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Reef-scale assessment of intertidal large benthic foraminifera populations on one tree Island, great barrier reef and their future carbonate production potential in a warming ocean

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Abstract

Populations of large benthic foraminiferans (LBFs) that inhabit coral reef platforms are major producers of calcium carbonate (CaCO3) in reef ecosystems. This study documented the population density of living intertidal LBF populations at One Tree Reef (OTR), southern Great Barrier Reef, in a community dominated by Marginopora vertebralis and Baculogypsina sphaerulata. Densities of 7.7 × 103 M. vertebralis individuals (ind.)/m2 and 4.5 × 105 B. sphaerulata ind./m2 were estimated for these populations in May 2011. We applied remote-sensing technology to determine reef-scale estimates of suitable Foraminifera habitats and used these to estimate overall stocks of LBF populations on the intertidal algal flat at OTR of ca. 2800 metric tons. The growth rate of M. vertebralis was determined in a laboratory study, and the data were used to calculate the annual CaCO3 production of the reef flat by the LBF population. The response of M. vertebralis to ocean warming was investigated using 3-week incubations at temperatures ranging from ambient sea surface temperature to +6°C. There were significant decreases in growth and concomitant CaCO3 production in 6°C warmer water, which resulted in shell dissolution of M. vertebralis. These results indicate that climate-driven ocean warming projected for the region will result in significant decreases in CaCO3 production in overall foraminiferan populations, although species-specific effects should be further investigated.

Keywords

carbonate, future, their, barrier, great, island, tree, one, populations, foraminifera, benthic, large, intertidal, assessment, scale, reef, ocean, warming, potential, production, GeoQuest

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Reef-Scale Assessment of Intertidal Large Benthic Foraminifera Populations on One Tree Island, Great Barrier Reef and Their Future Carbonate Production Potential in a Warming Ocean

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Steve S. Doo, Sarah Hamylton, and Maria Byrne (2012) Reef-scale assessment of intertidal large benthic Foraminifera populations on One Tree Island, Great Barrier Reef and their future carbonate production potential in a warming ocean. *Zoological Studies* **51**(8): xxx-xxx. Populations of large benthic foraminiferans (LBFs) that inhabit coral reef platforms are major producers of calcium carbonate ($CaCO_3$) in reef ecosystems. This study documented the population density of living intertidal LBF populations at One Tree Reef (OTR), southern Great Barrier Reef, in a community dominated by *Marginopora vertebralis* and *Baculogypsina sphaerulata*. Densities of 7.7×10^3 *M. vertebralis* individuals (ind.)/m^2 and 4.5×10^5 *B. sphaerulata* ind./m^2 were estimated for these populations in May 2011. We applied remote-sensing technology to determine reef-scale estimates of suitable Foraminifera habitats and used these to estimate overall stocks of LBF populations on the intertidal algal flat at OTR of ca. 2800 metric tons. The growth rate of *M. vertebralis* was determined in a laboratory study, and the data were used to calculate the annual $CaCO_3$ production of the reef flat by the LBF population. The response of *M. vertebralis* to ocean warming was investigated using 3-week incubations at temperatures ranging from ambient sea surface temperature to +6°C. There were significant decreases in growth and concomitant $CaCO_3$ production in 6°C warmer water, which resulted in shell dissolution of *M. vertebralis*. These results indicate that climate-driven ocean warming projected for the region will result in significant decreases in $CaCO_3$ production in overall foraminiferan populations, although species-specific effects should be further investigated.
http://zoolstud.sinica.edu.tw/Journals/51.8/xxx.pdf

Key words: Carbonate production, Foraminifera, Remote sensing, Great Barrier Reef, Algal flat.

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Large benthic foraminiferans (LBFs) are crucial to calcareous sediment production in tropical reefs, producing in excess of 1 kg calcium carbonate ($CaCO_3$)/m^2/yr, and at the global scale, contributing approximately 4.8% to the carbonate budget (Hallock 1981, Langer et al. 1997, 2008). Multiple reef-scale estimates of tropical coral reef carbonate production have noted the contribution of the Foraminifera to overall reef calcification (Yamano et al. 2000, Harney and Fletcher III 2003, Hart and Kench 2007). These protists have functionally important ecological and geological roles through fixing inorganic carbon (Smith and Wiebe 1977, Lee 2006), by accumulating $CaCO_3$ from their calcareous shells which produces sedimentary landforms such as coral cays (Yamano et al. 2000, Hohenegger 2006), and in buffering diurnal pH fluctuations in shallow-water environments (Santos et al. 2011).

