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, most reef scientists believe that the average cover of seaweed was very low in the natural state: perhaps less than 5%. 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.

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 (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.

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Here we illustrate this general problem by evaluating evidence from different methods of estimating the baseline state of coral reef communities, particularly 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, and because their abundance and cover are rarely quantified.

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 some reefs (McManus and Polsenberg 2004). Seaweeds are perceived as harmful invaders because they can reduce coral recruitment (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?

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 (Fig. 1)(Kaufman 1977, Brawley and Adey 1981). 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

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Caribbean at that time. Such lawns of dense turfs and 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).

Figure 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. A jpg file of the image can be downloaded here: http://figshare.com/articles/Figure_1/697526

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). Divers performing benthic surveys have a diminished ability to detect such macroalgae hidden from above. 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 (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."

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. 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).

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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 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* were 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, Precht and Aronson 2006 for the argument that *Diadema* were historically abundant). 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 1990). Thus, what is regarded as the coral-reef prototype may actually represent a highly shifted baseline due to historical fishing. Other aspects of the disturbance regime were also anomalous when the initial surveys of Caribbean reefs took place. For example, Jamaican reefs had not been impacted by a hurricane in nearly four decades (Woodley 1992). Woodley (1992) estimated the average return-time of hurricanes to Jamaica to be 6.5 years, leading him to suggest, "The luxuriant *Acropora* stands of the classic descriptions may therefore be atypical; one extreme of a variable condition." Although most scientists worked on reefs with high coral cover during the 1970s, some reefs at that time had considerable quantities of seaweed as a result of natural disturbances. For example, Belizean reefs damaged in 1961 by Hurricane Hattie remained dominated by macroalgae for more than a decade (Stoddart 1974). Bak (1977) reported, "Large parts of the reef terrace on the exposed coast [in the Lesser Antilles] are densely covered with the brown alga *Sargassum platycarpum*... In places the algal fields stretch over the drop-off down to the sediment plain at 40 m." Even some reefs off Jamaica and St. Croix had macroalgal cover greater than 10% (Adey and Steneck 1985, Liddell and Ohlhorst 1992).

Estimating the seaweed baseline: Quasi-pristine Pacific reefs

A second approach to understanding natural levels of seaweed abundance, which largely avoids this problem of shifting baselines, is to document the state of currently pristine or nearly pristine reefs (Vroom et al. 2006, Knowlton and Jackson 2008, Sandin et al. 2008). As a consequence of their remote locations, and in some cases due to legal protection, fishing and other direct human impacts are minimal on certain reefs in the central Pacific (Knowlton and Jackson 2008). The National Oceanic and Atmospheric Administration−Coral Reef Ecosystem Division (NOAA−CRED) surveys of 46 remote Pacific reefs (Vroom and Braun 2010, Vroom et al. 2010) found that macroalgal cover ranged from 10% to 30% and averaged 22% on atolls as remote and pristine as Johnston, Wake, Kingman, Palmyra, and the Northwest Hawaiian Islands (Fig. 2). The current state of these quasi-pristine reefs clearly suggests that natural levels of seaweed cover could be higher than the 2% estimate based on the early Caribbean surveys.

