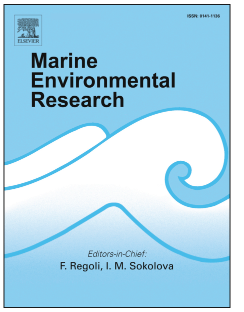
Article:

Knebel, Oliver, Carvajal, Carlos, Kench, Paul et al. (1 more author) (2023) Spatial pH variability of coral reef flats of Kiritimati Island, Kiribati. Marine Environmental Research. 105861. ISSN 0141-1136

https://doi.org/10.1016/j.marenvres.2022.105861

Journal Pre-proof



Spatial pH variability of coral reef flats of Kiritimati Island, Kiribati

Oliver Knebel, Carlos Carvajal, Paul Kench, Roland Gehrels

PII: S0141-1136(22)00306-3

DOI: https://doi.org/10.1016/j.marenvres.2022.105861

Reference: MERE 105861

To appear in: *Marine Environmental Research*

Received Date: 26 September 2022

Revised Date: 19 December 2022

Accepted Date: 25 December 2022

Spatial pH variability of coral reef flats of Kiritimati Island, Kiribati

Oliver Knebel[a,*,1], Carlos Carvajal[a], Paul Kench[b], Roland Gehrels[c]

[a] School of Environment, University of Auckland, New Zealand

[b]Department of Geography, National University of Singapore, Singapore

[c]Department of Environment and Geography, University of York

*Corresponding author: Oliver Knebel (Okne620@auklanduni.ac.nz)

[1]present address: Goethe-University, Department of Geoscience, Frankfurt am Main, Germany

Abstract

Ocean acidification poses a threat to carbonate-dominated marine systems, such as tropical coral reefs, as it impacts the ability of organisms to calcify. For assessing the susceptibility of coral reef flats to open ocean acidification it is crucial to better understand the dynamics between the carbonate chemistry of open ocean waters flowing onto coral reef flats and the ecological and hydrodynamic processes that locally modify seawater conditions.

In this study, variations in seawater pH and temperature were measured along cross-reef flat transects in high resolution (~0.3 m) and complemented by surveys of the benthic community composition and reef flat bathymetry.

Results that represent a snapshot in time suggest that reef flat hydrodynamic processes determine spatial pH modifications, with little influence of variations in benthic community composition. As mean reef flat pH largely equals ocean conditions, ocean acidification has had and will have an unhampered impact on narrow fringing reef flats.

Keywords: Acidification, Benthos, Coastal waters, Community composition, pH, Coral reef, reef flat, Kiritimati

1 Introduction

Anthropogenic inputs of nutrients, sediments, and pollutants to the oceans, combined with increased ocean uptake of CO_2 due to climate change, are altering the seawater carbonate chemistry of tropical coral reefs (Fabricius, 2005), as well as increasing open ocean acidification (Doney et al., 2020). Although different in causative mechanism, both processes result in a reduction of reef seawater pH and the calcium carbonate saturation state (Ω) that impacts the physiology of many calcifying reef organisms (Kroeker et al., 2013), as well as the overall state of reef ecosystems (Nagelkerken et al., 2016; Sunday et al., 2017). Most importantly, the ability of reef organisms to calcify is altered under reduced pH conditions (Albright et al., 2016, 2018). Additionally, coral mass bleaching events that result from global warming-induced thermal stress are causing a decline in coral reef calcification rates (Hughes et al., 2017). Notably, however, below the thermal stress threshold, increasing seawater temperatures enhance coral calcification (Cole et al., 2018). As a result, ocean acidification in combination with increasing seawater temperatures may shift reef carbonate budgets towards a negative state (Cornwall et al., 2021; Davis et al., 2021; Wolfe & Roff, 2021).

The seawater flowing on a coral reef originates from the adjacent ocean and therefore may inherit some of its initial properties. However, the seawater carbonate chemistry of coral reefs is further modified by a number of physical and biological processes and thus varies across spatial and temporal scales (Kayanne et al., 1995; Smith, 1973). The most important processes are the balance between Net Ecosystem Productivity (NEP) and Net Ecosystem Calcification (NEC; Gattuso et al., 1993). NEP is determined by the photosynthesis of autotrophic organisms that consume CO_2 and respiration by heterotrophic organisms that release CO_2, while NEC is determined by the dissolution of carbonates that absorbs CO_2 and the precipitation of carbonates that releases CO_2 (Suzuki et al., 1995). On a diurnal scale, reef water pH is elevated during the day, as photosynthesis is the predominant process during sunlight hours, but reduced during the night when calcification and respiration prevail (Kwiatkowski et al., 2016; Ohde & van Woesik, 1999).

Reported amplitudes of diurnal pH cycles of coral reefs range between 0.78 pH units and less than 0.05 pH units (Rivest et al., 2017). The benthic ecosystem composition of a reef influences the balance between NEP and NEC with macroalgae-dominated reefs being characterized by larger diurnal pH cycles than coral-dominated reefs (Anthony et al., 2013; Page et al., 2016). Seasonal changes in coral reef pH are usually multiple-folds smaller than the diurnal variability (Kayanne et al., 2005) and are driven to approximately equal amounts by changes in the temperature dependency of the carbonate dissociation constants and seasonal changes in the NEP/NEC balance (Albright et al., 2013; Gray et al., 2012). Other processes, such as coastal upwelling and river or groundwater discharge may also affect seasonal pH variations of a reef (Dong et al., 2017). Inter-annual variations in NEP/NEC of coral reef flats that again affect the seawater carbonate chemistry have been reported to occur in response to changes in benthic cover, especially after bleaching events (Davis et al., 2019; McMahon et al., 2019).

Spatial variations in reef pH have been linked to the geomorphic structure of the reef surface (Cyronak et al., 2019; Page et al., 2019). The concentration of the products of NEP and NEC varies depending on the volume of water at a given location and thus pH follows variations in water depth which are bathymetrically controlled. Furthermore, the local hydrodynamic conditions influence spatial variations in pH, as they determine the residence time of reefal waters (Falter et al., 2013; Platz et al., 2022; Zhang et al., 2012). For instance, fewer products of NEP and NEC can accumulate at a given location on the reef, if flushing (i.e., exchange between reef and open ocean water) is enhanced and consequently the residence time of reef water is reduced. For intertidal environments, such as coral reef flats, tidal fluctuations in sea level also play a major role in determining local seawater residence time that can even result in ponding, i.e., the temporary isolation of a body of water from the ocean (Albright et al., 2016, 2018; Wolfe et al., 2020). In addition, differences in the benthic community composition that drive local differences in the ratio between NEP and NEC have been reported to change pH conditions for downstream reef environments (Anthony et al., 2011; Kleypas et al., 2011). NEP and NEC have also been shown to vary spatially within a reef flat and may result in local variations of carbonate system parameters (Davis et al., 2019). Temperatures of reefal waters are controlled by solar heating and surrounding air temperatures and thus cycle diurnally with amplitudes ranging between more than 10 °C to less than 2 °C (Rivest et al., 2017). Spatial variations in temperature on reefs are primarily determined by the residence time that may vary across a reef depending on water depth and local hydrodynamics (Cyronak et al., 2019; Page et al., 2019).

Knowledge of the natural dynamics in coral reef pH and temperature is crucial for better understanding the impacts of anthropogenic processes on the seawater carbonate system and the biota of coral reefs. On reef flats, the variability in seawater pH and temperature is elevated compared to other reef environments and the open ocean, due to the low water levels (Cyronak et al., 2019; Knebel et al., 2021; Page et al., 2019). It is unclear if organisms dwelling on reef flats are less susceptible to anthropogenic reductions in pH and increasing thermal stress as natural exposure to variable pH and temperature conditions may have resulted in an enhanced resilience to these stressors (Clark et al., 2022; Rivest et al., 2017; Shaw et al., 2012). Intertidal habitats, such as coral reef flats, that locally differ from open ocean conditions, may also represent spatial refugia from ocean acidification and global warming (Wolfe et al., 2020). Furthermore, it has been suggested that shifts in reef flat benthic community structure may also change the mean pH conditions of downstream reef environments against the anthropogenically induced declining trend of pH in the open ocean (Andersson et al., 2014; Anthony et al., 2011; Kleypas et al., 2011). However, reef flat environments can also be affected by human interventions due to their accessibility and proximity to the shore (Ford et al., 2013).

This study examines the spatial variabilities in seawater pH on reef flats of the fringing reefs of Kiritimati Island, Kiribati, in the Central Pacific, as observed in May and June 2018. Seawater pH, temperature, salinity, bathymetry and benthos composition were quantified along transects on two reef flats that differ in their local oceanographic settings, and their proximity to human settlements. Furthermore, drivers and interrelations between the parameters measured are analysed, ultimately aiming to assess the susceptibility of coral reef flats to open ocean processes such as ocean acidification.

2 Materials and Methods

2.1 Study area

Kiritimati Island is a coral atoll in the equatorial central Pacific (01°52′N 157°24′W, Figure 1 A), where oceanographic conditions are characterized by upwelling of carbon-rich deep waters and thus relatively low surface water pH (~ 8.01±0.01, standard error; Lauvset et al., 2016) and relatively high nutrient concentrations (DeMartini et al., 2008). The local oceanography around Kiritimati Island is mainly controlled by easterly trade winds and the associated westward flowing South Equatorial Current (Walsh, 2011). Kiritimati Island is located directly to the west of the NINO3 region, which is an area where SST anomalies during El Niño events are highest within the equatorial central Pacific (Evans et al., 1999). During an El Niño event trade winds weaken, and thus equatorial upwelling is significantly reduced. Average annual SSTs vary between 24°C during La Niña and 30°C during El Niño conditions (Woodroffe et al., 2003), and average annual rainfall rates are low (~900 mm/year) but increase during El Niño events to up to 3000 mm/year (Morrison & Woodroffe, 2009). The average tidal range at Kiritimati is 1.5 m and El Niño events can cause a positive sea-level anomaly of up to 0.4 m for several months at a time compared to La Niña conditions (Woodroffe et al., 2012).

