#### **Original Article**

## Tidal cycle and time of day control pH levels in coastal habitats of the western Indian Ocean: the case of Mnazi and Chwaka Bays in Tanzania

Rushingisha George<sup>1</sup><sup>(b)</sup>, Blandina R. Lugendo<sup>2\*</sup><sup>(b)</sup>

<sup>1</sup> Tanzania Fisheries Research Institute (TAFIRI), PO Box 78850, Dar es Salaam, Tanzania <sup>2</sup> Department of Aquatic Sciences and Fisheries Technology (SoAF), University of Dar es Salaam, PO Box 60091, Dar es Salaam, Tanzania

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\* Corresponding author: blugendo@udsm.ac.tz

## Abstract

Ocean acidification, a progressive decrease in the pH and change in the carbonate chemistry of seawater caused by the uptake of carbon dioxide (CO<sub>3</sub>) from the atmosphere, is a growing crisis that threatens marine species. pH data relevant to a species' natural habitat in the coastal waters of the western Indian Ocean (WIO) is still sparse, limiting the capacity to undertake manipulative studies to better understand the impacts of ocean acidification on marine species. This study investigated tidal and day-night pH variations in mangrove, seagrass, and coral reef habitats of the WIO by using Tanzania as a case study. The mean pH of the studied coastal habitats was highest in seagrass (8.49  $\pm$  0.29), followed by coral reef (8.33  $\pm$  0.06), and lowest in mangrove (8.20  $\pm$  0.17). Seagrass habitats had the highest pH (9.06) during the day at low spring tides, mangrove habitats had the highest pH (8.45) during the day at high spring tides, and coral reef habitats had the highest pH (8.47) during the day at low tides. Seagrass habitats had the widest pH range (1.03), followed by mangrove habitats (0.54), while coral reef habitats had the narrowest range (0.23). The water with the highest pH during the day was transported to nearby mangrove habitats during incoming tides and to coral reef habitats during outgoing tides, resulting in the highest mean pH in mangrove and coral reef habitats during spring high and low tides, respectively. pH within the seagrass habitats correlated strongly and positively with changes in temperature (r=0.80), dissolved oxygen (r=0.84), and salinity (r=0.72), while pH in mangrove habitats correlated moderately and positively with dissolved oxygen (r=0.59). This study provides in-situ evidence on the pH fluctuations in the WIO's coastal habitats over time and space, with water from seagrass habitats capable of raising the pH of water in nearby mangrove and coral reef habitats during the day, thereby potentially helping in the mitigation of the effects of ocean acidification on these habitats.

Keywords: pH, ocean acidification, western Indian Ocean, mangroves, coral reefs, seagrasses

## Introduction

Ocean acidification (OA) is a progressive decrease in the pH and change in carbonate chemistry of seawater caused by carbon dioxide (CO<sub>2</sub>) absorption from the atmosphere (Doney *et al.*, 2009; Gattuso *et al.*, 2015). As a result, the pH of the open oceans has decreased from a previously stable value of 8.2 over the past century to a current value of 8.1, signifying a 30 % increase in acidity on average (Feely *et al.*, 2009; Orr, 2011). Based on the Intergovernmental Panel on Climate Change (IPCC) worst-case business-as-usual  $CO_2$  emissions scenario, biogeochemical models predict a further decrease in the pH of the open oceans, leading to an acidity increase of up to 150% by 2100 (Doney *et al.*, 2009; Feely *et al.*, 2009). Prediction of pH in coastal waters containing mangrove, seagrass, and coral reef habitats is, however, challenging because it is influenced by a complex set of factors such as community metabolism (a balance between primary productivity of vegetation cover and community respiration), eutrophication, inputs from the open ocean, underground freshwater discharge and rivers, and climatic factors (temperature and dissolved oxygen), some of which may be localized in nature (Hofmann *et al.*, 2011; Pacella *et al.*, 2018; Pauline *et al.*, 2011; Proum *et al.*, 2017; Unsworth *et al.*, 2012). As a result, natural pH variability may occur at much higher rates than the rate at which CO<sub>2</sub> decreases ocean pH.

