Two offshore coral species show greater acclimatization capacity to environmental variation than nearshore counterparts in southern Belize

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Abstract Coral reefs are enduring decline due to the intensifying impacts of anthropogenic global change. This widespread decline has resulted in increased efforts to identify resilient coral populations and develop novel restoration strategies. Paramount in these efforts is the need to understand how environmental variation and thermal history affect coral physiology and resilience. Here, we assess the acclimatization capacity of *Siderastrea siderea* and *Pseudodiploria strigosa* corals via a 17-month reciprocal transplant experiment between nearshore and offshore reefs on the Belize Mesoamerican Barrier Reef System. These nearshore reefs are more turbid, eutrophic, warm, and thermally variable than offshore reefs. All corals exhibited some evidence of acclimatization after transplantation. Corals transplanted from nearshore to offshore calcified slower than in their native habitat, especially *S. siderea* corals which exhibited 60% mortality and little to no net growth over the duration of the 17-month study. Corals transplanted from offshore to nearshore calcified faster than in their native habitat with 96% survival. Higher host tissue $\delta^{15}N$ in nearshore corals indicated that increased heterotrophic opportunity or nitrogen sources between nearshore and offshore reefs likely promoted elevated calcification rates nearshore and may facilitate adaptation in nearshore populations to such conditions over time. These results demonstrate that offshore populations of *S. siderea* and *P. strigosa* possess the acclimatization capacity to survive in warmer and more turbid nearshore conditions, but that local adaptation to native nearshore conditions may hinder the plasticity of nearshore populations, thereby limiting their utility in coral restoration activities outside of their native habitat in the short term.

Keywords Coral reefs · Climate change · Acclimatization · Isotopes · Reciprocal transplant · Heterotrophy · Belize

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Introduction

Coral reefs are facing unprecedented threats due to a combination of global stressors (e.g., ocean warming and acidification) coupled with local stressors (e.g., nutrient and sediment loading) (Hoegh-Guldberg et al. 2007). Rising temperatures and coral bleaching (i.e., the breakdown of the vital coral-Symbiodiniaceae partnership that sustains reef-building corals) associated with this warming is widely thought to be the biggest threat to the structure and function of coral reefs (Hughes et al. 2017). As the combined impacts of global and local stressors continue to mount, corals and their associated microbial and Symbiodiniaceae communities (collectively termed the 'coral

holobiont') may struggle to persist under changing environmental conditions predicted to occur with climate change.

Acclimatization and adaptation are two possible pathways for the survival and success of the coral holobiont in changing environmental conditions (Coles and Brown 2003). Acclimatization is a plastic change in the phenotype of an organism over its lifetime using its existing genomic repertoire (Baird et al. 2009; Liew et al. 2020; Ziegler et al. 2014), while adaptation is a change in the frequency of alleles in a population over generations in response to selection (Coles and Brown 2003). Corals exposed to more environmental heterogeneity *in-situ* may possess greater acclimatization potential to survive acute stress events (e.g., coral bleaching) and a reduced incidence of coral bleaching (Safaie et al. 2018). Acclimatization of the coral holobiont in response to thermal stress is often driven by changes in the Symbiodiniaceae and/or microbial community from more thermally sensitive species to more thermally tolerant species (Howells et al. 2013; Jones et al. 2008; Ziegler et al. 2014). However, acclimatization can also occur in the coral host, as corals living in warmer reef environments have shown fewer signs of physiological stress following exposure to acute temperature stress events than corals living in cooler environments (Kenkel et al. 2013a; Manzello et al. 2018). Additionally, exposure to high-frequency temperature variation has improved thermal tolerance via acclimatization that exceeds the impact of shifts to thermally tolerant Symbiodiniacea alone (Oliver and Palumbi 2011). Mechanisms of acclimatization in corals include: increased production of antioxidant enzymes, heat shock proteins, or fluorescent proteins, DNA methylation (epigenetic pathways), or other mechanisms of physiological plasticity (Baird et al. 2009; Liew et al. 2020; Ziegler et al. 2014). Understanding the environmental drivers and limitations of physiological acclimatization in thermally variable reefs is imperative to identify conservation priorities as reef restoration efforts expand (Safaie et al. 2018).

The acclimatization capacity of corals is constrained by genotype. For example, corals that already live at their absolute thermal maximum (i.e., $\sim$ 34 °C in the Southern Red Sea) show decreased capacity for physiological acclimatization to warming (Sawall et al. 2015), suggesting that absolute thermal maximums of modern corals can act as a barrier to acclimatization (Howells et al. 2013). Additionally, not all coral species are able to increase thermal tolerance through acclimatization (Camp et al. 2016) and local adaptation to native thermal regimes over generations can limit acclimatization potential as well (Howells et al. 2013). Nonetheless, thermal tolerance conferred via acclimatization in parent corals can be heritable (Putnam et al. 2018), indicating that corals that survive stressful conditions and then reproduce may be able to pass on advantages gained through acclimatization to larvae, which may improve the capacity for thermal tolerance of those species and reefs.

Many tropical coral reef environments that exhibit a high degree of thermal variation are located proximal to the coast in nearshore environments (Baumann et al. 2016; Camp et al. 2016; Oliver and Palumbi 2011). While corals can acclimatize to thermal stress and variation to a degree, this acclimatization is likely hindered by variability of other local scale factors, such as sedimentation, light availability, and nutrient enrichment. In the Caribbean, nearshore reefs are often degraded as a result of thermal stress combined with local land-based stressors, such as elevated sediment and nutrient concentrations (Baker et al. 2010; Baumann et al. 2016; Lapointe and Matzie 1996). As a result of these stressors, nearshore environments often exhibit lower coral diversity and cover than offshore reefs (Baumann et al. 2016; Camp et al. 2016), with some exceptions (Kenkel et al. 2015; McField et al. 2005). High nutrient loads in these nearshore environments may also lead to greater disease and bleaching incidence in corals and promote macroalgal growth, negatively impacting coral communities (Bellwood et al. 2004; Bruno et al. 2003; Lapointe et al. 2019). However, some nutrient loading can be beneficial to corals, providing a source of heterotrophic energy that results in increased growth rates (Mills et al. 2004; Tambutté et al. 2011), as well as mitigating thermal and UV stress (Sawall et al. 2015). The combined effects of increased temperature and nutrients on corals appear to be species specific (Faxneld et al. 2011), indicating that nearshore conditions may provide a beneficial growth environment for some species and a detrimental one for others. In spite of their degraded state, nearshore Caribbean reefs may harbor corals with a genetic or physiological advantage that allows them to persist in future ocean conditions, and corals from these reefs have been targeted for use in coral restoration efforts (Bowden-Kerby and Carne 2012; Morgan et al. 2016).

