Diverse coral communities in naturally acidified waters of a Western Pacific reef

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Abstract Anthropogenic carbon dioxide emissions are acidifying the oceans, reducing the concentration of carbonate ions ([CO_3^{2-}]) that calcifying organisms need to build and cement coral reefs. To date, studies of a handful of naturally acidified reef systems reveal depauperate communities, sometimes with reduced coral cover and calcification rates, consistent with results of laboratory-based studies. Here we report the existence of highly diverse, coral-dominated reef communities under chronically low pH and aragonite saturation state (Ω_{ar}). Biological and hydrographic processes change the chemistry of the seawater moving across the barrier reefs and into Palau's Rock Island bays, where levels of acidification approach those projected for the western tropical Pacific open ocean by 2100. Nevertheless, coral diversity, cover, and calcification rates are maintained across this natural acidification gradient. Identifying the combination of biological and environmental factors that enable these communities to persist could provide important insights into the future of coral reefs under anthropogenic acidification.

Humans release billions of tons of CO_2 into the atmosphere each year [*Keeling et al.*, 2005; *Solomon et al.*, 2007], to date, about 30% of this CO_2 has been absorbed by the ocean [*Canadell et al.*, 2007; *Le Quéré et al.*, 2009; *Sabine et al.*, 2011]. The resulting decline in seawater pH, Ω_{ar}, and [CO_3^{2-}], a process known as ocean acidification [*Raven et al.*, 2005], poses a significant threat to many marine ecosystems worldwide. Coral reefs are considered particularly vulnerable to ocean acidification because reef-building corals and calcifying algae use CO_3^{2-} to produce calcium carbonate ($CaCO_3$) skeletons that ultimately build the reef [*Kleypas et al.*, 1999]. Much of our current understanding of the impacts of ocean acidification on coral reef futures is shaped by results of controlled CO_2-manipulation experiments, and information from coral reef communities inhabiting naturally low pH environments suggest potential ecosystem-level consequences of prolonged exposure [*Manzello et al.*, 2008; *Crook et al.*, 2011; *Fabricius et al.*, 2011]. While none of these naturally more acidic coral reef environments are perfect analogs for anthropogenic ocean acidification [*Field et al.*, 2011], consistent patterns have emerged from these studies [*Manzello et al.*, 2008; *Crook et al.*, 2011; *Fabricius et al.*, 2011]. Typically, hard coral diversity is low; in some instances, the area of reef floor covered with live corals is reduced; and in eastern Pacific upwelling zones, elevated rates of bioerosion and low levels of abiogenic cementation result in reef structures that are highly porous and structurally fragile [*Manzello et al.*, 2008; *Crook et al.*, 2011; *Fabricius et al.*, 2011]. These observations, combined with the fact that today's most well-developed and diverse tropical reefs occur within a narrow geographic range characterized by open ocean [CO_3^{2-}] > 200 μmol kg^{-1} and Ω_{ar} > 3.3 [*Kleypas et al.*, 1999; *Hoegh-Guldberg et al.*, 2007], imply that coral communities may have limited capacity to adapt to levels of acidification projected for the 21st century [*Hoegh-Guldberg*, 2012] and that healthy coral reefs could cease to exist within this time frame [*Hoegh-Guldberg et al.*, 2007; *Hoegh-Guldberg*, 2011]. Here we report the existence of healthy, diverse coral reef communities living under levels of natural acidification approaching those projected for the tropical western Pacific open ocean by 2100. Understanding the combinations of genetic and/or environmental factors that enable coral communities to function under relatively extreme conditions of pH and Ω_{ar} will inform projections of reef futures under climate change and ocean acidification.

