

Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change

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Summary

Many coral reefs worldwide have undergone phase shifts to alternate, degraded assemblages because of the combined effects of overfishing, declining water quality, and the direct and indirect impacts of climate change [1–9]. Here, we experimentally manipulated the density of large herbivorous fishes to test their influence on the resilience of coral assemblages in the aftermath of regional-scale bleaching in 1998, the largest coral mortality event recorded to date. The experiment was undertaken on the Great Barrier Reef, within a no-fishing reserve where coral abundances and diversity had been sharply reduced by bleaching [10]. In control areas, where fishes were abundant, algal abundance remained low, whereas coral cover almost doubled (to 20%) over a 3 year period, primarily because of recruitment of species that had been locally extirpated by bleaching. In contrast, exclusion of large herbivorous fishes caused a dramatic explosion of

macroalgae, which suppressed the fecundity, recruitment, and survival of corals. Consequently, management of fish stocks is a key component in preventing phase shifts and managing reef resilience. Importantly, local stewardship of fishing effort is a tractable goal for conservation of reefs, and this local action can also provide some insurance against larger-scale disturbances such as mass bleaching, which are impractical to manage directly.

Results and Discussion

The ecosystem goods and services provided by healthy coral reefs are a key component in the economic, social, and cultural fabric of many tropical maritime countries [1, 9]. Until recently, land-based pollution and overfishing were considered to be the major threats to coral reefs. Today, reefs face additional pressure from thermal stress and emergent diseases that are closely linked to global warming [1–8]. In the most damaging case to date, 16% of the world's reefs were impacted in 1997–1998 by a regional-scale bleaching event that affected the Great Barrier Reef, vast tracts of the western Pacific, the Indo-Australian Archipelago, and the Indian Ocean [1, 10–11]. Climate-change projections indicate that similar events will reoccur with increased frequency in the coming decades [2, 12], highlighting the urgency of developing improved tools for managing reefs in the face of escalating threats [4–5, 13–15].

Here, we experimentally examine the resilience of coral-dominated assemblages on the Great Barrier Reef and the processes underlying a phase shift to macroalgal dominance (Figure 1A). We define resilience as the ability of reefs to absorb recurrent disturbances (e.g., from cyclones, outbreaks of predators, or coral bleaching events) and rebuild coral-dominated systems. Loss of resilience can lead to a phase or regime shift to an alternate assemblage that is typically characterized by hyperabundances of fleshy seaweeds or other opportunistic species. The experiment was designed to simulate the depletion of large predatory and herbivorous fishes caused by chronic overfishing [16–21] and to investigate their role in the regeneration of reefs after recent mass bleaching and the mortality of corals (see [Experimental Procedures](#)). The scale and timing of the experiment allowed us to measure the postbleaching dynamics of a rich coral assemblage (77 species represented by 4569 colonies were recorded by the end of the experiment), and its location provided us with a baseline comparison of an unusually intact fish fauna on heavily grazed reef crests within an established no-take area of the Great Barrier Reef Marine Park. This is the first replicated herbivore-exclusion experiment that explicitly examines herbivore-algae-coral interactions in the context of climate change. We demonstrate that exclusion of larger fishes profoundly erodes the resilience of coral reefs and their ability to regenerate after bleaching, with