Mangrove, seagrass, and coral reef habitats of the WIO are also subject to semi-diurnal tidal variability, with two high tides and two low tides during each day-night cycle, resulting in fluctuations in physicochemical variables such as salinity, temperature, and dissolved oxygen (George et al., 2018; Mahongo, 2014; Shaghude et al., 2012). These changes affect the pH of the water column by modulating community metabolism (photosynthesis and respiration) within habitats (Semesi et al., 2009a; Semesi et al., 2009b), allowing for a high degree of pH variability (day-night cycling) in the water column of these habitats. A study by Hofmann et al. (2011), which examined temporal changes in different coastal habitats, does not adequately represent pH variability in coastal habitats of the WIO. This is because the effect of tidal cycles on pH variability in mangrove, seagrass, and coral reef habitats was not considered. pH variations in such habitats could have a significant impact on the development of resistance in resident marine species, or they could combine with the persistent effects of OA to produce severe occurrences with significant consequences on resident marine species. In either case, understanding pH variations in mangrove, seagrass, and coral reef habitats as well as their underlying drivers is crucial for a better understanding of the effects of future OA on marine species. Therefore, the aim of this study was to characterise the pH variability in Tanzanian coastal habitats over space and time as well as their underlying drivers. In this study, we tested four hypotheses: (1) mangrove, seagrass, and coral reef habitats have different pH levels; (2) pH levels within mangrove, seagrass and coral reef habitats vary with tidal cycles; (3) pH levels within mangrove, seagrass, and coral reef habitats are higher during the day than at night, regardless of tidal cycle; and (4) water with a higher pH from seagrass habitats is flushed to nearby mangrove and coral reef habitats during the day at high tides, raising their pH and helping to mitigate the effects of OA in these habitats.

## Materials and methods Study area

This study was carried out in spatially isolated mangrove, seagrass, and coral reef habitats located in non-estuarine bays: Chwaka Bay in Unguja Island, Zanzibar, and in Mnazi Bay in Mtwara, Mainland Tanzania (Fig. 1). The climate along the Tanzanian coast is influenced by the northeast (NE) monsoon winds (which are present from November to April) characterized by heavy rainfalls, weak winds and high stable average air temperatures, and the southeast (SE) monsoon winds (which are present from June to September) characterized by weak rainfalls, strong winds and low stable average air temperatures (Mahongo, 2014). The inter-monsoon months (May and October) are comparatively calm. The monsoon season also creates two rainy seasons: heavy or long rains between March and May, and short rains, which occur irregularly between September and December (Francis and Mahongo, 2012; McClanahan, 1988). The coast is also characterised by semi-diurnal tides, consisting of two high tides and two low tides of approximately equal magnitude each day-night cycle, resulting in fluctuations in the physicochemical conditions of the water column that modulate biogeochemical processes and community metabolism within habitats, affecting pH of the water column (Cederlof et al., 1995; George, 2019; Shaghude et al., 2012). This study was conducted between September (2018) and July (2019), covering periods of both the NE and SE monsoons.

#### Study design

In each bay, large permanent plots (50 m x 50 m) in mangrove, seagrass, and coral reef habitats and their adjacent open ocean were marked using a Global Positioning System (GPS) and monitored during low and high spring tides during the NE and SE monsoons. Within each habitat at low spring tides, three 30 m transects were established using measuring tapes parallel to the shoreline to minimize the impact of depth gradient, as it has been demonstrated that water motion determines how much the local pH is influenced by vegetation metabolism (James et al., 2020). A 0.25 m x 0.25 m quadrat was randomly selected along each transect at a distance of approximately 10 m during low spring tides. In each quadrat, six measurements of pH, temperature, salinity and dissolved oxygen were taken for both the day (between 10:00 am and 3:00 pm) and night (between 10:00 pm and 3:00 am). Because the properties of the water column in shallow water habitats are similar, data (pH, temperature, salinity, and dissolved oxygen) were collected

at the surface of the water in a specific coastal habitat during high spring tides. *In-situ* measurements of pH, dissolved oxygen, salinity, and temperature were performed once during spring tides of each season over a 24-hour period covering high and low tides for each habitat within bays in order to capture the effect of the tidal cycle and time of day on pH levels. and compared between sites, time of the day, and tides. Prior to statistical analysis, the data were subjected to a Shapiro-Wilk test to determine their normality. The differences in mean pH levels between habitats were tested using a One-way Analysis of Variance (ANOVA), followed by the Tukey's test post-hoc for pairwise habitat comparisons. Furthermore, the differences in



Figure 1. Map of Tanzania showing locations of study sites (Mnazi and Chwaka Bays).

