

Sleeping Functional Group Drives Coral-Reef Recovery

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Summary

The world's coral reefs are in decline, with many exhibiting a phase shift from coral to macroalgal dominance [1–6]. This change is often associated with habitat loss and overharvesting of herbivorous fishes, particularly parrotfishes and surgeonfishes [6–9]. The challenge is to reverse this decline and enhance the resilience of coral-reef ecosystems [10, 11]. We demonstrate, by using a large-scale experimentally induced phase shift, that the rapid reversal from a macroalgal-dominated to a coral- and epilithic algal-dominated state was not a result of herbivory by parrotfishes or surgeonfishes. Surprisingly, phase-shift reversal was primarily driven by a single batfish species (*Platax pinnatus*), a fish previously regarded as an invertebrate feeder. The 43 herbivorous fishes in the local fauna played only a minor role, suggesting that biodiversity may not offer the protection we hoped for in complex ecosystems. Our findings highlight the dangers faced by coral reefs and other threatened complex ecosystems: Species or functional groups that prevent phase shifts may not be able to reverse phase shifts once they occur. Nevertheless, reversal is possible. The critical issue is to identify and protect those groups that underpin the resilience and regeneration of complex ecosystems.

Results and Discussion

Almost every ecosystem in the world is facing challenges from global warming, habitat modification, and overharvesting [12]. The decline in the condition of coral-reef ecosystems around the globe is well documented [1–6], with many reefs exhibiting phase shifts from coral-dominated healthy ecosystems to a degraded macroalgal-dominated state [1, 4, 5, 13]. In this world of declining biodiversity and ecosystem degradation, the most pressing challenge is, where possible, to reverse these trends and to facilitate recovery or regeneration [10, 11, 14]. With the exception of Kaneohe Bay, Hawaii [15],

there have been few documented examples of significant phase-shift reversals on coral reefs. Although it is well established that the loss of herbivores can trigger phase shifts on coral reefs [7, 8, 16], the corollary is not assured; whether the return of these herbivores can reverse the phase shifts is unknown. Here, we demonstrate that such a reversal is possible. By using a large-scale experimentally induced phase shift, we document the biological basis of rapid reversal from a macroalgal to a coral- and epilithic algal-dominated state and highlight the distinction between those fish species that are able to prevent and those that are able to reverse undesirable phase shifts.

We used a large-scale long-term exclusion experiment to simulate overfishing on the Great Barrier Reef. This triggered a phase shift from a system dominated by epilithic algae and corals to one overgrown by macroalgae and thus enabled us to directly examine the subsequent reversal after exposure to local herbivore populations. After excluding large fishes from 25 m² experimental plots for 3 years, macroalgal biomass in the two focal experimental plots increased from less than 100 g/m² to approximately 5.3 and 8.1 kg wet mass/m², respectively. In the 5 days after cage removal, the macroalgal thallus area had halved (Figure 1). After 8 weeks, macroalgal densities in experimental and control plots were indistinguishable, with virtually all macroalgae removed. Clearly, exposure to intact local herbivore fish populations (Figure 2) rapidly reversed the large-scale experimentally induced phase shift.

We documented the species responsible for this transition from macroalgal domination to epilithic algae and coral (by using remote underwater DV cameras, filming from dawn to dusk). Surprisingly, reversal of the phase shift through the direct removal of macroalgae was not a result of grazing by parrotfishes or surgeonfishes, the most abundant herbivores on reefs, nor any other of the 43 herbivorous species recorded in the vicinity. Recovery was primarily due to a single species, the batfish, *Platax pinnatus* (f. Ephippidae) (Figures 3 and 4). This species was consistently observed removing and ingesting large pieces of *Sargassum* (the dominant macroalgae) (see the Movies in Supplemental Data available with this article online). The batfish may also have contributed to algal removal by dislodging algae when feeding. This uningested material would therefore have entered the detrital food chain. *Platax* are relatively rare on the Great Barrier Reef (GBR) (with mean densities of 1.6 individuals per ha; Table S1). However, the batfish appeared to be attracted to the algal stands; the DV cameras regularly recorded one to three adult batfishes (approximately 30–40 cm total length and 2.5 kg each) feeding on the algae. Algal feeding is unusual for this species, which is usually reported to be a benthic invertebrate or plankton feeder [17], with sessile invertebrates normally predominating in its diet (Table S2).