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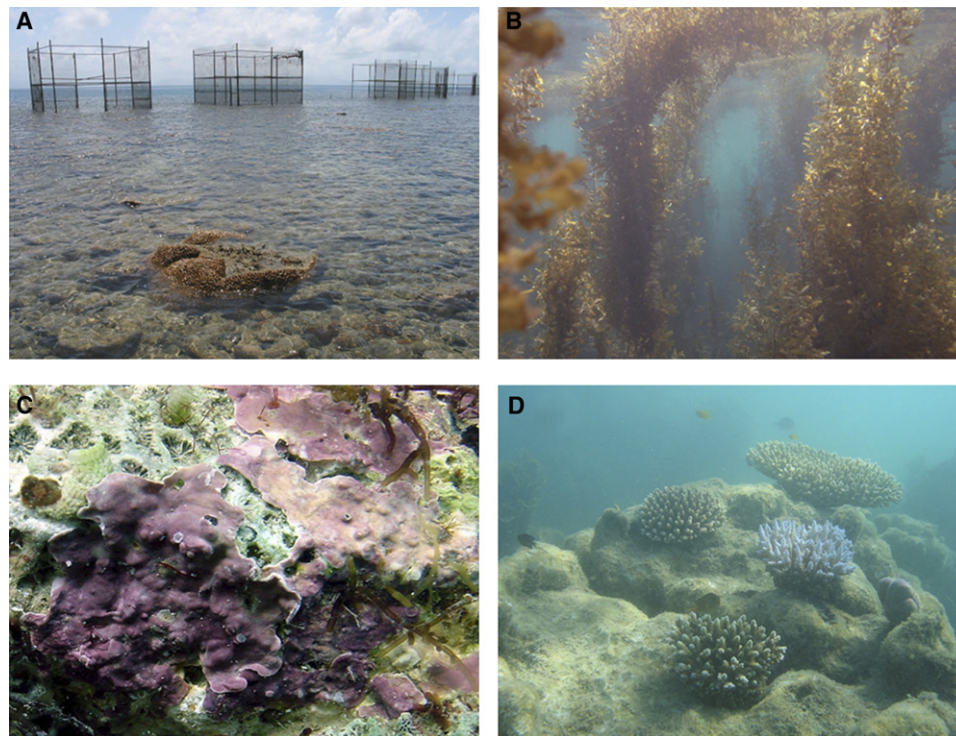


Figure 1. Experimental Phase Shifts on the Great Barrier Reef

(A) Roofless cages and partial cages constructed on the seaward edge of reef crest. Each structure is 5 × 5 m in area and 4 m tall. Note the 2 m high door in the cage in the center of the photograph, for access at low tide.

(B) Growths of *Sargassum* up to 3 m tall dwarf understory corals inside a fish-exclusion cage.

(C) When fishes were experimentally excluded, a foliose coralline alga, *Mesophyllum purpureus*, replaced shallow-water grazer-resistant species.

(D) Coral recruits settled on dead corals killed 5 years earlier by thermally induced bleaching in 1998. Grazing of the dead substrate by herbivores is crucial for settlement and early survival of corals and coralline algae.

major implications for reef ecology, conservation, and management.

Experimentally Induced Phase Shift

Our experimental exclusion of fishes replicated the paucity of medium and large fishes that is characteristic of chronically overfished reefs in S.E. Asia, the Caribbean, and elsewhere [16–19]. The biomass of herbivorous fishes inside cages (Figure 1A) was reduced to levels seven to ten times lower than in adjacent partial cages and open plots (0.45 ± 0.08 [S.E.], 4.29 ± 2.81 , and 3.12 ± 1.24 kg/m² per hr of video observation, respectively, $F = 7.79$, $p < 0.001$; Figure S1 in the Supplemental Data available with this article online). In response to the experimental exclusion of larger herbivorous fishes, benthic assemblages in the cages followed a fundamentally different trajectory over time, with upright fleshy macroalgae rather than corals and algal turfs becoming predominant, mimicking similar responses on many overfished and polluted reefs worldwide [4–8, 20–21].

In the aftermath of massive loss of corals on Orpheus Island in 1998 [10], roving herbivorous fishes continued to suppress the biomass of macroalgae and thus facilitated the recruitment of corals (Movie S1). In the partial cages and open plots where fish grazing was uninhibited, the cover of macroalgae (primarily the calcified red alga, *Galaxaura subfruticulosa*) averaged only 4.1% and 1.7% during the experimental period ($n = 16$

censuses), ranging up to a maximum of 10% and 7%, respectively (Figure 2A). In contrast, algal cover in the cages far exceeded the two control treatments throughout the experiment, reaching up to 91%, and averaging $56\% \pm 21\%$ (S.E.) after 30 months (repeated-measures ANOVA, $F = 3.82$, $p < 0.05$; Figure 2). By the end of the experiment, algal biomass in the cages was 9 to 20 times higher than in partial cages and open plots (1363 ± 234 , 146 ± 49 , and 68 ± 28 g wet weight per m², respectively; ANOVA, $F = 20.8$, $p < 0.001$). Over time, the species composition of macroalgae in the cages diverged dramatically from the other two treatments (Figure S2). Dense thickets of *Sargassum*, previously absent on the reef crest, grew to 3 m in height inside the cages, with maximum densities of greater than 1000 plants (holdfasts) per 25 m² and a biomass of up to 8.55 kg wet weight per m² (Figure 1B and Movie S2). Cover and species composition of crustose coralline algae also diverged in the three experimental treatments (Figure 1C and Figure S3).