Surface water (0–3 m) samples were collected at nine stations across the Palauan reef system (7.27 to 7.58°N; 134.39 to 134.56°E) (Figure 1) during both the wet (19–24 September 2011) and dry (25 March to 07 April 2012) seasons, from sunrise to sunset, and throughout the tidal cycle. As shown by previous studies [*Gattuso et al.*, 1993; *Silverman et al.*, 2007a, 2007b; *Shamberger et al.*, 2011], diurnal extremes in reef carbonate chemistry occur 0–2 h after sunrise and before sunset. Thus, these samples provide insight into both the seasonal and tidal range of carbonate chemistry, as well as the diurnal range at our sampling stations. The
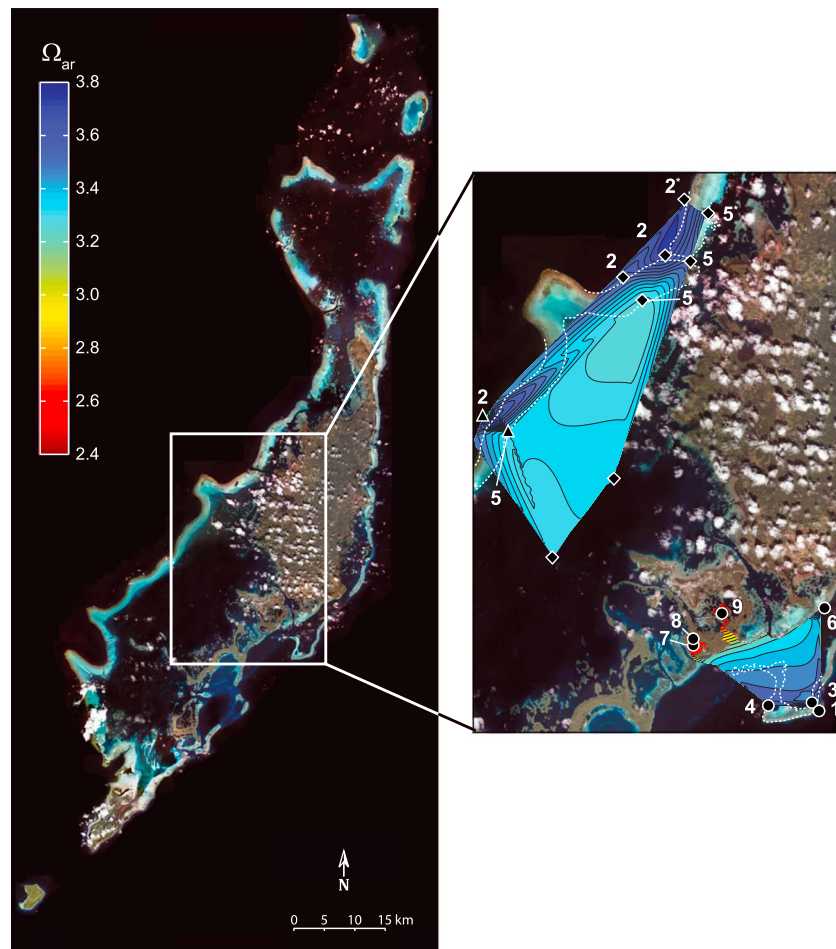
Figure 1. Satellite image of the main islands of Palau. IKONOS 4 m multispectral image provided by NOAA National Centers for Coastal Ocean Science, Silver Spring, Maryland. The inset shows aragonite saturation state (Ω_{ar}) colored contours and the locations where water samples were collected in 2011 (diamonds), 2012 (triangles), and both 2011 and 2012 (circles). Dotted white lines in the inset represent the edges of the barrier reefs. Site numbers are in order of distance from offshore waters with lower numbered sites being further offshore. Sites 7–9 are located in Rock Island bays. Data from sites without numbers are not discussed because there are no coral reefs at those locations. Data from sites with the same number were very similar and averaged together. Sites with asterisks show where ecological data (see Figure 4) were collected for sites with the same number.

