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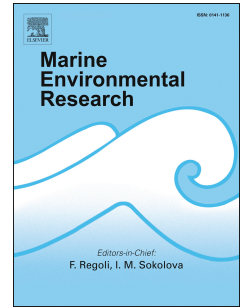
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1 **Spatial pH variability of coral reef flats of Kiritimati Island, Kiribati**

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8

9 Abstract

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

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

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

20
21 Keywords: Acidification, Benthos, Coastal waters, Community composition, pH, Coral reef, reef flat, Kiritimati

22 1 Introduction

23 Anthropogenic inputs of nutrients, sediments, and pollutants to the oceans, combined with increased ocean uptake of
24 CO₂ due to climate change, are altering the seawater carbonate chemistry of tropical coral reefs (Fabricius, 2005), as
25 well as increasing open ocean acidification (Doney et al., 2020). Although different in causative mechanism, both
26 processes result in a reduction of reef seawater pH and the calcium carbonate saturation state (Ω) that impacts the
27 physiology of many calcifying reef organisms (Kroeker et al., 2013), as well as the overall state of reef ecosystems
28 (Nagelkerken et al., 2016; Sunday et al., 2017). Most importantly, the ability of reef organisms to calcify is altered
29 under reduced pH conditions (Albright et al., 2016, 2018). Additionally, coral mass bleaching events that result from
30 global warming-induced thermal stress are causing a decline in coral reef calcification rates (Hughes et al., 2017).
31 Notably, however, below the thermal stress threshold, increasing seawater temperatures enhance coral calcification
32 (Cole et al., 2018). As a result, ocean acidification in combination with increasing seawater temperatures may shift
33 reef carbonate budgets towards a negative state (Cornwall et al., 2021; Davis et al., 2021; Wolfe & Roff, 2021).

34 The seawater flowing on a coral reef originates from the adjacent ocean and therefore may inherit some of its initial
35 properties. However, the seawater carbonate chemistry of coral reefs is further modified by a number of physical and
36 biological processes and thus varies across spatial and temporal scales (Kayanne et al., 1995; Smith, 1973). The most
37 important processes are the balance between Net Ecosystem Productivity (NEP) and Net Ecosystem Calcification
38 (NEC; Gattuso et al., 1993). NEP is determined by the photosynthesis of autotrophic organisms that consume CO₂
39 and respiration by heterotrophic organisms that release CO₂, while NEC is determined by the dissolution of carbonates
40 that absorbs CO₂ and the precipitation of carbonates that releases CO₂ (Suzuki et al., 1995). On a diurnal scale, reef
41 water pH is elevated during the day, as photosynthesis is the predominant process during sunlight hours, but reduced
42 during the night when calcification and respiration prevail (Kwiatkowski et al., 2016; Ohde & van Woesik, 1999).

43 Reported amplitudes of diurnal pH cycles of coral reefs range between 0.78 pH units and less than 0.05 pH units
44 (Rivest et al., 2017). The benthic ecosystem composition of a reef influences the balance between NEP and NEC with
45 macroalgae-dominated reefs being characterized by larger diurnal pH cycles than coral-dominated reefs (Anthony et
46 al., 2013; Page et al., 2016). Seasonal changes in coral reef pH are usually multiple-folds smaller than the diurnal
47 variability (Kayanne et al., 2005) and are driven to approximately equal amounts by changes in the temperature
48 dependency of the carbonate dissociation constants and seasonal changes in the NEP/NEC balance (Albright et al.,
49 2013; Gray et al., 2012). Other processes, such as coastal upwelling and river or groundwater discharge may also
50 affect seasonal pH variations of a reef (Dong et al., 2017). Inter-annual variations in NEP/NEC of coral reef flats that
51 again affect the seawater carbonate chemistry have been reported to occur in response to changes in benthic cover,
52 especially after bleaching events (Davis et al., 2019; McMahon et al., 2019).

53 Spatial variations in reef pH have been linked to the geomorphic structure of the reef surface (Cyronak et al., 2019;
54 Page et al., 2019). The concentration of the products of NEP and NEC varies depending on the volume of water at a
55 given location and thus pH follows variations in water depth which are bathymetrically controlled. Furthermore, the
56 local hydrodynamic conditions influence spatial variations in pH, as they determine the residence time of reefal waters
57 (Falter et al., 2013; Platz et al., 2022; Zhang et al., 2012). For instance, fewer products of NEP and NEC can
58 accumulate at a given location on the reef, if flushing (i.e., exchange between reef and open ocean water) is enhanced
59 and consequently the residence time of reef water is reduced. For intertidal environments, such as coral reef flats, tidal
60 fluctuations in sea level also play a major role in determining local seawater residence time that can even result in
61 ponding, i.e., the temporary isolation of a body of water from the ocean (Albright et al., 2016, 2018; Wolfe et al.,
62 2020). In addition, differences in the benthic community composition that drive local differences in the ratio between
63 NEP and NEC have been reported to change pH conditions for downstream reef environments (Anthony et al., 2011;
64 Kleypas et al., 2011). NEP and NEC have also been shown to vary spatially within a reef flat and may result in local
65 variations of carbonate system parameters (Davis et al., 2019). Temperatures of reefal waters are controlled by solar
66 heating and surrounding air temperatures and thus cycle diurnally with amplitudes ranging between more than 10 °C
67 to less than 2 °C (Rivest et al., 2017). Spatial variations in temperature on reefs are primarily determined by the
68 residence time that may vary across a reef depending on water depth and local hydrodynamics (Cyronak et al., 2019;
69 Page et al., 2019).

70 Knowledge of the natural dynamics in coral reef pH and temperature is crucial for better understanding the impacts
71 of anthropogenic processes on the seawater carbonate system and the biota of coral reefs. On reef flats, the variability
72 in seawater pH and temperature is elevated compared to other reef environments and the open ocean, due to the low
73 water levels (Cyronak et al., 2019; Knebel et al., 2021; Page et al., 2019). It is unclear if organisms dwelling on reef
74 flats are less susceptible to anthropogenic reductions in pH and increasing thermal stress as natural exposure to variable
75 pH and temperature conditions may have resulted in an enhanced resilience to these stressors (Clark et al., 2022;
76 Rivest et al., 2017; Shaw et al., 2012). Intertidal habitats, such as coral reef flats, that locally differ from open ocean
77 conditions, may also represent spatial refugia from ocean acidification and global warming (Wolfe et al., 2020).
78 Furthermore, it has been suggested that shifts in reef flat benthic community structure may also change the mean pH

79 conditions of downstream reef environments against the anthropogenically induced declining trend of pH in the open
80 ocean (Andersson et al., 2014; Anthony et al., 2011; Kleypas et al., 2011). However, reef flat environments can also
81 be affected by human interventions due to their accessibility and proximity to the shore (Ford et al., 2013).