The population densities of LBFs are controlled by environmental conditions, in particular temperature, solar radiation, and desiccation (Fisher 1966, Ross 1972, Severin 1987, Yassini and Jones 1995). Previous studies on sortids (e.g., *Marginopora vertebralis*) and Calcarinidae (e.g., *Baculogypsina sphaerulata*) indicated significant decreases in photosynthetic efficiency and growth in response to prolonged periods of increased temperatures (Reymond et al. 2011, Schmidt et al. 2011, Sinutok et al. 2011, Uthicke and Fabricius 2012, Uthicke et al. 2012). Warming in particular causes mortality and bleaching in the dinoflagellate-bearing foraminiferan, *M. vertebralis* (Uthicke et al. 2012). As the ocean warms due to climate change, it is expected that LBF communities will continue to experience stress from increased temperatures. In addition, anthropogenic stressors such as ocean acidification and coastal eutrophication (land runoff) are also deleterious to their physiology and growth (Osawa et al. 2011, Reymond et al. 2011, Fujita et al. 2011, Uthicke and Fabricius 2012, Uthicke et al. 2012). However, tolerance levels to stressors vary among LBF species with contrasting effects among species noted in some comparative studies (Fujita et al. 2011, Hikami et al. 2011, Osawa et al. 2011).

Despite the functional importance of LBFs in coral reef ecosystems, the extent to which carbonate production of living communities of benthic Foraminifera will be influenced by rising ocean temperatures at the overall reef scale is not well understood. Most studies have focused on the ecology

and population density of subtidal foraminiferans (e.g., Hallock 1981, Fujita et al. 2000, Hohenegger 2006), with only a few studies reporting on intertidal communities (Severin 1987, Yamano et al. 2000, Fujita et al. 2009). In many of those studies, reef-scale estimates were not possible due to spatial restrictions on the available LBF population datasets. The intertidal algal reef flat at One Tree Reef (OTR), southern Great Barrier Reef (GBR) provides extensive habitat for populations of common LBFs (*M. vertebralis* and *B. sphaerulata*), and we investigated these populations to estimate their density and the total amount of $CaCO_3$ stored. We classified ground-truthed remote sensing satellite images to upscale field data to the entire algal flat habitat at OTR, and by doing so, were able to estimate the total habitat of LBFs.

In consideration of the importance of temperature as a key factor affecting the persistence and resilience of benthic foraminiferan populations (Yassini and Jones 1995, Uthicke et al. 2012), we investigated the effects of increased temperatures on *M. vertebralis* to assess potential impacts of future ocean warming on this ecologically important species. In eastern Australia, the sea surface temperature (SST) has increased 0.2-1°C since 1970 and is projected to increase further by up to 6.4°C above current levels by 2100 (A1F1 scenario, IPCC 2007). We exposed *M. vertebralis* to thermal treatments ranging from the current ambient SST to scenarios that exceeded daytime low tidal temperatures (ca. +6°C). To support this analysis, the current thermal regime experienced by intertidal foraminiferan populations at OTR was determined using an in situ monitoring system for several months prior to the temperature experiments to understand the recent thermal history of *M. vertebralis* at OTR. These data were also used to relate our thermal treatments to in situ environmental conditions. Upper levels of warming (30 and 32°C) are commensurate with upper IPCC projections for SSTs by ca. 2100 (IPCC 2007). The growth response of *M. vertebralis* was used in conjunction with remote sensing imagery to estimate the potential effects of ocean warming on the overall carbonate production across the entire reef flat at OTR. These results provide an important baseline measurement of foraminiferan populations that will facilitate future assessments of changes in species density and assemblages in response to changing ocean conditions due to anthropogenic effects.

MATERIALS AND METHODS

Study site, sample collection, and population density

OTR (23°30'30"S, 152°5'30"E) is a high-latitude reef in the southern GBR with a coral cay (One Tree I., OTI) and a large lagoon enclosed by a reef crest characterized by an extensive algal flat habitat (Barbosa et al. 2010). Filamentous and turf macroalgae were hand-collected using a 7.6-cm-diameter core. Samples (n = 15) were collected in May 2011 during low tide at random-spaced locations along the algal flat (Figs. 1A, 2). Live *M. vertebralis* (> 1 mm) and *B. sphaerulata* (> 0.5 mm) were separated by species and visually inspected for pseudopodial projections and color using a dissecting microscope (Fig. 1B, C). The 2 species of *M. vertebralis* and *B. sphaerulata* were selected for this study due to their high density in this reef flat environment. Additional minor species found in our samples included *Amphistigina* sp. and *Peneroplis* sp. Isolated *B. sphaerulata* individuals (ind.) were counted in subsamples (~0.5 g) of the core samples, while all *M. vertebralis* specimens were isolated. Samples were then dried, counted, and weighed to determine a mean replicate weight.

To characterize the thermal regime experienced by the foraminiferan community on the OTR flat, temperature data (air and SSTs) and photosynthetically active radiation (PAR) were obtained from the reef monitoring system, Integrated Marine Observing System (IMOS: 23.49787S, 152.05275E; http://data.aims.gov.au/aimsrtds/map.xhtml?) from 15 Feb. to 10 May 2011 encompassing the period up to the date of sampling (Fig. 3). Air and PAR data were collected from the OTI relay station, and surface water temperatures were acquired from 1 m in depth.

