

Climate Change, Coral Loss, and the Curious Case of the Parrotfish Paradigm: Why Don't

John F. Bruno (/search?value1=John+F.+Bruno&option1=author&noRedirect=true)¹, Isabelle M. Côté (/search?value1=Isabelle+M.+C%C3%B4t%C3%A9&option1=author&noRedirect=true)

 View Affiliations

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ABSTRACT

Scientists have advocated for local interventions, such as creating marine protected areas and implementing fishery restrictions, as ways to mitigate local stressors. However, numerous reasons for why marine protected areas and the protection of herbivorous fish (especially parrotfish) have had little effect on coral resilience. One key explanation is the presence of numerous context dependencies of the five cascading links assumed by the managed-resilience hypothesis. If reefs cannot be saved by local actions alone,

Keywords

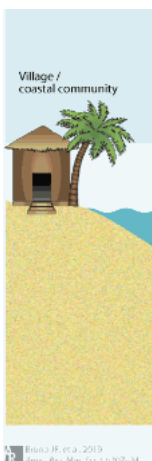
coral reef (/search?option1=pub_keyword&value1="coral reef"), **disturbance** (/search?option1=pub_keyword&value1="disturbance"), **parrotfish** (/search?option1=pub_keyword&value1="parrotfish"), **climate change** (/search?option1=pub_keyword&value1="climate change")

1. INTRODUCTION

Coral reefs provide numerous ecosystem services, including food (**Burke et al. 2011**) and economic benefits through fisheries and tourism, to hundreds of millions of people. Reefs also generate more than \$7 million per square kilometer annually (**Spalding et al. 2017**). Reefs also protect coastal communities from large waves generated by storms. However, building corals, many of which have been declining globally.

Figure 1

Ecosystem services provided by reefs and some of the geological and ecological features that support these benefits to people.



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Over the last 30–40 years, the average cover of living coral on tropical reefs has declined by approximately 50–75% in nearly all regions of the world (**Bruno et al. 2009**). This decline has led to a loss of reef complexity (**Alvarez-Filip et al. 2009, 2011**) and the diversity of reef inhabitants, including fishes and invertebrates (**Idjadi & Edmunds 2006, Jones et al. 2006**). Reefs also protect coastal communities from storms as the sea level rises depends on vertical reef accretion (**Beetham et al. 2017, Perry et al. 2018**), and reefs can accrete. Some putative localized factors causing coral population declines include increased water column turbidity, sedimentation, eutrophication and other forms of stress. Coral epidemics, which can occur on large scales (**Aronson & Precht 2001a, Willis et al. 2002**), can also cause coral loss, as can earthquakes and tsunamis (**Aronson et al. 2002**). The intensity—may become increasingly problematic in the future (e.g., **Altieri et al. 2017, Veron 2011, Webster et al. 2005**).

Coral-reef scientists have strongly advocated for marine protected areas (MPAs) and fishery restrictions in general as tools to better manage coral-reef fisheries and indirectly confer resilience to reef ecosystems in general and coral populations in particular (i.e., the managed-resilience hypothesis) (Bellwood et al. 2004, Mumby & Steneck 2008). Increased resilience is believed to be important for recovery from disturbances such as storms, disease outbreaks, and mass bleaching caused by ocean warming. Increased resilience is believed to be conferred by herbivorous fish and thereby lowering competition with space-monopolizing macroalgae (Mumby & Steneck 2008). This idea is appealing because it implies that MPAs and resilience management are the primary reef-conservation strategies for local, national, and international agencies and numerous nongovernmental organizations. The establishment of no-take MPAs and herbivore fishery management areas. A growing number of tropical nations have banned the harvest or sale of herbivorous fish, and there is a remarkably broad acceptance among scientists. A survey of 82 international coral-bleaching experts found that 94% believed that no-take MPAs were somewhat effective in achieving these goals, while 0% and 1% (respectively) thought MPAs and parrotfish protection were ineffective (some respondents had no opinion). But does conservation have any social consequences of these policies?

Here, we test the hypothesis that MPAs, and by extension parrotfish protection, increase the resilience of coral assemblages to large-scale disturbances. We examine the effects of large-scale disturbances, including storms, disease outbreaks, and acute periods of ocean warming. Our results indicate that MPAs have no general effect on coral loss and recovery from large-scale disturbances and local (mostly biotic) causes of coral loss and for synergies between these drivers. Finally, we discuss some of the potential costs of implementing ineffective policies.

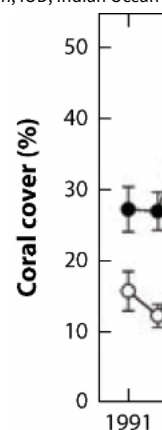
2. IS MANAGED RESILIENCE EFFECTIVE?

2.1. Managed-Resilience Theory

Resilience is the capacity of a system to resist (i.e., limit effects) and recover from a disturbance (Holling 1973, Nyström et al. 2000). In ecology, resilience is measured as the rate of recovery from a disturbance (the smaller the change, the higher the resistance), and recovery is measured as a rate or absolute time to return to the predisturbance state (the faster the recovery, the higher the resilience).