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

88 **2 Materials and Methods**

89 **2.1 Study area**

90 Kiritimati Island is a coral atoll in the equatorial central Pacific (01°52'N 157°24'W, Figure 1 A), where oceanographic
91 conditions are characterized by upwelling of carbon-rich deep waters and thus relatively low surface water pH (~
92 8.01±0.01, standard error; Lauvset et al., 2016) and relatively high nutrient concentrations (DeMartini et al., 2008).
93 The local oceanography around Kiritimati Island is mainly controlled by easterly trade winds and the associated
94 westward flowing South Equatorial Current (Walsh, 2011). Kiritimati Island is located directly to the west of the
95 NINO3 region, which is an area where SST anomalies during El Niño events are highest within the equatorial central
96 Pacific (Evans et al., 1999). During an El Niño event trade winds weaken, and thus equatorial upwelling is significantly
97 reduced. Average annual SSTs vary between 24°C during La Niña and 30°C during El Niño conditions (Woodroffe
98 et al., 2003), and average annual rainfall rates are low (~900 mm/year) but increase during El Niño events to up to
99 3000 mm/year (Morrison & Woodroffe, 2009). The average tidal range at Kiritimati is 1.5 m and El Niño events can
100 cause a positive sea-level anomaly of up to 0.4 m for several months at a time compared to La Niña conditions
101 (Woodroffe et al., 2012).

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

109

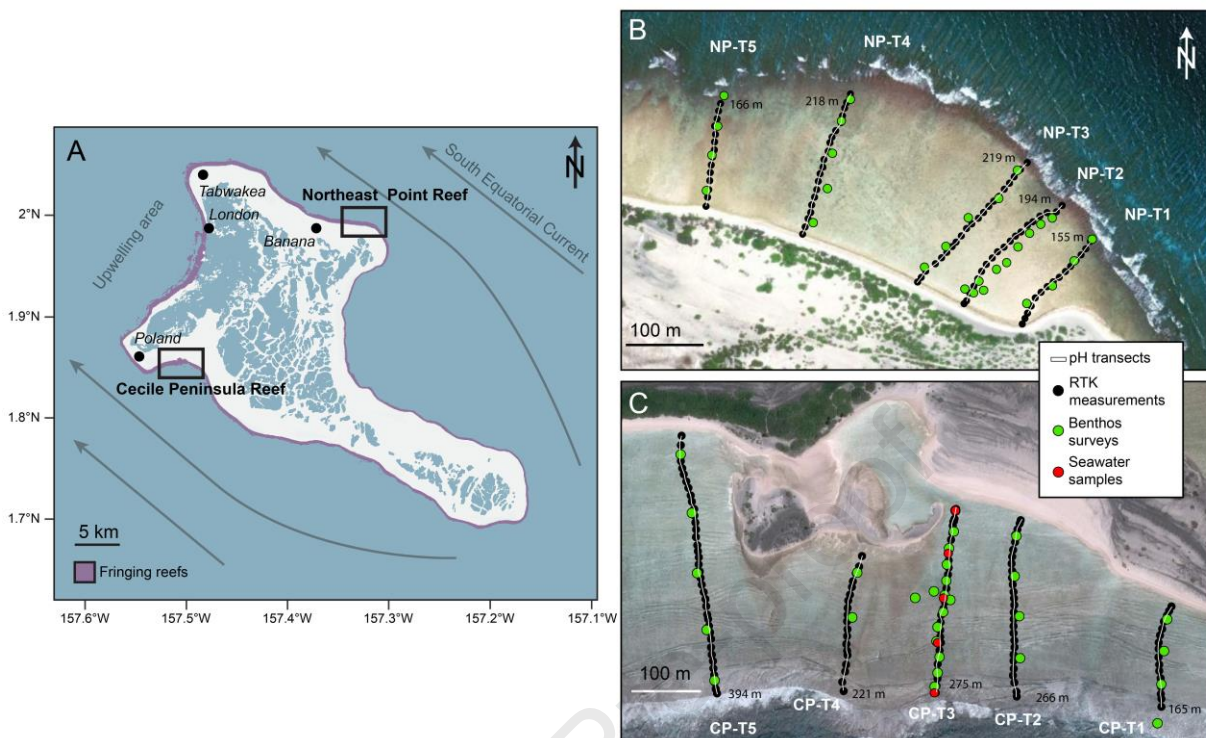


Figure 1 (A) Location map of Kiritimati Island, Kiribati, in the Central Pacific with study locations and major settlements (London: ~1900 inhabitants; Tabwakea: ~3500 inhabitants; Banana: ~1200 inhabitants; Poland: ~400 inhabitants). Also shown are the locations of fringing reefs around the island, 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.

110

111

112 2.2 Elevation Profiles

113 To document the bathymetry of the reef flat surface surveys were undertaken, from the shoreline to the reef edge,
 114 along 10 transects using a Trimble real-time kinematic (RTK) global position system with measurements taken every
 115 10 m (Figure 1 B and C). At each site survey measurements were tied to a local datum and surveys from both sites
 116 were reduced to a primary benchmark located 3.17 m above datum (WGS84), situated in the village of London on
 117 Kiritimati Island (Figure 1 A). Raw position data were corrected using Trimble RTX and the orthometric height was
 118 calculated relative to the WGS84 datum with the EGM-08 geoid model. Elevation data has an uncertainty of < 0.05
 119 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.
 120 At NP Reef, transects were 155 m to 219 m in length and spaced 50 m to 200 m from each other.

