.8
DIC (µmol/kg)	1914 ± 26	–	–	1934 ± 9	–	–
TA (µmol/kg)	2185 ± 55	–	–	2216 ± 10	–	–
pH(T)	7.96 ± 0.04	7.96 ± 0.03	7.97 ± 0.01	7.96 ± 0.00	7.96 ± 0.01	7.95 ± 0.02
Ωa	3.22 ± 0.39	–	–	3.29 ± 0.04	–	–
pCO_2 (µatm)	486.53 ± 56.85	–	–	479.79 ± 2.81	–	–
Average range						
Temperature (°C)	1.1 ± 0.6	0.7 ± 0.2	0.4 ± 0.1	0.5 ± 0.3	0.5 ± 0.2	0.4 ± 0.2
Salinity	2.4 ± 2.2	0.6 ± 0.3	0.8 ± 0.3	0.1 ± 0.1	0.9 ± 0.5	0.7 ± 0.4
DO (µmol/kg)	44.0 ± 8.8	44.4 ± 11.2	38.3 ± 6.9	32.8 ± 8.1	44.3 ± 13.2	49.6 ± 14.7
DIC (µmol/kg)	82 ± 25	–	–	64 ± 21	–	–
TA (µmol/kg)	98 ± 45	–	–	58 ± 20	–	–
pH(T)	0.11 ± 0.04	0.10 ± 0.07	0.07 ± 0.01	0.09 ± 0.02	0.05 ± 0.01	0.07 ± 0.02
Ωa	0.77 ± 0.42	–	–	0.51 ± 0.13	–	–
pCO_2 (µatm)	151.66 ± 69.79	–	–	121.19 ± 33.57	–	–

For the spatial surveys, range was calculated as the average range during each individual sampling survey (Punta Caracol, $n = 5$; Punta Vieja, $n = 4$), and for the temporal sampling regime range was calculated as the average diel range over a full 24 h period (Punta Caracol, $n = 17$; Punta Vieja, $n = 12$). Dashed lines imply that the parameter was not measured diel range (0.05 ± 0.01 and 0.07 ± 0.02, respectively; Table 1). Over any given day, the pH range varied from 0.04 to 0.07 at 3 m and 0.05 to 0.11 at 8 m.

3.3 Spatial Variability of Seawater Carbonate Chemistry Parameters from Boat Surveys

3.3.1 Punta Caracol

Average surface seawater temperature for all spatial surveys was 30.2 ± 0.5 °C, with a mean range of 1.1 ± 0.6 °C (Table 1). In general, seawater temperature was lower in the morning than the afternoon. During the afternoon surveys, surface seawater temperature showed an even spatial distribution while the first two morning surveys (November 11 and 12) revealed distinct spatial gradients with areas of colder surface seawater. These two surveys followed an intense rain event on the nights of November 10 and 11 (Fig. 2). Coincident with the colder temperatures, salinity was also lower with the lowest mean salinity (30.1 ± 1.2 psu) observed in the morning of November 11 and the greatest spatial gradient ranging from 28.5 to 33.9 psu in the morning of November 12 (Fig. 4). The mean seawater salinity for all surveys was 32.8 ± 1.6 psu with a mean salinity range of 2.4 ± 2.2 psu.

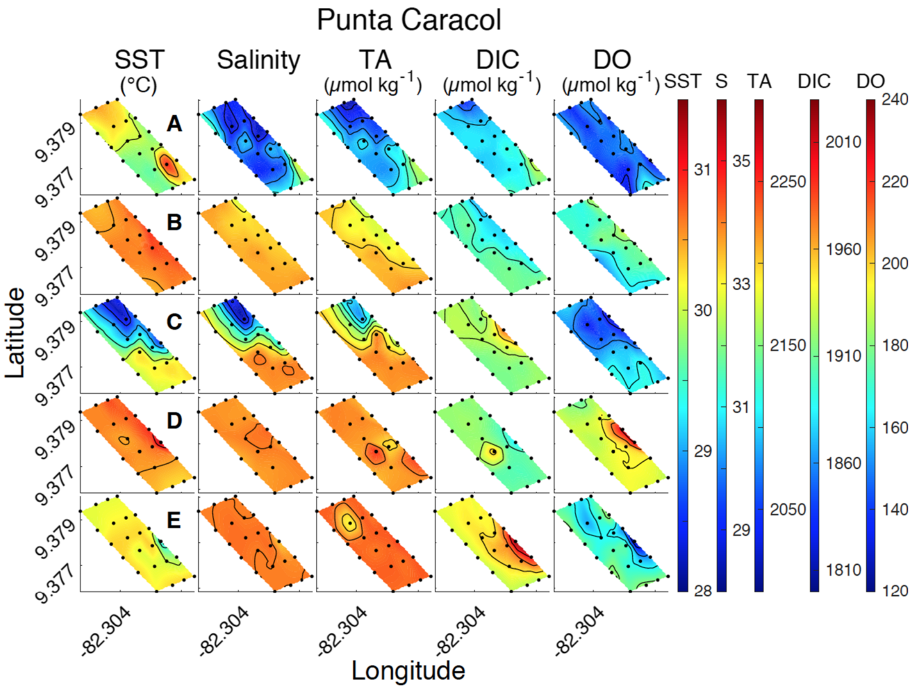

Fig. 4 Spatial contour plots from gridded interpolations (cubic interpolations using MATLAB griddata) of temperature, salinity, TA, DIC and DO across the spatial sampling stations over the course of the spatial surveys (**A**–**E**) at Punta Caracol. The black contour lines represent a change in each parameter unit as follows: 0.5 °C, 1 psu, 25 μmol kg^{-1} for TA and DIC, and 15 μmol kg^{-1} for DO. Survey times are as follows: **A** 9:30 AM November 11, 2015; **B** 2:30 PM November 11, 2015; **C** 6:45 AM November 12, 2015; **D** 1:00 PM November 12, 2015; **E** 7:20 AM November 13, 2015

