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Water motion and vegetation control the pH dynamics in seagrass-dominated bays

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Abstract

Global oceanic pH is lowering, which is causing great concern for the natural functioning of marine ecosystems. Current pH predictions are based on open ocean models; however, coastal zones are dynamic systems with seawater pH fluctuating temporally and spatially. To understand how coastal ecosystems will respond in the future, we first need to quantify the extent that local processes influence the pH of coastal zones. With this study, we show that over a single diurnal cycle, the total pH can fluctuate up to 0.2 units in a shallow seagrass-dominated bay, driven by the photosynthesis and respiration of the vegetation. However, these biologically controlled pH fluctuations vary significantly over small distances. Monitoring conducted at neighboring sites with contrasting hydrodynamic regimes highlights how water motion controls the extent that the local pH is altered by the metabolism of vegetation. The interactive effects of hydrodynamics and vegetation were further investigated with an in situ experiment, where the hydrodynamics were constrained and thus the local water residence time was increased, displaying the counteractive effect of hydrodynamics on the pH change caused by vegetation. With this research, we provide detailed in situ evidence of the spatial variation of pH within marine ecosystems, highlighting the need to include hydrodynamic conditions when assessing the pH-effects of vegetation, and identifying potential high-pH refuges in a future low pH ocean.

The substantial anthropogenic release of carbon dioxide (CO_2) into the atmosphere is causing a decrease in oceanic pH and altering the concentration of inorganic carbon species in seawater, a process termed ocean acidification (Sarmiento and Gruber 2006; Stocker et al. 2013). The worst-case scenario shows that by 2100, the global mean pH will decline 0.42 units; from 8.1 to 7.68 (RCP8.5 scenario, Pörtner et al. 2014), and under the best-case scenario, by 0.13 units to a mean global pH of 7.97 (RCP2.6 scenario, Pörtner et al. 2014). Ocean acidification represents a decrease in pH, an increase in dissolved CO_2 and a decrease in the concentration of CO_3^{2-}, at an unprecedented rapid rate (Hönisch et al. 2012). The decrease in CO_3^{2-} reduces the aragonite saturation state of the ocean, which is predicted to have negative consequences for calcification in the ocean (Hönisch et al. 2012; Pörtner et al. 2014). Future pH predictions are based on the open ocean, where the pH remains relatively stable, with measurements off the continental shelf of

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Additional Supporting Information may be found in the online version of this article.

California (U.S.) showing fluctuations of 0.02 units around a pH of 8.07 over 1 month (Hofmann et al. 2011). However, the coastal environment is much more dynamic, different ecosystems and environmental conditions can cause the pH to vary both temporally and spatially; often at magnitudes exceeding the trends predicted by global ocean pH models (Middelboe and Hansen 2007; Anthony et al. 2011; Hofmann et al. 2011; Kleypas et al. 2011; Duarte et al. 2013; Hendriks et al. 2014; Rivest et al. 2017). If we are to predict accurately how the coastal environment will respond to future lowering of seawater pH, it is vital to quantify the main drivers causing pH variability within the near coastal zone and the extent that diurnal pH fluctuations differ spatially.

Daytime photosynthesis and nighttime respiration cause large diurnal pH fluctuations in coastal areas with dense and highly productive photosynthetic organisms, such as coral, seagrass, or algae (Anthony et al. 2011; Hofmann et al. 2011; Kleypas et al. 2011; Buapet et al. 2013; Hendriks et al. 2014; Rivest et al. 2017). The assimilation of carbon during photosynthesis and release through respiration can occur at faster rates than the diffusion rate of carbon from the atmosphere, causing a variable seawater pH (Axelsson 1988; Buapet et al. 2013). Diverse diurnal pH fluctuations have been reported throughout the world in various coastal ecosystems, Rivest et al. (2017) observed pH fluctuations ranging from 7.84 at night up to 8.07 during the day on a relatively protected fringing coral reef in a lagoon within Moorea. Similar fluctuations have been observed in Mediterranean seagrass meadows, with pH ranging from 7.97 during the night vs. 8.19 within the canopy during the day (Hendriks et al. 2014). While in temperate regions, Saderne et al. (2013) reported larger fluctuations of 0.34 pH units in dense macrophyte communities in the Baltic Sea, and Koweek et al. (2018) reported a small fluctuation of 0.1–0.2 in an eelgrass community in California, U.S.A. The variability in these pH fluctuations can be explained by factors that affect the metabolic rates of organisms, such as temperature, light, seasonality, and nutrient availability (Axelsson 1988; Saderne et al. 2013; Hurd et al. 2014). But also, physical factors, such as the carbonate chemistry of the source water, depth, water residence time, and tidal regimes, which limit the spatial extent and magnitude that biological activity alters the surrounding seawater (Horst and Edmunds 2010; Unsworth et al. 2012; Cornwall et al. 2015; Hendriks et al. 2015; Koweek et al. 2018).

It has been suggested that the ability of photosynthesizing organisms to increase the local pH during the day could become a valuable ecosystem service in a future lower-pH ocean (Anthony et al. 2011; van Hooidonk et al. 2013;Hurd 2015 ; Koweek et al. 2018). By providing high pH conditions during the day that are more favorable for calcification, the habitats may provide a pH refuge for vulnerable organisms. However, current data indicate that pH refuges will be limited to specific locations where the balance between the metabolic pH-alteration rate and local physical conditions enable a significant increase in the local pH (Hurd 2015; Koweek et al. 2018). If we hope to identify habitats that will act as effective pH refuges, there is a need for further field measurements that examine the temporal and spatial pH variability in the coastal zone and capture the multitude of factors that influence seawater pH. These studies are particularly vital for ecosystems closely associated with vulnerable calcifying organisms, such as tropical seagrass meadows, which are an important habitat for many calcifying invertebrates, e.g., conch, spiny lobsters, and sea urchins (Heck and Wetstone 1977; Rios-Lara et al. 2007). It is also important to note that the identification of potential pH refuge areas needs to consider whether the habitat will survive future ocean acidification, and not be replaced by a more simple and opportunistic habitat (Connell et al. 2018).

The metabolic adjustment of seawater pH by vegetation is strongly dependent on the waters residence time around the photosynthesizing individuals (Koweek et al. 2018). A region of reduced flow, termed as velocity boundary layer (VBL), forms along the seafloor and around all stationary objects within aquatic environments (Hurd 2000). The size of VBLs is strongly dependent on the flow velocity (Hurd 2000; Hurd et al. 2014), with faster, more turbulent flow resulting in thinner boundary layers. Because the flow within VBLs is only laminar, the movement of solutes within VBLs is limited to diffusive transport, causing diffusive boundary layers (DBLs) to form around organisms that uptake and release solutes for metabolic processes, such as photosynthesis and respiration (Hurd 2000). A concentration gradient forms across the DBLs, when organisms utilize solutes at a faster rate than the diffusive movement of the solutes across the boundary layer. DBLs can thus have a distinct seawater chemistry compared to that of the bulk water (Hurd 2000; Cornwall et al. 2014), which can give rise to variability of seawater pH within marine ecosystems.