121 2.3 Seawater sampling

122 To quantify spatial variations in pH, temperature and salinity, measurements of these parameters were undertaken
123 along each of the 10 shore perpendicular transects (Figure 1 B and C). On Kiritimati Island, seawater reef flat pH
124 remains relatively stable at maximum values between 12:00 and 17:30, and similarly, remains relatively stable at
125 minimum values between 00:00 and 07:00 (Knebel et al., 2021). Therefore, measurements were taken, when possible,
126 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
127 (CP) and 21:34–22:58 (NP). Measurements were obtained using a sensor package consisting of a SeaFET pH-sensor
128 set to continuous mode, an RBR CTD logger and a GPS (Global Positioning System) tracker. The accuracy of the
129 SeaFET pH-sensor is 0.05 pH units and the precision is < 0.001 pH units. Measurements were performed around low
130 tide when spatial variations of parameters measured were expected to be strongest. A pH, temperature and salinity
131 measurement was taken every 0.3 m which corresponds to 361 measurements per transect on average ranging between
132 205 measurements along transect CP-T1 (night) and 601 along transect CP-T3 (day). Seawater samples were collected
133 along transect CP-T3 for quantification of the seawater carbonate system parameters (Dissolved Inorganic Carbon,
134 DIC; alkalinity, ALK; Aragonite saturation state, $\Omega_{\text{Aragonite}}$). Collection of seawater samples and processing of SeaFET
135 and RBR CTD logger data was performed as described in Knebel et al. (2021). Each set of transects was recorded
136 within 1.5 hours, and each individual transect was recorded within a 15-minute time period. Thus, the differences in
137 environmental conditions across and between transects at each site represent predominantly spatial variations, with
138 temporal variations kept to a minimum.

139 2.4 Benthic Ecology

140 To evaluate the potential influence of the reef flat benthos ecology on seawater pH, the benthic community
141 composition of CP and NP reef flat was documented. The composition of the benthos was determined following the
142 Line Intercept Transect (LIT) method (Leujak & Ormond, 2007) in May and June 2018. At 40 m intervals along each
143 transect, 10 m LITs were placed in an arbitrary orientation relative to the transect (Figure 1 B and C). Usually, 2 to 5
144 LITs were placed along transects, but along transects CP-T3 and NP-T2, the spatial resolution was increased to up to
145 15 LITs along transects. In total, 58 LITs were surveyed on both reef flats of which 57 were located on the reef flat
146 perpendicular transects and therefore used for statistical analysis along transects. However, all 58 LITs were used for
147 statistics related to the entire reef flats. On each 10 m LIT, the type of benthic cover was noted every 10 cm (100
148 observations), differentiated into 19 types of benthic cover (Table 1). Usually, the uppermost type of benthos visible
149 to the surveyor was recorded. However, in some cases, when multiple cover types were observed synchronously, all
150 were recorded (e.g., coralline red algae growing on a piece of rubble). All benthic cover types may contribute to reef
151 NEP and NEC in different ways (Cyronak et al., 2013; Kleypas et al., 2011; Romanó de Orte et al., 2021). However,
152 some benthos types were grouped, if observed only very occasionally and, if grouped benthos types represent similar
153 habitats (Table 1). In particular, dead skeletons and shells of corals and molluscs were grouped, as well as all types of
154 non-calcifying algae that were distinct from turf algae. Furthermore, “growing Halemida” which occurred only a few
155 times was grouped with coralline red algae that were widespread on the reefs. Finally, all species and growth forms

156 of “calcifying coral” were grouped. “Growing microatolls” were in most cases from the genus *Porites*. “Growing
157 branching coral sp.” and “Growing massive coral sp.” represent respective coral growth forms of unknown genus.

158

159 **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 <i>Porites</i>
	Dead massive coral				Green algae on dead coral	Growing <i>Halemida</i>	Growing <i>Acropora</i>
	Dead microatoll				Macroalgae		Growing branching coral sp.
	Dead gastropod						Growing massive coral sp.
	Dead bivalve						Growing microatolls

160

161

162 2.5 Data Processing and statistical analysis

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

170 For continuous variables, regression analyses were performed between all variables measured (Abundance of groups
171 of benthic cover types, distance to reef flat edge, elevation, pH, and temperature). However, as pH and temperature
172 measurements were performed during different days and times for CP and NP reefs, also temporal and not solely
173 spatial factors may have influenced observed variations in these variables between reefs. Thus, statistical tests for pH
174 and temperature between other variables were performed for each reef site separately. All tests were repeated
175 excluding CP-T5 as this transect contains ponded seawater close to the shore that may obscure potential relationships

176 in pH and temperature with other variables (see Figure 2 E, Figure 5 E). Similarly, all tests were also repeated
177 excluding NP-T5 as this transect showed a declining trend in temperature with increasing distance to the reef flat edge
178 that was different from all other transects (see Figure S4 i). Additionally, the Mantel test was used to infer correlations
179 between benthic community composition and continuous variables. To detect correlations between benthic community
180 composition and categorical variables (Reef site, transect, geomorphological zone) the ANOSIM and PERMANOVA
181 tests were performed. For resemblance-based permutation tests, the gower distribution was used as distance metric for
182 the benthic community composition and the Euclidean distance for the parameters tested. Furthermore, the spearman
183 method was used to quantify the correlation between variables.

184 **3 Results**

185 **3.1 Bathymetry**

186 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
187 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
188 flat was on average narrower compared to the CP reef flat. Also, the NP reef flat was significantly lower in elevation
189 (i.e. deeper) compared to CP reef flat ($t(176.65) = 7.79$, $p < 0.01$; Figure 2, Figure 3). Mean elevation along transects
190 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
191 on NP reef flat was 0.73 m above datum and a variability (σ) of 0.15 m. The bathymetric structure between both reef
192 flats revealed some differences. The inner CP reef flat was characterized by a moat parallel to the shore and an elevated
193 central reef flat and reef flat edge (Figure 2). The central area of NP reef flat was more planar, and the reef flat crest
194 was more elevated due to a more pronounced algal rim compared to CP reef flat (Figure 3).