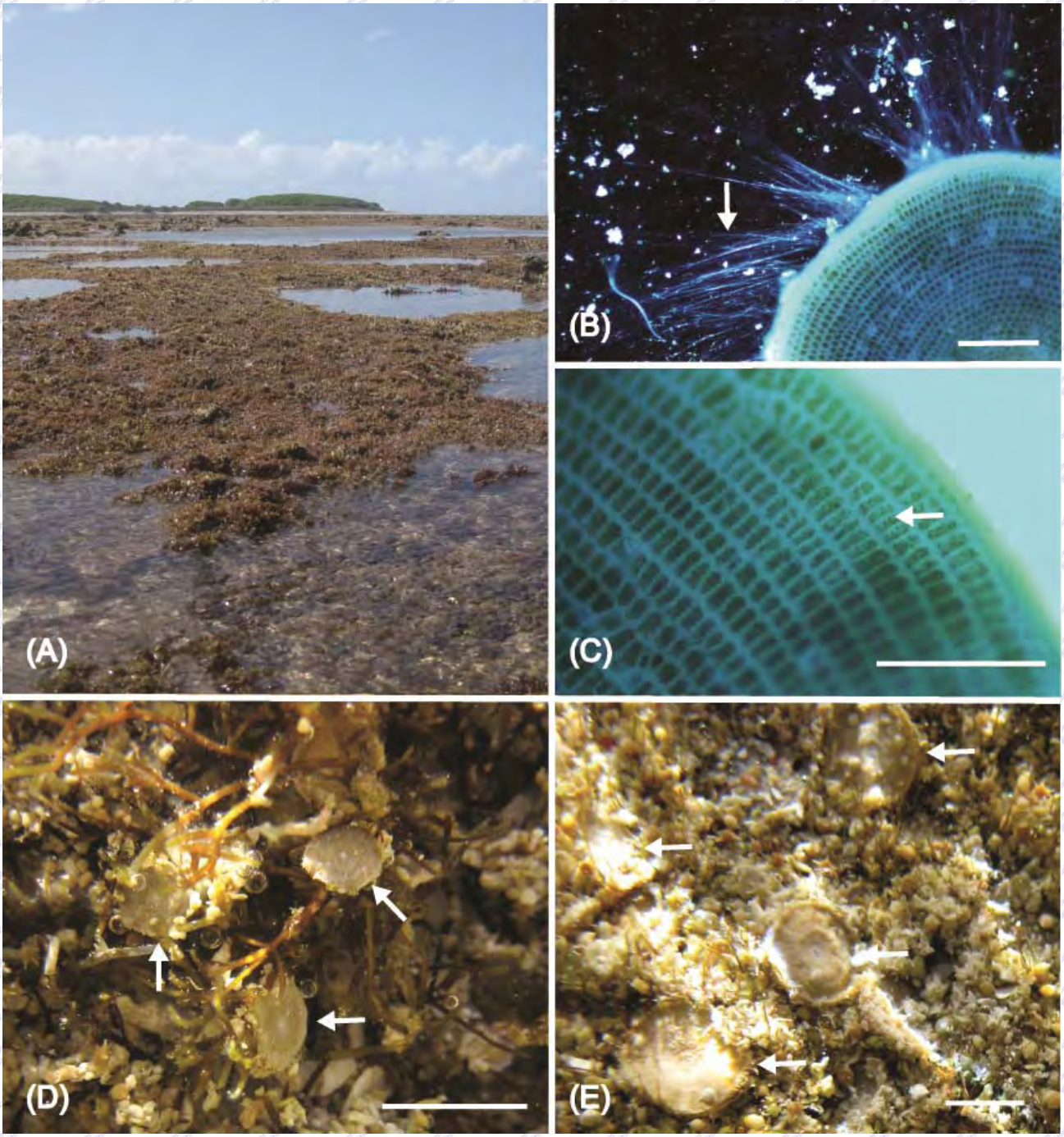

Fig. 1. (A) Algal flat habitat at One Tree Reef. (B) Pseudopodial projections of *Marginopora vertebralis* (white arrow); (C) algal symbionts of *M. vertebralis* (white arrow; photo credit: S. Eggins); (D) small *M. vertebralis* attached to algae (arrow); and (E) large specimens in nearby sediment depressions. Living *Baculogypsina sphaerulata* was found ubiquitously among both macroalgae and on the surface of sediment depressions. Scale bars (B, C), 1 mm; (D, E), 1 cm.

