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### **RESEARCH LETTER**

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### **Key Points:**

- Biogeochemical processes drive natural acidification in a coral reef system
- Despite natural acidification, coral communities appear healthy
- Coral cover, diversity, and calcification are maintained in acidified conditions

#### **Supporting Information:**

- Readme
- Figure S1
- Figure S2
- Figure S3
- Supplementary Figures & Tables

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# 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 ( $\Omega_{ar}$ ). 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<sub>2</sub> into the atmosphere each year [Keeling et al., 2005; Solomon et al., 2007], to date, about 30% of this CO<sub>2</sub> 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,  $\Omega_{arr}$  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<sub>3</sub>) 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<sub>2</sub>-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  $[CO_3^{2-}] > 200 \,\mu\text{mol}\,\text{kg}^{-1}$  and  $\Omega_{ar} > 3.3$  [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  $\Omega_{ar}$ 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

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**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 ( $\Omega_{ar}$ ) 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<sub>2</sub> 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  $\Omega_{ar}$  decrease with distance from offshore waters (Figures 1, 2, and supporting information Figure S1). Just inshore of the barrier reefs, average  $\Omega_{ar}$  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  $\Omega_{ar}$  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  $\Omega_{ar}$  is 3.26±0.16. This is at the previously estimated geographic  $\Omega_{ar}$  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  $\Omega_{ar}$  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  $\Omega_{ar}$  (Table S1). Rather, calcification, respiration, and dilution (mixing of

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**Figure 2.** (a) Average aragonite saturation state ( $\Omega_{ar}$ ) and (b) pH (seawater scale)  $\pm 1$  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  $\Omega_{ar}$  [*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)  $\Omega_{ar}$  (a) and pH (b) of all sites  $\pm 1$  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  $\Omega_{ar}$  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  $\Omega_{ar}$  between offshore and reef waters (Figure S2, supporting information). Calcification further lowers seawater  $\Omega_{ar}$  by consuming  $CO_3^{2^-}$  and adding  $CO_2$  to the system, while dissolution raises  $\Omega_{ar}$  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  $\Omega_{ar}$  as seawater moves across the barrier reefs and into the bays (Figure S3). Our calculations reveal that 68–99% of the difference in  $\Omega_{ar}$  between offshore source water and reef water is driven by net calcification by reef organisms (Figures 3 and S2). Respiration lowers  $\Omega_{ar}$  by consuming  $CO_2$ . At our barrier reef and exposed sites (sites 1–6), the dilution corrected DIC-TA data fall within the error of the modeled calcification relationship (Figure 3)



**Figure 3.** Observed average DIC versus average TA  $\pm$  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<sub>2</sub>, in addition to dilution and calcification. 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.

indicating an insignificant influence of photosynthesis and respiration on mean DIC and  $\Omega_{ar}$ . Photosynthesis and respiration rates may be high on the barrier reef and exposed sites but are approximately balanced and so do not significantly affect  $\Omega_{ar}$ . However, in the three sheltered Rock Island bay sites (sites 7–9), where  $\Omega_{ar}$ 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  $\Omega_{ar}$  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  $\Omega_{ar}$  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:  $0.89 \pm 0.02$  g cm<sup>-3</sup> yr<sup>-1</sup>) and low (site 9:  $0.91 \pm 0.02$  g  $\rm cm^{-3} \, yr^{-1}) \, \Omega_{\rm arr}$  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<sub>2</sub> 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  $\Omega_{ar}$  sites, hard coral richness averages 12 genera transect<sup>-1</sup> (Figure 4), higher than on the barrier reef and more exposed sites (8 to 10 genera transect<sup>-1</sup>) and higher than on neighboring Micronesian reefs (4 to 10 genera transect<sup>-1</sup>). At comparable  $\Omega_{arr}$  the naturally more acidic Papua New Guinea CO<sub>2</sub> seeps support 33% live coral cover and an average of 2.6 hard coral genera transect<sup>-1</sup> [Fabricius et al., 2011]. Likewise, although biogeographic factors 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,



