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REPORT

Growth tradeoffs associated with thermotolerant symbionts in the coral *Pocillopora damicornis* are lost in warmer oceans

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Abstract The growth and survival of reef corals are influenced by their symbiotic algal partners (*Symbiodinium* spp.), which may be flexible in space and time. Tradeoffs among partnerships exist such that corals with thermotolerant symbionts (e.g., clade D) resist bleaching but grow more slowly, making the long-term ecosystem-level impacts of different host–symbiont associations uncertain. However, much of this uncertainty is due to limited data regarding these tradeoffs and particularly how they are mediated by the environment. To address this knowledge gap, we measured growth and survival of *Pocillopora damicornis* with thermally sensitive (clade C) or tolerant (clade D) symbionts at three temperatures over 18–55 weeks. Warming reduced coral growth overall, but altered the tradeoffs associated with symbiont type. While clade D corals grew 35–40 % slower than clade C corals at cooler temperatures (26 °C), warming of 1.5–3 °C reduced and eliminated this growth disadvantage. These results suggest that although warmer oceans will negatively impact corals, clade D may enhance survival at no cost to growth relative to clade C. Understanding these genotype–environment interactions can help improve modeling efforts and conservation strategies for reefs under global climate change.

Keywords *Pocillopora damicornis* · *Symbiodinium* · Symbiosis · Climate change

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Introduction

The persistence of coral reef ecosystems under climate change scenarios depends on the ability of reef-building corals to survive and grow in warmer oceans. Rising seawater temperature is a major threat facing coral reefs, as thermal stress causes destabilization of the symbiosis between corals and their symbiotic algae (*Symbiodinium* spp.), a phenomenon known as coral bleaching. In association with climate warming, coral reef bleaching events worldwide are becoming more frequent and severe, often leading to mass coral mortality (Hoegh-Guldberg et al. 2007; Baker et al. 2008).

Susceptibility to bleaching varies widely among corals, in part due to differences in the type of *Symbiodinium* they host. Corals that associate with clade D *Symbiodinium* are more resistant to bleaching (Glynn et al. 2001; Berkelmans and van Oppen 2006), suggesting these corals have an advantage under climate change scenarios. Other corals may "switch" or "shuffle" (Baker 2003) their algal partners to associate with more clade D *Symbiodinium* as a mechanism to rapidly acclimatize to rising temperatures (Buddemeier and Fautin 1993; Baker 2001; Berkelmans and van Oppen 2006; Jones et al. 2008).

The increased thermal tolerance provided by clade D *Symbiodinium* may come at a cost of reduced carbon translocation (Cantin et al. 2009) or altered photokinetics and energetics (Jones and Berkelmans 2011, 2012) leading

to slower coral growth (Little et al. 2004; Jones and Berkelmans 2010). This tradeoff raises questions about whether *Symbiodinium* in clade D will ameliorate the effects of climate change on reefs by reducing bleaching or contribute to the long-term decline of reefs by reducing coral growth (Stat and Gates 2011; Ortiz et al. 2013b). Recent modeling work has predicted that coral cover on Caribbean reefs may actually decline faster in the presence of thermally tolerant symbionts, suggesting that clade D symbionts will have a deleterious ecosystem-level effect (Ortiz et al. 2013b). However, due to a paucity of data on the growth effects of different symbiont types, current models are constrained to assume a fixed negative growth effect of clade D (e.g., 50–60 % reduction; Ortiz et al. 2013a, b) that is environment-independent. In reality, the tradeoffs associated with different symbiont types may be mediated by numerous environmental variables.

To address this critical research gap, we conducted two experiments to evaluate growth of the major Indo-Pacific reef-building coral *Pocillopora damicornis* harboring either clade C (type C1b-c) or clade D (type D1) *Symbiodinium* at three temperatures (26, 27.5, and 29 °C). In particular, we tested the hypothesis that the growth disadvantage associated with thermally tolerant symbionts may be reduced as temperature increases. Understanding the interactive effects of symbiont type and environment on coral growth will improve our ability to model and predict coral reef futures under global climate change.