Remote sensing

The area of the algal flat habitat of living Foraminifera at OTR was estimated by performing a maximum-likelihood supervised classification on a Worldview-2 satellite image acquired on 9 Dec. 2009 (at a resolution of 1 m) (Fig. 2). Prior to classification, the image was corrected for the effects of the atmosphere and water column on light transfer (Lyzenga 1987, Cooley et al. 2002). For the atmospheric correction, the Fast-Line-of-sight Atmospheric Analysis of Spectral Hypercubes (FLAASH) algorithm was employed within ENVI 4.5 (Exelis Visual Information Solutions, Boulder, CO, USA) FLAASH provides a physics-based derivation of atmospheric properties, including the surface pressure, water vapor column, and aerosol and cloud overburdens. This was incorporated into a correction matrix for the purpose of inverting "radiance at the detector" measurements into "radiance at the water surface" values (Cooley et al. 2002). The water-column correction followed a methodology which assumed that vertical radiative transfer through the water column could be approximated to a logarithmic decrease in radiation with depth (Lyzenga 1987). Individual waveband data were log-transformed and regressed against each other to calculate a depth-invariant index for each band pair. This was calculated for multiple waveband pairs to generate a series of depth-invariant bands on which statistical image classification could be performed.

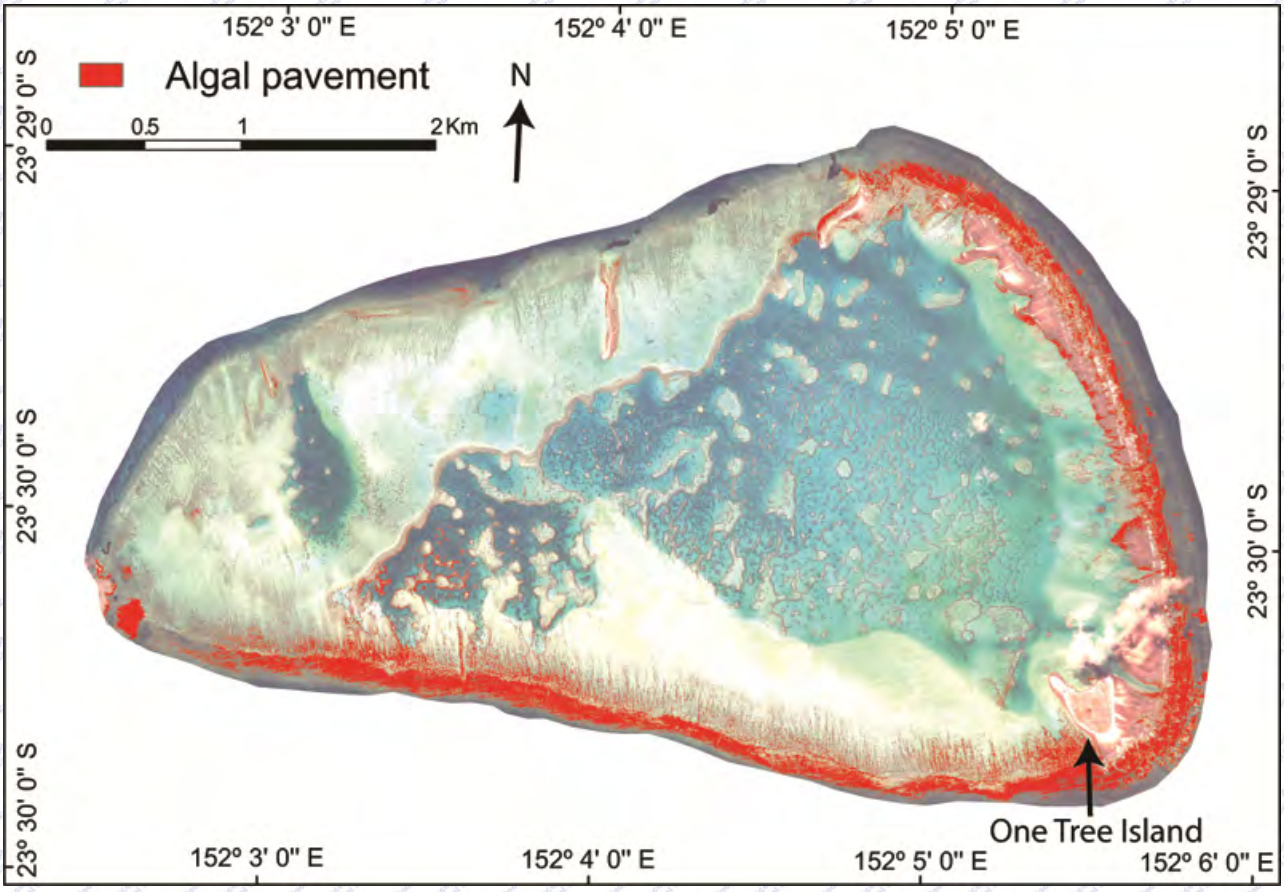

Fig. 2. Satellite image acquired with Worldview-2 sensor on 9 December 2009. Remote sensing data were classified and validated using a ground-truthed field dataset. Red color indicates areas identified as algal flat.