This study examines the environmental conditions on narrow reef flats (100-500 m in width) on either side of Kiritimati Island (Figure 1; Allen Coral Atlas, 2022). The Cecile Peninsula (CP) reef flat is located in the south of the island, a considerable distance from the main population centres, and located within an embayment in the broader southern atoll rim structure (Carilli & Walsh, 2012). Furthermore, CP reef flat has a quasi-lagoonal body of water impounded by a sand and gravel barrier behind the reef flat (Figure 1 C). The Northeast Point (NP) reef flat is located 25 km away on the northeastern shore of the atoll, along a sector that is more exposed to the open ocean, as well as the prevailing wind and wave regime and is closer to the main human settlements.

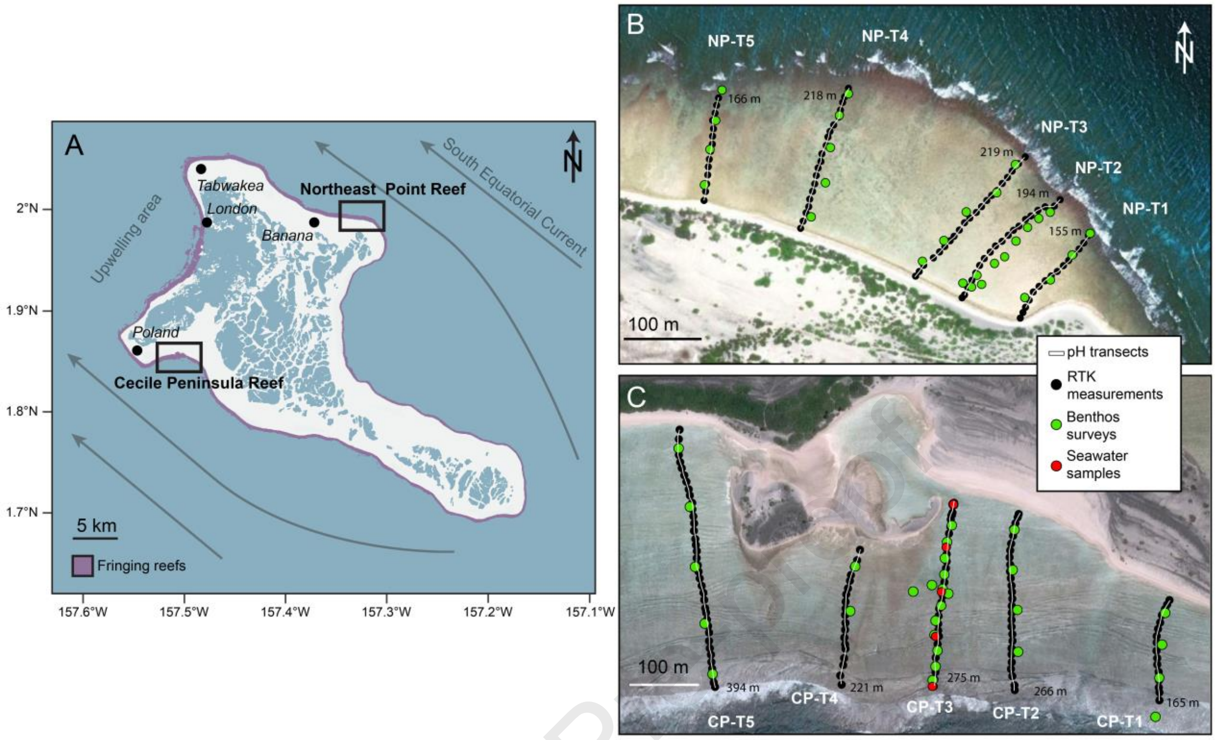


Figure 1 (A) Location map of Kiritimati Island, Kiribati, in the Central Pacific with study locations and major settlements (London: ~1900 inhabitants; Tabwakea: ~3500 inhabitants; Banana: ~1200 inhabitants; Poland: ~400 inhabitants). Also shown are the locations of fringing reefs around the island, major current directions, and the major upwelling area. (B) Satellite imagery of Northeast Point Reef and (C) Cecile Peninsula Reef with pH transects and locations of environmental measurements, as well as benthos surveys. Image credit: Allen Coral Atlas, Google Earth.

2.2 Elevation Profiles

To document the bathymetry of the reef flat surface surveys were undertaken, from the shoreline to the reef edge, along 10 transects using a Trimble real-time kinematic (RTK) global position system with measurements taken every 10 m (Figure 1 B and C). At each site survey measurements were tied to a local datum and surveys from both sites were reduced to a primary benchmark located 3.17 m above datum (WGS84), situated in the village of London on Kiritimati Island (Figure 1 A). Raw position data were corrected using Trimble RTX and the orthometric height was calculated relative to the WGS84 datum with the EGM-08 geoid model. Elevation data has an uncertainty of < 0.05 m (2σ). The 5 transects at CP Reef were 165 m to 394 m in length and spaced approximately 100 m to 200 m apart. At NP Reef, transects were 155 m to 219 m in length and spaced 50 m to 200 m from each other.

2.3 Seawater sampling

To quantify spatial variations in pH, temperature and salinity, measurements of these parameters were undertaken along each of the 10 shore perpendicular transects (Figure 1 B and C). On Kiritimati Island, seawater reef flat pH remains relatively stable at maximum values between 12:00 and 17:30, and similarly, remains relatively stable at minimum values between 00:00 and 07:00 (Knebel et al., 2021). Therefore, measurements were taken, when possible, within these intervals, in May and June 2018 at 11:15–12:44 (CP) and 13:09–14:13 (NP), as well as at 04:30–05:27 (CP) and 21:34–22:58 (NP). Measurements were obtained using a sensor package consisting of a SeaFET pH-sensor set to continuous mode, an RBR CTD logger and a GPS (Global Positioning System) tracker. The accuracy of the SeaFET pH-sensor is 0.05 pH units and the precision is < 0.001 pH units. Measurements were performed around low tide when spatial variations of parameters measured were expected to be strongest. A pH, temperature and salinity measurement was taken every 0.3 m which corresponds to 361 measurements per transect on average ranging between 205 measurements along transect CP-T1 (night) and 601 along transect CP-T3 (day). Seawater samples were collected along transect CP-T3 for quantification of the seawater carbonate system parameters (Dissolved Inorganic Carbon, DIC; alkalinity, ALK; Aragonite saturation state, $\Omega_{Aragonite}$). Collection of seawater samples and processing of SeaFET and RBR CTD logger data was performed as described in Knebel et al. (2021). Each set of transects was recorded within 1.5 hours, and each individual transect was recorded within a 15-minute time period. Thus, the differences in environmental conditions across and between transects at each site represent predominantly spatial variations, with temporal variations kept to a minimum.

2.4 Benthic Ecology

To evaluate the potential influence of the reef flat benthos ecology on seawater pH, the benthic community composition of CP and NP reef flat was documented. The composition of the benthos was determined following the Line Intercept Transect (LIT) method (Leujak & Ormond, 2007) in May and June 2018. At 40 m intervals along each transect, 10 m LITs were placed in an arbitrary orientation relative to the transect (Figure 1 B and C). Usually, 2 to 5 LITs were placed along transects, but along transects CP-T3 and NP-T2, the spatial resolution was increased to up to 15 LITs along transects. In total, 58 LITs were surveyed on both reef flats of which 57 were located on the reef flat perpendicular transects and therefore used for statistical analysis along transects. However, all 58 LITs were used for statistics related to the entire reef flats. On each 10 m LIT, the type of benthic cover was noted every 10 cm (100 observations), differentiated into 19 types of benthic cover (Table 1). Usually, the uppermost type of benthos visible to the surveyor was recorded. However, in some cases, when multiple cover types were observed synchronously, all were recorded (e.g., coralline red algae growing on a piece of rubble). All benthic cover types may contribute to reef NEP and NEC in different ways (Cyronak et al., 2013; Kleypas et al., 2011; Romanó de Orte et al., 2021). However, some benthos types were grouped, if observed only very occasionally and, if grouped benthos types represent similar habitats (Table 1). In particular, dead skeletons and shells of corals and molluscs were grouped, as well as all types of non-calcifying algae that were distinct from turf algae. Furthermore, "growing Halemida" which occurred only a few times was grouped with coralline red algae that were widespread on the reefs. Finally, all species and growth forms of "calcifying coral" were grouped. "Growing microatolls" were in most cases from the genus *Porites*. "Growing branching coral sp." and "Growing massive coral sp." represent respective coral growth forms of unknown genus.

Table 1 Groups of benthic cover types.

Hard substrate	**Dead corals/shells**	**Rubble**	**Silt/Sand**	**Turf algae**	**Other non-calcifying algae**	**Calcifying algae**	**Calcifying Corals**
Hard substrate	Dead branching coral	Rubble	Silt/Sand	Turf algae	Green algae on framework	Coralline red algae	Growing *Porites*
	Dead massive coral				Green algae on dead coral	Growing *Halemida*	Growing *Acropora*
	Dead microatoll				Macroalgae		Growing branching coral sp.
	Dead gastropod						Growing massive coral sp.
	Dead bivalve						Growing microatolls

2.5 Data Processing and statistical analysis

All calculations and processing of data were done using the program R (R Core Team, 2021). Calculation of seawater carbonate system parameters was achieved using the R-package "seacarb" (Gattuso et al., 2021) and the application of PERMANOVA-, ANOSIM-and Mantel-tests using the R-package "vegan" (Kenkel, 2006; Oksanen et al., 2020). Other statistical tests, such as PCA analysis, t-test, or regression analyses were performed using the respective built-in function in R. All pH measurements of this study are indicated in total scale and uncertainties of all parameters are indicated at 95 % confidence (2σ). The zonation of the reef flats in "shore", "reef flat" and "Crest" (Figure 2, Figure 3) was established based on the Allen Coral Atlas (2022).