carbonate chemistry of Palauan reef seawater is significantly different from open ocean source water (Figures 1 and 2). The full seawater CO_2 system calculated from total alkalinity (TA), dissolved inorganic carbon (DIC), salinity, and in situ temperature measurements shows that surface water pH, $[CO_3^{2-}]$, and Ω_{ar} decrease with distance from offshore waters (Figures 1, 2, and supporting information Figure S1). Just inshore of the barrier reefs, average Ω_{ar} values are 0.2 to 0.3 lower and pH values are 0.02 to 0.03 lower than they are offshore, declining further as water moves across the back reef, lagoon, and into the meandering bays and inlets that characterize the Rock Islands (sites 7–9) (Figures 1 and 2). These Rock Island coral communities inhabit seawater with average Ω_{ar} values of 2.7 or less, and as low as 1.9 (Figure 2). Among the nine stations occupied along our offshore-inshore transect, average Ω_{ar} is 3.26 ± 0.16. This is at the previously estimated geographic Ω_{ar} limit for coral reef accretion [*Kleypas et al.*, 1999; *Hoegh-Guldberg et al.*, 2007].

The relatively high levels of acidification of Palauan reef seawater are produced through a combination of natural biological processes and circulation patterns within the reef system. The specific processes and their relative contribution, particularly to the lowering of Ω_{ar} values, can be determined by comparing offshore source water temperature, salinity, TA, and DIC data to those measured at our reef sites (supporting information). Water temperatures inside the reef are within 1.3°C of offshore values, a difference that is too small to account for the large difference in Ω_{ar} (Table S1). Rather, calcification, respiration, and dilution (mixing of
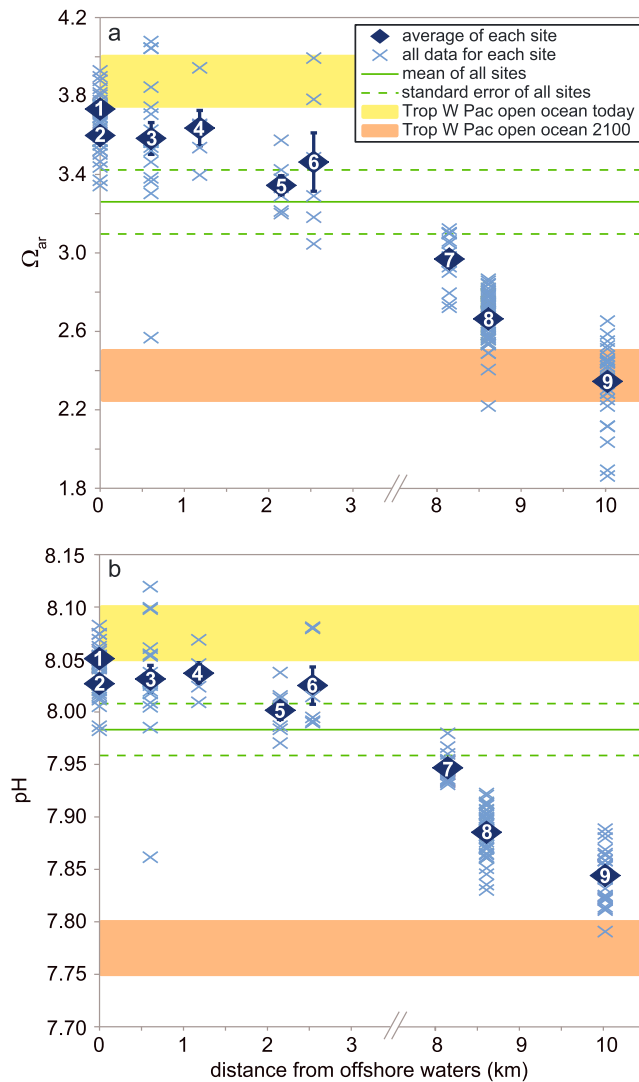
Figure 2. (a) Average aragonite saturation state (Ω_{ar}) and (b) pH (seawater scale) ± 1 standard error (dark blue diamonds with error bars) and all data collected (blue crosses) for each site versus distance from offshore waters (see supporting information). Shading represents the range of Ω_{ar} [*Steinacher et al.*, 2009] (a) and pH [*Denman et al.*, 2011] (b) in the tropical western Pacific open ocean in 2000 (yellow shading) and predicted for 2100 under the Intergovernmental Panel on Climate Change Special Report on Emissions Scenarios A2 emissions scenario (orange shading). Green horizontal lines represent the mean (solid line) Ω_{ar} (a) and pH (b) of all sites ± 1 standard error (dashed green lines) of all sites. Numbers on the symbols correspond to the site locations shown in Figure 1.

