Recovery of an Isolated Coral Reef System Following Severe Disturbance

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and aversive stimuli (23). The hypothesis can be formulated that the floral electric field reinforces the effectiveness of other floral cues. If true, an electric cue paired with a color cue should produce an enhanced learning outcome equivalent to that obtained with the test using color and scent. Differential conditioning was used to test this hypothesis. The same two green target hues were used as in (23), but olfactory cues were replaced with a patterned electric field (Fig. 3C). Bees were trained to discriminate between E-flowers of hue 120° HSB (hue, saturation, brightness) which offered a sucrose reward, and E-flowers of hue 140° HSB, which provided an aversive quinine solution (Fig. 4A). Bees learned to discriminate between the rewarding and aversive chargeless E-flowers either using color information alone ($n = 16$) or in combination with the patterned E-field ($n = 18$) (Fig. 4A). When learning color on its own, discrimination to 80% success (i.e., 8 out of the last 10 choices correct) took 35 ± 3 visits. When combined with the E-field pattern, the number of visits required was significantly reduced to 24 ± 3 ($T_{2\text{-sample; unequal}} = 2.86$, $P = 0.008$) (Fig. 4A). This demonstrates that the combination of two cues, E-field and hue, enhances the bee's ability to discriminate.

Our results show that electric field constitutes a floral cue. Contributing to a varied floral display aimed at pollinator senses, electric fields act to improve both speed and accuracy with which bees learn and discriminate rewarding resources. As such, electric field sensing constitutes a potentially important sensory modality, which should be considered alongside vision

and olfaction. The ubiquity of electric fields in nature and their integration into the bees' sensory ecology suggest that E-fields play a thus far unappreciated role in plant-insect interactions. The present study raises the possibility of reciprocal information transfer between plants and pollinators at time scales of milliseconds to seconds, much faster than previously described alterations in floral scent, color, or humidity (4, 18, 19). The remarkably accurate discrimination and learning of color patterns by bees was revealed by both laboratory and field training experiments (19, 21–23). Similarly, the present laboratory study reveals that floral electric fields occur in patterns and that they can be perceived. Hence, our study provides a framework for exploring the function and adaptive value of the perception of weak electric fields by bees in nature.

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Recovery of an Isolated Coral Reef System Following Severe Disturbance

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Coral reef recovery from major disturbance is hypothesized to depend on the arrival of propagules from nearby undisturbed reefs. Therefore, reefs isolated by distance or current patterns are thought to be highly vulnerable to catastrophic disturbance. We found that on an isolated reef system in north Western Australia, coral cover increased from 9% to 44% within 12 years of a coral bleaching event, despite a 94% reduction in larval supply for 6 years after the bleaching. The initial increase in coral cover was the result of high rates of growth and survival of remnant colonies, followed by a rapid increase in juvenile recruitment as colonies matured. We show that isolated reefs can recover from major disturbance, and that the benefits of their isolation from chronic anthropogenic pressures can outweigh the costs of limited connectivity.

Coral reefs are dynamic ecosystems periodically subjected to severe disturbances, such as cyclones, from which they typically recover at scales of one to two decades (1, 2). Today, this recovery is undermined by increasing anthropogenic pressures leading to global declines in coral cover (3, 4) and diversity (5, 6). Understanding the global degradation of coral reef ecosystems requires long-term data

on population and community dynamics, especially demographic processes (7–9). However, the rarity of such data has precluded a thorough assessment of the future of coral reef ecosystems in the IPCC report on climate change (10, 11), and current knowledge is mostly derived from studies of reef degradation (9, 12) rather than reef recovery. Here, we document the recovery of coral assemblages at Australia's largest oceanic reef

system, where changes in assemblage structure and key demographic parameters were quantified for 16 years, through a regime of disturbances beginning with a catastrophic mass bleaching event in 1998.

The Scott system of reefs is surrounded by oceanic waters on the edge of Western Australia's continental shelf. It is more than 250 km from the mainland and other reefs in the region, and more than 1000 km from a major center of urbanization (fig. S1). There is little fishing pressure at the reefs, apart from the harvesting of sea cucumber, trochus, and shark fin by Indonesian islanders using traditional fishing methods for more than 300 years (13, 14). Such oceanic reef systems may provide a critical refuge for coral reef assemblages because they are far removed from most direct anthropogenic pressures. Conversely, isolation and a consequent lack of connectivity may make such systems

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more susceptible to disturbances. Without an external supply of recruits, it is assumed that reefs will be very slow to recover from severe disturbance (15–18). However, the sensitivity of recovery to variation in larval supply and post-recruitment processes has not been investigated for a coral reef system through a full cycle of impact and recovery.