## Measurements of dissolved oxygen, salinity, pH and temperature

Dissolved oxygen, salinity and pH were manually measured by using an  $O_2$  electrode (FDO 925, WTW), salinity electrode (TetraCon 925, WTW) and a pH electrode (SenTix 940, WTW), respectively, connected to a multimeter (Multi 3430 WTW, Germany) one at a time. Prior to measurement, the pH meter was calibrated (three-point calibration; pH 4.10, 7.01, and 10.00) using a buffer that was purchased together with the instrument. This procedure allowed for the acquisition of reliable data. Electrodes also measured the temperature of water.

#### Statistical analyses

Mean and standard deviation for pH, temperature, salinity and dissolved oxygen values were computed

mean pH within habitats were tested using the T-test. The differences in dissolved oxygen, salinity and temperature between day-night time and between highlow tides within habitats were tested using a Two - way Analysis of Variance (ANOVA). Moreover, a spearman rank correlation analysis was performed to test the relationship between dissolved oxygen, salinity, temperature (predictors) and pH. The significance level was established at <0.05. All statistical analyses were performed using Python version 3.2.

#### Results

# pH variability in the mangrove, seagrass and coral reef habitats

The mean pH levels between mangrove, seagrass, and coral reef habitats varied significantly (Fig. 2). However, while the difference in mean pH levels between



**Figure 2.** Mean pH levels in seagrass, mangrove, and coral reef habitats. The dotted line indicates the mean pH of the adjacent open ocean. Error bars indicate standard deviations. The letters above the bars indicate significant differences in pH levels between mangrove, seagrass, and coral reef habitats (based on one-way ANOVA tests) at  $p \le 0.05$ . N = 16.

seagrass and mangrove habitats, and between seagrass and coral reef habitats was significant, the difference between mangrove and coral reef habitats was not (Fig. 2). Seagrass habitats had the highest mean pH of 8.49  $\pm$  0.29, followed by coral reef habitats with a mean pH of 8.33  $\pm$  0.06 and mangrove habitats with the lowest mean pH of 8.20  $\pm$  0.17. The adjacent open ocean had a mean pH of 8.16  $\pm$  0.05, which was 0.04 pH units lower than that of mangrove habitats, 0.33 pH units lower than that of seagrass habitats, and 0.17 pH units lower than that of coral reef habitats (Fig. 2).

## Tidal and day-night variability in pH levels in the mangrove, seagrass and coral reef habitats

Significant tide-dependent variations in mean pH levels were observed in mangrove and seagrass habitats, but not in coral reef habitats (Fig. 3; Table 1). The mean pH level in mangrove habitats was highest during the day at high spring tides  $(8.38 \pm 0.06)$ and lowest during the night at low spring tides (8.01  $\pm$  0.08). The mangrove habitats had a pH range of 0.54, with the highest pH (8.45) occurring in the day at high spring tides and the lowest pH (7.91) occurring during the night at low spring tides. In seagrass habitats, the mean pH was highest during the day at low spring tides (8.862  $\pm$  0.21) and lowest during the night at low spring tides (8.16  $\pm$  0.11). The pH range of the seagrass habitats was 1.03, with the highest pH (9.06) occurring in the day at low spring tides and the lowest pH (8.03) occurring during the night at low spring tides. The mean pH values for day high spring tides, day low spring tides, night high spring tides, and night low spring tides in coral reef habitats were  $8.34 \pm 0.01$ ,  $8.35 \pm 0.09$ ,  $8.30 \pm 0.06$ , and 8.33 $\pm$  0.06, respectively, and did not significantly differ from one another. The highest pH for the coral reef habitats was 8.47 and the lowest was 8.24, with a range of 0.23. Interestingly, the mean pH levels in seagrass,



**Figure 3.** Tidal variability in mean pH levels in mangrove, seagrass and coral reef habitats. The dotted line shows the mean of pH value of the adjacent open waters. Error bars indicate standard deviations. The letters above the bars indicate significant differences in pH levels between mangrove, seagrass, and coral reef habitats (based on one-way ANOVA tests) at  $p \le 0.05$ . N = 4.