offshore source water with low salinity rainwater and island runoff) appear to be the main factors driving the change in seawater chemistry. Dilution of reef water with freshwater can lower seawater Ω_{ar} because freshwater in this region has low [CO_3^{2-}]. Using our offshore salinity, TA, and DIC data; a previously established relationship between TA and salinity for the tropical Pacific open ocean [*Lee et al.*, 2006]; and the in situ reef seawater salinity, we estimate that dilution accounts for 1–17% of the difference in Ω_{ar} between offshore and reef waters (Figure S2, supporting information). Calcification further lowers seawater Ω_{ar} by consuming CO_3^{2-} and adding CO_2 to the system, while dissolution raises Ω_{ar} by producing CO_3^{2-} and consuming CO_2 (Figure S1). Because calcification (respiration) decreases (increases) TA and DIC in a 2:1 ratio, we can use our data to estimate the net contribution of calcification and dissolution to the lowering of Ω_{ar} as seawater moves across the barrier reefs and into the bays (Figure S3). Our calculations reveal that 68–99% of the difference in Ω_{ar} between offshore source water and reef water is driven by net calcification by reef organisms (Figures 3 and S2). Respiration lowers Ω_{ar} by producing CO_2 which increases seawater acidity and DIC without altering TA, whereas photosynthesis raises Ω_{ar} by consuming CO_2. At our barrier reef and
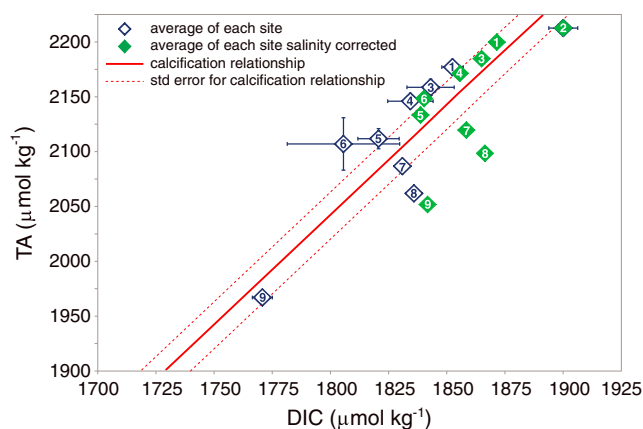
Figure 3. Observed average DIC versus average TA ± 1 standard error (open blue diamonds with error bars) for each site and salinity corrected values (filled green diamonds) estimated using the dilution relationship of *Lee et al.* [2006]. Dilution calculations are described in the supporting information. The solid red line is the modeled DIC versus TA relationship (slope = 2) if decreases in DIC and TA from average offshore values were due to calcification alone. Values to the right (left) of this line suggest significant respiration (photosynthesis) and/or the input of groundwater with high (low) CO_2, in addition to dilution and calcification. The error for the calcification relationship is represented by ± 2 standard error from the mean TA and DIC of the offshore data (red dotted lines). The error for the calcification relationship is based on the variability of the offshore data because this is the source water to the Palauan archipelago that coral reef calcification is altering. Numbers on the symbols correspond to the site locations shown in Figure 1.

