

REVIEW

Sea urchin *Diadema antillarum*: different functions in the structure and dynamics of reefs on both sides of the Atlantic

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ABSTRACT: The long-spined black sea urchin *Diadema antillarum* has been involved in phase shifts between 'desired' and 'undesired' states in the organization of shallow reefs on both sides of the Atlantic Ocean between 18 and 33° N, but with significantly different ecological outcomes. In the western Atlantic, high densities of *D. antillarum* previously exerted considerable grazing pressure on reefs where corals and turf algae were the main biological engineers; however, subsequent to a massive die-off of *D. antillarum* from disease in 1983–1984, many reefs have gradually become dominated by foliose algae. In contrast, hyperabundances of *D. antillarum* (>10 ind. m⁻²) in the eastern Atlantic have caused the elimination of erect vegetative frameworks with the subsequent creation of 'barrens'. As a result, this invertebrate is directly implicated in the 'health' of important components of the biogenic frameworks of reefs on both sides of the Atlantic Ocean. Efforts in the western Atlantic are concentrated on the restoration of populations of *D. antillarum* to enhance coral abundance, recruitment and survivorship, while ecologists and managers in the eastern Atlantic focus on possible mechanisms to control hyperabundances of this species. We believe that the disproportionate effects of a single herbivorous species in mediating transitions between alternate states on the 2 sides of the Atlantic Ocean may be a direct consequence of a decline in the resilience of coastal ecosystems to disturbance. This decline was principally caused by decreased diversity of many of the functional groups that inhabit the Atlantic Ocean; both the western and eastern Atlantic Ocean have experienced large reductions in predatory and other fish populations.

KEY WORDS: Sea urchins · Reefs · Alternate states · Regime shifts · Community organization · Atlantic Ocean · Bioengineers · *Diadema antillarum*

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INTRODUCTION

Anthropogenic disturbance and climate change have caused dramatic shifts in the organization and structure of many coastal communities, with the establishment of alternate stable states (Knowlton 2004). These changes are generally long lasting and difficult to reverse (Scheffer et al. 2001, Scheffer & Carpenter 2003, Folke et al. 2004, Hughes et al. 2005), resulting in severe economic loss (Bellwood et al. 2004). The extent

to which alternate states are stable or reversible is poorly understood, and this represents a major challenge for research and management of coastal reefs worldwide (Bellwood et al. 2004, Knowlton 2004). Moreover, regime shifts have important implications for the formulation of management strategies, as 'undesired' states (from a human perspective) with high resistance to restoration may develop.

Subtidal ecosystems are different on both sides of the Atlantic in the latitude belt between 18 and 33° N.

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This difference arises mostly because the warm-temperate region is situated almost 5° further south at the Atlantic coast of North America (Briggs 1974, Lüning 1990) compared to the eastern Atlantic; thus, coral reefs are asymmetrically distributed on either side of the Atlantic. Marine environments within this latitudinal belt in the western Atlantic comprise warm-temperate and tropical waters (Briggs 1974, Lüning 1990), including the northern USA coast of the Gulf of Mexico (SST range: 13 to 30°C) and a part of the Caribbean Sea (SST range: 24 to 30°C). In contrast, the eastern Atlantic comprises only warm-temperate waters (SST range: 16 to 24°C) (Briggs 1974, Lüning 1990). These different oceanographic regimes impose limitations on the development of marine ecosystem engineers (species that create more complex habitat), which result in the presence and dominance of different subtidal habitats on both sides of the Atlantic Ocean. For example, corals and turf algae in the warm tropical waters of the western Atlantic (e.g. the Caribbean Sea) structure the physical and biological components of their environment. In contrast, erect macroalgae provide the main biological substrate for many organisms in the eastern Atlantic (e.g. the Canarian and Madeira Archipelagos) where coral reefs do not exist.

Despite the existence of remarkable oceanographic and biogeographic barriers, certain widespread marine species are endemic to both sides of the Atlantic.

One of these species, the long-spined black sea urchin *Diadema antillarum* (Philippi) has been at the core of extensive research along both Atlantic coasts since the 1970s, although its ecological importance along the eastern Atlantic has only been highlighted in recent years (Alves et al. 2001, 2003, Tuya et al. 2004a,b). Genetic studies have revealed that populations of this echinoid from the western and eastern Atlantic have been isolated, in terms of their evolution, for more than 1.5 million years (Lessios et al. 2001). The aim of this study is to compare the different ecological functions that *D. antillarum* plays in the structure and dynamics of shallow reefs on both sides of the Atlantic between 18 and 33° N.

