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Ecosystems

Reef corals bleach to survive change

The bleaching of coral reefs, in which symbiotic algae are lost from reef-building invertebrates, is usually considered to be a drastic and damaging response to adverse environmental conditions^{1,2}. Here I report results from transplant experiments involving different combinations of coral host and algal symbiont that support an alternative view, in which bleaching offers a high-risk ecological opportunity for reef corals to rid themselves rapidly of suboptimal algae and to acquire new partners. This strategy could be an advantage to coral reefs that face increasingly frequent and severe episodes of mass bleaching as a result of projected climate change^{2,3}.

Coral reefs are built by symbioses between scleractinian (stony) corals and photosynthetic dinoflagellate algae. These diverse algae⁴ are important species because their loss during bleaching can lead to widespread coral mortality and degradation of reef ecosystems⁵. Different types of algal symbiont often show strong zonal patterns within their coral hosts that correspond to light intensity (shallow, 'high-light' algae or deep, 'low-light' algae)^{6–8}.

To investigate the effect of bleaching on the stability of these depth distributions, I reciprocally transplanted eight species of Caribbean scleractinian coral between 'shallow' (2–4 m) and 'deep' (20–23 m) sites in the San Blas archipelago, Panamá. I assessed transplanted and control colonies for bleaching after 8 weeks, and for mortality and changes in symbiont taxa after 12 months (Fig. 1).

'Upward' (deep-to-shallow) transplants showed significant bleaching after 8 weeks (11 of 24 colonies partially or severely bleached; 2 others pale), whereas 'downward' (shallow-to-deep) transplants showed less bleaching (0 of 37 colonies bleached; $\chi^2 = 20.7$, Fisher's exact $P < 0.0001$). Surprisingly, despite more extensive bleaching, upward transplants showed no mortality after 12 months (0 of 24 colonies dead), unlike downward transplants (7 of 37 colonies dead; $\chi^2 = 5.13$, Fisher's exact $P = 0.0358$). Control transplants showed no

