Potential Local Adaptation of Corals at Acidified and Warmed Nikko Bay, Palau

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Research Article

Keywords: Ocean warming and acidification, zooxanthellate coral coverage, Porites cylindrica

Posted Date: January 22nd, 2021

DOI: https://doi.org/10.21203/rs.3.rs-150437/v1

Abstract

Ocean warming and acidification caused by the increase of atmospheric carbon dioxide are now thought to be major threats to coral reefs on a global scale. Here we evaluated the environmental conditions and benthic community structures in semi-closed Nikko Bay at the inner reef area in Palau, which has high pCO_2 and seawater temperature conditions with high zooxanthellate coral coverage. This bay is a highly sheltered system with organisms showing low connectivity with surrounding environments, making this bay a unique site for evaluating adaptation and acclimatization responses of organisms to warmed and acidified environments. Seawater pCO_2/Ω_{arag} showed strong graduation ranging from 380 to 982 µatm (Ω_{arag}: 1.79-3.66) and benthic coverage, including soft corals and turf algae, changed along with Ω_{arag} while hard coral coverage did not. In contrast to previous studies, net calcification was maintained in Nikko Bay even under very low mean Ω_{arag} (2.44). Reciprocal transplantation of the dominant coral *Porites cylindrica* showed that the calcification rate of corals from Nikko Bay did not change when transplanted to a reference site, while calcification of reference site corals decreased when transplanted to Nikko Bay. Corals transplanted out of their origin sites also showed the highest interactive respiration (R) and lower photosynthesis (P) to respiration (P:R). The results of this study give important insights about the potential local acclimatization and adaptation capacity of corals to different environmental conditions including pCO_2 and temperature.

Introduction

The increase in atmospheric carbon dioxide (CO_2) causes both ocean warming and acidification simultaneously, which are now thought to be the major threats to coral reefs on a global scale[1,2]. Coral mass bleaching events are now occurring more frequently compared to the past, and ocean warming is predicted to further increase the susceptibility of corals to bleaching in the coming decades[3,4]. Some studies have indicated that zooxanthellate corals may have the ability to adapt to high temperature environments, such as by shuffling to Symbiodiniaceae types that have higher tolerances to warmer temperature[5,6]. In addition to global warming, the increase of seawater partial pressure of CO_2 (pCO_2) and the decrease of aragonite calcium carbonate saturation (Ω_{arag}) have been reported to decrease the calcification rates of most reef calcifiers including corals and crustose coralline algae (CCA)[7,8]. Meanwhile, it has been shown that the tolerance of organisms to high pCO_2 can differ among species and even within species[9]. Hence, there is now wide interest in understanding how reef organisms will respond to ocean warming and acidification at the community level, and to examine if organisms are able to acclimatize or adapt to these environmental changes.

Here we investigated a semi-closed bay (Nikko Bay) in the inner reef area in Palau (Fig. 1) with high pCO_2 and high-temperature conditions, and counter-intuitively, high coral coverage[10,11]. Nikko Bay's corals have shown little evidence of bleaching during the 1998-mass bleaching on other reefs of Palau and during the 2010-thermal stress event[12,10]. This bay is of particular interest because it is a highly sheltered system

with organisms showing low connectivity with surrounding populations[13]. CO_2 vent sites[14,15,16] and naturally acidified sites[17,18,19] have been found on coral reefs and utilized as essential models for evaluating the effects of ocean acidification at the ecosystem level. However, most of these systems are open or semi-closed lagoon ecosystems that continuously receive recruitment from the surrounding ocean, which may limit local adaptation of organisms to high pCO_2 conditions. Additionally, while CO_2 seeps shows highly temporal variability of pCO_2, the environment found within Nikko Bay is quite stable and has been suggested to be have been maintained for at least more than 5,000 years[11] and hence, corals may show adaptation or acclimatization responses to environmental conditions found within this bay. Finally, this unique bay provides opportunities to evaluate the effects of the co-stressors of ocean warming and ocean acidification at the community scale.

Here we evaluated the environmental conditions and benthic community structures along with the Ω_{arag} gradient found within the bay. We also conducted reciprocal transplantation experiments of the most dominant coral species, *Porites cylindrica*, to evaluate the potential acclimatization and adaptive responses of corals to warm and acidified conditions.

Results And Discussion

Seawater surface pH (total scale), Ω_{arag} and temperature (SST) showed a strong gradient at the entrance into the bay (Figs. 2a, b, e) and the seawater pH range (7.65–8.02) observed within the bay was equivalent to the ocean pH value from present to the value expected by the end of this century (IPCC 2013, RCP 8.5)[20]. The mean daytime seawater temperature within the bay was significantly warmer (31.8 ± 0.6°C, mean ± S.D.) and had lower pH (7.83 ± 0.06), lower $\Omega_{arag,}$ (2.44 ± 0.34) and higher pCO_2 (619 ± 104 µatm) compared to parameters outside the bay (30.4 ± 0.1°C, 8.02 ± 0.02, 391 ± 31 µatm, 3.63 ± 0.14, Wilcoxon-test, $p < 0.01$, Tables S2), respectively. The seawater pH at Nikko Bay showed diurnal variation, ranging from − 0.05 to 0.25, which was consistent with the range observed outside the bay (Fig. 1e, Table S2) and at other coral reefs[21]. This contradicts with most CO_2 vents where the seawater pH is highly variable temporally[14,15,16]. Average chlorophyll-*a* (Chl-*a*) and nutrient concentration values inside Nikko Bay were slightly but significantly higher than those outside the bay (Wilcoxon-test, $p < 0.01$, Fig. 2f-g, Table S1).

Daytime average total alkalinity (TA) and dissolved inorganic carbon (DIC) were significantly lower within the bay compared to outside the bay (Wilcoxon-test, $p < 0.01$, Figs. 2c, d, Table S2) and TA-DIC diagram indicated that the low pH and high pCO_2 within Nikko Bay were mainly caused by low seawater TA due to calcification and by high DIC due to respiration (Fig. 3). By using the calculated mean water residence time within the bay (71 days[11]), mean net calcification and net primary production (Pn) rates within the bay were calculated to be 22.7 mmol $CaCO_3$ m^{-2} d^{-1} and − 6.9 C mmol m^{-2} d^{-1}. This value was lower than the net calcification rate found at most reefs[22], however the positive net calcification at seawater Ω_{arag} of 2.44 within the bay contradicts with previous studies suggesting that coral reef formation is

restricted to seawater Ω_{arag} higher than ca. 2.8 (pCO_2 lower than 560 µatm)[23], and also with CO_2 seep studies indicating that reef development ceases where pH is lower than 7.7 (Ω_{arag} 2.1) in Papua New Guinea[14], and lower than 7.9 in the Mariana Islands[16].