It was particularly striking that local herbivore populations played only a limited role in the reversal because

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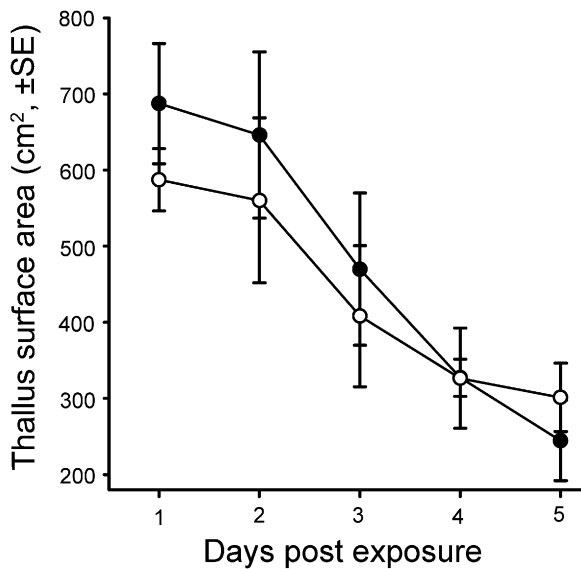


Figure 1. Rapid Reversal of an Experimentally Induced Phase Shift on a Coral Reef

After removal of 25 m² cages, fish herbivory reduced the macroalgal thallus area of a 3-year old algal stand by approximately half within 5 days. Thallus area is the mean area per 50 cm of stipe (±SEM); open and closed dots refer to the two experimental plots.

the Orpheus Island study site supports one of the world's best-protected reef fish faunas, with intact herbivore populations. It is located in the Great Barrier Reef Marine Park, where there is no fishery for herbivorous fishes, in an area that has been closed to all commercial and recreational fishing since 1987. Of the 43 herbivorous reef fish species present in the area, only two fed to any significant extent on the macroalgae, the two most abundant species, *Scarus rivulatus* and *Siganus doliatus* (Figure 3). Both species took small bites and possibly fed on epiphytic material rather than the *Sargassum* per se. The remaining species included 33 roving herbivores and comprised nine species of rabbitfishes (Siganidae), 15 parrotfishes (Labridae), seven surgeonfishes (Acanthuridae), and two rudderfish (Kyphosidae); none fed to any extent on the *Sargassum*.

The nature of the reversal in algal cover has profound implications for coral-reef management and highlights critical weaknesses in current approaches. Firstly, it reveals an unseen vulnerability based on the naïve assumption that functional groups that are believed to prevent phase shifts can also reverse phase shifts and thereby facilitate regeneration and rebuilding of ecosystems. Although the majority of herbivorous reef fishes feed on epilithic algae [18–21], it is well known that there are numerous guilds of herbivorous fishes on coral reefs [6, 9, 17, 20, 21]. However, what is most surprising is that despite more than 50 years of SCUBA-based research on coral reefs, we were totally unaware of the taxa responsible for reversing the most widely documented phase shift in reef ecosystems. Correlations between herbivorous fish densities and macroalgal densities may not be causal relationships. Parrotfishes and surgeonfishes appear to play a critical role in preventing phase shifts to macroalgae but when presented with

