Coral reef disturbance and resilience in a human-dominated environment

Magnus Nyström, Carl Folke and Fredrik Moberg

Facing a human-dominated world, ecologists are now reconsidering the role of disturbance for coral reef ecosystem dynamics. Human activities alter the natural disturbance regimes of coral reefs by transforming pulse events into persistent disturbance or even chronic stress, by introducing new disturbance, or by suppressing or removing disturbance. Adding these alterations to natural disturbance regimes will probably result in unknown synergistic effects. Simultaneously, humans are altering the capacity of reefs to cope with disturbance (e.g. by habitat fragmentation and reduction of functional diversity), which further exacerbates the effects of altered disturbance regimes. A disturbance that previously triggered the renewal and development of reefs might, under such circumstances, become an obstacle to development. The implications of these changes for reef-associated human activities, such as fishing and tourism, can be substantial.

Magnus Nyström, Carl Folke and Fredrik Moberg are at the Dept of Systems Ecology, Stockholm University, S-106 91, Stockholm, Sweden (magnusn@system.ecology.su.se; calle@system.ecology.su.se; fredrikm@system.ecology.su.se).

Early studies of coral reef ecology were generally limited to reefs in clear waters far from human or continental influences[1]. The typical coral reef was often described as a diversity oasis in an oceanic desert, with the prevailing opinion that reefs were closed, fragile climax systems found in areas with only small environmental fluctuations[2]. Over time, this view changed and coral reefs are now seen as dynamic systems subject to natural disturbances. Disturbance at an intermediate level has been suggested to be important for the high species diversity of reefs[3] and much research has focused on the ability of reefs to recover to their original state – the state that existed before disturbance[4]. During the past few decades, not only has the research experienced a process of change, but also the nature of disturbances themselves and the ability of many reefs to recover from them have changed[5,6]. A major contribution to this change is the increased human dominance of ecosystems[7]. In addition to human use (e.g. fishing and recreation) and abuse (e.g. destructive fishing and uncontrolled tourism), coral reefs have also become the passive receivers of environmental impacts caused by numerous local decisions taken by humans elsewhere, exemplified by global warming, eutrophication, overfishing, pollution and land-use change[5,6]. Therefore, the ability of coral reefs to return to the state prior to the disturbance should no longer be taken for granted[8,9]. Recent research has reconsidered the role of disturbance and has focused on coral reefs as dynamic ecosystems with multiple stable states[10–12].

Humans alter the natural disturbance regime of coral reefs

The disturbance regime

Coral reefs have been subjected to a wide spectrum of disturbances throughout their geological history and there have been recurrent global mass extinctions[13]. Consequently, it has been argued that present reef ecosystems are a product of only the past 45–50 million years of evolution[14]. During this period, coral reef disturbances have ranged from frequent minor pulses, such as grazing and predation, to large infrequent events, such as peaks of coral predator populations, hurricanes, and sea level and temperature changes[2] (Table 1). This dynamic set of interacting disturbances, occurring with different magnitude, duration, frequency and spatial distribution, is referred to as the natural disturbance regime of coral reefs. The effects of disturbance on corals and other reef-associated organisms are related to physical features, such as the location of the reef, its depth, local geography, topography, and other characteristics (including the morphology, behavior and life histories of reef organisms)[5]. Coral reef organisms have adapted and evolved within this spectrum of disturbances[13]. Although disturbance is detrimental to individual reef organisms, new substratum becomes available at various temporal and spatial scales[3]; this opens up patches of opportunity for renewal, development of the reef and for evolution[15]. The disturbance regime has been important for the development of species diversity, community structure and dynamics of coral reefs[14,16].

Human-altered disturbance

Recently, there has been an increasing awareness that humans can alter the temporal and spatial scales of natural disturbance regimes, and that this might affect coral reefs and their potential for recovery following disturbance[6,13,17,18]. In some cases, there is a rather clear-cut relationship between an altered disturbance regime and its human source, such as the clearing of coastal forests, which increases suspended sediments and nutrients in terrestrial runoff, causing direct and indirect effects on algal and coral growth and competition[12]. Moreover, logging activity can prolong sedimentation, transforming a short pulse disturbance into a more persistent disturbance. Even a modest increase in sedimentation might, in the long term, lead to changes in community structure in response to the sublethal stress on reef-building corals. Rejection of sediment requires energy, which increases the metabolic demands on the corals. Increased sedimentation also leads to increased water turbidity, allowing less sunlight for photosynthesis in the unicellular symbiont, zooxanthellae. This implies that less energy will be available for coral growth, reproduction and competition[19].