To evaluate the correlation among seawater carbonate chemistry and benthic community structure, six sites (N2-N7) along with the Ω_{arag} gradient (1.28–3.51) inside the bay and one site outside of Nikko Bay (N1) were selected for benthic community observation (Fig. 1, Table S3). Even though the seawater inside the bay was warmer and more acidified than the seawater outside the bay, hard coral coverage inside the bay (N2-N7) ranged from 34 to 82%, while the coverage at the N1 site outside the bay was 24% (Tables S4). There was no significant correlation between seawater Ω_{arag} and scleractinian hard coral cover (GLM, $p = 0.97$), CCA (GLM, $p = 0.68$), macroalgae, or seagrass coverage (GLM, $p = 0.06$, Fig. S1, Table S5). On the other hand, there was a significant increase in soft coral (= octocoral) coverage with an observed decrease of Ω_{arag} (GLM, $p = 0.01$), which follows previous results at a CO_2 vent at Iwotorishima in southern Japan showing high coverage of soft coral at a high pCO_2 site[15]. Turf algae coverage increased with Ω_{arag} (GLM, $p = 0.04$), contradicting with previous observations at a CO_2 vent in the Mariana Islands[16] (Table S5, Fig. S1). In Nikko Bay, the coral community was found to differentiate along with the Ω_{arag} gradient observed from the outer reef to the inner reef area[19]. Here we found that although coral coverage was not affected, the hard coral community structure showed differentiation among sites within the inner reef bay area, and this structure was mainly predicted by seawater Ω_{arag}, dissolved oxygen (DO), Chl-*a*, nitrate plus nitrite ($NO_3^- + NO_2^-$) concentration, pCO_2 and temperature (Fig. 4, Table S6). Site N1 (outside of the bay) was characterized by high Ω_{arag} (3.51), low pCO_2 (395 µatm), low temperature (29. 3°C), low Chl-*a* (0.55 µg/L), high DO (6.09 mg/L) and was dominated by *Acropora* spp. (coverage 16.5 ± 4.1%), while site N5 was characterized by low Ω_{arag} (1.28), high pCO_2 (1,305 µatm), high temperature (30.5°C), high Chl-*a* (1.68 µg/L), low DO (4.52 mg/L) and was dominated by Merulinidae spp. (15.6 ± 5.2%, Fig. 4, Tables S3-S5). Both *Acropora* spp. and massive *Porites* showed a slight but positive correlation with seawater Ω_{arag} (GLM, $p = 0.04$, Fig. S1, Table S5), suggesting that species belonging to these genera are sensitive to OA, though other environmental factors may also have interactively affected the coverage of those species. Branching *Porites* (mainly consisting of *Porites cylindrica*) showed the highest coverage, accounting for 22 to 79% of hard coral cover inside the bay (Fig. 4g, Table S4), and there was no significant correlation with branching *Porites* spp. and Ω_{arag} (GLM, $p = 0.16$, Table S5). These results suggest that the high coral cover observed within Nikko Bay is related to the potential acclimatization or adaptation capacity of corals such as *P. cylindrica* to high pCO_2 (low Ω_{arag}) seawater.

To determine this possibility, colonies of *P. cylindrica* were reciprocally transplanted between two inner reef bays; a reference site at Malakal Bay (site M1) and a site in Nikko Bay (site N5, Fig. 1) which had different seawater temperature and pCO_2 conditions (Table S7). As a result, it was found that while the calcification rate of *P. cylindrica* originating from M1 significantly decreased when transplanted to N5, the calcification rate of corals from N5 did not show significant differences when transplanted to either M1 and N5 (Fig. 5a, Table S8). Most previous tank experiments have reported a decrease of calcification

rates of *P. cylindrica* at high pCO_2[24, 25] or high pCO_2 and high temperature conditions[26]. Additionally, in contrast to massive *Porites*, *P. cylindrica* was found to have less capacity of up-regulating the calicoblastic calcifying fluid pH, suggesting a high sensitivity to increases of seawater pCO_2[27]. Additionally, the skeleton density of *P. cylindrica* did not show significant differences among sites (Fig. S2), again contradicting previous studies that showed lower skeleton density of corals at a CO_2 vent[28] and naturally acidified sites[29]. The net photosynthesis (Pn) rate of *P. cylindrica* transplanted to site N5 had a significantly higher value ($p = 0.04$) regardless of their origin (Fig. 5b, Table S8), which may be related to the slightly higher nutrient concentration at N5 site (Table S7). Respiration (R) rates showed interactive effects among transplanted site and origin site, and the R rate of both M1 and N5 corals was significantly lower when transplanted to their origin site (Fig. 5c, Table S8). As a result, there were also interactive effects among the transplanted site and origin site with regards to gross photosynthesis (Pg):R, with higher values when transplanted to their original site (Fig. 5d, Table S8), indicating higher energy acquirement of corals at their own origin site. Interestingly, the corals *Acropora pulchra*, *Porites lutea* and *Coelastrea aspera* in a semi-enclosed lagoon of New Caledonia with low pH, high temperature, low oxygen conditions but high coral coverage, were found to exhibit lower calcification, higher respiration (R) and lower Pg:R compared to corals outside of the lagoon[30]. Acclimatization of corals at the New Caledonia lagoon was suggested to be caused by high respiration through potentially high heterotrophy of corals within the lagoon, which has high organic carbon sedimentation[30]. A comparatively high heterotrophy of the corals in Nikko Bay is also suggested as zooplankton abundance (particularly copepod abundance) was observed to be higher at site N5 compared to reference site M1 (Fig. 6), and this may partially alleviate the effects of high temperature and high CO_2 by enhancing their energy availability[31,32]. However, taking into account that only the calcification rate of *P. cylindrica* at site M1 decreased when transplanted to site N5, potential epigenetic or genetic adaptation to the environmental conditions found within the bay appears to have occurred for Nikko Bay corals. This is also indicated by other findings that showed *Pocillopora acuta* within Nikko Bay had higher calcification rate when transplanted to their original site than out of the bay, while *P. acuta* from out of the bay were not able to survive when transplanted within the bay[33].