Greater water motion and waves increase the movement of solutes by advection in the bulk water, and reduce the size of boundary layers that form around aquatic organisms, with waves breaking up the boundary layers and refreshing the solutes at the organisms surface (Hurd 2000). In slow flow habitats, DBLs around organisms can become thick, and when vegetation is dense, the DBLs of multiple individuals can overlap. This often occurs in seagrass meadows and kelp forests, where dense canopies attenuate the flow, increasing the residence time of the water and creating boundary layers that encompass the entire canopy (Ackerman et al. 1993; Hurd 2000). Consequently, the thick DBLs in slow flow habitats are likely to result in large areas where seawater pH is influenced by the metabolizing vegetation. This could provide more favorable pH conditions for vulnerable marine taxa in the future, as photosynthesis by vegetation during light periods results in the removal of CO_2 from surrounding waters (Hurd 2015; Koweek et al. 2018). However, the release of CO_2 via respiration would result in these areas also experiencing low pH conditions during dark periods. The biogeochemical model developed by Koweek et al. (2018) highlights how the properties of the source water and the intensity of the water flow control the influence of the metabolic activity on the local pH, with low

flow conditions enabling vegetation to alter the pH in neighboring areas. Quantifying the extent that physical and biological forces drive changes in seawater pH within the natural environment is important for the accurate predictions of future pH conditions within dynamic coastal zones, and will allow for the identification of settings that may serve as high pH refuges. Furthermore, field studies evaluating the natural spatial and temporal variability within ecosystems can reveal the present-day tolerance of species, enabling predictions of their resilience to future global change (Botero et al. 2015). We study this using a model system of shallow tropical vegetation consisting predominantly of seagrass interspersed with calcifying macroalgae, growing adjacent to a fringing coral reef.

Shallow tropical seagrass meadows belong to the most productive ecosystems in the world (Duarte 1989), as the high light and temperature allow for consistently high photosynthetic rates, thereby giving potential for biotic processes to significantly impact the local seawater pH. To examine the spatial and temporal variability and quantify the extent that contrasting physical conditions influence the seawater pH in situ, we measured diurnal pH fluctuations concurrently with hydrodynamics along transects at three neighboring seagrass meadows with varying hydrodynamic regimes: wave-exposed, wave-sheltered, and current-dominated (unidirectional flow) over a 3-month period. We further explored the interactive effect of vegetation and hydrodynamics on the diurnal pH fluctuation by in situ manipulations of the water residence time (constant refreshment vs. high residence time, the latter being approximately 30 minutes), and biomass (bare, sparse, and dense cover of seagrass vegetation interspersed by calcifying macroalgae). With this research, the dominant processes driving the dynamic pH within seagrass vegetated bays are quantified.

Methods

Site description

Monitoring of diurnal pH fluctuations, waves, temperature, and light was conducted within three sites along the eastern coast of St Martin, Caribbean from September 2015 to February 2016 (Fig. 1). The eastern side of St Martin faces the Atlantic Ocean and is exposed to the Atlantic trade winds. A fringing coral reef extending along the eastern coast of St Martin protects the eastern bays from the largest waves coming from the Atlantic, and creates a relatively protected environment within shallow bays and lagoons (< 15 m depth). These shallow bays and lagoons are characterized by calcareous sediment that is often occupied by extensive seagrass meadows of the climax seagrass species, *Thalassia testudinum*. Sites were selected according to their contrasting hydrodynamic regimes. The southern end of Orient Bay (18.0826, −63.0119), a wave-exposed site that directly faces east, with only the fringing coral reef protecting it from the largest waves. The north-eastern corner of Baie de L'Embouchure (18.0770, −63.0154), a wave-sheltered site that is situated behind a small peninsula that shelters it from the trade winds and the prevailing swell coming from the Atlantic. Islets de L'Embouchure (18.0669, −63.0119), a site where incoming waves are forced between two islets situated 120 m off the shoreline creating a strong unidirectional flow (currents) through the site. Tidal currents are typically very low in St Martin, with tidal amplitudes of 0.2–0.3 m, and there are no freshwater inputs nearby any of the sites. Salinity ranges from 34.5 to 35.8, while coastal water temperature ranges from 34°C in the warmer months (July–September) to 26°C in the cooler months (December–February).

To estimate vegetation cover within the three sites with varying hydrodynamic regimes, 90 m long transects were placed along the seagrass meadow at each site, extending from near the landward edge of the meadows out toward the bay entrance (following the wave direction). A 0.3 × 0.3 m quadrat was placed at 60 random positions along the transects and percentage cover within the quadrat was estimated by eye. Photographs were also taken of each quadrat to validate the estimates using ImageJ (Schneider et al. 2012). Hydrodynamic forcing within each site was measured with self-logging pressure sensors (Wave gauge: OSSI-10-003C, Ocean Sensor Systems, Coral Springs, U.S.A.). Five wave gauges were placed along the transects used for the vegetation survey, in vegetated and unvegetated areas (as marked in Fig. 1), at each site. Measurements were conducted on six haphazardly chosen days from September 2015 to December 2015 with typical average wind conditions. The gauges were placed at a height of 0.1 m above the sediment, and pressure samples were recorded at a rate of 5 Hz in 7 min bursts every 15 min. In total, 100–150 bursts were recorded at each gauge deployment location after which the pressure measurements were processed to obtain the significant wave height at each location. To characterize the unidirectional flow at Islets of L'Embouchure (the other two sites had currents below detection limit, i.e., < 0.1 m s^{-1}), a mechanical flowmeter (Mechanical Flowmeter 2030R, General Oceanics, Miami, U.S.A.) was secured between two metal rods 0.1 m above the bed. Triplicate measurements were conducted at six locations within the site, with each measurement lasting 1 min.

Onset HOBO® pendant temp/light loggers (UA-002-64, Onset Computer Corporation, Bourne, U.S.A., temperature accuracy: ± 0.53°C, temperature resolution: 0.14°C at 25°C; spectral detection range: 150–1200 nm) were deployed on 0.1 m^2 plastic platforms at the sediment surface at the bay entrance (1.5 m depth), and within the main seagrass meadow (0.5–1.0 m depth) at each of the three sites. Temperature and light were logged every hour over the 3-month period that the pH measurements were conducted (October 2016, November 2016, January 2017). Light intensities, measured in lux, were converted to availability of photosynthetically active radiation (PAR) using the conversion from Valiela (1984): 1 μmol quanta (400–700 nm) m^{-2} s^{-1} = 51.2 lx.

pH monitoring

To measure the temporal and spatial pH variation within the three sites, pH measurements were manually conducted at