For continuous variables, regression analyses were performed between all variables measured (Abundance of groups of benthic cover types, distance to reef flat edge, elevation, pH, and temperature). However, as pH and temperature measurements were performed during different days and times for CP and NP reefs, also temporal and not solely spatial factors may have influenced observed variations in these variables between reefs. Thus, statistical tests for pH and temperature between other variables were performed for each reef site separately. All tests were repeated excluding CP-T5 as this transect contains ponded seawater close to the shore that may obscure potential relationships in pH and temperature with other variables (see Figure 2 E, Figure 5 E). Similarly, all tests were also repeated excluding NP-T5 as this transect showed a declining trend in temperature with increasing distance to the reef flat edge that was different from all other transects (see Figure S4 i). Additionally, the Mantel test was used to infer correlations between benthic community composition and continuous variables. To detect correlations between benthic community composition and categorical variables (Reef site, transect, geomorphological zone) the ANOSIM and PERMANOVA tests were performed. For resemblance-based permutation tests, the gower distribution was used as distance metric for the benthic community composition and the Euclidean distance for the parameters tested. Furthermore, the spearman method was used to quantify the correlation between variables.

3 Results

3.1 Bathymetry

The NP reef flat varied in width between 155 m and 219 m and CP reef flat between 165 m and 394 m (Figure 1 B and C). The average length of all transects on NP reef flat was 190.4 m and on CP reef flat 264.2 m. Thus, the NP reef flat was on average narrower compared to the CP reef flat. Also, the NP reef flat was significantly lower in elevation (i.e. deeper) compared to CP reef flat ($t(176.65) = 7.79$, $p < 0.01$; Figure 2, Figure 3). Mean elevation along transects on the CP reef flat was 0.86 m above datum with a variability (σ) of 0.13 m, and the mean elevation along transects on NP reef flat was 0.73 m above datum and a variability (σ) of 0.15 m. The bathymetric structure between both reef flats revealed some differences. The inner CP reef flat was characterized by a moat parallel to the shore and an elevated central reef flat and reef flat edge (Figure 2). The central area of NP reef flat was more planar, and the reef flat crest was more elevated due to a more pronounced algal rim compared to CP reef flat (Figure 3).

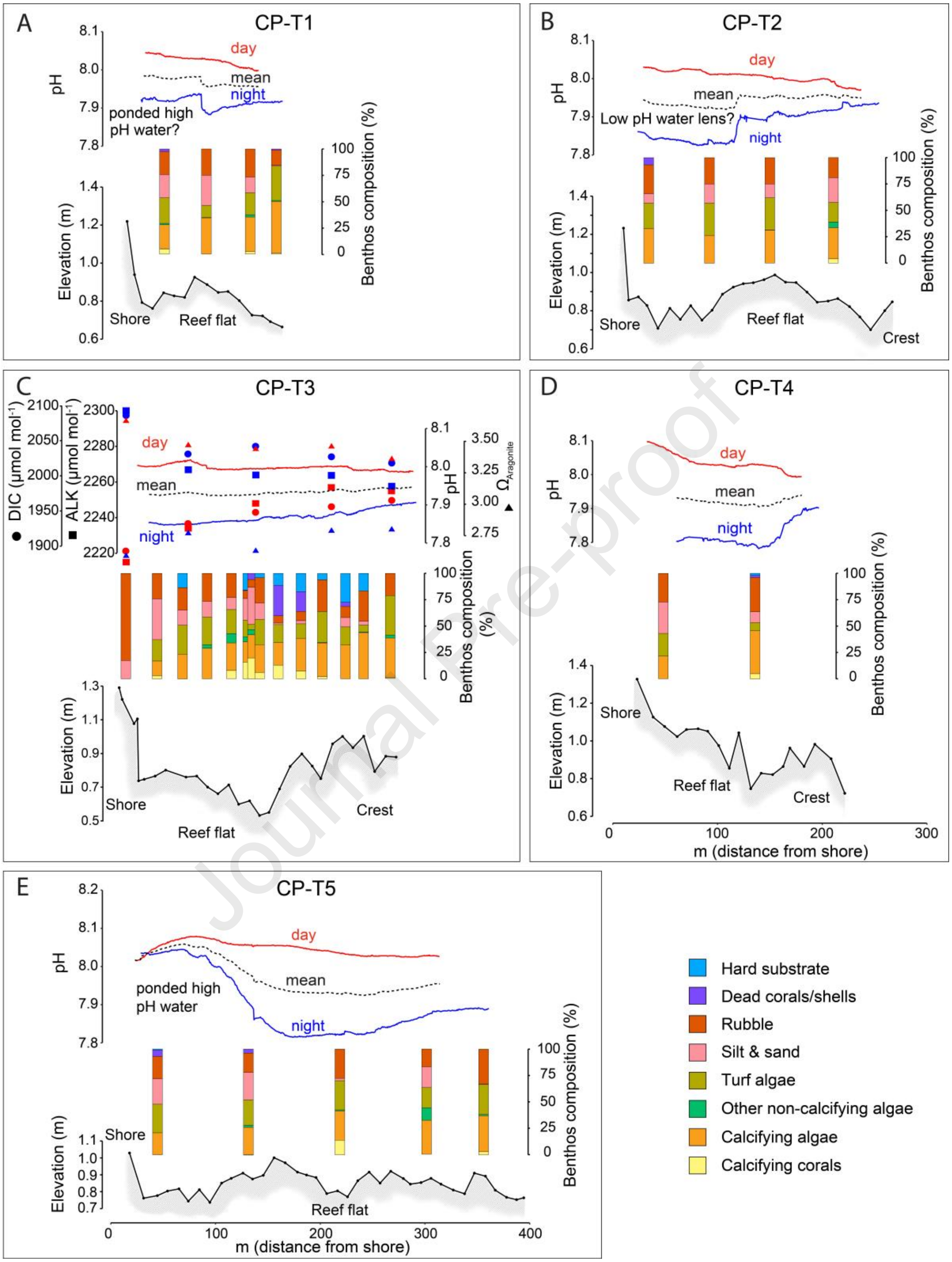


Figure 2 Results of measurements along transects on CP reef flat: Seawater pH during the day and night, as well as mean pH values; benthos composition; surface bathymetry from RTK measurements relative to WSG-84 datum. For transect CP-T3, seawater carbonate chemistry measurements are shown. The different geomorphological zones are also indicated. X-axis of E applies also for A and C, and x-axis of D also for B.

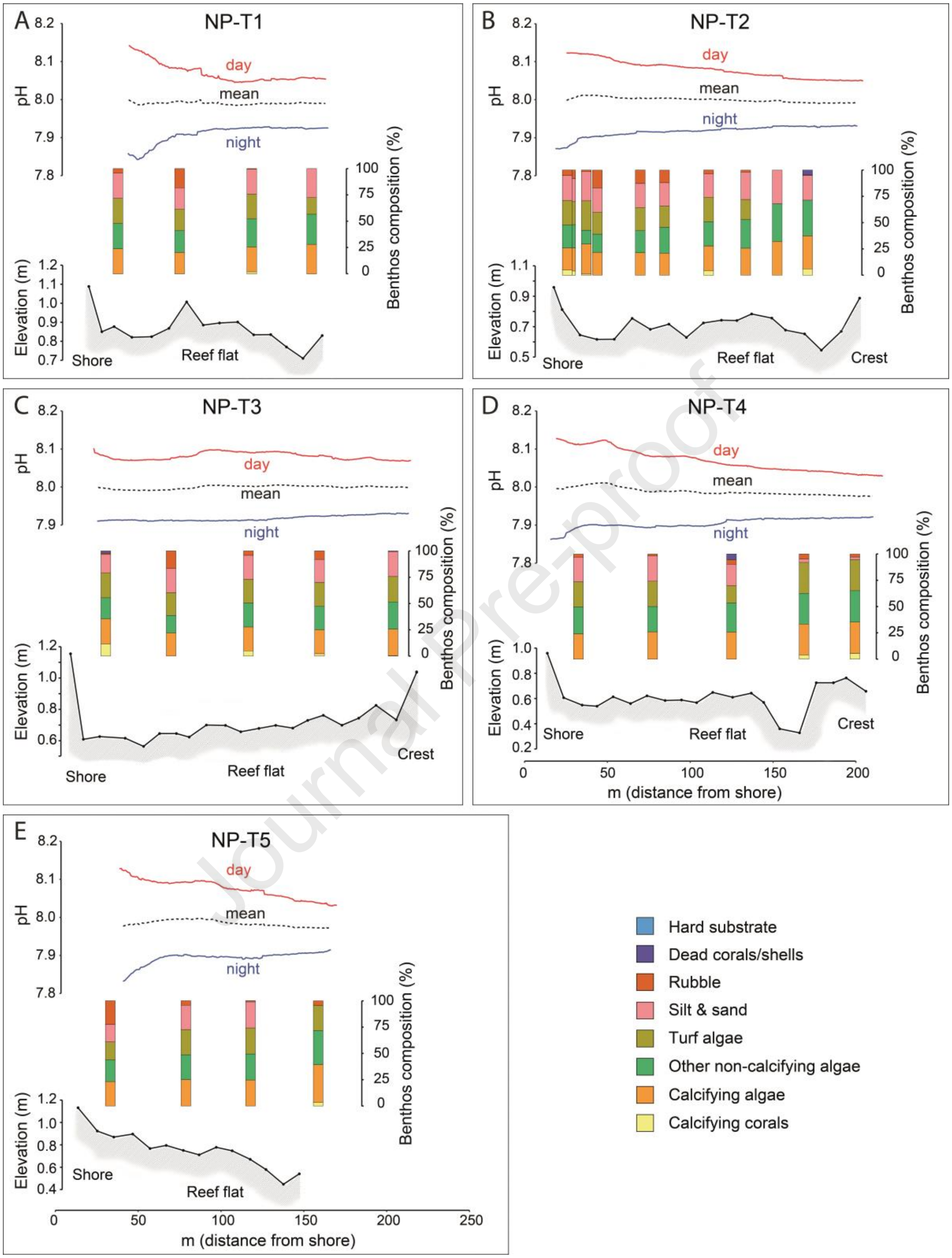


Figure 3 Results of measurements along transects on NP reef flat: Seawater pH during the day and night, as well as mean pH values; benthos composition; surface bathymetry from RTK measurements relative to WSG-84 datum. The different geomorphological zones are also indicated. X-axis of E applies also for A and C, and x-axis of D also for B.