The spatial distribution of TA tracked that of temperature and salinity, with the lowest mean TA (2092 ± 55 μmol kg^{-1}) observed in the morning of November 11, and the greatest spatial gradient observed in the morning of November 12 (Fig. 4). During the afternoon surveys, the spatial gradients were less defined although a distinct trend was noted on November 12. For the final morning survey on November 13, any spatial gradient was virtually absent across sampling stations except for at one station, where one suspicious outlier skewed the data (Fig. 4). The average TA for the spatial surveys was 2185 ± 55 μmol kg^{-1} with a mean range of 98 ± 45 μmol kg^{-1} (Table 1). For individual surveys, the range of TA variability varied from 55 to 154 μmol kg^{-1}. DIC and DO mostly tracked the observed gradients in other parameters, although some deviation from this was observed during the afternoon on November 12 and morning of November 13 (Fig. 4). In general, DIC and DO mirrored each other with high DIC corresponding to low DO and vice versa. In the mornings, DIC was highest and DO lowest at the stations along the shore and decreased and increased, respectively, in the offshore direction. Conversely, these gradients were reversed in the afternoon surveys (Fig. 4). The mean DIC for all surveys was 1914 ± 26 μmol kg^{-1} and the mean DO 166.8 ± 18 μmol kg^{-1} with mean spatial ranges of 82 ± 25 μmol kg^{-1} and 44 ± 9 μmol kg^{-1}, respectively (Table 1). The lowest spatial mean DIC and DO were observed on the morning of November 11 (1883 ± 20 μmol kg^{-1} and 147.3 ± 8.3 μmol kg^{-1}, respectively) following the rain event on November 10.

In general, gradients in pH, Ω_a and pCO$_2$ tracked closely to each other with pH and Ω_a inversely correlated to pCO$_2$. These gradients mostly followed those observed for salinity and TA (Fig. 5). One exception was observed in the morning of November 13 (Fig. 5) when gradients more closely followed DIC and DO, with the lowest pH and Ω_a, and highest pCO$_2$, recorded at stations close to shore, which increased and decreased, respectively, in the offshore direction (Fig. 5). The mean pH, Ω_a and pCO$_2$ for all spatial surveys were 7.96 ± 0.04, 3.22 ± 0.39, and 487 ± 57 μatm, respectively, with mean spatial ranges of 0.11 ± 0.04, 0.77 ± 0.42, and 152 ± 70 μatm, respectively (Table 1). The lowest mean pH and Ω_a, and highest pCO$_2$, were recorded in the morning of November 11 (7.89 ± 0.03, 2.60 ± 0.24, and 574 ± 47 μatm, respectively) following the rain event.

3.3.2 Punta Vieja

In general, seawater temperature followed the daily light cycle with cooler temperatures in the early mornings and warmer temperatures in the afternoon. Average seawater temperature for the spatial surveys was 29.9 °C ± 0.2 °C, which was marginally higher than the offshore reference station average of 29.7 °C ± 0.1 °C. Seawater temperature was generally uniform throughout the surveys; however, larger gradients began to form in the afternoon of November 17, when elevated temperatures were localized near the inner stations (Fig. 6). Average salinity was 34.2 ± 0.1 which was slightly lower than the offshore reference value of 34.4 ± 0.0 (Table 1). Spatial gradients in salinity were small with higher concentrations near the west/northwest stations, but were otherwise generally consistent between surveys with an average range of 0.1 ± 0.1 (Fig. 6; Table 1).

The spatial distribution in TA closely followed salinity where the lowest concentrations were observed near the offshore stations and increased moving inshore. The largest gradient in TA was recorded during the afternoon survey on November 17, with TA ranging from 2139 to 2225 μmol kg^{-1} (Fig. 6). The average TA for the spatial surveys was 2216 ± 10 μmol kg^{-1} with a mean range of 58 ± 20 μmol kg^{-1} (Table 1). Gradients in DIC closely matched those of TA, where the lowest concentrations were observed

