Mar Biol (2010) 157:1849–1856
DOI 10.1007/s00227-010-1456-y

ORIGINAL PAPER

The basics of acidification: baseline variability of pH on Australian coral reefs

Monica Gagliano · Mark I. McCormick · James A. Moore · Martial Depczynski

Received: 16 December 2009 / Accepted: 15 April 2010 / Published online: 15 May 2010

Abstract Ocean acidification is one of the key threats facing coral reef ecosystems, but there are few estimates of spatial and temporal variability in pH among reef habitats. The present study documents levels of spatial variability in pH among coral reef habitats (9 to 10), among locations separated by 100's km of latitude and between east (Great Barrier Reef, GBR) and west (Ningaloo Reef) coasts of Australia. Differences were found in pH between inshore and offshore waters along Ningaloo Reef (means 8.45, 8.53, respectively). Replicate assessments here ranged from 8.22 to 8.64. On the GBR, the range of values over all habitats and replicates was 0.39 pH units (7.98 to 8.37). There were minor but significant differences of 0.05 pH units between 5 consecutive days for habitats on average. Highest pH was recorded in filamentous algal beds maintained by the damselfish *Dischistodus perspicillatus*. Lowest pH was found in water extracted from sand-dwelling goby holes. While there were marked changes in pH over a 48-h sampling period among 4 habitats at Lizard Island (GBR), there was little evidence of a diel trend. Understanding how pH varies at scales that are relevant to organisms that live on shallow coral reefs is crucial for the design and interpretation of experiments that test the effects on organisms of the changes in water chemistry predicted to affect oceans in the future.

Communicated by U. Sommer.

M. Gagliano (✉)
Centre for Evolutionary Biology, School of Animal Biology and Centre for Microscopy, Characterisation and Analysis (CMCA), University of Western Australia, Crawley, WA 6009, Australia
e-mail: monica.gagliano@uwa.edu.au

M. I. McCormick · J. A. Moore
School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia

M. Depczynski
Australian Institute of Marine Science, University of Western Australia, Crawley, WA 6009, Australia

Introduction

Coral reefs are one of the world's most biologically diverse and economically important ecosystems. They are also one of the most vulnerable to the impacts of climate change (Caldeira and Wickett 2003; Doney et al. 2009). Increases in atmospheric carbon dioxide (CO_2) are leading to increased temperatures and ocean acidification. Concentrations of CO_2 in the atmosphere are the highest found in the last 740,000 years (Petit et al. 1999), driving increased CO_2 uptake by ocean surface waters. Through a series of chemical reactions, the additional CO_2 in water forms carbonic acid and leads to a decline in pH, thereby increasing ocean acidity and reducing the concentration of bioavailable carbonate ions by changing the carbonate–bicarbonate ion balance (Kleypas et al. 2006; Munday et al. 2007). There has been a decrease in the global ocean surface pH of 0.1 unit since 1750, with the lowest decrease in the tropics (0.06) and the highest decrease in higher latitudes (1.2) (Bindoff et al. 2007). Predictions suggest that by 2050, the surface waters will further decrease in pH by 0.2 to 0.3 units (Orr et al. 2005). Since pH is recorded on a negative log scale, a 0.1 reduction in pH represents a 30% increase in the concentration of H^+ ions in the ocean (Raven 2005). The mean pH of the world's open oceans ranges from 7.9 to 8.3, although within particular ocean locations, the within-year range in pH is usually below 0.05 units (Bindoff et al. 2007). There is considerable speculation about the impact

of acidification for organisms with carbonate skeletons, such as plankton and reef building corals (e.g. Hoegh-Guldberg et al. 2007; Iglesias-Rodriguez et al. 2008; Manzello et al. 2008), but the ramifications for most coral reef organism are poorly understood.

Acidification on the order of 0.1 pH unit will lead to slowing of the rates of accretion of coral skeletons, while pH reductions of more than 0.1 from current levels are predicted to cause a breakdown of existing carbonate deposits, whether they be supporting living tissue (Riebesell et al. 2000; Shirayama and Thornton 2005) or as part of the deposited reef matrix. Furthermore, given the critical role pH plays in mediating physiological reactions, low pH is expected to have significant effects on processes other than calcification. Although it is unclear how increasing acidity of the oceans will affect fish populations, a drop in ocean pH is expected to increase acidity in animal tissues and body fluids, causing long-term changes in metabolic functions, growth and reproduction (Fabry et al. 2008). Researchers agree that the effect of changes in pH will be most evident in the early developmental stages, which are less capable of homeostasis (Ishimatsu et al. 2004). Predictions include reduced fertilization rates, increased levels of skeletal abnormalities and higher embryo and larval mortality (Guinotte and Fabry 2008, Munday et al. 2008). To date, there are little data on which to base these predictions, but there is increasing interest in these issues, and most researchers now recognize that the study of physiological processes is a high priority in climate change research (Wilson et al. 2010).

