

Viewpoint

Is Jamaica a good model for understanding Caribbean coral reef dynamics?

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ABSTRACT

Caribbean reefs have experienced unprecedented changes in the past 40 years. A major hypothesis to explain shifts in reef community composition relates to declining herbivory. This hypothesis was developed largely based on observations of Jamaican reefs from the 1980s onward, but it is widely held to be relevant regionally. We use a region-wide dataset on benthic composition to examine how well the pattern of ecological change on Jamaican reefs is mirrored by other Caribbean reefs. The extent to which macroalgal cover exceeds coral cover on Jamaican reefs is an order of magnitude more extreme than seen elsewhere. We suggest that Jamaican reefs are not representative of the degradation trajectory of Caribbean reefs and management based on the Jamaican experience may not be relevant elsewhere. However, the recovery of Jamaican reefs following the return of urchins gives us hope that Caribbean reefs are more resilient to catastrophic disturbances than previously thought.

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1. Introduction

Coral reefs have changed radically over the past four decades (Gardner et al., 2003; Hughes et al., 2003; Bruno and Selig, 2007; De'ath et al., 2012). Regional-scale meta-analyses of reef-survey data have shown that coral cover on Caribbean reefs has declined on average from ~50% in the late 1970s to ~10% in the early 2000s (Gardner et al., 2003; Schutte et al., 2010). On some reefs, coral mortality has been followed by an increase in the cover of fleshy macroalgae, but the extent to which macroalgae have come to dominate Caribbean reefs is controversial (Bruno et al., 2009). The loss of coral and its replacement by macroalgae, if widespread, could have far-reaching consequences for reefs, including lower coral recruitment, increased bioerosion of the reef framework, diminished structural complexity, and reduced populations of fish and invertebrates that depend on that architecture (Mumby and Steneck, 2008).

The top-down model of Caribbean reef decline, originally derived from observations of Jamaican reefs (Hughes, 1989, 1994; Hughes et al., 1999), is perceived to be widely relevant as an explanation for changes on other reefs across the Caribbean region (Knowlton, 1992, 2001; Nyström et al., 2000, 2008; Jackson,

2001; Hughes and Tanner, 2000; Jackson et al., 2001; Knowlton and Jackson, 2001; Scheffer et al., 2001; Karlson, 2002; Elmqvist et al., 2003; Pandolfi et al., 2003; Scheffer and Carpenter, 2003; Bellwood et al., 2004; Steneck and Sala, 2005; Mumby et al., 2006, 2007; Mumby and Steneck, 2008; Mumby, 2009; Hughes et al., 2010, 2012; Sandin et al., 2010; Sala and Jackson, 2011). This model holds that both coral mortality and the associated phase shifts are primarily a consequence of low herbivory pressure (Knowlton, 1992; Hughes, 1994; Nyström et al., 2000; Jackson et al., 2001; Bellwood et al., 2004). The depletion of large predators, which occurred centuries ago (Jackson, 2001; Jackson et al., 2001), the subsequent switch to overfishing of herbivores, and finally the mass mortality in 1983–1984 of the herbivorous sea urchin *Diadema antillarum* from disease (Lessios, 1988), triggered a proliferation of macroalgae, which was directly responsible for increased coral mortality (Jackson et al., 2001; Hughes et al., 2010). But is this model applicable to other Caribbean reefs? If not, what are the implications for the management of reefs across the region?

Here, we ask whether Jamaican reefs are in fact good models for understanding ecological change on Caribbean coral reefs at a regional scale through the 1980s and 1990s, the period during which live coral cover declined most abruptly across the region. We compare the relative abundance of living corals and macroalgae through time on reefs in Jamaica and reefs elsewhere in the Caribbean. We suggest that Jamaican reefs are not representative of what has occurred in the Caribbean in general and speculate on

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the reasons for their uniqueness and the implications for our outlook of Caribbean reefs.

2. Materials and methods

2.1. Data acquisition

Time-series of data on hard-coral and macroalgal cover for reef sites within the wider Caribbean basin (including Florida and The Bahamas) were obtained through electronic and manual literature searches, as well as direct personal communication with reef scientists, site managers and institutional librarians. Electronic literature searches were conducted using the Science Citation Index (SCI) and Aquatic Sciences and Fisheries Abstracts (ASFA) from 1981 to 2001 and 1988 to 2001, respectively, covering a period of extensive changes on Caribbean reefs (Gardner et al., 2003; Schutte et al., 2010). All relevant references cited in these publications were also checked. The only selection criterion employed was that a study reported percent cover of both target benthic components—hard corals and macroalgae—with replicated measurements, from a site within the region.

2.2. Temporal trends in coral and macroalgal cover

We defined macroalgae as all larger, erect, and anatomically complex algal forms with canopy heights usually >10 mm (Steneck, 1988). Crustose coralline algae and algal turfs were not considered in this analysis because of their functional differences and because many reef-monitoring programs do not differentiate between turfs and other non-erect algal forms.