Materials and methods

Experiment 1: growth at 26 °C

Pocillopora damicornis colonies ($n = 58$) were collected from Uraba, Panama in August 2010 and transported to the University of Miami's Coral Resource Facility (CRF). Colonies from this area are known to comprise Type 1 and 3 lineages of *Pocillopora* (Pinzon and LaJeunesse 2011; Cunning et al. 2013), although lineages were not identified in this study. Approximately 20 fragments (~2 to 5 cm) were taken from each colony and mounted on labeled, weighted microcentrifuge tubes using hot glue. From August 2010 until March 2013, fragments were grown in a single indoor semi-recirculating 233-L tank maintained at 26 ± 0.5 °C. Recirculating seawater was treated by a UV-sterilizer, protein skimmer, and 10-µM canister filter, while continuously supplemented with 1 µM-filtered seawater pumped directly from Biscayne Bay at a rate of 1 L h^{-1}. Light was provided by two 80 W Giesemann T5 fluorescent bulbs delivering approximately 100 µmol quanta m^{-2} s^{-1} PAR (at position of corals) on a 14 h:10 h light:dark cycle. Growth was monitored over a 55-week period by taking buoyant weight measurements for $n = 349$ fragments on June 1, 2011 and June 19, 2012.

Experiment 2: effect of temperature on growth

In March 2013, 6–20 additional fragments were cut from each of 58 colonies that had been maintained under the conditions described for Experiment 1. Fragments were transferred to a set of four outdoor semi-recirculating experimental tank systems at the CRF (see Gillette 2012) where they recovered from fragmentation and acclimated to new conditions for 30 d (at 26 °C) prior to temperature manipulations. Each tank system consisted of a 350-L fiberglass tank used for experimentation mounted above a 500-L covered fiberglass sump tank used for temperature control, with seawater continuously recirculating between tanks. Temperature was maintained within 0.1 °C by submersible titanium heaters and heat exchangers supplied with chilled (~18 °C) fresh water. Each tank received a constant input of 5 µM-filtered seawater (0.2 L min^{-1}) from Biscayne Bay. Seawater was also recirculated within each upper tank to provide continuous flow around coral fragments. Shadecloth over the tanks reduced ambient irradiance by ~90 % (~50 µmol quanta m^{-2} s^{-1} midday irradiance at position of corals), and AT-Films Super 4 Agricultural Foil blocked ~90 % of UVA and UVB.

After 30 d of acclimation at 26 °C, coral fragments from each colony were divided and distributed evenly among three temperature treatments: 26, 27.5, and 29 °C ($n = 133$–197 fragments per clade per temperature). Water temperature was increased in the warmer treatments at a rate of 0.5 °C d^{-1} so that final temperatures were reached on April 26, 2013. Temperature treatments were maintained for 125 d and rotated among the four independent tank systems every 5–7 d in order to control for tank effect (a fourth unoccupied tank allowed rotation to take place without altering the temperature histories of the corals). HOBO data loggers (Onset Corp.) recorded water temperature in each tank throughout the experiment.

Symbiont community characterization

One tissue sample was taken from each coral colony in August 2010 and September 2012 for characterization of *Symbiodinium* communities by qPCR. DNA was extracted using a modified organic extraction protocol (Baker et al. 1997), and qPCR assays targeting specific actin loci in *Symbiodinium* clades C and D were performed as described in Cunning and Baker (2013). Only clades C and D were assayed because no stable symbioses with other *Symbiodinium* clades have ever been reported for eastern Pacific *Pocillopora* (LaJeunesse et al. 2008, 2010; Pettay et al. 2011; Pinzon and LaJeunesse 2011; McGinley et al. 2012;

Silverstein et al. 2012; Cunning and Baker 2013). Therefore, we assumed clades C and D comprised the entire symbiont community and calculated their proportions following Cunning et al. (2013) to categorize each colony as C- or D-dominated (i.e., "C colonies" or "D colonies").

Coral growth measurements

Coral growth was measured by buoyant weights of coral fragments at the beginning and the end of each experiment. Corals were suspended in seawater beneath an analytical balance and buoyant weight recorded to the nearest milligram. To account for the positive buoyancy of the caps to which each coral was mounted, 65 mg was added to each measurement (mean weight of $n = 5$ caps; corals whose mass did not exceed this positive buoyancy were excluded). A jet of water was used to remove any trapped air in the caps prior to weighing. In Experiment 2, bleaching (bleached vs. non-bleached) and mortality (total and partial) were assessed visually for each fragment at intervals of 54, 95, and 125 d.

