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COMMUNITY STRUCTURE, CIRCULATION AND SEAWATER PH IN A CORAL REEF ECOSYSTEM (MOOREA, FRENCH POLYNESIA)

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Abstract. Seawater pH measurements across different reef settings in Cook's Bay (Moorea, French Polynesia) taken during October and November 2008 were compared and related to circulation and community composition in the reef flat, fringing reef, lagoon and bay. pH is thus an easy measure of seawater carbonate chemistry, which can be altered by community metabolism. Current velocity and percent cover of coral were greatest across the reef flat, yet no significant difference in seawater pH was found between the algal ridge and the lagoon. However, pH variations were discernable between the surface water from the fringing reef, which had the highest percent cover of algae, and water sampled at depth in the lagoon and bay. This study thus brings a better understanding of pH differences within a reef ecosystem and can serve as a benchmark for monitoring ocean acidification.

Key words: coral reef; community structure; circulation; calcification; carbonate chemistry; French Polynesia; pH.

INTRODUCTION

Coral reef ecosystems are very rich and diverse habitats that can be differentiated between several distinct environments, which vary in terms of geology, community structure, circulation and other factors. One setting includes the barrier reef flat, which shelters the lagoon from wave exposure. This area is relatively shallow and characterized by an abundance of live coral and a very rich marine biota. Water from the open ocean flows across the reef flat and towards the lagoon due to gradients in water level and radiation stress from breaking waves (Hench 2005), also implying that the residence time of water is short across this distance since current is strong. On the other hand, the lagoon is a much deeper environment where organic matter and calcium carbonate ($CaCO_3$) from the reef flat are deposited. This zone is too deep for algae or coral to subsist and is unique in that water can stagnate there for extended periods of time before being expelled through the pass (Watanabe 2006).

As a result of the considerable biogeochemical differences found between coral reef settings, the chemistry of seawater will be affected differently depending on where it flows in the reef system. Notably, community metabolism, which varies in accordance with community composition, can significantly modify the carbonate chemistry of surrounding seawater through the processes of photosynthesis, respiration and calcification. Though many marine organisms such as algae,

fish, crustaceans and other invertebrates contribute greatly to overall community metabolism, corals have been shown to be one of the main factors affecting the carbonate chemistry of seawater in reef ecosystems since they are the most prominent biological feature on the reef flat (Smith 1973). This is mainly due to the fact that corals produce large calcified structures through the precipitation of $CaCO_3$, a process known as calcification, which releases carbon dioxide (CO_2) into the water column according to the following equilibrium:

$$Ca^{2+} + 2\ HCO_3^- \leftrightarrow CaCO_3 + CO_2 + H_2O$$
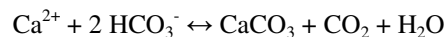
The molar ratio of CO_2 released per $CaCO_3$ precipitated is 0.6 at 25°C for standard oceanic conditions. Coral calcification also accounts for >10% of the total precipitation of $CaCO_3$ in the world's oceans (Gattuso et al. 1997). The dissolved CO_2 released then reacts with water to form carbonic acid (H_2CO_3) which affects pH according to the following equilibrium (Gattuso et al. 1995):

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3^- \leftrightarrow 2\ H^+ + CO_3^{2-}$$
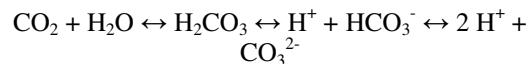
An increase in $[H^+]$ due to CO_2 input from calcification thus causes pH to decrease, or in other words for the surrounding seawater to become more acidic. Oppositely, the dissolution of $CaCO_3$ takes up CO_2, which leads to an increase in pH.

Similarly, the organic carbon metabolism of corals involves the production and degradation of

organic matter through photosynthesis and respiration, which decreases and increases DIC, respectively. However, based on a study of the community metabolism at the Tiahura barrier reef in Mo'orea (Gattuso et al. 1993), coral respiration is of the same order of magnitude as photosynthesis, therefore implying that net productivity is close to zero. It is therefore safe to assume that organic carbon metabolism in corals only plays a minor role in net carbon fluxes. Coral reef ecosystems, mostly barrier reef flats, have therefore been shown to be net sources of CO_2 due to their low net fixation of CO_2 through photosynthesis and rather significant release of CO_2 caused by the precipitation of $CaCO_3$. Subsequently, as water flows across a barrier reef flat largely dominated by live coral and is chemically altered by coral metabolism, it should theoretically be enriched in CO_2 and therefore also be more acidic (lower pH) at the end of the reef flat in comparison to 'new', open ocean water immediately crossing the algal ridge. However, if the reef happens to be in an algal-dominated state it will act as a CO_2 sink rather than a source, which is usually only true in a coral-dominated state (Gattuso et al. 1997).

High rates of $CaCO_3$ precipitation are also often associated with high rates of photosynthesis, which can result in a diurnal calcification pattern. For instance, the CO_2 released from calcification or respiration can be taken up through photosynthesis instead of being released into the atmosphere, which poses a problem when trying to differentiate the net effect of separate metabolic processes on the overall CO_2 budget (Gattuso et al. 1995). Nonetheless, this study will only take into account the overall effect of community metabolism on seawater pH rather than seeing how each metabolic process affects it independently.