P. cylindrica from N5 was also found to host two types of *Cladocopium* subclade C1[34] (former *Symbiodinium* 'Clade C'), as well as *Durusdinm*[34] (former *Symbiodinium* 'Clade D'), which are known to be tolerant to high temperatures[35], while *P. cylindrica* from the other sites only hosted *Cladocopium* subclade C1 (Fig. S3). These differences in Symbiodiniaceae, particularly at the most sheltered Nikko Bay site, may be another adaptation mechanism of corals to the environment found within Nikko Bay. However, molecular studies evaluating the potential genetic differentiation of those host corals within the bay are first needed before implying the occurrence of local adaptation. However, for further understand, molecular studies evaluating the potential genetic differentiation of those host coral within the bay are essentially needed before evaluation for the local adaptation possibility.

From the present study, the coral community structure was found to change according to the seawater environmental conditions within the bay, and corals living within the bay such as *P. cylindrica* can maintain their fitness in the warmed and acidified conditions found within the bay. However, interpretation of these results to future climate change should be taken carefully, as several other environmental factors including Chl-*a*, DO, inorganic nutrient concentration and light intensity also varied among sites. Additionally, corals within this bay have been suggested to have been continuously exposed to the unique environment found within Nikko Bay for more than 5,000 years[11], while climate change will occur within a few hundred years. Nevertheless, these results give important insights about the potential acclimatization and adaptation capacity of corals to different environmental conditions, even at small spatial scales, on coral reefs.

Methods

Water quality measurements. The carbonate chemistry including total alkalinity (TA), dissolved inorganic carbon (DIC), aragonite saturation (Ω_{arag}), and water quality parameters including chlorophyll-*a* (Chl-*a*), turbidity (FTU), dissolved oxygen (DO) and inorganic nutrients (DIN, DIP) were measured once each during daytime and nighttime from 40 sites around Nikko Bay (Supplementary Fig. S1, Tables S1, S2).

Water quality measurements in Nikko Bay were conducted during daytime before sunset (15:00–18:00) and nighttime around sunrise (5:00–8:00) between 17 to 19 November, 2014 at 40 sites (Fig. 1). Seawater temperature, salinity, depth, Chl-*a*, and turbidity (FTU) were measured by vertical casting using a multi-parameter sensor (AAQ-Rinko, JFE Advantech). Salinity was calibrated by a salinometer (PORTASAL 8410A, Guildline Instruments), and Chl-*a* (3 replicates) by a fluorometer (Trilogy, Turner Designs). Surface water samples for TA, DIC (2 replicates) and nutrient (DIN, DIP) measurements (4 replicates) were collected from the same sites and measured using an auto burette titrator (ATT-05, Kimoto Electronic Co. Ltd.) standardized by certified reference materials obtained from A. Dickson Laboratory (Scripps Institution of Oceanography), and a nutrient autoanalyzer (AACSIII, BRAN + LUEBEE), respectively. Carbon chemistry was calculated from TA, DIC using CO2SYS[36] with the constants of Mehrbach et al. (1973)[37] and aragonite solubility of Mucci (1983)[38].

Mean net calcification and primary production in Nikko Bay were calculated from the differences between the average of lagoon TA and DIC (n = 80 data each, Table S2) and offshore end-members, the average depth of the bay (18 m), and the mean water residence time within the bay (71 days[11]), by simply assuming these TA and DIC differences were accumulated in the bay during this residence time. For the calculation TA and DIC were normalized at S = 33.02 which was the mean salinity of Nikko Bay.

Benthic community survey. Benthic coverage including coral community cover (at the genus level) was determined by taking 0.5 X 0.5 m photo-quadrats every meter along five 50 m transects at 3 m depth. A total of 50 photographs were taken per transect and per depth at each site; representing an area of 12.5 m^2 of benthos per depth and site. We measured coral community composition and water quality of one

site outside of Nikko Bay (N1) and six sites within Nikko Bay (N2-N7) at a similar depth (~ 5 m) showing different Ω_{arag} conditions (1.39–3.45) for the analyses.

Sites N1 to N5 were surveyed in November 2015 while sites N6 and N7 in August 2014. No major disturbance within Nikko Bay (e.g. bleaching event) was observed between the two benthic survey dates. Benthic photographs were analyzed using CPCe software[39]. The benthic substrate directly below five random points per photograph was classified into benthic categories. The benthic categories included live corals (to the genus level), fleshy macroalgae (identified to the genus level), turf algae, other invertebrates (e.g. sponges, ascidians, gorgonians), crustose coralline algae (CCA), and non-living substrates (e.g. bare rock, rubble, sand). The percentage cover of benthic categories at each site and depth was the result of the average of percentage cover among the five transects. Surface water quality for these seven sites was measured using the AAQ-Rinko, and for water samples taken at 3 m depth to measure TA, DIC and nutrients.

Transplantation experiment. Two nubbins of 5 cm length were collected from 12 *Porites cylindrica* colonies in September 2015 from Nikko Bay (sites N5) and reference site at Malakal Bay (site M1) at 2–3 m depth, respectively. M1 site was selected as the reference site because the coral community structure was similar to Nikko Bay and dominated by *P. cylindrica*, while seawater carbonate chemistry and seawater temperature were close to the conditions found outside the bay such as at site N1. After bringing all samples to Palau International Coral Reef Center (PICRC), all nubbins were glued onto the top of plastic bolts, and transplanted back to the same site from which they were collected. After one month, all nubbins were recovered and buoyant wet weight was measured for all nubbins. Thereafter, coral nubbins were reciprocally transplanted to the two sites, with each one nubbin of 12 colonies collected from the 2 sites transplanted to each 2 sites (n = 24 per site) for 18 days. During transplantation, both seawater temperature and light intensity were logged at 10 min intervals using a temperature data logger (CO-UA-002, HOBO, Onset Corp.) and light sensor logger (DEFI-L, JFE Advantech), respectively. Additionally, seawater was sampled on October 17 for measurement of Chl-*a* (3 replicates), nutrients (4 replicates), and suspended solids (3 replicates). Seawater carbonate chemistry (TA and DIC) was measured by collecting 2 replicate water samples 3 times (17 Oct, 28 Oct and 5 Nov) during transplantation. pH and temperature loggers (EXO2 Multiparameter Sonde, YSI) were also deployed at the three transplantation sites for ca. 5 days. The pH data for the loggers were calibrated using NIST buffers and are therefore reported in NBS scale.