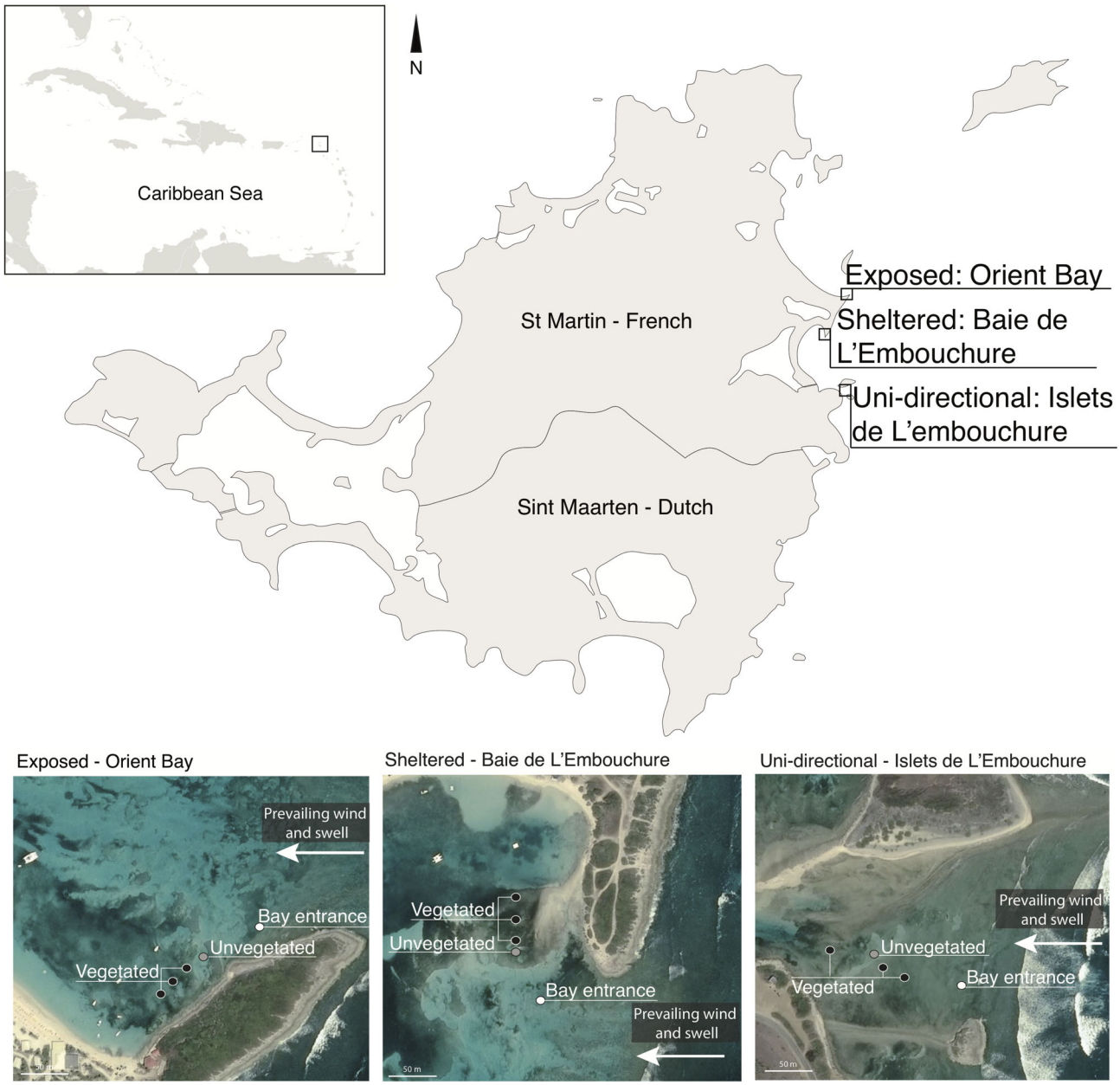

Fig. 1. Map of the three study sites with contrasting hydrodynamic regimes, on St Martin, Caribbean. The satellite images of the sites are marked with the positions where the pH and wave measurements were taken: vegetated (black circles), unvegetated (gray circles), and bay entrance (white circles).

multiple positions and at set time points within each site. Measurements were done twice a month for 3 months (October 2015, November 2015, January 2016) on the same day the wave measurements were made (haphazardly chosen). For a single diurnal cycle, the measurements were conducted every 3 h from 06:00 h (just before sunrise) to 21:00 h (3 h after sunset), with six diurnal cycles being measured in total at each site over the 3-month period. To measure spatial variability at each site, diurnal measurements were taken at five different positions along the transects: three positions within the seagrass meadow (vegetated, 0.5–1 m depth), one in a neighboring unvegetated area adjacent to the seagrass meadow (unvegetated, 1–1.5 m depth), and one at the bay entrance where no vegetation was present (1–1.5 m depth; Fig. 1). The bay entrance position is considered to be representative of the source water entering the seagrass meadows, due to the prevailing easterly wind and swell from the Atlantic Ocean (Johns et al. 2002) ensuring that the seawater at this location has limited upstream influences except the fringing coral reef. To minimize disturbance of the sampling zone, the positions were carefully approached by

snorkeling, and 60 mL water-tight polypropylene plastic sampling containers that had been rinsed with seawater nearby to the sampling position, were opened and closed 0.05 m above the seafloor. Duplicate measurements were taken at each position, and it was ensured that no headspace existed in the sampling containers. The pH was directly measured on shore < 15 min after first collection with a ROSS Ultra epoxy gel-filled pH/ATC electrode connected to an Orion Star A325 portable meter (Thermo Fisher Scientific™, Waltham, U.S.A.). The order that the samples were measured was randomized, to ensure that there was no bias from potential changes in the pH of the samples over the time between collection and measurement. No detectable change in the pH of the water samples over the measurement time was observed, with differences in duplicate measurements remaining < 0.01 units, below the detection limit of the pH meter. The pH meter was calibrated in the morning before the initial measurements for each diurnal cycle, and a built-in temperature sensor ensured that pH values were temperature-corrected. Because measurements were conducted in the field, the pH was measured at different temperatures throughout the day (*see* Supporting Information Fig. S1d for measuring temperature). Values of pH were corrected with TRIS buffer as described in Dickson et al. (2007), and total pH (pH_T) is reported, with values being defined as the concentration of hydrogen ion on the total hydrogen ion scale, thereby resolving the difference in ionic strength between NBS pH buffers and seawater.

In situ pH experiment

An in situ experiment investigating the effect of vegetation and water refreshment on the diurnal pH fluctuation was conducted at the unidirectional flow site. This site was chosen for the experiment location, as there was a large area of uniform depth and seagrass coverage, and a lack of pH difference between vegetated and unvegetated areas during the monitoring period indicated that water residence times were low. In March 2017, nine plots were marked out, measuring 0.3×0.3 m at a depth of 0.4 m. Plots were positioned > 2 m apart, to ensure there was no interaction between them. Each plot was randomly assigned one of three vegetation treatments: (1) bare, where all of the seagrass was cut below the sediment level but leaving rhizomes and roots still intact, (2) sparse vegetation, which had 50% of the seagrass removed, and (3) dense vegetation treatment, where the seagrass was left unaltered. For one full diurnal cycle, enclosures were set up around one plot of each of the vegetation treatments, which were randomly selected, while the remaining two plots of each vegetation treatment were left open. The enclosures consisted of a 0.3×0.3 m metal frame extending out of the water with 150 μm plastic around the frames to create an enclosure with a high residence time and a volume of 36 L. The tops of the enclosures were left open above the water to allow for water-atmospheric gas-exchange (*see* Fig. 2a), and sand bags were placed around the base to prevent leakage (*see* Fig. 2b). pH was measured in each plot (with or without enclosure) every 3 h from sunrise (06:00 h) to sunset (18:00 h), following the same procedure as described in the pH monitoring, for 1.5 d. Following this period, the enclosures were moved to a new vegetation plot, until all of the nine plots were measured over a full diurnal cycle with and without the enclosures. A full diurnal cycle per plot was considered a single replicate, with measurements on the three replicate plots being done over three diurnal cycles.

The water residence time within the enclosures was measured by injecting 1 mL of a 2.1 g L^{-1} stock solution of