Adding CO_2 to the water through calcification consequently leads to an increase in partial pressure of CO_2 (pCO_2) in seawater in relation to the atmosphere, which drives CO_2 from the water to the atmosphere and therefore increases atmospheric CO_2 (Gattuso et al. 1993). Oppositely, if atmospheric pCO_2 is greater than that of seawater, oceanic CO_2 will increase until equilibrium is reached. This is of major concern today as atmospheric CO_2 is increasing drastically due to fossil fuel emissions, which in turn causes oceanic CO_2 to rise as well. As a result, the Earth's oceans are becoming more acidic and pH is predicted to decrease by 0.4 units by 2100 (McNeil 2007). Although the actual effects remain unclear, ocean acidification is expected to have a profound impact on ocean chemistry, biogeochemical cycles,

marine organisms and ecosystems. Ocean models predict that acidification will lead to a decrease in aragonite and calcite saturation levels, which will negatively impact aragonitic and calcifying organisms such as corals, plankton and shellfish. Reduced surface ocean pH can also impact the speciation of nutrients and metals, which are major determinants of primary production (Turley 2008).

This study first seeks to determine if community metabolism in a coral reef ecosystem leads to measurable changes in the pH of seawater, as pH is an easy measure of carbonate chemistry. Secondly, this study investigates if the pH of seawater is affected differently in separate reef settings, such as shallow reef flat environments and the deep lagoon, which vary in terms of geology, community composition and circulation. Coral and algal cover, as well as seawater circulation will be measured in each reef environment to determine if there is a correlation with changes in seawater pH. Finally, since there are only few records of ocean pH worldwide, the data gathered in this study can serve as a baseline for monitoring ocean acidification.

METHODS

Study site

The overall study area was located in Cook's Bay, on the North coast of Moorea, in French Polynesia (coordinates: -17.48° S, -149.83° W) (Fig. 1). The different reef settings studied include the barrier reef flat, the fringing reef, the lagoon and the bay.

Vertical mixing rates and current velocity

First, vertical mixing was measured in order to determine if the water column across the barrier reef flat was thoroughly mixed. If seawater in this area was stratified, water samples would be taken different depths since distinct water layers could potentially have different chemical properties. On the other hand, if the water column was well-mixed across the entire reef flat, surface water would likely have had the same characteristics as water near the substrate. This eliminates the need to take samples at different depths. Since water across the reef flat and the fringing reef was shown to be well-mixed, only surface water samples were taken at these sites. Although vertical mixing rates could not be measured in the lagoon and in the bay, this study assumes these sites were stratified with depth, therefore requiring both surface and deep water samples.
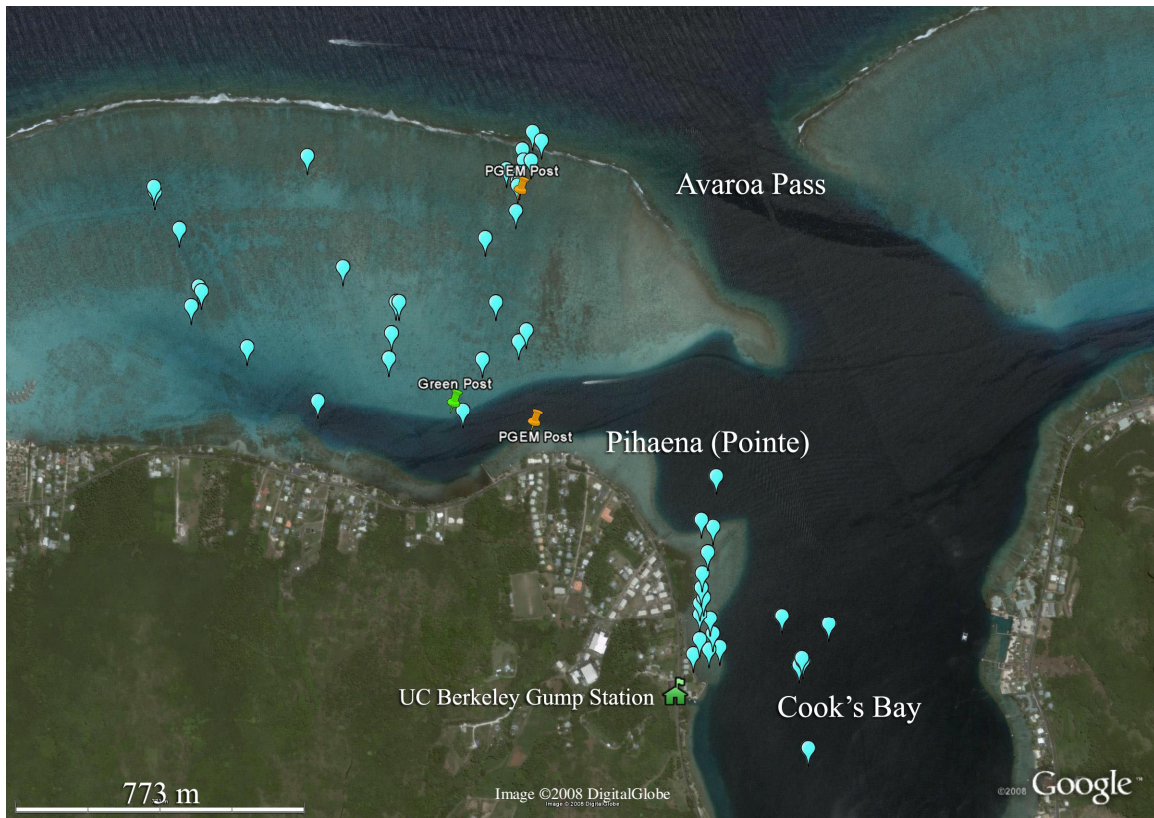
FIG. 1. Location of individual sample sites (blue tear drop markers) and other landmarks in Cook's Bay