9.2

Tidal cycle	Mean	SD	Minimum	Maximum
Day high tide	8.34	0.06	8.34	8.45
Day low tide	8.16	0.07	8.06	8.20
Night high tide	8.24	0.15	8.11	8.37
Night low tide	8.01	0.08	7.91	8.08
Day high tide	8.52	0.05	8.45	8.55
Day low tide	8.86	0.21	8.68	9.06
Night high tide	8.42	0.11	8.33	8.55
Night low tide	8.16	0.11	8.03	8.25
Day high tide	8.34	0.01	8.33	8.35
Day low tide	8.36	0.09	8.25	8.47
Night high tide	8.30	0.06	8.24	8.36
Night low tide	8.33	0.06	8.24	8.37
	Tidal cycle   Day high tide   Day low tide   Night high tide   Day high tide   Day low tide   Night high tide   Day low tide   Night low tide   Day high tide   Day high tide   Night low tide   Day low tide   Night low tide   Night high tide   Night low tide   Night low tide   Night low tide	Tidal cycleMeanDay high tide8.34Day low tide8.16Night high tide8.24Night low tide8.01Day high tide8.52Day low tide8.86Night high tide8.42Night low tide8.16Day high tide8.34Day low tide8.36Night low tide8.30Night high tide8.33	Tidal cycle   Mean   SD     Day high tide   8.34   0.06     Day low tide   8.16   0.07     Night high tide   8.24   0.15     Night low tide   8.01   0.08     Day high tide   8.52   0.05     Day low tide   8.86   0.21     Night high tide   8.42   0.11     Night low tide   8.36   0.01     Day high tide   8.34   0.01     Day high tide   8.36   0.09     Night high tide   8.36   0.09     Night high tide   8.36   0.09     Night high tide   8.33   0.06	Tidal cycleMeanSDMinimumDay high tide8.340.068.34Day low tide8.160.078.06Night high tide8.240.158.11Night low tide8.010.087.91Day high tide8.520.058.45Day low tide8.860.218.68Night high tide8.420.118.33Night high tide8.160.118.33Day high tide8.340.018.33Day high tide8.360.098.25Night high tide8.360.068.24Night high tide8.330.068.24

Table 1. The mean, standard deviation (SD), minimum and maximum pH values recorded in mangrove, seagrass, and coral reef habitats (n=4).

mangrove, and coral reef habitats were higher during the day than at night, and were lower than that of adjacent open water in the mangrove habitats at night by 0.02 pH units (Fig. 4).

## Day-night variability in water temperature, dissolved oxygen and salinity

The mean temperature in mangrove habitats did not vary significantly between day-night cycles (F=2.82, p>0.05) or tides (F=0.96, p>0.05), with both the highest (35.79 °C) and the lowest (25.29 °C) values recorded during the daytime low spring tide (Table 2). Similarly, the mean salinity in mangrove habitats did not vary significantly between day and night (F=0.37, p<0.05) or between tides (F=169, p>0.05), with both

the highest (39.70%) and the lowest (17.10%) values recorded during low spring tide during the day. The mean dissolved oxygen value in the mangrove habitats, on the other hand, varied significantly between tides (F=14.58, p<0.05), but not between day and night (F=1.25, p>0.05), with the highest value (14.65 ml/L) recorded during high spring tide during the day, and lowest value (7.66 ml/L) recorded during low spring tide during the day (Table 2).

The mean temperature in seagrass ecosystems fluctuated significantly between tides (F=4.48, p<0.05) and between day and night (F=15.50, p<0.05). The highest value (35.08 °C) was recorded during daytime low spring tide, and the lowest (26.33 °C) during



Figure 4. Day-night variability in mean pH in the mangrove, coral reef and seagrass habitats. The dotted line shows the mean of pH of the adjacent open waters. Error bars indicate standard deviations. The letters above the bars indicate significant differences in pH levels between mangrove, seagrass, and coral reef habitats (based on one-way ANOVA tests) at  $p \le 0.05$ . N = 8.

