Viewpoint

Coral reef baselines: How much macroalgae is natural?

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ABSTRACT

Identifying the baseline or natural state of an ecosystem is a critical step in effective conservation and restoration. Like most marine ecosystems, coral reefs are being degraded by human activities: corals and fish have declined in abundance and seaweeds, or macroalgae, have become more prevalent. The challenge for resource managers is to reverse these trends, but by how much? Based on surveys of Caribbean reefs in the 1970s, some reef scientists believe that the average cover of seaweed was very low in the natural state: perhaps less than 3%. On the other hand, evidence from remote Pacific reefs, ecological theory, and impacts of over-harvesting in other systems all suggest that, historically, macroalgal biomass may have been higher than assumed. Uncertainties about the natural state of coral reefs illustrate the difficulty of determining the baseline condition of even well studied systems.

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1. Introduction

To restore and manage ecosystems properly, we need to know what they looked like and how they operated before humans began to deplete, alter, and otherwise degrade them (Dayton et al., 1998). The pristine or natural state of a population or community is called the baseline in conservation biology, and it serves as a guide for setting conservation and restoration targets. Unfortunately, scientists rarely have reliable information on baselines because in most cases quantitative data are not collected until long after the resource has been modified (Pauly, 1995; Dayton et al., 1998). This is particularly true for marine communities, which can be difficult and expensive to monitor.

Ecologists use a variety of approaches and sources of information to estimate the baseline states of populations and communities: historical data such as ships' logs and naturalists' observations (Jackson, 1997), fossil and archeological information (Wing and Wing, 2001; Aronson et al., 2002), molecular-genetic techniques (Lessios et al., 2001, Roman and Palumbi, 2003), and even relationships between abundance and body mass (Levitan, 1992; Jennings and Blanchard, 2004). We have not, however, constructed a logical framework for choosing the target baseline for situations in which different techniques provide conflicting portraits of the pristine condition.

Here we illustrate this general problem by evaluating evidence from different methods of estimating the baseline state of coral reef communities, in terms of the abundance of seaweeds, or macroalgae. We use macroalgal cover as a key indicator of reef state, based on a broad consensus of coral reef scientists (Steneck, 1988; Liddell and Ohlhorst, 1992; Steneck and Dethier, 1994; Steneck and Sala, 2005). We define macroalgae as large, anatomically complex algal forms, including erect calcifying species but not filamentous algal turfs. Even erect, calcifying green algae, such as species of *Halimeda*, have increased on many reefs around the world over the last several decades and are thought to have a negative impact on coral populations (Szmant, 2001; Nugues et al., 2004; Smith et al., 2006; Birrell et al., 2008). Conceptual models of coral reef ecology frequently pool algae in this way (Hughes et al., 2010), rather than attempting to predict or depict the specific effect and dynamic of each coral-algal species pair. Algal turfs are not included in this category because far less is known about their effects on adult and juvenile corals (but see Birrell et al., 2005), and because their abundance and cover are rarely quantified accurately (Littler et al., 1987, Aronson et al., 1994, Miller et al., 2003).

2. Coral reef degradation and the missing baseline

Coral populations around the world began to decline several decades ago from a variety of causes including oceanic warming, storms, outbreaks of predators and diseases, and poor land-use practices that cause nutrient and sediment pollution. The loss of once-dominant corals, combined with the over-harvesting and die off of key grazers, has enabled seaweeds to increase in abundance on many reefs (McManus and Polsenberg, 2004). Seaweeds are perceived as harmful invaders because they can reduce coral

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recruitment (Kuffner et al., 2006, Box and Mumby, 2007; Idjadi et al., 2010; Rasher and Hay, 2010), potentially slowing the recovery of coral populations from natural and anthropogenic disturbances. Managers are thus charged with maintaining "reef resilience" by promoting grazing and minimizing the proportion of the substrate covered by macroalgae (Hughes et al., 2005; Mumby et al., 2007). But what quantity of seaweed is natural on a coral reef, and how much is too much – or too little?

3. Estimating the seaweed baseline: The Jamaican prototype

One answer is based on historical surveys of a handful of reefs off Jamaica and St. Croix, U.S. Virgin Islands in the late 1970s and early 1980s (Adey and Steneck, 1985; Liddell and Ohlhorst, 1992; Hughes, 1994) from which average macroalgal cover was estimated to be approximately 2% (Côté et al., 2005; Schutte et al., 2010). These studies preceded the impacts of strong hurricanes on both islands in the 1980s and the regional mass mortality in 1983–1984 of the echinoid *Diadema antillarum*, an important herbivore. Descriptive accounts (Van den Hoek et al., 1975; Adey et al., 1977; Littler et al., 1987) support the view that very low (<3%) seaweed cover was typical of some Caribbean reefs at that time; however, given the very small number of reefs that were sampled and the potential for biases in the selection of sites, the generality of this finding is unclear.