Eighteen days after transplantation, all nubbins were recovered and buoyant wet weight of all nubbins were measured to calculate the calcification rate according to Davis (1989)[40]. Additionally, photosynthesis and respiration rates were measured for 9 out of 12 nubbins of each conditions. Coral nubbins (36 nubbins in total) were placed individually in airtight glass container (volume = 400 ml) filled with the seawater collected from the same site where the corals were transplanted under LED light (250 µmol photon m^{-2} s^{-1}) and dark conditions. Seawater was continuously stirred during the incubation and the oxygen concentration was measured at 0, 20 and 40 minutes using an oxygen sensor (Fibox3, PreSens). After all measurements, the surface areas of all nubbins were measured using the aluminum

foil technique[41] and all calcification, photosynthesis and respiration rates were calculated and normalized by the surface area.

Zooplankton. Zooplankton were sampled at night after sunset for three days (11, 12 and 13 March 2016) from three sites (N5, N7, and M1) using a 100 m Nansen plankton net (30 cm diameter). Horizontal tows were conducted 5 times at 1–3 m depth per site, and the filtered volume was recorded with a flowmeter. Zooplankton samples were split and one-half of the sample was preserved in 5% borated-buffered formalin. Individual numbers of all zooplankton and copepods of the formalin fixed samples were counted under microscope.

Statistical methods. Differences in seawater qualities inside and outside Nikko Bay were analyzed using Wilcoxon signed-rank test. Redundancy analysis (RDA) was conducted as a constrained ordination technique to relate the coral communities to seawater environmental variables. Input for the RDA consisted of coral coverage data that were first transformed using the decostand function in the vegan package. In the present case, the Hellinger distance was used. Generalized linear models (GLMs, family = quasipoisson) were used to evaluate the relation between Ω_{arag} and coral and other benthic coverage. The calcification rate of the transplantation experiment was evaluated with a Generalized Linear Mixed Effects model (family = Gamma) with origin site and transplanted site and its interaction as fixed effects and colony as random effect. Net photosynthesis, respiration (log transformed) and Pg:R (log transformed) of the transplantation experiment were evaluated with a linear mixed-effect model (REML) with origin site and transplanted site and its interaction as fixed effects and colony as random effect. Tukey's HSD test was conducted when there was a significant interaction. Difference of zooplankton and copepod abundance among sites were tested with student t-test. All statistical analyses were conducted using R (version 3.6.3)[42].

Declarations

Acknowledgement

We are grateful to Asap Bukurrou, Arius Merep, Seiji Nakaya, Geraldine Rengiil, Randa Jonathan, Geory Mereb and all staff of the Palau International Coral Reef Center for their support and assistance during this work. This work was supported by funding from the Japan International Cooperation Agency (JICA)-Japan Science and Technology (JST) SATREPS program, and the Japan Society for the Promotion of Science (JSPS) KAKENHI, grant numbers 16H05772, and 20H05790.

Author Contribution

H.K. led the research planning study design, all authors contributed to data collection, H.K., A.W., A.T. and T.K. conducted data analyses, H.K. produced figures, H.K led the writing of the manuscript and all authors contributed to the final manuscript preparation.

Competing interests: The authors declare no competing interests.