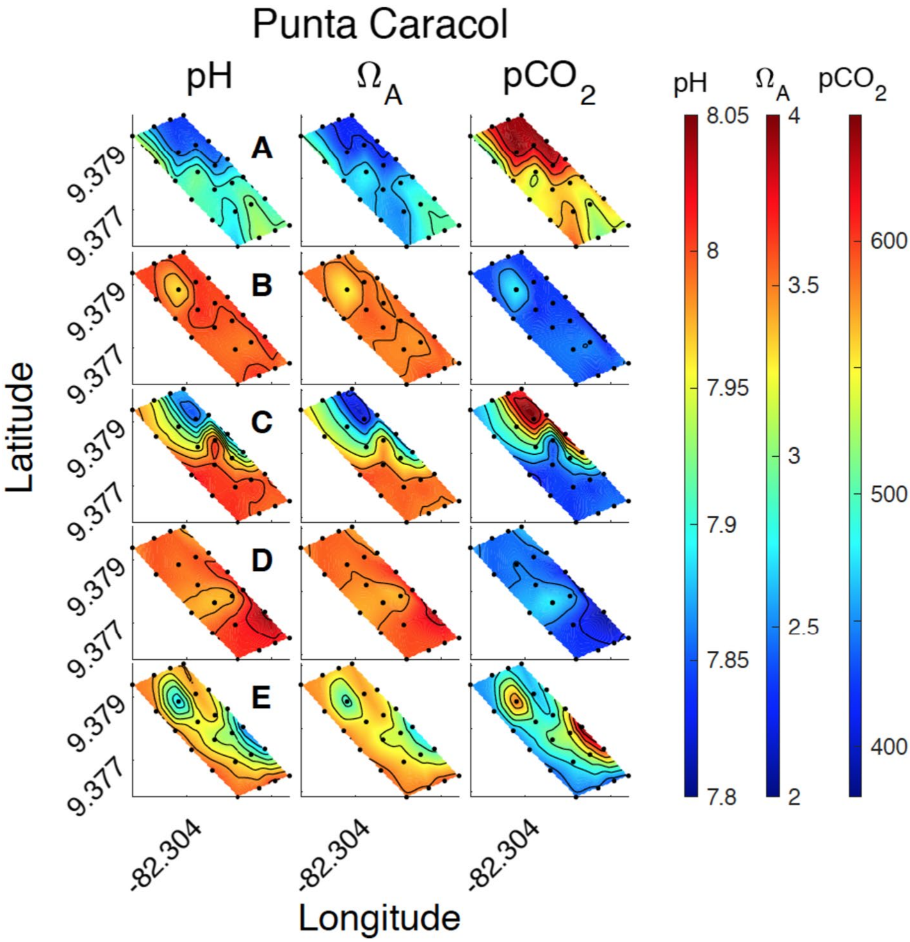

Fig. 5 Spatial contour plots from gridded interpolations (cubic interpolations using MATLAB griddata) of pH_T, Ω_a, and pCO_2 across the spatial sampling stations over the course of all surveys (**A**–**E**) at Punta Caracol. The black contour lines represent a change in each parameter as follows: 0.02, 0.3, and 30 µatm, respectively. Survey times are as follows: **A** 9:30 AM November 11, 2015; **B** 2:30 PM November 11, 2015; **C** 6:45 AM November 12, 2015; **D** 1:00 PM November 12, 2015; **E** 7:20 AM November 13, 2015

offshore and increased in the inshore direction (Fig. 6). Conversely, gradients in DO were weaker and reversed in direction with increased concentration in the offshore direction (Fig. 6). The mean DIC and DO were generally consistent between surveys (1934 ± 9 µmol kg^{-1} and 177.6 ± 6.2 µmol kg^{-1}, respectively) with mean spatial ranges of 64 ± 21 µmol kg^{-1} and 33 ± 8 µmol kg^{-1}, respectively (Table 1).

Seawater pH, Ω_a, and pCO_2 showed general gradients in the inshore to offshore direction, with some isolated exceptions (e.g., afternoon of November 17; Fig. 7). The gradients were most strongly apparent in the pH and pCO_2 data. Gradients in Ω_a followed the same spatial pattern, but were less defined (Fig. 7). The mean pH, Ω_a, and pCO_2 for all surveys were 7.96 ± 0.00, 3.29 ± 0.04, and 480 ± 3 µatm, respectively, with mean spatial ranges of 0.09 ± 0.02, 0.51 ± 0.13, and 121 ± 34 µatm, respectively (Table 1).

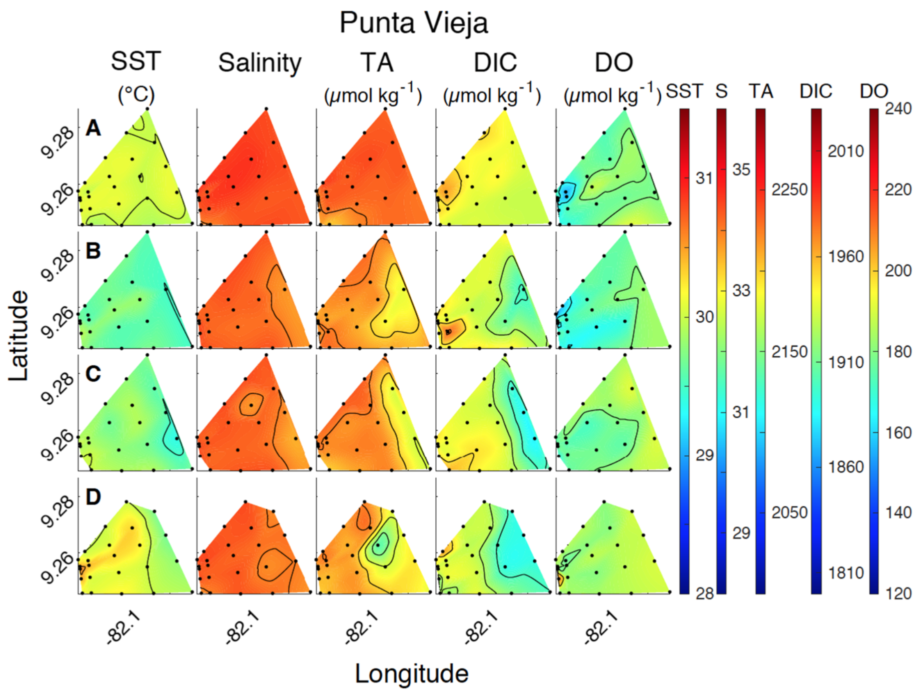

Fig. 6 Spatial contour plots from gridded interpolations (cubic interpolations using MATLAB griddata) of temperature, salinity, TA, DIC and DO across the spatial sampling stations over the course of the spatial surveys (**A**–**D**) at Punta Vieja. The black contour lines represent a change in each parameter unit as follows: 0.5 °C, 1 psu, 25 μmol kg^{-1} for TA and DIC, and 15 μmol kg^{-1} for DO. Survey times are as follows: **A** 9:30 AM November 16, 2015; **B** 7:00 AM November 17, 2015; **C** 11:00 AM November 17, 2015; **D** 2:30 PM November 17, 2015