While detailed records of water temperature have been collected at a range of temporal and spatial scales for decades, there is a paucity of data on how pH varies naturally on biologically relevant spatial and temporal scales. In general, pH has been collected for open oceans rather than inshore biologically rich coastal zones (e.g. Pelejero et al. 2005). Understanding the extent of variation in pH among microhabitats inhabited by reef organisms and how this changes over a range of temporal scales is vital if we are to experimentally examine how global predictions of pH change may affect the development of marine organisms. In fact, different marine organisms are likely to experience not only different levels of pH within a specific microhabitat (e.g. sessile organisms) but may also be exposed to a variable range of values as they move across habitats (e.g. fishes). One may expect that some habitats may be more variable in pH than others through differences that include the numbers of respiring or photosynthesizing organisms; the stability of the water mass (flushing rates) and hence the presence and thickness of boundary layers; or the history of the water mass before it impinges on a particular site. The present study aimed at describing the levels of spatial variability in pH, spanning 100's kms in tropical latitude down to among reef microhabitats, and over a 48-h period among microhabitats, in order to establish a foundation for future studies where pH values are a proposed causal agent for change and variability among biotic groups.

Materials and methods

Sample locations

To assess spatial variability in the pH of tropical water over the continental shelf, samples were collected at three sampling scales from December 2007 to July 2008: (a) locations along the northern and central Great Barrier Reef spanning approximately 510 km of latitude; (b) within reef and beyond reef locations along Ningaloo Reef in Western Australia spanning 95 km of latitude; and (c) from 10 microhabitats within 2 sites 50 m apart on the leeward side of Lizard Island on the northern Great Barrier Reef (Fig. 1 and Table 1). In addition, at two sites at Lizard Island, samples were collected every 2 h over a 48-h period to examine the levels of variation in pH over the diel period over 4 habitat types. Because of its effects on temperature and hence to account for its potentially confounding effects on pH readings, salinity was measured at Ningaloo (Sandy Bay, near Yardie Creek, midway down Ningaloo Reef) using a CTD, and at Lizard Island using an Autosal salinity meter. It was found to be similar (range 34.7–34.9 ppt and 34.4–35.2 ppt, respectively).

Water sampling and pH measurement

Samples were collected in 50-ml syringes and analysed for pH and temperature within 10 min of collection. In between collection and analysis, samples were kept in a water bath of ambient water from the collection site. Syringes were rinsed with ambient seawater prior to sample collection, and each sample was carefully collected in ~20 s. Water temperature was recorded at the time of collection. Samples were analysed using a WTW pH315i meter with a sentix H electrode, recorded in millivolts and converted to pH by a 4-point pH temperature compensation curve that accounts for temperature conditions at the time of analysis (and collection) and hence ensures standardized pH values. The meter was calibrated for the National Bureau of Standards (NBS) scale using 4 fresh buffer solutions (WTW pH 4 & 7, Fisher pH 8 and Ricca pH 10) kept at the same temperature as the samples.

Northern and central Great Barrier Reef

Water samples were collected from a range of habitats (Table 1) from the leeward side of Lizard Island, a mid-shelf reef on the northern Great Barrier Reef, during