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Figures

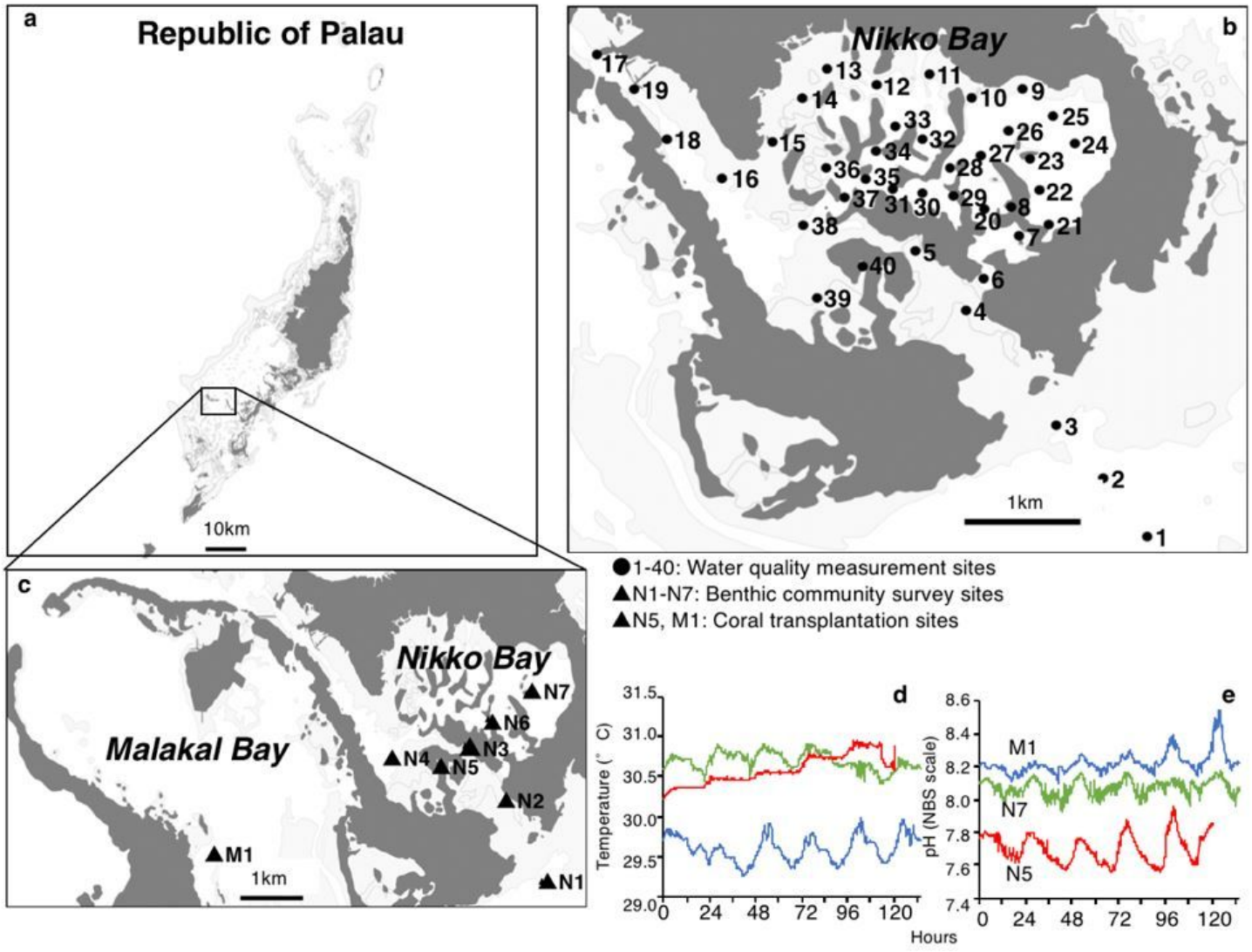

Figure 1

Map showing study sites and seawater temperature and pH at 3 sites (M1, N7, N5). (a) Map of the Republic of Palau. (b) The 40 locations where seawater quality was measured around Nikko Bay. (c) The seven sites (N1-N7) where benthic communities were surveyed and the reference site at Malakal Bay (M1) where the coral Porites cylindrica experiment was conducted. The coral P. cylindrica was sampled from sites M1 and N5 for reciprocal transplantation experiment. (d) Diurnal seawater temperature and (e) pH (NBS scale) measured at Malakal Bay (M1) and two sites at Nikko Bay (N7 and N5). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

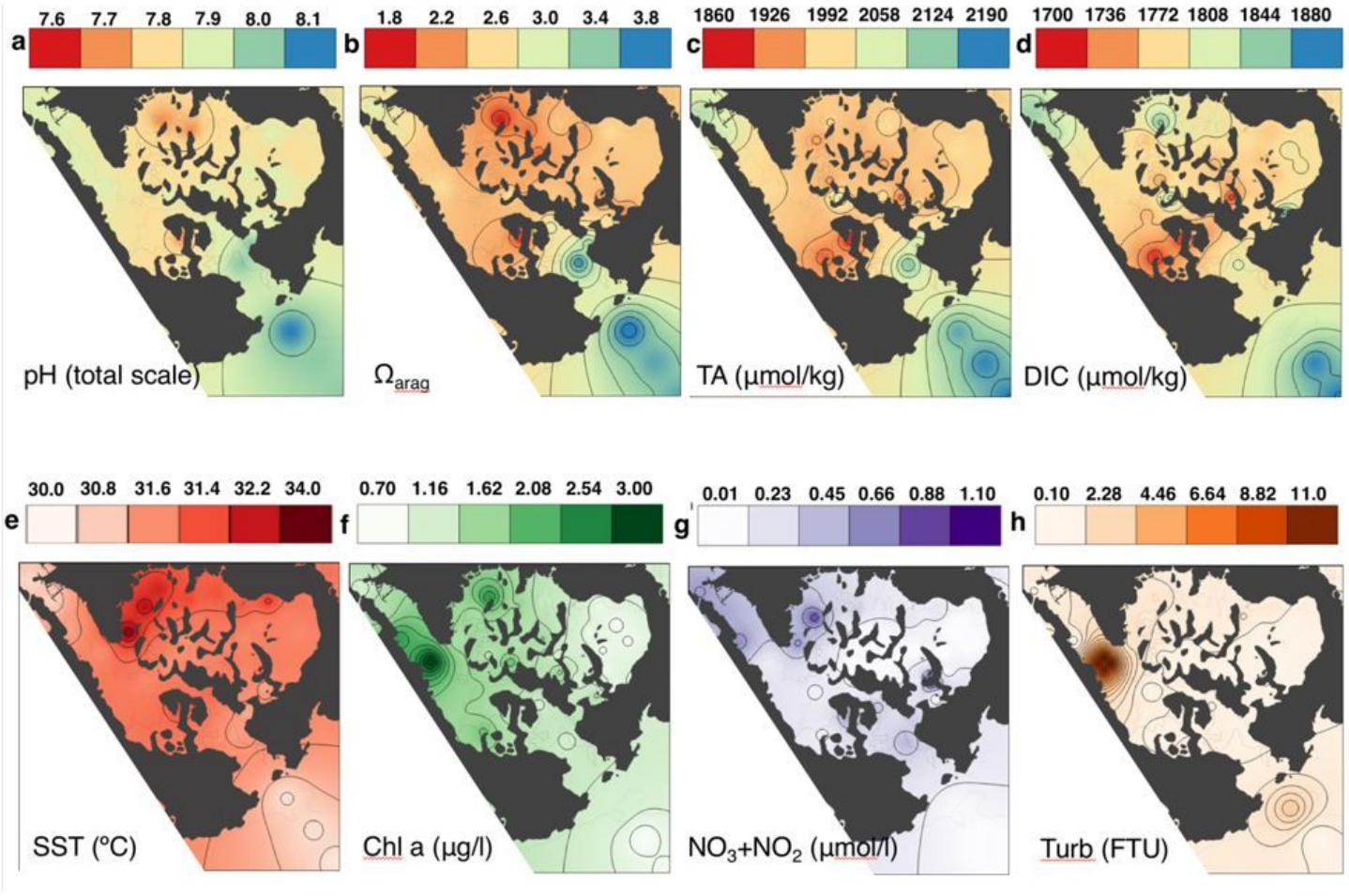

Figure 2

Spatial gradient of (a) pH (total scale), (b) aragonite saturation state (Ωarag), (c) total alkalinity (TA, µmol equivalent kg-1), (d) dissolved inorganic carbon (DIC, µmol kg-1), (e) sea surface temperature (SST, °C), (f) chlorophyll-a (Chl-a, µg L-1), (g) nitrate + nitrite (NO2- +NO3-, µmol L-1) and (e) turbidity (FTU) in sea surface water during daytime around Nikko Bay. See Table S1 and S2 for details. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

