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REPORT

Neighboring colonies influence uptake of thermotolerant endosymbionts in threatened Caribbean coral recruits

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Abstract Intervention strategies to enhance coral resilience include manipulating associations with algal endosymbionts. While hosting thermotolerant *Durusdinium trenchii* can increase bleaching thresholds in Caribbean coral adults, its effects remain largely unknown during their early life stages. Here, we tested if *Orbicella faveolata* recruits could establish symbiosis with *D. trenchii* supplied by nearby "donor" colonies and examined the resulting ecological trade-offs to evaluate early Symbiodiniaceae manipulation as a scalable tool for reef restoration. We exposed aposymbiotic recruits to 29 °C or 31 °C and to fragments of *Montastraea cavernosa* (containing *Cladocopium* ITS2 type C3) or *Siderastrea siderea* (containing *D. trenchii*). After 60 days, recruits reared with *D. trenchii* donors hosted nearly three times more *D. trenchii* than those with *Cladocopium* donors, suggesting that recruits can acquire Symbiodiniaceae from nearby corals of different species. Temperature did not affect symbiont identity. Next, donor colonies were removed and surviving recruits were maintained for three months at ambient temperatures, after which a subset was exposed to a 60-day heat stress. Recruits previously reared at 31 °C survived twice as long at 34 °C as those reared at 29 °C, suggesting that pre-exposure to heat can prime recruits to withstand future thermal stress. Furthermore, recruits hosting primarily *D. trenchii* survived twice as long at 34 °C as those hosting little or no *D. trenchii*. However, the proportion of *D. trenchii* hosted was negatively correlated with polyp size and symbiont density, indicating a trade-off between growth (of both host and symbiont) and heat tolerance. These findings suggest that, while donor colonies may be effective sources for seeding coral recruits with thermotolerant symbionts, practitioners will need to balance the likely benefits and costs of these approaches when designing restoration strategies.

Keywords Coral · Symbiosis · Recruits · Symbiodiniaceae · *Durusdinium trenchii* · *Orbicella faveolata*

Introduction

Scleractinian corals are ecosystem engineers, building reefs that support one quarter of all marine biodiversity and contributing billions of dollars to global economies annually through fisheries, tourism, and coastline protection (Jones et al. 1994; Wells et al. 2006). However, coral reefs are declining rapidly as multiple stressors outpace their natural capacity to evolve and threaten the critical ecosystem services they provide (Hughes and Connell

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1999; Hughes et al. 2003; Pandolfi et al. 2003; Wild et al. 2011). A major cause of recent decline is coral bleaching (Hughes et al. 2017), a phenomenon wherein stressful environmental conditions destabilize the partnership between corals and Symbiodiniaceae, prompting ejection of the algae by the coral hosts (Knowlton and Rohwer 2003; Weis 2008). However, some corals survive these bleaching episodes, recovering or even maintaining their symbioses while neighboring colonies perish (Baker et al. 2004; LaJeunesse et al. 2010; Cunning et al. 2016). One factor contributing to this resilience is the type(s) of Symbiodiniaceae hosted within the corals; when stressful conditions subside, bleached corals can reacquire algae (Jones and Yellowlees 1997; Boulotte et al. 2016; Cunning et al. 2016). Termed "symbiont shuffling" (Baker 2003), this process involves shifts in the relative abundance of different symbiont types within the host, which can replace the numerically dominant symbiont and alter the community function (Buddemeier and Fautin 1993; Toller et al. 2001; Baker 2001; Stat et al. 2008).

Many members of the Symbiodiniaceae genus *Durusdinium* are particularly tolerant to thermal stress (Glynn et al. 2001; Baker et al. 2004; Rowan 2004) and may prove critical for the persistence of reefs. Most prevalent after bleaching events or on reefs characterized by extreme or highly variable conditions (Baker et al. 2004; Fabricius et al. 2004; LaJeunesse et al. 2009, 2010), *Durusdinium* is widely distributed (albeit at generally low abundance) among locations and hosts worldwide (Silverstein et al. 2012). During recent marine heatwaves, corals hosting this genus have maintained their symbioses while nearby colonies bleached (Glynn et al. 2001; Baker et al. 2004; LaJeunesse et al. 2009; Kemp et al. 2014), and many bleached colonies have recovered with predominantly *Durusdinium*, increasing the holobiont's subsequent bleaching threshold by ~ 1–2 °C (Berkelmans and van Oppen 2006; Silverstein et al. 2015). Thus, symbiont shuffling and relative increases in *Durusdinium trenchii* represent mechanisms of rapid ecological acclimatization and potential tools for researchers to enhance coral heat tolerance (Baker et al. 2004; Silverstein et al. 2015; Cunning et al. 2018; National Academies 2019).

However, despite its thermotolerance benefits, hosting *D. trenchii* may be accompanied by physiological trade-offs that impact whether symbiont shuffling is sustainable at the ecosystem scale. Studies have found reduced calcification, growth rates, lipid stores, and egg size in corals hosting *D. trenchii* under non-stressful temperatures (Little et al. 2004; Jones and Berkelmans 2011; Poquita-Du et al. 2020), suggesting that this symbiont may compromise long-term reef recovery (Ortiz et al. 2013; Pettay et al. 2015). Consequently, we must consider the benefits and costs of *D. trenchii* in the context of predicted stress exposure as we assess approaches to increase reef resilience.

While laboratory studies have manipulated algal partners in adult Caribbean corals to enhance stress tolerance (Silverstein et al. 2015; Cunning et al. 2016, 2018), the capacity of Caribbean coral juveniles to acquire *D. trenchii* and the associated eco-physiological trade-offs are not well understood. Many corals are broadcast spawners, beginning life as aposymbiotic larvae that acquire Symbiodiniaceae "horizontally" from their environment (Coffroth et al. 2006). Since a recruit's algal partners influence fitness (Mieog et al. 2009), early establishment of environmentally appropriate symbioses may enhance survival (Chamberland et al. 2017; Quigley et al. 2017a). Various processes may govern symbiont acquisition and selection during early ontogeny (Little et al. 2004), but few studies have tracked the biotic and abiotic factors shaping symbiotic partnerships in young Caribbean corals. Indeed, Quigley et al. (2018) urged that research be directed at optimizing Symbiodiniaceae delivery to boost juvenile survival.