The vertical mixing rate across the barrier reef flat was therefore determined by using fluorescein dye (Sigma, Acid Yellow 73). For each test, approximately 5 mL of dye were released into the water column near the substrate, using a pre-filled 10 mL disposable syringe to allow for a more precise injection point and to prevent excess dye from leaking out before the injection. The time and horizontal distance it took for the dye to travel from the bottom of the water column to the surface were measured with a digital watch timer and a transect tape. This test was performed at various locations across the reef flat to account for the possibility of localized changes in current or turbulence, such as directly behind a large coral head or in a wide open area, which might significantly impact vertical mixing rates.

Secondly, current velocity was measured to find out how long it took for a body of seawater to travel across the barrier reef flat or fringing reef. Assuming water crossing the reef flat mixes thoroughly, the product of concentration change multiplied by water volume transport across the reef flat equals the net rate at which a component X, such as dissolved CO_2, changes. Dividing that by the reef area gives the rate of change per unit area (Smith 1973). This signifies that a greater

water volume transport or higher current velocity will lead to a lesser rate of change per unit area for seawater. For instance, if flow across a coral-dominated reef flat is very sluggish, water will spend more time filtering through corals and will therefore have a greater chance of being chemically altered by coral metabolism.

Current velocity was thus determined by releasing 5 mL of dye at mid-depth and measuring how far it traveled in an interval of 2 minutes. Both time and horizontal distance of travel were taken into account. This test was executed at the beginning, middle and end of the barrier reef flat, as well as along the fringing reef. Tests were repeated several times at each location to account for possible variations in velocity and volume transport of water due to wave size, tidal conditions, wind direction or large geological obstructions (i.e. massive *Porites* coral heads).

Community composition

Community composition across separate reef settings was estimated to determine if these were algal or coral-dominated, which is important in relating these differences with possible seawater pH variations between environments.

Live coral cover across the barrier reef flat was estimated by a 263-meter line transect that extended from the algal ridge to the lagoon, in alignment with the PGEM boundary (starting point: -17.477525° N, -149.830584° S; end point: -17.480082° E, -149.830417° W). The transect tape was held down using dive weights and pieces of coral rubble in order to conserve a straight line.

The percentage cover of coral and algae along the fringing reef was estimated by placing a ½ m^2 quadrant at 30 random points encompassed in a fictitious rectangle drawn along fringing reef, aligned in the North-South direction. The dimensions of the rectangle are as follows (Fig. 2):

- -17.486761° N, -17.490265° S
- -149.825586° E, -149.826025° W
- Area: 18,381 m^2, Perimeter: 874 m

FIG. 2. Random quadrat points within a rectangle along the fringing reef.

The random points within the rectangle were computed using a random point generator by GeoMidpoint (http://www.geomidpoint.com/random/) and the geographic coordinates for each point were then imported into Google Earth Pro. The coordinates were sorted in a South to North order using Microsoft Excel and subsequently located using a Garmin® eTrex handheld GPS device.

Seawater sampling and pH measurements

Surface water samples were taken across the barrier reef flat at the algal ridge on the West side of Avaroa Pass, at the yellow PGEM post approximately 100 meters South of the algal ridge crest, at the end of the reef flat near the lagoon, and at several points in between. Samples were also taken in the lagoon near Pihaena Point and in the center of Cook's Bay, both at the surface and at 20

meters deep. Finally samples were taken along the fringing reef on the West side of Cook's Bay, directly in front of the UC Berkeley Gump Research Station. Sampling sites along the fringing reef were determined using the same random point generator as that mentioned above. For all other sites, GPS coordinates were recorded in Universal Transverse Mercator (UTM) coordinates using a handheld GPS device. All GPS points taken were then converted to Geographic (decimal degrees) coordinates using an online converter (http://home.hiwaay.net/~taylorc/toolbox/geography/geoutm.html) and imported into Google Earth Pro v. 4.3.7. Water samples points and other useful landmarks (such as the PGEM boundary posts) were marked on a map (Fig. 1).