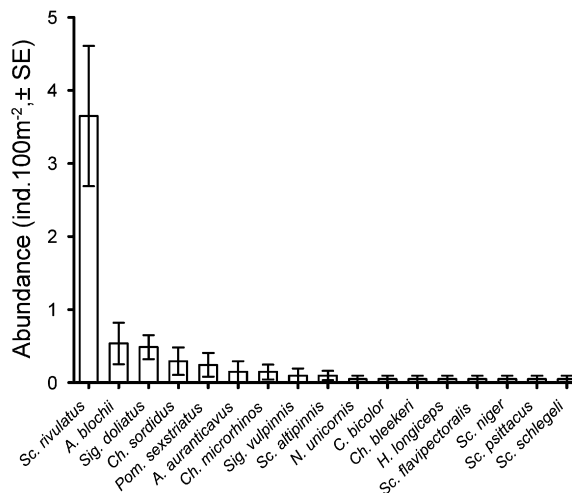


Figure 2. Densities of Nominally Herbivorous Fishes in the Study Location

Pioneer Bay, Orpheus Island, on the Great Barrier Reef has intact protected herbivorous fish populations. Species (mean density ± SEM) are as follows (from left to right): *Scarus rivulatus*, *Acanthurus blochii*, *Siganus doliatus*, *Chlorurus sordidus*, *Pomacanthus sexstriatus*, *Acanthurus auranticavus*, *Chlorurus microrhinos*, *Siganus vulpinus*, *Scarus altipinnis*, *Naso unicornis*, *Cetoscarus bicolor*, *Chlorurus bleekeri*, *Hipposcarus longiceps*, *Scarus flavipectoralis*, *Scarus niger*, *Scarus psittacus*, and *Scarus schlegelii*. *Pomacanthus sexstriatus* is provisionally included although it is likely to have been feeding predominantly on epiphytic algae and sponges. Roving herbivorous species present but not recorded in the visual censuses include the following: *Acanthurus dussumieri*, *A. grammoptilus*, *A. nigricauda*, *A. xanthopterus*; *Kyphosus cinerascens*, *K. vaigiensis*; *Bolbometopon muricatum*, *Scarus chameleon*, *Sc. dimidiatus*, *Sc. ghobban*, *Sc. quoyi*; *Siganus corallinus*, *S. canaliculatus*, *S. javus*, *S. lineatus*, *S. puellus*, *S. punctatissimus*, *S. punctatus*, and *S. spinus*.

intact stands of macroalgae, their ability to remove the algae may be limited.

Secondly, the results have implications for the presumed relationships between “herbivorous” fishes and algae on coral reefs. A rich herbivore biodiversity may not offer the protection that one might assume [22–24]. Functional redundancy may be more restricted than species richness would suggest. The fishes that are included in censuses, like the majority of herbivores in the present study, may have only a limited interaction with macroalgae. Indeed, based on current knowledge, one of the most important macroalgal feeders at this location (i.e., batfishes) would not be considered herbivores and would not be included in traditional censuses. Monitoring programmes would therefore fail to detect changes or declines in this critical functional group. This oversight could lay the foundation for an undetected loss of resilience and eventual ecological surprises as the system flips to an alternate state [6, 10, 11, 13, 25]. Likewise, inclusion experiments can tell us little about ecosystem-level interactions if the most relevant species are overlooked.

It is probable that other species play a comparable role to batfishes in other reef systems. Indeed, the species responsible for such reversals are likely to vary along many spatial and temporal scales and will, in some cases, include more traditional herbivorous species. For example, rabbitfishes, rudderfishes, nasine surgeonfishes in

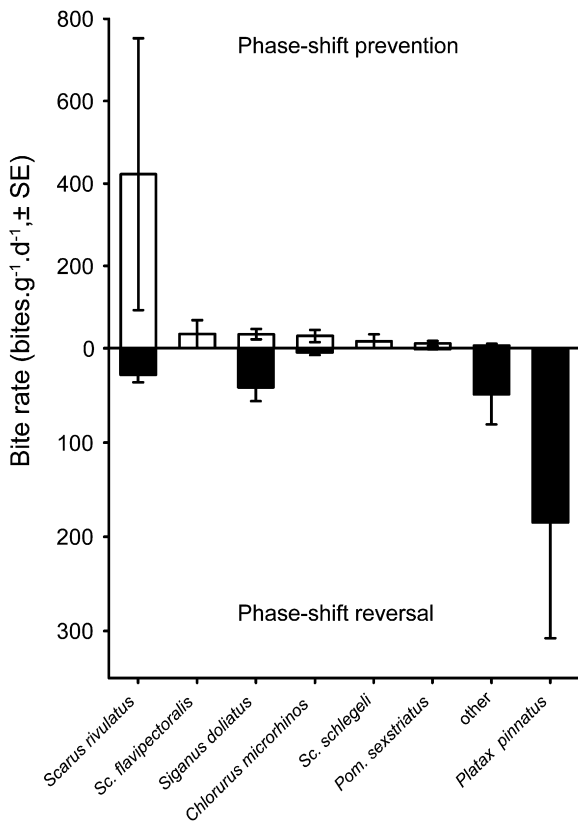


Figure 3. Patterns of Herbivory that Prevent and Reverse Algal-Coral Phase Shifts