Data analysis

For Experiment 1, growth was analyzed by regression of (log-transformed) final buoyant weight against (log) initial buoyant weight, with symbiont type as a fixed factor and parent colony as a nested factor. Only coral fragments that did not fuse to other fragments and did not experience partial mortality during the experiment were included in the growth analysis ($n = 283$ fragments). For Experiment 2, growth was analyzed by regression of (log-transformed) final buoyant weight against (log) initial weight, with symbiont type and temperature as fully crossed fixed factors and parent colony as a nested factor to account for the variation due to parent genotype. Only coral fragments that survived to the final time point and had not suffered major partial mortality (>50 % tissue loss) were included in the analysis ($n = 590$ fragments). The significance of each factor in these models was tested by partial F tests comparing the full model to reduced models lacking each factor. Growth rates (mg g^{-1} $week^{-1}$) were calculated by comparing adjusted mean weights (±SEM) for each group of corals to initial mean weight of all corals. Differences among treatment groups were assessed post hoc by two-tailed Student's t tests with $\alpha = 0.05$.

Mortality at the end of Experiment 2 (three levels: dead, partial mortality, or healthy) was analyzed by a nominal logistic model with temperature and symbiont type as fully crossed fixed factors and colony as a nested effect ($n = 664$ fragments). Significance of each factor was assessed with Likelihood-ratio chi-square tests comparing the full model to reduced models lacking each factor. Fragments that experienced mortality early in the experiment (within the first interval) were assumed to have been affected by fragmentation and transplantation stress rather than temperature and were therefore excluded from the analysis. All analyses were conducted in JMP v10.0.

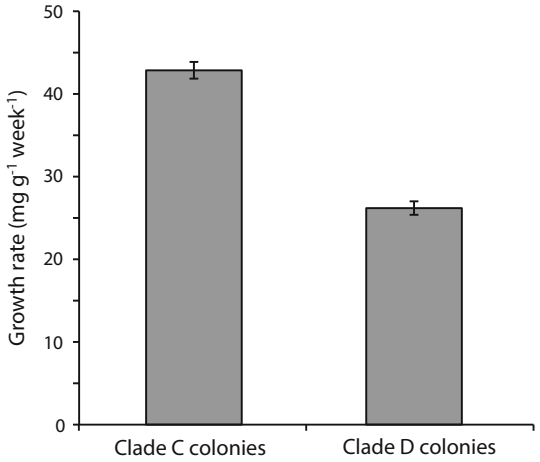

Fig. 1 Growth of clade C and D corals indoors under artificial lighting at 26 °C over 18 weeks (Experiment 1). Clade D corals ($n = 134$) grew 39 % slower than clade C corals ($n = 149$; student's t test, $P < 0.0001$). *Error bars* represent SEM

Results

Symbiont community characterization

All corals were categorized as clade C colonies (>98.1 % clade C) or clade D colonies (>99.5 % clade D), although 23 % of colonies contained background levels of the other clade. Several studies have identified the particular clade C and D symbionts hosted by *Pocillopora* in the eastern Pacific as ITS2 types C1b-c and D1, respectively (LaJeunesse et al. 2007, 2008; Cunning and Baker 2013). The dominant symbiont clade did not change in colonies between August 2010 (before Experiment 1) and September 2012 (before Experiment 2) and was therefore assumed to be stable throughout both experiments. Indeed, the dominant symbionts in eastern Pacific *Pocillopora* colonies are highly stable over time, even following bleaching events (LaJeunesse et al. 2007; McGinley et al. 2012; Cunning and Baker 2013). All fragments from the same colony were assumed to have the same dominant symbiont clade, as intracolony variation in the dominant symbiont clade is exceedingly rare in *Pocillopora* (LaJeunesse et al. 2007, 2008; Pettay et al. 2011; Cunning and Baker 2013).

Experiment 1: growth at 26 °C

Coral growth at 26 °C was significantly influenced by symbiont clade ($F = 161.3$, $df = 1$, $P < 0.0001$) and host

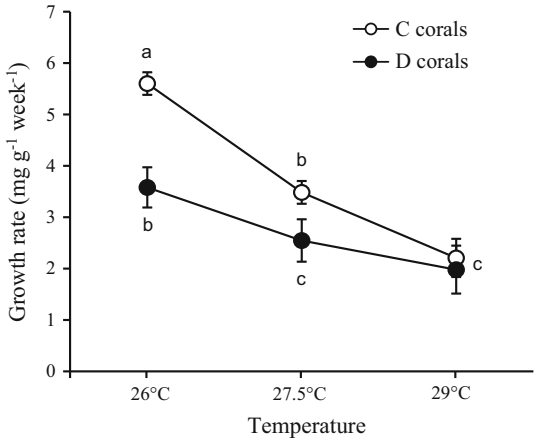

Fig. 2 Growth of clade C and D corals at different temperatures over 55 weeks (Experiment 2). Sample sizes for 26, 27.5, and 29 °C treatments are $n = 177$, 164, and 62 for clade C fragments, and $n = 72$, 66, and 50 for clade D fragments. *Error bars* represent SEM. Group means that do not share a *letter* are significantly different ($\alpha = 0.05$)