To ground reference the satellite image and validate the image classification, 350 snapshots of 30 s of oblique underwater video footage were collected from a boat over a wide range of reef system coverage at OTR. Each video footage record was viewed in turn, and the percent cover of individual benthic components was estimated. Of the 350 records collected, 50 were used as training areas to calibrate the classification algorithm, and the remaining 300 were used to assess the overall accuracy of the output map.

Temperature-growth experiment

Impacts of temperature on *M. vertebralis* growth were investigated on specimens haphazardly collected from algal flats and acclimated for 2 d in aquaria at ambient (26°C) temperature. Six specimens were then haphazardly placed into replicate borosilicate glass vials (20 mL) with 7 sub-

replicate vials per treatment replicate. The vials were placed in temperature-controlled water baths set to 26°C (ambient controls) and 3 near-future warming treatments at 28, 30, and 32°C in 0.5-µm-filtered lagoon seawater (FSW) collected at high tide. Specimens were incubated in the experimental treatments for 21 d, and experimental FSW at the designated temperature was changed every 3 d. The protists were carefully monitored for color changes that may have indicated thermal bleaching in response to the treatments. Growth was determined using digital images of individual *M. vertebralis* taken at the start and end of the 3-wk treatment using ImageJ (National Institute of Health, Bethesda, MD, USA), and the percentage surface area growth per day was calculated. For each replicate, growth of the 6 specimens was pooled to determine a replicate mean surface area change for the analysis. Growth data were analyzed by a one-way analysis of variance (ANOVA) with temperature as a fixed factor. Assumptions of the ANOVA (normality and homoscedasticity of the data) were met as respectively tested with Shapiro-Wilk's W and Levene's tests.

To predict changes in weight, a power regression analysis of the diameter and weight of individual foraminifers (n = 300) was used to correlate the surface area measured in this study with individual $CaCO_3$ weight (Fig. 4A). To calculate potential reef-scale effects of calcium carbonate production, the estimated turnover rate of 1 *M. vertebralis*/yr of a similar sortid species, *Amphisorus hemprichii,* was used to predict the annual production of this species (Zohary et al. 1980), and an estimated turnover rate of 11 *B. sphaerulata*/yr was also used (Hallock 1981). All statistical analyses were performed using JMP9 (Cary, NC, USA).

RESULTS

Population density

On the intertidal algal flat (Fig. 1A), small *M. vertebralis* (< 1 cm) individuals were attached to macroalgae, while larger conspecifics (> 1 cm) occupied nearby sediment-filled depressions (Fig. 1D, E). *Baculogypsina sphaerulata* was ubiquitously found among all habitats (Fig. 1D, E). Counts of *M. vertebralis* in samples indicated a mean population density of 7.7×10^3 ind./m^2 (SE = 1.4×10^3 ind./m^2, n = 15) and an approximate annual $CaCO_3$ production of 71.7 g/$m^{2/}$yr. *Baculogypsina sphaerulata* had a mean density of 4.55×10^5 ind./m^2 (SE = 1.66×10^5 ind./m^2, n = 15) and an average annual $CaCO_3$

production of ca. 2.86×10^3 g/m^2/yr based on the estimated yearly turnover rate of 11 *B. sphaerulata*/yr (Hallock 1981).

Reef-scale assessment

The classification produced a map that was found to be 81% accurate on the basis of the accuracy assessment dataset of 300 video footage records. Based on the remote sensing classification, the area of the algal flat habitat at OTR was estimated to be 0.96 km^2 (Fig. 2). Thus, based on the available habitat and observed population densities, approximately 73,000 kg of $CaCO_3$ was estimated to be stored in living *M. vertebralis* and 270,000 kg in *B. sphaerulata* on the OTR algal flat at the time of our May 2011 sampling. Based on estimates of yearly turnover rates of similar species (*Amphisorus hemprichii*, a sortid similar to *M. vertebralis* (Zohary et al. 1980) and *B. sphaerulata* (Hallock 1981)), an estimated total of 2800 metric tons of $CaCO_3$ is produced yearly by these 2 populations on the OTR flat, with *B. sphaerulata* having a greater contribution (~97%) to $CaCO_3$ production.

Thermal environment of the reef flat

In the austral summer, *M. vertebralis* regularly experienced subaerial exposure, resulting in ambient environmental temperatures of 26-31°C at OTR (Fig. 3A). During spring and daytime low tides, particularly high levels of warming were observed due to radiative effects of sunlight (PAR), as evidenced in much higher surface seawater temperatures compared to air temperatures (Fig. 3A, B). In the months prior to the experiments, SSTs (at high tide) ranged 25-29°C. Thus *M. vertebralis* experienced temperatures 2-4 °C above ambient SSTs in pulses at low tide during this period.