3.2 Seawater pH, temperature, and salinity

Mean pH on CP reef flat was 7.95±0.08 pH units while the NP reef flat had a mean value of 7.99±0.03 pH units. Although both mean pH values are significantly different ($t(3124) = -43.17$, $p < 0.01$) it cannot be excluded that this difference is due to the fact that measurements were recorded not synchronously. Ocean pH of this region (8.01±0.01 pH units; Lauvset et al., 2016) is within the error of mean pH values for both reef flats. The mean diel pH range was 0.14±0.12 pH units on CP reef flat and 0.17±0.08 pH units on NP reef flat which is similar to diel pH ranges reported for other reefs in Northern Line Islands (Price et al., 2012). Measurements along transect CP-T3 in other carbonate system parameters revealed mean values in ALK of 2256.1±22.2 µmol mol^{-1}, in DIC of 1989.8±59.6 µmol mol^{-1}, and in $\Omega_{Aragonite}$ of 3.1±0.4. Mean seawater temperature at both locations was 28.4±2.0 °C on CP reef flat and 28.2±1.8 °C on NP reef flat which is significantly different ($t(6718.6) = 6.56$, $p < 0.01$). The mean diel temperature range on CP and NP reef flats were both 1.7±1.6 °C. Measurements of seawater pH and temperature showed significant correlations across transects measured during the day ($r^2 = 0.14$, $p < 0.01$) and night ($r^2 = 0.19$, $p < 0.01$), as well as between all measurements ($r^2 = 0.75$, $p < 0.01$; Figure 4 A, Table S1).

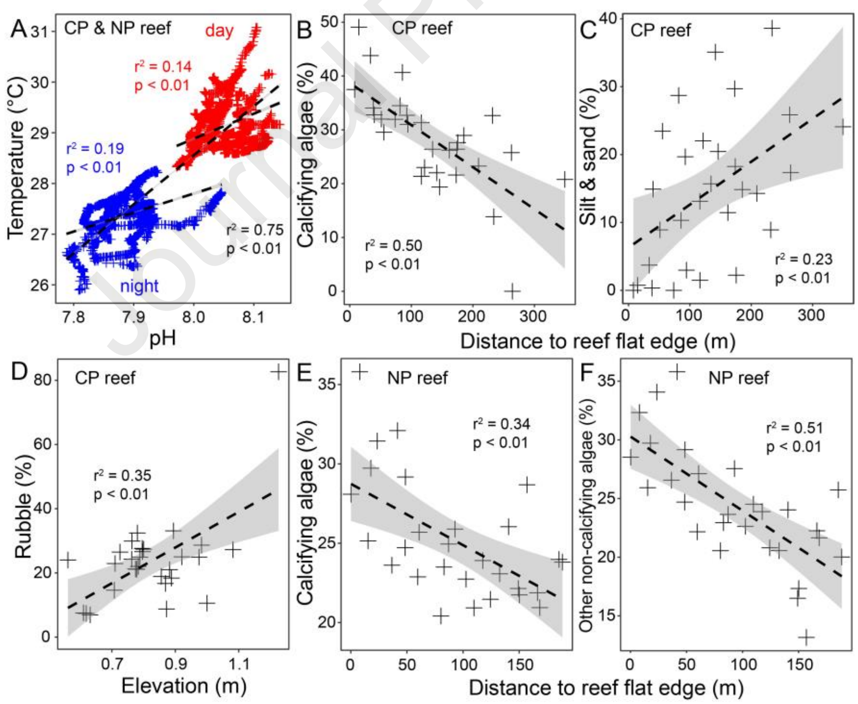


Figure 4 Linear regressions between (A) synchronous measurements in pH and temperature on both reefs. Linear regressions between distance to reef flat edge and the relative abundance of (B) calcifying algae and (C) silt & sand, as well as between elevation relative to datum and the relative abundance of (C) rubble on CP reef flat. Linear regressions between distance to reef flat edge and the relative abundance of (E) calcifying algae and (F) "other non-calcifying algae".

Along the majority of transects from both locations (NP and CP reef flats) the diel pH and temperature ranges increased from the outer reef flat towards the shoreline (Figure 2, Figure 3, Figure S3 and Figure S4). The diel pH range of all pH transects on CP reef flat excluding the very long transect CP-T5 revealed the highest level of correlation with distance from reef flat edge fitted to a linear function ($r^2 = 0.33$, $p < 0.01$; Figure 5 A–E, Table S2). Similarly, on NP reef flat, the diel pH range revealed the highest correlation with distance to reef flat edge ($r^2 = 0.45$, $p < 0.01$, Figure 5 F–J, Table S3). Also, the diel temperature ranges on CP ($r^2 = 0.46$, $p < 0.01$) and NP reef ($r^2 = 0.33$, $p < 0.01$) correlated strongest with the distance from the reef flat edge (Table S2, Table S3). The diel range in other carbonate system parameters (DIC, ALK and $\Omega_{Aragonite}$) also increased towards the shore (Figure 2C). In contrast, across-reef flat transects from both sites showed that diel pH and temperature ranges exhibit no strong correlation with elevation (Table S2, Table S3).

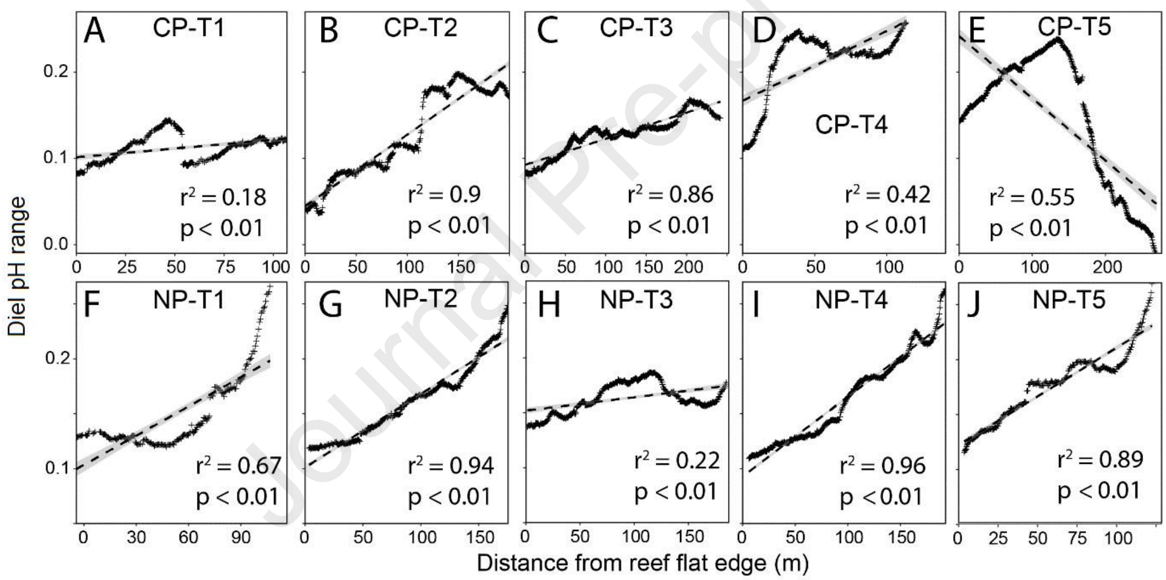


Figure 5 Linear regression between distance from reef flat edge and diel pH range for each transect.

Variations of pH were observed along all cross-reef transects (Figure 2 and Figure 3). On the CP reef flat, pH varied on average by 0.06±0.06 pH units during the day (range 8.10–7.99 pH units) and 0.12±0.12 pH units during the night (range 8.05–7.79 pH units). Similarly, at NP reef flat, pH varied on average by 0.08±0.06 pH units during the day (range 8.14–8.03 pH units) and 0.06±0.06 pH units during the night (range 7.93–7.83 pH units). Furthermore, on the CP reef flat, abrupt changes of pH along transects corresponding to changes in reef flat bathymetry and thus water depth were observed. For instance, nightly pH increased by 0.06 pH units across a space of 7 m along transect CP-T1 at the transition to lower reef surface elevation (Figure 2 A). In contrast, along the neighbouring transect (CP-T2) pH abruptly decreased by 0.08 pH units over 6 m when deeper waters were encountered (Figure 2 B). Along the very wide CP-T5 transect, night-time pH increased by 0.23 units reaching values similar to those observed during the day close to the shoreline (Figure 2 E).

Mean salinity on both reefs was 34.9±0.4 PSU. The diel range in salinity was low with 0.2±0.2 PSU on CP reef flat and 0.4±0.4 PSU on NP reef flat and did not show a consistent trend along transects (Figure S3 and S4). The variability (σ) in salinity along transects was also only small with 0.22 PSU during the day and 0.13 PSU during the night. Year-long monitoring showed that salinity variability on CP reef flat was more pronounced during rainfall events (Knebel et al., 2021). This highlights that the results of this study represent only a snapshot in time and temporal variations in the spatial patterns of pH, temperature, salinity, and benthos compositions were not quantified.

