## brief communications

## **Coral bleaching**

## Thermal adaptation in reef coral symbionts

any corals bleach as a result of increased seawater temperature, which causes them to lose their vital symbiotic algae (*Symbiodinium* spp.) unless these symbioses are able to adapt to global warming, bleaching threatens coral reefs worldwide<sup>1-3</sup>. Here I show that some corals have adapted to higher temperatures, at least in part, by hosting specifically adapted *Symbiodinium*. If other coral species can host these or similar *Symbiodinium* taxa, they might adapt to warmer habitats relatively easily.

Around Guam, species of the coral genus *Pocillopora* each associate with at least two *Symbiodinium* taxa, one of which, according to ecological data<sup>4</sup>, seems to be more tolerant of high temperature. I tested whether this could be the case by comparing photosynthetic responses of the taxa, labelled according to their genotype, *Symbiodinium C* and *Symbiodinium D* (ref. 4) (for methods, see supplementary information). I measured the maximum quantum yield of photosystem II (PSII) as the ratio of variable chlorophyll fluorescence ( $F_v/F_m$ )<sup>5</sup> in *P. verrucosa*. In *P. damicornis*, I measured photosynthesis from oxygen flux.

Symbiodinium C and D respond in opposite ways to temperature, as indicated by their differing  $F_v/F_m$  (Fig. 1a). Compared with a control temperature of 28.5 °C, a temperature of 31.3 °C did not affect Symbiodinium C, but it increased  $F_v/F_m$  in Symbiodinium D; a temperature of 32.0 °C decreased  $F_v/F_m$  in Symbiodinium C, whereas Symbiodinium D maintained an increased  $F_v/F_m$ . Although  $F_v/F_m$  was similar in Symbiodinium Cand Dat 28.5 °C, at 32.0 °C Symbiodinium C could be identified by its lower  $F_v/F_m$ . After the temperature treatments, corals were kept at 28.5 °C; after three and four days,  $F_v/F_m$  in treated Symbiodinium C remained lower than in controls (P=0.02)and unchanged from the value recorded at 32.0 °C (P > 0.2), whereas  $F_v/F_m$  in control and treated Symbiodinium D had become similar (P > 0.2; Wilcoxon paired-sample tests).

A long-lasting decrease in  $F_v/F_m$ , as observed in *Symbiodinium C*, indicates that chronic photoinhibition resulted from damage to PSII (refs 5–7). Repeated measures (Wilcoxon paired-sample tests) show that the decrease in  $F_v/F_m$  in *Symbiodinium C* at 32.0 °C compared with 31.3 °C (P=0.02) was accompanied by a 20% increase (P=0.02) in the minimum chlorophyll fluorescence in the dark-acclimated state ( $F_o$ ) and no change (P>0.5) in  $F_m$ , confirming chronic photoinhibition<sup>5</sup>. Over the same time, both  $F_o$ and  $F_m$  decreased by 13% (P=0.02) in control *Symbiodinium C*, suggesting an increase in photoprotection<sup>7</sup>.  $F_o$  and  $F_m$  did not change in *Symbiodinium* D under control or treatment conditions ( $P \ge 0.2$ ).

Whereas chronic photoinhibition of *Symbiodinium C* indicates temperature sensitivity and predicts coral bleaching<sup>1,6,7</sup>, the increased  $F_v/F_m$  in treated *Symbiodinium D* indicates photoprotection. For *Symbiodinium D*, the relationship between  $F_v/F_m$  and irradiance

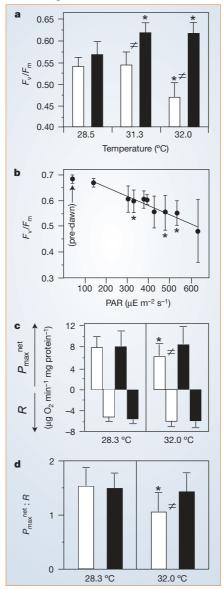


Figure 1 Photosynthesis in corals hosting Symbiodinium C (white bars) or D (black bars). a, Afternoon values of maximum quantum yield of photosystem II ( $\mathit{F_v/F_m}$ ) in Pocillopora verrucosa (mean and s.d.; n = 7); asterisks indicate differences (P < 0.05) between corals at 28.5 °C and the same corals at 31.3 °C or 32.0 °C; inequalities indicate differences (P<0.05) between Symbiodinium C and D (both, Wilcoxon paired-sample tests). **b**, Afternoon values of  $F_v/F_m$ (mean  $\pm$  s.d., n=7) in *P. verrucosa* hosting *Symbiodinium D* at 28.5 °C, plotted against daily average irradiance (PAR, photosynthetically available radiation; between 10:00 and 14:00); slope is not equal to zero (t-test, P < 0.001); pre-dawn (three-day average) shows overnight recovery of  $F_v/F_m$  compared with preceding afternoons (asterisks: P = 0.02, Wilcoxon paired-sample test). **c**,  $P_{max}^{net}$ (positive) and R (negative, measured in the dark) of P. damicornis (mean and s.d.; n = 9). **d**,  $P_{\text{max}}^{\text{net}:R}$  from data summarized in **c**. In **c**, d, asterisks as in a; inequalities indicate differences between Symbiodinium C and D (P < 0.05, Mann–Whitney U-test).

exposure, which quantifies dynamic photoinhibition (reversible and protective) of PSII (refs 8, 9; Fig. 1b), shows that increased temperature mimicked a 30% decrease in habitat irradiance at 28.5 °C. Photoprotection by increased temperature reflects the temperature dependence of photosynthetic pathways<sup>10</sup>. Thus, I conclude that *Symbiodinium D* is a high-temperature specialist. Plant models<sup>9</sup> indicate that photoinhibition similar to that relieved by warmer temperatures in *Symbiodinium D* reduces daily carbon gain by 6–10%.

Oxygen-flux measurements independently support these conclusions and extend them to another host species at the whole-coral level. Increased temperature affected only corals hosting *Symbiodinium C*: maximum net photosynthesis ( $P_{max}^{net}$ ) decreased; respiration (R) was not affected (Fig. 1c). At the higher temperature, the ratio of  $P_{max}^{net}$  to R ( $P_{max}^{net}$ :R) decreased by 31%, making corals hosting *Symbiodinium C* less autotrophic than corals hosting *Symbiodinium D* (Fig. 1d). Temperature did not affect numbers or the chlorophyll a of *Symbiodinium C* or D ( $P \ge 0.5$ , Wilcoxon paired-sample tests), so the decreased autotrophy did not result from lost symbionts.

Symbiodinium can differ physiologically owing to their acclimatization to different environments3, which probably include different host species. However, because I controlled for these variables, the differences observed here are regarded as intrinsic symbiont adaptations that apparently contribute significantly to whole-coral physiology. Adaptation to higher temperature in Symbiodinium D can explain why Pocillopora spp. hosting them resist warm-water bleaching whereas corals hosting Symbiodinium C do not (personal observations). It can also explain why Pocillopora spp. living in frequently warm (more than 31.5°C) habitats host only Symbiodinium D (ref. 4), and, perhaps, why those living in cooler habitats predominantly host Symbiodinium C (ref. 4). These observations, which may apply to other corals<sup>11</sup>, indicate that symbiosis recombination<sup>12</sup> may be one mechanism by which corals adapt, in part, to global warming<sup>3</sup>.

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