Habitat	Variable	Tidal cycle	Mean	SD	Minimum	Maximum
Mangrove	Temperature	Day high tide	28.90	1.50	27.01	30.55
		Day low tide	32.65	4.95	25.29	35.79
		Night high tide	28.84	1.04	27.45	29.66
		Night low tide	27.90	0.61	27.33	28.76
	Salinity	Day high tide	37.75	0.50	37.00	38.00
		Day low tide	32.72	10.6	17.10	39.70
		Night high tide	37.75	0.50	37.00	38.00
		Night low tide	35.92	1.87	34.30	38.00
	Dissolved oxygen	Day high tide	14.23	0.56	13.56	14.65
		Day low tide	9.86	1.98	7.66	11.54
		Night high tide	14.19	0.48	13.65	14.61
		Night low tide	11.76	2.79	9.31	14.64
Seagrass	Temperature	Day high tide	29.11	0.62	28.65	30.02
		Day low tide	34.14	1.13	32.73	35.08
		Night high tide	28.45	0.74	27.64	29.38
		Night low tide	27.45	0.85	26.33	28.33
	Salinity	Day high tide	37.75	0.50	37.00	38.00
		Day low tide	38.57	1.29	37.37	40.00
		Night high tide	37.75	0.96	37.00	39.00
		Night low tide	37.00	1.15	36.00	38.00
	Dissolved oxygen	Day high tide	14.02	0.50	13.68	14.69
		Day low tide	15.29	0.79	14.49	15.99
		Night high tide	14.13	0.59	13.54	14.72
		Night low tide	11.45	0.58	10.91	12.02
Coral reef	Temperature	Day high tide	29.12	0.62	28.65	30.02
		Day low tide	28.62	1.19	27.47	29.69
		Night high tide	28.43	0.62	27.72	29.11
		Night low tide	28.73	0.49	28.16	29.36
	Salinity	Day high tide	37.75	0.50	37.00	38.00
		Day low tide	38.25	0.96	37.00	39.00
		Night high tide	37.75	0.50	37.00	38.00
		Night low tide	37.75	0.50	37.00	38.00
	Dissolved oxygen	Day high tide	14.11	0.59	13.50	14.72
		Day low tide	14.55	0.28	14.12	14.72
		Night high tide	14.06	0.56	13.58	14.59
		Night low tide	13.99	0.56	13.46	14.52

night-time low spring tide. Salinity within seagrass beds, on the other hand, did not vary significantly with tides or between day-night cycles (p>0.05). The highest salinity value (40.00‰) was, however, recorded during low spring tide during the day while the lowest value (36.00‰) was recorded during low spring tide at night. The mean dissolved oxygen in seagrass ecosystems varied significantly between day-night samplings (F=10.55, p<0.05), but not with tides (F=1.76, p>0.05), with the highest value (15.99 ml/L) recorded during daytime low spring tide and the lowest value (10.91 ml/L) reported during low spring tide at night (Table 2). The mean temperature, salinity and dissolved oxygen in the coral reef habitats did not vary significantly between tides and day-night cycles (p>0.05). The highest temperature (30.02 °C) was recorded during daytime high spring tide and the lowest (27.47 °C) during daytime low spring tide. The highest salinity (39.00‰) was recorded during low spring tide in the daytime, while the lowest value (37.00‰) stayed constant independent of time of day or tide status. The highest dissolved oxygen value (14.72 ml/L) was recorded during high and low spring tides during the day, and lowest value (13.46 ml/L) recorded during low spring tide at night (Table 2).



Figure 5. Relationship between pH and temperature, salinity and dissolved oxygen in A) mangrove, B) seagrass and C) coral reef habitats.

## Correlation between pH and other environmental variables

pH in mangrove habitats associated only modestly and positively with dissolved oxygen (r=0.59), whereas pH in seagrass habitats significantly and positively linked with variations in temperature (r=0.80), dissolved oxygen (r=0.84), and salinity (r=0.72). pH in the coral reef habitats was found to be weakly and negatively related to salinity (r=-0.08) but moderately and positively related to temperature (r=0.44) and dissolved oxygen (r=0.41).

#### Discussion

This study found that the tidal cycle and time of day (day or night) controls pH levels in mangrove, seagrass, and coral reef habitats of Tanzania and the WIO. As a result, mangrove, seagrass, and coral reef habitats experience large pH fluctuations, indicating that resident marine species are subject to wide pH ranges, which should be considered in future experimental studies evaluating the effects of OA on marine species. Water with the highest pH from seagrass habitats is transported to nearby mangroves during incoming daytime high tides as well as to nearby coral reefs during outgoing daytime low tides, raising their pH levels and helping to mitigate OA on these habitats. These results will guide management strategies to safeguard healthy seagrass meadows that maintain high primary productivity and act as refugia against OA.