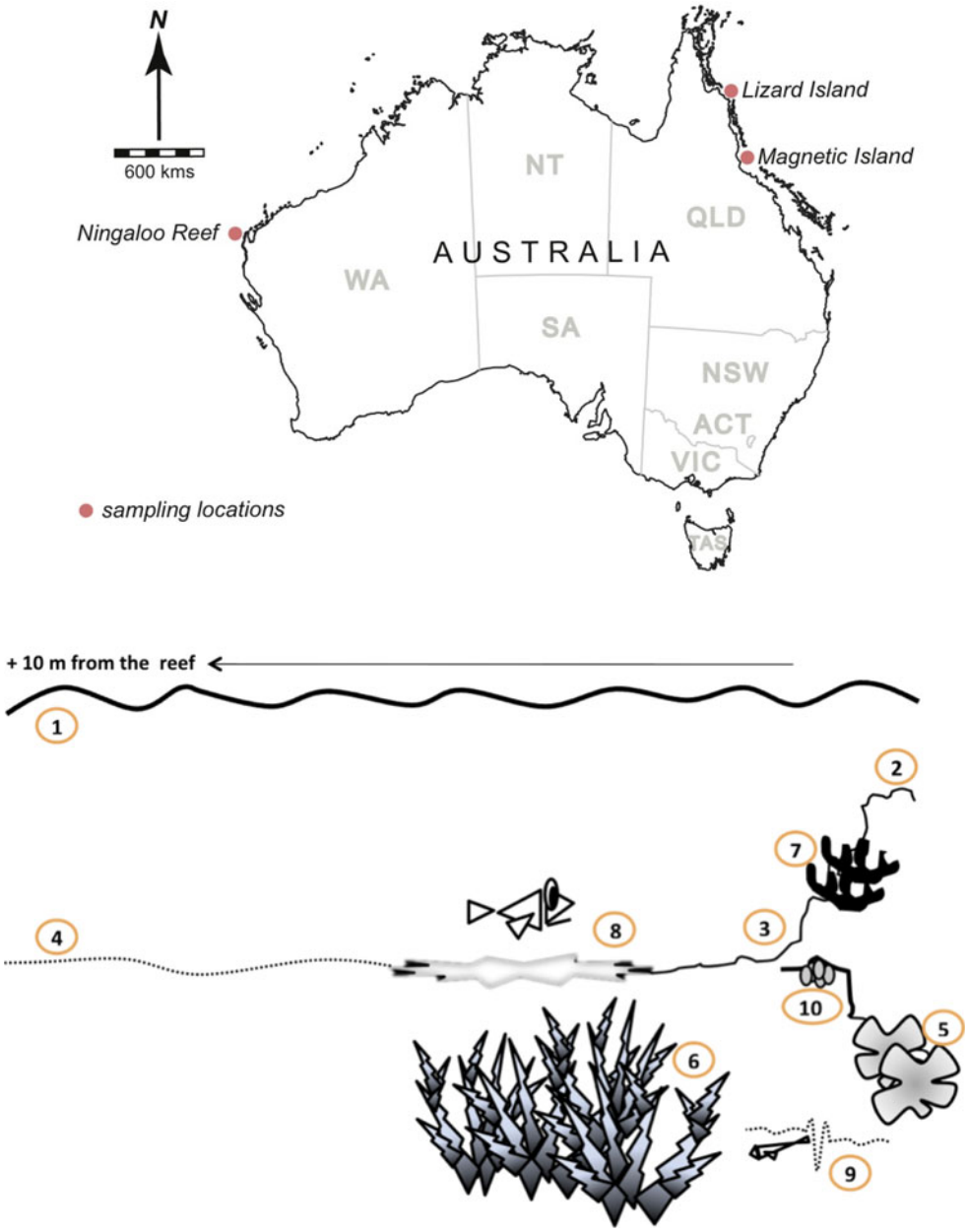

Fig. 1 Location of pH sampling in tropical Australia and schematic diagram (not in scale) of the sampled microhabitats. *Numbers* refer to microhabitat descriptions as per Table 1

December 2007, and two inshore coral reefs on the central GBR (Magnetic Island and Bay Rock), during April 2008. Ten habitats were sampled at the leeward side of Lizard Island within a shallow (3 m depth) lagoonal location on the reef edge. Water samples were collected and analysed once per day (11:30 to 14:30) for each of 5 days over a 6-day period (3rd to 9th December 2007), with three replicate samples collected for each habitat spread over a 100-m strip of reef and within the same part of the tide.

In addition, at a back-reef site at Magnetic Island (Picnic Bay, 19°9′52.56′′S, 146°51′10.28′′E) and a similar site at Bay Rock 12 km north-west (19°7′5.49′′S, 146°45′ 7.81′′E), nine habitats at the same depth were sampled during a single sampling exercise (10th April 2008). Damselfish (*Pomacentrus amboinensis*) nest sites were only sampled at Lizard Island, since they were not breeding during the April sampling event. Three replicate water samples were collected and analysed from each habitat by location combination, with samples collected 50 m apart and within the same part of the tide.

Ningaloo Reef

Eleven sampling stations were sampled along the coast of Western Australia spanning the northern section of Ningaloo Reef. Six stations 0.2 to 1 km off the reef edge were sampled (offshore), while five inshore stations among the lagoonal reef matrix were also sampled (inshore). At 10 of

Table 1 Habitats over which water samples were collected by 50-ml syringe

Habitat	Description
1. Subsurface	Within 5 cm of the water surface at least 10 m from the reef edge
2. Reef top	50 cm above the reef substratum on the reef crest
3. Reef bottom	50 cm above the reef substratum on the reef slope
4. Open sand	Within 3 cm of the sand 10 m from reef edge
5. Soft coral	Within the convolutions of a *Sacrophyton* sp. soft coral
6. Staghorn hard coral	Within branches of an *Acropora* branching hard coral
7. *Pocillopora* hard coral	Within branches of a *Pocillopora* hard coral
8. Algal garden	Gardening damselfish, *Dischistodus perspicillatus*, filamentous algal bed over sand. Water sample from between filaments
9. Goby hole	Within the hole of a sand goby
10. Damselfish nest	*Pomacentrus amboinensis* nest site; often under an upturned clam shell (a low-flow environment)

these stations, surface samples were collected, while at 5 stations, samples were also collected from the reef bottom; this yielded the following station replication: offshore surface, 6 stations; offshore bottom, 3 stations; inshore surface, 4 stations; inshore bottom, 2 stations. At each station, 5 replicate water samples were collected and analysed for pH.