Herbivory Boosts the Resilience of Coral Assemblages to Global Warming

In tandem with the changes in macroalgae and corallines, the trajectory of coral reassembly after the 1998 bleaching event diverged markedly in the fish-exclusion cages compared to the partial cages and open plots (Figure 2B). Initially, the most prevalent taxa (accounting for >80% of coral cover) were branching *Porites*

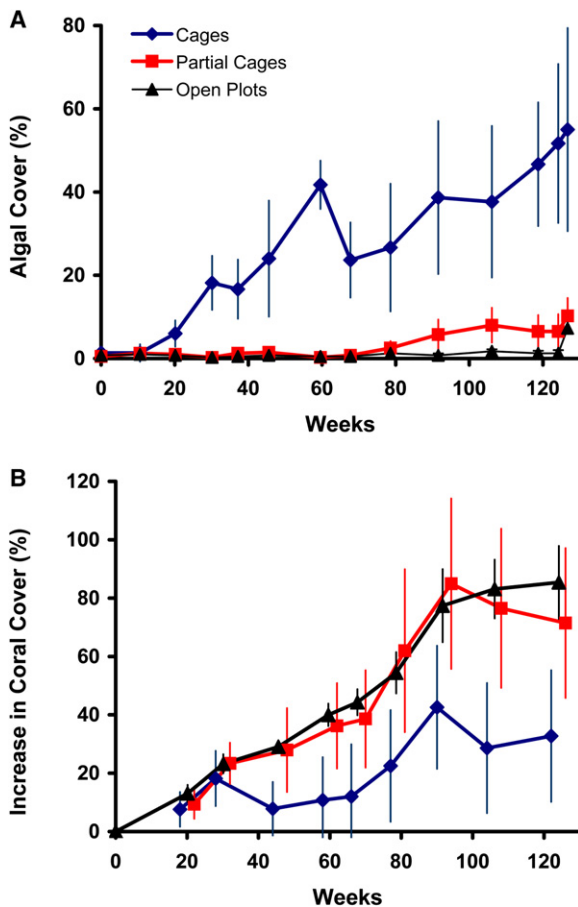


Figure 2. Contrasting Trajectories of Macroalgae and Corals after Exclusion of Fishes

(A) Macroalgal cover. Error bars are SE.
 (B) Relative coral cover over time among three experimental treatments. Absolute coral cover after 130 weeks was $7.7\% \pm 1.0\%$ (S.E.), $19.2\% \pm 2.3\%$, and $20.2\% \pm 2.2\%$ in the three treatments (see text for analysis). Census dates were the same for all treatments and are slightly staggered in the plots for clarity. Error bars are SE.

cylindrica, massive *Porites* spp. (especially *P. lobata* and *P. rus*), and massive faviids (principally heads of *Goniastrea*, *Favia*, and *Montastrea* spp.) that had survived the bleaching event 2 years prior to the initiation of the experiment. Alcyonacean soft corals and branching hard corals, particularly a diverse suite of *Acropora* species, were virtually eliminated from shallow sites by bleaching [10], and only a few small recruits were present ($<0.1\%$ cover) when the experiment began in 2000. In the fish-exclusion cages, total coral cover grew from $6.0\% \pm 0.8\%$ (S.E.) to $7.7\% \pm 1.0\%$ after 30 months. Coral cover increased much more quickly inside the partial cages and open plots, reaching $19.2\% \pm 2.3\%$ and $20.2\% \pm 2.2\%$, respectively (RM-ANOVA, $F = 3.82$, $p < 0.05$). In relative terms, coral cover increased by 28% inside the cages compared to 68% for partial cages and 83% for open plots (Figure 2B).

The divergence in coral cover among treatments was attributable to both lower recruitment and higher mortality of established corals after the experimental reductions of fish biomass (Figures 3A and 3B). A total of