**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 ( $\Omega_{ar}$ ) ± 1 standard error. Numbers on symbols correspond to the site locations shown in Figure 1.

where daytime  $\Omega_{ar}$  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  $\Omega_{ar}$  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  $\Omega_{ar}$  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  $\Omega_{ar}$  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<sub>2</sub> groundwater discharge, experience low but relatively stable pH and  $\Omega_{ar}$  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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### Diverse Coral Communities in Naturally Acidified Waters of a Western Pacific Reef

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### **Supporting Information**

### Sites

In September 2011 and March-April 2012 we collected 228 water samples at 9 different sites throughout the Palauan archipelago for TA and DIC analyses in order to characterize the spatial and temporal variability of the seawater CO<sub>2</sub> system within Palau. Samples were collected on the ocean side (sites 2 in Figure 1) and lagoon edge (sites 5 in Figure 1) of the northwestern barrier reef at Ngaremlengui; on the ocean side (site 1 in Figure 1) and lagoon edge (sites 3 and 4 in Figure 1) of the southeastern barrier reef at Uchelbeluu; in the northwestern lagoon (two unnumbered sites in Figure 1); at the edge of a southeastern fringing reef at Airai (site 6 in Figure 1); and within Risong Bay (sites 7 and 8 in Figure 1) and Nikko Bay (site 9 in Figure 1) in the Rock Islands.

Distance from offshore waters was determined using the ruler tool in Google Earth. For exposed sites (sites 3-6), a straight line perpendicular to the nearest barrier reef was measured from the site to approximately 300 m ocean ward of the barrier reef crest where breaking waves can be seen in the satellite image. For Rock Island sites (sites 7-9), the shortest path between islands from the site to approximately 300 m ocean ward of the nearest barrier reef crest was measured. The same offshore point was used for all three Rock Island sites.

### **Data Collection and Analyses**

In situ temperature was measured in 2011 with TidbiT v2 water temperature data loggers produced by Onset with a manufacturer stated accuracy of 0.2 °C and in 2012 with a RBR XR-620 CTD with a manufacturer stated temperature accuracy of  $\pm 0.002$  °C. Surface water (0-3 m) samples were collected multiple times a day between sunrise and sunset and on 3-9 separate days for each site from a Niskin bottle into 300 ml glass bottles (TA/DIC) and 125 ml glass bottles (salinity). Approximately 5 ml were removed from each bottle to allow headspace for expansion and each TA/DIC sample was poisoned with 50 µl saturated mercuric chloride solution immediately after collection to inhibit biological activity and then sealed with screw tops and tape. TA and DIC analyses were performed with a Versatile INstrument for the Determination of Total inorganic carbon and titration Alkalinity (VINDTA) produced by Marianda Marine Analytics and Data. The VINDTA uses coulometric titration for DIC analysis and an open cell potentiometric titration for TA analysis. DIC and TA measurements were standardized with certified reference materials obtained from Andrew Dickson at Scripps Institution of Oceanography [Dickson, 2001; Dickson et al., 2007]. Analyses of replicate samples yielded a mean precision of  $\sim 2 \mu mol \text{ kg}^{-1}$  and  $\sim 1 \mu mol \text{ kg}^{-1}$  for DIC and TA analyses, respectively (n = 9 pairs).

Ecological data were provided by the Palau International Coral Reef Center (PICRC). At each site where teams of PICRC divers collected ecological data, five 50 m transects (the same transect length was used in *Fabricius et al.* [2011]) were laid on the reef at 3 and 10 m depth. For each transect, a photograph was taken at every meter, resulting in 50 photographs per transect. PICRC analyzes their coral ecological data to the genus level. To estimate coral cover, coral richness (number of coral genera), and coral diversity (Shannon diversity index), the photographs were analyzed using Coral Point Count with Excel extensions (CPCe) [*Kholer and Gill*, 2006]. Five random points from each quadrat were used to determine coral cover. Data from the 50 quadrats were averaged to provide the mean for each transect and the five transects were averaged to provide the mean for each depth at each site. Genus richness and diversity data were extracted from the transects and averaged for the depth at each site. Note that richness can be more useful for comparisons across regions than the Shannon diversity index which is sensitive to differences in evenness.