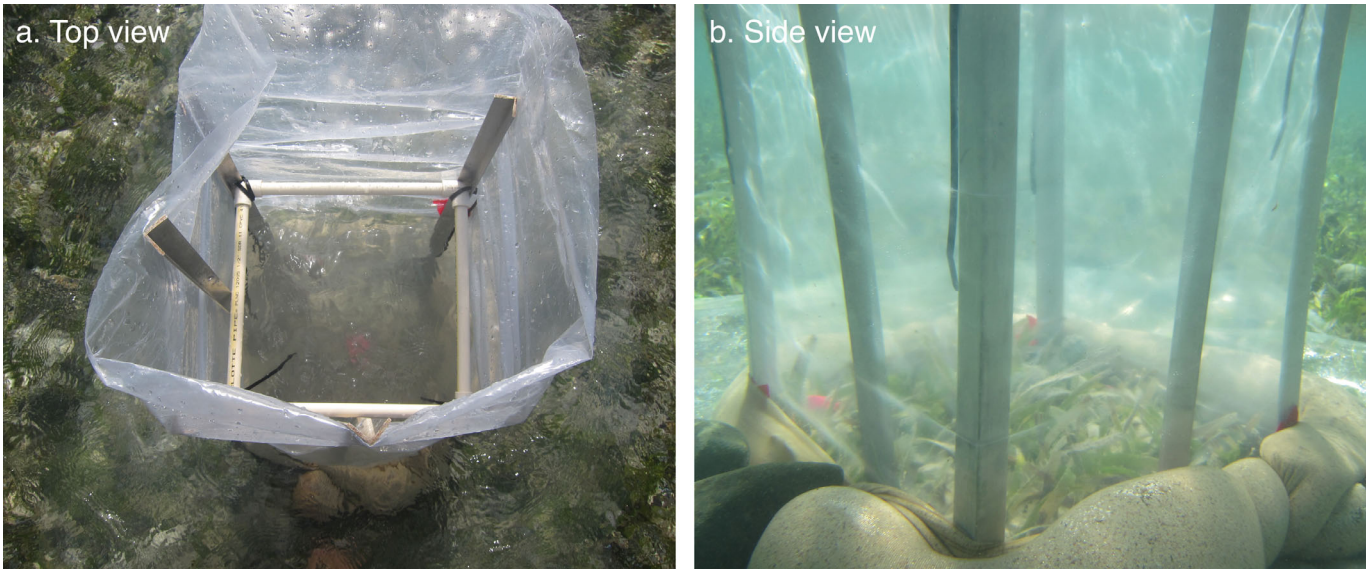

Fig. 2. Photos show the enclosures from above (**a**) where they were left open so air–sea gas exchange could occur, and how water residence times were increased by enclosing the plots with plastic lining weighed down with sand bags (**b**).

Uranine dye into the center of the enclosures, and logging the exponential decline in concentration over time with a Cyclops-7F™ Submersible Sensor connected to a DataBank™ Handheld Datalogger (Turner Designs). The water residence time was measured twice in each enclosure, once just after the enclosure had been set up and again near the end of the diurnal cycle. The use of thin, flexible plastic allowed for water movement within the enclosures as passing waves from the outside cause the plastic around the enclosures to oscillate, ensuring the plots were well mixed and boundary layer formation was reduced. This was supported by the injection of Uranine dye into the enclosures, which took 5–10 s to disperse throughout the enclosure after first being injected, suggesting a well-mixed environment inside the enclosures. The water residence time outside of the enclosures was below the detection limit, and the dye was instantly undetectable after injection into the water; therefore, the water outside of the enclosures was considered to be constantly refreshed with a low residence time.

Statistics

Values presented throughout the results and within the figures represent the mean ± the 95% confidence interval (CI). The difference in the above ground biomass and the significant wave heights recorded at each of the three water motion sites was tested with a one-way ANOVA. The range in pH (pH_{max}–pH_{min}) during a daily set of pH measurements from 06:00 h (before sunrise) to 21:00 h (3 h after sunset) for the long-term monitoring data, and 06:00 h (before sunrise) to 18:00 h (after sunset) for the in situ experimental data was used for statistical analyses. All statistical analyses were conducted in RStudio with R version 3.3.3. Normality and homoscedasticity of the data were tested, and passed these assumptions. A p value < 0.05 was considered significant.

A linear mixed effects model was produced with "lmerTest" package in R version 3.3.3, to test the differences in the observed pH ranges between the three sites with contrasting hydrodynamic regimes (sheltered, exposed, or unidirectional) and the three positions with each site (bay entrance, vegetated, or unvegetated). Site and position were considered fixed effects, with position being nested within the site, to test the variation both within and between the three sites. The date measurements made was included as a random effect. A linear regression was additionally used to quantify the effects of site, vegetation cover, and wave forcing (using the significant wave height at each measurement location) on the measured pH ranges. Both vegetation cover and wave forcing were considered nested within site. The in situ experiment was analyzed with a linear mixed effects model, to test the fixed effects of water residence time and vegetation on the pH range measured, with measuring day included as a random effect. Normality and homoscedasticity of both data sets were tested and passed these assumptions.

A backward elimination of the factors in all the models was conducted, and model selection was based on Akaike information criterion. Least squares means with 95% CIs and t-tests (with the corresponding t values, where df indicates the degrees of freedom) were calculated with the "lsmeans" package for both the monitoring and in situ experiment linear mixed effects models. For the monitoring data, contrasts were made between treatments from the same site or position to test for significant differences, and for the in situ experiment, contrasts were made for all of the interactions.

The overall mean pH over a 24-h period was calculated for the pH monitoring data. As measurements were not conducted between 21:00 and 06:00 h (for safety reasons), a linear regression using pH values from 21:00 to 06:00 h was used to estimate the pH at midnight and 03:00 h. Here, the assumption is made that respiration occurred continuously and pH declined at a linear rate throughout the night, with seawater pH being at its lowest point just before-sunrise (06:00 h). This assumption is supported by the continuous pH measurements from within a tropical seagrass meadow, reported by Cyronak et al. (2018).

All data available at 4TU. Centre for Research Data (doi:10.4121/uuid:ef9221c0-7dff-4c27-99b3-3414c444267f).

Results

Site description

The three neighboring study sites experienced similar temperature and light levels over the course of the monitoring period (Supporting Information Fig. S1). Temperature ranged from 30°C to 32°C at all sites at the beginning of the monitoring period in October 2015, and reduced to 26–28°C by late January 2016. The light levels did not significantly differ between the sites, a mean daily PAR of 12.9 ± 0.7 mol d^{-1} (95% CI, $n = 310$) was recorded at the sheltered site, 12.5 ± 0.8 mol d^{-1} ($n = 296$) at the exposed site, and 13.6 ± 1.0 mol d^{-1} ($n = 289$) at the unidirectional site.

Seagrass cover varied between the sites, with the sheltered site having the greatest benthic cover of seagrass with a mean of 89.0% ± 8.3% across the site ($n = 60$; Fig. 3a). Seagrass cover at the exposed site was more patchy than at the sheltered site, and when seagrass was present it was more sparse. A mean seagrass cover of 61.1% + 7.4% ($n = 60$; Fig. 3b) was present at the exposed site. The unidirectional flow site also had a sparser cover of seagrass than the sheltered site, with a mean vegetated cover of 74.7% ± 7.4% ($n = 60$; Fig. 3c) across the site.

The significant wave height at the bay entrance was comparable across the three sites, with the exposed and sheltered site experiencing a mean significant wave height of 0.25 ± 0.007 m ($n_{shel.} = 116$, $n_{exp.} = 119$) and the unidirectional flow site experiencing a slightly lower significant wave height of 0.20 ± 0.008 m ($n_{uni.} = 94$). At the sheltered site, the waves were attenuated as they traveled through the site, reducing to 0.13 ± 0.006 m ($n = 116$) at the