This study investigated whether temperature and/or neighboring adult corals could enhance *D. trenchii* uptake in juvenile *Orbicella faveolata*, an important reef-building species listed as threatened under the Endangered Species Act. First, we tested the hypothesis that elevated temperature and/or proximity of *D. trenchii* "donor" colonies increases *D. trenchii* abundance in recruits during symbiosis establishment. Next, we examined the physiological trade-offs, such as polyp size and algal cell density, of hosting *D. trenchii*. Finally, we tested if symbiont community and/or previous heat exposure impacted recruit survival during a heat stress trial.

Methods

Larval rearing and settlement

This experiment utilized newly settled *Orbicella faveolata* recruits collected as gametes during a spawning event six days after the full moon in August 2018 from Horseshoe Reef in Key Largo, FL (25.1388°N, 80.2950°W). At this location, multiple *O. faveolata* colonies were previously mapped, genotyped, and observed to spawn (Miller et al. 2018; Fisch et al. 2019). Gamete bundles were collected from eight colonies in conical mesh nets with 50-mL Falcon tubes at the apices, then capped and brought to the boat. Gametes from all parents were pooled in 2-L plastic containers and diluted with filtered seawater (FSW) as bundles broke apart to reach a sperm concentration of ~ 10^6 cells/mL following Hagedorn et al. (2009). Batches of mixed gametes were transported to a field laboratory in Key Largo, FL, where larvae were maintained in

FSW as they developed. Fresh FSW was provided and dead larvae were removed several times daily.

Four days post-fertilization, ~ 4000 larvae were transported to an indoor laboratory at the Rosenstiel School of Marine and Atmospheric Science, placed in one-micron FSW, and supplied with 108 ceramic plugs (2.5 cm diameter) to facilitate settlement. Plugs had one-mm grooves in the top and were previously preconditioned at Emerald Reef (near Miami, FL) for three weeks to develop a "reef-like" biofilm (Hadfield 2011). After two days, settlers were counted under a microscope. For standardization, only recruits on the top face of plugs were tracked and sampled for the subsequent experiment (n = 1,595).

Experiment 1: Symbiodiniaceae uptake

Plugs were distributed randomly into 12 new 2.5-gallon aquaria, so that each contained nine plugs and approximately 133 settlers. Aquaria were supplied with one-micron FSW (to exclude Symbiodiniaceae cells) and immersed in one of two 50-gallon seawater tanks to maintain temperatures, held at 31 and 29 °C. The maximum monthly mean (MMM) temperature on Horseshoe Reef is ~ 30 °C (according to Pathfinder 5.0 and Coral Reef Watch—R. van Hooidonk, pers. comm.), so these temperatures were within the scope of what recruits might naturally experience. The 31 °C treatment was designed to exert only mild heat stress on recruits without high mortality. Light (150–300 µmol quanta m − 2 s − 1, measured by an Apogee Underwater Quantum PAR Meter MQ-210) was maintained on a 12 h light–dark cycle using 400 W metal halide pendant lights (IceCap Inc., USA). Irradiance and temperature were recorded with a HOBO Pendant® data logger (Onset Computer Corporation MX2202). One ~ 6 cm^2 fragment of *Siderastrea siderea* was placed into half of the aquaria at each temperature. These fragments originated from a single colony and were known to host > 95% *D. trenchii*. In each of the other aquaria, we placed one ~ 6 cm^2 fragment of *Montastraea cavernosa* hosting *Cladocopium* (exclusively ITS2 type C3, confirmed by ITS2 amplicon sequencing [MiSeq]) (Hume et al. 2019). One 4 W submersible pump (VicTsing CAAA3-HG16) was placed into each aquarium to distribute heat and symbiont cells. With two temperatures and two symbiont sources, the experiment consisted of four treatments conducted in triplicate (Fig. 1).

Recruits were maintained in their respective treatments for 60 days. FSW was replaced every other day, and algae were manually removed from plugs to prevent overgrowth and/or competition with recruits. To minimize differences in light and flow, positions of aquaria and plugs were shuffled weekly.

Observation and tissue sampling

At least once per week, a dissecting microscope was used to count the number of: (1) surviving recruits and (2) recruits visibly infected with symbionts (Fig. 2a, b). When infection was first observed in all aquaria (day 21) and again after 60 days in their treatments, three to five recruits from each aquarium were sacrificed using a razor blade (Figs. 1, 2c). To standardize sampling, only solitary polyps not clumped with others were sacrificed (Fig. 2d). Sacrificed recruits were placed in individual 1.5-mL microcentrifuge tubes with 200 µL of 1% SDS + DNAB and incubated at 65 °C for one hour. Genomic DNA was extracted from SDS archives following modified organic extraction methods (Rowan and Powers 1991; Baker and Cunning 2016).

Growth and symbiont density

After 60 days, donor fragments were removed and aquaria were reduced by 1 °C per day to reach 27 °C (the ambient temperature of incoming seawater in Bear Cut, FL). After this, temperature tracked local seasonal fluctuations, eventually reaching 22 °C three months later (January 2019).

Five months (150 days) after settlement, a random sample of recruits from each of the four original treatments was photographed under a dissecting microscope with QCapture Suite Plus. Only solitary polyps were photographed to maximize accuracy of area measurements (Fig. 2d). ImageJ was used to calculate recruit skeletal area in mm^2. R was used to create generalized linear models (GLMs) comparing recruit area by experimental treatments. A subset of the photographed recruits was then sacrificed to measure symbiont identity and density at the time of growth measurements.

Experiment 2: Heat stress trial

To assess whether previous exposure to elevated temperature and/or *D. trenchii* dominance increased tolerance to future thermal stress, a subset of recruits were subjected to heat stress in late January 2019 (day 150), three months after the end of Experiment 1. Three recruits per aquarium (nine per treatment) were sampled to characterize Symbiodiniaceae communities at the start of heat stress. However, since sampling these small recruits required sacrificing them, we could not directly sample Symbiodiniaceae in recruits used in the heat stress trial. For analysis, aquaria were therefore split into categories based on the mean proportion of *Durusdinium* hosted on day 150 ("low" = < 0.25, "intermediate" = 0.25–0.75, "high" = > 0.75).