Here, we employ a reciprocal transplant experiment to assess the relative physiological acclimatization capacity and/or extent of local adaptation of two stress-tolerant Caribbean coral species (Darling et al. 2012). *Pseudodiploria strigosa* and *Siderastrea siderea* corals were collected from nearshore and offshore environments on the Belize Mesoamerican Barrier Reef System (MBRS) and transplanted for 17 months (December 2017–July 2019). Coral colonies were collected from a more thermally variable and nutrient-rich nearshore reef and a more thermally stable and nutrient poor offshore reef, fragmented, and transplanted such that fragments of each genotype were present in both reef locations. We hypothesized that corals from nearshore habitats would possess more plastic

responses to novel environmental conditions than their offshore counterparts. This study has wide reaching implications for coral restoration, as many current restoration methods involve harvesting resilient corals and transplanting them between reefs (Bowden-Kerby and Carne 2012; Lirman and Schopmeyer 2016).

Methods

Sea surface temperature and carbonate chemistry data assessment

To characterize the recent thermal history of the two sites used in this experiment, daily 1-km horizontal resolution sea surface temperature (SST) estimates were acquired for the period of 2003–2019 from the Jet Propulsion Laboratory's Multi-Scale High Resolution SST (JPL MUR SST) records via the NOAA ERDDAP server (https://coastwatch.pfeg.noaa.gov). Previous research has demonstrated that MUR SST better estimates *in-situ* temperatures than other SST products on the MBRS, although it has been shown to underestimate temperatures at depth, and that it is an ideal fit for site characterization due to its lack of cloud contamination and high spatial resolution (Baumann et al. 2016). In-situ temperature was monitored for the duration of the experiment (17 months) using HOBO® V2 data loggers placed at the depth of the table nurseries (1.7 m at False Caye and 3 m at Silk Caye). Monthly carbonate chemistry data were collected from NOAA ACCRETE ocean acidification product suite (Cai et al. 2010) at 0.1° × 0.1° resolution from January 2016–December 2017 (two years of data predating the experiment). Only data from discrete grid cells that contained each site were utilized.

Study sites description

Field work was conducted at a nearshore reef site (False Caye, 16.602554° N, 88.340223° W) and an offshore site (Silk Caye, 16.45026° N, 88.04360° W) on the southern portion of the Belize MBRS. Nearshore reefs on the Belize MBRS have previously been characterized as having greater annual seawater temperature variations and higher incidence of temperatures exceeding the published regional coral bleaching threshold of 29.7 °C than offshore reefs (Aronson et al. 2002; Baumann et al. 2016). Additionally, remotely sensed chlorophyll-*a* has historically been ~ 5 times higher and more variable (due to land-based influences) on nearshore reefs compared to offshore reefs since 2003 (Baumann et al. 2016).

Satellite Sea Surface Temperature (SST) records (2003–2019) reveal that the annual average SST at False Caye 28.23 °C ± 0.02 (SE) was 0.08 °C greater than at Silk Caye (28.15 °C ± 0.02; Table S1) over the past 16 years. Average *in-situ* temperatures over the experimental period were 0.4 °C warmer at False Caye (28.58 ± 0.07 °C) than at Silk Caye (28.18 ± 0.06°; Fig S1A). The average annual range of SST was 0.7 °C greater at False Caye (6.05 °C ± 0.21) than at Silk Caye (5.32 °C ± 0.19; Table S1) over the past 16 years. Diel temperature range (*in-situ*) was 27% higher (ANOVA $p < 0.01$) at False Caye (1.08 °C ± 0.01) than at Silk Caye (0.85 °C ± 0.01) over the experimental interval (Table S1). Daily temperature range was most different between the two sites over the summer interval, when mean temperatures exceeded 30 °C at False Caye (30.07 °C). Additionally, relative differences in *in-situ* light level were assessed over four months (Oct 2018–Jan 2019) as a proxy for sedimentation using HOBO Pendant® loggers placed at the depth of each nursery table (1.7 m at False Caye and 3 m at Silk Caye). Light levels were higher at Silk Caye than at False Caye across the late summer and early winter months (ANOVA $p < 0.01$) despite the shallower table depth at False Caye (Fig S1B).

Experimental design

A reciprocal transplant study was conducted utilizing coral colonies collected at False Caye (nearshore) and Silk Caye (offshore) at a depth of 1.5–4 m. In December 2017, six colonies of *S. siderea* and six colonies of *P. strigosa* were collected from both False Caye and Silk Caye (total of 12 colonies per species between the two sites). Spherical coral colonies of approximately the same size were collected from each site, with an average volume of 4792 cm^3 ± 625 cm^3 (S.E.). Colonies were collected with hammer and chisel and transported to shore in seawater. Each colony was sectioned into 13 roughly equally sized fragments using a 10-inch wet tile saw (RIDGID) creating a total of 312 fragments across all colonies. The saw was lubricated by natural seawater during sectioning and cleaned thoroughly with seawater and fresh water between each colony. Immediately after sectioning, each fragment was rinsed with seawater and placed into a bin of clean seawater. One fragment from each colony was immediately flash-frozen on dry ice to serve as a pre-transplantation sample (T0 control). Twelve fragments of each colony were glued to plastic Petri dishes with pre-drilled holes in them with high viscosity cyanoacrylate superglue (Glue Masters LLC). Petri dishes were labeled with colored livestock ear tags (Allflex) to denote colony and fragment number. Livestock tags were glued to the underside of each Petri dish to prevent biofouling and allow for easy identification of each fragment. After gluing, each fragment was rinsed with seawater, buoyantly weighed, and stored in a bin of clean

seawater until placement back on the *in-situ* nursery tables. Fragments were placed back on the *in-situ* nursery tables on the same day as weighing at the nearshore shore. However, due to logistical concerns and time required to clean and weigh each fragment, all coral fragments were overnighted in plastic bins in low wave energy reef flats at Little Water Caye (1–2 m depth) before being placed back on *in-situ* nursery tables. Plastic bins were covered with nitex mesh to decrease light stress and no visible bleaching or fragment damage occurred. A portion of the originally collected offshore coral colonies were kept overnight before sectioning in the same manner at the beginning of the experiment. Coral fragments were placed onto plastic-coated wire mesh nursery tables provided by Fragments of Hope Ltd. at False Caye (nearshore) and Silk Caye (offshore) using all weather zip ties. These tables were installed onto the substratum using rebar. For each colony, six fragments were placed on a table nursery in their native reef environment and six fragments were transplanted to table nurseries in their nonnative reef. This fully reciprocal experimental design created a native and nonnative (transplant) treatment for each site. The four treatments are defined as follows: Nearshore Native (corals collected at False Caye and placed on the False Caye nursery), Offshore Native (corals collected at Silk Caye and placed on the Silk Caye nursery), Offshore Transplant (corals collected nearshore at False Caye and transplanted offshore to the Silk Caye nursery), and Nearshore Transplant (corals collected offshore at Silk Caye and transplanted nearshore to the False Caye nursery).