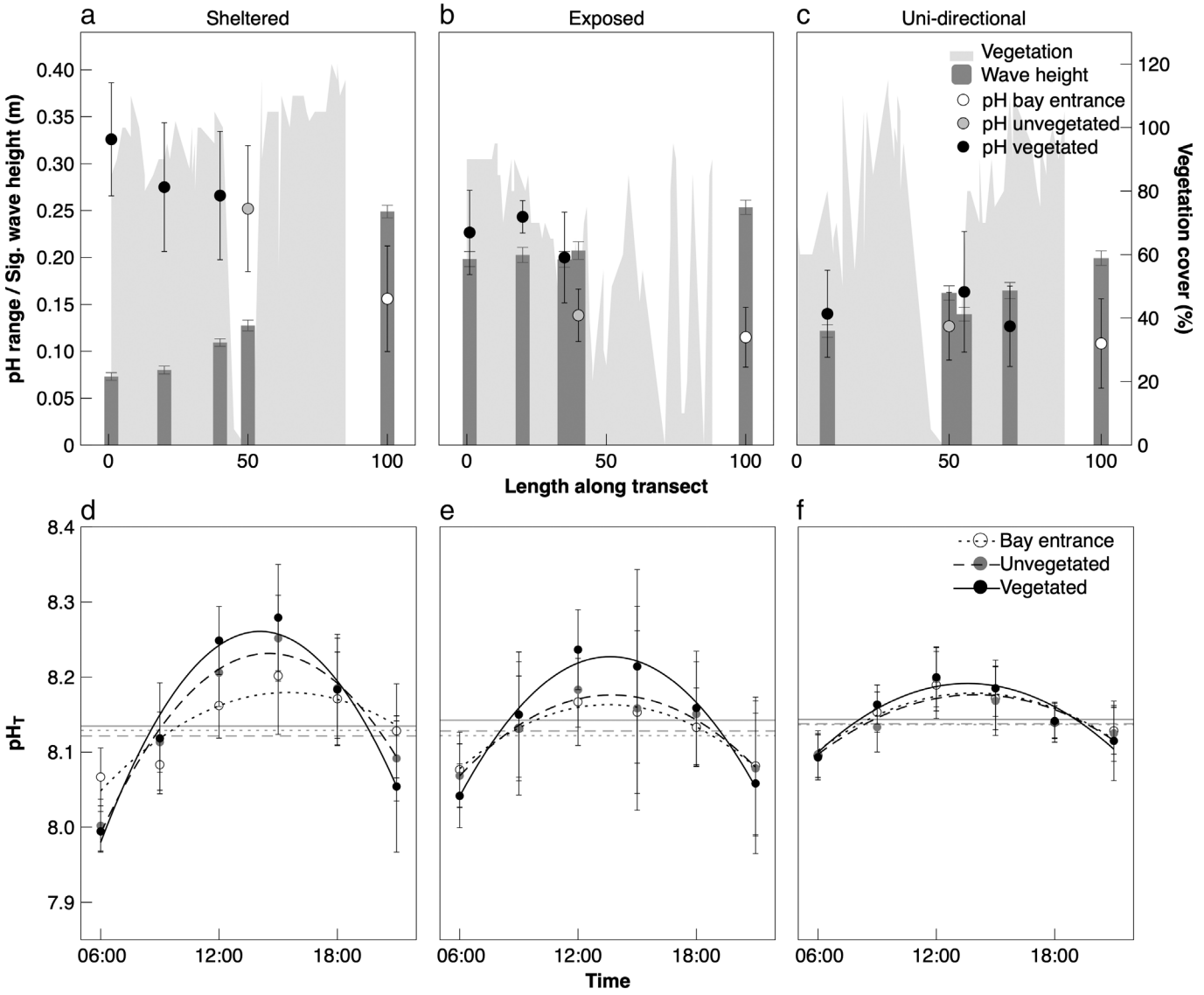

Fig. 3. The significant wave height (m; dark gray bars), vegetation cover (%; light gray area) and mean diurnal pH range (circles) along the transects at the sheltered (a), exposed (b) and unidirectional flow (c) sites. The pH was measured in vegetated (black circles), unvegetated (gray circles) and bay entrance (white circles) positions within each site. Time series data of wave, temperature, and light conditions during monitoring period can be observed in Supporting Information Fig. S1. Plots (**d**–**f**) show the mean seawater pH_T (measured on the total pH scale) over a light cycle at vegetated (black circles and solid line), unvegetated (gray circles and long-dashed line), and bay entrance positions (white circles and dotted line) within the three sites. The horizontal gray lines show the overall daily mean pH for vegetated (solid line), unvegetated (long-dashed line), and bay entrance positions (dotted line). Points and bars represent means ± 95% CIs (n_{pH} = 3–6, n_{waves} = 94–119).

unvegetated position (50 m from the bay entrance), and further reducing to < 0.1 m in the vegetated positions, 60–100 m from the bay entrance (Fig. 3a). Wave attenuation was much less at the wave-exposed site, with a mean significant wave height of 0.21 ± 0.009 m (n = 98) measured at the unvegetated position that was 60 m from the bay entrance, and 0.20 ± 0.008 m (n = 117) at the innermost vegetated position, 100 m from the bay entrance (Fig. 3b). Small uniform waves traveled through the unidirectional flow site, with significant wave heights ranging between a mean of 0.14 ± 0.007 (n = 113) at the unvegetated position and 0.12 ± 0.007 (n = 111) at the vegetated site 90 m downstream of the bay entrance position (Fig. 3c). In contrast to all other sites, the unidirectional flow site had a constant current velocity of around of 0.15 ± 0.05 m s^{-1} (n = 18), while currents were negligible at the other sites.

Spatial pH variability

A distinct diurnal pH fluctuation was observed at all sites (Fig. 3d–f), with the lowest recorded pH being observed before

sunrise and the highest pH being recorded at midday or the early afternoon. The magnitude in which seawater pH fluctuated throughout a diurnal cycle differed significantly according to the site and the position within the site (linear mixed effects model, $F_{6,28} = 28.92$, $p < 0.001$, Supporting Information Table S1). At all sites, the diurnal pH fluctuated the least within the bay entrance positions, where the largest mean significant wave heights were recorded and no vegetation was present (Fig. 3a–c). Although there were diurnal pH fluctuations with varying magnitudes within and between the sites, the daily mean pH was between 8.12 and 8.14 (Fig. 3d–f) at all locations.

The pH at the bay entrance of the sheltered site fluctuated by 0.16 ± 0.05 units ($n = 5$) throughout a diurnal cycle, ranging from 8.07 ± 0.04 ($n = 5$) at sunrise to 8.20 ± 0.08 ($n = 3$) by 15:00 h, corresponding to a 25.9% change in [H^+] (Fig. 3d). Vegetated positions within the sheltered site exhibited significantly greater fluctuations than the bay entrance ($t = 10.08$, df = 28, $p < 0.001$). In the vegetated position 60 m downstream from the bay entrance, the mean diurnal pH fluctuation was 0.27 ± 0.07 ($n = 5$) units, while at the landward edge of the meadow (100 m downstream from bay entrance), a mean diurnal pH fluctuation of 0.33 ± 0.06 ($n = 5$) was recorded (Fig. 3a). This diurnal fluctuation ranged from a mean pH of 8.00 ± 0.02 ($n = 5$) at sunrise (06:00 h), up to a mean pH of 8.28 ± 0.08 ($n = 3$) by the afternoon (15:00 h; Fig. 3d), corresponding to a 47.5% decrease in the concentration of hydrogen ions ([H^+]) over 9 h. The unvegetated position of the sheltered site exhibited a diurnal pH fluctuation of 0.25 ± 0.07 ($n = 5$), significantly less than the pH within the vegetated positions ($t = 4.39$, df = 28, $p < 0.001$), but significantly more than that at the bay entrance ($t = 5.69$, df = 28, $p < 0.001$).

The exposed site also exhibited a significant difference in the diurnal pH fluctuations between the bay entrance and the vegetated positions ($t = 7.68$, df = 28, $p < 0.001$), although this difference was slightly less than what was observed at the wave-sheltered site. A diurnal pH fluctuation of 0.12 ± 0.03 ($n = 6$) was recorded at the bay entrance of the exposed site, ranging from 8.07 ± 0.06 ($n = 6$) at sunrise to a maximum pH of 8.17 ± 0.06 ($n = 6$) at midday (12:00 h; Fig. 3e). This diurnal pH fluctuation at the bay entrance corresponds to a 20.6% decrease in [H^+] over 6 h. A significantly greater pH fluctuation of 0.22 ± 0.04 ($n = 18$) was observed within the three vegetated positions; 60–100 m downstream from the bay entrance (Fig. 3b). Within vegetated positions, the pH ranged from 8.04 ± 0.04 ($n = 6$) at sunrise to 8.24 ± 0.06 ($n = 6$) at midday (12:00 h), a 36.9% decrease in [H^+]. The pH at the unvegetated position of the exposed site did not significantly differ from the vegetated areas and bay entrance.