It is also possible that the high coral cover of the Caribbean "baseline" reefs led to an underestimation of macroalgal cover. Algal lawns cultivated by the territorial threespot damselfish, *Stegastes planifrons*, have historically been abundant on Caribbean reefs (Precht et al., 2010) and were reported to be so in St. Croix and Jamaica at the time of the early surveys (Kaufman, 1977, Brawley and Adey, 1977; Fig. 1). Kaufman (1977) reported that 10–40% of the surface area of the forereef at Discovery Bay, Jamaica was covered by the algal lawns of damselfish in the 1970s, and that he had observed similar "processes" elsewhere in the Caribbean at that time. Such lawns, primarily made up of dense turfs with some macroalgae, dominate the bases of many colonies of branching species of *Acropora* today, even on some of the world's most isolated and pristine reefs (Fig. 1).

How could macroalgal cover have been as low as 0–3% on reefs with high densities of *Stegastes* territories? One plausible answer is that macroalgae were undercounted when obscured by canopy-forming acroporid corals (Goatley and Bellwood, 2011). Plating, Indo-Pacific acroporid corals can facilitate an understory of high macroalgal biomass by providing a refuge from most herbivores (Fig. 1). Thus, divers performing benthic surveys, especially with photography and videography in such multilayered assemblages, have a diminished ability to detect such macroalgae hidden from above (Foster et al., 1991). Macroalgal abundance, therefore, could be routinely underestimated on reefs with high coral cover, at least on reefs dominated by branching and plating acroporids.

Underestimates of macroalgal cover in the coral-dominated state could be skewing our perception about spatio-temporal dynamics of coral and macroalgal cover, especially on reefs from which acroporids have now been lost (Aronson and Precht, 2001). In fact, Goatley and Bellwood (2011) argued, "While phase-shifts to algal dominated states are among the most reported effects following disturbances on coral reefs our results suggest that in some cases, apparent shifts could simply be due to the canopy effect, with the removal of the coral canopy unveiling a pre-existing algal-dominated state."

4. Shifting Caribbean baselines

Because many reef scientists began their careers in the Caribbean during the 1970s, the field in general has largely adopted the condition of Caribbean reefs of this era – particularly Jamaican reefs – as the archetypal natural state (Côté et al. 2013). Caribbean reefs of the 1970s, however, were probably not representative of pre-human, pristine reefs. By the time scientists began studying coral reefs, people had been harvesting plants and animals from them for centuries (Wing and Wing, 2001; Pandolfi et al., 2003) and had significantly altered several aspects of community structure (Knowlton and Jackson, 2008).

Regardless of what the true cover of macroalgae was in the 1970s, deriving the Caribbean (or global) baseline from the results of early Caribbean surveys assumes grazing intensity was close to natural levels. We doubt this assumption is valid. Overfishing has caused the loss of large piscivores, particularly sharks, barracudas and groupers from most of the world's reefs (Sandin et al., 2008; Stallings, 2009). This wholesale removal of top predators probably increased grazing and grazer populations (McClanahan and Shafir, 1990; Sale et al., 2005; Valentine and Heck, 2005; Madin et al., 2010), at least initially before herbivores like parrotfishes were overfished as well. Inflated benthic grazing could have artificially suppressed seaweed cover on what we – perhaps erroneously – consider our archetypal reefs.

For example, there is evidence that densities of *Diadema* may have been unnaturally high on some Caribbean reefs during the 1970s because their predators, including triggerfish and hogfish, had been removed by fishing (Hay, 1984; Aronson, 1990; Levitan, 1992; Hughes, 1994; Knowlton and Jackson, 2001; but see Jackson, 1997, Lessios et al., 2001, Precht and Aronson, 2006 for the argument that *Diadema* were historically abundant). Herbivory by echinoids (at high densities) is generally far more effective at reducing algal cover than herbivorous fishes (McClanahan, 1995; Precht and Aronson, 2006). Similar dynamics have been documented in the western Indian Ocean, where overfishing facilitated the growth of sea-urchin populations, increasing grazing to the point that it was detrimental to corals (McClanahan, 1995). Thus, what is regarded as the coral-reef prototype may actually represent a highly shifted baseline due to historical fishing.

Fig. 1. Association between acroporid corals and macroalgae. (left) *Acropora cervicornis* thicket from Discovery Bay, Jamaica in 1978. Note thick understory of *Dictyota* and *Amphiroa* adjacent to a territory of the threespot damselfish, *Stegates planifrons*. Photo credit: William Precht. (center) *Stegates*-occupied branching-*Acropora* thicket from Ningaloo Reef, Western Australia, 2010. Photo credit: John Bruno. (right) High biomass of macoalgae underneath a plating acroporid coral from Ningaloo Reef, Western Australia, 2010. Photo credit: John Bruno.