exposed sites (sites 1–6), the dilution corrected DIC-TA data fall within the error of the modeled calcification relationship (Figure 3) indicating an insignificant influence of photosynthesis and respiration on mean DIC and Ω_{ar}. Photosynthesis and respiration rates may be high on the barrier reef and exposed sites but are approximately balanced and so do not significantly affect Ω_{ar}. However, in the three sheltered Rock Island bay sites (sites 7–9), where Ω_{ar} levels are extremely low (Figures 1 and 2), the corrected DIC-TA data fall to the right of the calcification line indicating an additional input of DIC (Figure 3). This input of DIC may reflect respiration occurring within the bays (by the benthic community and microbial decomposition of organic matter), or discharge of groundwater with elevated CO_2 due to terrestrial respiration. Our calculations reveal that in situ respiration and/or groundwater discharge contributes between 17 and 30% of the difference in Ω_{ar} between offshore source water and reef water at the Rock Island sites (Figure S2). Residence time of seawater in the Rock Island bays is likely to be much longer than at the well-flushed exposed sites, enabling calcification and respiration to drive Ω_{ar} to very low levels.

Average annual calcification rates of massive *Porites* corals from 2007 to 2009 (supporting information), calculated from 3-D Computerized Tomography scan images of skeletal cores (method described in *Crook et al.* [2013]), are comparable on reefs with high (site 4: 0.89 ± 0.02 g cm^{-3} yr^{-1}) and low (site 9: 0.91 ± 0.02 g cm^{-3} yr^{-1}) Ω_{ar}, suggesting that calcification by at least one dominant reef-building species is maintained under relatively acidic conditions. This result is contrary to predictions based on laboratory manipulation experiments but consistent with findings at CO_2 seeps in Papua New Guinea [*Fabricius et al.*, 2011]. Three additional indices were thus examined to assess the health of the coral communities across Palau's natural acidification gradient: percentage of live coral cover, coral diversity (Shannon diversity index), and coral taxonomic richness (number of coral genera). This analysis reveals patterns different from those observed in other naturally more acidic reef systems. In the Rock Island bay sites ($\Omega_{ar} \leq 2.7$), coral cover is maintained at relatively high levels: 32 to 63%, significantly higher than the western Pacific average of 25% (Figure 4 and supporting information Figure S4) [*Bruno and Selig*, 2007]. Hard coral diversity is also high, averaging 1.7, compared with 1.1 to 1.6 on the barrier reef and more exposed sites within Palau (Figure 4). Although genus richness is a somewhat crude measure of coral community health, it is widely measured and useful for comparing coral reef systems where diversity data have not been reported. In Palau's naturally low Ω_{ar} sites, hard coral richness averages 12 genera transect^{-1} (Figure 4), higher than on the barrier reef and more exposed sites (8 to 10 genera transect^{-1}) and higher than on neighboring Micronesian reefs (4 to 10 genera transect^{-1}). At comparable Ω_{ar}, the naturally more acidic Papua New Guinea CO_2 seeps support 33% live coral cover and an average of 2.6 hard coral genera transect^{-1} [*Fabricius et al.*, 2011]. Likewise, although biogeographic factors
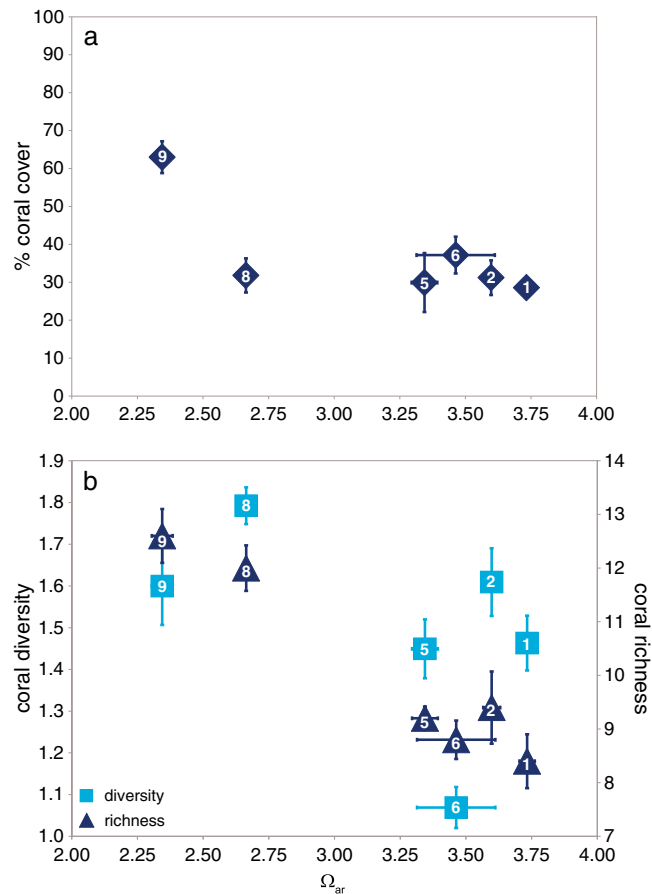
Figure 4. (a) Average percentage of live coral cover, (b) coral diversity (light blue squares), and coral richness (number of coral genera per transect) (dark blue triangles) versus aragonite saturation state (Ω_{ar}) ± 1 standard error. Numbers on symbols correspond to the site locations shown in Figure 1.