3.4 Comparing Punta Caracol and Punta Vieja

Despite both study locations maintaining similar spatiotemporal averages in salinity and temperature, Punta Caracol exhibited greater variability in both parameters. Both sites exhibited stratification, with cooler, fresher water lying on top of warmer, saltier water (Fig. 2). Mean DO and pH for the temporal measurements were nearly identical between sites and sampling depths, although measurements at 3 m in Punta Caracol showed more extreme pH minimums than the other sites on a few occasions. However, because some of these extremes were not accompanied by similar extremes in the DO data, we cannot ascertain whether they were real. The mean pH from the spatial surveys was the same between the sites (Table 1). Mean TA, DIC, DO, and Ω_a were qualitatively slightly higher at Punta Vieja compared to Punta Caracol (Table 1). In addition, Punta Caracol experienced greater spatial variability in all parameters compared to Punta Vieja despite a much smaller survey area.

To further assess variability between the sites, seawater samples collected on a transect between Punta Caracol and Punta Vieja, revealed distinct gradients in TA and DIC during both morning and afternoon. In general, these parameters decreased from Punta Caracol toward Punta Vieja. The transect mean TA and DIC were greater in the morning (2215 ± μmol kg^{-1} and 1927 ± 18 μmol kg^{-1}) than the afternoon (2203 μmol and

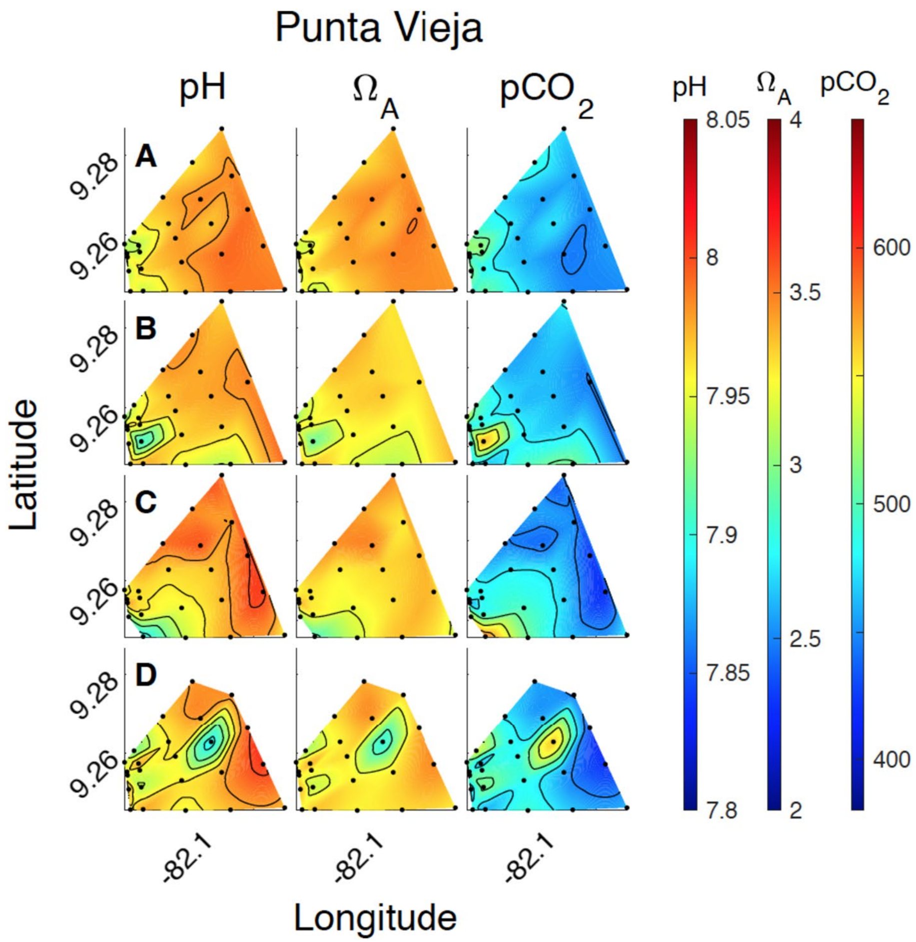

Fig. 7 Spatial contour plots from gridded interpolations (cubic interpolations using MATLAB griddata) of pH_T, Ω_a, and pCO_2 across the spatial sampling stations at Punta Vieja over the course of all surveys (**A**–**D**). The black contour lines represent a change in each parameter as follows: 0.02, 0.3, and 30 µatm, respectively. Survey times are as follows: **A** 9:30 AM November 16, 2015; **B** 7:00 AM November 17, 2015; **C** 11:00 AM November 17, 2015; **D** 2:30 PM November 17, 2015

1905 ± 7 µmol kg^{-1} Fig. 8). In spite of this, mean pH was similar between morning and afternoon (7.98 ± 0.02 and 8.00 ± 0.02). In addition, the spatial gradient in pH was not as clear in the afternoon as it was in the morning, when pH gradually decreased from Punta Caracol toward Punta Vieja.