195

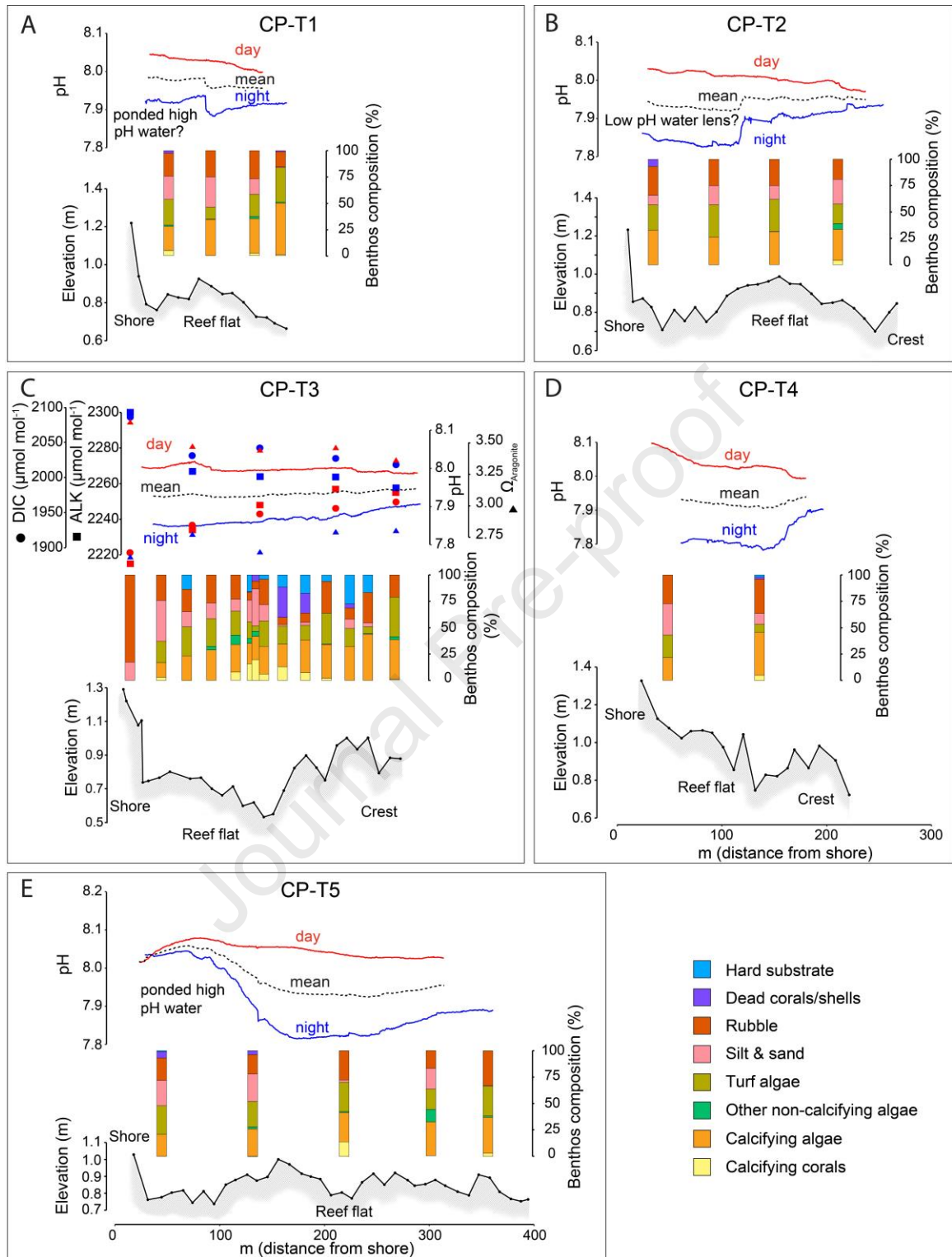


Figure 2 Results of measurements along transects on CP reef flat: Seawater pH during the day and night, as well as mean pH values; benthos composition; surface bathymetry from RTK measurements relative to WSG-84 datum. For transect CP-T3, seawater carbonate chemistry measurements are shown. The different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