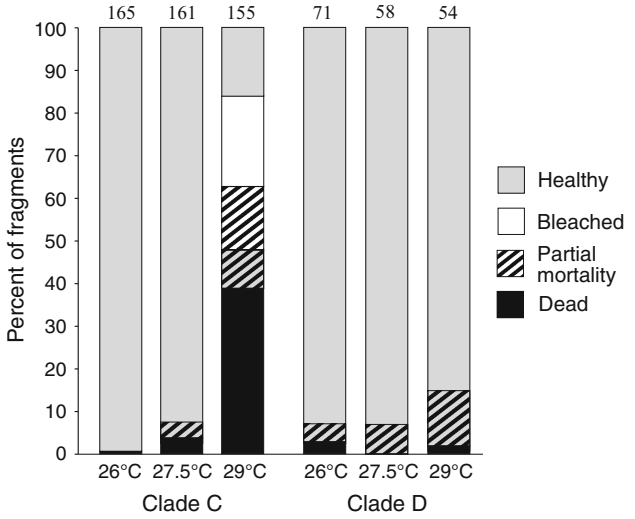

Fig. 3 Bleaching and mortality of clade C and D corals at different temperatures. After 125 d, living coral fragments in each treatment group were visually assessed to record significant partial mortality (>50 % tissue loss) and bleaching (white tissue). *Numbers above each column* indicate sample size

colony ($F = 19.3$, $df = 37$, $P < 0.0001$). Relative to clade C corals ($n = 149$), growth of clade D corals ($n = 134$) was 39 % lower (26.2 ± 0.8 vs. 42.9 ± 1.0 mg g^{-1} week^{-1}; Fig. 1).

Experiment 2: effect of temperature on growth

Coral growth in this experiment ranged from ~2 to 6 mg g^{-1} week^{-1} and was also influenced by host colony ($F = 6.5$, $df = 54$, $P < 0.0001$). Growth decreased at warmer temperatures regardless of symbiont type ($F = 29.9$, $df = 2$, $P < 0.0001$). However, the reduction in growth was more severe for corals with clade C ($n = 403$) than clade D ($n = 188$; symbiont:temperature interaction, $F = 3.59$, $df = 2$, $P < 0.05$). Compared to 26 °C, growth of clade C corals at 27.5 and 29 °C was reduced by 38 and 61 %, respectively, while growth of clade D corals was reduced by 29 and 45 % (Fig. 2). Within-temperature comparisons indicate that relative to clade C corals, growth of clade D corals was reduced at 26 °C by 36 %, while at 27.5 °C by 27 %. At 29 °C, clade D and C corals grew the same amount (Fig. 2). When bleached fragments were excluded, growth at 29 °C was still not different between C and D corals ($t = -1.2$, $P > 0.2$).

Experiment 2: mortality and bleaching

Mortality in response to temperature was significantly different between corals with clade C and D symbionts (symbiont:temperature interaction, $\chi^2 = 24.4$, $df = 4$, $P < 0.0001$) and was also influenced by host colony ($\chi^2 = 173.1$, $df = 108$, $P < 0.0001$). Mortality occurred mostly among clade C corals at 29 °C, of which 39 % were dead and 24 % suffered major partial mortality by the end of the experiment (Fig. 3). Among the clade C corals at 29 °C that remained alive, 59 % were bleached. Bleaching was not observed in clade C corals at 26 or 27.5 °C, or in any clade D corals. These corals also had low rates of total and partial mortality (<6 % overall; Fig. 3) that could not be distinguished statistically.

Discussion

In Experiment 1, we found that clade D corals grew 39 % slower than clade C corals at 26 °C (indoors under artificial lighting; Fig. 1). Similar reductions in growth associated with clade D symbionts were observed in adult *Acropora millepora* (29–38 %: Jones and Berkelmans 2010), with even greater reductions in juveniles (Little et al. 2004; Mieog et al. 2009). Reduced growth may be caused by decreased carbon translocation by clade D symbionts (Cantin et al. 2009) and has been cited as a tradeoff to the thermal tolerance clade D confers on its hosts (Jones and Berkelmans 2010, 2011; Stat and Gates 2011).