Seagrass habitats had the greatest mean pH levels, which, when compared to nearby mangrove and coral reef habitats, show that seagrass productivity (the balance between photosynthesis and respiration) affects the pH of its surrounding waters (Hendriks *et al.*, 2014; Pacella *et al.*, 2018). The observed differences

in pH levels and dissolved oxygen (DO) between day and night also suggested that the effect of seagrasses was related to their productivity (Pacella et al., 2018). Daytime photosynthesis and nightime community respiration have different effects on pH levels in coastal habitats (Semesi et al., 2009b). Seagrasses remove carbon from the water column during photosynthesis (Borum et al., 2007; Brodersen et al., 2018; Larkum et al., 2007), lowering the partial pressure of  $CO_9$  and thus the amount of dissolved inorganic carbon in the water column. As a result, the pH of the water column rises (Brodersen et al., 2018; Olsen et al., 2018). During the nighttime, however, seagrass photosynthesis is inactive, and community respiration is high, resulting in an increased partial pressure of  $\mathrm{CO}_2$  and, thus, dissolved inorganic carbon in the water column (Brodersen et al., 2018; Olsen et al., 2018; Pedersen et al., 2016). As a result, the pH of the water column decreases (Hofmann et al., 2011). These could explain why the highest and lowest pH values in seagrass habitats were observed during low spring tides in the day and night, respectively, resulting in the observed highest pH range. In light of these findings, it is important to take into account the day-night pH variations in coastal habitats when designing new experimental studies aimed at better understanding the effects of OA on resident marine species. Despite the fact that this study focused on pH, future studies should include assessments of total alkalinity, partial pressure of CO<sub>9</sub>, and dissolved inorganic carbon as indicators of OA to better understand the changing seawater carbonate chemistry in the WIO.

Lowest pH levels in mangrove habitats compared to seagrass and coral reef habitats have been linked to river inflow and underground discharge (Pauline et al., 2011). Because Chwaka and Mnazi Bays are non-estuarine, the lowest pH levels observed during low spring tides were primarily caused by groundwater discharge. During incoming daytime high tides, water with the highest pH from nearby seagrass habitats is transported to mangrove habitats, helping to raise the pH of water in these habitats. Similarly, during outgoing day low tides, seagrass habitats raise the pH of water coming from mangrove habitats, preventing the water with the lower pH from reaching coral reefs. Low pH water inhibits coral calcification processes and, in extreme conditions, may cause reef dissolution (Kroeker et al., 2013). The ability of seagrass habitats to mitigate the effects of OA on nearby mangrove and coral reef habitats is dependent on their health and has been shown to decline with disturbances (Carstensen and Duarte, 2019).

Climate change-related stressors such as freshwater flooding, anoxia, and ocean warming are threatening seagrass survival (García et al., 2013; George, 2019; Rasmusson et al., 2020). Positive correlations between pH and salinity, dissolved oxygen, and temperature were found in this study, and these relationships are discussed separately. A positive correlation between pH and O<sub>9</sub> shows the influence of primary productivity and community respiration on pH. Healthy seagrass habitats have been shown to support high primary productivity, producing water with high pH and O<sub>9</sub> levels that will be transported to adjacent coastal habitats (Hendriks et al., 2014; Semesi et al., 2009a; Semesi et al., 2009b; Unsworth et al., 2012). On the other hand, degraded habitats with low primary productivity, have been shown to compromise the ability of seagrass habitats to mitigate OA (Van Dam et al., 2021). Eutrophication-induced hypoxia has become a major threat to seagrass survival because it reduces plant primary productivity, reducing the ability of seagrass habitats to mitigate the effects of OA in coastal areas (Che et al., 2022). Increased water temperatures have been linked to increased primary productivity of tropical seagrasses, and, as a result, rising pH in their water column during the day (George et al., 2018; George et al., 2020). On the other hand, temperatures over optimal ranges of tropical seagrasses can impair primary productivity, and, consequently, lower the pH of the water column (Carstensen and Duarte, 2019). Increased flood occurrences in coastal areas are predicted to lower pH in mangrove, nearby seagrass, and coral reef habitats, increasing the effects of OA on these ecosystems (Orr, 2011). Therefore, these findings suggest that minimizing disturbances in coastal habitats will improve the capacity of seagrass habitats to absorb CO<sub>9</sub> from the water column and, in turn, increase their capacity to elevate the pH of surrounding mangrove and coral reef habitats.