We sought to determine the extent to which reefs were dominated in terms of percent cover by either live coral or macroalgae. Because the term 'dominance' is ill-defined in the ecological literature, for this study we opted to avoid any index with an arbitrary threshold cover (e.g., 50%, Bruno et al., 2009). Instead, we considered the differences in percent cover of corals and macroalgae, with positive values reflecting relatively more coral than macroalgae. Percent-cover difference was calculated for every reef in each year of the study period. Yearly averages and their associated standard errors were then calculated separately for Jamaican and other Caribbean sites.

3. Results and discussion

A total of 229 shallow-water reef sites (<20 m deep) from 71 separate studies across the Caribbean reported concurrent cover of coral and macroalgae. The sites were distributed evenly around the region (similar to the distribution shown in Gardner et al. (2003), but with the addition of sites in St. Lucia and Saba). Overall, the time-series of coral and macroalgal cover spanned the years 1977–2001.

Pre-1982 data on benthic composition are only available from Jamaican reefs (Fig. 1). These early data suggest that Jamaican reefs had much more coral than macroalgae until 1980, after which the relative difference in cover between these two benthic components began to decline markedly. By 1984, macroalgal cover exceeded coral cover on Jamaican reefs. The difference between macroalgal and coral cover peaked in 1992, with reefs having on average 70% higher absolute cover of macroalgae than living coral. Corals recovered and macroalgae declined between 1992 and 1999, the last year of our dataset for Jamaica.

The pattern for other Caribbean reefs was superficially similar but quantitatively different. On non-Jamaican reefs, the difference between coral and macroalgae also declined from 1984 to 1994 and remained relatively stable for the remainder of the time series.

However, in contrast to Jamaican reefs, macroalgal cover very rarely exceeded coral cover on non-Jamaican reefs (Fig. 1).

Jamaican reefs have long been held up as the archetypal example of reef degradation in the Caribbean (Precht and Aronson, 2006). Our results call into question the suitability of Jamaican reefs as models for the study of coral-reef dynamics for the Caribbean region (see also Aronson and Precht, 2006; Bruno et al., 2009; Dudgeon et al., 2010).

Two catastrophic events have critically affected the balance between living corals and macroalgae on Caribbean reefs. One is the loss of the formerly dominant acroporid corals due to white-band disease, which began in the late 1970s and continued throughout the 1980s and 1990s (Gladfelter, 1982; Aronson and Precht, 2001). The other is the pathogen-induced mass mortality of the herbivorous sea urchin *D. antillarum* in 1983 (Lessios, 1988). The epizootic had repercussions on reef benthos and fishes (Hughes et al., 1987; Liddell and Ohlhorst, 1986; Robertson, 1991). Both events had regional-scale ecological impacts, and in the absence of other localized conditions and events they should have generated similar patterns of temporal change in coral and macroalgal cover across Caribbean reefs.

However, Jamaica was characterised by site-specific events and prior conditions that triggered a larger-than-average response (Hughes, 1989). Most notable were Hurricane Allen in 1980, which caused extensive direct coral mortality (Woodley, 1980), and subsequent coral losses due to predation and breakage-induced disease (Knowlton et al., 1981, 1990). Hurricane damage to corals increases with the time elapsed since the last storm (Gardner et al., 2005), and the effects of Hurricane Allen were particularly severe because they occurred after an unusually long, hurricane-free period (Woodley, 1992). Thus, 1980 marked the beginning of a rapid change in the relative abundance of coral and macroalgae on Jamaican reefs. The precipitous shift that followed was likely compounded by the extreme importance of *Diadema* as a grazer (Sammarco, 1982; Carpenter, 1986; Precht and Aronson, 2006; Idjadi et al., 2010; Sandin and McNamara, 2011) in the near-absence of herbivorous fishes, which had been overexploited for decades (Aronson, 1990; Hughes, 1994), if not centuries (Jackson, 2001; but see Precht and Aronson, 2006; Baisre, 2007). Indeed, from

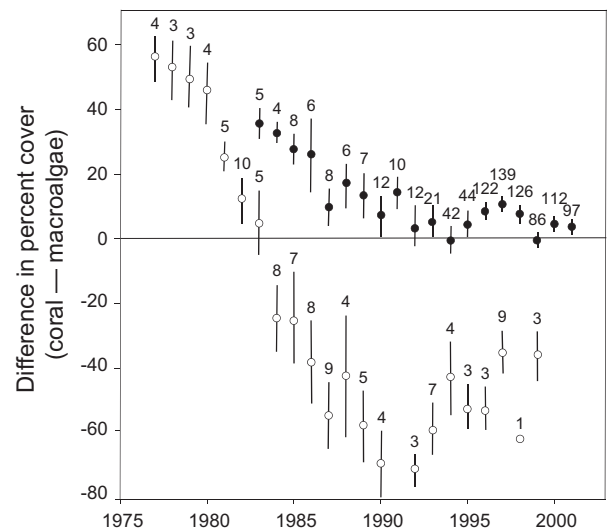


Fig. 1. Magnitude of the difference between percent cover of live coral and macroalgae on Caribbean reefs in each year between 1977 and 2001. Means (\pm se) are shown separately for Jamaican sites (open circles) and all other sites (filled circles). Positive values indicate that the cover of coral was higher than that of macroalgae. Numbers above the error bars show the number of sites contributing to each mean.

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