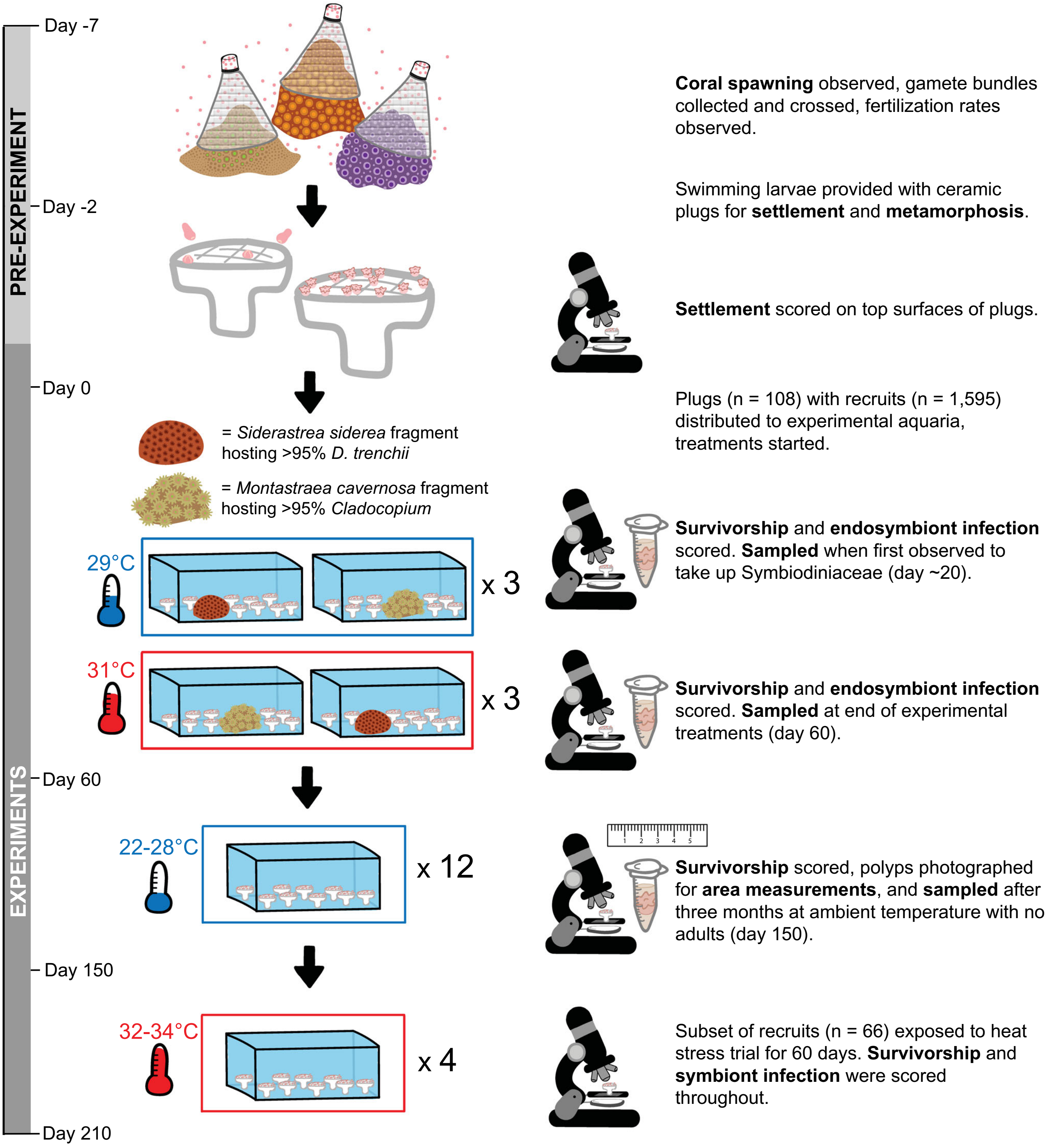

Fig. 1 Sequence of experimental treatments and sampling events described in this study

Two or three plugs from each aquarium were placed into new aquaria with FSW, where temperature was increased from 22 to 28 °C over six days, and then to 32 °C over 48 h. At this point, all recruits (n = 66) were infected with symbionts. About half the recruits (n = 32) were pre-exposed to mild heat stress (reared at 31 °C during Experiment 1), while the other half (n = 34) were naïve to heat stress (reared at 29 °C). Temperature was maintained at 32 °C for ten days, then raised to 33 °C for ten days, then raised to 34 °C for 40 days. Every two to five days, recruits were scored as “healthy,” “pale,” “bleached,” or “dead” using a fluorescence microscope. After 60 days, all