3.5 Assessing Reef Metabolism Based on TA–DIC Relationships

The slopes of the TA–DIC linear regressions (type II, major axis) at Punta Caracol varied between the normalized and non-normalized data. The raw TA–DIC data had a slope of 2.48 with an R^2 of 0.67. In contrast, normalizing the data with a zero end-member produced a slope of 0.71 with a strong positive correlation ($R^2 > 0.96$)

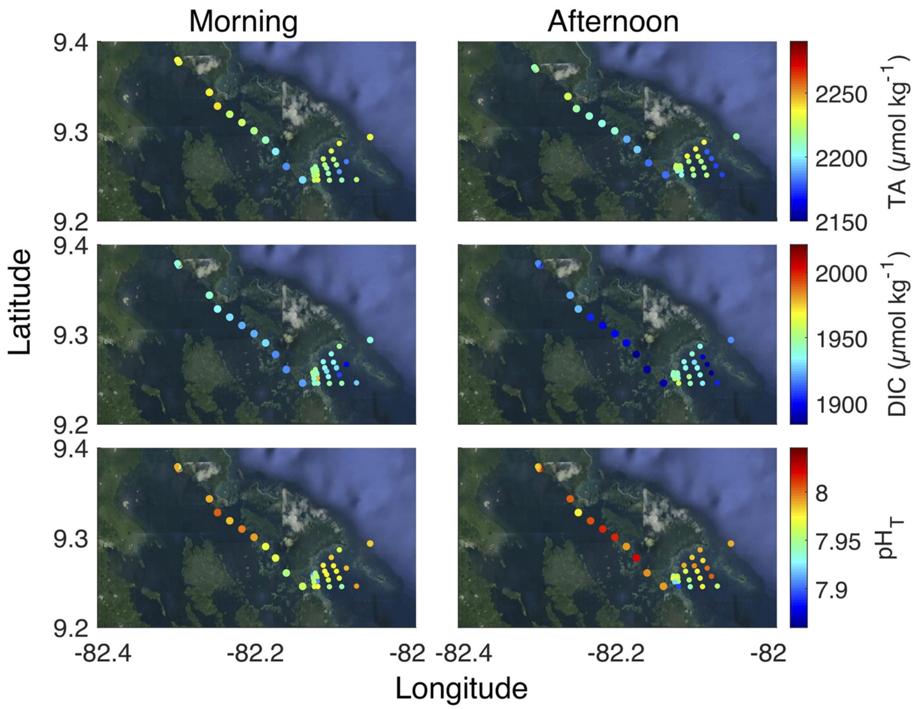

Fig. 8 Comparison of morning and afternoon concentrations of TA (μmol kg^{-1}), DIC (μmol kg^{-1}), and pH_T shown as a transitional continuum from Punta Caracol to Punta Vieja, including the offshore reference station. Map imagery from Google

(Fig. 9), and the nonzero end-member further reduced the slope to 0.64 with an R^2 of 0.59 (Fig. 9). Conversely, the slope of the normalized data at Punta Vieja did not change regardless of end-member used (slope = 0.86; R^2 = 0.58; Fig. 9); however, it did slightly decrease from the raw data (slope = 1.01; Fig. 9). Relative to the open ocean end-member, Punta Caracol mostly exhibited excess alkalinity during both the morning and afternoon, although the values in the morning were typically higher than during the afternoon. Some instances of alkalinity depletion were observed during both morning and afternoon. DIC was generally depleted relative to offshore during the afternoon while mostly excess DIC was observed in the morning. These observations combined with the slope of the linear II regression (0.64) suggest that Punta Caracol was dominated by net $CaCO_3$ dissolution during morning and afternoon, heterotrophy during the morning, and autotrophy during the afternoon. In contrast, excess TA and DIC relative to the open ocean was observed at Punta Vieja for the majority of observations regardless of the time of the day, although early morning values were typically higher with respect to both TA and DIC. These observations combined with the slope of the linear II regression (0.86) indicate that Punta Vieja was dominated by heterotrophy and $CaCO_3$ dissolution.

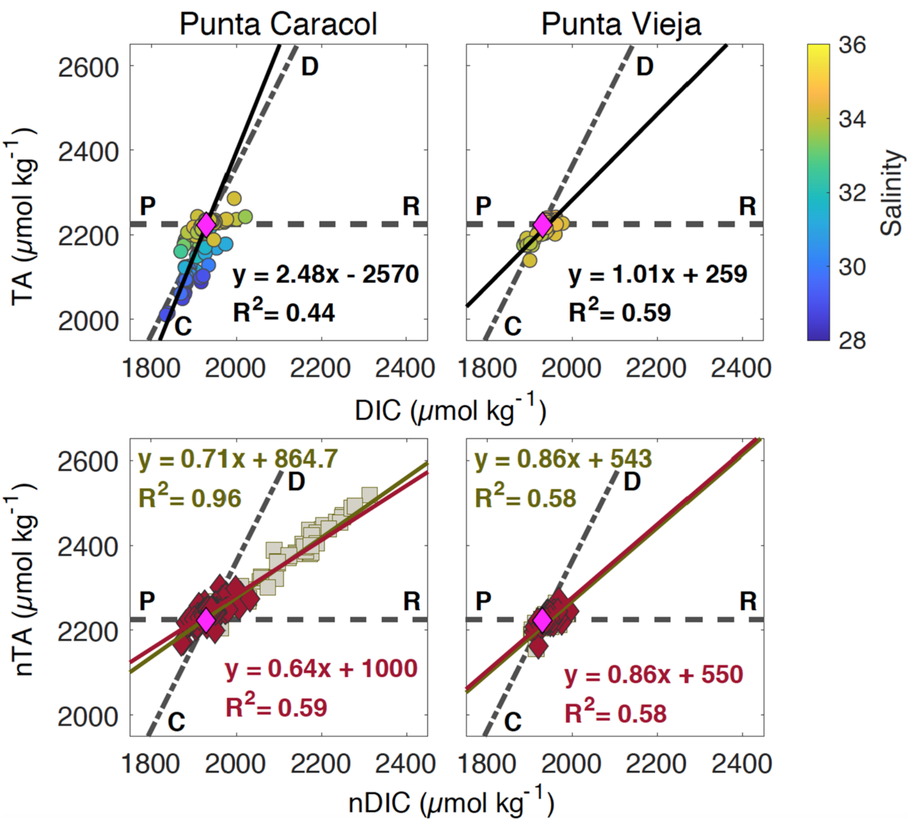

Fig. 9 Salinity-normalized and non-salinity-normalized TA–DIC diagrams using data collected from the spatial surveys. The pink diamond represents the offshore reference station average. Dashed lines show the organic (*P*/*R*; production/respiration) and inorganic (*C*/*D*; calcification/dissolution) metabolic pathways. Solid black lines in the upper plots show the best fit line from a type II major axis linear regression. The bottom two plots show salinity-normalized TA–DIC relationships using two different end-members. Gray squares show the salinity-normalized zero end-member data, and the red diamonds show the salinity-normalized nonzero end-member data