In other situations, the source is more diffuse, thus leading to debates on whether the disturbance is natural or human-induced. This is the case for the proposed relationship between persistent harvesting pressure on

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Table 1. The natural disturbance regime of coral reefs[a]

Process	Spatial extent	Frequency	Duration
Predation and grazing	1–10 cm	Weeks to months	Minutes to days
Coral collapse (bioerosion)	1 m	Months to years	Days to weeks
Bleaching or disease of individual corals	1 m	Months to years	Days to weeks
Storms	1–100 km	Weeks to years	Days
Hurricanes	10–1000 km	Months to decades	Days
Mass bleaching	10–1000 km	Years to decades	Weeks to months
Crown-of-thorns outbreaks	10–1000 km	Years to decades	Month to years
Epidemic disease	10–1000 km	Months to century	Years
Sea-level or temperature change	Global	10^4–10^5 years	10^3–10^4 years

[a]Data adapted from Ref. 50.

predator and grazing fish, and the increased frequency of outbreaks of the coral-eating crown-of-thorns starfish (*Acanthaster planci*)[20] and the rock-boring sea urchin (*Echinometra mathaei*)[21]. It has also been suggested that human-induced eutrophication might cause more frequent outbreaks of the crown-of-thorns starfish[20], as well as diseases such as black-band disease[22].

Impacts on a regional level might be generated when several local, but widely distributed, disturbances interact[13]. It then becomes even more difficult to trace the origin of the disturbances, as illustrated by a frequently cited case where Caribbean coral reefs shifted from coral to algal dominance as a result of a combination of overfishing, eutrophication, hurricanes and diseases[12,17,23,24] (Box 1; Fig. 1).

Another debated issue is the role of human activity in the observed increase in mass-bleaching events, as hypothesized by Hoegh-Guldberg[18] among others. He predicted that global warming will increase the frequency of mass bleaching of the coral reefs of the world, and that it will occur annually in Southeast Asia and the Caribbean by the year 2020, in the Great Barrier Reef between the year 2030 and 2040, and in the central Pacific by the year 2040 (Box 2).

Chronic disturbance, synergistic effects and recovery

A major difference between many human-induced and natural disturbances is their persistence. Natural disturbances tend to occur in a pulsed manner[9] (e.g. hurricanes and coral predator outbreaks), whereas human-induced disturbances often appear in a more persistent manner and slowly accumulate (e.g. nutrient enrichment and pollution), or occur so frequently that there is little time for recovery (e.g. high fishing pressure)[9,12,25]. Even a low level of such chronic background stress can have severe impacts on a coral reef ecosystem over time, in terms of decreased reproduction and growth rates, and impaired defense mechanisms of corals against predators, competitors and diseases[26,27]. The process of recovery following natural disturbances is reduced further by such background stress. For example, it has been found that after an extreme low-tide event, recovery of reefs chronically impacted by oil spills is much slower than that of nearby unpolluted reefs[28].

In addition, humans generate toxic substances that might further inhibit recovery by interfering with the chemical signals required for reproductive synchrony, metamorphosis and settlement[19]. Such substances often have no equivalent in nature and reef organisms are thus poorly adapted to withstand them. Adaptations to large-scale infrequent disturbances are also few, because organisms tend not to experience a sufficiently strong selective pressure to resist such infrequent events[29]. In addition, large-scale disturbances, such as volcanic eruptions, earthquakes and hurricanes, tend to alter currents, reef topography and substratum availability[30]. These factors can prevent larval settlement and survival, thus increasing the time for coral re-establishment[31].

The timing of disturbance is also important. If reefs are affected during crucial periods, such as during coral spawning events, dispersal or settlement of coral larvae, the impact of the disturbance is likely to be enhanced. For example, coral spawning often occurs during the rainy season when coastal pollution generally reaches its peak owing to increased land runoff[26].