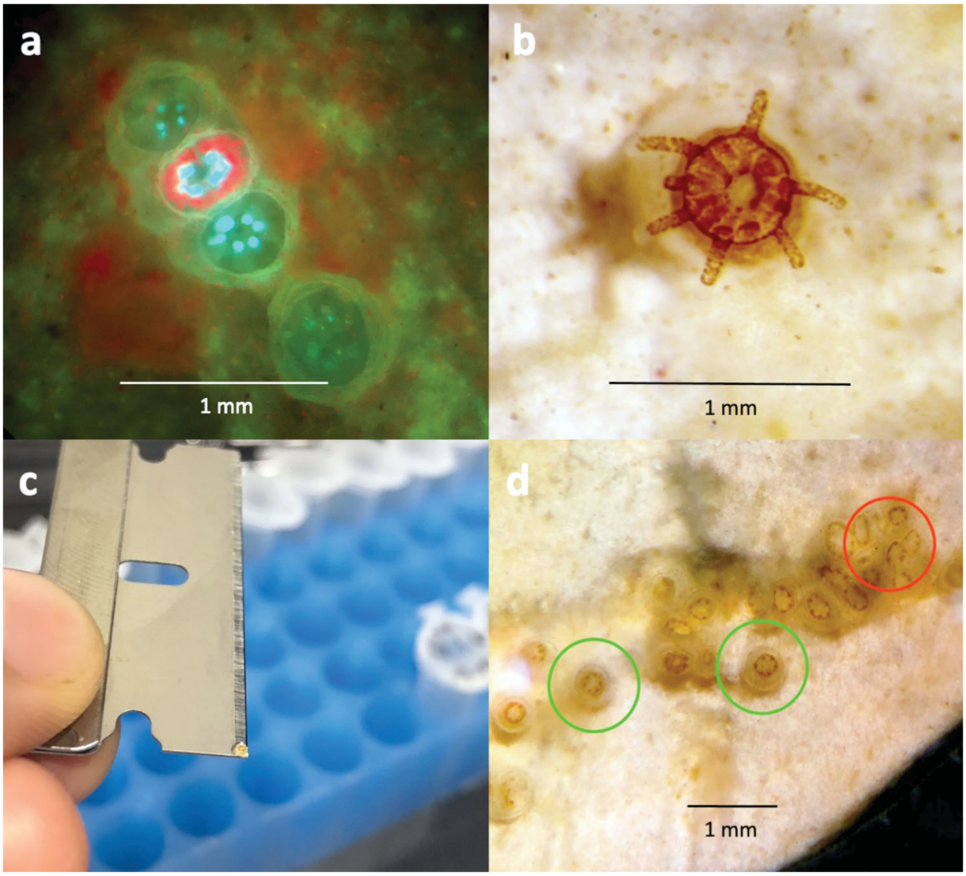

Fig. 2 **a** Symbiodiniaceae infection was scored visually, aided by violet light filters to view red chlorophyll fluorescence in symbiont cells. **b** A one-month-old *Orbicella faveolata* recruit infected with Symbiodiniaceae. **c** Individual recruits were sacrificed using a razor blade. **d** Recruits circled in green are examples of well-separated polyps, which were chosen for sampling. Recruits circled in red are clumped together without clear separation, and were not chosen for sampling

remaining living recruits were sacrificed for symbiont community analysis. GLMs were created in R to test how prior heat exposure and proportion *Durusdinium* impacted survival and bleaching during heat stress.

Symbiodiniaceae identification and quantification

Quantitative PCR (qPCR) assays were used to identify Symbiodiniaceae to genus level and quantify symbiont-to-host (S:H) cell ratios for each recruit sampled. Since *O. faveolata* commonly hosts members of *Symbiodinium*, *Breviolum*, *Cladocopium*, and *Durusdinium* (Kemp et al. 2015), assays targeting specific actin loci for each genus were performed using a QuantStudio 3 Real-Time PCR Instrument (Applied Biosystems, USA). Assays for *O. faveolata*, *Symbiodinium*, and *Breviolum* followed reactions described in Cunning and Baker (2013), whereas *Cladocopium* and *Durusdinium* assays were multiplexed as described in Cunning et al. (2015). The StepOneR software package in R was used to quality-filter assay results, calculate relative abundance of each symbiont, and compute S:H cell ratios. The Kaplan–Meier estimate was used to calculate the fraction of surviving recruits in each treatment over time (Goel et al. 2010). GLMs were created to compare the effects of experimental treatments and their interactions on survivorship, symbiont infection rates, algal community composition, and S:H cell ratios.

Results

Experiment 1: Symbiodiniaceae uptake

Survivorship and Symbiodiniaceae infection

Recruit survivorship did not vary significantly among treatments. In all treatments, the proportion of recruits visibly infected with Symbiodiniaceae increased over time (Fig. 3). Differences in proportion of infected recruits were driven primarily by temperature ($p < 0.0001$) and to a lesser extent by donor symbionts ($p = 0.048$). After 14 days, a significantly higher proportion of recruits reared at 29 °C were infected with symbionts compared with those reared at 31 °C, which were delayed in their infection by $\sim$ 5–20 days (Fig. 3). At 43 days at 31 °C, a significantly higher proportion of recruits reared with *D. trenchii* donors were visibly infected compared to those with *Cladocopium* donors ($p = 0.005$).

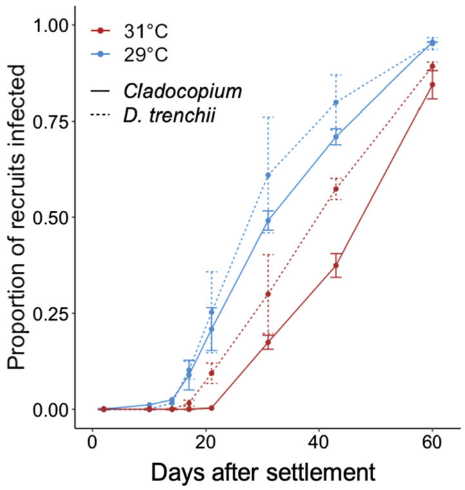

Fig. 3 Symbiodiniaceae infection in recruits varied with temperature ($p < 0.0001$) and symbiont treatments ($p = 0.048$). Error bars represent ± SEM

Symbiodiniaceae identity and abundance

Recruits in all treatments hosted *Symbiodinium*, *Breviolum*, and *Durusdinium*, but *Cladocopium* was not detected. After 60 days, *D. trenchii* was dominant (> 90% of symbiont community) or co-dominant (10–90% of community) in 58.3% of recruits. The proportion of *D. trenchii* in recruits varied significantly with donor symbiont type but not with temperature (Fig. 4). Recruits reared with *D. trenchii* donors hosted higher proportions of *D. trenchii* (48.3 ± 34.9%) than those reared near *Cladocopium* donors (17.8 ± 24.9%) ($p = 0.03$).

S:H cell ratios varied with symbiont community composition (Fig. 5) and showed significant interactions with time ($p = 0.046$). For recruits < 150 days old, log S:H cell ratio decreased with increasing proportion of *Symbiodinium*, while at 150 days the opposite trend was observed (Fig. 5a). As proportion of *Breviolum* in recruits increased, the log S:H cell ratio also increased ($p < 0.001$, Fig. 5b). Conversely, as proportion of *D. trenchii* increased in recruits, the log S:H cell ratio decreased ($p < 0.001$, Fig. 5c).