3.2 Benthos composition

The results of the benthos survey correspond to previous surveys of reef benthos cover on Kiritimati Island (Sandin et al., 2008). Example images of the benthos at both reef flats can be found in the supplementary (Figure S1 and Figure S2). The CP reef flat was characterized by a higher fraction of "rubble", but a lower fraction of green algae, especially "other non-calcifying algae", compared to NP reef flat (Figure 6 A). Furthermore, coral cover on CP reef flat was slightly higher compared to NP reef flat. The benthic community structure between both reef sites was significantly different as ANOSIM ($r = 0.52$, $p < 0.01$) and PERMAONVA ($r^2 = 0.36$, $p < 0.01$) tests revealed, but no significant difference was found between the transects of each reef flat (Table S4 and S5). The significant difference in elevation and the apparent difference in width between CP and NP reef flats may supersede any potential relationship between both parameters and the benthic community composition. Thus, to further explore the influence of these parameters on the benthos composition, both reef flats were studied separately. Results for both reefs combined can be found in Table S1. Significant correlations between distance to reef flat edge and the fraction of "calcifying algae" ($r^2 = 0.50$, $p < 0.01$; Figure 4 B) and "silt and sand" ($r^2 = 0.23$, $p < 0.01$; Figure 4 C) were found on CP reef flat (Table S2), and the fraction of "calcifying algae" ($r^2 = 0.34$, $p <0.01$, Figure 4 E) and "other non-calcifying algae" ($r^2 = 0.51$, $p < 0.01$; Figure 4 F) on NP reef flat (Table S3). These observations can be attributed to the typical zonation of reef flats with elevated abundances of calcifying algae, mainly coralline red algae, on the algal rim, and more silt and sand closer to the shore (Figure 2, Figure 3). This is further supported by the significant difference in benthic community composition between the geomorphological zones of CP reef flat ($r^2 = 0.15$, $p = 0.02$) and NP reef flat ($r^2 = 0.27$, $p < 0.01$) as deduced from PERMANOVA tests (Table S5) and visible in PCA diagrams (Figure 6 B and C). Reef flat elevation also significantly correlated with the fraction of calcifying algae on NP reef flat ($r^2 = 0.15$, $p = 0.05$; Table S3) and the fraction of rubble on CP reef flat ($r^2 = 0.35$, $p < 0.01$; Table S3), although this can be attributed to an outlier (Figure 4 C). This outlier represents overwash sediment that accumulated at the narrow outlet of the quasi-lagoonal body of water behind the reef flat (i.e., the most shoreward LIT along CP-T3, Figure 1B, Figure 2 C). The results of Mantle tests also showed that the benthos composition significantly varied with elevation on CP ($r = 0.31$, $p < 0.01$) and NP reef flats ($r = 0.22$, $p < 0.01$; Table S7 and S8).

For CP reef flat, results from Mantel tests revealed no relationship between benthos composition and the mean, diel range, day and night values in pH or temperature (Table S7). On NP reef flat, Mantel tests revealed significant correlations between mean ($r = 0.42$, $p < 0.01$) and day pH ($r = 0.29$, $p < 0.01$) with benthos composition (Table S8).

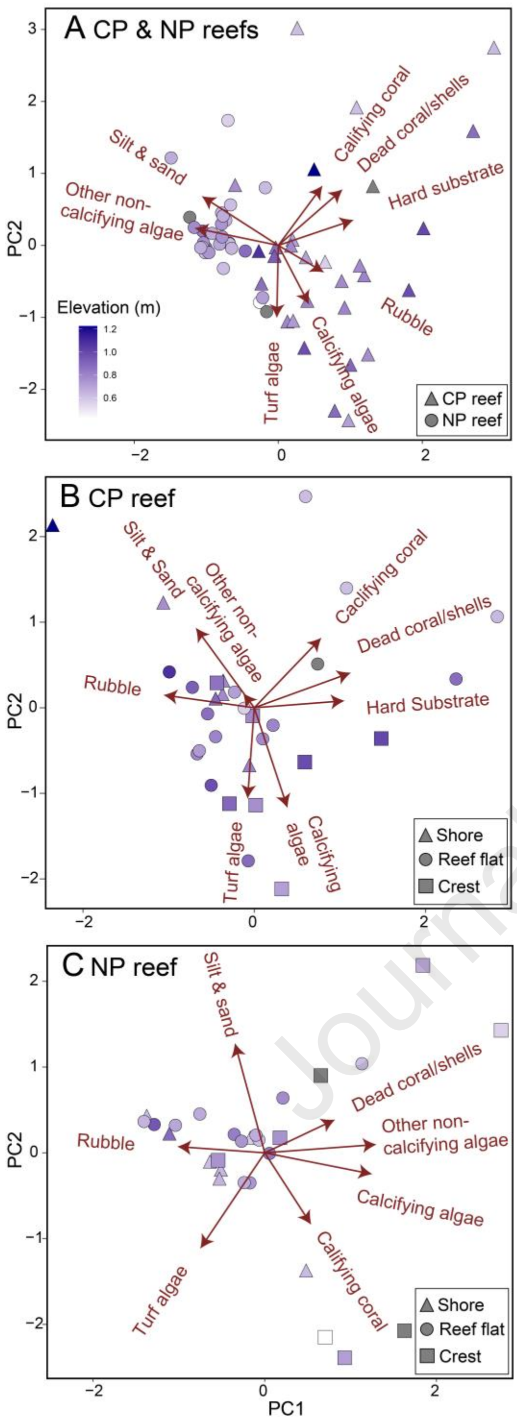


Figure 6 PCA diagrams of the benthic community structure recorded on (A) both reefs, (B) CP, and (C) NP reef flats. For all diagrams, colours indicate the elevation relative to datum for each LIT where the higher elevation corresponds to shallower water depth. For (A), symbols indicate reef sites, and for (B) and (C) colours indicate the geomorphological zones of the reef.

269

4 Discussion

4.1 Seawater pH and temperature variations

Along transects, seawater pH and temperature ranges revealed the strongest correlation with distance from the reef flat edge, when fitted to a linear function. It should be noted that these cross-reef flat observations are at very shallow water depths only (maximal ~ 1 m depth), which differ from similar transects spanning various reef habitats including deeper water (> 15 m depth; Cyronak et al., 2019). Cyronak et al. (2019) reported that diel pH and temperature ranges showed the highest level of correlation with water depth, best fitted to a power function. Furthermore, Guadayol et al. (2014) also found a linear relationship between the diel pH range with distance to reef flat edge, but an exponential relationship between the diel pH range and water depth for deeper waters. This difference reflects that in shallower and deeper waters different mechanisms prevail in determining the diel ranges in pH and temperature. The ratio between the products of NEP/NEC and water volume is much higher at shallower water levels than in deep water. This results in an elevated diel pH range in shallower water compared to deeper water (Page et al., 2019). Similarly, smaller volumes of water at shallower water levels heat up or cool down more rapidly than larger volumes of water at higher depths resulting in a negative correlation between diel temperature range and water depth. However, on shallow reef flats where variations in water depth are only small, diel pH and temperature ranges may be predominantly determined by the seawater residence time (Guadayol et al., 2014). Seawater exchange with the ocean declines across the reef flats towards the shore and consequently, seawater residence time increases with distance from the outer edge of the reef flat (McCabe et al., 2010). At locations with elevated seawater residence time, the products of NEP and NEC are integrated over a longer time period before dilution through exchange with open ocean water. Likely, this results in the observed positive correlation between diel pH and temperature ranges with distance to the reef flat edge. Other carbonate system parameters, including DIC, ALK and $\Omega_{Aragonite}$, also showed a pronounced diel variability closer to the shore (Figure 2 C). DIC is primarily influenced by diel changes in the balance between photosynthesis and respiration (i.e. NEP) with elevated photosynthetic rates reducing DIC during the day, while changes in ALK can be solely attributed to changes in the balance between calcification and dissolution (i.e. NEC) with enhanced calcification during the day reducing ALK (Cyronak et al., 2018). Furthermore, the elevated aqueous CO_2 concentration at night shifts the carbonate equilibrium, reducing the carbonate ion concentration of the seawater, and thus $\Omega_{Aragonite}$. The diel ranges in DIC, ALK and $\Omega_{Aragonite}$ increase when moving further shoreward across the reef flat (Figure 2 C). Again, these relationships can be best explained by increasing seawater residence times due to reduced horizontal mixing with distance to the reef flat edge.

No strong correlations between diel cycles in pH and temperature and benthos composition were found (Table S6 and S7). This contradicts a previous study from reefs in the proximity to Kiritimati Island in the Northern Line Islands that found that spatial variations in the diel pH range may be influenced by variations in the benthic community composition (Price et al., 2012). On the other hand, Hannan et al. (2020) also identified abiotic factors as the main drivers of variations in diel cycles between reefs.

Furthermore, especially along the shallower transects on the CP reef flat, abrupt changes in pH were observed. These changes are not a function of the distance from the reef flat edge and do not necessarily occur with similar magnitude (but in opposing directions), during day and night. These observed variations in pH did not appear to coincide with changes in the benthic community composition. Instead, changes in reef flat bathymetry best explain observed spatial variations of pH. However, the abrupt changes of pH along a transect cannot be explained by changes in bathymetry alone as an increase in water depth can result in an abrupt positive as well as a negative shift in pH, recorded during the same time of a day (compare Figure 2 A and B). Instead, we propose that the observed spatial pH variability likely reflects the local flow patterns of water on the reef flat with possible ponding in some locations. For instance, seawater with an elevated pH during the night between 0 and 100 m from shore along CP-T5 (see Figure 2 E, Figure 7) represents seawater that had not been exchanged with ocean water since the water level had dropped in the afternoon when pH values had been higher due to the stimulated reefal photosynthesis during the day. Furthermore, a lens of low pH water (by ~0.08 pH units) can be observed in the areas close to the shore of CP-T2, CP-T3 and CP-T4, as well as in the central area of CP-T5 (Figure 7). In CP-T2 this lens causes an abrupt drop of pH at 110 m from shore (see Figure 2 B). This low pH water lens may be explained by water draining out of the quasi-lagoonal body of water to the North of CP-T4 as the water level drops during the outgoing tide and then is directed westwards by the northwestward flowing South Equatorial Current. This interpretation aligns with previous studies that found that hydrodynamic forcing through mainly wave action and the tidal cycle, and to a lesser degree wind, has the strongest influence on spatial variations of the reefal seawater residence time and parameters of the seawater carbonate system (Hannan et al., 2020; Zhang et al., 2012). However, the exact hydrological regime of CP reef flat remains speculative as flow directions or seawater residence times were not recorded.