All samples were taken during falling tide, within two hours of low tide, using 75 mL plastic, screw-top vials. Deep water samples were taken with the aid of a Niskin bottle (Forestry Suppliers Inc., Water Mark). These were then stored in the shade to keep water temperature from rising. Weather conditions, wind direction and swell size were recorded for each sample instance. When rainfall occurred, sampling was postponed until the following day, as this could have had a significant impact on surface water pH values. Water temperature was also measured at each site using an alcohol thermometer, which was placed within 0.5 meters from the surface.

The water samples were then measured for pH within a few hours after sampling. The pH was measured using a pH meter (Extech Instruments ExStik® EC500 pH/Conductivity/TDS/Salinity/Temperature Meter), which was calibrated on a weekly basis using a pHydrion® Tri-Chek Buffer Capsule Set (pH 4.00, 7.00, 10.00) (though expired in 2005, solutions appeared to be accurate). The pH probe was placed directly into each sample vial and the pH was recorded approximately 30 seconds later, when readings were stable. The vials were shaken during the pH reading to allow for the water in the vials to mix. The pH meter was cleaned with Kimwipes® after each measurement to avoid contamination. After measurements were completed, the vials were rinsed out with freshwater and set to dry until the next sampling instance. Additional measurements of water chemistry could not be performed due to the lack of proper instruments.

Experiment: Change in seawater pH over time in tanks containing live coral

Live and healthy *Pocillopora* coral heads were collected from the barrier reef flat on the East side

of Avaroa Pass using a chisel and hammer. Approximately 693 cm^3 of coral were placed in each of the 3 plastic buckets that were used as tanks, which were also each filled with 3.8 L of seawater. A fourth bucket, filled only with seawater, was used as a negative control. The water in each tank remained stagnant for the remainder of the experiment. The seawater pH and temperature were measured immediately after the coral was placed into the buckets and every 15 minutes thereafter for a total of one hour. This experiment was repeated 3 times and the results were averaged. The coral specimens were then replaced in their original environment once the experiment was over.

Statistics and graphs

All statistics were computed using the statistical analysis software JMP® 7.0.1. The graphs of the variability in seawater pH across the reef flat (Fig. 5) and between different reef settings (Fig. 6) were also made using the same program. The graph of pH vs. time for the experiment was made using Microsoft® Office Excel 2003.

RESULTS

Experiment

As expected, seawater pH measurements in both treatments and controls at minute 1 showed nearly identical values (average 8.15 vs. 8.17 respectively, Fig. 3). Throughout the experiment, seawater pH in the controls stayed practically constant with an average end value of 8.15 at minute 60, while the seawater pH in the tanks containing coral dropped significantly over time, with an average end value of 7.97.

A Repeated Measures Multivariate Analysis of Variance (MANOVA) was used to measure the treatment effects relative to controls and to test for changes in seawater pH over time. The results indicated both effects of the treatment and time (Table 1). A significant interaction between treatment and time indicates that the decrease in seawater pH in the treatments compared to the controls was significant.
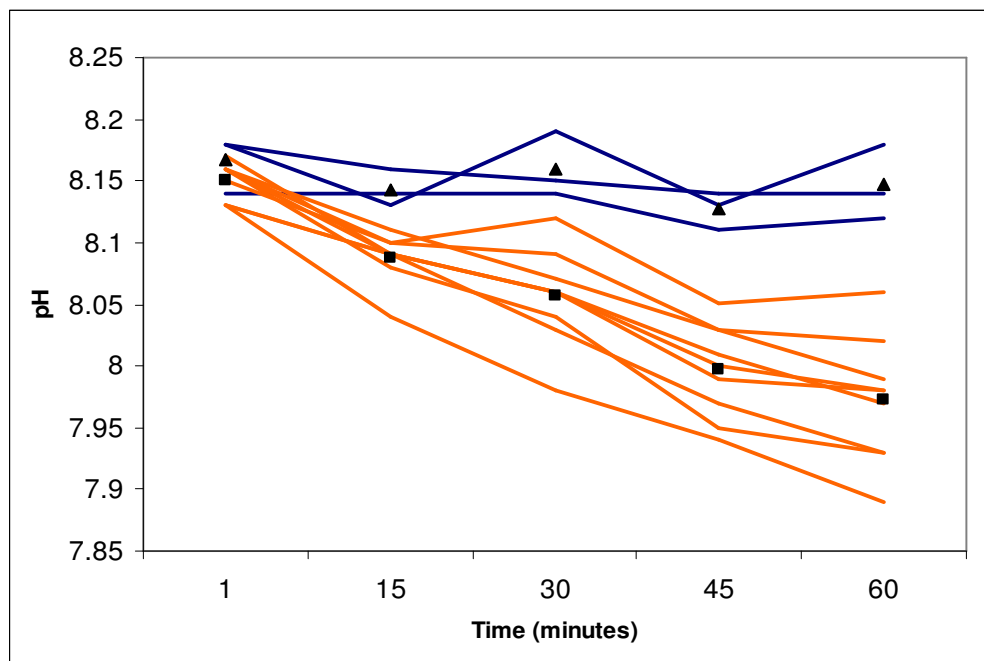

Fig. 3. Change in seawater pH vs. time in tanks containing live *Pocillopora* coral. Blue lines denote control tanks, orange lines experimental tanks. Triangular and square markers show pH averages for the controls and tanks, respectively, over time.