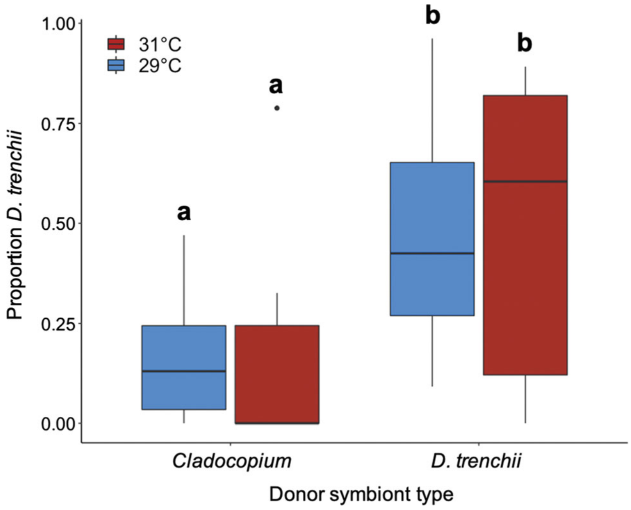

Fig. 4 Proportion of *Durusdinium trenchii* in recruits reared near *D. trenchii* donors and *Cladocopium* donors after 60 days

Polyp area

After 5 months, polyp size varied significantly with Symbiodiniaceae communities. Mean polyp area increased with proportion *Breviolum* ($p = 0.005$, Fig. 6b) and decreased with increasing proportion of *D. trenchii* ($p = 0.006$) (Fig. 6c). There was no significant relationship between polyp size and previous temperature treatment or proportion of *Symbiodinium* (Fig. 6a).

Experiment 2: Heat stress trial

During the heat stress trial, both previous heat exposure and symbiont community impacted survivorship. Recruits previously reared at 31 °C survived over twice as long at 34 °C as those reared at 29 °C, independent of their symbionts ($p < 0.001$) (Fig. 7a). In addition, recruits hosting primarily *D. trenchii* at the start of heat stress survived over twice as long at 34 °C as recruits with low proportions of *D. trenchii* and 50% longer than recruits with intermediate proportions of *D. trenchii* ($p < 0.001$) (Fig. 7b). Recruits with high proportions of *Symbiodinium* and *Breviolum* experienced reduced survivorship (Fig. S1). Survivorship during heat exposure was positively correlated with proportion of *D. trenchii* ($p = 0.006$), negatively correlated with proportion of *Symbiodinium* ($p = 0.022$), and not correlated with *Breviolum*.

Similarly, both previous temperature treatment and Symbiodiniaceae communities influenced bleaching resistance. During heat stress, recruits previously reared at 31 °C and/or hosting high proportions of *D. trenchii* maintained symbiosis longer than those reared at 29 °C and/or hosting intermediate or low proportions of *D. trenchii* (Figs. S2, S3). At the end of the trial, the two recruits scored as "pale" and "symbiotic" hosted only *D. trenchii*. Symbiodiniaceae were not detected in the 13 "bleached" recruits (Figs. S2, S3).

Discussion

Manipulating symbiosis establishment in recruits

This study tested a novel, scalable approach for introducing thermotolerant *Durusdinium trenchii* into coral hosts at a

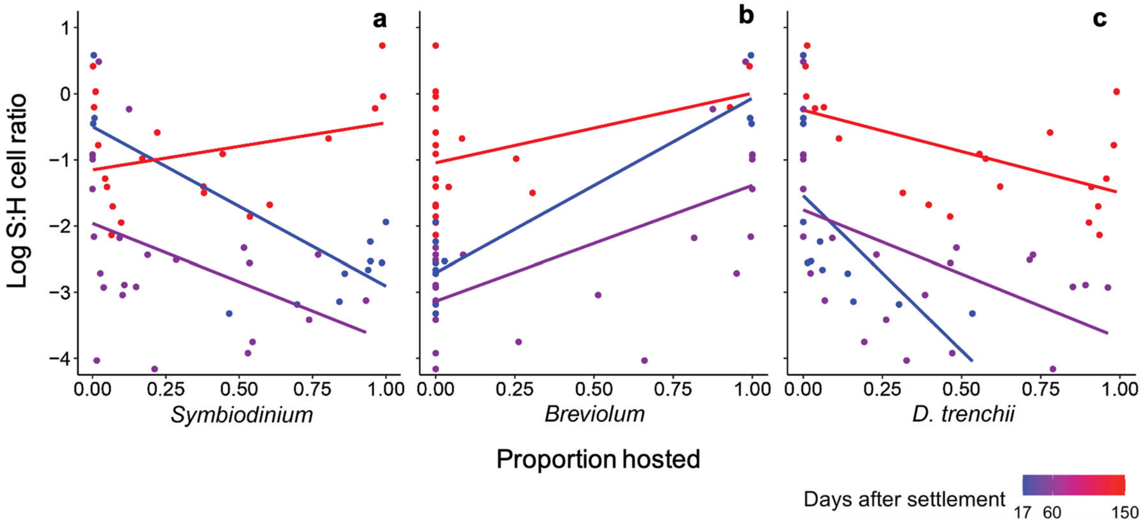

Fig. 5 Symbiodiniaceae density varies with community composition in recruits. Log S:H cell ratio shows **a** no relationship with proportion of *Symbiodinium*, **b** positive correlation with proportion of *Breviolum* ($p < 0.001$), and **c** negative correlation with proportion of *D. trenchii* ($p < 0.001$). Points were jittered to minimize overlap