Hence, the natural disturbance regime contributes to the dynamic development of coral reefs. However, humans have altered this disturbance regime by introducing new disturbances and by changing natural disturbances. The latter includes human activities leading to the transformation of pulse events into persistent disturbance or even chronic stress, and also the suppression or removal of disturbances essential for maintaining natural dynamics of coral reefs[32] (e.g. loss of grazing due to overfishing). The combination of these impacts might generate compounded perturbations[17] unfamiliar to most coral reef organisms, leading to unpredictable synergistic effects and ecological surprises[5,15,25].

Box 1. Phase shift in Caribbean coral reefs

The coral reefs in the Caribbean region have undergone a dramatic transition over the past two to three decades, from hard coral to fleshy algae dominance[12,23,41]. The factors behind this change are not completely understood but it reflects a combination of natural (hurricanes and disease) and anthropogenic (overfishing and nutrient increase) disturbances acting in synergy. By the late 1960s, fish biomass had been heavily reduced, and by the late 1970s the reefs around Jamaica were extensively damaged, resulting from direct and indirect effects of overfishing[23]. Because large predatory fish were continuously overfished, herbivorous fish became the new target species. When the number of herbivorous fish declined, the sea urchin *Diadema antillarium* was able to increase in abundance, because the two groups shared the same algal resources[23]. *Diadema* subsequently became the keystone herbivore. In 1981, Hurricane Allen struck the area and most of the branching coral species were killed or damaged, resulting in new open substratum becoming available for colonization by fast growing algae. Despite high levels of nutrients, the density of benthic algae was kept low by the efficient grazing *Diadema*, and coral recolonization took place. However, in 1982 and 1983, the sea urchin population suffered from a species-specific pathogen that reduced the population by 99% in some areas. Because all major grazers were then low in numbers, they were not able to prevent the establishment of algae, resulting in a dramatic change in the abundance ratio between coral and benthic algae[10,12]. Brown fleshy algae became overwhelmingly abundant and prevented coral larvae settlement. Even large old coral colonies were out-competed by the fast growing macroalgae. This case demonstrates how the loss of diversity within the functional group of herbivores resulted in reduced resilience. A disturbance that could previously be buffered by a diverse functional group of herbivores, became the trigger that caused an ecosystem with reduced resilience to shift from a coral-dominated state to one dominated by algae. The extent to which this phase shift is irreversible is still unclear.

Humans alter the capacity of reefs to cope with disturbance

Ecosystem resilience and disturbance

The capacity of ecosystems to cope with disturbance is determined by characteristics such as genetic variability within populations, diversity within and among functional groups, and variability and connectedness of habitats[33,34]. It has been suggested that in spite of increasing human influence, reef scientists have often ignored anthropogenic effects or worked on those rare reefs still free of people[1]. Hence, the literature dealing with the potential for coral reef ecosystem recovery has generally focused on rates of recovery following natural disturbances, rather than tackling the question of whether recovery will occur at all. In the 1970s and early 1980s, several coral reef researchers argued that human influences could prolong recovery[4,28], but it was implicitly assumed that eventually recovery to the former state would occur.

In recent years, many ecologists have reconsidered the role of disturbance in the context of complex systems[15,35]. A new understanding of ecosystem dynamics has developed that recognizes multiple-equilibria, nonlinearity and threshold effects[11,36], vividly portrayed as phase shifts in the coral reef literature[10,23].

These two different ways of interpreting ecosystem development have resulted in two definitions of resilience. The traditional definition and most widespread usage of the resilience concept concentrates on stability near a single equilibrium state, where resistance to disturbance and the speed of return to equilibrium is emphasized. The second definition focuses on ecosystems in a dynamic, non-equilibrium environment with multiple stable states, where phase shifts might occur (Fig. 2). This definition is consistent with 'ecosystem resilience' as proposed by Holling[15,32], reflecting the magnitude of disturbance that can be absorbed by a system before it shifts from one stable state (or stability domain) to another[15].