Diel periodicity in pH

Diel sampling was conducted at a back-reef site at Lizard Island. To determine whether there were diel trends in the pH among habitats, 5 replicate water samples were collected from one 50-m stretch of shallow reef edge (4 m maximum depth) every 2 h for 48 h (15 to 16th December 2007). Habitats were subsurface, open sand, *Pocillopora* hard coral and *Dischistodus perspicillatus* algal garden (see Table 1 for full description). Individual patches of habitat (for *Pocillopora* colonies and algal gardens) were resampled to reduce small-scale spatial variability confounding comparisons through time.

Analyses

To determine whether there were differences in pH between shelf position (inshore and offshore waters) along Ningaloo Reef and with depth (surface and bottom waters), a 2-way analysis of variance (ANOVA) was undertaken. Sampling station was analysed separately as surface and bottom waters were not sampled at each station. For GBR sampling, ANOVAs were undertaken to test for the equality of means among habitats and locations. Assumptions of normality and homoscedasticity were examined using residual analyses. In all but the first analysis, assumptions of ANOVA were met. Transformation did not improve the normality of the Ningaloo dataset, so raw data were analysed with α set to a conservative 0.01 and results interpreted with caution. Repeated measures ANOVA was used to test for differences among the four habitats sampled over the 48-h sampling period since the same replicate sites were sampled through time. The assumption of sphericity was tested with a Mauchley test and was found to be non-significant.

Results

Great Barrier Reef

The range of values over all habitats and replicates was 0.39 pH units (7.98 to 8.37). There were significant differences in the pH among the 10 habitats sampled within the Lizard Island lagoon ($F_{9,36} = 3.433$, $P = 0.004$; Fig. 2). Highest mean pH values of 8.18 were recorded in the beds of filamentous algae maintained by *D. perspicillatus*. Lowest mean pH values of 8.11 were found in water extracted from sand goby holes. There was also a significant difference in pH over the 5 days of sampling across all microhabitats ($F_{4,36} = 3.433$, $P < 0.0001$), but these were relatively minor with differences of 0.05 pH units between consecutive days. The temperature over all 5 sampling days was 28°C.

There was a significant difference in pH among the 9 microhabitats between Magnetic Island and Bay Rock back-reefs (Habitat × Location: $F_{8,34} = 12.934$, $P < 0.0001$). The Magnetic Island location showed marked differences in pH among habitats, while there were no differences among habitats at the Bay Rock location (Fig. 3). pH sampled within *D. perspicillatus* algal gardens and over open sand was significantly higher than either subsurface or reef bottom samples (Fig. 3). At Magnetic Island, the pH ranged over 0.11 units (8.11 to 8.22) among samples, while at Bay Rock pH ranged only 0.04 units (8.14 to 8.18).

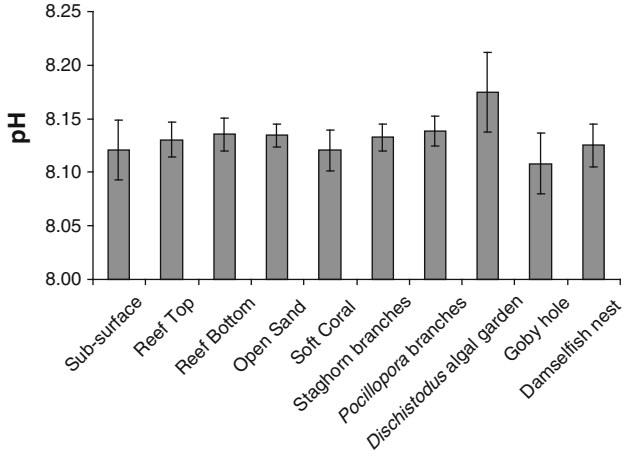

Fig. 2 Comparison of mean pH among 10 habitats sampled over a 5-day period within the Lizard Island lagoon. *Error bars* represent 95% confidence limits

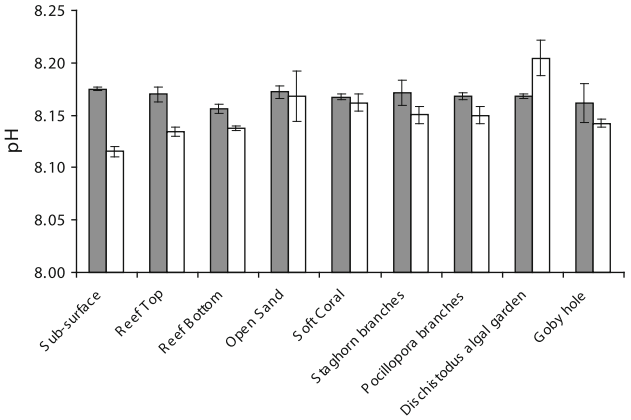

Fig. 3 Comparison of mean pH among 9 habitats sampled at two locations (Magnetic Island, *grey bars*; Bay Rock, *white bars*) on the central Great Barrier Reef. *Error bars* represent 95% confidence limits