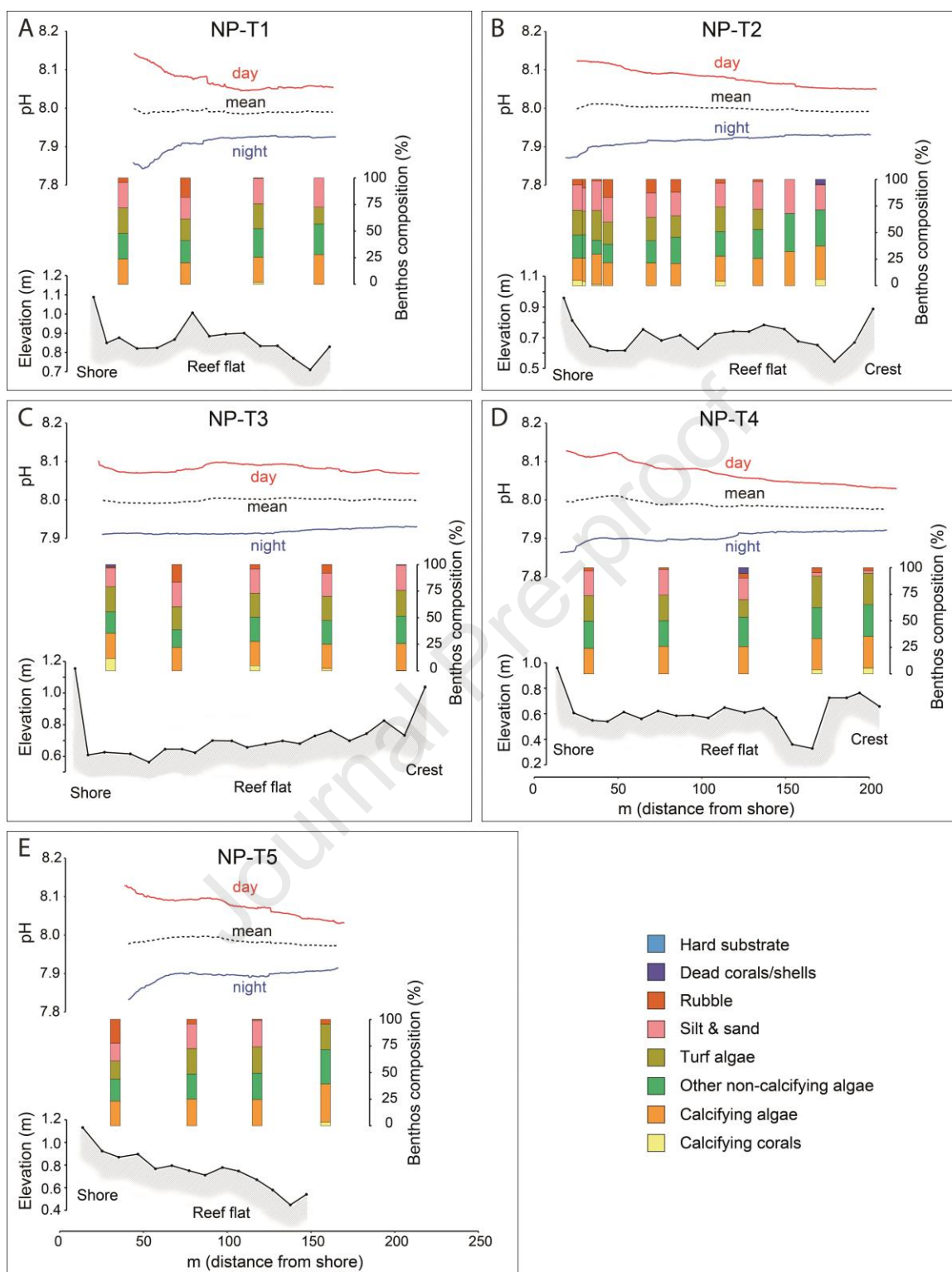


Figure 3 Results of measurements along transects on NP reef flat: Seawater pH during the day and night, as well as mean pH values; benthos composition; surface bathymetry from RTK measurements relative to WSG-84 datum. The different geomorphological zones are also indicated. X-axis of E applies also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

196

197 3.2 Seawater pH, temperature, and salinity

198 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.
 199 Although both mean pH values are significantly different ($t(3124) = -43.17$, $p < 0.01$) it cannot be excluded that this
 200 difference is due to the fact that measurements were recorded not synchronously. Ocean pH of this region (8.01 ± 0.01
 201 pH units; Lauvset et al., 2016) is within the error of mean pH values for both reef flats. The mean diel pH range was
 202 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
 203 for other reefs in Northern Line Islands (Price et al., 2012). Measurements along transect CP-T3 in other carbonate
 204 system parameters revealed mean values in ALK of $2256.1 \pm 22.2 \mu\text{mol mol}^{-1}$, in DIC of $1989.8 \pm 59.6 \mu\text{mol mol}^{-1}$, and
 205 in $\Omega_{\text{Aragonite}}$ of 3.1 ± 0.4 . Mean seawater temperature at both locations was $28.4 \pm 2.0 \text{ }^\circ\text{C}$ on CP reef flat and $28.2 \pm 1.8 \text{ }^\circ\text{C}$
 206 on NP reef flat which is significantly different ($t(6718.6) = 6.56$, $p < 0.01$). The mean diel temperature range on CP
 207 and NP reef flats were both $1.7 \pm 1.6 \text{ }^\circ\text{C}$. Measurements of seawater pH and temperature showed significant correlations
 208 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
 209 measurements ($r^2 = 0.75$, $p < 0.01$; Figure 4 A, Table S1).

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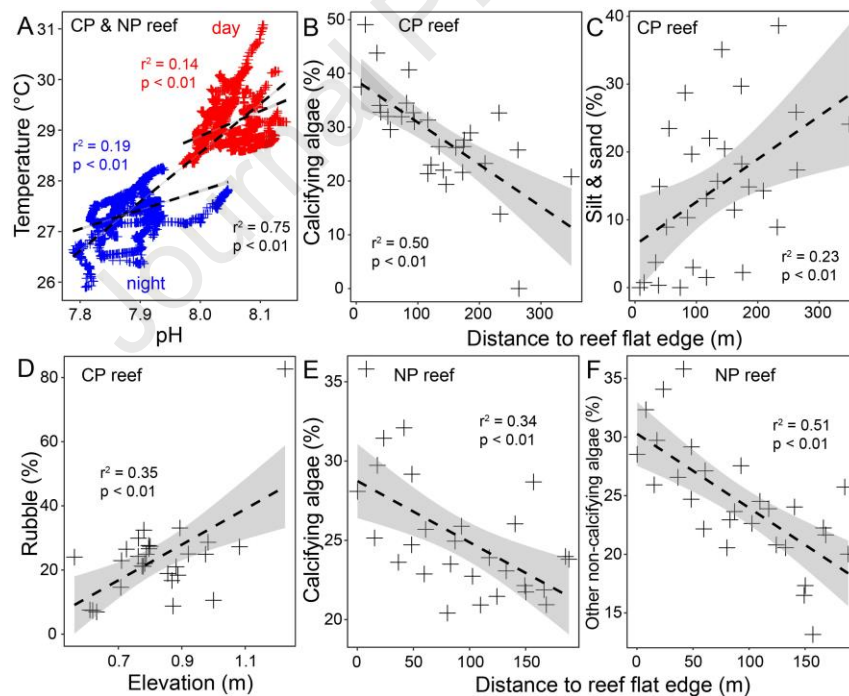


Figure 4 Linear regressions between (A) synchronous measurements in pH and temperature on both reefs. Linear regressions between distance to reef flat edge and the relative abundance of (B) calcifying algae and (C) silt & sand, as well as between elevation relative to datum and the relative abundance of (D) 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”.

211

212 Along the majority of transects from both locations (NP and CP reef flats) the diel pH and temperature ranges increased
 213 from the outer reef flat towards the shoreline (Figure 2, Figure 3, Figure S3 and Figure S4). The diel pH range of all
 214 pH transects on CP reef flat excluding the very long transect CP-T5 revealed the highest level of correlation with
 215 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
 216 reef flat, the diel pH range revealed the highest correlation with distance to reef flat edge ($r^2 = 0.45$, $p < 0.01$, Figure
 217 5 F–J, Table S3). Also, the diel temperature ranges on CP ($r^2 = 0.46$, $p < 0.01$) and NP reef ($r^2 = 0.33$, $p < 0.01$)
 218 correlated strongest with the distance from the reef flat edge (Table S2, Table S3). The diel range in other carbonate
 219 system parameters (DIC, ALK and $\Omega_{\text{Aragonite}}$) also increased towards the shore (Figure 2C). In contrast, across-reef flat
 220 transects from both sites showed that diel pH and temperature ranges exhibit no strong correlation with elevation
 221 (Table S2, Table S3).