TABLE 1. Repeated measures multivariate analysis of variance measuring between and within treatment effects.

MANOVA	F	DF	P
Between Treatment			
pH	27.5	1, 10	0.0004
Within Treatment			
Time	34.6	4, 7	0.0001
Treatment * Time	19.7	4, 7	0.0007

Reef system

Concerning circulation across the barrier reef flat, vertical mixing time was found to average only 63 seconds over a short horizontal distance (no more than 5 meters), implying that water flowing across this area was not stratified.

Current speed across the barrier reef flat averaged 7.67 m/min (Table 2) and water flow was oriented perpendicular to the algal ridge and towards the lagoon, as expected (Fig. 4). The current along the fringing reef was much slower (2.5 m/min) and was mostly directed towards shore. The current speed was also much more variable across the reef flat than on the fringing reef since it is dependent on radiation stress from breaking waves.

TABLE 2. Average current speed (±1 standard error) and direction across the reef flat and fringing reef.

Location	Current (m/min)	Direction
Reef Flat	7.67 ± 16	SSW
Fringing Reef	2.5 ± 1	SE

The reef flat is approximately 625 meters across, starting from the initial sampling site on the algal ridge to the start of the lagoon (measured from Google Earth). Since the average current velocity across this distance is 7.67 m/min, water was estimated to take approximately 1h 20 min to travel across the reef flat.

TABLE 3. Percent live coral cover vs. algal cover across the reef flat and fringing reef.

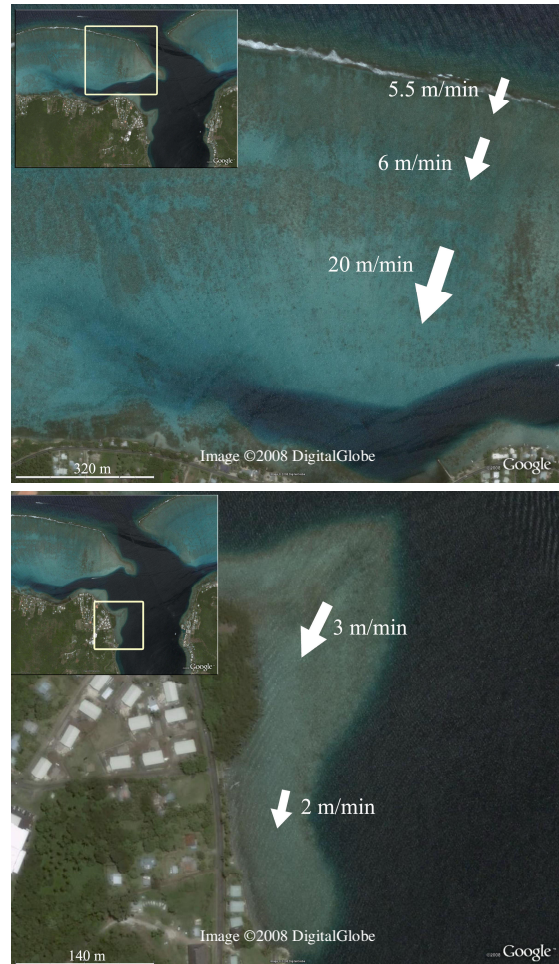| Location	Coral (%)	Algae (%)
Reef Flat	22.3	0
Fringing Reef	2.13	28.3

FIG. 4. Current speed and direction across the reef flat (top) and the fringing reef (bottom), shown by white arrows.

Live coral cover along the transect performed across the barrier reef flat averaged 22.3 %, compared to 2.13% throughout the fringing reef (Table 3). While no algae was observed across the reef flat, 28.3% of the fringing reef was covered in macroalgae.

TABLE 4. Average water temperature in °C (±1 standard error) at different locations.

Location	Water Temp (°C)
Reef Flat (Surface)	27.6 ± 3.8
Fringe Reef (Surface)	30.3 ± 1.5