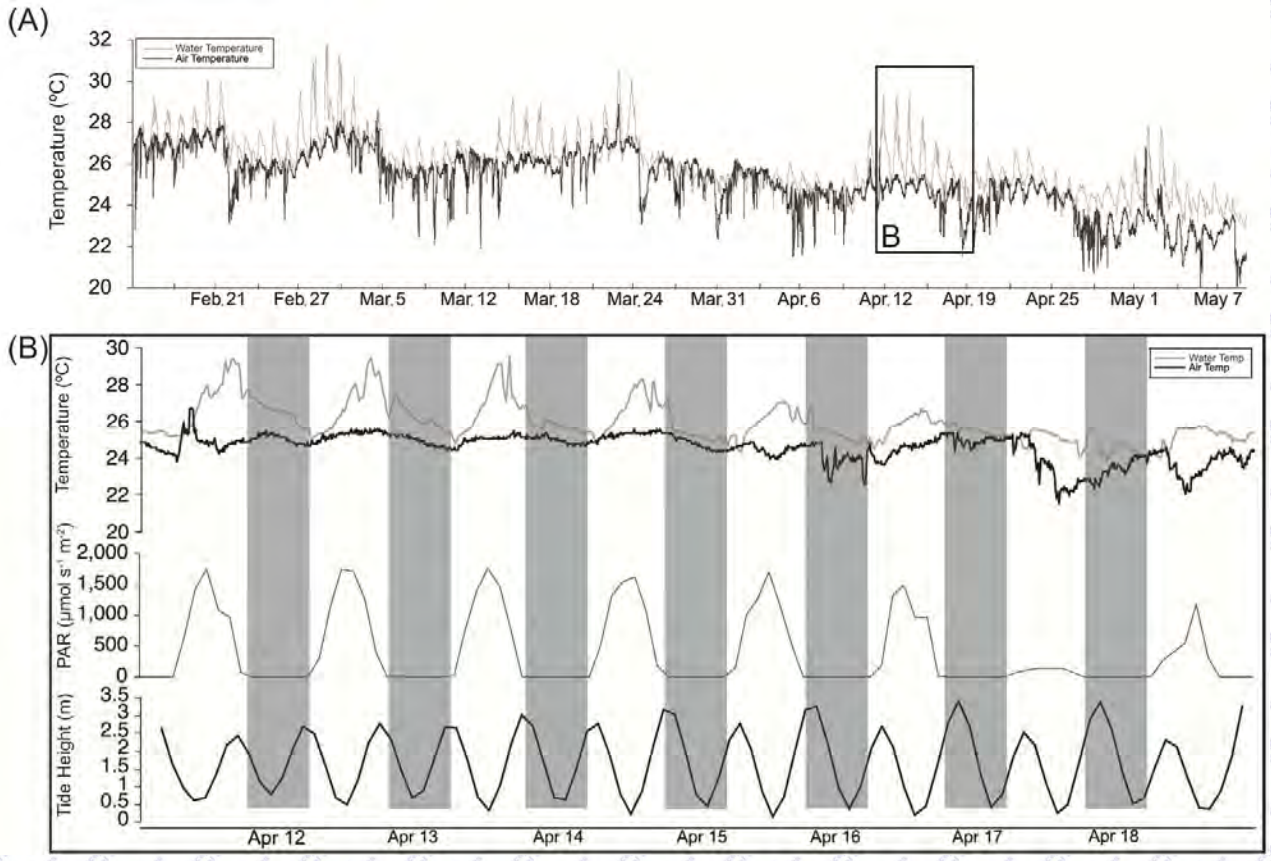

Fig. 3. Physical parameters at One Tree Reef from in situ sensor data (http://data.aims.gov.au/aimsrtds/map.xhtml?) representing (A) surface water (1 m) and air temperature collected 15 Feb.~10 May 2011 for characterization of the thermal regime over a tidal cycle, and (B) a week-long temporal subset of the surface water and air temperature dataset, encompassing combined spring and daytime low tides on the surface water (1 m) temperature. Photosynthetically active radiation (PAR) was high during low tidal height, leading to increased surface water temperatures. Gray shading indicates nighttime.

Growth response of *M. vertebralis* to temperature treatments

There was a significant negative effect of temperature on the growth of *M. vertebralis* ($F_{3,24}$ = 6.21, p = 0.003). According to Tukey's post-hoc test, the highest temperature treatment (+6°C) was deleterious to growth, resulting in an observed 130% decrease in shell diameter (Fig. 4B). Using regression analyses of the diameter to calculate the shell weight (Fig. 4A), this would indicate that on a reef-scale assessment based on remote sensing data, a 140% decrease in calcification would be predicted at the highest warming temperature (Fig. 4C).