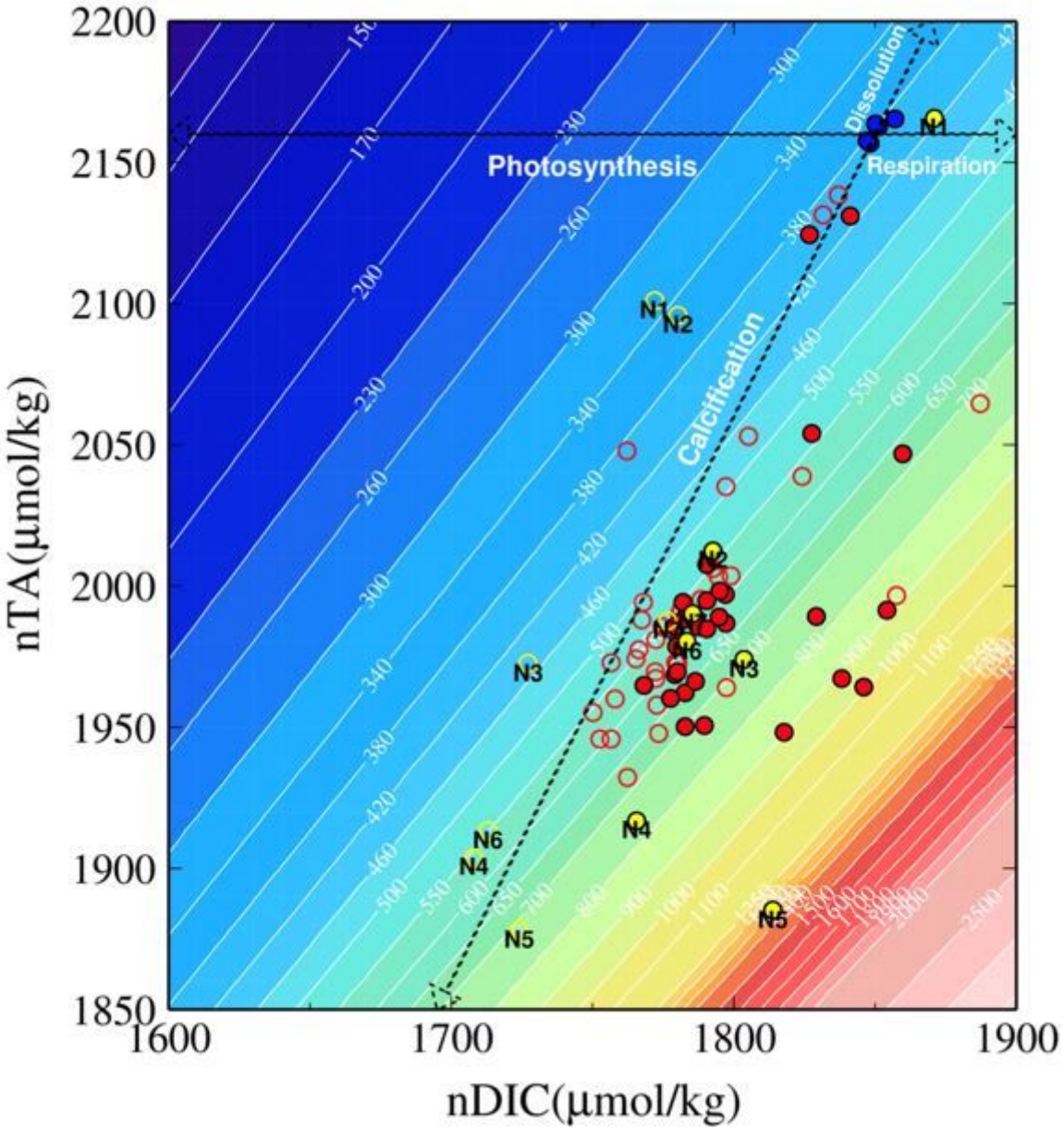

Figure 3

Salinity normalized TA-DIC diagram for the seawater collected around Nikko Bay. Data are normalized at the mean Nikko Bay salinity of 33.02 during the survey. Yellow symbols indicate data collected from N1 to N7 (Fig. 1c) during daytime (open) and at nighttime (filled). Red symbols indicate samples collected at other sites in Nikko Bay during daytime (open) and at nighttime (filled). Blue symbols indicate data collected at far offshore sites as end members. Trend lines indicating calcification, dissolution, photosynthesis, and respiration are drawn from these offshore end member values. Contours indicate pCO2 isolines calculated at S = 33.02 and T = 30 oC.