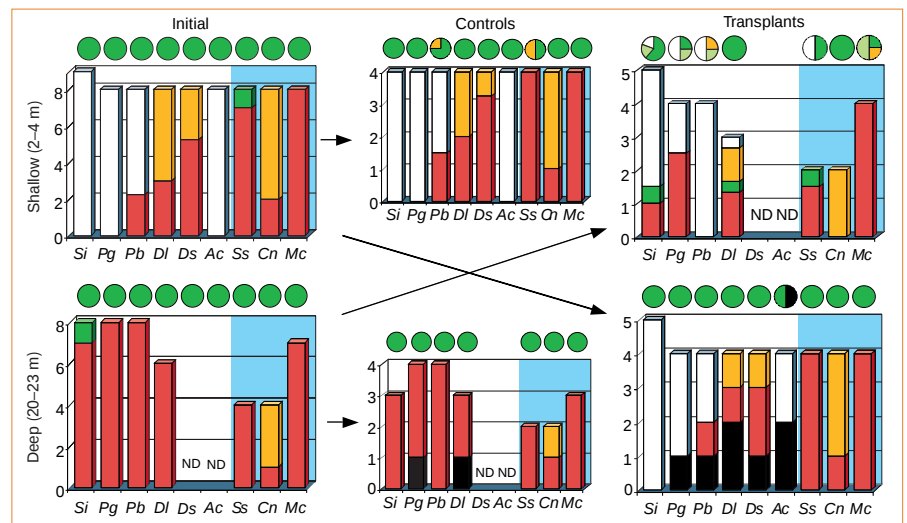


Figure 1 Symbiont diversity and mortality responses to bleaching in transplanted corals. Bars show symbiont community structure (*Symbiodinium* clades A–D) before transplantation and 12 months after transplantation: white, A; orange, B; red, C; green, D; black, dead. Pie charts indicate bleaching status of host colonies before transplantation and 8 weeks after transplantation: dark green, healthy; light green, pale; orange, partial bleaching; white, severe bleaching; black, dead. Vertical axes, number of colonies; horizontal axes, coral species. Si, Pg, Pb, Dl, Ds and Ac (white background) have strong light-related patterns of symbiont diversity; Ss, Cn and Mc (blue background) exhibit no light-related patterns of symbiont diversity. Control colonies accompanied the transplanted corals to their new location before being returned immediately to their original depths. ND, no data: Ds and Ac were very rare at the deeper location and underwent shallow-to-deep transplantation only (at similar depths nearby they were not uncommon and contained 'low-light' algae). Diagonal arrows indicate direction of transplantation. Si, *Stephanocoenia intersepta*; Pg, *Porites astreoides* (green); Pb, *Porites astreoides* (brown); Dl, *Diploria labyrinthiformis*; Ds, *Diploria strigosa*; Ac, *Acropora cervicornis*; Ss, *Siderastrea siderea*; Cn, *Colpophyllia natans*; Mc, *Montastraea cavernosa*.

significant bleaching or mortality.

Changes in the structure of symbiont communities explained these surprising patterns of bleaching and mortality. Surveys of restriction-fragment-length polymorphisms in genes encoding large-subunit ribosomal RNA^{4,8} identified four groups of *Symbiodinium* algae (termed A, B, C, and a previously unassigned clade, D^{4,8,9}) from these coral hosts. Five of the eight coral host species showed strong intraspecific patterns of depth zonation in their symbionts; the other three showed no such patterns⁸ (Fig. 1). Transplanted coral species that hosted different algae at deep and shallow sites adjusted their algae distributions to their new depths only when transplanted upwards (12 of 16 colonies), and not when transplanted downwards (1 of 25 colonies; $\chi^2 = 22.7$, Fisher's exact $P < 0.0001$).

These results reveal an unexpected relationship between acute stress-induced bleaching (sudden exposure to increased irradiance after upward transplantation), adaptive change in symbiont communities, and reduced coral host mortality. This contrasts with a lack of bleaching in response to chronic stress (lower sustained irradiance after downward transplantation), no change in symbiont communities, and increased coral mortality. Together, these findings support the view (first proposed by theorists¹⁰) that coral bleaching can promote rapid response to environmental change by facilitating compensatory change in algal symbiont communities.

Without bleaching, suboptimal host–symbiont combinations persist, leading eventually to significant host mortality.

Reef corals are flexible associations that can switch or shuffle symbiont communities in response to environmental change^{4,8,10,11}. However, there may be costs involved, as shown by higher mortality in the five coral species that vary their algae with depth (9 of 79 colonies) than in the three species that do not (0 of 39 colonies; $\chi^2 = 4.81$, Fisher's exact $P < 0.0289$).

Changes in symbiont communities may be slow unless existing symbionts are first removed, suggesting that established symbionts have a significant competitive home advantage over invasive (or low-abundance) symbionts. Coral bleaching can rapidly remove these symbionts, facilitating their replacement by alternative algae that are better suited to the new environmental conditions. Furthermore, the process of community change, which is facilitated by bleaching, may provide a window for unusual opportunistic symbionts to colonize hosts (and/or proliferate inside them)^{9,11,12}, as shown by the behaviour of *Symbiodinium* A and D in upward-transplant experiments.

Symbiosis recombination may help to resolve the paradox of reef corals as environmentally fragile yet geologically long-lived associations¹³. Despite the extreme risks involved^{1,2}, and the likely high incidence of mortality in some regions (such as that resulting from the 1997–98 El Niño¹⁴),

bleaching may ultimately help reef corals to survive the recurrent and increasingly severe warming events projected by current climate models of the next half-century³. Bleaching is an ecological gamble in that it sacrifices short-term benefits for long-term advantage. This counters conventional wisdom that bleaching is detrimental from all perspectives, and supports the role of symbionts as adaptive agents^{10,11}.