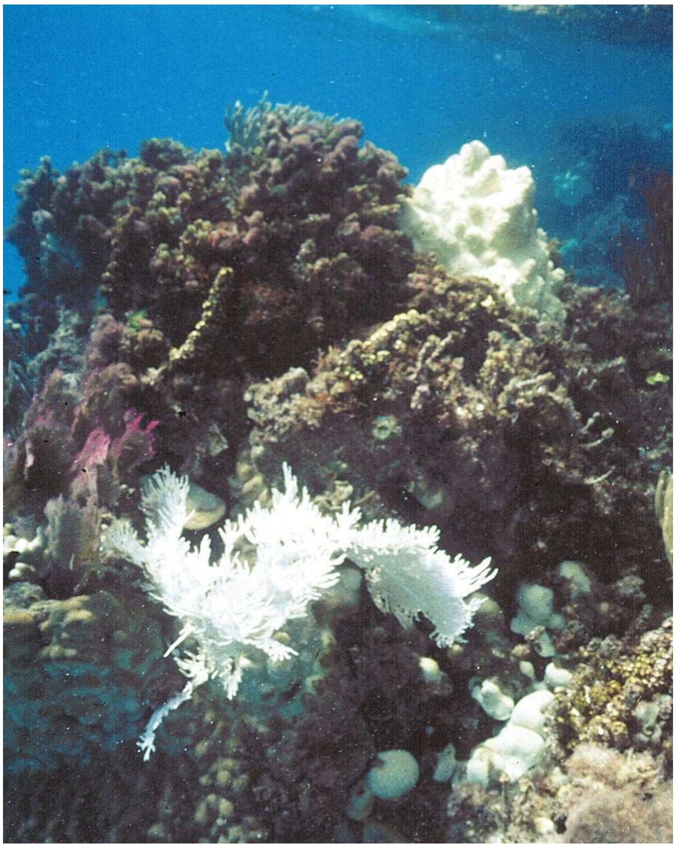

Fig. 1. A patch reef dominated by brown fleshy algae (e.g. *Turbinaria* spp. and *Sargassum* spp.) during the extensive bleaching event in 1998 at Glovers Reef Atoll, Belize. Photo by I. Nordemar.

The distribution, abundance and dynamic interactions of species, at several spatial and temporal scales, play an important role in ecosystem resilience following disturbance[37,38]. After disturbance, new successional pathways become available, allowing chance events and new species compositions and interactions to define the equilibrium state. The direction of ecosystem development will depend on which sources of resilience are present for self-organization[36]. Functional diversity, the existence of species that fill similar ecological roles, is important in this context[39]. It provides potential alternative ways to maintain key-functions of the ecosystem in the face of change[34,35,37]. For example, high species diversity within the functional group of herbivores increases the probability that algal grazing after disturbance will remain sufficiently intense to maintain the substrate in a suitable state for coral larvae to settle[23,33]. Following large-scale destruction and extensive mortality within a reef, the relative dependency on external sources for ecosystem resilience will increase. Water currents contribute to resilience by carrying coral and fish larvae from surrounding areas to damaged reefs[40]. The distance to the source reef will influence the species composition after disturbance because dispersal is a function of the swimming capabilities of adults and reproduction strategies among corals (e.g. the release of fully developed larvae versus the release of gametes).

The concept of ecosystem resilience thus captures the ability to resist, reorganize and re-establish from disturbance, as well as maintaining a diversity of options for