### **Calculations**

The full seawater CO<sub>2</sub> system was calculated using salinity, temperature, TA, and DIC data using an Excel Workbook Visual Basic for Applications translation of the original CO2SYS program [*Lewis and Wallace*, 1998] by Pelletier, Lewis, and Wallace at the Washington State Department of Ecology, Olympia, WA. The CO2SYS program was run with carbonate constants from *Mehrbach et al.* [1973] refit by Dickson and Millero [1987].

Calculations were performed to determine the relative contributions of dilution, calcification, and respiration to decreased  $\Omega_{ar}$  at our sites compared to offshore levels (Supplementary Figure S2).  $\Omega$  is defined as the product of the concentration of calcium ions ([Ca<sup>2+</sup>]) and CO<sub>3</sub><sup>2-</sup> divided by the stoichiometric solubility product for the form of CaCO<sub>3</sub> (such as aragonite, which corals produce) being investigated (K<sup>\*</sup><sub>sp</sub>):  $\Omega = [Ca^{2+}][CO_3^{2-}]/K^*_{sp}$ . A decrease (increase) in [CO<sub>3</sub><sup>2-</sup>], therefore, results in a decrease (increase) in  $\Omega$ . Dilution relationships between TA and salinity and between DIC and salinity were developed by mixing water with the average TA, DIC, temperature, and salinity of our offshore sites (averages of site 1 and 2 data, Supplementary Table S1) with fresh water. The TA of the fresh water end member was calculated with the S-TA relationship of *Lee et al.* [2006] for the tropical Pacific open ocean, the average temperature of our Palau sites, and salinity = 0. The DIC of the fresh water end member was calculated from the estimated TA at salinity = 0 assuming a 9:1 ratio of bicarbonate to carbonate ion concentration and that TA is well approximated by carbonate alkalinity (i.e. only carbonate and bicarbonate ions contribute to TA). To bound our estimates, calculations were also performed with dilution relationships using TA and DIC equal to zero for the fresh water end member. Both sets of calculations produced similar results with dilution accounting for 1 - 21 % and 2 - 30 % of the difference in  $\Omega_{ar}$  between offshore and reef waters, using the S-TA relationship of *Lee et al.* [2006] and zero TA and DIC for the freshwater end members, respectively.

To quantify the contribution of calcification to decreased  $\Omega_{ar}$  at our sites compared to offshore levels, it was assumed that dilution, calcification, and dissolution of CaCO<sub>3</sub> are the only processes that affect TA within the Palauan archipelago. Therefore, the differences between average offshore TA and the average TA measured at each site represent decreases in TA due to dilution and calcification combined (TA<sub>meas</sub> = TA<sub>dilut+cal</sub>). The DIC change due to dilution plus calcification (DIC<sub>dilut+cal</sub>) was calculated from the average measured TA for each site using the dilution relationship described above and assuming a 2:1 decrease in TA:DIC for every mole of CaCO<sub>3</sub> produced. The green squares in Supplementary Figure S2 show  $\Omega_{ar}$  at each site calculated from TA<sub>dilut+cal</sub>, DIC<sub>dilut+cal</sub>, and average *in situ* temperature and salinity. The difference between the  $\Omega_{ar}$  due to dilution and calcification combined (green squares in Supplementary Figure S2) and the  $\Omega_{ar}$  due to dilution alone (light blue dashed line in Supplementary Figure S2) gives the contribution of calcification to lowered  $\Omega_{ar}$  at each of our sites (see green arrow in Supplementary Figure S2). Our calculations show that calcification