Buoyant weight measurements were taken for each coral fragment in the experiment, and a subset of fragments were collected at three time points (3 months after transplantation, March 2018, $n = 35$; 9 months after transplantation, October 2019, $n = 37$; and 17 months after transplantation, May 2019, $n = 46$).

Calcification and survivorship

At each time point, each fragment was buoyantly weighed for quantification of net calcification rates (Jokiel et al. 1978) using an Ohaus Scout® portable balance (Ohaus, Parsippany, NJ). A hook was affixed to the bottom of the balance to allow for hanging weights to be measured and the balance was placed over a bucket of seawater. Salinity and temperature of the seawater were quantified with an YSI 30 probe (Yellow Springs Incorporated, Yellow Springs, Ohio). Percent change in skeletal growth was calculated as the difference between initial weights and other time points (3, 9, and 17 months after transplant) to represent net change in weight (gross weight gain + net dissolution). Buoyant weight of each fragment at each time point was standardized to the surface area of each fragment at the start of the experiment. Coral fragments with no live tissue cover were considered dead for survival analysis, and missing fragments were omitted from the calcification analysis.

Symbiodiniaceae density and chlorophyll-a

Fragments collected and preserved during 0 and 3, 9, and 17 months after transplantation were sectioned into four rectangular or triangular sub-fragments (dependent on colony geometry). The length, width, and height (when applicable) of each fragment were calculated using calipers or a NIST certified ruler (Fisher Scientific, Hampton, NH). Surface area of each fragment was calculated based on these measurements and the geometry of each individual fragment (Veal et al. 2010). Tissue was airbrushed from one sub-fragment from each parent colony using deionized water. The resulting slurry was homogenized using a Tissue-Tearor® handheld homogenizer (BioSpec, Bartlesville, Oklahoma). One mL of the resulting homogenized slurry was aliquoted for Symbiodiniaceae density analysis as per Kenkel et al (2015). Briefly, a 1:1 mixture of formalin and Lugol's iodine was added to the aliquot to stain Symbiodiniaceae cells for counting. Symbiodiniaceae densities were determined by conducting replicate ($n = 3$–8) cell counts of 10 µL samples using a hemocytometer and compound microscope (100 × magnification) and counts were standardized to the surface area of their respective sub-fragment.

The remaining tissue slurry was centrifuged at 4400 rpm for 3 min to pellet out the Symbiodiniaceae portion. Coral animal fraction (supernatant) was poured off, leaving the Symbiodiniaceae pellet behind. Chlorophyll-a was extracted from the Symbiodiniaceae pellet for 24 h. using a 90% acetone dark incubation at − 20 °C (Kenkel et al. 2015). Samples were diluted by adding 0.1 mL of extracted chlorophyll-*a* sample to 1.9 mL of 90% acetone. Extracted chlorophyll-*a* content was measured using a Turner Design 10-AU fluorometer with the acidification method (Parsons et al. 1984) and expressed as µg of chlorophyll-*a* per cm^2 of coral tissue surface area. If sample values were too high or too low to read on the fluorometer, samples were reanalyzed by either diluting or concentrating the sample, respectively.

Energy reserves

Total soluble proteins, lipids, and carbohydrates of the coral holobiont were measured for all frozen fragments and normalized to biomass (ash free dry weight, AFDW), following methods modified from Rodrigues and Grottoli (2007). Sample preparation details for energy reserve analyses can be found in the Supplementary Methods.

Protein content was quantified colorimetrically for each sample using a Bradford Assay (Pierce™ Coomassie Protein Assay Kit). Total lipids of the coral holobiont were extracted following the Folch Method (Folch et al. 1956) and measured on a plate reader at 540 nm (following methods modified from Cheng et al. 2011). Carbohydrates were quantified utilizing a sulfuric acid incubation (Masuko et al. 2005) and read on a plate reader at 485 nm. Additional details on each energy reserve assay are available in the Supplementary Methods. All energy reserve values are reported as mg energy reserve per mg AFDW. Total energy reserves were calculated as the gravimetric sum (mg) of protein, lipid, and carbohydrate values for each sample.

Coral host tissue stable isotopes

Samples were prepared for stable isotope analysis following a methods from Wall et al (2019) and Maier et al (2010). A sub-fragment of each coral was airbrushed using milliQ water. The resulting supernatant was homogenized using a Tissue-Tearor handheld homogenizer. The homogenized slurry was filtered through a 20-µm mesh sieve to remove any residual carbonate. Filtered slurry was centrifuged at 2000*g* for three minutes and the resulting liquid (coral host layer) was decanted off into a clean conical tube. The pellet was suspended in five mL milliQ water and centrifuged again. The resulting liquid layer was added to the coral host layer in a clean conical tube. The coral host layer was then frozen at − 80 °C. The pellet (Symbiodiniaceae portion) was re-suspended in 5–10 mL milliQ, vortexed, and frozen at − 80 °C. Following freezing, all samples were lyophilized (freeze-dried). Approximately one mg (± 0.1 mg) of each freeze-dried sample was placed into a tin capsule and folded into a ball. Samples were placed into 96-well plate and kept in a desiccator until analyzed. $\delta^{15}N$ (a measure of the ratio of ^{15}N:^{14}N in a sample relative to that of a standard) and $\delta^{13}C$ (a measured of the ratio of ^{13}C:^{12}C in a sample relative to that of a standard) were assessed at the Duke Environmental Stable Isotope Laboratory. The samples were combusted at 1020 °C in a Carlo-Erba NA1500 elemental analyzer via a ThemoFinnigan Conflo III to a ThermoFinnigan Delta + XL IRMS. $\delta^{13}C$ values of coral host tissues are reported relative to the Vienna Peedee Belemnite Limestone Standard (V-PDB) at a precision of 0.1 ‰. The $\delta^{15}N$ values of coral host tissues are reported relative to an atmospheric N_2 standard at a precision of 0.1‰.