In our second experiment, we investigated how this tradeoff is affected by changes in the environment (e.g., temperature). In this experiment, clade D corals grew 36 % slower than clade C corals at 26 °C. Although different conditions preclude comparison of absolute growth rates, the 36 % reduction in D corals closely matches that of 39 % in Experiment 1 at the same temperature. At warmer temperatures, growth rates decreased for all corals, indicating they were above their thermal optima defined by

Gaussian temperature–growth relationships (Marshall and Clode 2004). However, warming also eliminated the growth disadvantage of clade D: at 27.5 °C, clade D reduced growth by only 27 % relative to clade C, while at 29 °C, clade D did not reduce growth at all, indicating a significant genotype–environment interaction. In contrast to this finding, Jones and Berkelmans (2010) found no effect of temperature (23 vs. 29 °C) on growth of *A. millepora* with clade C or D *Symbiodinium* and no interaction between temperature and symbiont type. These different findings may be explained by unique thermal growth optima for different host–symbiont associations (Marshall and Clode 2004); in particular, the lack of a temperature effect in Jones and Berkelmans (2010) may be a result of their temperature treatments (23 and 29 °C) lying on either shoulder of the Gaussian curve for *A. millepora* growth, while our temperature treatments (26–29 °C) may have captured the decreasing right shoulder for growth of *P. damicornis*. In addition, the longer duration of our experiments (18–55 vs. 4 weeks; Jones and Berkelmans 2010) may have allowed sufficient time for environmental impacts on the photokinetics and energetics of different symbiont types (Jones and Berkelmans 2011, 2012) to manifest in skeletal growth. While additional research is needed to elucidate these complex interactions (Smith et al. 2008; Mieog et al. 2009), our findings show that warming reduces growth of *P. damicornis* more severely when hosting clade C, causing their growth advantage over clade D corals to be lost after 1.5–3 °C of warming, which is expected before the end of this century (Meehl et al. 2007).

Importantly, the loss of a growth advantage in clade C corals is only relevant for those corals that survive. We found that less than half of clade C corals at 29 °C escaped complete or partial mortality and less than half of those remained unbleached. The significant bleaching and mortality that occurred among (and only among) clade C corals at 29 °C (Fig. 3) reflects the well-documented thermal sensitivity of *Pocillopora* with clade C (Glynn et al. 2001; LaJeunesse et al. 2007, 2010; Cunning and Baker 2013). However, some clade C corals at 29 °C (16 %) still remained healthy, suggesting that at least some corals with thermally sensitive symbionts may still survive, possibly due to local adaptation (Howells et al. 2011) and/or host-derived thermal tolerance (Baird et al. 2009; Gillette 2012). However, even the 16 % of healthy clade C corals at 29 °C grew no faster than clade D corals, showing that the lost growth advantage is not simply due to bleaching. Furthermore, the growth advantage of clade C corals was significantly reduced at 27.5 °C although no bleaching occurred.

Taken together, these bleaching, mortality, and growth data suggest that warming will have a major impact on the relative success of corals with clade C and D partnerships. While clade C corals have a significant growth advantage in the absence of thermal stress, warmer oceans may cause significant mortality among these thermally sensitive partnerships while eliminating the growth advantage of those that survive. By contrast, clade D partnerships may greatly enhance thermotolerance and survival at little to no cost in growth, relative to clade C. Although other tradeoffs to hosting clade D may still exist (e.g., reduced energy stores and reproductive output; Jones and Berkelmans 2011), these trends suggest that clade D symbionts may have beneficial ecosystem-level effects on reefs under climate change scenarios. Switching or shuffling toward clade D-dominated symbiont communities (Baker 2003) may allow corals to rapidly acquire these advantages and acclimatize to warmer environments (Berkelmans and van Oppen 2006; Jones et al. 2008; Correa and Baker 2011). However, important considerations for future studies are the impacts of not only rising baseline temperatures, but also greater seasonal and local temperature variation and maxima.

In summary, this work reveals that genotype–environment interactions may be important in driving many coral traits, and further work to quantify these interactions may directly inform modeling efforts to predict the fate of coral reefs (Ortiz et al. 2013a, b), and conservation strategies to protect them (Pandolfi et al. 2011). Nevertheless, the slower growth of all corals at higher temperatures, regardless of symbiont type, suggests that reefs are being pushed beyond their thermal growth optima and that warming must be curbed to ensure the future persistence of these ecosystems.

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