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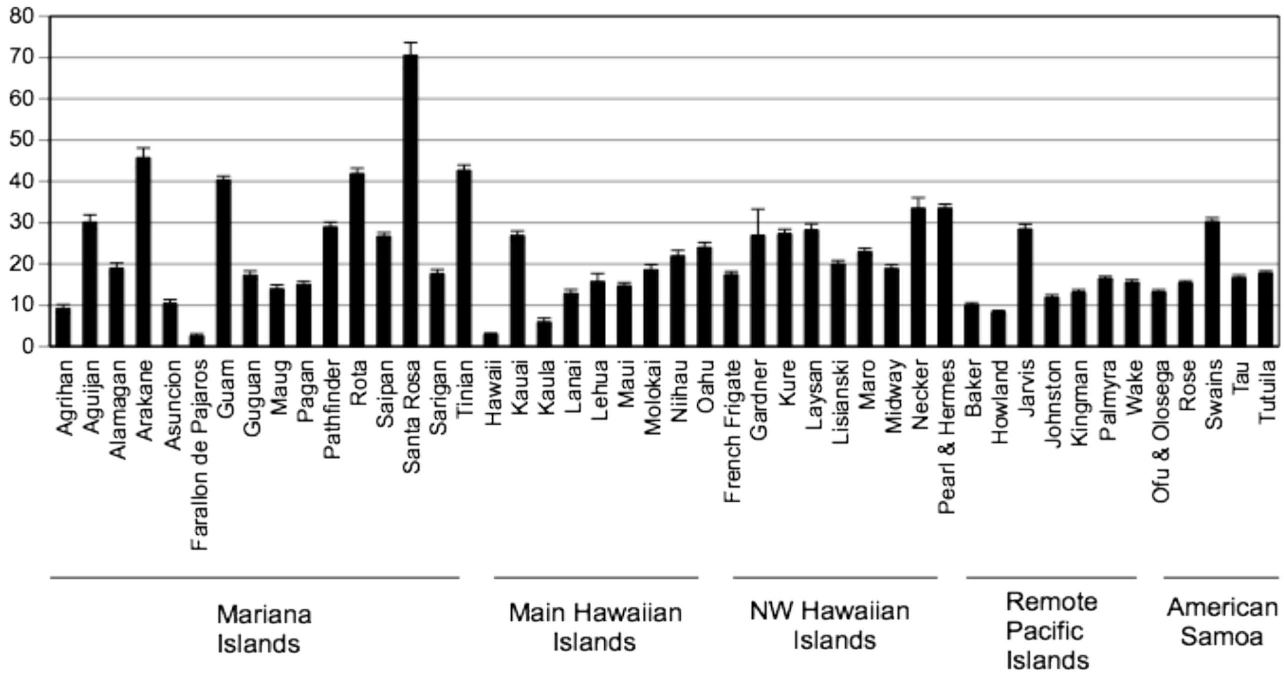

Figure 2. Percentage of the seafloor covered by macroalgae on 46 Pacific reefs based on NOAA−CRED towed-diver surveys performed between 2000 and 2009. Redrawn from Vroom 2011 (Fig. 2C). Values are site-means ± 1 SE. An eps file of the image can be downloaded here: http://dx.doi.org/10.6084/m9.figshare.697550

Unfortunately, using remote Pacific reefs as regional or global baselines also has several limitations. For example, they are clearly being impacted by global stressors, particularly ocean warming (Alling et al. 2007, Halpern et al. 2008, Selkoe et al. 2009). Additionally, they are probably not representative of reefs in other regions, specifically those closer to continents or large islands, which are generally less nutrient-limited and might be expected to have even higher seaweed baselines.

Baseline distributions

Reefs, like all communities, have always been disturbed. Even long ago in the pre-human past, reefs were dynamic, non-equilibrial systems and were not fixed in climax states of coral dominance (Woodley 1992, Connell et al. 1997, Vroom et al. 2006). In his long-term monitoring study of shallow reefs on the Great Barrier Reef, Connell documented repeated fluctuations of macroalgal cover between 15% and 85% due to natural disturbances and community succession (Connell et al. 2004). Because coral and seaweed cover fluctuate naturally (and quasi-independently; (Bruno et al. 2009, Colvard and Edmunds 2011, McClanahan et al. 2011a, 2011b)), there is no single baseline for a healthy reef. There is instead a range of state values and a regional-historical average, which is not the same as a maximum or minimum value measured on a pristine reef in a late stage of succession. At any time, a proportion of reefs in any given region will be in various states of recovery from natural disturbances (Emslie et al. 2008). Those reefs exhibit reduced coral cover and sometimes increased macroalgal cover, shifting the mean benthic composition away from the state of fully recovered reefs (Bruno and Selig 2007).

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The natural state of reefs is also highly context-specific. The abundances in space and time of different functional groups of algae are related to a combination of biotic and abiotic factors, including competition, grazing, nutrient availability, wave action, temperature, and irradiance (Steneck and Dethier 1994). Baselines, therefore, necessarily vary along environmental gradients (Vroom and Braun 2010). For example, cyclones are rare within 5° of latitude of the equator because of the weakness of the Coriolis effect. Equatorial reefs, therefore, might be expected to have higher coral and lower seaweed baselines. On the other hand, reefs growing at their latitudinal extremes, such as those in Florida, show marked seasonal dynamics, with as much as 30% variation in the absolute cover of macroalgae between winter and summer (Lirman and Biber 2000). Coral reefs also exist across a range of nutrient availability and benthic primary productivity, so seaweed biomass should vary significantly even in the absence of anthropogenic disturbances (Vroom and Braun 2010). Dayton et al. (1998) described a similar phenomenon in kelp forests of southern California, which are strongly influenced by oceanographic cycles such as the El Niño–Southern Oscillation (ENSO), resulting in striking temporal variability in what is natural. ENSO drives similarly coupled physical–biological fluctuations in the tropical eastern Pacific, where the meaning of "natural" in terms of temperature, productivity, species interactions and community structure can vary enormously on annual to millennial time scales (Glynn and Colgan 1992, Toth et al. 2012).