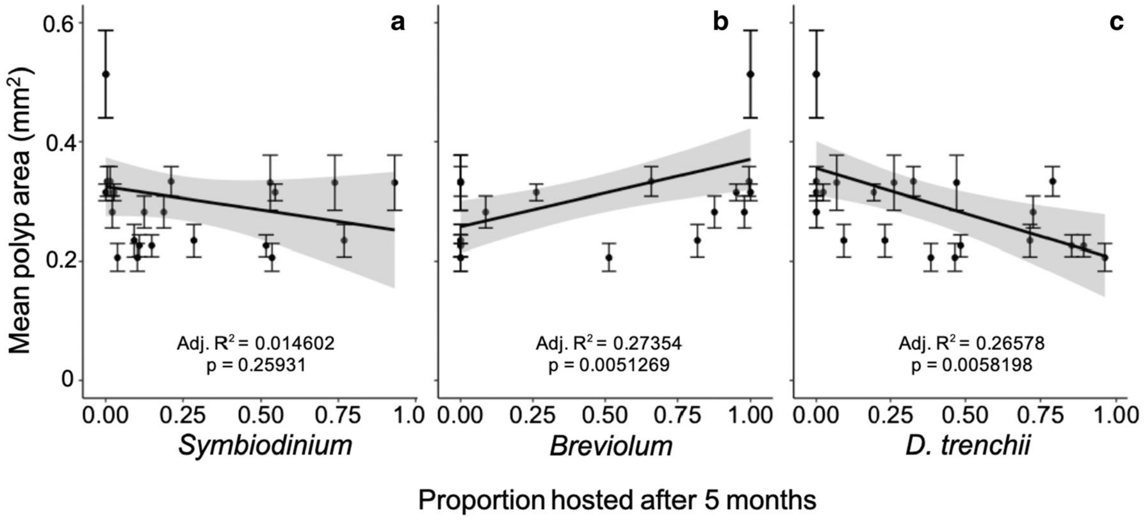

Fig. 6 Correlation of polyp area with proportion of **a** *Symbiodinium*, **b** *Breviolum*, and **c** *D. trenchii*. Each point represents the mean size of polyps on one plug. Error bars represent ± SEM. Points were jittered to prevent overlap

key stage in their life history. Our results indicate that temperature and/or symbionts in neighboring colonies can affect: (1) rates of infection in *O. faveolata* recruits, (2) Symbiodiniaceae assemblages acquired during initial symbiosis establishment, and (3) the future thermal tolerance of recruits.

In Experiment 1, temperature impacted the onset of symbiosis while donor colonies influenced initial Symbiodiniaceae community composition. Infection was delayed in recruits reared at 31 °C, suggesting that even minimal heat exposure can slow algal acquisition in recruits by ~ 5–20 days (Fig. 3). Abrego et al. (2012) similarly found that *Acropora tenuis* and *A. millepora* recruits at 31 °C acquired symbionts significantly later than those at 28 °C. Delayed infection could prove detrimental, particularly in the field, because juvenile corals rely on the fixed carbon their endosymbionts provide to grow and surpass size-escape thresholds (Doropoulos et al. 2012; Chamberland et al. 2017). Although we hypothesized that elevated temperature would favor acquisition of *D. trenchii* (Cunning et al. 2015; Abrego et al. 2012), we found no significant effect of temperature on the algal species hosted, suggesting that availability outweighs temperature in determining the dominant symbiont(s) in *O. faveolata* recruits. However, it is also possible that 31 °C was not hot

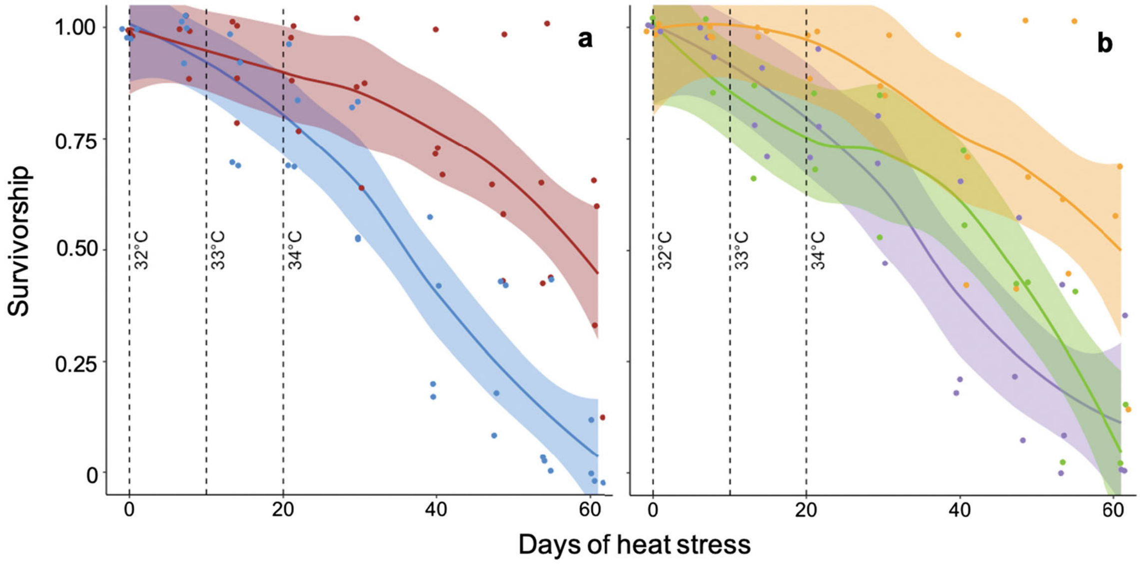

Fig. 7 Heat stress trial revealed highest survivorship in recruits **a** previously reared at 31 °C and **b** hosting high proportions of *D. trenchii*. In panel (a), red points indicate recruits reared at 31 °C and blue points indicate those reared at 29 °C. In panel (b), orange points indicate recruits hosting high proportions of *D. trenchii* at the start of heat stress (> 0.75), green indicates intermediate proportions (0.25–0.75), and purple indicates low proportions (< 0.25). Points were jittered to minimize overlap. Lines indicate smoothed data (method = "loess"), and shaded areas indicate ± SEM

enough to favor *D. trenchii* acquisition in recruits from Key Largo, FL.