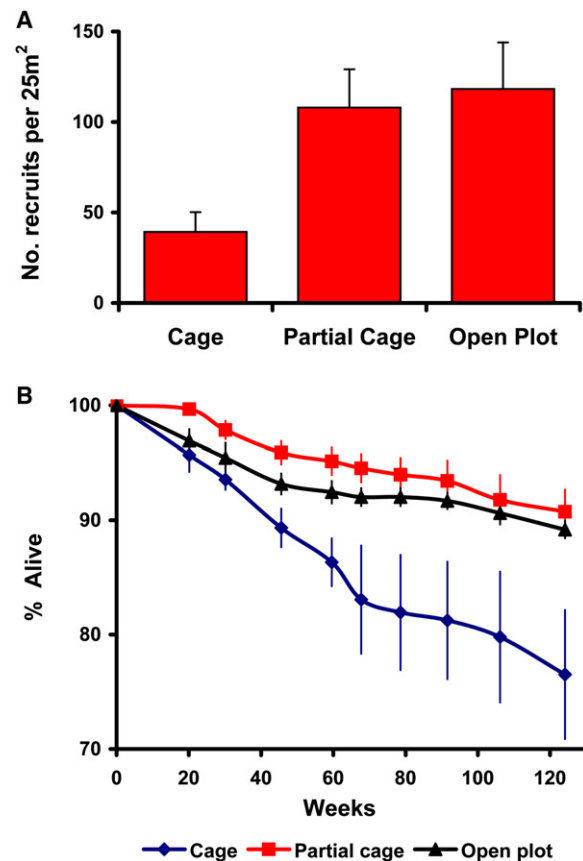


Figure 3. Demographic Responses of Corals

(A) Recruitment of corals into the three experimental treatments. Error bars are SE.

(B) Mortality of coral colonies originally present in cages, partial cages, and open plots. Error bars are SE.

1062 new recruits from 26 coral genera were recorded in the three treatments at the end of the experiment (Figure 1D). Overall, coral recruitment in cages was approximately two-thirds lower (39 ± 11 recruits per 25 m^2 , compared to 108 ± 26 for partial cages and 118 ± 21 in the open plots; ANOVA, $F = 150.9$, $p < 0.001$; Figure 3A). *Acropora*, which was virtually eliminated in 1998 from the reef crest at Orpheus Island by bleaching [10], accounted for 246 of the recruits, representing 23% of the total. The dominant adult genus, *Porites*, had only two recruits in the cages, compared to 45 elsewhere (19 in partial cages, 26 in open plots; $F = 12.49$, $p = 0.003$). Similarly, *Acropora* recruits were three times more abundant in partial cages and open plots ($F = 7.7$, $p = 0.011$). In contrast, *Fungia* and *Euphyllia* were more abundant inside cages, where together they comprised 18% of the recruits compared to only 3% in each of the two other treatments. A principal component analysis summarizes the striking divergence in the composition of coral recruits in cages compared to partial cages or open plots (Figure 4). Recruit assemblages in the partial cages and open plots were indistinguishable.

The suppression of coral recruitment inside cages is unlikely to have been an experimental artifact for two reasons. First, the considerable size of the cages and

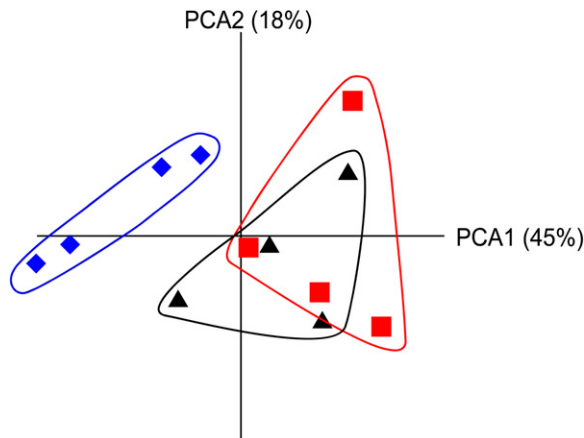


Figure 4. A Principal Component Analysis Showing the Divergent Coral Assemblages in Cages versus Other Experimental Treatments. Cages are colored blue, partial cages are colored red, and open plots are colored black. Each symbol represents one of the $4 \times 25 \text{ m}^2$ replicates in each experimental treatment. The first two axes explain 63% of the variation among the 12 experimental replicates.

the absence of a roof minimized caging effects (e.g., because of reduced water flow or shading from the cage structure). Light levels in the cages supported luxuriant algal growth, and macroalgae and juvenile fishes recruited in great numbers into them. Second, the partial-cage treatment did not show an intermediate reduction in numbers of newly recruited corals (Figure 3B). Juvenile *Fungia* and *Euphyllia* (and the coralline alga, *Mesophyllum purpurescens*) are normally found in deeper water and on shaded vertical surfaces and are rare on shallow reef crests. Consequently, the divergent response by juvenile corals among the experimental treatments (Figure 4) is more likely to reflect a range of tolerances to shading by the dense stands of *Sargassum* than differences among experimental treatments in the rate of delivery of larvae by currents.