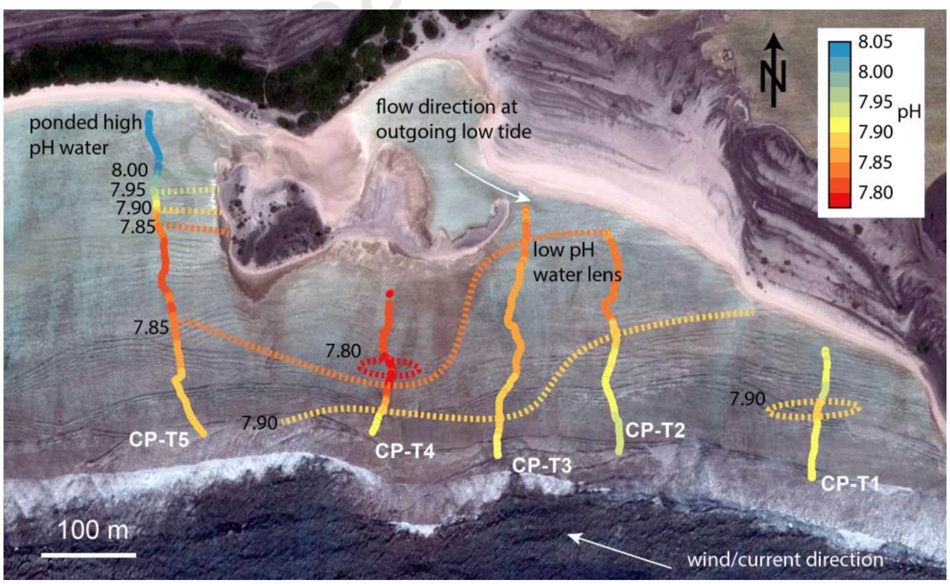


Figure 7 Seawater pH measurements along transects on CP reef flat during the night and outgoing low tide. Dashed lines illustrate estimated areas of similar pH values between transects. Wind direction (ESE) from Time and Date AS (2022). Image credit: Google Earth.

Measurements of seawater pH and temperature showed significant correlations (Figure 5A). First, pH and temperature measurements performed at day or night correlate as relative differences of both parameters follow similar controls. Second, all pH and temperature measurements correlate as daytime pH is elevated due to enhanced reef photosynthesis when also the temperature is elevated, and night-time pH is reduced due to prevailing reef calcification when water temperatures are also low.

4.2 Variations in benthic community structure

Both reef flats significantly differed regarding the composition of the benthic community (Figure 6 A). Although significant, the difference between mean pH conditions was only small (0.04 pH units) and was likely a result of the difference in time seawater conditions were recorded. Differences in nutrient concentrations have been used as an explanation for differences in reef ecosystem composition between Kiritimati Island and other Line Islands with higher nutrient concentrations being associated with algae-dominated benthic communities (Sandin et al., 2008). However, the observed difference in CP and NP benthic community composition is not consistent with this hypothesis as upwelling conditions and thus nutrient concentrations are expected to be similar at both sites (Figure 1 A). Furthermore, the proximity of NP reef flat to human settlements, thus being more affected by fishing and sewage, might have contributed to the observed difference. Most likely, the differences in benthos composition result from the difference in reef geomorphology with NP reef flat being significantly lower in elevation promoting the growth of green algae especially “other non-calcifying algae”, and CP reef flat being characterized by more overwash sediments resulting in an increased fraction of rubble on the benthos suppressing algae growth. An enhanced geomorphological activity on CP reef flat is also evident from aerial and satellite imagery (Figure 8).

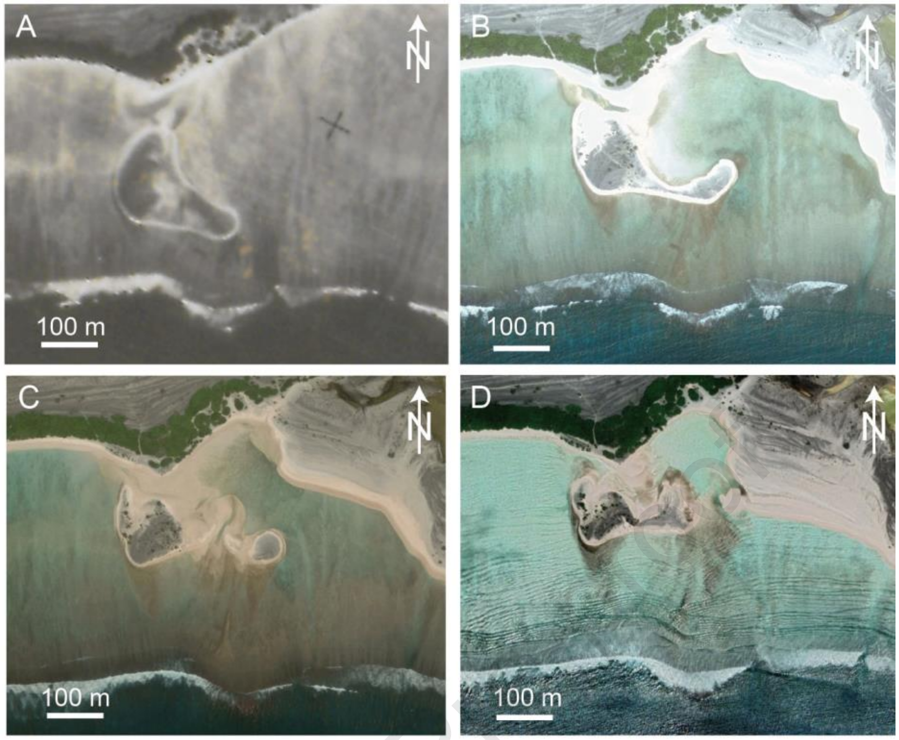


Figure 8 Aerial photography and satellite imagery from CP reef flat recorded before this study was conducted in (a) 1957, (b) 2006, (c) 2013, and afterwards in (d) 2020. Image credit: Secretariat of the South Pacific (SPC), Google Earth.

Variations in benthos composition along transects revealed the strongest correlations with geomorphological parameters, especially distance to reef flat edge (Figure 4 B–F), but also geomorphological zone, and bathymetry (i.e., variations in elevation; Figure 6 B and C). Also, non-linear relationships between reef bathymetry and benthos composition were observed, such as, for instance, the elevated relative abundance of corals in deeper and more sheltered areas of the reef flat (see Figure 2 A, C, and E, Figure 3 C). For NP reef flat, also some significant correlations between reef benthos composition and pH conditions were found (Table S3, Table S8). However, the latter relationship likely results from the fact that the abundances of "other non-calcifying algae" and "calcifying algae", as well as mean and day pH on NP reef flat all significantly linearly correlate with distance to reef flat edge, rather than a causal dependency (Figure 4 E and F, Table S3).

5 Conclusions

Environmental surveys on the narrow reef flats of Kiritimati Island revealed that spatial variations of pH and temperature at a given location on the reef flat were predominantly controlled by the distance to the reef flat edge and the local bathymetry. The amplitude of diel pH and temperature ranges linearly increased towards the shore with distance to reef flat edge, very likely as seawater residence time increased across the reef flat towards the shore. Furthermore, local pH and temperature conditions appeared to be modified by local hydrodynamics (e.g., flow patterns) that are bathymetrically controlled. Similarly, spatial variations in benthic community composition were primarily linked to the geomorphological structure of the reef flat with little evidence for a relationship between benthic community structure and local seawater pH or temperature conditions.

While many previous studies have shown that temporal variations in reef seawater pH result from diel oscillations in the NEP/NEC ratio and are consequently driven by the activity of the benthic community (Gattuso et al., 1993; Kwiatkowski et al., 2016; Smith, 1973), spatial variations in pH as observed on the narrow reef flats of Kiritimati Island could not be linked to variations in the benthic community structure. Thus, mean pH conditions on narrow reef flat systems of fringing reefs are primarily determined by the ocean pH conditions off reef. This finding implies that narrow reef flat environments are prone to open ocean processes such as anthropogenic ocean acidification and compensation for a decline in ocean pH through shifts in the benthic community structure may only be possible for downstream reef environments with large seawater residence times.

Acknowledgements

The authors would like to thank the Royal Society Te Apārangi Marsden Fund New Zealand for funding this project (Project no. UOA1513, to P.K.). Furthermore, R.G. was funded by the Worldwide University Network Research Mobility Programme and the Quaternary Research Association (UK). We are also grateful to Emma J. Ryan, Brendan Hall, David Wackrow and Natalia Abrego from the University of Auckland for their help in preparing and conducting the fieldwork. We would like to thank Kim Currie and Judith Murdoch from the University of Otago for measuring the carbonate chemistry of seawater samples and Mike Beckwith from the University of York for processing the elevation data. Furthermore, we are also thankful to Gavin Foster for his feedback on the PhD thesis chapter that preceded this manuscript.

Fieldwork was undertaken under Research Permit No. 010/16, provided by the Ministry of Environment, Lands and Agricultural Development, Government of Kiribati.