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Population control

African elephants and contraception

Protected from hunting and provided with access to water-holes during droughts, elephant numbers can double in a decade, severely damaging natural vegetation and the many species dependent upon it. Culling is an effective but controversial control strategy, so Fayrer-Hosken *et al.*¹ have assessed the efficacy of using immunocontraception through vaccination, concluding that this could be a practical way of controlling elephant numbers. However, an intervention feasible in reproductive physiology may not be a practical way to control a population. Fayrer-Hosken *et al.* have not considered calculations^{2,3} that undermine the practicality of their method, nor alternative management strategies.

Controlling elephants in Kruger National Park, South Africa, by immunocontraception would necessitate treatment of 2,250 cows each year over an initial period of 11 years (ref. 3). Even if individual treatments were 100% effective, the costs would be likely to exceed the total management budget of the South African national parks. The best results of Fayrer-Hosken *et al.* involved two of ten elephants becoming

pregnant, and that was after receiving two booster vaccinations.

The effectiveness of this method may be less than claimed. Of the control group, 89% became pregnant within a year. This seems high, exaggerating the difference between treated and control groups. Data from 813 adult cows culled in Kruger National Park between 1979 and 1994 showed that 51% (range, 36–77%) were pregnant. This is to be expected: gestation lasts 22 months and the calving interval is 44 months (ref. 2), so about 50% of a sample of cows should be pregnant. Thus, on average, females go for 22 months without becoming pregnant. In a random sample of females monitored for 12 months, only 55% (not 89%) should therefore become pregnant.

Between 16 and 1,846 elephants of all age classes and both sexes were culled annually in Kruger National Park from 1967 to 1994. We share the desire to reduce culling and have sought methods to do so. Removing or sterilizing 250 subadult females each year should reduce population growth to zero^{2,3}. Moreover, densities of greater than 0.37 elephants per square kilometre result in reduced population growth rates — probably due to reduced reproductive output by newly sexually matured females or to increased calving intervals². Culling, as conducted, maintained densities at which population growth was near its maximum. Culls should be delayed for one year after counts exceed 0.37 elephants per square kilometre to allow density dependence to reduce numbers naturally². Culls may still be necessary, but they would then be much less frequent and involve far fewer animals.

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Fayrer-Hosken et al. reply — Pimm and van Aarde question the feasibility of controlling elephant numbers by immunocontraception, arguing that the sterilization or removal of 250 subadult cows each year is the answer to population growth. However,

there are no known safe methods of sterilizing free-roaming African elephants. Moving 250 subadult females to another park is impractical as there are very few areas able to receive elephants from Kruger National Park without becoming confronted with an elephant overpopulation problem of their own.

This number of subadult cows cannot be moved without disrupting the social order within their herds. Keeping them in their herds would mean that (assuming a mean herd size of 12.4, as shown in our study, and an average of 3 subadult females per herd) Kruger National Park would have to move 1,033 elephants — an unrealistic and expensive proposition. Hence the only practical way to remove 250 subadult females would be to cull them, which Pimm and van Aarde agree is an unacceptable solution.

We have shown that immunocontraception using porcine zona pellucida (pZP) works in the African elephant, although its long-term effectiveness in controlling populations is still being evaluated in South Africa. The cost and speed of field delivery have not been assessed for vaccinating large groups of elephants. However, contrary to the calculations of population modellers^{1,2}, immunocontraception has worked in herds of wild horses and white-tailed deer³.

Preserving these magnificent creatures and their genetic contribution for the future is a common goal. On the basis of a single administration of a multiple-release pZP vaccine that is being developed for use in horses (I. K. M. Liu, personal communication), it should be possible to reduce the first three vaccinations used in our original study to a single dose and so minimize the stress, cost and labour of elephant immunocontraception.

We therefore question Pimm and van Aarde's criticism regarding the practicality of field immunocontraception for Kruger Park's elephant herds. It is our judgement that preserving these animals through immunocontraception is a realistic strategy that would save elephants without having to kill them.

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