Statistical analyses

Fully interactive three-way mixed models were used to assess the impacts of species, time point, and transplant treatment on all parameters (growth, protein, lipid, carbohydrate, total energy reserves, endosymbiont density, endosymbiont chlorophyll-*a*, coral host $\delta^{13}C$, and coral host $\delta^{15}N$) using the function *lmer* in the *R* package *lme4* (Bates et al. 2013). The best fit model structure was assessed using AIC (Tables S3, S4), with a random effect of colony in all model structures. For lipid concentrations, all mixed models resulted in a singular fit, so a simple linear model was used. Parametric bootstraps (1500 iterations) were performed to model 95% confidence intervals (Wilcox 2010). Mean and non-overlapping bootstrapped 95% confidence intervals were interpreted as statistically clear differences between treatments (Fig. 2, 4, S2, S3). A Kaplan–Meier estimate of survival was used to assess the effect of transplant treatment on survival using the package *survival* in *R* (Therneau 2015). Cox proportional hazard models, with colony as a random effect and nearshore native corals as controls, were performed using *coxme* in *R* (Therneau 2018). The relationships between measured response variables (energy reserves, Symbiodiniaceae physiology, and isotope values) values in collected fragments of each coral species at 3 and 9 months after transplant were assessed using a principal component analysis (PCA) on a scaled correlation matrix. Data from 0 and 17 months after transplantation were excluded from the PCA due to missing buoyant weight and isotope data, respectively. A PERMANOVA (*adonis* function in *R* package, *vegan* (Oksanen et al. 2013)) was used to assess the effects of transplant treatment and time after transplant on the relationship between response variables for each coral species.

Results

Survivorship

Pseudodiploria strigosa fragments exhibited 100% survival at 3-month and 9-month post-transplantation in all four treatments. Similarly, *P. strigosa* maintained 100% survival 17-month post-transplantation in both the nearshore and offshore native treatments. However, survival was reduced to 96% (1 of 25 fragments) and 92% (2 of 26 fragments) in nearshore and offshore transplant treatments after 17 months, respectively. There was no significant effect of transplant treatment on the survival of *P. strigosa* over the course of this 17-month study time ($p = 0.1477$; Fig. 1a; Table S2).

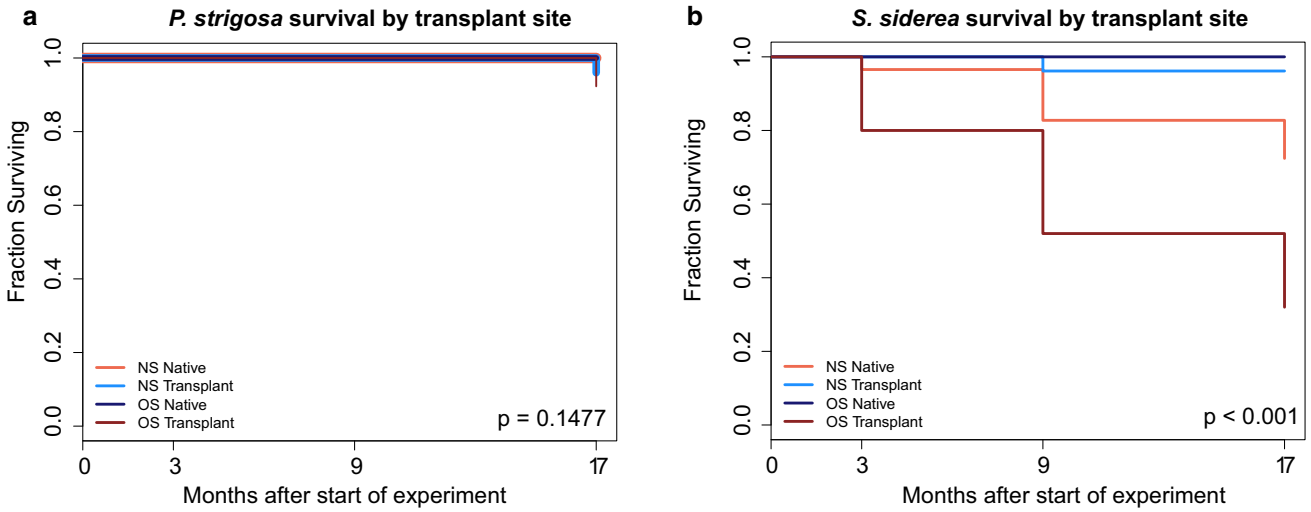

Fig. 1 Survivorship curves for **a** *P. strigosa* and **b** *S. siderea* by treatment and time after transplant. Colors represent the four treatments

Siderastrea siderea fragments exhibited 100% survival throughout the experiment in the offshore native treatment only (Table S2; Fig. 1b). *Siderastrea siderea* fragments in the nearshore transplant treatment exhibited only a single mortality event 9 months after transplantation, resulting in 96% survival 17 months after transplant. Conversely, survival declined at all time points in both the nearshore native and offshore transplant treatments, resulting in 72% and 32% survival, respectively. Transplant treatment had a significant effect on survival of *S. siderea* ($p < 0.001$ Fig. 1b; Table S2).

Net coral calcification

Across all transplant treatments, *P. strigosa* corals maintained net calcification at each time point (Fig. 2; Table S5; Fig S3). Nearshore native fragments showed a significantly greater change in weight over 17 months than did offshore transplant corals (the same genotypes moved to the offshore environment), increasing their weight by 150% compared to just 77% in offshore transplant corals (Fig. 2a; Table S5). Additionally, nearshore transplant fragments showed a greater change in weight over 17 months than did offshore native fragments, growing by 148% compared to 114% (Fig. 2; Table S5).

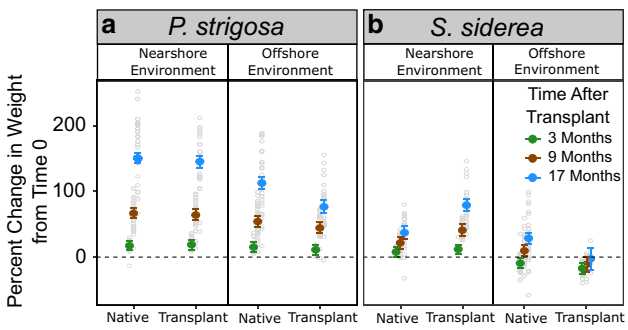

Fig. 2 Percent change in buoyant weight from T0 for **a** *P. strigosa* and **b** *S. siderea* by treatment and time after transplant. The four treatments are labeled on the x-axis and colors represent time after transplant. Colored points represent modeled population means and error bars are modeled 95% confidence intervals. Confidence intervals that do not overlap represent statistically clear differences between populations. Open circles are individual fragment values

Net calcification was observed across three of the four transplant treatments in *S. siderea*, while offshore transplant corals failed to maintain net growth, even after 17 months in their new environment (Fig. 2b; Table S5; Fig S2). Offshore transplant *S. siderea* corals exhibited net dissolution (net skeletal loss) for the first nine months of the study (Fig. 2b; Table S5). As with *P. strigosa*, nearshore native fragments showed a significantly greater increase in weight over 17 months than did offshore transplant corals (37% change in weight compared to 8%; Fig. 2b; Table S5) and nearshore transplant corals also showed greater change in weight over 17 months than did offshore native corals (Fig. 2b; Table S5). Indeed, nearshore transplant *S. siderea* exhibited the greatest change in weight of all *S. siderea* corals in the experiment (80% change in weight compared to − 2.5%; Fig. 2b; Table S5).