In all treatments, recruits acquired *Symbiodinium*, *Breviolum*, and *D. trenchii*. This result is consistent with studies of other coral species, which found that recruits can initially host a variety of different algal partners (Coffroth et al. 2001; Little et al. 2004; Mieog et al. 2009; Cumbo et al. 2013, 2018). Field surveys have reported that *O. faveolata* adults associate with *Symbiodinium, Breviolum, Cladocopium*, and *Durusdinium* throughout their range and even within the same colony (Rowan and Knowlton 1995; Rowan et al. 1997; Kemp et al. 2015). In this study, the presence of *D. trenchii*-dominated *Siderastrea siderea* colonies enhanced the proportion of *D. trenchii* two- to threefold in *O. faveolata* recruits. Nearby corals may influence Symbiodiniaceae availability by discharging algal cells that persist in the sediments and water column, increasing the rate of acquisition by recruits (Coffroth et al. 2006; Nitschke et al. 2016; Ali et al. 2019). *D. trenchii* has been shown to be highly infectious in aposymbiotic recruits, although its abundance typically declines during ontogeny (Abrego et al. 2009; McIlroy and Coffroth 2017; Pollock et al. 2017).

No recruits acquired detectable levels of *Cladocopium*, including those in aquaria with *M. cavernosa* donors hosting ITS2 type C3, which is considered "homologous" (native) to *O. faveolata* in the Florida Keys (Kemp et al. 2015). Throughout its range, *O. faveolata* commonly hosts C3, C7, and/or C12 in areas of low irradiance around a colony's base or deeper than 3 m (Rowan and Knowlton 1995; Thornhill et al. 2009; Kemp et al. 2015; Hauff et al. 2016). Irradiance in our experiments (150–300 micromoles quanta m − 2 s − 1) may have resembled a shallow reef where *Symbiodinium* and *Breviolum* (particularly *Breviolum* ITS2 type B1) are preferred, preventing uptake of *Cladocopium* (Rowan et al. 1997; LaJeunesse 2002; Thornhill et al. 2009). Furthermore, fewer recruits with *Cladocopium* donors were infected after 43 days compared to those with *D. trenchii* donors (Fig. 3b). Together, these findings indicate a possible shortage of environmentally appropriate symbionts in this treatment.

Since *Symbiodinium* and *Breviolum* were detected in recruits but not in donors, these algae must have been present at low density either in unsampled parts of donor fragments, the FSW, or the biofilm on the settlement plugs. As such, these algae were likely much less abundant than *Cladocopium* and *D. trenchii*, which were presumably shed by donors during the experiment to regulate symbiont density in their tissues (Fitt et al. 2001). Therefore, the differential acquisition of *Symbiodinium* and *Breviolum* despite their relative scarcity suggests a degree of specificity in recruits under these conditions. Although Symbiodiniaceae communities in the parent colonies are unknown, surveys have identified *Breviolum* (particularly B1) as a dominant partner for *O. faveolata* in Florida (Thornhill et al. 2009; Kemp et al. 2015), so it is not surprising that recruits readily hosted *Breviolum*.

Heat tolerance in *O. faveolata* recruits hosting *D. trenchii*

Recruits reared at 31 °C survived significantly longer during the subsequent heat stress trial than those reared at 29 °C, regardless of dominant symbiont type (Fig. 7a), suggesting that pre-exposure to mild thermal stress may increase a juvenile's resilience against future, more severe heat waves. It should be noted that in nature, coral recruits are unlikely to experience heat stress at 5 months post-settlement. Since most broadcast spawning corals are born during the warmest time of year, they might more plausibly face heat stress either prior to three months or one year after settlement. However, our results show that recruits can be preconditioned to heat, and that this effect may last at least three months after heat exposure ends. Future studies should test how long recruits retain thermal tolerance after pre-exposure.

Symbiodiniaceae community composition also impacted survivorship under heat stress. Recruits that started the trial with the highest proportion of *D. trenchii* (> 0.75) survived significantly longer than recruits with low and intermediate proportions of *D. trenchii* for a similar decline in survivorship (Fig. 7b). This agrees with previous studies reporting increased heat tolerance and bleaching resistance in adult *O. faveolata* hosting *D. trenchii* (Kemp et al. 2014; Cunning et al. 2018; Manzello et al. 2018). Acroporid juveniles from the Great Barrier Reef also survived better under thermal stress when hosting *D. trenchii* compared with other symbionts (Mieog et al. 2009; Abrego et al. 2012; Quigley et al. 2020; but see Abrego et al. 2008). Together, these findings suggest that *D. trenchii* may enhance coral survival during vulnerable early life stages in the face marine heatwaves that can often coincide with, or shortly follow, coral spawning events.

Although this study primarily focused *D. trenchii*, we recognize that other Symbiodiniaceae taxa can potentially increase the thermal tolerance of coral hosts (Abrego et al. 2008; Hume et al. 2015). However, *D. trenchii* has dominated the literature in the Caribbean, and when present it usually ranks most thermotolerant among symbionts in the region (Swain et al. 2017), including in *O. faveolata*. As such, given our study species and location, we targeted *D. trenchii* for these experiments.

Trade-offs of hosting *D. trenchii*

Symbiodiniaceae cell density varied with algal community composition in *O. faveolata* recruits. At all-time points, log S:H cell ratio was negatively correlated with the proportion of *D. trenchii* (Fig. 5c) and positively correlated with the proportion of *Breviolum* (Fig. 5b). Fewer symbionts per host cell could indicate slower colonization or proliferation rates for *D. trenchii*, differences in cell size between symbiont species (Jones and Yellowlees 1997; LaJeunesse et al. 2018), or a host-regulated reduction in symbiont density when hosting *D. trenchii*. This low cell S:H cell ratio may also help explain the heat tolerance observed in recruits hosting *D. trenchii*, since high Symbiodiniaceae density can increase bleaching susceptibility (Cunning and Baker 2013).