accounts for 68 - 99 % and 64 - 98 % of the difference in  $\Omega_{ar}$  between offshore and reef waters, using the S-TA relationship of ref. 19 and zero TA and DIC for the freshwater end members, respectively. However, most of our sites require another process to bring  $\Omega_{\text{ar}}$  to the observed levels (dark blue arrows in Supplementary Figure S2); photosynthesis-respiration and groundwater discharge are likely candidates; the available data do not enable us to distinguish between the two. Our calculations show the barrier reef and exposed sites (sites 3-6) as net photosynthesizing and the Rock Island sites (sites 7-9) as net respiring (Supplementary Figure S2). However, changes in DIC due to net photosynthesis on the barrier reef and exposed sites are insignificant compared to changes due to calcification. This is shown in Figure 3 where the salinity corrected DIC-TA data fall within the error of the calcification relationship. However, in the Rock Islands, changes in DIC due to respiration and/or high CO<sub>2</sub> groundwater discharge are significant and account for 17 – 30 % and 18 – 32 % of the difference in  $\Omega_{ar}$  between offshore and reef waters using the S-TA relationship of ref. 19 and zero TA and DIC for the freshwater end members, respectively. The influence of net respiration and/or groundwater input in the Rock Island bays is evident in Figure 3 which shows that the salinity corrected data fall to the right of the modeled calcification line.

Modern calcification rates of *Porites* corals at sites 4 and 9 were determined by averaging 2007-2009 rates. 2010 and 2011 calcification rates were excluded from average modern rates so they would not reflect the influence of a bleaching event that occurred throughout the Palauan archipelago in 2010. A full description of spatial and temporal variability in coral calcification will be published elsewhere.

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Figures



**Figure S1.** Average carbonate ion concentration  $[CO_3^{2^-}]$  (a) and  $pCO_2$  (b)  $\pm 1$  standard error (dark blue diamonds with error bars) and all data collected (blue crosses) for each site versus distance from offshore waters. Shading represents the range of  $[CO_3^{2^-}]$  [*Feely et al.*, 2009] (a) and  $pCO_2$  [*Steinacher et al.*, 2009] (b) in the tropical western Pacific open ocean in 2000 (yellow shading) and predicted for 2100 under the IPCC SRES A2 emissions scenario (orange shading). Green horizontal lines represent the mean (solid line)  $[CO_3^{2^-}]$  (a) and  $pCO_2$  (b) of all sites  $\pm 1$  standard error of all sites (dashed green lines). Numbers on the symbols correspond to the site locations shown in Figure 1.



**Figure S2.** Average  $\Omega_{ar}$  versus average salinity  $\pm 1$  standard error (dark blue diamonds with error bars). The solid dark blue horizontal line represents average offshore  $\Omega_{ar}$ . The blue dashed dilution line represents the relationship between  $\Omega_{ar}$  and salinity when average offshore water (average of site 1 and site 2 data) mixes with low salinity water. Green squares represent average  $\Omega_{ar}$  calculated for each site if dilution and calcification were the only processes affecting  $\Omega_{ar}$ . Numbers on the diamonds correspond to the site locations shown in Figure 1. The light blue arrows illustrate the change in  $\Omega_{ar}$  from offshore levels due to dilution alone, using sites 6 and 9 as examples. The green arrows illustrate the change in  $\Omega_{ar}$  due to photosynthesis-respiration and/or groundwater discharge alone.



**Figure S3.** Average total alkalinity (TA) (a) and dissolved inorganic carbon (DIC) (b)  $\pm 1$  standard error (dark blue diamonds with error bars) and all data collected (blue crosses) for each site versus distance from offshore waters. Green horizontal lines represent the mean (solid line) TA (a) and DIC (b) of all sites  $\pm 1$  standard error of all sites (dashed green lines).



**Figure S4.** Photographs of Palauan coral reef communities. Site 9 (see Figure 1) in the Rock Islands where mean  $\Omega_{ar} = 2.34 \pm 0.04$  (a) and the lagoon side of the southeastern barrier reef at site 3 (see Figure 1) where mean  $\Omega_{ar} = 3.58 \pm 0.08$  (b).