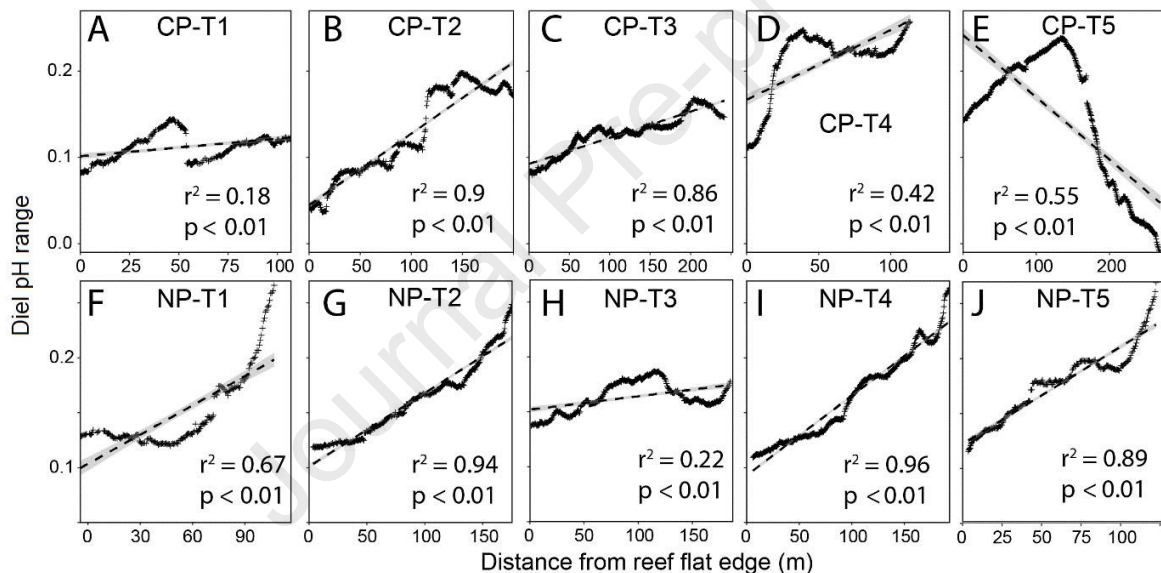


Figure 5 Linear regression between distance from reef flat edge and diel pH range for each transect.

222

223 Variations of pH were observed along all cross-reef transects (Figure 2 and Figure 3). On the CP reef flat, pH varied
 224 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
 225 (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
 226 (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
 227 CP reef flat, abrupt changes of pH along transects corresponding to changes in reef flat bathymetry and thus water
 228 depth were observed. For instance, nightly pH increased by 0.06 pH units across a space of 7 m along transect CP-T1
 229 at the transition to lower reef surface elevation (Figure 2 A). In contrast, along the neighbouring transect (CP-T2) pH
 230 abruptly decreased by 0.08 pH units over 6 m when deeper waters were encountered (Figure 2 B). Along the very

231 wide CP-T5 transect, night-time pH increased by 0.23 units reaching values similar to those observed during the day
232 close to the shoreline (Figure 2 E).

233 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
234 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
235 (σ) in salinity along transects was also only small with 0.22 PSU during the day and 0.13 PSU during the night. Year-
236 long monitoring showed that salinity variability on CP reef flat was more pronounced during rainfall events (Knebel
237 et al., 2021). This highlights that the results of this study represent only a snapshot in time and temporal variations in
238 the spatial patterns of pH, temperature, salinity, and benthos compositions were not quantified.

239

240 **3.2 Benthos composition**

241 The results of the benthos survey correspond to previous surveys of reef benthos cover on Kiritimati Island (Sandin
242 et al., 2008). Example images of the benthos at both reef flats can be found in the supplementary (Figure S1 and Figure
243 S2). The CP reef flat was characterized by a higher fraction of “rubble”, but a lower fraction of green algae, especially
244 “other non-calcifying algae”, compared to NP reef flat (Figure 6 A). Furthermore, coral cover on CP reef flat was
245 slightly higher compared to NP reef flat. The benthic community structure between both reef sites was significantly
246 different as ANOSIM ($r = 0.52$, $p < 0.01$) and PERMANOVA ($r^2 = 0.36$, $p < 0.01$) tests revealed, but no significant
247 difference was found between the transects of each reef flat (Table S4 and S5). The significant difference in elevation
248 and the apparent difference in width between CP and NP reef flats may supersede any potential relationship between
249 both parameters and the benthic community composition. Thus, to further explore the influence of these parameters
250 on the benthos composition, both reef flats were studied separately. Results for both reefs combined can be found in
251 Table S1. Significant correlations between distance to reef flat edge and the fraction of “calcifying algae” ($r^2 = 0.50$,
252 $p < 0.01$; 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
253 the fraction of “calcifying algae” ($r^2 = 0.34$, $p < 0.01$, Figure 4 E) and “other non-calcifying algae” ($r^2 = 0.51$, $p < 0.01$;
254 Figure 4 F) on NP reef flat (Table S3). These observations can be attributed to the typical zonation of reef flats with
255 elevated abundances of calcifying algae, mainly coralline red algae, on the algal rim, and more silt and sand closer to
256 the shore (Figure 2, Figure 3). This is further supported by the significant difference in benthic community composition
257 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
258 deduced from PERMANOVA tests (Table S5) and visible in PCA diagrams (Figure 6 B and C). Reef flat elevation
259 also significantly correlated with the fraction of calcifying algae on NP reef flat ($r^2 = 0.15$, $p = 0.05$; Table S3) and the
260 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
261 C). This outlier represents overwash sediment that accumulated at the narrow outlet of the quasi-lagoonal body of
262 water behind the reef flat (i.e., the most shoreward LIT along CP-T3, Figure 1B, Figure 2 C). The results of Mantle
263 tests also showed that the benthos composition significantly varied with elevation on CP ($r = 0.31$, $p < 0.01$) and NP
264 reef flats ($r = 0.22$, $p < 0.01$; Table S7 and S8).