The message is that the distributions of baseline states for coral reefs and other habitat types are region-specific. Great care should be taken when using information about the baseline-range in one location to make inferences about the degree of degradation in another. Ideally, we would have science-based baseline distributions for each region and even for different habitats (i.e., different reef zones). Unfortunately, the necessary data do not exist, leaving substantial uncertainties about the natural state of coral reefs.

Lessons from other systems

To investigate trophic cascades, ecologists experimentally remove carnivorous predators from model communities. Humans have effectively replicated this work in an uncontrolled fashion at far larger scales by removing carnivorous vertebrates for sustenance, profit, and sport from nearly every ecosystem on the planet. In most cases, the depletion of such predators weakens trophic cascades and reduces plant biomass. Marine examples include kelp forests, salt marshes and rocky subtidal habitats (Silliman et al. 2005, Steneck and Sala 2005). For rocky subtidal communities at temperate latitudes, Steneck and Sala (20005) observed, "Where large predators remained, lobsters, crabs, and herbivorous sea urchins were rare [and] kelp was abundant." There are also many terrestrial examples, such as tropical rainforests in which losses of carnivores lead to the rapid depletion of plant biomass and greatly reduced seedling survival (Terborgh et al. 2001). The explosion of deer and elk in North America due primarily to the removal of their predators and the subsequent overgrazing of herbaceous plants, is another salient example (Ripple and Beschta 2006, 2011).

Considering ecological theory and experiences in other systems, it should not be surprising that some pristine reefs have more seaweed than some fished reefs. Trophic cascades, mediated by both consumptive and non-consumptive effects of predators on herbivores, could explain the higher than expected cover of seaweeds observed on remote, pristine reefs. Unfished or lightly

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fished reefs are typically dominated by large predators such as sharks, snappers, and groupers (Steneck and Sala 2005, Sandin et al. 2008). As a result, herbivores are scarce and spend most of their time hiding rather than foraging (Sandin et al. 2008, Madin et al. 2010), thereby inducing a numerically and behaviorally mediated trophic cascade in favor of increased macroalgal cover and biomass.

Conclusions

Different approaches to assessing the macroalgal baseline for the world's coral reefs lead to different baseline estimates – an unfortunate reality that leads to considerable ambiguity for managers and causes confusion in the literature. Most reef scientists would agree that a reef with > 50% seaweed coverage has been substantially degraded or has at least shifted to a macroalgal-dominated phase (McManus and Polsenberg 2004). But what about a Caribbean reef with 10% seaweed cover or a central Pacific reef with 15% cover? Should managers consider such reefs healthy, at least in terms of macroalgae, or should they intervene by promoting herbivory or limiting (to the degree possible) human activities that promote the growth of seaweeds? These are not merely hypothetical questions since such values of seaweed coverage in the neighborhood of 10−15% represent recent averages for much of the world (Bruno et al. 2009). We can all recognize near-pristine and highly degraded reefs, yet most the world's reefs fall along a continuum between these extremes. This matters for reef management because having too little algae on a reef could be as disruptive as having too much. Macroalgae and other primary producers are, after all, a critical component of coral reef food webs and the targets of conservation and restoration in many other types of nearshore marine environments. Recent work indicates that seaweeds are at least as threatened by anthropogenic climate change as reef-building corals (Wernberg et al. 2011). Furthermore, over-promoting herbivory could cause rapid bioerosion and structural homogenization (McClanahan 1990).

We conclude with four recommendations:

1) Scientists and managers should be aware that there is no single baseline; rather, there is a baseline distribution. This may seem obvious, but it is often forgotten when the state of a given reef or the effectiveness of a local management plan is evaluated.

2) Some reefs in any given region will inevitably have high seaweed coverage and low coral coverage. This is a simple result of the natural disturbance regimes that reefs have always experienced, and no form of local management can avoid this reality (Emslie et al. 2008).

3) The natural coverage of seaweed varies along bathymetric and environmental gradients and among regions. Scientists should recognize that it is unrealistic to expect nearshore, continental reefs and those in equatorial upwelling regions, both with high natural levels of nutrient availability, to look exactly like remote, oligotrophic atolls.

4) Macroalgal cover is just one of several key metrics of reef state (McClanahan et al. 2011a). Developing context-specific baseline distributions of seaweed for management and restoration is an important goal, but we also need to know the natural range of other important characteristics of reef ecosystems.

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