

Coral bleaching

# Thermal adaptation in reef coral symbionts

Many 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 to maximum 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 C* and *D* at 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 ( $P\geq 0.2$ ).

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

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* ( $P\geq 0.5$ , Wilcoxon paired-sample tests), so the decreased autotrophy did not result from lost symbionts.

*Symbiodinium* can differ physiologically owing to their acclimatization to different environments<sup>3</sup>, 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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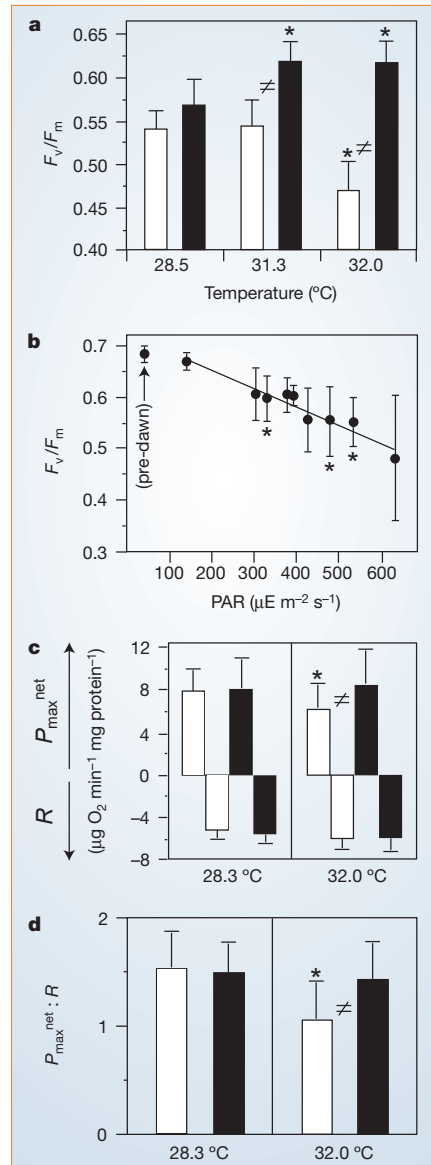
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Supplementary information accompanies this communication on Nature's website.

Competing financial interests: declared none.



**Figure 1** Photosynthesis in corals hosting *Symbiodinium C* (white bars) or *D* (black bars). **a**, Afternoon values of maximum quantum yield of photosystem II ( $F_v/F_m$ ) 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**,  $P_{max}^{net}:R$  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).