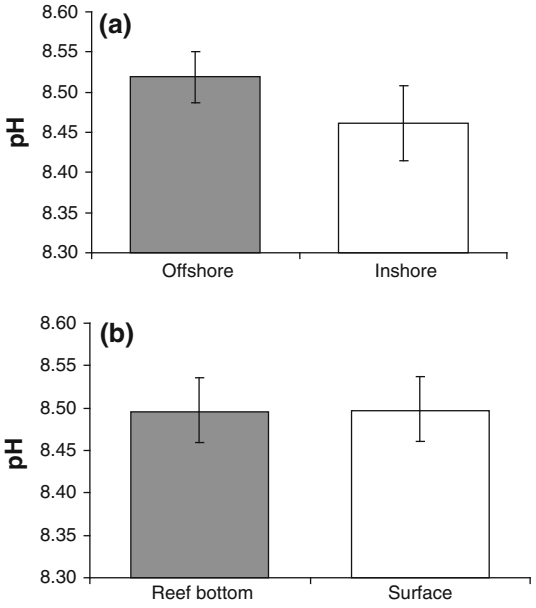

Fig. 4 Comparison of mean pH from Ningaloo Reef in Western Australia spanning 95 km of coastline from North-west Cape in the north to Coral Bay in the south. **a** Stations were positioned inside the reef matrix (Inshore, *white bars*) and on the outside of the outer reef (Offshore, *grey bars*) and **b** samples were collected from the surface (*white bars*) or from the reef bottom (*grey bars*). *Error bars* represent 95% confidence limits

Ningaloo Reef

There was a difference between the pH of inshore and offshore waters along Ningaloo Reef ($F_{1,71} = 6.800$, $P = 0.011$), with offshore waters less acidic than inshore waters around the reef matrix (means 8.53 vs. 8.45; Fig. 4a) and about 20% greater pH variability in inshore than offshore waters. Overall, there was no difference in pH between the bottom and surface samples ($F_{1,71} = 0.174$, $P = 0.677$; Fig. 4b). The temperature range across all Ningaloo Reef sampling stations was 23 to 24°C.

Diel changes in pH

There were significant differences in mean pH levels between the 2 days ($F_{1,16} = 1076.6$, $P < 0.001$; all habitats pooled for each day) and among the habitats sampled over the 2 days ($F_{3,16} = 3.621$, $P = 0.036$). Specifically, seawater pH on day 1 was significantly lower than on day 2, and pH readings over *D. perspicillatus* algal gardens were significantly higher than among the branches of *Pocillopora* colonies, although there were no other statistical differences in pH among other habitats. Over the 48-h continuum period, there were significant pH fluctuations ($F_{23,368} = 97.600$, $P < 0.0001$), and the nature of the changes differed with habitat sampled (Time x Habitat: $F_{69,368} = 2.285$, $P < 0.0001$). These differences in pH through time were mainly due to differences that occurred in all habitats at 3 pm of day 1 and 5 pm of day 2 (Fig. 5).

Interestingly, there were also trends in the variability among replicate observations that were consistent among habitats, with high variability shown at 9 pm of day 1, 5 pm of day 2 and 9 pm of day 2. These consistent trends among habitats through time may be due to the tidal cycle bringing water of different pH into the sampling site (Fig. 5). During these periods, the ranges of pH among replicates within a habitat were high and spanned about 0.2 pH units. For instance, at 9 pm of day 1, there was a spike in variability for all habitats, with readings between 8.02 and 8.20 in the surface waters and 7.93 and 8.17 among the branches of *Pocillopora* colonies. These spikes lasted less than 2 h, which was the temporal resolution of sampling.