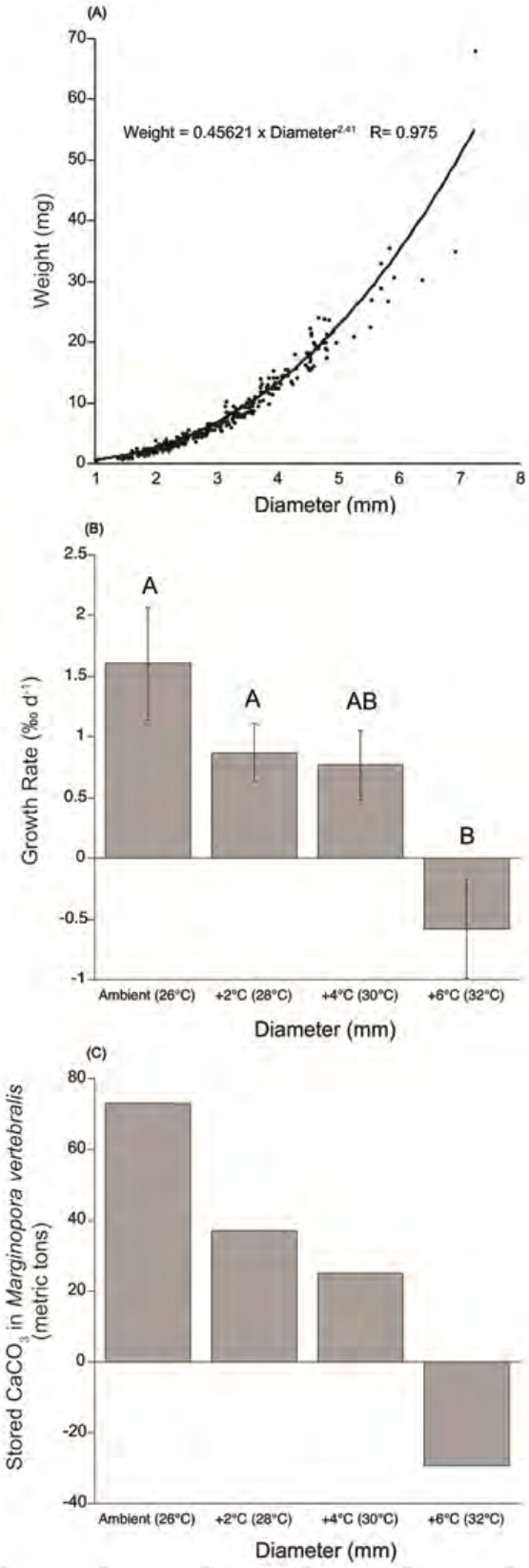

Fig. 4. (A) A regression analysis indicated a strong correlation of *Marginopora vertebralis* diameter with shell weight. (B) Growth results of *M. vertebralis* in experimental treatments after 3-week

temperature treatments. Letters indicate Tukey's honest significant difference post-hoc test. (C) Estimates of overall $CaCO_3$ decreases due to warming in both *M. vertebralis* scaled up from a remote sensing image of the total habitat.

DISCUSSION

Our study adds to the few studies that employed remotely sensed satellite images to scale up *in situ* and laboratory measurements of the intertidal foraminiferan population sizes and further expanded laboratory measurements to estimate their functional contribution to carbonate production across the entire reef flat under different temperature regimes. These results provide a baseline assessment for future studies on sediment production dynamics of these species at OTR and a basis for regional comparisons. Field studies of subtidal LBF communities of *Amphisorus kudakajimensis* estimated populations of $> 1.3 \times 10^6$ ind./m^2 in the Ryukyu Is., Japan (Fujita et al. 2000), and of 6.0×10^5 ind./m^2 for *B. sphaerulata* at Kudaka I., Japan (Sakai and Nishihara 1981). These communities of LBFs were similar in local densities to those observed here on the OTR flat.

Due to the vast area of algal flat habitat suitable for LBFs here at OTR, our estimates of living storage of 73,000 kg $CaCO_3$ of *M. vertebralis*, and 270,000 kg $CaCO_3$ of *B. sphaerulta* represent a large potential for carbonate production on this tropical reef flat. Although the prominence and importance of algal-flat Foraminifera populations at OTR have been known for decades (Davies and West 1981), it is likely that both species in this study experience large seasonal fluctuations in population related to reproductive cycles (Sakai and Nishihara 1981, Fujita et al. 2000). In addition, previous studies on reef-scale foraminiferan communities observed differences in windward and leeward population compositions either due to direct wave effects or indirect macroalgal compositions (Fujita et al. 2009, Osawa et al. 2011). Although we did not distinguish between these areas, an effort was made to sample the entire reef flat to obtain an overall mean. Regardless, monitoring differences between the windward and leeward sides of OTR would be helpful in estimating longer-term population dynamics in terms of both biological (primary productivity) and geological (sediment dynamics) processes.