The diurnal pH fluctuations observed at the unidirectional flow site varied the least between the positions compared to the exposed and sheltered sites. A mean pH of 8.09 ± 0.02 ($n = 6$; Fig. 3f) was observed at all positions at sunrise, with pH ranges of 0.11 ± 0.05 units ($n = 6$) observed at the bay entrance, and 0.16 ± 0.06 pH units ($n = 6$) within the vegetated position 55 m downstream from the bay entrance (Fig. 3c). The change in magnitude of the diurnal pH fluctuation between the bay entrance and the vegetated areas was statistically significant ($t = 2.27$, df = 28, $p < 0.03$), and corresponded to a 20.6 decrease in [H^+] at the bay entrance and a 22.4% decrease in [H^+] at vegetated positions between sunrise and midday.

Analyzing the observed pH fluctuations within each site revealed that the magnitude of the fluctuations is positively correlated with vegetation cover (Fig. 4a), with wave forcing (measured as significant wave height) displaying a counteracting effect (Fig. 4b). The extent of the influence of vegetation cover and wave forcing did vary significantly at the three

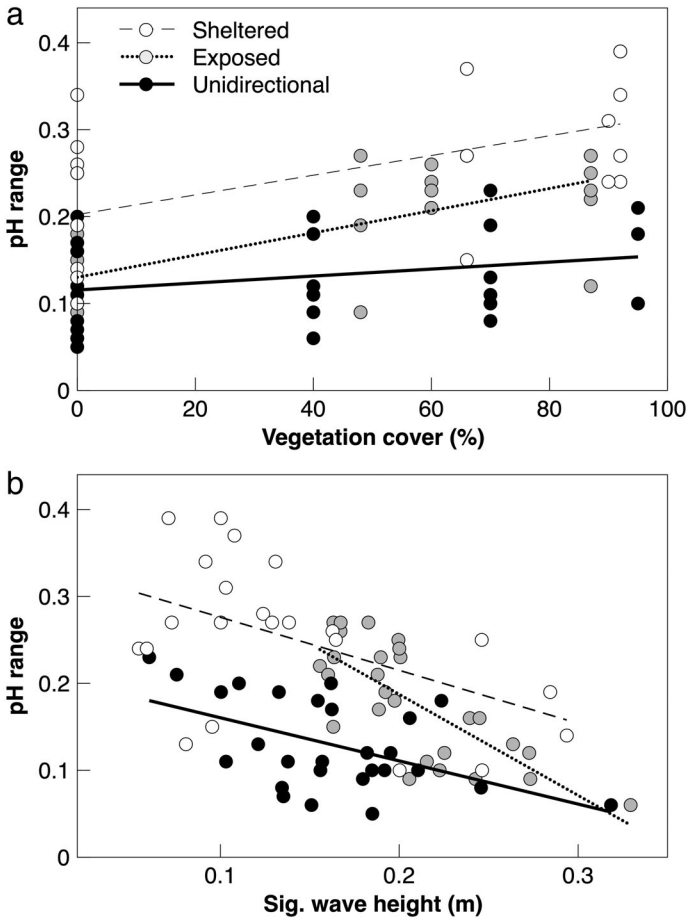

Fig. 4. The relation of the diurnal pH range as observed within the three sites with contrasting hydrodynamic regimes, plotted against the significant predictors; percent vegetation cover (**a**) and significant wave height (**b**). Different colors of the points indicate the sheltered (white points and dashed line), exposed (gray points and dotted line), and unidirectional (black points and solid line) sites. Each point represents values from a single diurnal cycle, and the lines indicate the linear trend of the individual factors. The linear regression analysis for these trend lines can be found in Supporting Information Table S2.

sites, reflecting their contrasting hydrodynamic regimes. The statistical interaction between wave forcing and vegetation cover was not significant and was dropped from the model. Vegetation cover is the strongest predictor for the observed pH range at the sheltered site, with the pH range increasing by 0.008 units for every 10% increase in vegetation cover ($t = 2.00$, df = 67, $p = 0.049$; Supporting Information Table S2). The seagrass meadow at the sheltered site is characterized by significant wave heights of < 0.12 m, with larger waves only occurring at the bay entrance (Fig. 3). Although there is a trend of wave forcing counteracting the pH adjustment by the vegetation (Fig. 4b), the uneven scatter of wave measurements results in this trend not being significant. At the exposed site, the positive correlation between vegetation cover and pH range follows the same significant trend that is observed at the sheltered site (estimate = 0.0009, $t = 2.77$, df = 67, $p = 0.007$; Fig. 4a). However, the larger waves that travel through the site (Fig. 3) result in a significant counteracting effect of wave forcing on the magnitude of the pH range ($t = -3.20$, $p = 0.002$; Fig. 4b), and overall, cause pH ranges that are significantly less than at the sheltered site (Figs. 3, 4). Contrastingly, the unidirectional site is characterized by a strong current that runs through the entire site (0.15 ± 0.05 m s^{-1}), which leads to this site having an overall lower ΔpH estimate within the regression model compared to the sheltered and exposed sites (Fig. 4; Supporting Information Table S2). Vegetation did not significantly affect the pH range at the unidirectional site, while the wave forcing further reduced the observed diurnal pH fluctuation ($t = -2.18$, df = 67, $p = 0.03$; Fig. 4b).

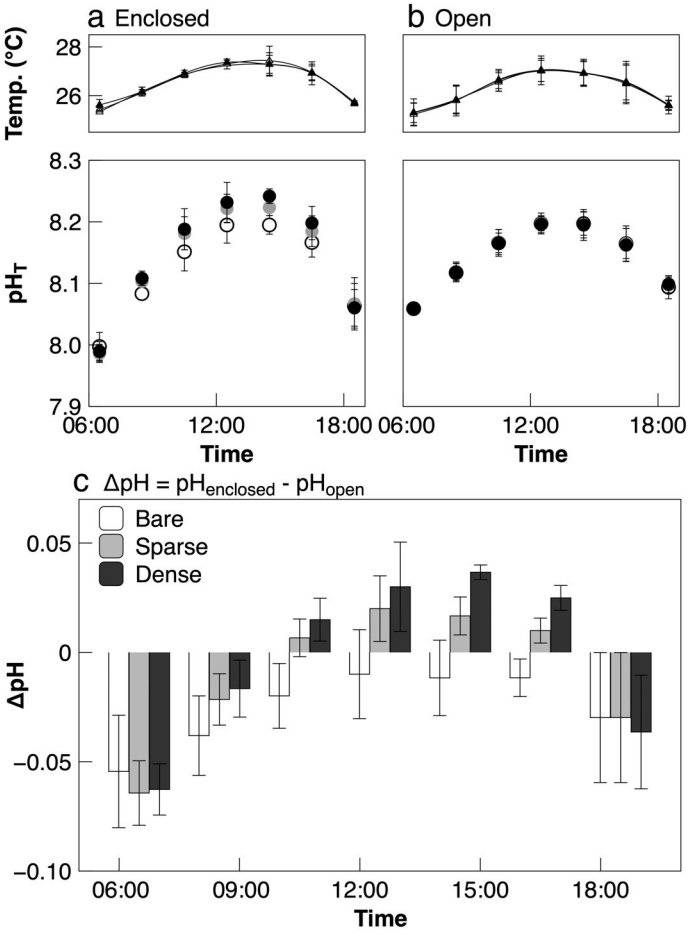

Fig. 5. Diurnal seawater temperature and pH_T (total pH scale) measurements from an in situ enclosure experiment with bare (white points), sparse (gray points), and dense vegetation (black points). Plots were either enclosed with high water residence times (30 min) (**a**) or were left open for constant refreshment (**b**). The difference between the pH of the open (low residence time) and enclosed (high residence time) treatments throughout the day can be seen in the ΔpH (**c**). Points and bars represent means ± 95% CIs ($n = 3$).