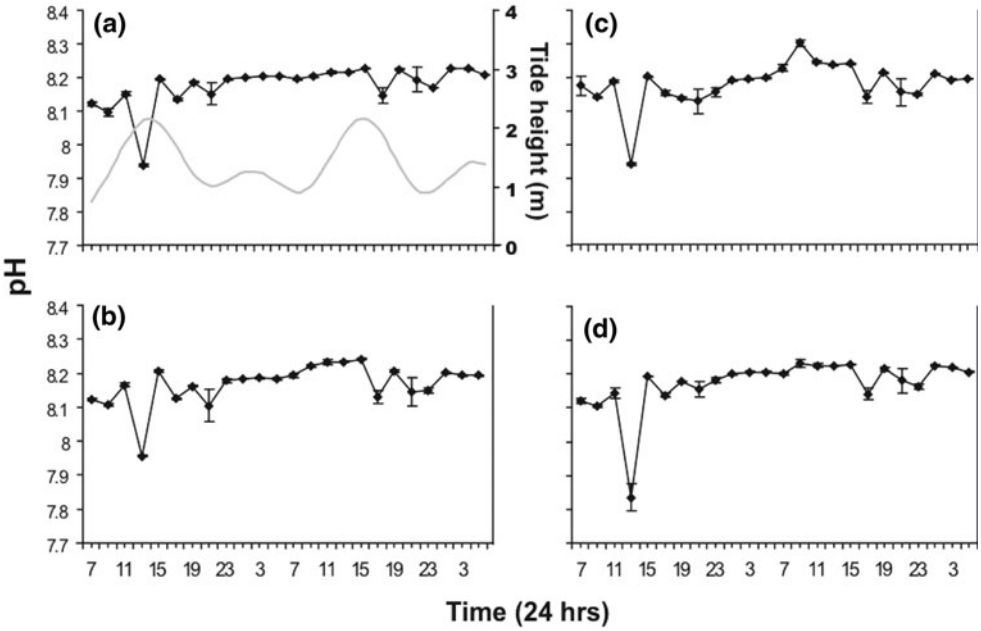

Fig. 5 Change in mean pH (±SE) of water samples from 4 habitats from the shallow back-reef at Lizard Island, together with the tidal heights (*grey line*), over a 48-h period. pH was sampled every 2 h. Habitats were: **a** subsurface; **b** *Pocillopora damicornis*; **c** *D. perspicillatus* algal garden; **d** open sand

Discussion

While much attention has recently been focused on the importance of the decreasing pH of the world's oceans (e.g. Fine and Tchernov 2007; Hoegh-Guldberg et al. 2007; Guinotte and Fabry 2008), few data are available on the levels of spatial and temporal variability of pH in coastal waters, particularly with respect to coral reefs. Documenting the temporal and spatial variability in pH that organisms must presently cope with is the first step to understanding how organisms may respond to changes in pH predicted to occur in the future (e.g. Orr et al. 2005). Evidence from the present study suggests that there are consistent differences at small spatial and temporal scales and that these differences can be of the order of 0.4 pH units.

Ocean scale differences in the coastal pH from the present study conform to the general predictions from indirect measurements of ocean pH (Pelejero et al. 2005). Ocean pH was higher along Ningaloo Reef on the west coast of Australia than from locations sampled along the east coast on the Great Barrier Reef (8.5 ± 0.014 SE, 8.14 ± 0.003 SE, respectively). This may in part be due to the difference in the timing of sampling, but this is also a problem associated with the global estimates of pH trends (Pelaejero et al. 2005 supplementary material). Large-scale data generally originate from the Global Data Analysis Project (Raven 2005), which averages over the top 50 m and has little coverage over most of the Great Barrier Reef. Differences in pH between east and west coast locations may be due to differences in biological productivity, which is a fundamental link for the transport of particulate organic carbon from the surface and its sedimentation into the ocean's interior (Raven and Falkowski 1999). If this is the case, the present findings may indicate that the eastern GBR locations had lower biological production when sampled (summer and autumn) compared to western Ningaloo locations, which were sampled in winter. Simultaneous measurements over broad spatial scales would be required to quantify the trends in pH without seasonal confounding.

Results from Ningaloo indicated that locations sampled 0.2–1 km off the reef exhibited higher pH values (i.e. lower acidity) than those sampled over the reef matrix (8.53 vs. 8.45). Unfortunately, there are few data sets that are spatially or temporally comparable to the present study. Suzuki et al. (1995) sampled a single water sample every 50 m from the inner reef flat to the outer slope on a fringing reef at Ishigaki Island, Japan, obtaining readings of ~8.4 across the shallow inner reef flat and rising to a maximum of 9 on the reef crest, with a sample taken off the reef slope recording 8.3. However, pH was measured 3 h after the water samples were collected, and biological activity within the samples may have substantially changed the pH in this study. Schmalz and Swamson (1969) found very little difference in the pH of water samples collected from a windward and a lagoon site over three 24-h periods at Eniwetok Atoll, Marshall Islands. Studies of carbonate chemistry suggest that lower pH over the reef may be due to the release of CO_2 during calcification on reefs, which generally exceeds the reduction in CO_2 through photosynthesis, resulting in reef waters having elevated pCO2 and a lower pH than nearby oceanic waters (Kawahata et al. 1997; Suzuki et al. 2001). It is likely that trends in pH across the GBR will be much greater than observed here for Ningaloo because of the much wider lagoon, and much greater levels of freshwater input bringing with it lower salinity and

terrestrial components (some of which will influence alkalinity; Hinga 2002). This might be especially relevant to those inshore reefs (e.g. Magnetic Island) that are exposed to significant terrigenous run-off, which may affect the chemical composition of particulate matter suspended in the water column and hence may have a direct bearing on resulting pH. The generality of the potential cross-shelf trend in pH found in the present study obviously requires further research.

Overall, fluctuations in pH among microhabitats were generally subtle, and such differences were relatively stable over time. For example, differences of only 0.07 units were recorded for any of the 10 microhabitats sampled at Lizard Island, and habitat-specific differences measured over the 5-d sampling period at this location were only of 0.05 pH units over consecutive days. Lowest pH values were recorded for sand goby holes, where flow was likely to be relatively low and biological respiration high, while the lowest values were recorded over the filamentous algal beds of a gardening damselfish. Differences in pH were found to be less distinct at the Magnetic Island and Bay Rock (GBR) locations, with the latter showing no difference in pH among the 9 sampled habitats. The higher pH readings over *D. perspicillatus* algal gardens are probably due to algal photosynthesis driving the carbonate–bicarbonate equilibrium to lower pCO_2 and elevating pH. All microhabitats were sampled around midday when pH is typically highest for algal beds (Middelboe and Hansen 2007). It is noteworthy that algal beds maintained by *Dischistodus* spp. damselfishes are known to be important settlement and nursery habitats for the juveniles of many wrasses and parrotfishes (Green 1998). These fishes sit within the algal beds among the fronds and are likely to be exposed to different pH levels during their early development compared to fishes that may live in the open water column, such as many planktivores. Understanding these small-scale differences in pH among habitat will be crucial for the design and interpretation of laboratory studies that simulate the impact of ocean acidification on marine organisms.