Symbiodiniaceae physiology

Symbiodiniaceae densities varied seasonally in *P. strigosa* with higher densities occurring in winter (Pre-transplantation: Dec 2017) and early summer months (3 months after transplantation: March 2018, 17 months after transplantation: May 2019) (Fig. 3a; Table S11). Densities were 3–6 orders of magnitude lower in late summer (9 months after transplantation, September 2018) than in other seasons in

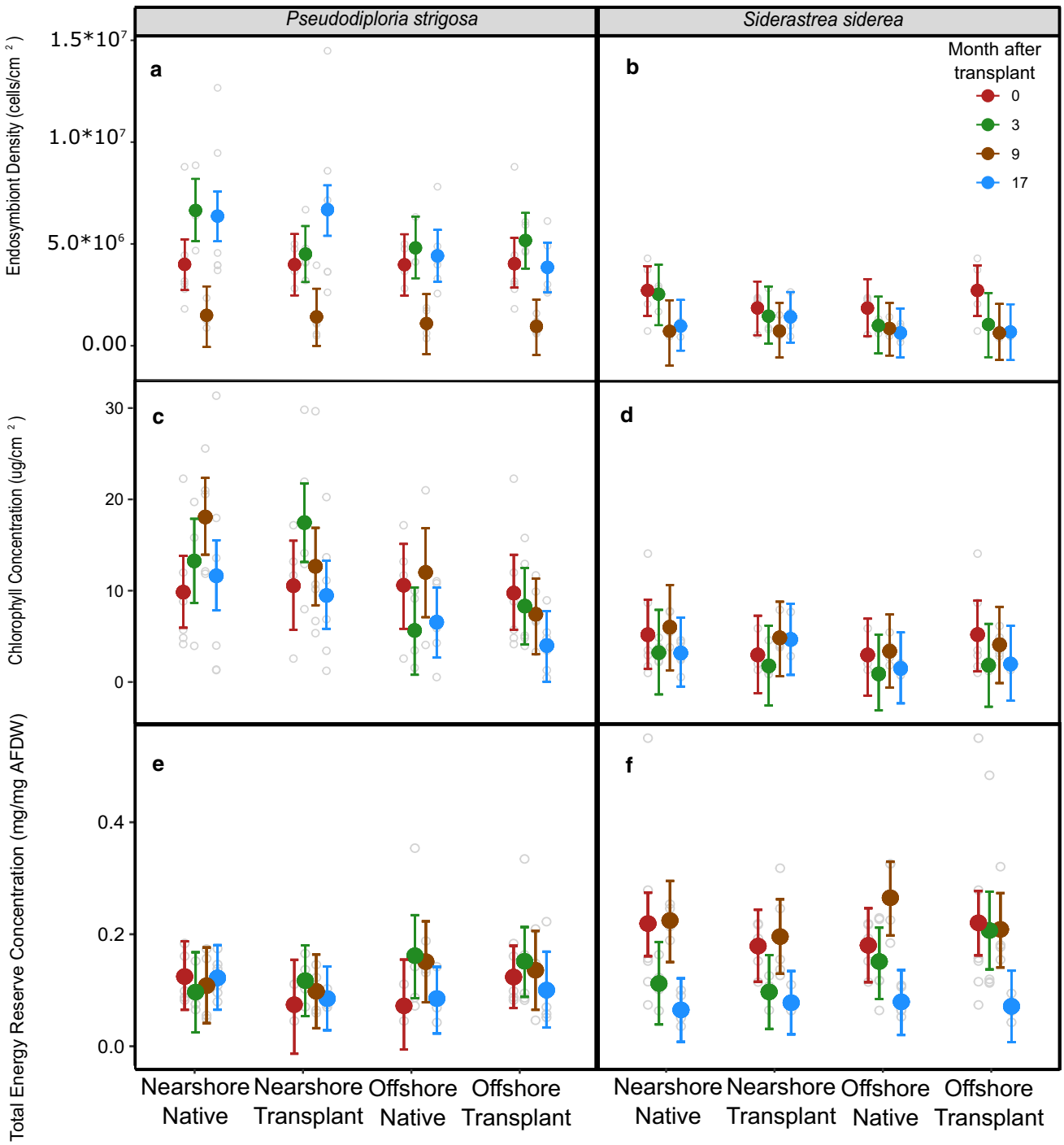

Fig. 3 Endosymbiont density (**a**, **b**), Chlorophyll-*a* concentration (**c**, **d**), and Total energy reserves (**e**, **f**) in *P. strigosa* (left), and *S. siderea* (right) by treatment and time after transplant (months). The four treatments are labeled on the x-axis and colors represent time after transplant. Colored points represent modeled population means and error bars are modeled 95% confidence intervals. Confidence intervals that do not overlap represent statistically clear differences between populations. Open circles are individual fragment values

P. strigosa, though these values were not always clearly different from all other time points (Fig. 3a; Table S11). There were no statistically clear differences in Symbiodiniaceae densities across time points or treatments in *S. siderea* (Fig. 3b; Table S11).

There were no clear differences in chlorophyll-*a* across time points within a treatment in *P. strigosa* corals (Fig. 3c; Table S11). However, chlorophyll-*a* was clearly higher in nearshore native *P. strigosa* corals at three and nine months after transplantation than in offshore

transplant *P. strigosa* at nine and 17 months after transplantation (Fig. 3c; Table S11). There were no clear differences in chlorophyll-*a* concentration between time points or treatments in *S. siderea* corals (Fig. 3d; Table S11).

Total energy reserves

There were no differences in total energy reserves (coral host + Symbiodiniaceae) between time points or treatments in *P. strigosa* (Fig. 3e; Table S7). There were no differences in total energy reserves zero-, three-, and nine-month post-transplantation in *S. siderea* (Fig. 3f; Table S7); however, total energy reserves were lowest 17 months after transplantation in all treatments (Fig. 3f; Table S7). There were no differences in protein concentrations across time points within a treatment in *P. strigosa*, but carbohydrate and lipid concentrations were elevated 3 months after transplant relative to T0 in offshore natives (Fig S4A, C, E). Overall, no value of protein, carbohydrate, or lipid concentration dropped below T0 values in *P. strigosa* (Fig S4A, C, E). In *S. siderea*, protein concentrations declined between 9 and 17 months after transplantation in offshore natives but no differences were observed in other treatments (Fig S4B). Carbohydrates declined between T0 and 17 months after transplantation in nearshore transplant *S. siderea*, while there were no clear differences in other treatments (Fig S4D). There were no differences in lipid concentrations in *S. siderea* across time points or treatments (Fig S4F).