4 Discussion

Despite differences in reef geomorphology, benthic community structure, proximity to terrestrial ecosystems, freshwater and anthropogenic inputs, and the open ocean, the observed average conditions and diel variability of seawater parameters were remarkably similar between Punta Caracol and Punta Vieja (Fig. 2; Table 1). This was particularly true for the high-resolution temporal data collected at 3 m and 8 m; in contrast, the differences in spatial variability of physical and chemical parameters in the surface (< 0.5 m) were greater between the two sites (Table 1). These differences in spatial variability appeared to be mainly driven by focused freshwater inputs at Punta Caracol as well as differences in depth across the sampling areas with larger metabolic imprint in shallow areas. This was evident from salinity gradients coincident with gradients in TA, DIC, and DO (as well as pH, Ω_a, and pCO_2) following rain events (Figs. 4 and 5). A small creek just north of the sampling grid at Punta Caracol appeared to be the source of the majority of this freshwater input, which explains the lower mean, and greater variability in salinity and other parameters at this site compared to Punta Vieja. During dry periods at Punta Caracol, the spatial variability in DIC, DO, and pH was driven by benthic metabolism that was amplified by depth gradients across the survey area, with the shallowest depths showing the greatest changes from morning to afternoon (Figs. 4 and 5). Notably though, while the spatial averages of TA, DIC, and DO were qualitatively slightly lower at Punta Caracol compared to Punta Vieja, the averages of surface seawater pH, Ω_a, and pCO_2 were similar at the two sites (Table 1). However, the spatial variability was greater at Punta Caracol than Punta Vieja. Based on this larger spatial variability, one might interpret that the benthic community at Punta Caracol was exposed to a wider range of conditions, but it is evident from the autonomous sensors at 3 m and 8 m depths that this was not the case, as the most prominent differences were restricted to the very top surface layer (Table 1). The comparable variability recorded by the autonomous sensors indicated that the benthic metabolic influence on seawater chemistry was similar between the two sites.

Although the direct influence of freshwater was readily evident in surface chemistry at Punta Caracol, freshwater inputs can modify many other biogeochemical processes and seawater chemistry parameters. In particular, terrestrially derived freshwater inputs are often enriched in organic matter and/or nutrients and could amplify net respiration through increased remineralization of organic matter, while stimulating primary production via nutrient addition (e.g., Fabricius 2005; Cai et al. 2010; Larsen and Webb 2009; Ringuet and Mackenzie 2005; Fagan and Mackenzie 2007). Such metabolic alterations can shift the dominant biogeochemical processes on a reef, and consequently, the seawater chemistry. Given the direct inputs of freshwater at Punta Caracol and its effect on surface chemistry variability, it was expected that this location might experience a greater influence of organic matter and nutrient inputs on biogeochemical processes than Punta Vieja. This could be further amplified by its partial isolation from the Caribbean Sea and being completely surrounded by terrestrial environments. However, the pH and DO data (i.e., mean and average diel range) from 3 and 8 m depths did not reveal any clear evidence of differences in net reef metabolism between the two sites resulting from terrestrial inputs of water with lower pH and oxygen levels. Typically, these parameters, including the diel variability, are influenced by additional factors such as community composition and biomass, flow rates and trajectory, as well as the seawater residence time at each site (Zhang et al. 2012; Lowe and Falter 2015; Page et al. 2018). Yet, the average flow rate between the sites differed by only 0.01 m s^{-1}, and the flow direction was predominantly unidirectional (Fig. 3), so it is unlikely that current speeds had any major influence on the biogeochemical diel variability.

Depending on flow trajectory and mixing rates with freshwater or offshore water, the cumulative modification of properties such as DIC and TA ("chemical memory") of the seawater could be different. These changes are not necessarily discernible from oxygen and pH data alone because changes in pH are dependent on the relative ratio of DIC and TA (Andersson et al. 2014). Nonetheless, despite contrasting properties between the two sites, the diel variability in pH and oxygen during the study period were similar at all sensor locations, and therefore, no major differences in net reef metabolism or in dominant biogeochemical processes were detected between the two sites. Similarly, a recent study from Kane'ohe Bay in Hawaii did not detect substantial differences in seawater pH and oxygen variability between a range of different reef habitats (Page et al. 2018). Instead, it was proposed that the prevailing biogeochemical conditions and temporal variability were most strongly correlated with water depth, and thus, controlled by the biomass-to-water-volume ratio rather than the benthic community composition, with the exception of areas of extremely high coral cover (Page et al. 2018; Cyronak et al. 2020).