References

Albright, R., Caldeira, L., Hosfelt, J., Kwiatkowski, L., Maclaren, J. K., Mason, B. M., Nebuchina, Y., Ninokawa, A., Pongratz, J., Ricke, K. L., Rivlin, T., Schneider, K., Sesboüé, M., Shamberger, K., Silverman, J., Wolfe, K., Zhu, K., & Caldeira, K. (2016). Reversal of ocean acidification enhances net coral reef calcification. *Nature*, *531*(7594), 362–365. https://doi.org/10.1038/nature17155

Albright, R., Langdon, C., & Anthony, K. R. N. (2013). Dynamics of seawater carbonate chemistry, production, and calcification of a coral reef flat, central Great Barrier Reef. *Biogeosciences*, *10*(10), 6747–6758. https://doi.org/10.5194/bg-10-6747-2013

Albright, R., Takeshita, Y., Koweek, D. A., Ninokawa, A., Wolfe, K., Rivlin, T., Nebuchina, Y., Young, J., & Caldeira, K. (2018). Carbon dioxide addition to coral reef waters suppresses net community calcification. *Nature*, *555*(7697), 516–519. https://doi.org/10.1038/nature25968

Allen Coral Atlas. (2022). *Imagery, maps and monitoring of the world's tropical coral reefs.*

Andersson, A. J., Yeakel, K. L., Bates, N. R., & de Putron, S. J. (2014). Partial offsets in ocean acidification from changing coral reef biogeochemistry. *Nature Climate Change*, *4*(1), 56–61. https://doi.org/10.1038/nclimate2050

Anthony, K. R. N., A. Kleypas, J., & Gattuso, J. P. (2011). Coral reefs modify their seawater carbon chemistry - implications for impacts of ocean acidification. *Global Change Biology*, *17*(12), 3655–3666. https://doi.org/10.1111/j.1365-2486.2011.02510.x

Anthony, K. R. N., Diaz-Pulido, G., Verlinden, N., Tilbrook, B., & Andersson, A. J. (2013). Benthic buffers and boosters of ocean acidification on coral reefs. *Biogeosciences*, *10*(7), 4897–4909. https://doi.org/10.5194/bg-10-4897-2013

Carilli, J., & Walsh, S. (2012). Benthic foraminiferal assemblages from Kiritimati (Christmas) Island indicate human-mediated nutrification has occurred over the scale of decades. *Marine Ecology Progress Series*, *456*, 87–99. https://doi.org/10.3354/meps09684

Clark, V., Mello-Athayde, M. A., & Dove, S. (2022). Colonies of Acropora formosa with greater survival potential have reduced calcification rates. *PLoS ONE*, *17*(6 June). https://doi.org/10.1371/journal.pone.0269526

Cole, C., Finch, A. A., Hintz, C., Hintz, K., & Allison, N. (2018). Effects of seawater pCO2 and temperature on calcification and productivity in the coral genus Porites spp.: an exploration of potential interaction mechanisms. *Coral Reefs*, *37*(2), 471–481. https://doi.org/10.1007/s00338-018-1672-3

Cornwall, C. E., Comeau, S., Kornder, N. A., Perrs, C. T., van Hooidonk, R., DeCarlo, T. M., Ptatchett, M. S., Anderson, K. D., Browne, N., Carpenter, R., Diaz-Pulido, G., D'Olivo, J., Doo, S. S., Figueiredo, J., Fortunato, S. A. V., Kennedy, E., Lantz, C. A., McCulloch, M. T., González-Rivero, M., … Lowe, R. J. (2021). Global declines in coral reef calcium carbonate production under ocean acidification and warming. *PNAS*, *118*(21). https://doi.org/10.1073/pnas.2015265118/-/DCSupplemental

Cyronak, T., Andersson, A. J., Langdon, C., Albright, R., Bates, N. R., Caldeira, K., Carlton, R., Corredor, J. E., Dunbar, R. B., Enochs, I., Erez, J., Eyre, B. D., Gattuso, J. P., Gledhill, D., Kayanne, H., Kline, D. I., Koweek, D. A., Lantz, C., Lazar, B., … Yamamoto, S. (2018). Taking the metabolic pulse of the world's coral reefs. *PLoS ONE*, *13*(1). https://doi.org/10.1371/journal.pone.0190872

Cyronak, T., Santos, I. R., & Eyre, B. D. (2013). Permeable coral reef sediment dissolution driven by elevated pCO 2 and pore water advection. *Geophysical Research Letters*, *40*(18), 4876–4881. https://doi.org/10.1002/grl.50948

Cyronak, T., Takeshita, Y., Courtney, T. A., DeCarlo, E. H., Eyre, B. D., Kline, D. I., Martz, T., Page, H., Price, N. N., Smith, J., Stoltenberg, L., Tresguerres, M., & Andersson, A. J. (2019). Diel temperature and pH variability scale with depth across diverse coral reef habitats. *Limnology And Oceanography Letters*, *5*(2), 193–203. https://doi.org/10.1002/lol2.10129

Davis, K. L., Colefax, A. P., Tucker, J. P., Kelaher, B. P., & Santos, I. R. (2021). Global coral reef ecosystems exhibit declining calcification and increasing primary productivity. *Communications Earth and Environment*, *2*(105). https://doi.org/10.1038/s43247-021-00168-w

Davis, K. L., McMahon, A., Kelaher, B., Shaw, E., & Santos, I. R. (2019). Fifty years of sporadic coral reef calcification estimates at One Tree Island, Great Barrier Reef: Is it enough to imply long term trends? *Frontiers in Marine Science*, *6*(282). https://doi.org/10.3389/fmars.2019.00282

DeMartini, E. E., Friedlander, A. M., Sandin, S. A., & Sala, E. (2008). Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Marine Ecology Progress Series*, *365*, 199–215. https://doi.org/10.3354/meps07501

Doney, S. C., Busch, D. S., Cooley, S. R., & Kroeker, K. J. (2020). The Impacts of Ocean Acidification on Marine Ecosystems and Reliant Human Communities. *Annual Review of Environment and Resources*, *45*(1), 1–30. https://doi.org/10.1146/annurev-environ-012320-083019

Dong, X., Huang, H., Zheng, N., Pan, A., Wang, S., Huo, C., Zhou, K., Lin, H., & Ji, W. (2017). Acidification mediated by a river plume and coastal upwelling on a fringing reef at the east coast of Hainan Island, Northern South China Sea. *Journal of Geophysical Research: Oceans*, *122*(9), 7521–7536. https://doi.org/10.1002/2017JC013228

Evans, M. N., Fairbanks, R. G., & Rubenstone, J. L. (1999). The thermal oceanographic signal of El Niño reconstructed from a Kiritimati Island coral. *Journal of Geophysical Research: Oceans*, *104*(C6), 13409–13421. https://doi.org/10.1029/1999jc900001

Fabricius, K. E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. *Marine Pollution Bulletin*, *50*(2), 125–146. https://doi.org/10.1016/j.marpolbul.2004.11.028

Falter, J. L., Lowe, R. J., Zhang, Z., & McCulloch, M. (2013). Physical and Biological Controls on the Carbonate Chemistry of Coral Reef Waters: Effects of Metabolism, Wave Forcing, Sea Level, and Geomorphology. *PLoS ONE*, *8*(1). https://doi.org/10.1371/journal.pone.0053303

Ford, M. R., Becker, J. M., & Merrifield, M. A. (2013). Reef Flat Wave Processes and Excavation Pits: Observations and Implications for. *Journal of Coastal Research*, *29*(3), 545–554. https://doi.org/10.2307/23486338

Gattuso, J.-P., Epitalon, J.-M., Lavigne, H., Orr, J., Gentili, B., Hagens, M., Hofmann, A., Mueller, J.-D., Proye, A., Rae, J., & Soetaert, K. (2021). *Seacarb: Seawater Carbonate Chemistry* (3.2.16).

Gattuso, J.-P., Pichon, M., Delesalle, B., & Frankignoulle, M. (1993). Community metabolism and air-sea CO2 fluxes in a coral reef ecosystem (Moorea, French Polynesia). *Marine Ecology Progress Series*, *96*, 259–267.

Gray, S. E. C., Degrandpre, M. D., Langdon, C., & Corredor, J. E. (2012). Short-term and seasonal pH. *Global Biogeochemical Cycles*, *26*(3). https://doi.org/10.1029/2011GB004114

Guadayol, Ò., Silbiger, N. J., Donahue, M. J., & Thomas, F. I. M. (2014). Patterns in temporal variability of temperature, oxygen and pH along an environmental gradient in a coral reef. *PLoS ONE*, *9*(1). https://doi.org/10.1371/journal.pone.0085213

Hannan, K. D., Miller, G. M., Watson, S. A., Rummer, J. L., Fabricius, K., & Munday, P. L. (2020). Diel pCO2 variation among coral reefs and microhabitats at Lizard Island, Great Barrier Reef. *Coral Reefs*, *39*(5), 1391–1406. https://doi.org/10.1007/s00338-020-01973-z

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., Babcock, R. C., Beger, M., Bellwood, D. R., Berkelmans, R., Bridge, T. C., Butler, I. R., Byrne, M., Cantin, N. E., Comeau, S., Connolly, S. R., Cumming, G. S., Dalton, S. J., Diaz-Pulido, G., … Wilson, S. K. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, *543*(7645), 373–377. https://doi.org/10.1038/nature21707

Kayanne, H., Hata, H., Kudo, S., Yamano, H., Watanabe, A., Ikeda, Y., Nozaki, K., Kato, K., Negishi, A., & Saito, H. (2005). Seasonal and bleaching-induced changes in coral reef metabolism and CO2 flux. *Global Biogeochemical Cycles*, *19*(3), 1–11. https://doi.org/10.1029/2004GB002400

Kayanne, H., Suzuki, A., & Saito, H. (1995). Diurnal Changes in the Partial Pressure of Carbon Dioxide in Coral Reef Water. *Science*, *296*, 214–216. https://doi.org/10.1126/science.269.5221.214

Kenkel, N. C. (2006). On selecting an appropriate multivariate analysis. *Canadian Journal of Plant Science*, *86*(3), 663–676. https://doi.org/10.4141/P05-164

Kleypas, J. A., Anthony, K. R. N., & Gattuso, J. P. (2011). Coral reefs modify their seawater carbon chemistry - case study from a barrier reef (Moorea, French Polynesia). *Global Change Biology*, *17*(12), 3667–3678. https://doi.org/10.1111/j.1365-2486.2011.02530.x

Knebel, O., Carvajal, C., Standish, C. D., Vega, E. de la, Chalk, T. B., Ryan, E. J., Guo, W., Ford, M., Foster, G. L., & Kench, P. (2021). Porites Calcifying Fluid pH on Seasonal to Diurnal Scales. *Journal of Geophysical Research: Oceans*, *126*(3). https://doi.org/10.1029/2020JC016889

Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S., Duarte, C. M., & Gattuso, J. P. (2013). Impacts of ocean acidification on marine organisms: Quantifying sensitivities and interaction with warming. *Global Change Biology*, *19*(6), 1884–1896. https://doi.org/10.1111/gcb.12179