Extreme water temperatures leading to mass coral bleaching occurred in all regions of the world in 1998 (19), and the Scott Reef system was severely affected. Seawater temperatures at Scott Reef rose rapidly during February 1998 and remained above average for the next 2 months (fig. S2). The NOAA satellite estimate of the cumulative degree heating weeks, a measure of the severity of the temperature anomaly, was 13.3°C; this remains the most extreme temperature anomaly recorded at Scott Reef (20). Catastrophic mortality of corals across the entire reef system occurred over the next 6 months

to depths of 20 m. Along permanent transects at replicate sites across Scott Reef (13), between 80 and 90% of live coral was lost from the reef crest (~3 m) and reef slope (~9 m), and almost 70% from the upper reef slope (~6 m) (fig. S3A). On the reef slope, the coral assemblage changed markedly and the number of genera decreased by half (Fig. 1 and fig. S3). The reductions in coral cover were followed by recruitment failure to settlement tiles (21), which were redeployed (n = 108) at the permanent transects on the reef slope (13). In the years before the bleaching, the total number of recruits was between 2600 and 5600; this had decreased to zero a year later, clearly indicating that larvae were locally derived. For 6 years, recruitment rates were <6% of those prior to the disturbance (Fig. 2), and initial increases in coral cover were driven by the growth of remnant corals. On the basis of these rates of change, recovery was projected to take decades. Within

12 years, however, coral cover, recruitment, generic diversity, and community structure were again similar to the prebleaching years (Figs. 1 and 2 and fig. S3).

The decline in recruitment after the mass mortality of corals in 1998 was caused by the drastic reduction in local brood stock (Fig. 3) and a negligible supply of larvae from neighboring reefs hundreds of kilometers away (22, 23). However, no phase shift to macroalgae was observed; the substrata made available by the death of corals was colonized by fine turfing and coralline algae (Fig. 1) and not by macroalgae, sponges, or other organisms that can exclude and outcompete corals (24, 25). The already high densities of herbivorous fishes also increased after the loss of coral (Fig. 1), probably in response to the changes in turfing algae (26); this finding suggests a surplus grazing capacity within the system that assisted subsequent coral recruitment and survival (27). Consequently, a high proportion of the coral larvae were produced locally, settled, and survived. The
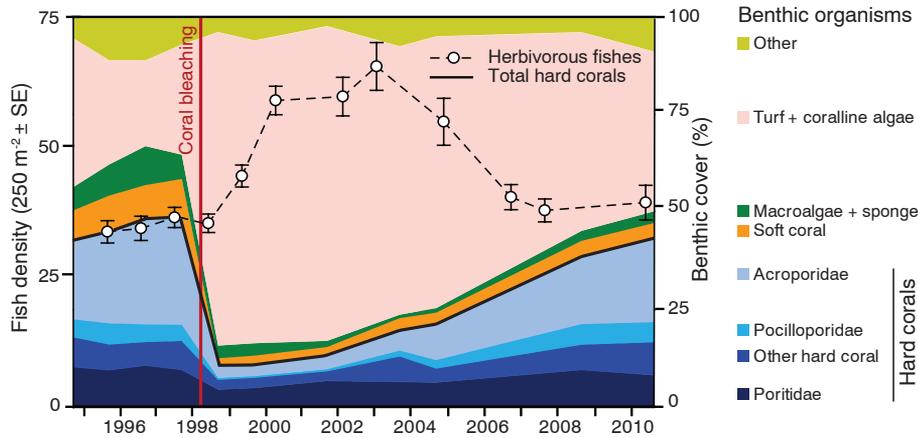
Fig. 1. Temporal dynamics in benthic communities on the reef slope at Scott Reef. Marked declines in the cover of corals (especially Acroporidae) followed the mass coral bleaching in March 1998. There was a corresponding increase in the cover of fine turfing and coralline algae, but the cover of sponges, macroalgae, and other benthic organisms remained low. The mean (±SE) density of herbivorous fishes increased for several years after the mass bleaching event. Coral assemblages had mostly recovered by 2010, despite two cyclones (2004 and 2007), an outbreak of disease (2009), and a moderate bleaching event (2010).