Based on system scale analysis of surface seawater TA–DIC data relative to open ocean conditions, Punta Vieja reflected net heterotrophy at all times while Punta Caracol appeared autotrophic during afternoon surveys and heterotrophic during morning surveys (Fig. 10). However, one must recognize that the data from Punta Caracol (~0.07 km^2) reflect variability at smaller, more localized spatial scales while the data from Punta Vieja (~16 km^2) represent an integrated signal from multiple habitats and communities over a much larger spatial scale (see Cyronak et al. 2018 and Takeshita et al. 2018 for a detailed discussion). The observed net heterotrophy at this larger scale can only be attributed to external inputs and remineralization of organic material, which is not surprising, given the local geography and adjacent terrestrial environments (Suzuki et al. 2001; Suzuki and Kawahata 2003; Fagan and Mackenzie 2007). The oxygen data also support this conclusion, as it was predominantly undersaturated (< 100%) at this larger scale. Thus, despite Punta Viejo's direct connection to the open ocean, the results show that its seawater chemical conditions were directly or indirectly strongly influenced by the nearby terrestrial systems and the associated supply of organic material during the study period. This chemical imprint was likely enhanced by the relatively slow mixing and replenishment of near shore and inshore waters with open ocean waters.

Irrespective of the trophic status, both locations appeared to undergo net dissolution of $CaCO_3$ minerals as inferred from alkalinity repletion relative to offshore samples and based on the assumption that $CaCO_3$ formation and dissolution were the dominant processes affecting TA. Although this assumption is valid for most coral reef environments, the potentially large input of dissolved organic material and nutrients in Bocas del Toro could significantly affect the TA balance and must be noted (Brewer and Goldman 1976; Cai and Wang 1998; Courtney et al 2021). However, by salinity normalizing TA–DIC data

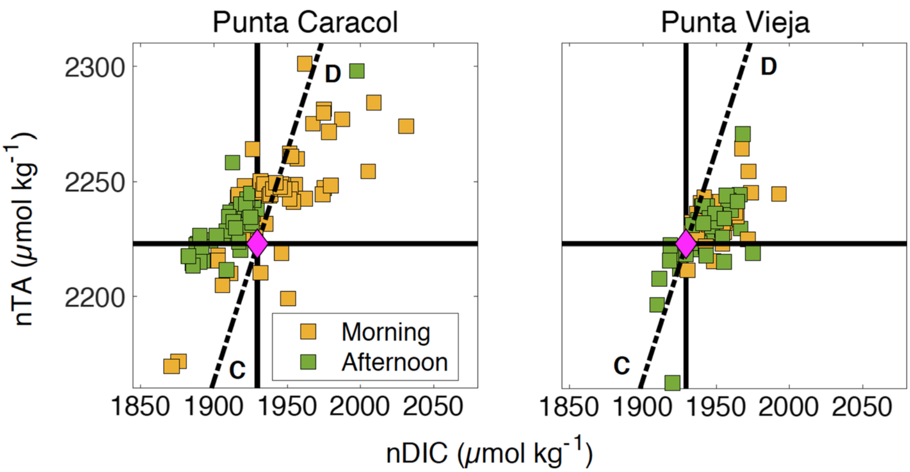

Fig. 10 Zoomed in view of salinity-normalized nonzero end-member TA–DIC data from Punta Caracol and Punta Vieja. Yellow squares represent data from morning surveys ($n=3$ at Punta Caracol and $n=2$ at Punta Vieja), and green squares represent data from afternoon surveys ($n=2$ at Punta Caracol and $n=2$ at Punta Vieja). The pink diamond reflects the offshore reference station average TA and DIC concentration, with the solid black lines extending the value to the edge of the plot. The dashed black line depicts the theoretical inorganic (calcification/dissolution) metabolic pathway

to a derived nonzero TA–DIC end-member, the TA contribution from the end-member is partly accounted for, although the composition of this end-member is clearly associated with uncertainty. Regardless, observations of net heterotrophy from other reef environments have frequently been associated with net $CaCO_3$ dissolution (Courtney et al. 2018; Melendez et al. 2018; Muehllehner et al. 2016; Stoltenberg et al. 2020) as decomposition of organic material drives seawater Ω in sediments and microenvironments below equilibrium ($\Omega < 1$), causing $CaCO_3$ dissolution (Andersson and Gledhill 2013; Drupp et al. 2016; Eyre et al. 2018). As a result, net dissolution is observed despite that the water column seawater aragonite saturation state is well above saturation ($\Omega > 3$), which can be attributed to the undersaturated microenvironments, the activity of chemical bioeroders, and the occurrence of metastable carbonate minerals that are more soluble than aragonite (Andersson 2015). However, given the short duration of the study, it is not possible to conclude whether the condition of net dissolution was ephemeral or chronic at the study site, and additional observations are needed. Based on a globally distributed experimental study, Eyre et al. (2018) concluded that most coral reef sediments will transition to net dissolution at a water column aragonite saturation state of 2.92 ± 0.16, which is slightly lower than the mean seawater Ω observed at Punta Caracol (3.22 ± 0.39) and Punta Viejo (3.29 ± 0.04) (Table 1). Although none of the study locations in the Eyre study are directly comparable to Punta Caracol or Punta Viejo, the highest rates of sediment dissolution were observed in Kaneohe Bay, Hawaii, which is also strongly influenced by terrestrial inputs of organic material and nutrients (Hoover and Mackenzie 2009).

In addition to terrestrially driven heterotrophy on reefs, this trophic state can also be driven by lateral advection of organic material from highly productive offshore blooms onto reefs resulting in increased feeding by corals (e.g., Yeakel et al. 2015; Fox et al. 2018). The prevailing hypothesis suggests that this would lead to increased reef-scale calcification rather than dissolution (e.g., Yeakel et al. 2015). However, despite conditions of net reef-scale $CaCO_3$ dissolution as a result of terrestrially derived organic material, some studies suggest that this additional nutrition could still prove beneficial to the success and growth of individual corals (Watanabe et al. 2006; Shamberger et al. 2014). One possible explanation for this is that a significant proportion of $CaCO_3$ dissolution occurs in sediments that quantitatively masks calcification by individual calcifiers and reef structures, which still may deposit $CaCO_3$ at high rates (Andersson et al. 2009; Eyre et al. 2018). However, the interpretation of such a scenario will depend on the chemical footprint of the observations as well as the spatial and temporal scales that are being considered. Most reefs contain large amounts of both modern and relict carbonate sediments that could undergo dissolution, but even so, if calcifiers are negatively affected by an increased frequency of abnormal heating events, long-term acidification and deoxygenation, such dissolution offers little respite to maintaining the success of calcifying coral reef communities in the long term.