265 For CP reef flat, results from Mantel tests revealed no relationship between benthos composition and the mean, diel
266 range, day and night values in pH or temperature (Table S7). On NP reef flat, Mantel tests revealed significant
267 correlations between mean ($r = 0.42$, $p < 0.01$) and day pH ($r = 0.29$, $p < 0.01$) with benthos composition (Table S8).
268

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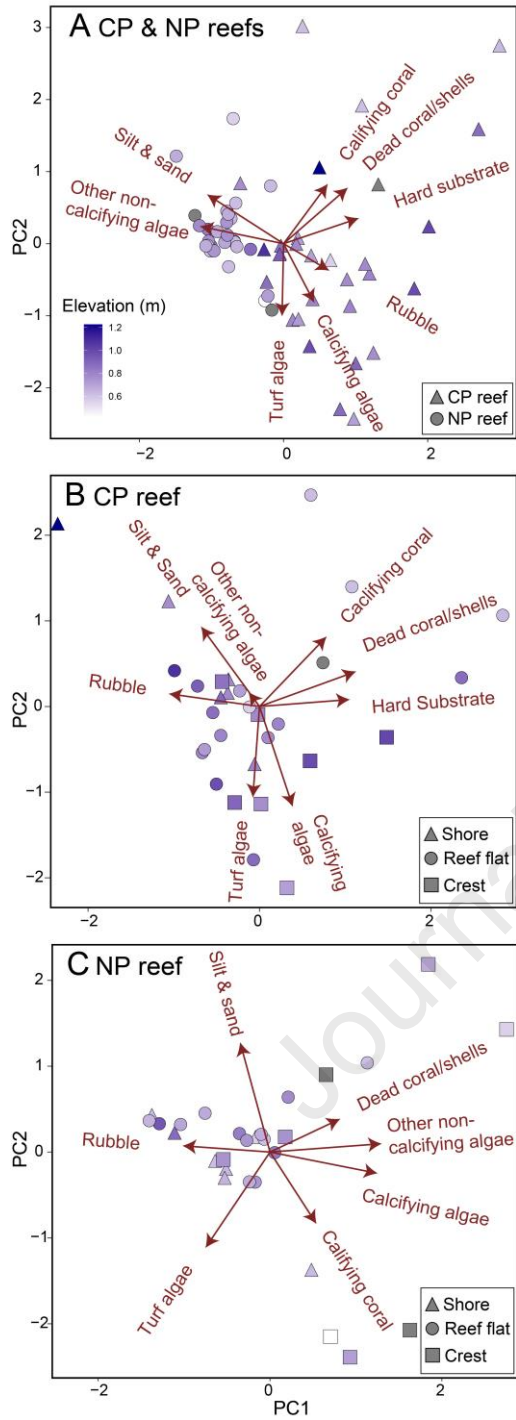


Figure 6 PCA diagrams of the benthic community structure recorded on (A) both reefs, (B) CP, and (C) NP reef flats. For all diagrams, colours indicate the elevation relative to datum for each LIT where the higher elevation corresponds to shallower water depth. For (A), symbols indicate reef sites, and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

270 4 Discussion

271 4.1 Seawater pH and temperature variations

272 Along transects, seawater pH and temperature ranges revealed the strongest correlation with distance from the reef
273 flat edge, when fitted to a linear function. It should be noted that these cross-reef flat observations are at very shallow
274 water depths only (maximal ~ 1 m depth), which differ from similar transects spanning various reef habitats including
275 deeper water (> 15 m depth; Cyronak et al., 2019). Cyronak et al. (2019) reported that diel pH and temperature ranges
276 showed the highest level of correlation with water depth, best fitted to a power function. Furthermore, Guadayol et al.
277 (2014) also found a linear relationship between the diel pH range with distance to reef flat edge, but an exponential
278 relationship between the diel pH range and water depth for deeper waters. This difference reflects that in shallower
279 and deeper waters different mechanisms prevail in determining the diel ranges in pH and temperature. The ratio
280 between the products of NEP/NEC and water volume is much higher at shallower water levels than in deep water.
281 This results in an elevated diel pH range in shallower water compared to deeper water (Page et al., 2019). Similarly,
282 smaller volumes of water at shallower water levels heat up or cool down more rapidly than larger volumes of water at
283 higher depths resulting in a negative correlation between diel temperature range and water depth. However, on shallow
284 reef flats where variations in water depth are only small, diel pH and temperature ranges may be predominantly
285 determined by the seawater residence time (Guadayol et al., 2014). Seawater exchange with the ocean declines across
286 the reef flats towards the shore and consequently, seawater residence time increases with distance from the outer edge
287 of the reef flat (McCabe et al., 2010). At locations with elevated seawater residence time, the products of NEP and
288 NEC are integrated over a longer time period before dilution through exchange with open ocean water. Likely, this
289 results in the observed positive correlation between diel pH and temperature ranges with distance to the reef flat edge.
290 Other carbonate system parameters, including DIC, ALK and $\Omega_{\text{Aragonite}}$, also showed a pronounced diel variability
291 closer to the shore (Figure 2 C). DIC is primarily influenced by diel changes in the balance between photosynthesis
292 and respiration (i.e. NEP) with elevated photosynthetic rates reducing DIC during the day, while changes in ALK can
293 be solely attributed to changes in the balance between calcification and dissolution (i.e. NEC) with enhanced
294 calcification during the day reducing ALK (Cyronak et al., 2018). Furthermore, the elevated aqueous CO_2
295 concentration at night shifts the carbonate equilibrium, reducing the carbonate ion concentration of the seawater, and
296 thus $\Omega_{\text{Aragonite}}$. The diel ranges in DIC, ALK and $\Omega_{\text{Aragonite}}$ increase when moving further shoreward across the reef flat
297 (Figure 2 C). Again, these relationships can be best explained by increasing seawater residence times due to reduced
298 horizontal mixing with distance to the reef flat edge.