Herbivory that prevents phase shifts (open bars) is dominated by adult parrotfishes feeding on the epilithic algal matrix. Herbivory on macroalgae during the phase-shift reversal (filled bars) is dominated by the batfish *Platax pinnatus*. In the reversal the “other” category is primarily juvenile *Scarus rivulatus* less than 20 cm and *Siganus doliatus* less than 10 cm along with 14 other roving herbivore species. Bite rates are expressed as the mean number of bites per day standardized by body mass ($g \pm SEM$).

the Indo-Pacific, and sparismatine parrotfishes in the Caribbean are likely, based on their diet, behavior, and feeding mode, to play a significant role in macroalgal to epilithic algal phase-shift reversals [9, 20, 26–28]. Although several studies have documented the removal of macroalgae by fishes in both the Indo-Pacific and Caribbean, the taxa responsible remain largely unknown [26, 29]. Clearly, our understanding of fish-algal interactions and phase shifts on coral reefs requires a re-evaluation.

The induced phase shifts in this study occurred on plots of 25 m², which were considerably larger and maintained over a longer period than in previous experiments. Previously, most large cages were less than 1 m in length and remained in place for less than 1 year [16, 29–31]. Our experimental design enabled us to evaluate the capacity of the system to remove significant stands of naturally growing algae rather than isolated transplanted pieces [32]. The estimated removal rates, even from such large stands, indicate that batfish browsing is of system-wide significance. Based on algal removal rates (700 g/m²/day = 35 kg/day from 50 m² of cages) the fish in the vicinity of the cages would be

able to remove an estimated 12,750 kg over 12 months. Compared with long-term algal-biomass accumulation (a mean algal biomass of 6.7 kg/m² after 30 months = 2.5 kg/m²/year), the total algal removal would equate to the annual biomass accumulation over 5,100 m². On this basis, batfishes in the study site would be able to clear macroalgae from the 5-m-wide reef crest for a distance of approximately 1.02 km.

The rapid removal of macroalgae from the experimental plots effectively marked the reversal of a phase shift to a macroalgal-dominated state. However, in some ways this marks only the beginning of a process of reversal. Available evidence suggests that coral growth and recruitment will be favored in the absence of macroalgae [29, 33]. However, the full expression of coral recovery will be manifest over longer time frames than the 8 weeks required for termination of the macroalgal phase and may take years or decades.

Batfishes have not previously been associated with coral-algal interactions and associated phase shifts. As such, they represent a “sleeping functional group,” i.e., a species or group of species capable of performing a particular functional role but which does so only under exceptional circumstances. *Platax* are relatively rare on the GBR and currently have no specific legislative protection. Their vulnerability to overexploitation is enhanced by their size, sensitivity to spear fishing, and propensity for recruiting in coastal or mangrove areas [17]. Indeed, the resilience of inshore GBR reefs may be closely tied to the fate of mangroves and their suitability for batfish recruitment.

Furthermore, batfishes may represent one of the last intact herbivore populations capable of reversing phase shifts on the inner GBR reefs. Other macroherbivores that are capable of removing significant quantities of macroalgae are under threat. Green turtles are one of the largest known herbivores on coral reefs and play a major role as herbivores in seagrass beds and potentially on reefs [34, 35]. Declining turtle numbers would therefore represent a serious weakening of a significant functional group and a potential loss of reef resilience. Indeed, the GBR has already effectively lost a large potential sleeping functional group, dugongs. At their high historical population levels, dugongs may have supplemented seagrasses with other marine plant resources [36, 37]. If *Platax* is the last grazer of large macroalgal stands on inshore coral reefs, the capacity of the GBR reefs to recover from a phase shift to macroalgae could be compromised. If so, it becomes imperative that phase shifts are prevented and that existing regeneration mechanisms are enhanced by the effective protection of critical functional groups.