δ¹⁵N and δ¹³C isotopes

Nearshore native corals had ~ 20% higher $\delta^{15}N$ values than offshore native corals in both species (Fig. 4a, b; Table S12, S13). Coral transplanted to the offshore had ~ 18% higher $\delta^{15}N$ values than offshore native corals in both species (Fig. 4a, b; Table S12, S13). *Siderastrea siderea* fragments transplanted to the nearshore had ~ 13% lower $\delta^{15}N$ values than nearshore native corals, while *S. siderea* transplanted to the offshore had ~ 19% higher $\delta^{15}N$ values than offshore native corals (Fig. 4b; Table S12). There were no statistically clear differences in $\delta^{15}N$ across time points in in *S. siderea.* Additionally, There were no statistically clear effects of transplant treatment or time point on Transplant $\delta^{13}C$ in either species, though corals native to or transplanted to the nearshore had marginally lower $\delta^{13}C$ *values*(Fig. 4a; Table S12, Table S13).

Principal component analysis

Principal component analysis and PERMANOVA of measured response variables identified significant effects of transplant treatment and number of months after transplant on coral holobiont physiology in both species ($p < 0.01$ in both species; Fig. 5a, b). In *P. strigosa* there is considerable overlap between all transplant treatments and both time points, yet slight differences are visible due to elevated carbohydrate and lipid concentrations in offshore native corals compared to other treatments (Fig. 5a). Differences between time points in *P. strigosa* are driven by higher symbiont density 3 months after transplant and higher calcification rates 9 months after transplant (Fig. 5a). In *S. siderea*, nearshore and offshore native treatments are separated by higher calcification rates, lipid concentration, and $\delta^{15}N$ values in nearshore natives, while transplanted corals (nearshore and offshore transplant) overlap with both native treatment and have characteristics of both sites (Fig. 5b). Differences between time points in *S. siderea* are driven by higher symbiont density, $\delta^{13}C$ values, and $\delta^{15}N$ values 3 months after transplant and higher protein and carbohydrate concentrations 9 months after transplant (Fig. 5b).

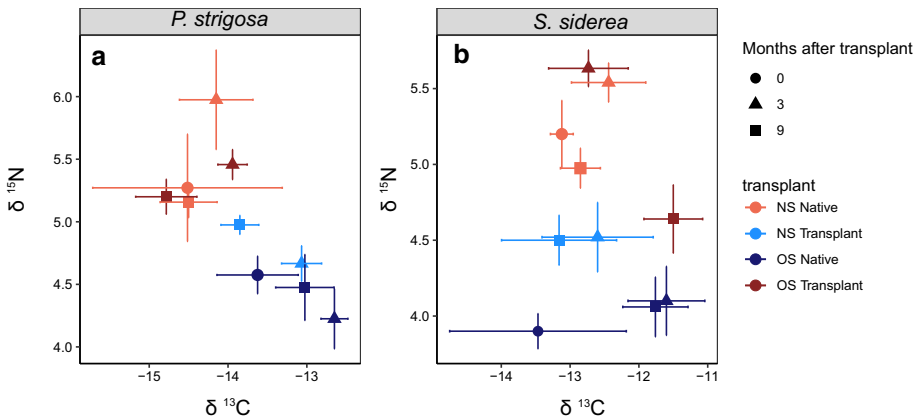

Fig. 4 $\delta^{13}C$ and $\delta^{15}N$ for **a** *P. strigosa* and **b** *S. siderea* by treatment and time after transplant. Colors points represent modeled treatment means and symbols represent time after transplant. Error bars are modeled 95% confidence intervals. Confidence intervals that do not overlap represent statistically clear differences between populations

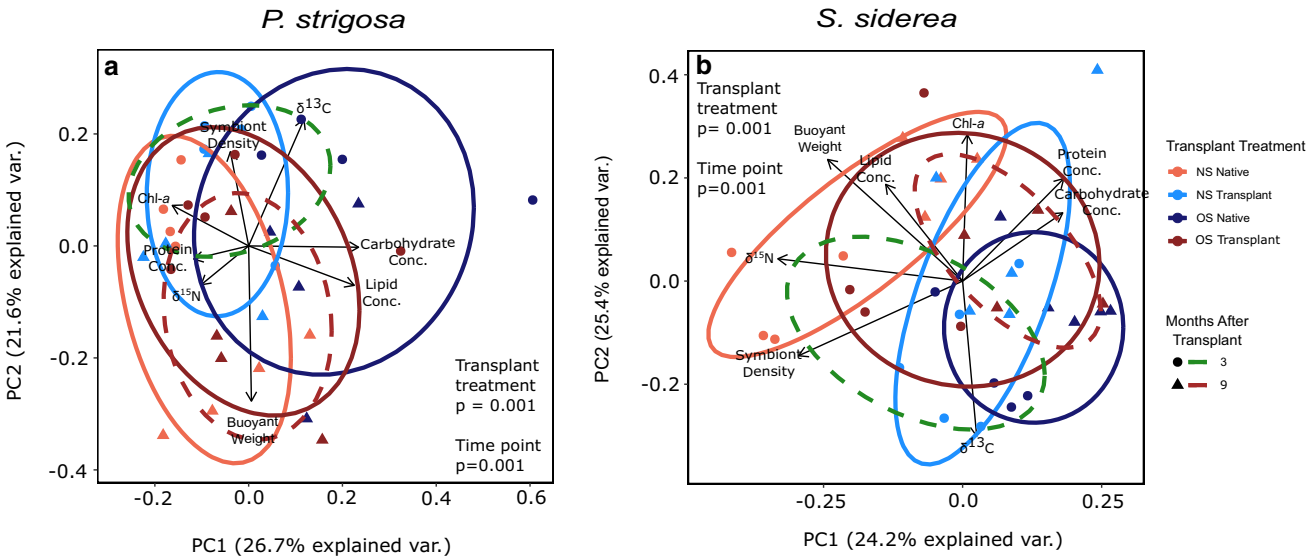

Fig. 5 Principal Component Analysis of physiological parameters for **a** *P. strigosa* and **b** *S. siderea* by treatment and time after transplant. Colored points represent PCA scores for each fragment, colored ellipses denote transplant treatments (solid lines) and time points (dashed lines), and arrows show the effects of all parameters included in the PCA