Box 2. Coral bleaching and future effects

Corals obtain most of their food from the photosynthesizing microalgae (zooxanthellae) that live symbiotically within their transparent tissue. Bleaching occurs when the algae (or their pigment) are lost and the white calcium carbonate skeleton of the coral becomes visible. Bleaching is a general stress response when corals are exposed to extremes of temperature, UV radiation, salinity and pollutants[6,18,25]. Mortality of corals is largely determined by the magnitude of the disturbance and duration of the disruption of the symbiosis. In 1979, bleaching was so widely distributed that local disturbances could not account for the event. Since then, mass bleaching has occurred every 3 to 4 years[6]. The 1997–1998 bleaching event was the most geographically widespread and severe ever recorded[43]. It was probably owing to damage by elevated sea water temperatures, linked to one of the strongest El Niño events of this century[6,18]. It has been projected that bleaching will become more frequent, widespread and intense unless global warming is arrested[18]. Although some remain skeptical about the coupling of bleaching and global warming, there is little doubt among researchers that normal periods of elevated water temperatures will have more severe effects in the future, owing to the additive effects from other human-altered disturbances (e.g. increased sedimentation, overfishing and eutrophication)[6,18,43]. In addition, the ability of a reef to remain in a coral-dominated state after bleaching might be inhibited if larval sources are being damaged by anthropogenic disturbances[43]. Bleached reefs can also lose resilience owing to loss of species diversity within functional groups. For example, many bleached Indo–Pacific reefs might have become more susceptible to the Porites line-disease, owing to an increased relative abundance of the temperature tolerant *Porites* spp.[43]. There is a strong suggestion that coral reef organisms and communities possess adaptive and acclimative mechanisms to respond to climate change[13]. For example, corals can alter the relative abundance of several distantly related strains of zooxanthellae, thus they might host a larger proportion of high-temperature-tolerant zooxanthellae after a bleaching event[51]. Whether these responses to environmental change will be sufficient for corals to cope with more frequent bleaching events (and global change in general) in the future is still being debated, but many researchers fear that we have already crossed the environmental response threshold[13].

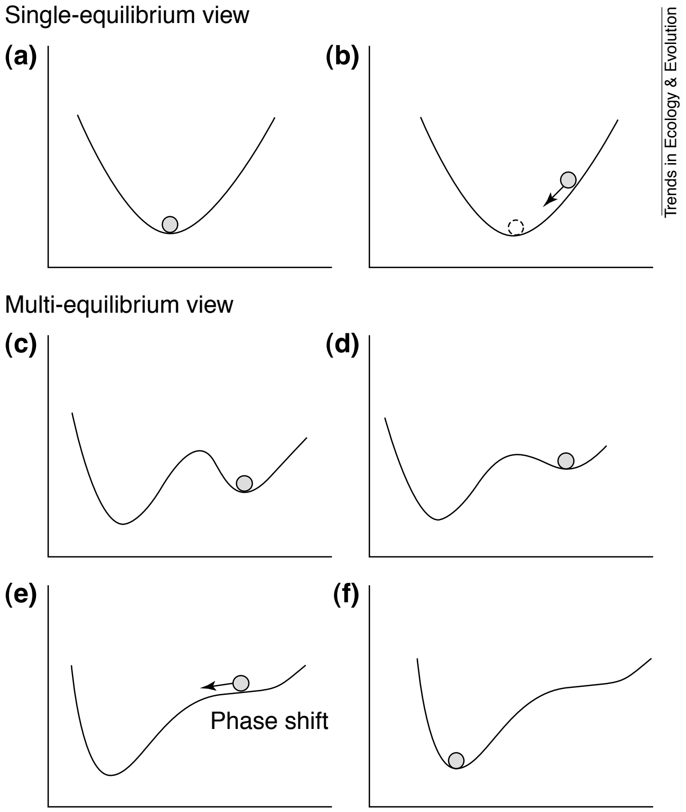

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Fig. 2. The 'ball-and-topography analogy' after Holling *et al.*[36], depicting two different views of coral reef ecosystem dynamics. In single-equilibrium models, resistance to disturbance (a) and speed of return (b) to a single equilibrium are of primary interest. In multi-equilibrium models, more than one equilibrium exists and a system can slide from one to another stable state or equilibrium. In (c) a coral reef is in a stable state of coral dominance and in (d) the reef is still dominated by corals, but ecosystem resilience has decreased (e.g. because diversity within the functional group of grazers has been reduced). Consequently, the system is progressively becoming more susceptible to disturbances that could previously be absorbed (e.g. hurricanes and diseases). Such events might now lead to a phase shift (e) to algal dominance and might cause the loss of essential ecosystem services. In this new state (f), the recolonization of corals is inhibited and therefore the shift might be irreversible, on a human timescale, unless it is actively managed. *Reproduced, with permission, from Ref. 36.*

development and evolution[15]. This concept broadens the perspective from recovery at the site impacted by disturbance to include the sources of resilience of the surrounding areas that are required for self-organization and reorganization to sustain the reef in a coral-dominated stable state.