Surface water temperature averaged 27.6 °C across the reef flat and 30.3 °C along the fringing reef (Table 4). A t test showed that mean water temperature was significantly higher along the fringing reef (t = 5.28, DF = 14, P < 0.0001). Water temperature could not be measured at depth in the bay or lagoon due to lack of proper instruments.
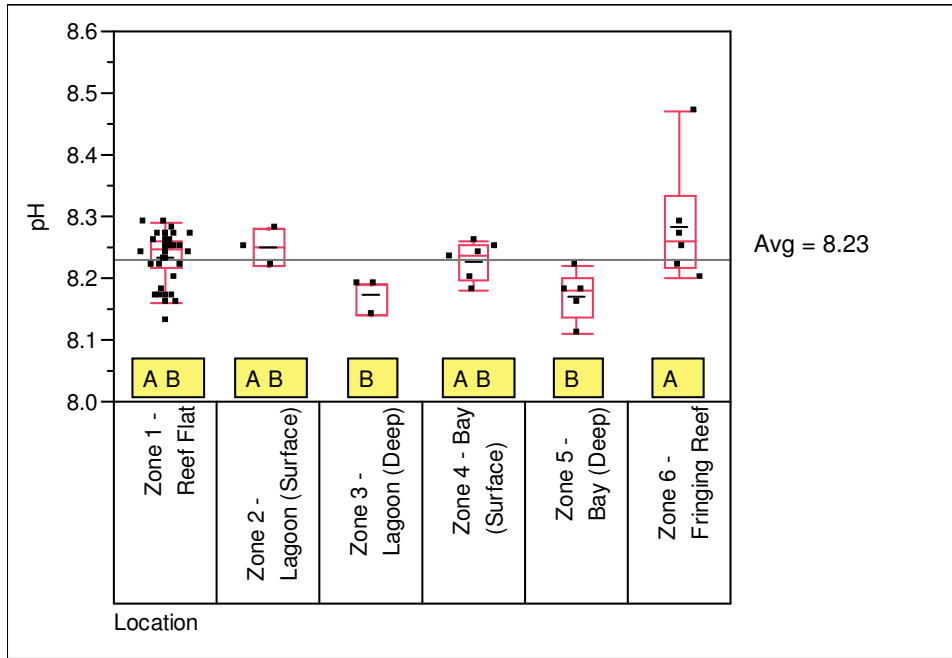
FIG. 5. Variability in seawater pH across lagoon and reef macroenvironments. Mean pH values that share the same letters are not significantly different (see text). All water samples were taken at the surface, except in the bay and lagoon where samples were also taken at 20 meters depth.
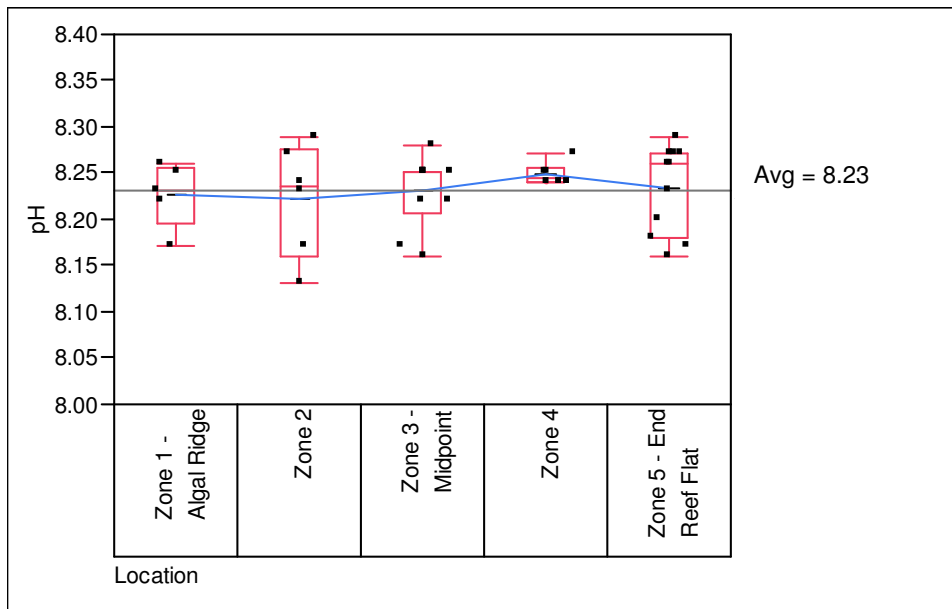

FIG. 6. Variability in seawater pH across the Reef Flat. Surface water samples were taken at the algal ridge, at the end of the reef flat, and at 3 points in between.

The surface water pH across the reef flat, the lagoon and the bay were very similar (8.23, 8.25 and 8.23 respectively, Fig. 5), while the pH of deep water in the bay and lagoon was notably lower (8.17) (more acidic). Though seawater pH along the fringing reef showed the greatest variability, it was higher than at any other site (8.28).

An Analysis of Variance showed that there were statistically significant differences in seawater pH across the lagoon and reef macroenvironments (F ratio = 4.0994, DF = 5, P < 0.0031).

Using Tukey's HSD (Honestly Significant Differences) test, the pH measurements for separate zones were compared with each other to

see if there is a significant difference between them. Mean pH values not connected by the same letter (shown by A or B) are therefore significantly different. Measurements of seawater pH at Zones 3 and 5 (Lagoon and Bay at depth) were significantly different than those at Zone 6 (Fringing Reef) only. However, pH at Zones 1, 2 and 4 (Reef Flat, Lagoon and Bay Surface) were not significantly different.

Seawater pH measurements at the beginning, middle and end of the reef flat showed nearly identical values, while it was slightly higher in Zone 4 (Fig. 6). Variability was greatest at site 2, also shown by a higher standard deviation, and least at site 4, with a lower standard deviation.

An Analysis of Variance showed no statistically significant difference in seawater pH across the reef flat (F ratio = 0.3431, DF = 4, P < 0.8469).