In the Caribbean, where many coral-algal phase shifts have been documented [2–9], the importance of sleeping functional groups could be critical. Here, the reduced level of functional redundancy, the loss of turtles and other macro herbivores, and a history of human impacts [5, 6, 8] all emphasize the current vulnerability of Caribbean coral-reef ecosystems. In this system, the spadefish (*Chaetodipterus faber*, f. Ephippidae) represents a promising candidate for effective macroalgal removal and could easily surpass its Indo-Pacific congeneric counterparts. Because the spadefish grows to a larger size than most Indo-Pacific batfishes and occurs

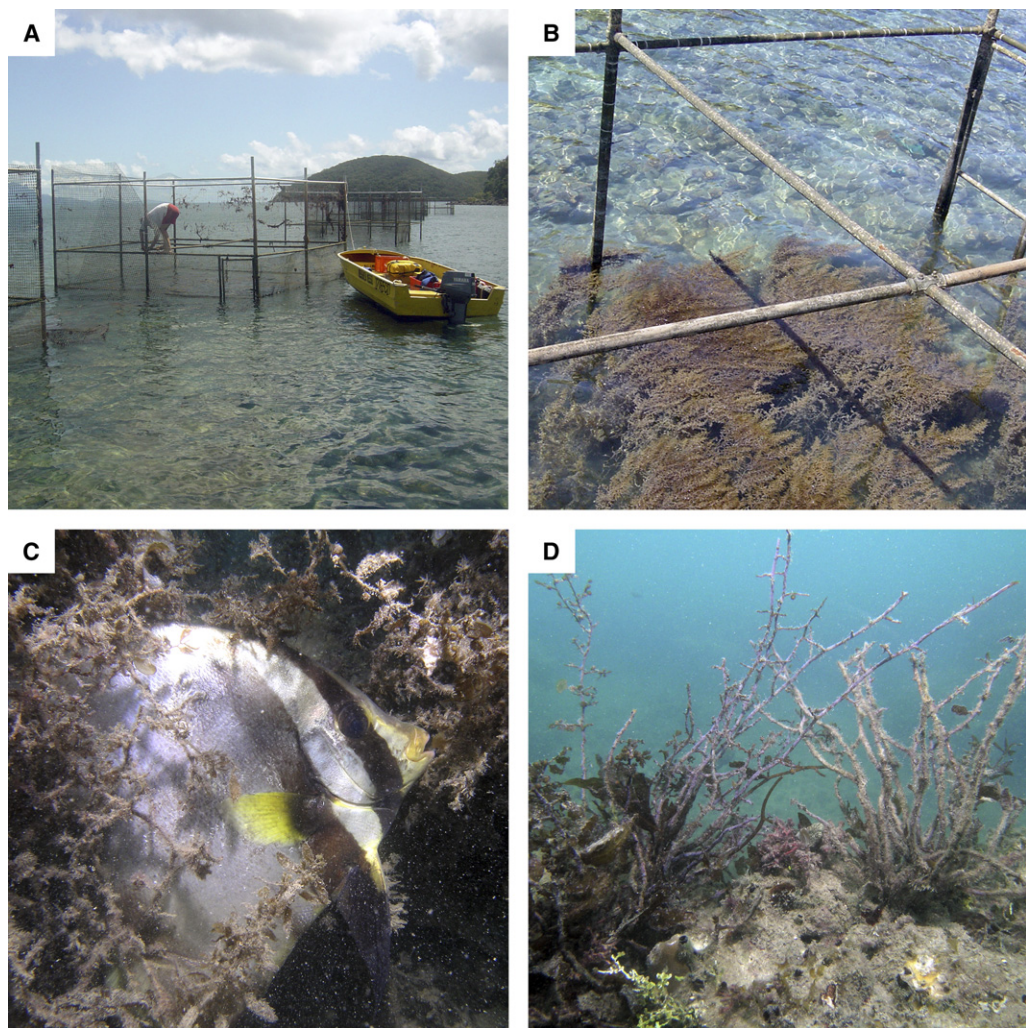


Figure 4. Rapid Reversal of an Experimentally Induced Phase Shift on a Coral Reef

- (A) Experimental cages (each 25 m²) simulate overfishing and trigger a phase shift from corals and epilithic algae to macroalgae.
(B) After 32 months, the cage mesh was removed, exposing intact macroalgal stands (approx 5 to 8 kg algae/m²) to resident herbivores.
(C) Adult *Platax pinnatus* were primarily responsible for the reversal of the phase shift.
(D) *Sargassum* showing initial signs of fish browsing.

in large schools, it may be a particularly effective sleeping functional group.