In this study, pH changes observed over a 48-h period were mainly due to large spikes in acidity that occurred across most of the 4 habitats sampled. This is in contrast to findings from previous studies where pH fluctuations followed clear diel trends. For example, Schmalz and Swanson (1969) found marked differences in pH over a 24-h period among three parts of a bay in Bermuda and at 2 sites on Eniwetok Atoll. Minimum values were recorded just before dawn and maximum values in the late afternoon just before sunset. Yates and Halley (2006) found similar pattern of changes in pH within a closed system calcification incubation chamber on a shallow (1–2 m depth) reef flat at Molokai, Hawaii. Again, lowest values were recorded in the early morning, while highest values were typically in the late afternoon. Suzuki et al. (1995) reported diel variations of up to 1 pH unit for surface water samples collected over a transect across a shallow fringing reef flat on Ishigaki Island, Japan, with lower values at night than during the day. Ohde and van Woesik (1999) collected sub-surface water samples found diurnal changes of up to 0.7 pH units at 3 sites within a coral reef atoll near Okinawa, Japan, with lowest values at night. The lack of a diel pattern in pH in the present study may be due to the location of the site at the mouth of a flushing lagoon. While the back-reef study site is near the entrance of a large lagoon, currents over the 24-h period were minimal (<5 cm/s) and appeared to have no link to the tidal cycle. The spikes in pH found in the temporal series for all four habitats suggest that the site is influenced by pulses of water whose chemistry have been influenced by factors outside the habitats sampled.

The few studies that have quantified differences in pH among reef habitats have shown levels of variability that span 0.4 to 1 unit. These are high given that the oceans are predicted to display a 0.5 unit decrease in pH by 2100 (Raven 2005). Understanding the levels of spatial variability in pH and the extent and magnitude of fluctuations through time is crucial for the design of controlled experiments that mimic field conditions. Much effort has been directed at understanding how changes in pH will affect the physiological capacity and survival of marine organisms under predicted climate change scenarios. However, many current predictions are based on values which may not necessarily reflect the true environmental conditions specific to the organism(s) under study, or the scale (e.g. microhabitat) at which changes might be experienced by wild animals. This study has shown that different marine organisms experience not only different levels of pH within a specific microhabitat (e.g. sessile organisms) but may also be exposed to a variable range as they move over the reef to conduct their daily activities (e.g. fishes). Hence, without accounting for this natural variability, we may be limiting the power of our current experimental effort.

Acknowledgments Research funding was provided by the ARC Centre of Excellence for Coral Reef Studies. MG was funded by the AIMS@JCU joint venture under a postdoctoral fellowship scheme. We would like to thank M. Holcomb, H. Baumann, C. Goatley, T. Holmes, J. Scannell, S. DeJong, J. Colquhoun, D. Ceccarelli and K. Lema for assistance in the field. M. Holcomb provided salinity measurements from Lizard Island, while D. Krikke provided measurements for Ningaloo.

References

Bindoff NL, Willebrand J, Artale V, Cazenave A, Gregory J, Gulev S, Hanawa K, Le Quéré C, Levitus S, Nojiri Y, Shum CK, Talley LD, Unnikrishnan A (2007) Observations: oceanic climate change and sea level. In: Solomon S, Qin D, Manning M, Chen Z,

Marquis M, Averyt KB, Tignor M, Miller HL (eds) Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, pp 384–432

Caldeira K, Wickett ME (2003) Anthropogenic carbon and ocean pH. Nature 425:365

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: the other CO_2 problem. Ann Rev Mar Sci 1:169–192

Fabry VJ, Seibel BA, Feely RA, Orr JC (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. ICES J Mar Sci 65:414–432

Fine M, Tchernov D (2007) Scleractinian coral species survive and recover from decalcification. Science 315:1811

Green A (1998) Spatio-temporal patterns of recruitment of labroid fishes (Pisces: Labridae and Scaridae) to damselfish territories. Environ Biol Fish 51:235–244

Guinotte JM, Fabry VJ (2008) Ocean acidification and its potential effects on marine ecosystems. Ann NY Acad Sci 1134:320–342

Hinga KR (2002) Effects of pH on coastal phytoplankton. Mar Ecol Prog Ser 238:281–300