The significant growth reductions in *M. vertebralis* recorded in response to elevated temperatures were similar to those reported in previous studies of this species in prolonged (30-d) +5°C treatments above ambient conditions (Uthicke et al. 2012). In addition to the decrease in the

calcification rate in the Foraminifera in response to increased temperature (e.g., Fujita et al. 2011, Uthicke et al. 2012), we also observed shell dissolution in the +6°C treatment. Although this shrinking effect was not previously reported, an earlier study indicated that increased thermal stress reduced the calcite crystal width and produced overall negative calcification, i.e., dissolution (Sinuok et al. 2011). This sensitivity to warming indicates that *M. vertebralis* might not cope well with further increases in air and sea temperatures, although we did not observe bleaching as seen elsewhere (Uthicke et al. 2012). Alternatively, *M. vertebralis* may migrate to deeper depths with more-suitable habitats. One cause of the reduced calcification we observed is likely decreased photosynthesis/primary productivity as documented in previous studies of *M. vertebralis* in a laboratory-based study and from specimens collected at natural CO_2 seeps in Papua New Guinea (Uthicke and Fabricius 2012, Uthicke et al. 2012). In addition, thermal stress was documented to reduce protein expression in the rate-limiting enzyme, RuBisCO (Doo et al. 2012), possibly leading to further changes in pH in the microenvironment of the foraminiferan test (Köhler-Rink and Kühl 2000). This highlights the particular ecological importance of the associated algal symbionts to reef primary production and individual foraminifer holobiont $CaCO_3$ production.

Although the 2 species investigated in this study have similar ecological roles on tropical reefs, there are likely differences in test diagenesis post-mortem. Transport of *B. sphaerulata* into the OTR lagoon where its shells accumulate requires less wave energy and wind forcing than advection of the larger *M. vertebralis* (Davies and West 1981). Due to the high turnover rate of *B. sphaerulata* (Hallock 1981), this species is a particularly important component of carbonate lagoon sediments (Scoffin and Tudhope 1985), and plays a key role in sediment accumulation over time which supports the formation and maintenance of sedimentary landforms (coral sand cays) (Yamano et al. 2000). Test dissolution and decreased growth at higher temperatures would reduce the lagoon sediment supply at OTR where foraminiferan shells constitute a significant portion of the lagoon sediments (Davies and West 1981). As the $CaCO_3$ shells of LBFs buffer daily diurnal biogeochemical cycles of carbonate sands and pore water exchange (Santos et al. 2011), a decrease in Foraminifera production would also impact sediment dynamics and the associated fauna. In addition, a recent local study at OTR highlighted the ecological importance of the living fauna such as sea cucumbers, which plays key roles in reef dissolution rates at the reef scale by buffering the dissolution of calcareous tests in the acidic holothurian gut (Schneider et al. 2011). Although our study did not test the effects of thermal stress on *B. sphaerulata*, it is likely that there were also significant effects on growth, as seen in other Calcarinadae (Schmidt et al. 2011). Overall, decreased calcification by intertidal foraminiferan populations in a warming ocean as indicated by our results would likely have a negative effect on future reef health. With increasing global

temperatures, reef-scale measurements of population fluxes will be a valuable addition to evaluating future responses of tropical reefs to a changing climate.

As seen in other intertidal invertebrates (Somero 2010), it is likely that the thermal history of the Foraminifera will influence their resilience to stress from increased temperatures. Investigations of thermal responses of foraminiferan populations from environmentally distinct areas, such as the intertidal LBF population documented in this study, in relation to more-stable subtidal populations may identify more-robust species and populations. In the months prior to our study, *M. vertebralis* experienced warming of 2-4°C above ambient SSTs in pulses at low tide. This was evident from our experimental results, which indicated a degree of resiliency up to +4°C for this species. Our experiments indicated that long-term +6°C treatments were deleterious to *M. vertebralis* growth, but it is currently not known how *M. vertebralis* will respond in the field with potential recovery from the stress provided by the incoming tide. This warrants further study into possible acclimation (phenotypic plasticity) and adaptation (genetic) mechanisms of the response to stress and potential reductions in size due to air and ocean warming, as models predict smaller body sizes in animals due to global warming (Sheridan and Bickford 2011). Differences in algal symbionts of *M. vertebralis* (dinoflagellate) and *B. sphaerulata* (diatom) were also documented in a recent study to be key to the resilience in a Calcarindae species of Foraminifera to withstand ocean acidification stress (Hikami et al. 2011), emphasizing the importance of host-symbiont relationships in Foraminifera.

As the cnidarian-dinoflagellate symbiosis in corals was documented to vary in terms of thermal tolerance (Coffroth and Santos 2005, Wang et al. 2012), further study directed at both host- and symbiont-specific responses of benthic Foraminifera to ocean warming would be beneficial to our understanding of the mechanistic causes of reduced calcification seen in this and previous studies. Remote sensing techniques used in this study provided a useful tool for estimating potential reef-scale changes in population densities of these calcifiers. Establishment of an ongoing program that combines repeated acquisition of satellite images with in situ sampling of intertidal populations will be useful for future monitoring efforts of habitat fluxes. As the deleterious effects of ocean warming on invertebrate species are becoming increasingly evident (Somero 2010, Byrne 2011), the ability to quantify reef-scale changes will be crucial for ecological forecasts of both population standing stocks and functional turnover.

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