In situ pH experiment

The flow at the unidirectional site was considered to cause constant refreshment due to the strong current, while the water residence time within the enclosures averaged 30 ± 2 minutes ($n = 18$). Temperature varied from 25.4°C in the morning up to 27.5°C in the afternoon within the enclosures, and from 25.3°C up to 27.0°C in the plots without enclosures (Fig. 4a,b). The water residence time and vegetation density (bare, sparse, and dense) showed an interactive effect on the pH (Fig. 5; linear mixed effects model: $F_{2,15} = 10.43$, $p = 0.002$).

When there was constant refreshment and the water residence time was low, the vegetation had no significant effect on the pH range, with pH increasing from an average of 8.05 ± 0.01 ($n = 9$) at sunrise to a peak of 8.22 ± 0.01 ($n = 9$) by 14:30 h in all three vegetation treatments (Fig. 5b), a 32.4% change in [H$^+$]. Within the enclosed plots with high water residence times, however, the presence of dense vegetation significantly increased the magnitude of the range in pH when compared to bare plots ($t = 5.915$, df = 15, $p < 0.001$, Fig. 5a). Densely vegetated plots had on average a pH of 7.99 ± 0.02 ($n = 3$) at sunrise, and by the early afternoon (14:30 h) had reached a maximum pH of 8.24 ± 0.01 ($n = 3$), corresponding to a 43.8% change in [H$^+$] throughout the day. Enclosed plots with sparse vegetation were not significantly different from plots with dense vegetation, and experienced a 41.1% change in [H$^+$] throughout the day. The [H$^+$] in bare enclosed plots changed by 36.9%, starting at a pH of 8.00 ± 0.02 ($n = 3$) at sunrise, and reaching an average pH of 8.20 ± 0.01 ($n = 3$) by the early afternoon, which was a significantly lower pH range than in the sparse and densely vegetated enclosure plots (Supporting Information Table S3).

Enclosed plots with high water residence times (~ 30 min) experienced significantly greater diurnal fluctuations in pH compared with the corresponding open vegetation plots with constant refreshment (bare: $t = 5.86$, df = 15, $p < 0.001$; sparse: $t = 10.29$, df = 15, $p < 0.001$; dense: $t = 12.15$, df = 15, $p < 0.001$, Fig. 5c). Bare, enclosed plots with high water residence times had a lower pH throughout the entire course of the day than that of corresponding open bare plots with constant refreshment (Fig. 5c). While sparse and densely vegetated, restricted plots had significantly lower pH values in the

early morning and late evening than the corresponding open plots with constant refreshment, however, by late morning through to later afternoon exhibited a higher pH (Fig. 5c).

Discussion

This study displays the counteracting effect that hydrodynamic forcing has on the alteration of pH by biological metabolism, causing the pH within coastal ecosystems to vary remarkably over a spatial scale of meters. Small hydrodynamic forces (waves) and dense seagrass cover at the sheltered site meant that the metabolism by vegetation had a strong influence on the pH. Diurnal pH fluctuations at the sheltered site occurred at a similar magnitude to those observed where refreshment was restricted within densely vegetated plots during the field experiment. A similar spatial trend of the seawater pH was apparent at the wave-exposed site, at a smaller magnitude however, with the stronger hydrodynamic forces and sparser seagrass cover leading to a reduced influence of the seagrass metabolism on the local seawater pH. Even though the vegetation cover was consistently high at the unidirectional flow site, the fast current that flowed through the site strongly reduced the metabolic influence on the seawater pH by the vegetation. With this research, we illustrate the significant spatial and temporal variability of pH within a tropical seagrass ecosystem. Furthermore, we provide direct evidence for the hydrodynamic setting driving spatial variability of seawater pH within vegetated coastal zones.

pH fluctuations in vegetated ecosystems

Photosynthesis and subsequent respiration at night by tropical seagrass meadows results in significant seawater pH fluctuations within the vegetated areas of bays and lagoons, due to the uptake and release of CO_2. This metabolic adjustment of the local seawater pH at the sheltered and exposed sites was comparable to the 0.25 pH fluctuation observed within a tropical coral reef by Rivest and Gouhier (2015), and the 0.24 pH fluctuation observed in a Mediterranean seagrass meadow by Hendriks et al. (2014). The observed mean diurnal pH fluctuations within the inner seagrass meadow of the sheltered site resulted in a maximum daytime pH 0.18 units above the global mean seawater pH of 8.10. Whereas after a night of respiration, the mean pH in the meadow was 0.14 units lower than that of the oceanic pH. This pH fluctuation occurs regularly over a single day, but compared to global ocean models (Caldeira and Wickett 2005), is equivalent to pH predictions that span from preindustrial times to the mid-21st century (year ~ 2050). Although the overall mean daily pH is not significantly affected, such large diurnal pH fluctuations emphasize the distinction between the dynamic coastal zone and the stable open ocean (Hofmann et al. 2011; Montalto et al. 2014). Recognizing these fluctuating conditions within the coastal zone is highly important if we are to understand the physiological tolerance of coastal species and their ability to respond to changes in their environment (Botero et al. 2015; Boyd et al. 2016; Thomsen et al. 2017). This is particularly necessary for global change studies, where it has been shown that averaging temporal fluctuations and exposing organisms to static conditions compared with a naturally fluctuating regime can result in alternative physiological responses (Cornwall et al. 2013*a*; Montalto et al. 2014; Boyd et al. 2016), possibly leading to biased conclusions.

Adding to the complexity of temporally fluctuating pH within the coastal zone is the spatial heterogeneity of pH, varying both within and between sites. Monitoring of the pH at sites with contrasting hydrodynamic regimes displays how spatial variability of pH corresponds with the hydrodynamic setting. Strong advection processes at the unidirectional flow site limit the residence time of the water within the vegetated areas, thereby restricting the magnitude of the metabolically driven pH fluctuation from increasing as the water flows through this site, and resulting in a uniform pH environment across the site. This is in contrast to the exposed and sheltered sites, which have a strong hydrodynamic regime at the bay entrance, but which attenuates toward the shoreline, consequentially resulting in an increase in the magnitude of the pH fluctuations within the seagrass meadows. The effect of hydrodynamic forcing on the biological adjustment of seawater pH has been precisely measured in the laboratory (Hurd et al. 2011; Cornwall et al. 2013*b*, 2015); however, field measurements of this effect are limited and often complicated by varying weather conditions (Cyronak et al. 2018), and factors causing variable metabolic rates, such as light and nutrient availability. With the in situ experiment in this study, we were able to provide direct evidence from the field, which showed that the spatial variability observed within these tropical seagrass meadows is driven by the refreshment rate counteracting the metabolic-adjustment of seawater pH by vegetation.