Human impacts on ecosystem resilience

Modern reefs might always have possessed several features that favor multiple stable states[11]. However, studies from the Pleistocene coral reef fossil record suggest that reefs have shown remarkable persistence in their community structure for tens to hundreds of thousands of years, in spite of global environmental change and disturbance[16]. A unique feature of recent decades is that shifts from one stable state to another might have become more frequent and less reversible and that shifts are influenced, even driven, by human impact. A growing body of literature addresses phase shifts in coral reefs in relation to human activities[10–12,23,24,41,42] (Box 1).

Human modification of the marine environment might result in loss of diversity within and among functional groups (e.g. reef framework builders and grazers)[41], leading to simplification of coral reef habitats, reduced functional plasticity[23] and decreased ability to buffer disturbance. Coral reefs with decreased diversity within functional groups might still maintain ecological functions[8,39], but when faced with an additional disturbance they might reach a critical threshold and shift into another stable state in which large-scale degradation and loss of essential ecosystem services could occur[6,11,16,23,41].

Many coral reefs depend on larval sources outside their own boundaries[40]. They also rely on community interactions with other reefs and other ecosystems in the seascape[33]. The capacity of coral reefs to self-organize can be inhibited by human activities in several ways. For example, human activities have depleted larval sources[43]. They have also 'cut-off' disturbed sites from source areas either by altering dispersal routes (e.g. through land-fill, channel construction or reef mining, which lead to changes in currents) or by creating local pollution barriers that coral larvae must cross on their way to the impacted reef[26]. Loss of such spatial ecosystem resilience implies that reorganization and re-establishment might be severely hampered.

Coral reef communities might therefore shift into other stable states in two different ways – either through a change in the original disturbance regime or as a result of a reduction in ecosystem resilience. In reality, there is generally a combination of both. For example, it has been shown that chronic stress alone does not necessarily lead to a phase shift[11,23]. However, loss of ecosystem resilience, in a situation of chronic eutrophication and exploitation of herbivores, becomes visible when coral regrowth and recolonization are inhibited following a natural disturbance; thus the reef shifts from a state of coral dominance to one of algal dominance[12] (Box 1).

A challenge for coral reef management

In pace with increasing human dominance of ecosystems, natural disturbance regimes are altered and compounded perturbations created[17]. In a seascape environment that has been modified by humans, the ability of coral reefs to buffer the disturbance regime and reorganize themselves is also changed. In a world of human dominance, will the rate at which organisms adapt to the new disturbance regime be fast enough? It has become increasingly clear that the response of reefs to the combination of natural and anthropogenic disturbances will be difficult to understand and manage without considering multiple stable states[11]. It is possible that the escalating human alteration of the disturbance regime and resilience of coral reefs has triggered research on multiple stable states of reefs. In systems with ample resilience, shifts from one stable state to another are not an issue. However, such systems are becoming increasingly scarce. Reef recovery, in terms of percentage cover, species abundance or physical structure after disturbance, can no longer be taken for granted in a seascape strongly influenced by human activities. For example, the same currents that contribute to increasing the connectivity between coral reefs in the seascape, might also become a threat to ecosystem resilience by carrying pollutants, nutrients or diseases[39]. It can no longer be assumed that dispersal and natural variation among local assemblages in the seascape will buffer perturbations. Instead, the capacity to renew, reorganize and re-establish reefs after disturbance has to be actively managed at the regional level. This will involve many sectors of society, not only in the coastal zone but also further up in the drainage basin.

Scientists are increasingly addressing this challenge. For example, the importance of marine reserves for reef conservation is well developed in the literature[44], including the role of upstream and downstream reefs[40], and the management of disturbance[29]. Monitoring ecosystem performance[45] and managing seascape resilience to increase the chances of reefs reorganizing after disturbance are other challenges[33]. Managing for seascape resilience provides insurance to society in terms of sustaining a flow of ecosystem services[46]. In a world of human dominance this might seem to be an almost impossible task. Luckily, in seascape management practice there are cases to learn both from traditional societies[47–49] and from modern settings, such as the Great Barrier Reef Marine Park (http://www.dist.gov.au/science/pmsec/15meet/gbr/done.html).

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