Fig. 2. Stock-recruitment relationship for corals on the reef slope at Scott Reef. The mass bleaching in 1998 caused an 80% decline in coral cover (mean percent ± SE) and a 94% decline in recruitment (mean number per tile ± SE) of the dominant coral taxa, the genus *Acropora*, over 6 years (note axis break for recruit density; recruitment was not measured in 2007). A decade after the mass bleaching, cover and recruitment were similar to or higher than before the disturbance.
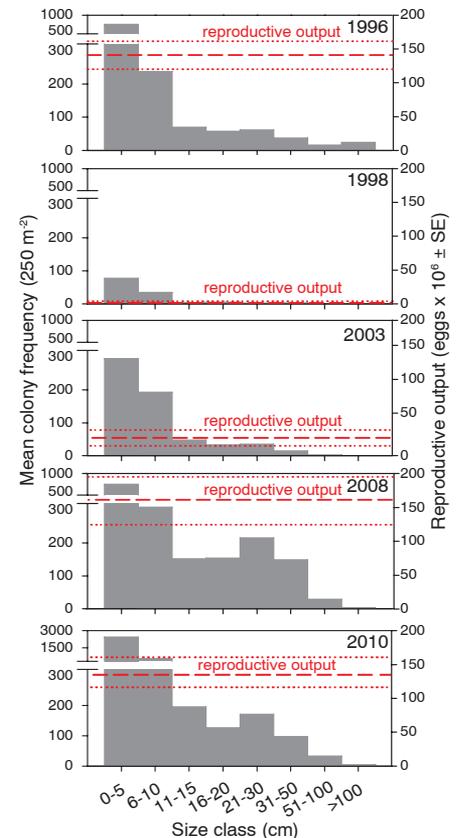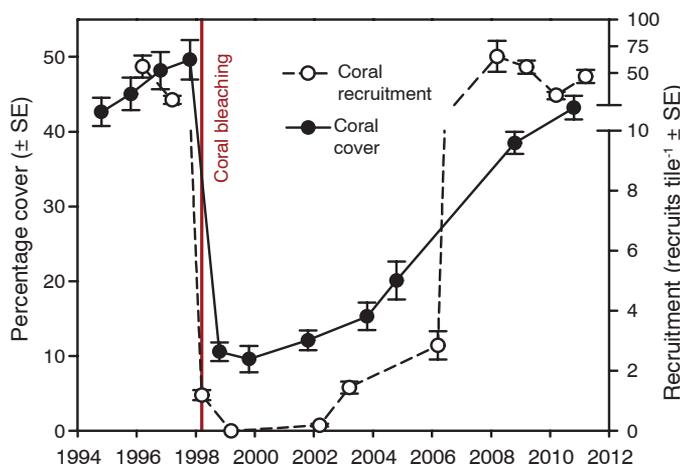

Fig. 3. Temporal dynamics in size structure and reproductive output of *Acropora* on the reef slope at Scott Reef. The mean reproductive output (solid red line) and SE (dashed red lines) were calculated from the assemblage size structure and size-specific fecundity of the most common species, *A. spicifera*. In 2008, a decade after the mass bleaching, the reproductive output was similar to before the disturbance, coinciding with the rapid increase in coral recruitment (Fig. 2).

mean survival of recruits (<5 cm; n = 1281) of branching (*Acropora*) and massive (*Goniastrea*) corals during the recovery period (*13*) ranged from 83 to 93% each year (fig. S4), which is far higher than the <50% survival of recruits on reefs experiencing chronic pressures (*28*, *29*). Indeed, the mean survival of all (n = 5333) colonies was consistently higher than 80% each year, apart from the lower survival (>53% year^{-1}) of some larger (>15 cm) branching corals at sites exposed to cyclonic waves in 2007 (fig. S4). High survival and growth resulted in rapid rates of transition through increasing colony size classes, with corresponding increases in brood stock and reproductive output (*13*) (Fig. 3). Reproductive output and recruitment were similar to predisturbance levels within a decade of the bleaching, and 2 years later, coral cover and community structure had also recovered.

The recovery of corals at Scott Reef after the 1998 mass bleaching may have been even faster if not for a series of more moderate disturbances, including two cyclones, an outbreak of disease, and a second bleaching. This demonstrates that even coral reefs with a negligible supply of larvae from outside can recover relatively quickly from disturbances in the absence of chronic human pressures. Other ecosystems have displayed a similar resilience when environmental conditions were not fundamentally altered by human activities (*30*). Our results suggest that addressing local pressures, such as pollution and overfishing, is as important to the recovery of coral reefs as the establishment of networks of marine protected areas (MPAs). Managing local pressures to promote resilience will be critical to preventing the global degradation of coral reefs, with climate change likely to cause additional severe disturbances in the near future.

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Mechanism-Based Covalent Neuraminidase Inhibitors with Broad-Spectrum Influenza Antiviral Activity

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Influenza antiviral agents play important roles in modulating disease severity and in controlling pandemics while vaccines are prepared, but the development of resistance to agents like the commonly used neuraminidase inhibitor oseltamivir may limit their future utility. We report here on a new class of specific, mechanism-based anti-influenza drugs that function through the formation of a stabilized covalent intermediate in the influenza neuraminidase enzyme, and we confirm this mode of action with structural and mechanistic studies. These compounds function in cell-based assays and in animal models, with efficacies comparable to that of the neuraminidase inhibitor zanamivir and with broad-spectrum activity against drug-resistant strains in vitro. The similarity of their structure to that of the natural substrate and their mechanism-based design make these attractive antiviral candidates.

The envelope of the influenza virus contains two immunodominant glycoproteins, hemagglutinin (HA) and neuraminidase (NA), that play key roles in viral infection and spread. HA effects attachment of the virus to the host cell through its interaction with surface sialic acids, thereby initiating entry. Once the virus has replicated, the NA cleaves sialic acids from the viral and cell surfaces, allowing the virus progeny to spread to uninfected cells. On the basis of the notion that potent and specific viral NA inhibitors should function to reduce viral spread, structure-based inhibitor design programs have

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