ECOLOGICAL FUNCTION OF *DIADEMA ANTILLARUM*

Biotopes in the western Atlantic

Decreases in fish populations in the last century have altered the structure of functional groups of herbivores on many reefs, especially during the last 3 decades (Edmunds & Carpenter 2001, Gardener et al. 2003, Pandolfi et al. 2003, Bellwood et al. 2004). In response, herbivory has shifted from being fish-dominated to becoming echinoid-dominated (Bellwood et al. 2004) (Fig. 1). In this respect, a major ecological consequence

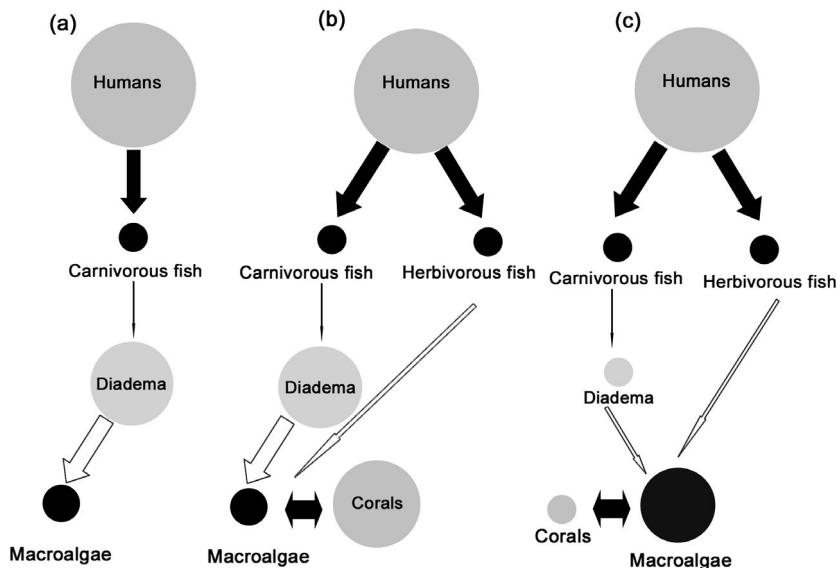


Fig. 1. Schematic representation of functional food webs on both sides of the Atlantic Ocean in the latitude-belt between 18 and 33°N: (a) eastern Atlantic, (b) western Atlantic prior to the 1983–1984 massive disease-induced die-off of *Diadema antillarum*, and (c) western Atlantic after the disease outbreak. Size of circles is proportional to the approximate biomass of each group; single-headed black arrows indicate predation; single-headed outline arrows indicate herbivory; width of the arrows reflects strong (wide) or weak (narrow) interactions; double-headed black arrows represent strong interspecific competition

of the massive die-off from disease of *Diadema antillarum* in the western Atlantic during 1983–1984 has been the abundant growth of erect algae (Lessios 1988a, Lessios 1988b, Hughes 1994, Bellwood et al. 2004). Without the grazing pressure exerted by high densities of *D. antillarum*, many reefs where corals and turf algae were the main biological reef engineers have gradually become dominated by erect foliose macroalgae (Hughes 1994, Edmunds & Carpenter 2001, Bellwood et al. 2004). Macroalgae outcompete corals by directly overgrowing them, or by occupying available space and thus inhibiting outward growth of existing colonies and recruitment of new colonies (Williams & Polunin 2001 and references therein). Over the last few years, reduced macroalgal cover and increased abundance of juvenile corals has resulted from natural recovery of *D. antillarum* populations at some sites in the Caribbean (Edmunds & Carpenter 2001, Miller et al. 2003), and through

experimental manipulation of *D. antillarum* abundance in the Florida Keys (Nedimyer & Moe 2003). This recovery provides evidence of the initiation of a reversal from a 'less desirable' macroalgal stable state to a coral-dominated system, suggesting that macroalgae dominance of Caribbean reefs is not an irreversible consequence of natural and anthropogenic disturbances (Edmunds & Carpenter 2001).