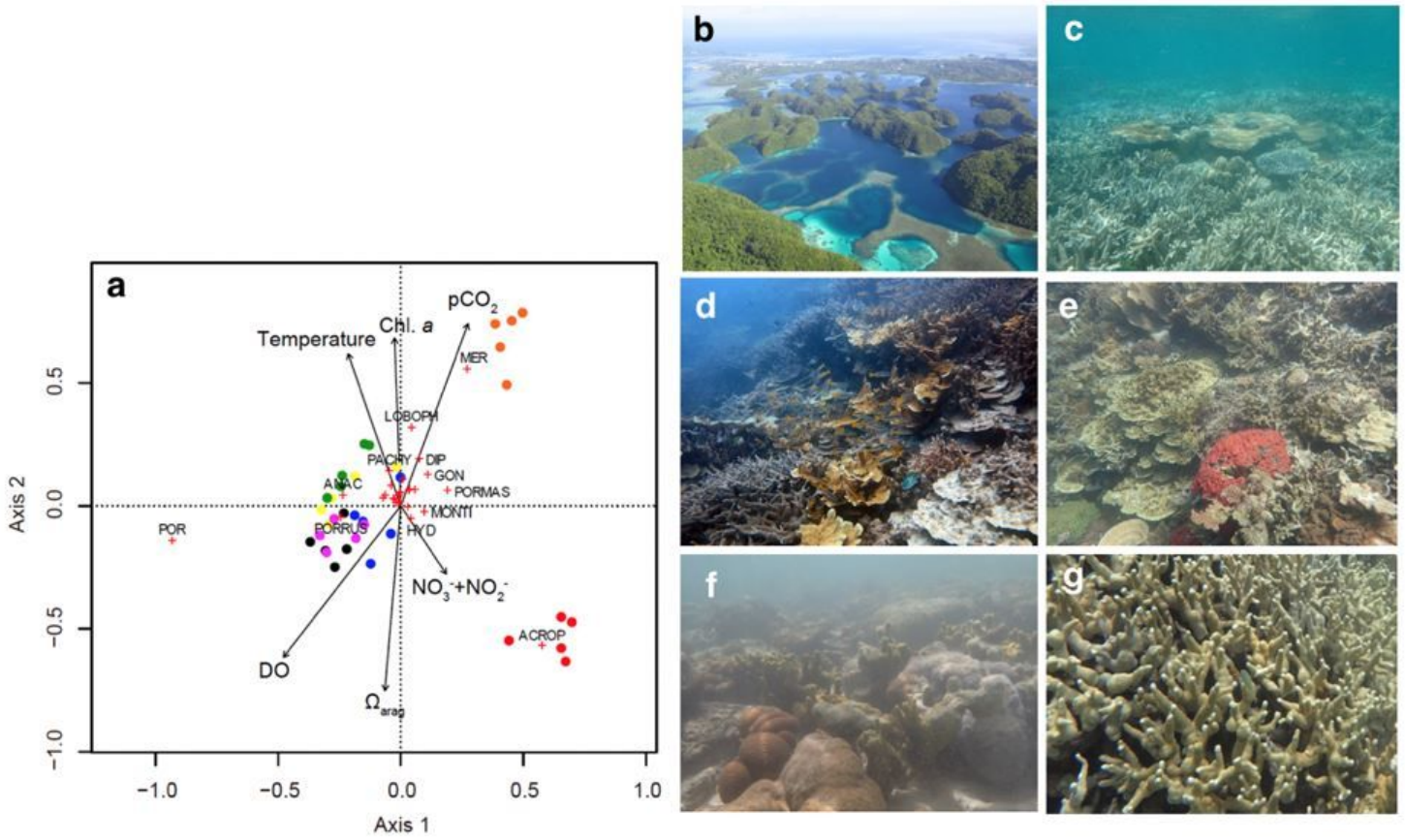

Figure 4

Redundancy analysis (RDA) for water quality and hard coral community at seven sites around Nikko Bay (N1-N7) and image of sites with different benthic communities. (a) Ordination of coral community based on redundancy analysis (Eigenvalue axis 1: 0.1795, Eigenvalue axis 2: 0.1035). Arrows represent significant seawater environmental variables, and their direction and length indicate their contributions to variation along those axes. Dots indicate transect lines with colors distinguishing study sites: red: N1, black: N2, blue: N3, yellow: N4, light blue: N5, green: N6, pink: N7. Genera/families of hard corals are indicated by plus symbols; selected genera are indicated by codes: LOBOPH: Lobophyllia spp., ACROP: Acropora spp., ANAC: Anacropora spp., MONTI: Montipora spp., MER: Merulinidae, DIP: Dipsastrea spp., GON: Goniastrea spp., HYD: Hydnophora spp., PACHY: Pachyseris spp., POR: branching Porites spp., PORMAS: massive Porites spp., PORRUS: Porites rus. (b) aerial image of Nikko Bay, (c) image of site N1 (Ωarag = 3.51), a reef outside of Nikko Bay mainly covered by Acropora spp., (d) image of site N6 (Ωarag = 2.41) within Nikko Bay mainly covered by Porites spp., Pachyseris spp. and Anacropora spp., (e) image of site N7 (Ωarag = 2.36) (f) image of site N5 (Ωarag = 1.28) mainly covered by Merulinidae and Porites spp, and (g) image of the most dominant coral Porites cylindrica.