Similar studies are generally lacking in the WIO region. However, a study by Camp *et al.* (2016) in three locations in the Atlantic, Indian, and Pacific Oceans found similar trends, with seagrass habitats consistently having a higher mean pH ( $8.15 \pm 0.01$ ) than the nearby outer-reef habitats ( $8.12 \pm 0.03$ ), and mangrove habitats having a lower mean pH ( $8.04 \pm 0.01$ ). Camp *et al.* (2016) reported day-night pH variations that were similar to the current findings, with high pH during the day time associated with CO<sub>2</sub> uptake during photosynthesis and low pH at night associated with CO<sub>2</sub> release during respiration in the absence of photosynthesis. This study concentrated on non-estuarine bays, therefore it is suggested that future research should concentrate on estuarine coastal habitats in order to obtain a complete picture of pH dynamics in WIO coastal habitats.

### Conclusions

The tidal cycle and time of day control pH levels in mangrove, seagrass, and coral reef habitats of the WIO, resulting in large pH fluctuations in these coastal habitats. As a result, resident marine species in mangrove, seagrass, and coral reef habitats face wide pH ranges, which should be considered in future manipulative studies evaluating the effects of OA on marine species from coastal habitats. Water with the highest pH from seagrass habitats is transported to nearby mangroves during incoming daytime high tides and to nearby coral reefs during outgoing daytime low tides, raising their pH levels and helping to mitigate OA on these habitats. To better understand the changing seawater carbonate chemistry in costal habitats of the WIO, future studies should include assessments of total alkalinity, pCO<sub>3</sub>, and dissolved inorganic carbon as indicators of OA not covered in this study.

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### References

- Borum J, Sand-Jensen K, Binzer T, Pedersen O, Greve TM (2007) Oxygen movement in seagrasses. In: Seagrasses: biology, ecology and conservation. Springer, Dordrecht. pp 255-270
- Brodersen KE, Kühl M, Nielsen DA, Pedersen O, Larkum AW (2018) Rhizome, root/sediment interactions, aerenchyma and internal pressure changes in seagrasses. In: Seagrasses of Australia. Springer, Cham. pp 393-418
- Camp EF, Suggett DJ, Gendron G, Jompa J, Manfrino C, Smith DJ (2016) Mangrove and seagrass beds provide different biogeochemical services for corals threatened by climate change. Frontiers in Marine Science 3: 52
- Carstensen J, Duarte CM (2019) Drivers of pH variability in coastal ecosystems. Environmental Science & Technology 53 (8): 4020-4029

- Cederltif U, Rydberg L, Mgendi M, Mwaipopo O (1995) Tidal exchange in tropical lagoon: Chwaka Bay, Zanzibar. Ambio 24: 7-8
- Che X, Zhang T, Li H, Zhang L, Liu, J (2022) Effect of hypoxia on photosystem II of tropical s seagrass *Enhalus acoroides* in the dark. Photochemistry and Photobiology 98 (2): 421-428
- Doney SC, Fabry VJ, Feely, RA, Kleypas JA (2009) Ocean acidification: the other CO<sub>2</sub> problem. Annual Review of Marine Science 1: 169-192
- Feely RA, Doney SC, Cooley SR (2009) Ocean acidification: Present conditions and future changes in a high-CO<sub>2</sub> world. Oceanography 22 (4): 36-47
- Francis J, Mahongo SB (2012) Analysis of rainfall variations and trends in coastal Tanzania. Western Indian Ocean Journal of Marine Science 11 (2): 121-133
- García R, Holmer M, Duarte CM, Marbà N (2013) Global warming enhances sulphide stress in a key seagrass species (NW Mediterranean). Global Change Biology 19 (12): 3629-3639
- Gattuso JP, Magnan A, Billé R, Cheung WW, Howes EL, Joos F, Turley C (2015) Contrasting futures for ocean and society from different anthropogenic  $CO_2$  emissions scenarios. Science 349 (6243): aac4722
- George R, Gullström M, Mangora MM, Mtolera MS, Björk M (2018) High midday temperature stress has stronger effects on biomass than on photosynthesis: a mesocosm experiment on four tropical seagrass species. Ecology and Evolution 8 (9): 4508-4517
- George R (2019) Seagrasses in warming oceans: physiological and biogeochemical responses. Doctoral dissertation. Stockholm University Press, Stockholm. 98 pp
- George R, Gullström M, Mtolera MS, Lyimo TJ, Björk M (2020) Methane emission and sulfide levels increase in tropical seagrass sediments during temperature stress: A mesocosm experiment. Ecology and Evolution 10 (4): 1917-1928
- Hendriks IE, Olsen YS, Ramajo L, Basso L, Steckbauer A, Moore TS, Duarte CM (2014) Photosynthetic activity buffers ocean acidification in seagrass meadows. Biogeosciences 11 (2): 333-346
- Hofmann GE, Smith JE, Johnson KS, Send U, Levin LA, Micheli F, Martz TR (2011) High-frequency dynamics of ocean pH: a multi-ecosystem comparison. PloS One 6 (12): e28983
- James RK, van Katwijk MM, van Tussenbroek BI, van Der Heide T, Dijkstra HA, van Westen RM, Bouma TJ (2020) Water motion and vegetation control the pH dynamics in seagrass-dominated bays. Limnology and Oceanography 65 (2): 349-362