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742

Iglesias-Rodriguez MD, Halloran PR, Rickaby REM, Hall IR, Colmenero-Hidalgo E, Gittins JR, Green DRH, Tyrrell T, Gibbs SJ, von Dassow P, Rehm E, Armbrust EV, Boessenkool KP (2008) Phytoplankton calcification in a high-CO_2 world. Science 320:336–340

Ishimatsu A, Kikkawa T, Hayashi M, Lee KS, Kita J (2004) Effects of CO_2 on marine fish: larvae and adults. J Oceanogr 60:731–741

Kawahata H, Suzuki A, Goto K (1997) Coral reef ecosystems as a source of atmospheric CO2: evidence from pCO_2 measurements of surface waters. Coral Reefs 16:261–266

Kleypas JA, Feely RA, Fabry VJ, Langdon C, Sabine CL, Robbins LL (2006) Impacts of Ocean Acidification on Coral Reefs and other marine calcifiers: a guide for future research, Report of a workshop held 18–20 April 2005, St. Petersburg, FL, sponsored by NSF, NOAA, and the US Geological Survey

Manzello DP, Kleypas JA, Budd DA, Eakin CM, Glynn PW, Langdon C (2008) Poorly cemented coral reefs of the eastern tropical Pacific: possible insights into reef development in a high-CO_2 world. Proc Nat Acad Sci USA 105:10450–10455

Middelboe AL, Hansen PJ (2007) High pH in shallow-water macroalgal habitats. Mar Ecol Prog Ser 338:107–117

Munday PL, Jones GP, Sheaves M, Williams AJ, Goby G (2007) Vulnerability of fishes of the Great Barrier Reef to climate change. In: Johnson JE, Marshall PA (eds) Climate change, the Great Barrier Reef. Great Barrier Reef Marine Park Authority and Australian Grenhouse Office, Australia, pp 357–391

Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for coral reef fishes. Fish Fish 9:261–285

Ohde S, van Woesik R (1999) Carbon dioxide flux and metabolic processes of a coral reef, Okinawa. Bull Mar Sci 65:559–576

Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RA, Gnanadesikan A, Gruber N, Ishida A, Joos F, Key RM, Lindsay K, Maier-Reimer E, Matear R, Monfray P, Mouchet A, Najjar RG, Plattner G, Rodgers KB, Sabine CL, Sarmiento JL, Schlitzer R, Slater RD, Totterdell IJ, Weirig M, Yamanaka Y, Yool A (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686

Pelejero C, Calvo E, McCulloch MT, Marshall JF, Gagan MK, Lough JM, Opdyke BN (2005) Preindustrial to modern interdecadal variability in coral reef pH. Science 309:2204–2207

Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola J-M, Basile I, Bender M, Chappellaz J, Davisk M, Delaygue G, Delmotte M, Kotlyakov VM, Legrand M, Lipenkov VY, Lorius C, Pepin L, Ritz C, Saltzmank E, Stievenard M (1999) Climate and atmospheric history of the past 420, 000 years from the Vostok ice core, Antarctica. Nature 399:429–436

Raven JA (2005) Ocean acidification due to increasing atmospheric carbon dioxide. The Royal Society, London, p 59

Raven JA, Falkowski PG (1999) Oceanic sinks for atmospheric CO_2. Plant Cell & Environment 22:741–755

Riebesell U, Zondervan I, Rost B, Tortell PD, Zeebe RE, Morel FMM (2000) Reduced calcification of marine plankton in response to increased atmospheric CO_2. Nature 407:364–367

Schmalz RF, Swanson FJ (1969) Diurnal variations in the carbonate saturation of seawater. J Sediment Petrol 39:255–267

Shirayama Y, Thornton H (2005) Effect of increased atmospheric CO_2 on shallow water marine benthos. J Geophys Res 110: doi:10.1029/2004JC002618

Suzuki A, Nakamori T, Kayanne H (1995) The mechanism of production enhancement in coral reef carbonate systems: model and empirical results. Sediment Geol 99:259–280

Suzuki A, Kawahata H, Ayukai T, Goto K (2001) The oceanic CO_2 system and carbon budget in the Great Barrier Reef, Australia. Geophys Res Lett 28:1243–1246

Wilson SK, Adjeroud M, Bellwood DR, Berumen ML, Booth D, Marie Bozec Y, Chabanet P, Cheal A, Cinner J, Depczynski M, Feary DA, Gagliano M, Graham NAJ, Halford AR, Halpern BS, Harborne AR, Hoey AS, Holbrook SJ, Jones GP, Kulbiki M, Letourneur Y, De Loma TL, McClanahan T, McCormick MI, Meekan MG, Mumby PJ, Munday PL, Öhman MC, Pratchett MS, Riegl B, Sano M, Schmitt RJ, Syms C (2010) Crucial knowledge gaps in current understanding of climate change impacts on coral reef fishes. J Exp Biol 213:894–900

Yates KK, Halley RB (2006) CO_3^{2-} concentration and pCO_2 thresholds for calcification and dissolution on the Molokai reef flat, Hawaii. Biogeosci 3:357–369