DISCUSSION

The experiment consequently showed that coral metabolism had a measurable effect on the pH of seawater in the tanks, since it decreased significantly over time in comparison to that in the controls. Since the water temperature and salinity in the tanks remained nearly constant and because coral was the only organism present and thus the only contributor to changes in carbonate chemistry – apart from the probability of there being microalgae or small plankton already present in the seawater – the decrease in pH was therefore probably due to a net release of CO_2 from coral calcification and respiration, which agrees with the findings of Frankignoulle et. al (1994) that calcification is a well-recognized source of CO_2 to the surrounding water.

Since it takes more than one hour for water to cross the barrier reef flat, which was dominated by healthy coral, seawater pH was expected to be lower at the end of the reef flat compared to the beginning of the reef flat, near the algal ridge, since it took less than 15 minutes for there to be a significant decrease in seawater pH in the experiment treatments. This hypothesis was thus based on the assumption that coral is the main contributor to community metabolism across the reef flat since it is the most prominent biological structure. Additionally, a study on CO_2 fluxes across the coral-dominated Tiahura barrier reef flat in Mo'orea showed that reef metabolism decreased seawater CO_2 (Gattuso et al. 1993), implying a decrease in seawater pH. However, the results did not show any significant gradient in seawater pH from the algal ridge to the lagoon.

This trend was therefore unexpected and did not match that of the experiment, most likely due to disparities between the natural reef system and the experimental setting. First, a major difference between the experiment and a natural reef system includes the fact that seawater in the treatments was stagnant for the duration of each trial, which is not the case across the reef flat, where water is constantly flowing.

Furthermore, though the reef flat was coral-dominated, the reef biomass also included many other organisms that were unaccounted for, yet undoubtedly had an impact on seawater carbonate chemistry. The estimates made on community composition were therefore inaccurate due in part to the fact that the transects performed across the reef flat only took into account coral and algal cover. Additionally, these only provided a 'top view' estimate of visible coral and algae and did not consider any algae or coral on the underside of rocks or coral heads, which could have had a significant impact on the results. In other words, since pH showed no gradient, perhaps implying that there was no net change in dissolved CO_2 across the reef flat, a reasonable hypothesis is that the effects of primary production across the reef flat equaled respiration and calcification. Moreover, a study by Odum (1955) showed that pH actually increased across the reef flat on Eniwetok Atoll even though live coral cover was comparable to that on the reef flat examined in this study. However, Odum's study took into account the percent cover of encrusting algae, which made up 23% of the biomass component and therefore significantly contributed to community metabolism.

Additionally, as mentioned by Gattuso et al. (1997), if community metabolism had actually led to an increase in the pCO_2 of seawater, the net increase in dissolved CO_2 could not have been fully accounted for since CO_2 would have escaped into the atmosphere across the air-sea interface until an equilibrium was reached. However, according to Smith (1973), these fluxes are very sluggish and depend on the turbulence present at the interface, implying that they should not have had a significant impact on this study.

Lastly, no significant differences in seawater pH were found across this area due the possibility that the sample size was not large enough or because the instruments used to measure pH were not necessarily accurate enough. Though temperature remained constant across the reef flat, possible variations in seawater salinity, which could not be measured due to the lack of proper instruments, could have also had an impact on the

results, since pH depends heavily on both these factors.

Nevertheless, significant differences in seawater pH were found across the different reef settings. The pH along the fringing reef was significantly higher and water was therefore more basic than water sampled at depth in the lagoon and in the bay. Otherwise, all other surface water samples were not significantly different from each other. Contrasting pH values between the fringing reef and deep water were therefore most likely caused by the strong dissimilarities between both environments.

First, the fringing reef is a particular setting in that there is a significant amount of plant detritus and human waste near shore. This area is also subject to surface runoff, which includes soil, pesticides, fertilizers and other pollutants, which is detrimental to the health of the reef as it leads to eutrophication and increased water turbidity, subsequently suppressing coral growth and favoring the development of macrophytes. Instead, there is a high percent cover of algae, which increases with proximity to shore. Most of the coral present on the fringing reef is therefore constricted to the border of the lagoon, since the water is less turbid and most likely less polluted farther from shore. In comparison to the barrier flat, the fringing reef thus has a much lower percent cover of coral, and a greater abundance of algae. Assuming that algae and coral metabolism are the main factors affecting water chemistry in this location, a higher percent cover of algae along the fringing reef implies a higher rate of photosynthesis, which subsequently decreases dissolved CO_2 and increases seawater pH. This hypothesis is supported by a study on CO_2 fluxes of a macroalgal-dominated fringing reef community in Moorea, which was shown to be a CO_2 sink (Gattuso et al. 1997). The fringing reef is also a much shallower environment in comparison to the rest of the reef system, causing water temperature there to be significantly higher. Higher temperature thus decreases the solubility of gases, meaning $[CO_3^{2-}]$ will be large, subsequently increasing pH. Though not measured, salinity was probably higher on the fringing reef since there is a higher rate of evaporation due to higher water temperature, which also has a positive impact on pH. Lastly, the water flow across the fringing reef was much slower than that across the reef flat, and was directed towards shore. The rate of change of water pH should have therefore been greater along the fringing reef since water had a longer residence time in this environment.