### Tables

**Table S1.** Average temperature, salinity, and carbonate chemistry data  $\pm 1$  standard error. Site numbers correspond to those in Figure 1.

site #	Ν	temp (°C)	salinity	TA (µmol kg⁻¹)	DIC (µmol kg⁻¹)	$\Omega_{ar}$	pCO <sub>2</sub> (µmol)	рН	CO3 <sup>2-</sup> (µmol kg <sup>-1</sup> )
1	18	29.5 ± 0.1	33.4 ± 0.0	2177.0 ± 3.7	1852.5 ± 4.6	$3.73 \pm 0.03$	360.5 ± 4.6	$8.05 \pm 0.00$	227.5 ± 1.8
2	17	28.9 ± 0.1	33.9 ± 0.1	2212.6 ± 4.7	1900.0 ± 6.2	$3.60 \pm 0.03$	392.0 ± 6.3	8.03 ± 0.01	220.6 ± 1.9
3	18	29.6 ± 0.1	$33.4 \pm 0.0$	2146.0 ± 5.0	1834.4 ± 9.8	$3.58 \pm 0.08$	379.4 ± 15.8	8.03 ± 0.01	218.1 ± 4.9
4	7	29.7 ± 0.2	33.4 ± 0.1	2158.7 ± 7.2	1843.0 ± 10.1	$3.64 \pm 0.09$	372.2 ± 11.1	8.04 ± 0.01	221.2 ± 5.3
5	7	29.7 ± 0.1	33.4 ± 0.1	2111.8 ± 9.2	1820.7 ± 8.9	$3.34 \pm 0.05$	402.2 ± 9.6	8.00 ± 0.01	203.6 ± 3.0
6	6	$29.6 \pm 0.3$	33.1 ± 0.3	2107.0 ± 23.9	1805.6 ± 24.1	3.46 ± 0.15	378.3 ± 19.6	$8.03 \pm 0.02$	210.3 ± 8.9
7	17	29.5 ± 0.2	$33.2 \pm 0.0$	2086.7 ± 1.6	1830.9 ± 1.9	$2.97 \pm 0.03$	464.5 ± 4.1	$7.95 \pm 0.00$	180.6 ± 1.7
8	51	30.0 ± 0.1	$33.2 \pm 0.0$	2062.0 ± 1.0	1835.9 ± 1.7	$2.66 \pm 0.02$	544.7 ± 4.5	$7.89 \pm 0.00$	161.6 ± 1.0
9	26	30.2 ± 0.2	32.2 ± 0.1	1967.1 ± 5.3	1770.7 ± 4.3	2.34 ± 0.04	586.1 ± 7.5	$7.84 \pm 0.00$	141.1 ± 2.2

**Table S2.** Average  $\Omega_{ar} \pm 1$  standard error for a barrier reef site (site 3) and the Rock Island bay sites (sites 7-9) during incoming and outgoing tides and during the rainy (September) and dry (March) seasons. N is shown in parentheses. Site numbers correspond to those in Figure 1.

	site 3	site 7	site 8	site 9
September 2011:				
average all data	3.53 ± 0.10 (14)	2.92 ± 0.05 (9)	2.53 ± 0.06 (7)	2.37 ± 0.05 (18)
ave incoming tide	3.71 ± 0.13 (4)	2.94 ± 0.12 (3)	2.53 ± 0.04 (2)	2.36 ± 0.09 (6)
ave outgoing tide	3.48 ± 0.05 (5)	2.90 ± 0.08 (4)	2.53 ± 0.11 (4)	2.34 ± 0.11 (8)
March 2012:				
average all data	3.78 ± 0.11 (4)	3.03 ± 0.03 (8)	2.68 ± 0.02 (44)	2.28 ± 0.03 (8)
ave incoming tide	3.61 ± 0.09 (2)	2.94 ± 0.01 (2)	2.63 ± 0.04 (10)	2.24 ± 0.12 (2)
ave outgoing tide	-	3.09 ± 0.01 (4)	2.73 ± 0.02 (22)	2.29 ± 0.03 (5)