We observed a significant negative correlation between the proportion of *D. trenchii* and polyp size after 5 months, consistent with previous studies reporting reduced growth in juvenile and adult corals hosting *D. trenchii* (Little et al. 2004; Cantin et al. 2009; Jones and Berkelmans 2010; Pettay et al. 2015; but see Yuyama and Higuchi 2014; Quigley et al. 2020). For instance, Little et al. (2004) found that acroporid recruits infected with *Cladocopium* grew 2–3 times faster than those hosting *Durusdinium*. Under ambient, non-stressful conditions, *D. trenchii* is less photochemically efficient than *Breviolum* and *Cladocopium* (Cunning et al. 2018) and thus may have less photosynthate available for the coral host. Although dominant Symbiodiniaceae type explained up to 30% of variation in polyp size after 5 months, algal communities detected at the time of photographing and sampling provided only a "snapshot" assessment and do not necessarily represent previous communities that may have contributed to growth earlier in ontogeny. However, due to their small size (< 1 mm in diameter), it was impossible to sample a recruit's symbiont community without sacrificing it. Consequently, some of the unexplained variation in polyp size could be due to changes in symbiont communities over time. Algal density could also impact growth, because fewer Symbiodiniaceae cells in coral tissues may translate to less carbon produced and delivered to the host. Thus, the smaller size of recruits hosting *D. trenchii* may result from their low symbiont density, and not necessarily from these symbionts being individually stingy or "selfish" (Stat and Gates 2008). However, our finding that recruits hosting predominantly *Breviolum* were largest after five months contradicts a study by McIlroy et al. (2016) reporting significantly faster growth in *O. faveolata* recruits harboring *Symbiodinium* compared to *Breviolum*. This may be attributed to different experimental conditions that favored *Breviolum* in the present study.

Growth rates can help determine winners and losers in coral reef ecosystems, which are highly competitive for space and light. Like many organisms, corals attain some refuge in size whereby predators and competitors are less likely to harm larger individuals. Field studies of *Pocillopora damicornis* and *Siderastrea radians* juveniles reported significant increases in survivorship with colony size (Raymundo and Maypa 2004; Vermeij and Sandin 2008). Combined with environmental stressors such as ocean acidification that already compromise coral growth (Hoegh-Guldberg et al. 2007; Doropoulos et al. 2012), hosting *D. trenchii* could further prolong the vulnerability that comes with small size and prevent population recovery (Ortiz et al. 2013). With these potential trade-offs, it will be important to take many factors into account when assessing the net risks versus benefits of *D. trenchii* in enhancing coral restoration strategies.

Implications for reef restoration and resilience

In recent years, researchers, practitioners, and managers have recognized the importance of sexually derived coral stock to expanding the genetic diversity and spatial scale of reef restoration efforts (Baums et al. 2019; Randall et al. 2020). However, strategies for maximizing the early post-settlement survival of reared and outplanted juveniles need to be advanced. Specifically, efforts to: (1) reduce the risk of predation or competition, (2) promote early, beneficial associations with Symbiodiniaceae, and (3) enhance stress tolerance prior to outplanting can minimize juvenile mortality and strengthen the impact of restoration efforts (Quigley et al. 2018).

Since most reef-building corals spawn during the warmest time of year, recruits are likely to experience heat stress during their first few months of life, a threat that will intensify with continued climate change. As such, boosting the thermal resilience of new generations of corals should be a priority of reef restoration efforts, and practitioners concerned about bleaching risk may benefit by rearing recruits near *D. trenchii* donors (in situ or ex situ) to increase uptake of this algae. Even if it is replaced later by a preferred symbiont (Abrego et al. 2009; Poland and Coffroth 2017), *D. trenchii* may enable recruits to resist heat stress during their critical first months on the reef. However, some species appear to be relatively inflexible during initial algal uptake, favoring specific symbionts (Weis et al. 2001; Quigley et al. 2017b). Manipulating these juveniles to host *D. trenchii* may not be feasible. Similarly, the relative benefit of hosting *D. trenchii* likely varies among species (Cunning et al. 2018). Therefore, restoration practitioners should test how *D. trenchii* impacts the particular coral(s) they work with before incorporating it into their efforts.

Given its associated physiological trade-offs, there is a risk that *D. trenchii* may reduce corals' competitive ability and prolong recovery following disturbances (Ortiz et al. 2013). Nevertheless, since a majority of the world's reefs are projected to experience annual severe bleaching by mid-century (van Hooidonk et al. 2014), coral persistence may soon depend more on heat tolerance than growth. Under elevated temperature, *D. trenchii* confers a photochemical advantage to its hosts and relative growth trade-offs may decrease or even disappear at progressively higher temperatures (Cunning et al. 2015, 2018). Thus, under a "new normal" of repeated or chronic heat stress, *D. trenchii* may increase coral survival without compromising growth relative to other symbiont genera. Stakeholders should therefore consider climate projections when deciding if *D. trenchii* may help or harm the reefs they manage in the long-term.

Going forward, it will be important to determine whether recruits can be primed with *D. trenchii in-situ* as part of existing restoration pipelines. Without the constraints of laboratory space, field methods to boost *D. trenchii* uptake could help practitioners rear large numbers of thermally tolerant coral juveniles for outplanting. However, even if *D. trenchii* proves advantageous during thermal anomalies, it may be lost from corals over time in the absence of heat stress (Thornhill et al. 2006; LaJeunesse et al. 2009). Therefore, future studies should examine the longevity of manipulated symbiont communities in outplanted recruits, and identify conditions that promote *D. trenchii* dominance and maintain its benefits for hosts.

Finally, our finding that nearby colonies enhance *D. trenchii* uptake in recruits may inform the potential for symbiont community feedbacks within and between generations. While it was historically present at low abundances in some corals and locations, *D. trenchii* has rarely served as the dominant, preferred symbiont (e.g., LaJeunesse 2002) unless colonies experienced environmental stress or extremes (Baker et al. 2004; Fabricius et al. 2004; Kennedy et al. 2015; Silverstein et al. 2015). However, warming oceans and recurring bleaching events may favor *D. trenchii* at the ecosystem level, because it colonizes newly settled recruits and adults recovering from bleaching (Nitschke et al. 2016; Boulotte et al. 2016), and colonies that cannot shift to environmentally appropriate partnerships perish (LaJeunesse et al. 2010; Grottoli et al. 2014).

It remains uncertain whether the proliferation of *D. trenchii* on coral reefs will promote resilience or hinder recovery. As studies continue to disentangle the relationships between Symbiodiniaceae identity, coral physiology, and environmental variability, we can begin to predict context-dependent trade-offs within the coral holobiont and use our findings to inform reef restoration. If early infection with *D. trenchii* increases thermal tolerance in coral juveniles without severely compromising other aspects of fitness, practitioners may choose to rear them near *D. trenchii*-dominated adult colonies, boosting their resilience before outplanting them onto the reef.

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Declarations

Conflicts of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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