Mortality rates of older coral colonies, which had survived bleaching and were already established when the experiment began, were more than double in the cages (24.2% after 30 months compared to 9.8% for partial cages and 11.3% for open plots (Figure 3B; RM-ANOVA, $F = 4.29$, $p < 0.05$). Recruitment was insufficient to counter these losses in the cages, where the total number of coral colonies decreased by an average of 72 ± 32 per 25 m^2 (a 26% decline). In contrast, counts of corals increased by 43 ± 21 (16%) and 39 ± 24 (14%) per 25 m^2 in partial cages and open plots, respectively. In addition to changes in mortality of corals, we also recorded significant differences in sublethal indices of coral condition attributable to indirect impacts of herbivorous fishes (see Supplemental Data).

Conclusions

Implications for Coral-Reef Management

The spatial and temporal scales of our experiment (300 m^2 , 30 months) was sufficiently large that we successfully generated a phase shift to macroalgal dominance. The increased numbers of small fishes inside

the cages may be due partially to reduced rates of predation or to the enhanced settlement and migration of juveniles into the dense algal canopies that formed after the exclusion of large roving herbivores. Ironically, the small herbivores and detritivores that dominated the cages may have promoted blooms of fleshy seaweeds by removing filamentous epiphytes and sediment from the surfaces of macroalgae that were too large or well-defended for them to consume. These findings provide robust experimental evidence for trophic cascades or top-down control—changes in the structure of food-webs and species composition (e.g., enhanced recruitment of fishes and increased algal biomass) due to reduction in the abundance of medium and large fishes [18, 20, 22]. After 30 months, we removed the mesh from cages to allow entry once more to roving herbivores and predators. Cover of macroalgae in the newly accessible cages declined rapidly because of intense grazing, from 53% to 13% after 12 days and to approximately 0 after 30 days [23]. Juvenile fishes in the former cages declined much faster than the algae, by 98% after only 3 days, presumably because of predation. In the Caribbean, Mumby et al. [24] tested the potential importance of marine no-take areas for safeguarding parrotfish and their ability to control blooms of turf and fleshy seaweeds. They found a greater biomass of parrotfishes and less macroalgae inside a no-take reserve, consistent with the experimental results presented here (although the abundance of adult and juvenile corals was not reported). Our large-scale experiment provides direct evidence that overfishing of herbivores affects more than just the targeted stocks and can also influence the resilience of coral reefs to climate change.

Process-oriented research, exemplified by the experimental manipulations presented here, provides a more rigorous basis for coral-reef management than conventional approaches. In particular, the current focus on descriptive mapping and monitoring of reefs needs to be substantially broadened for better understanding of critical processes that underlie resilience. Our results demonstrate that loss of coral-reef resilience can be readily quantified with several metrics (e.g., depletion of key functional groups of fishes, reduced rates of coral recruitment and population regeneration, sublethal impacts, etc.). Furthermore, our findings show that local management efforts in support of resilience can afford significant protection against threats that are much larger in scale. Preventing coral bleaching is not a tractable management goal at meaningful spatial or temporal scales, and a long-term solution will require global reductions of greenhouse gases over decadal timeframes. On the other hand, supporting resilience in anticipation of bleaching and other recurrent disturbances can be achieved locally by changing destructive human activities (e.g., overfishing and pollution) and thereby reducing the likelihood of undesirable phase shifts. Achieving this outcome will require the linking of ecological resilience to social and governance structures and involve scientists, other stakeholders, environmental managers, and policy makers [25–26]. A resilience-based approach represents a fundamental change of focus, from reactive to proactive management, aimed at sustaining the socioeconomic and ecological value of coral reefs in an increasingly uncertain world.

Experimental Procedures

Study Site and Experimental Treatments

The fish-exclusion experiment was undertaken on the inner Great Barrier Reef, in Pioneer Bay on the leeward coast of Orpheus Island (18°36'S, 146°29'E), a high-island approximately 10 km offshore from the Australian mainland. Like many continental reefs in Australasia, the reef fauna is highly diverse, with a benthos dominated by massive and branching scleractinians and alcyonacean soft corals. The water is turbid (typical horizontal visibility is 5–8 m), and the typical tidal range is 3–3.5 m. The sheltered reef fringing the lee of the island seldom experiences breaking waves except during rare storms and cyclones. Fishing has been banned in Pioneer Bay since 1987.