contribute to the generally low numbers of genera on eastern Pacific and Caribbean reefs, within these systems, coral richness declines with increasing levels of acidity. For example, reefs of the Galapagos and Gulf of Panama, where daytime Ω_{ar} averages 2.7 and 2.9, respectively [*Manzello*, 2010], support six hard coral genera although coral cover can be high in monospecific stands [*Cortes*, 1997]. Similarly, reefs of the Yucatan Peninsula, where groundwater discharge causes natural acidification, support just two genera of hard coral where Ω_{ar} values are less than 2.5, compared to seven genera on nearby unaffected reefs [*Crook et al.*, 2011]. Thus, among the handful of naturally low pH, low Ω_{ar} coral reef sites identified to date, Palau is currently unique in maintaining extraordinarily dense and diverse coral communities.

None of the naturally acidified reefs that exist today, including Palau, provide an exact representation of the chemical conditions and adaptive pressures coral communities will face as CO_2 levels continue to rise over the course of this century. In the eastern Pacific, for example, low Ω_{ar} is coupled with large seasonal swings in temperature, significantly elevated nutrient concentrations, and a community structure heavily influenced by biogeography [*Glynn and Colgan*, 1992; *Manzello et al.*, 2008; *Manzello*, 2010]. Where discharge of high CO_2 groundwater causes natural acidification, there are concurrent increases in TA, DIC, and nutrient concentrations [*Crook et al.*, 2011]. At volcanic CO_2 seeps [*Fabricius et al.*, 2011], the scale of connectivity is generally larger than the acidified area so that larvae of many species are continuously recruited from external, unaffected source populations, limiting selective pressure for adaptation [e.g., *Cigliano et al.*, 2010]. On Palau, natural acidification is caused by a combination of hydrographic processes; calcification by barrier, patch, and bay reefs; CO_2 emitted through respiration; and influences from the land, not solely by absorption of excess CO_2. Despite the fact that none of these sites provide a perfect analog for global ocean acidification due to anthropogenic CO_2, information from each of them provides important clues about the potential responses

of coral reef communities to future levels of acidification. Coral communities that occupy Palau's relatively acidic reef areas developed over thousands of years, and unlike the communities in the CO_2 vent sites and areas of high CO_2 groundwater discharge, experience low but relatively stable pH and Ω_{ar} over tidal and seasonal cycles (Table S2). By comparing conditions and community responses among the full spectrum of naturally acidified coral reef sites, we will gain insight into the factors that enable healthy coral communities to persist under relatively acidic conditions.

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