In contrast, the deeper submarine environments found in the lagoon or the bay have a very different biological makeup than any of the other sites sampled. Unlike the reef flat or fringing reef, coral and algae are not present at depth since photosynthesis does not occur in the euphotic zone, implying that there is no biological uptake of CO_2 in this zone. Though not measured, water temperature is undoubtedly lower at depth compared to surface waters, subsequently increasing the solubility of gases. There is also an increase in pCO_2 at depth due to the oxidation of decaying organic material from the reef flat or adjacent land, which accumulates in the lagoon and in the bay. Moreover, increasing pressure and decreasing temperature with depth lead to an increase in the solubility of $CaCO_3$, which redissolves when calcified organisms die and sink into deep water, releasing calcium and carbonate ions back into solution, subsequently decreasing pH. However, the increase in solubility of $CaCO_3$ in the deep lagoon and bay is probably only very minor since these zones are only 20 to 40 meters deep, implying that pH is lower for other reasons.

In conclusion, though reliable values of seawater pH are not easily obtained by direct measurement since seawater is a concentrated solution, meaning the effective concentration of a dissolved ion is almost invariably less than the true concentration due to ion pairing among dissolved species in seawater, and because it can be affected by a large numbers of factors that are in themselves difficult to determine, this study can serve as a basic survey of pH variations in a coral reef ecosystem. A better understanding of seawater carbonate chemistry is thus fundamental in determining community metabolism and the health of coral reefs. Furthermore, the seawater pH data will potentially serve as a baseline for monitoring ocean acidification, which poses a major threat to the calcifying organisms that make up these reefs.

ACKNOWLEDGMENTS

LITERATURE CITED

Frankignoulle, M., C. Canon, and J.-P. Gattuso. 1994. Marine calcification as a source of carbon dioxide: Positive feedback of increasing atmospheric CO-2. Limnology and

Oceanography **39**:458-462.

Gattuso, J.-P., D. Allemand, and M. Frankignoulle. 1999a. Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry. American Zoologist **39**:160-183.

Gattuso, J.-P., M. Frankignoulle, and S. V. Smith. 1999b. Measurement of community metabolism and significance in the coral reef CO2 source-sink debate. Proceedings of the National Academy of Sciences of the United States of America **96**:13017-13022.

Gattuso, J.-P., C. E. Payri, M. Pichon, B. Delesalle, and M. Frankignoulle. 1997a. Primary production, calcification, and air-sea CO2 fluxes of a macroalgal-dominated coral reef community (Moorea, French Polynesia). Journal of Phycology **33**:729-738.

Gattuso, J. P., D. Allemand, and M. Frankignoulle. 1997b. Interactions between the carbon and carbonate cycles at organism and community levels in coral reefs. American Zoologist **37**:170A.

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

Gattuso, J. P., M. Pichon, and M. Frankignoulle. 1995. Biological control of air-sea CO-2 fluxes: Effect of photosynthetic and calcifying marine organisms and ecosystems. Marine Ecology Progress Series **129**:307-312.

Gattuso, J. P., M. Pichon, J. Jaubert, M. Marchioretti, and M. Frankignoulle. 1996. Primary production, calcification and air-sea CO-2 fluxes in coral reefs: Organism, ecosystem and global scales. Bulletin de l'Institut Oceanographique (Monaco) **0**:39-46.

Jokiel, P. L., K. S. Rodgers, I. B. Kuffner, A. J. Andersson, E. F. Cox, and F. T. Mackenzie. 2008. Ocean acidification and calcifying reef organisms: a mesocosm investigation. Coral Reefs **27**:473-483.

Kawahata, H., A. Suzuki, and K. Goto. 1997. Coral reef ecosystems as a source of atmospheric CO2: evidence from PCO2 measurements of surface waters. Coral Reefs **16**:261-266.

McNeil, B. I. and R. J. Matear. 2007. Climate change feedbacks on future oceanic acidification. Tellus Series B Chemical and Physical Meteorology **59**:191-198.

Odum, H. T. and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef on Eniwetok Atoll. Ecol Monogr **25**:291-320.

Pelejero, C., E. Calvo, M. T. McCulloch, J. F. Marshall, M. K. Gagan, J. M. Lough, and B. N. Opdyke. 2005. Preindustrial to modern interdecadal variability in coral reef pH. Science (Washington D C) **309**:2204-2202.

Salvat, B., A. Aubanel, M. Adjeroud, P. Bouisset, D. Calmet, Y. Chancerelle, N. Cochennec, N. Davies, A. Fougerousse, R. Galzin, E. Lagouy, C. Lo, C. Monier, C. Ponsonnet, G. Remoissenet, D. Schneider, A. Stein, M. Tatarata, and L. Villiers. 2008. Monitoring of French Polynesia coral reefs and their recent development. Revue D Ecologie-La Terre Et La Vie **63**:145-177.

Smith, S. V. and J. A. Marsh. 1973. Organic carbon production on windward reef flat of Eniwetok-Atoll. Limnology and Oceanography **18**:953-961.

Turley, C. 2008. Impacts of changing ocean chemistry in a high-CO2 world. Mineralogical Magazine **72**:359-362.