Sleeping functional groups are arguably the most difficult to detect and protect because we do not know which species are important until conditions change. It is clear that a two-pronged approach is needed for enhancing reef resilience [1, 6, 13, 38], with protection for both the species that prevent phase shifts and those that facilitate reversal and recovery. We can no longer assume that simply reintroducing or protecting the species that prevented phase shifts will result in a reversal and permit regeneration.

Experimental Procedures

The Caging Experiment

Experimental cages were located on the reef crest in Pioneer Bay, Orpheus Island in the central Great Barrier Reef (18°35'S, 146°28'E). Each cage was 25 m² in area (5 m × 5 m) and 5 m high (the top extended above high water eliminating the need for a roof). The 35 mm cage mesh simulated overfishing by excluding all roving

fish species greater than 10 cm total length but permitting access by smaller individuals. Herbivore biomass within the cages was censused with video recordings at the end of the experimental period and was seven to ten times lower than in adjacent plots. Cages were monitored and the mesh cleaned every 7–10 days for the 30-month experimental period. There were four replicate cages, half cages, and control plots. Only cages exhibited a phase shift to macroalgae. Algal growth within cages resulted from colonization and proliferation of resident algae on natural substrata. Removal of the mesh at the end of the experiment exposed a 25 m² thicket of attached macroalgae (predominantly *Sargassum*). The composition of the stand represented the product of local algal recruitment and survival in the absence of macroherbivores. Pioneer Bay is a sheltered location, and there was no evidence of algae being dislodged by the minimal physical activity of waves or currents (see the [Supplemental Data](#) for water-movement values).

Feeding Observations

To minimize observer effects, we recorded feeding activity by using four digital videos (Sony DCR-TRV950E cameras in Amphibico housings). After 3 years, the cage mesh was removed at dusk (18:20–19:00), and video recording initiated before dawn the following day. The two cages with the highest algal biomass (approximately

5–8 kg/m² wet weight) were selected for detailed observations. Within each cage, a random 1 m² area was censused each day with paired video cameras (to record the full >2 m length of the algal thallus) filming continuously from dawn (05:20) to dusk (18:40), with obligatory tape changes every 90 min. All tapes were analyzed (13 hr 20 min per day × 5 days, × 2 sites, and × 2 cameras per site; a total of 267 hr) recording the species and sizes of fishes present as well as the location and number of bites taken. Background levels of herbivory, which prevented phase shifts, were recorded in adjacent control plots with the same sampling design as above (but because no macroalgae were present, a single camera was used to record the m² area). Because bite size is scaled to body mass, the estimated impact of feeding is standardized by the estimated biomass of each individual (number of bites × body mass in g). The biomass of each fish was estimated with published length-weight relationships of the form $W = aL^b$ [39, 40]. W is the weight in grams, L is the total length in cm, and a and b are parameters estimated by least-squares regression. Length-weight relationships were obtained for several taxa based on specimens from the area. These relationships did not differ significantly from the published values so for consistency, published values were used throughout.

Algal Area, Volume, and Mass

To estimate the change in algal thallus surface area, we acquired digital images of the quadrats directly from DV tapes (used for fish-feeding analyses above). Images were captured for both cages at approximately the same time (06:30–07:30) for the 5 days after the removal of the cage mesh. The height and surface area of each clearly visible *Sargassum* thallus within each quadrat was calculated with the image-analysis software UTHSCSA ImageTool v3.0. For comparative purposes, the surface area of each thallus was standardized per 50 cm thallus height. Estimated algal removal rates are conservative in that we express only decreases in area; the 3D loss of material and decrease in mass would be proportionally much greater. Total initial algal biomass was estimated based on a length-weight regression for *Sargassum* growing in the local region (mass [g] = 1.7 e-5 × length [cm]^{3.0739}; $r^2 = 0.9179$).

Herbivorous Fish Densities

Herbivorous fish densities in the vicinity of the experimental plots were recorded with eight 5 min stratified visual censuses [41]. Fishes included in these censuses were those species that remove algal material when feeding. Although detritus may be the major nutritional constituent in the diet of many of these fishes [20, 21], from an ecosystem perspective algal removal remains the critical factor [42, 43]. Quantification was limited to roving herbivorous species; benthic territorial herbivores did not bite the macroalgae.

Supplemental Data

Supplemental Data include Experimental Procedures, two tables, and two movies and can be found with this article online at <http://www.current-biology.com/cgi/content/full/16/24/2434/DC1/>.

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