

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^{1–3}. 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 data⁴, 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)⁵ 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 photoinhibition⁵. Over the same time, both F_o and F_m decreased by 13% ($P=0.02$) in control *Symbiodinium C*, suggesting an increase in photoprotection⁷. 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^{1,6,7}, the increased F_v/F_m in treated *Symbiodinium D* indicates photoprotection. For *Symbiodinium D*, the relationship between F_v/F_m and irradiance

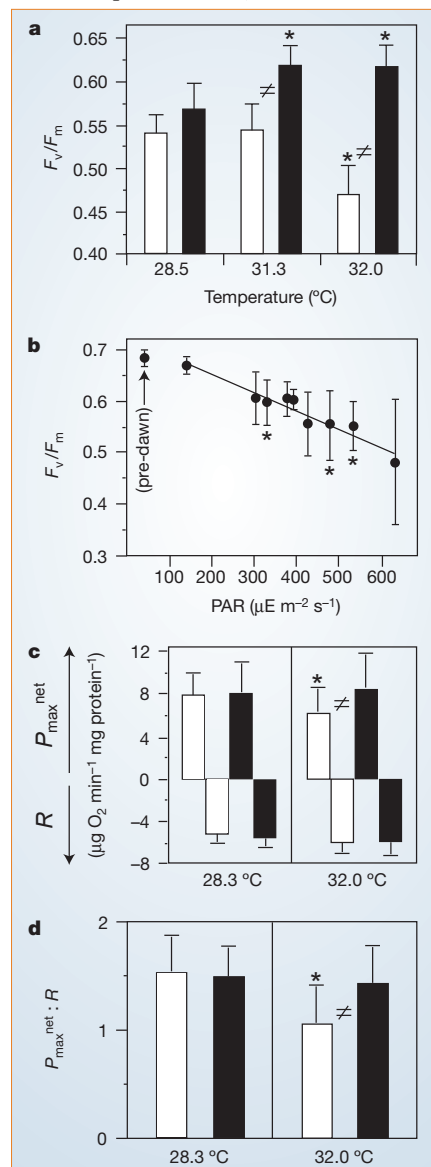


Figure 1 Photosynthesis in corals hosting *Symbiodinium C* (white bars) or *D* (black bars). **a**, Afternoon values of maximum quantum yield of photosystem II (F_v/F_m) in *Pocillopora verrucosa* (mean and s.d.; $n=7$); asterisks indicate differences ($P < 0.05$) between corals at 28.5 °C and the same 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).

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 pathways¹⁰. Thus, I conclude that *Symbiodinium D* is a high-temperature specialist. Plant models⁹ 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 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 corals¹¹, indicate that symbiosis recombination¹² may be one mechanism by which corals adapt, in part, to global warming³.

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