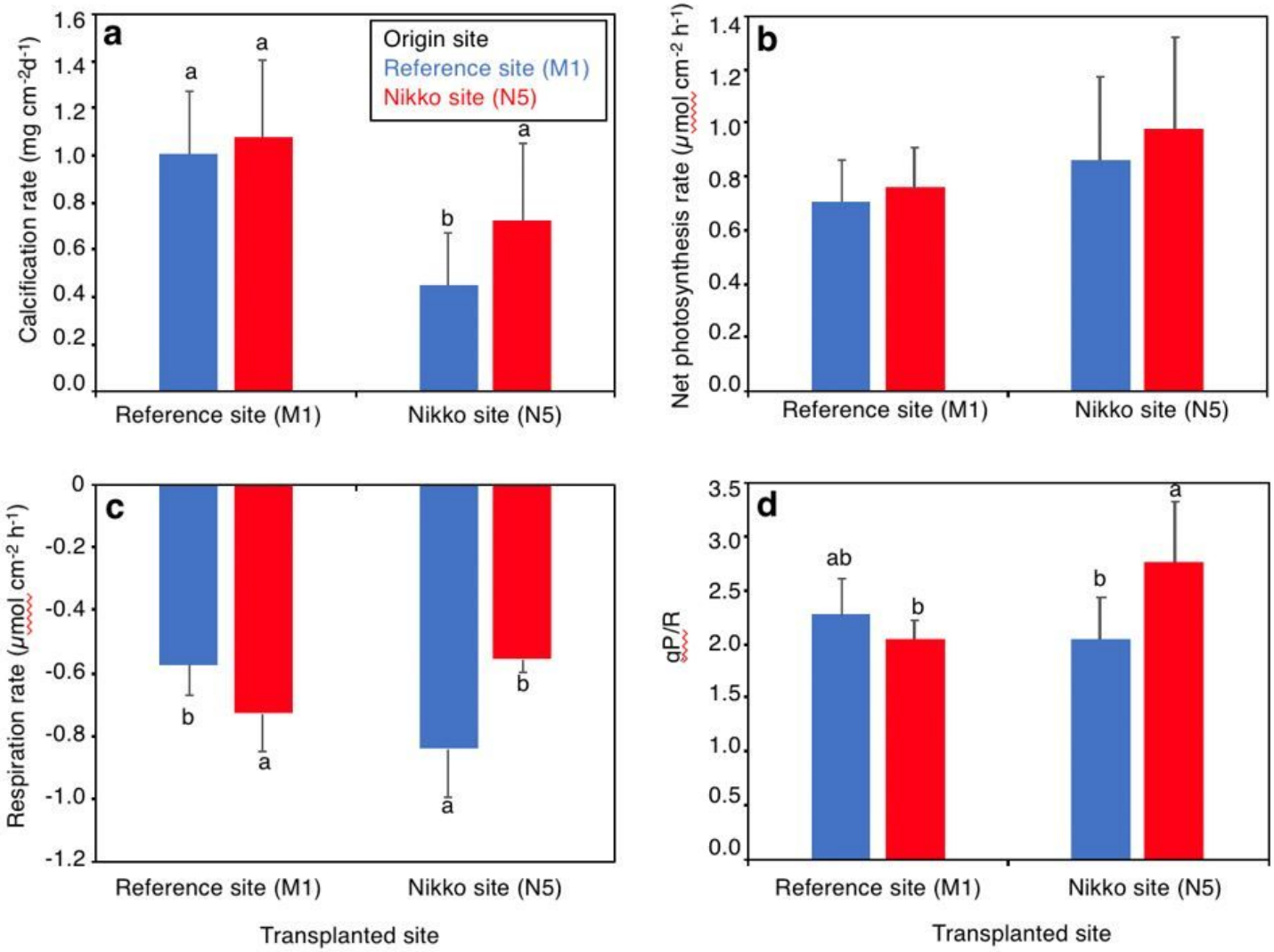

Figure 5

Metabolism of the coral Porites cylindrica reciprocally transplanted between the reference site (M1) and Nikko Bay site (N5). (a) Calcification rate (n = 12), (b) net photosynthesis rate (Pn, n = 9), (c) respiration rate (R, n = 9), and (d) gross photosynthesis ratio to respiration (Pg : R, n = 9) of P. cylindrica originated from the reference site M1 (blue) and Nikko Bay site N5 (red), and reciprocally transplanted for 18 days to either sites. Bars with different lower letters show significant differences among them (Tukey-Kramer HSD, $p < 0.05$).

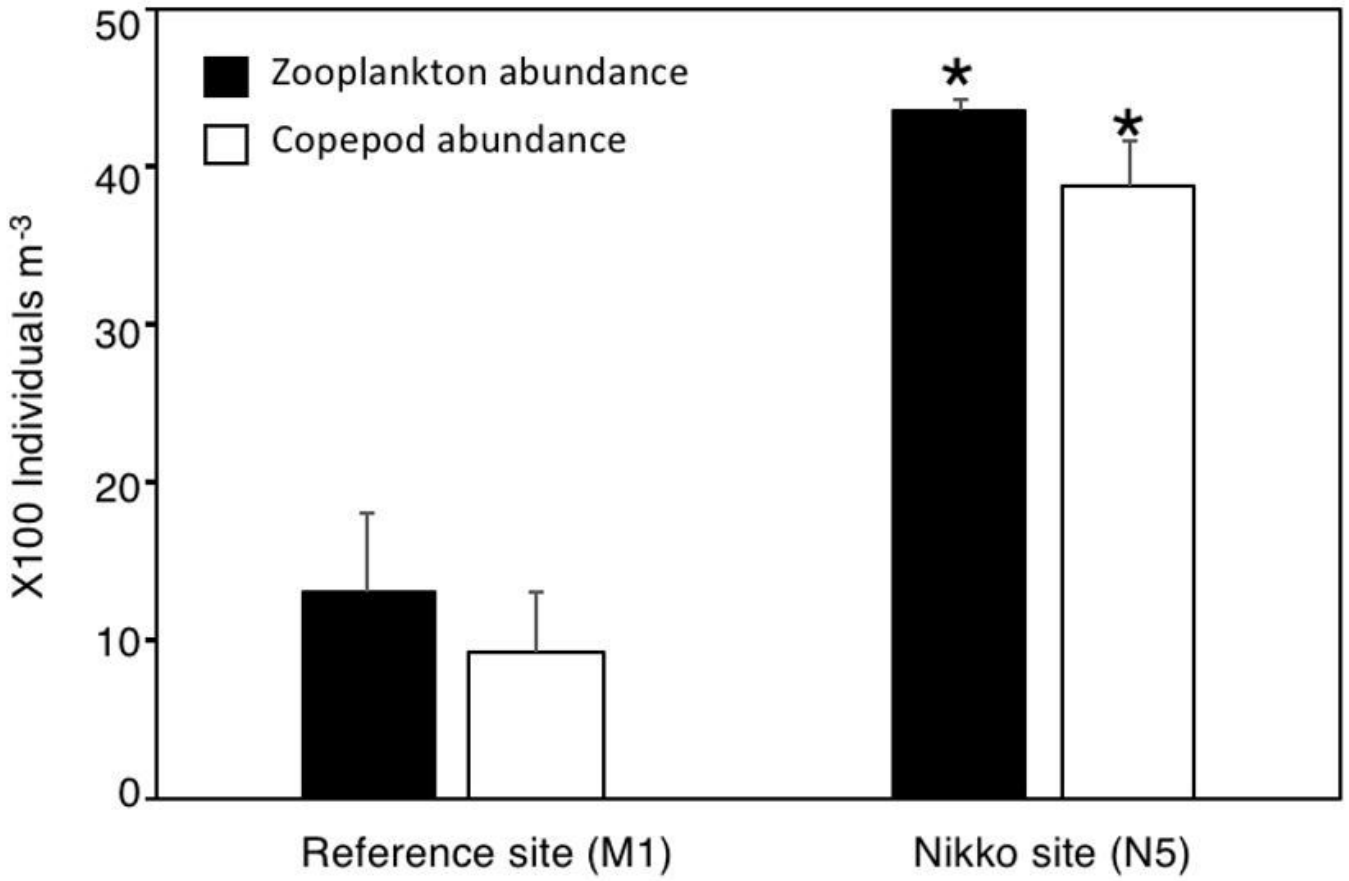

Figure 6

Zooplankton (black bar) and copepod (write bar) abundances at reference site (M1) and Nikko Bay site (N5). Average and S.D. for 3 nights plankton net sampling at each site. Asterisks show significant differences between the two sites (student t-test, $p < 0.05$).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

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