Discussion

Evidence for acclimatization in two transplanted coral species over 17 months

Pseudodiploria strigosa corals from nearshore and offshore reefs of the Belize Mesoamerican Barrier Reef System possessed the acclimatization capacity necessary to succeed following transplantation regardless of native reef environment as evidenced by positive growth, low mortality, and maintenance of energy reserves in all treatments (Fig. 1a, 3a, 4e). Additionally, principal component analysis of host and Symbiodiniaceae physiology revealed that transplanted *P. strigosa* retain some similarities with corals from their native environments, but also show significant overlap with corals native in their transplant environments (Fig. 5a). Thus, *P. strigosa* can acclimatize when transplanted to new reef environments (Coles et al. 2018). Notably, acclimatization of nearshore transplant (offshore to nearshore) *P. strigosa* appears limited. Nearshore transplant (offshore to nearshore) *S. siderea* performed similarly to nearshore native conspecifics, showing positive growth and low mortality (Fig. 1b, 3b) which is indicative of acclimatization (Coles et al. 2018). Principal component analysis revealed clear differences between nearshore and offshore native *S. siderea* populations and that both nearshore and offshore transplant populations appear to overlap both native populations, indicating that some degree of acclimatization occurs in both transplant populations (Fig. 5b). However, offshore transplant (nearshore to offshore) *S. siderea* corals showed over 60% mortality and did not show positive growth for up to 17-month post-transplant (Fig. 1b, 3b), possibly due to UV light exposure. While both coral species show evidence of acclimatization, these slow growth rates and high mortality rates in offshore transplants suggest limited acclimatization capacity in response to this treatment (Kenkel et al. 2015).

Plasticity (acclimatization) in coral growth and calcification responses, similar to what was observed in offshore to nearshore transplants in this study, has also been observed in the Red Sea (Sawall et al. 2015). Additionally, corals that possess flexibility or plasticity in their utilization and acquisition of heterotrophic energy may be more likely to succeed in nearshore conditions, where sediment and nutrient concentrations are elevated (Grottoli et al. 2006). Corals transplanted from offshore to nearshore in this study demonstrate elevated growth rates and greater heterotrophic energy utilization in tissues, providing evidence that they are able to acclimatize to warmer, more variable, and higher nutrient conditions. Conversely, corals transplanted from nearshore to offshore show depressed growth rates, suggesting that they are not able to acclimatize successfully to offshore conditions in the short term. In order to parse the relative roles of acclimatization and genetic adaptation in the responses observed in this study, further research into genetic divergence between sites and transplant treatments is needed.

Local adaptation to nearshore conditions limits acclimatization potential of two nearshore coral species over 17 months

Corals of both species transplanted from nearshore to offshore (offshore transplants) grew significantly slower than nearshore native and offshore native corals in both species (Fig. 1a, b). As transplants performing worse than natives within a treatment is an indicator of local adaptation within the transplanted population (Kawecki and Ebert 2004), these results demonstrate nearshore *S. siderea* and *P. strigosa* corals may be locally adapted to nearshore conditions (low light, high sedimentation and nutrient loads, warmer and more variable temperatures than offshore), a phenomenon previously observed in other corals species (Howells et al. 2013; Kenkel et al. 2015). Such local adaptation to the nearshore environment appears to limit acclimatization potential in nearshore corals to offshore environments (Howells et al. 2013) in the short term. Local genetic adaptation of the coral host has been shown in previous studies, where genes associated with immune function and apoptosis were upregulated in corals native to highly variables reefs, regardless of what environment they were transplanted to (Palumbi et al. 2014). Additional genetic evidence of local adaptation was seen in nearshore corals in Florida that performed transcriptional frontloading through upregulation of metabolic genes in order to improve thermotolerance (Kenkel et al. 2013b). Local genetic adaptation to thermal regimes can also be attributed to the Symbiodiniaceae, as chlorophyll retention has previously been shown to be higher in corals native to high variability reefs regardless of current environment (Barshis et al. 2014; Howells et al. 2013). Local adaptation is also possible through changing of dominant Symbiodiniaceae species (Baker et al. 2013; Pandolfi et al. 2011). Our results do not show clear evidence of a native reef effect on Symbiodiniaceae chlorophyll concentrations. Thus, further research into mechanisms underlying local adaptation in these populations, including genotyping and Symbiodiniaceae community analysis, is needed.

High mortality coupled with low growth rates in *S. siderea* offshore transplants and low growth rates in *P. strigosa* offshore transplant corals may have been driven, at least in part, by increased UV radiation exposure in the offshore environment relative to nearshore. Short-term increases in UV radiation exposure can cause bleaching in some coral species (Gleason and Wellington 1993) and can also lead to slower growth (Gleason 1993) in calm, clear water down to a depth of at least 12 m (Gleason and Wellington 1993). Such calm and clear water conditions occur at the offshore reef site as it is located in the back reef behind the reef crest but is also nearly 30 km from shore, leading to diminished land-derived sedimentation. The UV levels were likely higher offshore compared to nearshore, but Symbiodiniacea cell density and chlorophyll-*a* concentrations did not clearly differ between native and transplant corals of either species (Fig. 3a–d), indicating that UV bleaching was not a persistent stressor for offshore transplanted corals over this 17-month experiment. However, it appears that nearshore native and transplant corals had slightly higher chlorophyll-*a* concentrations in *P. strigosa*, possibly associated with lower light conditions (Fitt et al. 2000), suggesting possible adaptation to low light conditions in nearshore natives and acclimatization to lower light in nearshore transplants.

Nearshore growth advantage driven by increased heterotrophy and/or terrestrial N sources

In *P. strigosa* and *S. siderea* corals transplanted from offshore to nearshore (nearshore transplant) grew significantly faster than offshore native corals (Fig. 2a, b), indicating that offshore corals of both species likely possess the acclimatization capacity to survive and thrive in warmer, more variable, and nutrient-rich conditions than their native environment provides. These findings also demonstrate that the nearshore environment may provide a more optimal environment for growth than the offshore reef for some species. Previous research on *S. siderea* and *P. strigosa* on the Belize MBRS revealed that nearshore corals have historically grown faster than offshore conspecifics, possibly due to warmer temperatures or nutrient loading nearshore that do not exceed a threshold that would cause stress (Baumann et al. 2019).