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

304 Furthermore, especially along the shallower transects on the CP reef flat, abrupt changes in pH were observed. These
305 changes are not a function of the distance from the reef flat edge and do not necessarily occur with similar magnitude

306 (but in opposing directions), during day and night. These observed variations in pH did not appear to coincide with
 307 changes in the benthic community composition. Instead, changes in reef flat bathymetry best explain observed spatial
 308 variations of pH. However, the abrupt changes of pH along a transect cannot be explained by changes in bathymetry
 309 alone as an increase in water depth can result in an abrupt positive as well as a negative shift in pH, recorded during
 310 the same time of a day (compare Figure 2 A and B). Instead, we propose that the observed spatial pH variability likely
 311 reflects the local flow patterns of water on the reef flat with possible ponding in some locations. For instance, seawater
 312 with an elevated pH during the night between 0 and 100 m from shore along CP-T5 (see Figure 2 E, Figure 7)
 313 represents seawater that had not been exchanged with ocean water since the water level had dropped in the afternoon
 314 when pH values had been higher due to the stimulated reefal photosynthesis during the day. Furthermore, a lens of
 315 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
 316 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
 317 Figure 2 B). This low pH water lens may be explained by water draining out of the quasi-lagoonal body of water to
 318 the North of CP-T4 as the water level drops during the outgoing tide and then is directed westwards by the
 319 northwestward flowing South Equatorial Current. This interpretation aligns with previous studies that found that
 320 hydrodynamic forcing through mainly wave action and the tidal cycle, and to a lesser degree wind, has the strongest
 321 influence on spatial variations of the reefal seawater residence time and parameters of the seawater carbonate system
 322 (Hannan et al., 2020; Zhang et al., 2012). However, the exact hydrological regime of CP reef flat remains speculative
 323 as flow directions or seawater residence times were not recorded.
 324

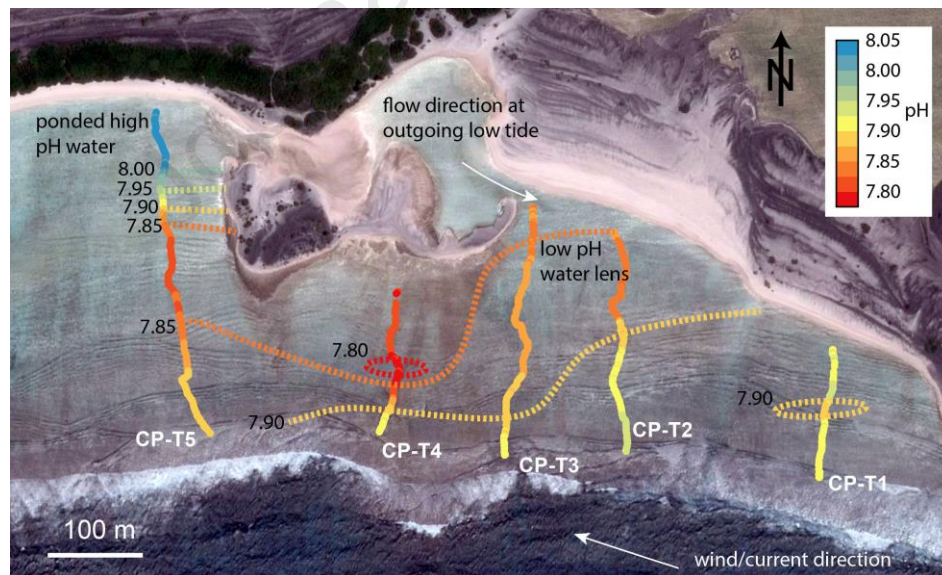


Figure 7 Seawater pH measurements along transects on CP reef flat during the night and outgoing low tide. Dashed lines illustrate estimated areas of similar pH values between transects. Wind direction (ESE) from Time and Date AS (2022). Image credit: Google Earth.

325

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

331 4.2 Variations in benthic community structure

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

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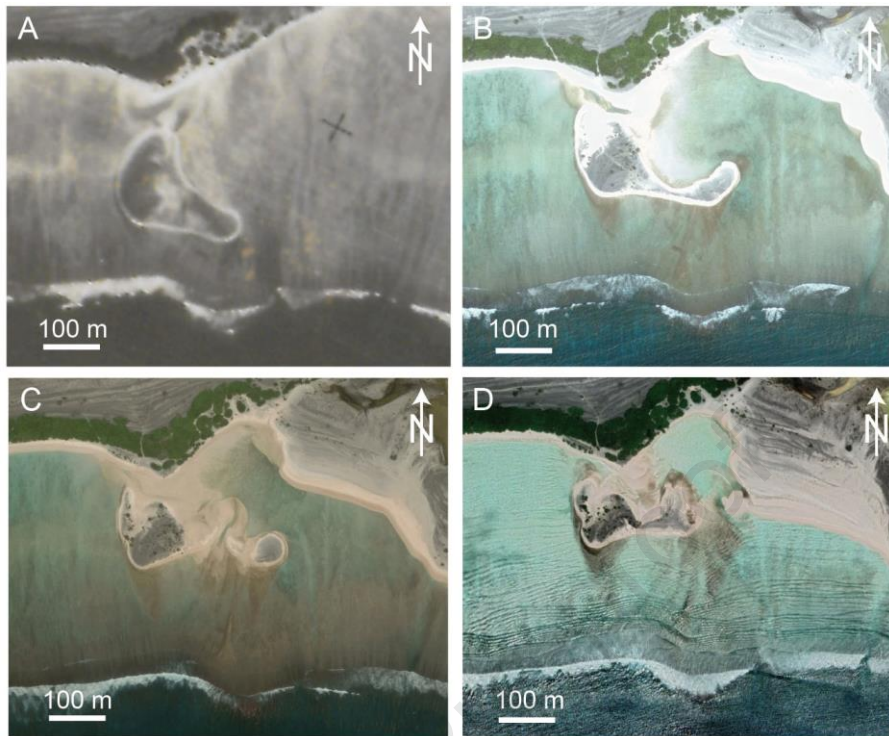


Figure 8 Aerial photography and satellite imagery from CP reef flat recorded before this study was conducted in (a) 1957, (b) 2006, (c) 2013, and afterwards in (d) 2020. Image credit: Secretariat of the South Pacific (SPC), Google Earth.

346

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

356 **5 Conclusions**

357 Environmental surveys on the narrow reef flats of Kiritimati Island revealed that spatial variations of pH and
 358 temperature at a given location on the reef flat were predominantly controlled by the distance to the reef flat edge and
 359 the local bathymetry. The amplitude of diel pH and temperature ranges linearly increased towards the shore with
 360 distance to reef flat edge, very likely as seawater residence time increased across the reef flat towards the shore.
 361 Furthermore, local pH and temperature conditions appeared to be modified by local hydrodynamics (e.g., flow

362 patterns) that are bathymetrically controlled. Similarly, spatial variations in benthic community composition were
363 primarily linked to the geomorphological structure of the reef flat with little evidence for a relationship between
364 benthic community structure and local seawater pH or temperature conditions.

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

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

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- 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

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

Carlos Carvajal: Conceptualization, Investigation, Project administration

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