There was evidence for the fringing coral reefs influencing the source seawater at the study sites, with a diurnal pH fluctuation of 0.11–0.16 existing at the bay entrances at all sites. Prevailing easterly swell and winds drive water from the Atlantic into the Eastern bays of St Martin (Johns et al. 2002), this water passes a fringing coral reef 50–100 m upstream from the bay entrance sampling positions. Coral reefs have been shown to influence the local pH through their own metabolism (Horst and Edmunds 2010; Kleypas et al. 2011; Jokiel et al. 2014), with reported diurnal fluctuations of 0.23–0.25 pH units (Hofmann et al. 2011; Rivest and Gouhier 2015). Without direct measurements within the fringing coral reef, we are unable to calculate the degree to which this metabolically influenced seawater was diluted before reaching the bay entrance of the sites. However, this observed fluctuation of the pH at the bay entrance at all three sites provides evidence that plumes of metabolically influenced pH seawater can travel downstream from the site of original modification, altering the seawater chemistry of neighboring communities (Koweek et al. 2018). The further doubling of the magnitude of the seawater pH fluctuation within the seagrass meadow highlights the strong effect that seagrass meadows alone have on the local seawater pH. The

adjustment of pH by larger areas of upstream communities most likely explains why there was a pH fluctuation of 0.17 within all vegetation treatments with constant refreshment during the in situ experiment.

Vegetated ecosystems as pH refuges

By the end of the century, seawater pH is expected to reduce by a further 0.13–0.42 units (Pörtner et al. 2014), lowering the average oceanic pH from 8.1 (Hofmann et al. 2011) down to 7.97–7.70. This rapidly lowering pH creates unfavorable conditions for calcifying organisms (Ries et al. 2009; Koch et al. 2013), as $[H^+]$ increases and $[CO_3^{2-}]$ declines, causing a reduction in the aragonite saturation state of the seawater. The large pH fluctuations within the seagrass meadows did not affect the overall average seawater pH across a day cycle, but instead created a period of high pH conditions during the day which extended up to 0.18 units above the mean open ocean pH. The future reduction of pH by ocean acidification could be thus partially counteracted within sheltered vegetated bays during the day. The nighttime respiration of the vegetation and associated organisms, however, will exacerbate the lowering pH, potentially limiting the effectiveness of pH refuges. Calcifying organisms that can tolerate low nighttime pH, or mobile organisms that can move between habitats, could take advantage of the high pH conditions within sheltered vegetated sites.

The ability to regulate calcification depending upon external environmental factors has been shown in a number of species, and would allow those organisms to benefit from the transient pH conditions within pH refuges. Mytilid mussels, both adults and larvae, have been shown to adjust their rate of calcification depending upon whether pH conditions are favorable or not (Frieder et al. 2014; Wahl et al. 2018). Mussel larvae only required high pH conditions for a few hours to develop normally when grown in a high pCO_2 treatment (Frieder et al. 2014). Additionally recruits of the stony coral *Seriatopora caliendrum* calcified more in naturally fluctuating conditions; compared to stable ambient or high pCO_2 conditions (Dufault et al. 2012). Alternatively, mobile organism may be able to utilize the spatial variability of coastal pH, moving to more favorable conditions as required. Many zooplankton and crustacean larvae have been shown to inhabit seagrass canopies during the day, but vertically migrate up the water column during the night (Robertson and Howard 1978). This daily migration is traditionally thought to be a strategy against predation, but could additionally allow the organisms to benefit from the high pH conditions during the day within the seagrass canopy, while escaping the low pH conditions at night.

The ability to tolerate or escape unfavorable conditions for calcification does not extend to all marine species. Adult coralline macroalgae negatively responded to fluctuating low-pH conditions and the associated changes in carbonate chemistry (Cornwall et al. 2013*a*), and although this was reported to not impact the production of new coralline macroalgae recruits, further experiments on the new recruits showed that their growth was reduced in conditions with a fluctuating pH (Roleda et al. 2015). Low pH conditions may require additional energy expenditure by pH-sensitive marine organisms, as they are forced to more strongly regulate cellular pH to maintain the appropriate H^+ gradients (Schulz and Riebesell 2013). Such a response was hypothesized by Agostini et al. (2013) to contribute to the low levels of ATP measured within corals at night. The lower pH conditions at night may therefore limit the suitability of sheltered vegetated habitats in acting as pH refuges for some organisms.

Because diurnal pH fluctuations within vegetated environments are recurring, and therefore, predictable, it would be expected that the organisms inhabiting these environments would be acclimated to natural diurnal fluctuations (Botero et al. 2015). Whether this adaptation to fluctuating pH extends to being resistant to future pH changes is of high interest. Bivalve larvae from a pH-variable site were found to be less affected by high pCO_2 conditions than those growing within a more-stable pH environment (Thomsen et al. 2017). While a multigenerational study displayed the ability of oyster larvae (*Saccostrea glomerata*) to acclimate or adapt to changing conditions over just one or two generations (Parker et al. 2013). It was found that oyster larvae spawned from adults that were grown in elevated pCO_2 were more resilient to high pCO_2 than those from adults grown under ambient pCO_2. Contrastingly, Noisette et al. (2013) collected temperate coralline algae from areas with different levels of pH heterogeneity and subjected them to future pCO_2 conditions. Their results showed no increased resilience of coralline algae individuals growing in heterogeneous conditions; however, confounding light factors as well as the use of adult individuals may have contributed to this result. Further experiments are required, utilizing a variety of taxa, to determine whether species inhabiting areas with fluctuating pH conditions are more resilient to the global lowering of oceanic pH.

The limited seasonal changes and relatively constant conditions in tropical environments results in uniform diurnal pH fluctuation within tropical seagrass meadows throughout the year (Hofmann et al. 2011; Hendriks et al. 2014), making them effective and reliable habitats at providing a high pH refuge during the day. Seagrass are well recognized for their flow-attenuation capabilities (Fonseca and Cahalan 1992; Hansen and Reidenbach 2012), which can increase the water residence time within the seagrass canopy, and likely contributes to the large pH fluctuations observed within the meadows. When connected to coral reefs, seagrass meadows act as nursery habitats for reef fish, urchins, lobster, conch, and nursing sharks (Rios-Lara et al. 2007; Nagelkerken 2009). The dense seagrass canopy provides shelter and a protected, low water motion environment for these vulnerable early-life stages (Gillis et al. 2014). The importance of seagrass meadows as nurseries is likely to be made even greater by their ability to raise the surrounding pH and provide a high-pH refuge for vulnerable

early-life stages of organisms in a future low pH ocean. In addition, photosynthetic rates of seagrass are expected to increase with higher concentrations of CO_2 in the ocean (Zimmerman et al. 1997; Invers et al. 2001; Campbell and Fourqurean 2013), potentially leading to larger pH fluctuations within vegetated habitats and an increased metabolic effect on pH in areas with stronger hydrodynamic settings. Field studies have shown, however, that this increase in metabolism due to high CO_2 is dependent upon the availability of nutrients and light, which could limit the extent that seagrass metabolism increases in the future (Apostolaki et al. 2014). Further investigations into how metabolically driven pH fluctuations in vegetated communities may change under different global change scenarios would be valuable.

The pH within the coastal zone is both temporally and spatially dynamic, making it difficult to accurately predict future ocean acidification conditions. While the metabolism of vegetation alters the local pH, water motion is a primary factor controlling the pH levels that organisms encounter. In sheltered regions, the high-pH conditions during the day could potentially create high pH refuges that provide conditions favorable for calcification. However, the positive day effects are reversed at night, with respiration by the vegetation causing a lower pH than the surrounding bulk water. In regions with strong hydrodynamic forcing, the physical processes override biological influences on the pH, leading to much more stable pH conditions. If we are to conserve and promote ecosystems that create diverse pH conditions in the coastal zone, particularly those that provide high pH areas where calcification is promoted, we need to increase our accuracy in predicting the spatial variation in coastal pH. Incorporating high-resolution measurements of in situ conditions, such as hydrodynamic forcing and vegetation density, is a first step in increasing our ability to develop accurate pH prediction models of coastal areas.

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Conflict of Interest

None declared.

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