Multiple laboratory experiments have shown increased tolerance to acidification (and other environmental perturbations) if corals are provided additional nutrition (e.g., Edmunds 2011; Drenkard et al. 2013; Towle et al. 2015) and similar inferences have been made from field studies (e.g., Crook et al. 2012; Shamberger et al. 2014). For example, Shamberger et al. (2014) reported healthy coral communities within a semi-enclosed bay in Palau exposed to low seawater Ω, but with a potential plentiful supply of nutrition and nutrients from the surrounding terrestrial environments. Similarly, in Puerto Morelos, Mexico, where seawater is frequently undersaturated owing to inflow of naturally acidic groundwater, the presence of healthy corals has been hypothesized as a result of elevated inorganic nutrient concentrations in the groundwater providing nutritional energy that may offset any potential negative effects of acidification (Crook et al. 2012). Despite the persistence of corals under these conditions, only a few species appeared tolerant to such low levels of seawater Ω and pH, as coral density and biodiversity increased with distance away from the source of groundwater (Crook et al. 2012). Similar decreasing trends in biodiversity have been observed at reefs influenced by CO_2 vents in Papua New Guinea (Fabricius et al. 2011), which appear related to species-specific tolerance to low pH conditions (e.g., *Porites*) rather than the supply of additional nutritional resources as the abundance of corals was not affected. In contrast, at a CO_2 vent site in Okinawa, Japan, soft corals dominated the coral community under acidified conditions (Inoue et al. 2013). Based on the carbonate chemistry data of the present study, it is not possible to ascertain whether any potential differences between the reefs in Punta Caracol and Punta Vieja are related to this, as the means and variability of biogeochemical parameters were remarkably similar. However, these data only represent a snapshot in time, and a longer study would be required to fully characterize these differences.

In the context of OA, it is of interest to understand whether reefs influenced by large terrestrial inputs, such as the reefs in Bocas del Toro, are more or less sensitive to the long-term changes in seawater Ω and pH of adjacent offshore waters. Input of nutrients and organic matter certainly influence water quality, including turbidity, light, and seawater Ω and pH, and may ultimately control the community structure and distribution, potentially favoring species that are more tolerant to changes in seawater chemistry. Drastic changes in coral community structure and shifts from corals to macroalgae dominance have been observed in multiple places such as throughout the wider Caribbean (Hughes 1994; McManus and Polsenerg 2004; Jackson et al. 2014), in the Reunion Island (Montaggioni et al. 1993; Chazottes et al. 2002), and in Kane'ohe Bay, Hawaii (Smith et al. 1981; Jokiel et al. 1993) where multiple drivers including terrigenous input of organic material (e.g., sewage) and nutrient discharge have correlated with declines in coral cover and reef growth (Smith et al. 1981; Montaggioni et al. 1993; Jokiel et al. 1993; Chazottes et al. 2002; Jackson et al. 2014). In the case of Bocas, reefs in Almirante Bay have undergone a shift in dominance from branching *Porites* species to *Agaricia tenuifolia* in mid-depth waters since the 1970s (Aronson et al. 2004, 2014). This is thought to be because the latter are more tolerant of high nutrient concentrations and high sedimentation rates than other Caribbean corals (Sebens et al. 2003).

5 Conclusion

The seawater conditions found on the reefs in Bocas del Toro do not represent typical oligotrophic coral reef conditions; rather, the reefs are heavily influenced by terrestrial runoff and anthropogenic organic pollution (Aronson et al 2014, Seeman et al. 2014). In particular, heavy rainfall and terrigenous runoff exerted a large influence on the spatial variability in seawater carbonate chemistry and the trophic status of the reefs during the time of the study. Despite differences in the magnitude of surface variability in physiochemical parameters between the study sites, seawater conditions below the surface were remarkably similar. In general, the results of this study highlight the potential influence of freshwater input on near-shore carbonate chemistry and demonstrate how biogeochemical processes can be misinterpreted unless they are evaluated with the consideration of non-negligible external inputs of TA and DIC via freshwater. Thus, a more complete understanding of the dominant biogeochemical processes at the reefs in Bocas del Toro would require the characterization of different end-members as well as the contribution from inorganic nutrients and organic acids and bases to TA. Given the current threat of OA to coral reefs worldwide, Bocas del Toro and similar reef systems, influenced by large terrestrial inputs, deserve further attention to better understand the mechanisms that allow these reefs to thrive and persist. Continuing to measure seawater chemistry conditions across a broad range of habitats and environmental conditions on spatial and temporal scales is critical to further our progress in understanding potential effects of climate change and other anthropogenic stressors while taking into account natural variability. Moreover, spatiotemporal variability across an array of habitats can provide context for more ecologically relevant experimental conditions that incorporate natural ranges, and exposure times, and can help us understand the distribution of organisms.

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Author contributions AJA and DIK designed the study; AJA, DIK, MT, and LL deployed instruments and collected all samples; MG and RT analyzed samples, KP, TC, and AJA analyzed the data; KP and AJA wrote the first draft of manuscript with subsequent input from all co-authors.

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Data availability BCO-DMO https://www.bco-dmo.org/project/737878.

Code availability Not applicable.

Declarations

Competing interests The authors declare no competing interests.

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