Slightly warmer average temperatures nearshore (0.8 °C; Fig S1A; Table S1) may play a role in faster nearshore coral growth rates compared to offshore, as increases in temperatures up to and slightly above a coral's thermal optimum have been shown to increase coral growth rates via a metabolic effect (Castillo et al. 2014; Jokiel and Coles 1977; Marshall and Clode 2004). As growth rates were higher at the nearshore site than the offshore site, and low mortality was observed nearshore over the 17-month study, it is likely that the thermal limit for each species was not met (or greatly surpassed) in the nearshore environment (Jokiel and Coles 1977). Indeed, it is possible that these two stress-tolerant corals have thermal optima that correspond to nearshore conditions, allowing them to thrive in nearshore growth conditions, although some mortality was observed in nearshore native *S. siderea* corals, possibly indicating that nearshore conditions are not always ideal for the survival and acclimatization of this species. Increasing temperatures associated with climate change coupled with continued coastal development may also reverse the trend we see here,

forcing temperatures, nutrients, and /or sediment levels above stress thresholds.

Increased growth rates in nearshore transplant compared to offshore native corals could also be driven by increased heterotrophic opportunity or differences in nutrient sources. Increased concentrations of suspended particulate matter have been shown to correlate with elevated coral growth rates elsewhere in the Caribbean (Tomascik and Sander 1985), suggesting that increased heterotrophic opportunity could potentially enable higher growth rates nearshore (Houlbreque and Ferrier-Pages 2009). As both *P. strigosa* and *S. siderea* corals have been shown to metabolize N ingested from sediment and particulates (Mills et al. 2004; Mills and Sebens 2004), and *S. siderea* appears to show greater asexual budding in high sediment conditions (Foster 1980), it is likely that these two species are able to utilize N from sediments to aid in calcification at nearshore sites. Though elevated nutrient levels correlated with elevated growth rates in these stress-tolerant coral species, nutrient enrichment may be damaging to the ecosystem at-large due to stimulation of macroalgal growth and cover and diminished coral diversity at nearshore sites compared to offshore sites (Baumann et al. 2016; De'ath and Fabricius 2010). Should nearshore nutrient levels increase too much, they may negatively impact coral growth rates, as shown in Mo'orea (Gil 2013). Additionally, differences in coral genotypes across environments and treatments may also have impacted growth rates, as growth rates between genotypes subjected to the same conditions have been shown to vary by up to 200% (Papke et al. 2021).

Enrichment in $\delta^{15}N$ in nearshore corals compared to offshore corals (Fig. 4a, b) indicates differing sources of DIN and DON utilized by corals in nearshore vs offshore environments (Heikoop et al. 2000; Nahon et al. 2013; Wall et al. 2019). Possible nearshore sources of enriched $\delta^{15}N$ include sewage ($\sim$ 10‰; Baker et al. 2010; Katz 2004), mangrove leaf detritus ($\sim$ 5‰;Wooller et al. 2003), terrestrial sediments (Mills et al. 2004), and agricultural runoff. Higher $\delta^{15}N$ in consumer tissues is often indicative of higher tropic position (DeNiro and Epstein 1981; Sturaro et al. 2019), suggesting that nearshore corals may utilize more heterotrophically acquired energy than offshore corals. However, due to tightly coupled recycling mechanisms between corals and their associated symbionts, it can be hard to tie enrichment in $\delta^{15}N$ to increased heterotrophy (Reynaud et al. 2009). Thus, nearshore corals and those transplanted to the nearshore from the offshore likely utilize different (more terrestrial, anthropogenic, and/or mangrove derived) DIN and DON, sources than offshore corals and may also increase heterotrophic N utilization to enhance growth rates.

Other environmental factors

The role variable pCO_2 plays in the differential growth seen between nearshore and offshore corals in this study appears minor. As experimental corals were sectioned and skeleton was exposed during the experiment, dissolution of skeleton was possible (Rodolfo-Metalpa et al. 2011). However, TA and Ω_{Ar} were lower on the nearshore reef (False Caye) than the offshore reef (Silk Caye) in 2016 and 2017 (Fig S2), meaning increased dissolution rates should occur nearshore. Additionally, elevated nutrients can lead to increased bioerosion and net community calcification (Rice et al. 2020; Silbiger et al. 2018). Yet net growth rates were higher nearshore compared to offshore, suggesting that negative effects of carbonate chemistry in the nearshore may have been offset by heterotrophic opportunity or temperature based metabolic effects over this time frame (17 months), though there may also be inherent resilience to high pCO_2 conditions in Belizean *S. siderea* populations (Bove et al. 2019).

High densities of parrotfish on reefs with low coral cover (e.g., nearshore reefs) may impact the growth and survival of coral populations on such reefs (Burkepile 2012). Parrotfish are selective corallivores and do not preferentially graze on *P. strigosa* in Belize, but have been shown to graze on *S. siderea* (Rotjan and Lewis 2006). As fish use of coral ecosystems decreases as sedimentation increases, the nearshore site is less likely to be impacted by corallivory than the offshore site (DeMartini et al. 2013). Thus, *S. siderea* growth rates on the offshore site may have also been slowed due to corallivory.

The offshore site has been shown to have higher wave exposure and flow rates than the nearshore site, although both sites have moderate to high wave exposure (Chollett and Mumby 2012). Flow rates as slow as 5 cm/s have proven sufficient to reduce the boundary layer around the coral in order to allow for more rapid oxygen and nutrient transfer (Shashar et al. 1993), though lower flow rates correlate with lower photosynthesis and respiration rates, and lower calcification rates in laboratory studies (Dennison and Barnes 1988; Schutter et al. 2010). Increasing water velocity has been shown to increase P uptake, growth rates, and respiration rates in corals while it can decrease bleaching incidence (Atkinson and Bilger 1992; Nakamura and Yamasaki 2005; Sebens et al. 2003). As such, coral metabolism and growth rates may also be influenced by differential flow rates between offshore and nearshore sites.

Conclusion

Our results suggest that nearshore and offshore populations of *P. strigosa* and *S. siderea* possess some acclimatization potential to respond plastically to changing environmental conditions, but that this acclimatization potential appears greater in offshore populations. Nearshore populations may be locally adapted to native conditions, and this local adaptation may limit their acclimatization potential in other habitats in the short term. As such, some corals native to nearshore environments may not be ideal candidates for coral restoration practices focused on restoration of offshore environments, though physiological responses to environmental heterogeneity are likely species and region specific. However, replicating our transplant study with additional species and longer time frames is recommended as restoration efforts in the Caribbean become more urgent due to Stony Coral Tissue Loss Disease and increasingly severe bleaching events.

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Data Accessibility Data and code associated with this manuscript are available at https://github.com/jbaumann3/Belize-RT-Baumann-et-al-2021-

Declaration

Conflict of interest The authors declare that no conflict of interest exists.

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