The three experimental treatments were (1) four 5 × 5 m fully-meshed roofless cages for excluding all large and medium fishes (Figure 1C), (2) four partially meshed cage controls that afforded access along 50% of each perimeter to control for any effects of the caging structure, and (3) four open plots. Each of the 12 replicates was 25 m² in area. The cage and partial cage framework consisted of eight 4-m-tall vertical lengths of 50-mm-diameter tubular steel (at each corner and midway along each side), three horizontal lengths along each side at the bottom, middle, and top, and an internal cross of tubing that connected horizontally between the four middle vertical uprights. We anchored the vertical tubes by sliding them over a 2 m steel bar that was hammered halfway into the substrate and cemented in place. Eight stays were also attached to each cage to prevent them from lifting. A door to each cage (2 × 0.8 m) provided access at all tide levels. The 4 m height of the cages and partial cages obviated the need for a roof because they extended a few decimeters above water at high tide, and the base always remained submerged. The plastic mesh on cages and partial cages (1 cm² for the bottom 2 m, and 2 cm² for the top 3 m) was scrubbed every 7–10 days to prevent fouling. A weighted net sealed the bottom. After 30 months, we removed the mesh from cages and partial cages and closely followed the immediate response of fishes and macroalgae. *Diadema* sea urchins are rare at this location. Three were removed from the cages (100 m²) at the start of the experiment.

Numbers and Sizes of Herbivorous Fishes

The abundance of herbivorous fishes in each treatment was measured after 28 months with 90 hr of high-resolution remote video. In each of the 12 cages, partial cages, and open plots, five randomly placed 1 m² quadrats were censused for 90 min with remote video cameras (so that diver effects could be eliminated). Recording was undertaken within 90 min of high tide between 1000 and 1600, with randomly allocated times among treatments. Fish were identified to species, and their body lengths were recorded and converted to biomass with standard length-weight regressions.

Response of Macroalgae and Coralline Algae

Fleshy macroalgae and noncoralline crusts were identified *in situ* to genus, and their abundance in each of the 12 plots was estimated on a six-point categorical scale (0 = "absent," 1 = "rare," 2 = "uncommon," 3 = "common," 4 = "abundant," and 5 = "dominant"). A total of thirteen censuses were made, and two were made after the removal of the mesh. In addition, the percentage of macroalgal cover was measured from 16 photographic censuses (0.25 m² resolution) of 2 × 2 m quadrats located centrally within each cage, partial cage, and open plot. Abundances of crustose coralline algae were measured initially and after 26 months from photographs of 33 permanently marked 10 × 10 cm quadrats (two to four quadrats distributed among each of the 12 replicate plots). At the final census, macroalgae were first removed from the quadrats, by brushing to expose overgrown corallines, and then the quadrats were rephotographed. Samples of live and dead corallines were collected for taxonomic identification.

Responses of Corals

Coral cover, survivorship of colonies, and cover of macroalgae was estimated from digital photographs (0.25 m² resolution, 16 censuses) of 2 × 2 m areas positioned centrally within each of the 12 experimental areas. In addition, all corals greater than 1 cm in the experiment were identified (to species, where possible) and mapped

initially in September 2000 and again in April 2003, with a grid of 100 × 0.25 m² quadrats covering each of the 12 experimental plots. A comparison of the two censuses yielded data on recruitment (arrival of new colonies) and coral composition.

Coral tissue thickness, an index of biomass and physiological condition, was measured with calipers after 2 years in 64 colonies of *Porites cylindrica* from within two cages and outside. Those colonies from within cages were (1) positioned at least 10 cm away from the nearest clump of macroalgae, (2) shaded or (3) partially overgrown by macroalgae. Reproductive output of corals was measured in 90 experimental fragments of *Montipora digitata* that were placed 17 weeks before spawning outside and within two cages, the latter either positioned in the open or beneath clumps of macroalgae (principally *Padina*). After 14 weeks, fragments were collected and decalcified for an estimation of egg size, number of eggs per polyp, and number of reproductive polyps.

Supplemental Data

Supplemental Data include additional Experimental Procedures, three figures and two movies and are available with this article online at <http://www.current-biology.com/cgi/content/full/17/4/360/DC1/>.

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