Biotores in the eastern Atlantic

In the eastern Atlantic, the scenario differs markedly. Removal of top predators during the last few decades as a consequence of overfishing has been linked to hyperabundances (>10 ind. m⁻²) of sea urchins (predominantly *Diadema antillarum*), with the subsequent elimination of erect vegetative frameworks and the creation of barrens as an alternate stable state (Fig. 1) (Tuya et al. 2004a). This process follows the classical trophic-cascade paradigm of subtidal temperate rocky reefs (Sala & Zabala 1996, Estes et al. 1998, Pinnegar et al. 2000, Shears & Babcock 2003, Graham 2004), in that urchin barrens may be considered as a global phenomenon mediated by overexploitation of inshore resources (Sala et al. 1998, Knowlton 2004). Consequently, *D. antillarum* plays an important ecological role in the organization of rocky reefs across the eastern Atlantic, as this species determines the composition and structure of benthic algal communities by inhibiting the development of the physical structure and primary resources provided by macroalgae (Alves et al. 2001, 2003, Tuya et al. 2004a,b). In this case, the lack of a vegetative framework imposes important limitations on the available food and refuge for a great number of species, with the establishment of an 'undesired' stable state dominated by crustose algae and barren habitat. Empirical evidence of natural reversals from a 'barren state' to a macroalgal-dominated system is still sparse.

'Desired' versus 'undesired' states

Diadema antillarum is therefore currently involved in the dominance and persistence of 'desired versus undesired' states in the organization of reefs on both sides of the Atlantic Ocean, but with completely opposite scenarios. In other words, this sea urchin is directly implicated in the phase shifts (sensu Knowlton 2004) of the major components of the biogenic frameworks of reefs on both sides of the Atlantic (Fig. 1). Ironically, efforts in the western Atlantic are concentrated on the restoration of populations of *D. antillarum* to enhance coral abundance, recruitment and survivor-

ship (Edmunds & Carpenter 2001, Nedimyer & Moe 2003), whereas ecologists and managers in the eastern Atlantic focus on possible mechanisms to control and decrease the hyperabundances of this species and thus allow erect macroalgae to recolonise unvegetated (barren) areas. Nonetheless, before 1983, efforts should have been focused in the same direction on both sides of the Atlantic (H. A. Lessios pers. comm.), principally because both the western and eastern Atlantic experienced large reductions in predatory and herbivorous fish populations. The mass mortality of *D. antillarum* in the western Atlantic was the cause of currently opposite situations on either side of the Atlantic.

It has been speculated that hyperabundances of *Diadema antillarum* in the 1970s across the Caribbean, principally associated with the elimination of competitors (herbivorous fish) and predators (carnivorous fish) through overexploitation, may have contributed to the species' own demise in 1983–1984 (Bellwood et al. 2004). At this time a pathogen spread throughout the Caribbean and reduced numbers of *D. antillarum* by 2 orders of magnitude (Lessios et al. 1984, Lessios 1988b) and precipitated the growth of macroalgae on coral reefs with the subsequent loss of coral cover (Bellwood et al. 2004, Hughes et al. 2005). However, no massive die-off event has been recorded in the eastern Atlantic over the last several decades, where mean local densities can easily reach up to 10 ind. m⁻². If the species' own demise is linked to its hyperabundance, the why have mass mortalities not occurred in the eastern Atlantic? Apparently, such a die-off would directly benefit the recovery of the main bioengineers (erect macroalgae) of the shallow hard bottoms of the eastern Atlantic.

CONCLUSIONS

Distortion of food webs by humans, induced by selectively removing top predators and herbivores, has damaged the resilience of marine systems (Myers & Worm 2003, Hughes et al. 2005), with the establishment of 'undesired' alternate organizational states (Knowlton 2004, Hughes et al. 2005). We believe that the disproportionate effects of a single herbivorous species *Diadema antillarum* in mediating transitions ('phase shifts') between alternate states on both sides of the Atlantic Ocean may be a direct consequence of a decline in the resilience of coastal ecosystems to disturbance. This decline was principally caused by decreasing diversity of predatory and/or herbivorous fish, and concomitant reductions in the diversity of many functional groups that inhabit the Atlantic Ocean (Myers & Worm 2003). As a result, the structural and functional

properties of the emergent dominant states differ significantly from the original states, resulting in less valuable ecosystems with fewer 'goods and services' being generated for society.

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