- Kroeker KJ, Kordas RL, Crim R, Hendriks IE, Ramajo L, Singh GS, Gattuso JP (2013) Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. Global Change Biology 19 (6): 1884-1896
- Larkum AW, Drew EA, Ralph PJ (2007) Photosynthesis and metabolism in seagrasses at the cellular level. In: Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht. pp 323-345
- Mahongo SB (2014) Annual to inter-decadal variability of surface air temperature along the coast of Tanzania. Western Indian Ocean Journal of Marine Science 13 (2): 109-124
- McClanahan TR (1988) Seasonality in East Africa's coastal waters. Marine Ecology Progress Series 44: 191-199
- Olsen YS, Fraser MW, Martin BC, Pomeroy A, Lowe R, Pedersen O, Kendrick GA (2018) *In situ* oxygen dynamics in rhizomes of the seagrass *Posidonia sinuosa*: impact of light, water column oxygen, current speed and wave velocity. Marine Ecology Progress Series 590: 67-77
- Orr JC (2011) Recent and future changes in ocean carbonate chemistry. Ocean Acidification 1: 41-66
- Pacella SR, Brown CA, Waldbusser GG, Labiosa RG, Hales B (2018) Seagrass habitat metabolism increases short-term extremes and long-term offset of CO<sub>2</sub> under future ocean acidification. Proceedings of the National Academy of Sciences 115 (15): 3870-3875
- Pauline CY, Matson PG, Martz TR, Hofmann GE (2011) The ocean acidification seascape and its relationship to the performance of calcifying marine invertebrates: Laboratory experiments on the development of urchin larvae framed by environmentally-relevant pCO<sub>2</sub>/pH. Journal of Experimental Marine Biology and Ecology 400 (1-2): 288-295

- Pedersen O, Colmer TD, Borum J, Zavala-Perez A, Kendrick GA (2016) Heat stress of two tropical seagrass species during low tides–impact on underwater net photosynthesis, dark respiration and diel in situ internal aeration. New Phytologist 210 (4): 1207-1218
- Proum S, Santos JH, Lim LH, Marshall DJ (2018) Tidal and seasonal variation in carbonate chemistry, pH and salinity for a mineral-acidified tropical estuarine system. Regional Studies in Marine Science 17: 17-27
- Rasmusson LM, Buapet P, George R, Gullström M, Gunnarsson PC, Björk M (2020) Effects of temperature and hypoxia on respiration, photorespiration, and photosynthesis of seagrass leaves from contrasting temperature regimes. ICES Journal of Marine Science 77 (6): 2056-2065
- Semesi IS, Beer S, Björk M (2009a) Seagrass photosynthesis controls rates of calcification and photosynthesis of calcareous macroalgae in a tropical seagrass meadow. Marine Ecology Progress Series 382: 41-47
- Semesi IS, Kangwe J, Björk M (2009b). Alterations in seawater pH and CO<sub>2</sub> affect calcification and photosynthesis in the tropical coralline alga, *Hydrolithon* sp.(Rhodophyta). Estuarine, Coastal and Shelf Science 84 (3): 337-341
- Shaghude YW, Mahongo SB, Muzuka A, Nyandwi N (2012) Physical and geological processes in Chwaka Bay. People, nature and research: Past, present and future of Chwaka Bay, Zanzibar, Tanzania. pp 41-55
- Unsworth RK, Collier CJ, Henderson GM, McKenzie LJ (2012) Tropical seagrass meadows modify seawater carbon chemistry: implications for coral reefs impacted by ocean acidification. Environmental Research Letters 7 (2): 024026
- Van Dam B, Lopes C, Zeller MA, Ribas-Ribas M, Wang H, Thomas H (2021) Corrigendum: Overstated potential for seagrass meadows to mitigate coastal ocean acidification. Frontiers in Marine Science: 1959