Kwiatkowski, L., Albright, R., Hosfelt, J., Nebuchina, Y., Ninokawa, A., Rivlin, T., Sesboüé, M., Wolfe, K., & Caldeira, K. (2016). Interannual stability of organic to inorganic carbon production on a coral atoll. *Geophysical Research Letters*, *43*(8), 3880–3888. https://doi.org/10.1002/2016GL068723

Lauvset, S. K., Key, R. M., Olsen, A., Heuven, S. van, Velo, A., Lin, X., Schirnick, C., Kozyr, A., Tanhua, T., Hoppema, M., Jutterström, S., Steinfeldt, R., Jeansson, E., Ishii, M., Pérez, F. F., Suzuki, T., & Watelet, S. (2016). A new global interior ocean mapped climatology: the 1°x1° GLODAP version 2. *Earth Syst. Sci. Data*, *8*, 325–340. https://doi.org/10.5194/essd-8-325-2016

Leujak, W., & Ormond, R. F. G. (2007). Comparative accuracy and efficiency of six coral community survey methods. *Journal of Experimental Marine Biology and Ecology*, *351*(1–2), 168–187. https://doi.org/10.1016/j.jembe.2007.06.028

McCabe, R. M., Estrade, P., Middleton, J. H., Melville, W. K., Roughan, M., & Lenain, L. (2010). Temperature variability in a shallow, tidally isolated coral reef lagoon. *Journal of Geophysical Research: Oceans*, *115*(12). https://doi.org/10.1029/2009JC006023

McMahon, A., Santos, I. R., Schulz, K. G., Scott, A., Silvermann, J., Davis, K. L., & Maher, D. T. (2019). Coral Reef Calcification and Production After the 2016 Bleaching Event at Lizard Island, Great Barrier Reef. *Journal of Geophysical Research: Oceans*, *124*, 4003–4016. https://doi.org/10.1029/2018JC014698

Morrison, R. J., & Woodroffe, C. D. (2009). The soils of kiritimati (christmas) Island, Kiribati, Central Pacific: New information and comparison with previous studies. *Pacific Science*, *63*(3), 397–411. https://doi.org/10.2984/049.063.0308

Nagelkerken, I., Russell, B. D., Gillanders, B. M., & Connell, S. D. (2016). Ocean acidification alters fish populations indirectly through habitat modification. *Nature Climate Change*, *6*(1), 89–93. https://doi.org/10.1038/nclimate2757

Ohde, S., & van Woesik, R. (1999). Carbon dioxide flux and metabolic processes of a coral reef, Okinawa. *Bulletin of Marine Science*, *65*(2), 559–576.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). *vegan: Community Ecology Package*.

Page, H. N., Andersson, A. J., Jokiel, P. L., Rodgers, K. S., Lebrato, M., Yeakel, K., Davidson, C., D'Angelo, S., & Bahr, K. D. (2016). Differential modification of seawater carbonate chemistry by major coral reef benthic communities. *Coral Reefs*, *35*(4), 1311–1325. https://doi.org/10.1007/s00338-016-1490-4

Page, H. N., Courtney, T. A., de Carlo, E. H., Howins, N. M., Koester, I., & Andersson, A. J. (2019). Spatiotemporal variability in seawater carbon chemistry for a coral reef flat in Kāneʻohe Bay, Hawaiʻi. *Limnology and Oceanography*, *64*(3), 913–934. https://doi.org/10.1002/lno.11084

Platz, M. C., Arias, M. E., & Byrne, R. H. (2022). Reef Metabolism Monitoring Methods and Potential Applications for Coral Restoration. *Environmental Management*, *69*(3), 612–625. https://doi.org/10.1007/s00267-022-01597-9

Price, N. N., Martz, T. R., Brainard, R. E., & Smith, J. E. (2012). Diel Variability in Seawater pH Relates to Calcification and Benthic Community Structure on Coral Reefs. *PLoS ONE*, *7*(8). https://doi.org/10.1371/journal.pone.0043843

R Core Team. (2021). *R: A language and environment for statistical computing. R Foundation for Statistical Computing*. https://www.r-project.org/

Rivest, E. B., Comeau, S., & Cornwall, C. E. (2017). The Role of Natural Variability in Shaping the Response of Coral Reef Organisms to Climate Change. In *Current Climate Change Reports* (Vol. 3, Issue 4, pp. 271–281). Springer. https://doi.org/10.1007/s40641-017-0082-x

Romanó de Orte, M., Koweek, D. A., Cyronak, T., Takeshita, Y., Griffin, A., Wolfe, K., Szmant, A., Whitehead, R., Albright, R., & Caldeira, K. (2021). Unexpected role of communities colonizing dead coral substrate in the calcification of coral reefs. *Limnology and Oceanography*, *66*(5), 1793–1803. https://doi.org/10.1002/lno.11722

Sandin, S. A., Smith, J. E., DeMartini, E. E., Dinsdale, E. A., Donner, S. D., Friedlander, A. M., Konotchick, T., Malay, M., Maragos, J. E., Obura, D., Pantos, O., Paulay, G., Richie, M., Rohwer, F., Schroeder, R. E., Walsh, S., Jackson, J. B. C., Knowlton, N., & Sala, E. (2008). Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS ONE*, *3*(2). https://doi.org/10.1371/journal.pone.0001548

Shaw, E. C., McNeil, B. I., & Tilbrook, B. (2012). Impacts of ocean acidification in naturally variable coral reef flat ecosystems. *Journal of Geophysical Research: Oceans*, *117*(3). https://doi.org/10.1029/2011JC007655

Smith, S. v. (1973). Carbon Dioxide Dynamics: A Record of Organic Carbon Production, Respiration, and Calcification in the Eniwetok Reef Flat Community. *Limnology and Oceanography*, 106–120. https://doi.org/10.4319/lo.1973.18.1.0106

Sunday, J. M., Fabricius, K. E., Kroeker, K. J., Anderson, K. M., Brown, N. E., Barry, J. P., Connell, S. D., Dupont, S., Gaylord, B., Hall-Spencer, J. M., Klinger, T., Milazzo, M., Munday, P. L., Russell, B. D., Sanford, E., Thiyagarajan, V., Vaughan, M. L. H., Widdicombe, S., & Harley, C. D. G. (2017). Ocean acidification can mediate biodiversity shifts by changing biogenic habitat. *Nature Climate Change*, *7*(1), 81–85. https://doi.org/10.1038/nclimate3161

Suzuki, A., Nakamori, T., & Kayanne, H. (1995). The mechanism of production enhancement in coral reef carbonate systems: model and empirical results. *Sedimentary Geology*, *99*(3–4), 259–280. https://doi.org/10.1016/0037-0738(95)00048-D

Time and Date AS. (2022). *timeanddate.com*. https://www.timeanddate.com/weather/kiribati/kiritimati/historic?month=5&year=2018

Walsh, S. M. (2011). Ecosystem-Scale Effects of Nutrients and Fishing on Coral Reefs. *Journal of Marine Biology*, *2011*, 1–13. https://doi.org/10.1155/2011/187248

Wolfe, K., Nguyen, H. D., Davey, M., & Byrne, M. (2020). Characterizing biogeochemical fluctuations in a world of extremes: A synthesis for temperate intertidal habitats in the face of global change. *Global Change Biology*, *26*(7), 3858–3879. https://doi.org/10.1111/gcb.15103

Wolfe, K., & Roff, G. (2021). Global predictions of coral reef dissolution in the Anthropocene. *Communications Earth and Environment*, *3*(42). https://doi.org/10.1038/s43247-022-00363-3

Woodroffe, C. D., Beech, M. R., & Gagan, M. K. (2003). Mid-late Holocene El Niño variability in the equatorial Pacific from coral microatolls. *Geophysical Research Letters*, *30*(7), 1358–1361. https://doi.org/10.1029/2002GL015868

Woodroffe, C. D., McGregor, H. V., Lambeck, K., Smithers, S. G., & Fink, D. (2012). Mid-Pacific microatolls record sea-level stability over the past 5000 yr. *Geology*, *40*(10), 951–954. https://doi.org/10.1130/G33344.1

Zhang, Z., Falter, J., Lowe, R., & Ivey, G. (2012). The combined influence of hydrodynamic forcing and calcification on the spatial distribution of alkalinity in a coral reef system. *Journal of Geophysical Research: Oceans*, *117*(4). https://doi.org/10.1029/2011JC007603

Spatial pH variability of coral reef flats of Kiritimati Island, Kiribati

Oliver Knebel[a,*,1], Carlos Carvajal[a], Paul Kench[b], Roland Gehrels[c]

[a] School of Environment, University of Auckland, New Zealand

[b]Department of Geography, National University of Singapore, Singapore

[c]Department of Environment and Geography, University of York

*Corresponding author: Oliver Knebel (Okne620@auklanduni.ac.nz)

[1]present address: Goethe-University, Department of Geoscience, Frankfurt am Main, Germany

- Spatial variations in reef flat pH primarily followed bathymetrically controlled hydrodynamics
- The diel range in pH increased towards the shore, likely with increasing seawater residence time
- Variations in benthos community composition did not exert an influence on spatial pH variability
- Mean pH conditions of narrow fringing reef flats are primarily determined by open ocean conditions

Oliver Knebel: Conceptualization, Formal analysis, Investigation, Data curation, Writing - Original Draft, Visualization, Project administration

Carlos Carvajal: Conceptualization, Investigation, Project administration

Paul Kench: Conceptualization, Investigation, Resources, Writing - Review & Editing, Supervision, Funding acquisition, Project administration

Roland Gehrels*:* Investigation, Data Curation, Writing - Review & Editing, Funding acquisition

Declaration of interests

☐ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☒ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Oliver Knebel reports financial support was provided by Royal Society of New Zealand Marsden Fund. Roland Gehrels reports financial support was provided by Worldwide Universities Network. Roland Gehrels reports financial support was provided by Quaternary Research Association.