Figure 2

Example of a long-term field study that measured the effect of disturbances on coral cover in unfished (protected) and fished sites. Abbreviations: ENSO, El Niño–Southern Oscillation; IOD, Indian Ocean Dipole.



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In the context of the protection of coral-reef ecosystems from ocean warming, numerous mechanisms and management actions that could increase resilience have been proposed. Increased coral cover (Burkepile & Hay 2006, Burkepile et al. 2009, Mumby et al. 2006, Williams & Polunin 2001). Increased herbivory is assumed to decrease competition for space, thereby theoretically increasing the postdisturbance recovery rate of coral populations. The hypothesized interaction chain leading from management to coral cover includes: (1) management (protection) of parrotfishes (and other herbivores) on algae (primarily macroalgae); (2) algae on coral recruitment, growth, and survival; and (3) coral recruitment on rates of postdisturbance recovery from storms and other acute disturbances (Shaver et al. 2017). Therefore, in theory, mitigating these local-scale stressors should increase the resilience of coral reefs.

Figure 3

The theoretical multistep interaction chain linking the management (protection) of parrotfishes [generally through targeted bans or fishery closures (marine protected areas or marine reserves)] with coral cover.



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2.2. Field Tests of Managed Resilience

Despite near-universal buy-in from coral-reef scientists, nongovernmental organizations, and governmental agencies, there is virtually no evidence in support of large-scale disturbances in 66 MPAs and 89 unprotected control sites (**Table 1**). The study outcomes have been remarkably consistent: They found no significant protection benefited functionally important coral species (e.g., acroporids and massive, framework-building species), which provide a disproportionate amount of cover averaged across studies immediately after a disturbance tended to be greater, not smaller, inside MPAs [$12.3\% \pm 5.5\%$ (mean \pm 1 SE)] than it was on unprotected sites ($d.f. = 14, p = 0.43$) (**Figure 4**).

Table 1

Characteristics and outcomes of 18 tests of the managed-resilience concept

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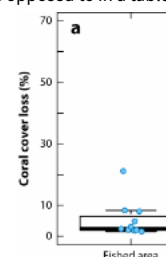
Reference	Location	
Bégin et al. 2016	Saint Lucia, Caribbean	No
Bood 2006	Belize, Caribbean	No
Coelho & Manfrino 2007	Little Cayman, Caribbean	No
Darling et al. 2010	Kenya	No
Graham et al. 2008	Indian Ocean	No
Graham et al. 2015	Seychelles	No
Halpern et al. 2013	Solomon Islands	No
Harris et al. 2014	Seychelles	No
Huntington et al. 2011	Belize, Caribbean	No
Jones et al. 2004	Papua New Guinea	No
Manfrino et al. 2013	Little Cayman, Caribbean	No
McClanahan 2008	Kenya	No
McClanahan et al. 2001	Kenya	No
Miller et al. 2009	US Virgin Islands, Caribbean	No
Mumby & Harborne 2010	Bahamas, Caribbean	Yes
Muthiga 2009	Kenya	No
Russ et al. 2015	Philippines	No
Toth et al. 2014	Florida Keys	No

We considered only direct empirical field tests that measured change in absolute coral cover within at least one protected area [marine protected areas (MPAs) and fully protected or no-take marine reserves] and one control area (change over time after a disturbance) disturbances. The MPAs come from 15 countries (and two regions of the United States—the Florida Keys and the US Virgin Islands) and a wide range of reef types and biogeographic regions.

^aB, bleaching or warming event; C, cyclone or hurricane; D, disease; S, sediment.

Figure 4

Results of a meta-analysis of published studies measuring the effectiveness of local protection [i.e., marine protected areas (MPAs)] in reducing the effects of large-scale disturbances on (a) the loss in absolute coral cover. In each study, we recorded the mean disturbance impacts (coral cover per year) and recovery rates (percentage change in coral cover per year). We extracted values presented in a figure (as opposed to in a table).



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All 18 studies measured the effectiveness of well-enforced no-take reserves for coral protection. For example, one year before the establishment of three no-take reserves, coral cover was similar at protected and control sites (Toth et al. 2014). Nearly all of the coral loss, especially in the reserves, was due to partial or whole-colony mortality of ecological framework-building species. Postsettlement survival appeared to be low (van Woesik et al. 2014). Significant coral loss occurred even though a previous study found that abundances of herbivores were higher in the no-take reserves, as has been observed elsewhere (Mumby et al. 2006). Likewise, Harris et al. (2014) found that two isolated and well-protected macroalgal dominance despite the absence of fishing and the high densities of herbivorous fishes.

In one case (out of 18 studies), the authors interpreted their results as supporting the managed-resilience hypothesis for coral reefs. Mumby & Harborne (2009) However, the measured increase in absolute coral cover in the reserve was very small (1.3% across four stations over 2.5 years), and the total coral cover was similar to the recovery rate of ~4% annually on unprotected reefs (as reported by Graham et al. 2011) and the average rate of 1.5% annually across all 155 sites (including 100 corals that have been replacing the formerly dominant taxa across the western Atlantic for several decades (Green et al. 2008) at a significant cost to ecosystem health. The coral taxa upon which conservation efforts are focused (i.e., mainly *Orbicella* and *Acropora* spp. in the Caribbean) will benefit from herbivore and seaweed removal and recruitment of these framework-building species. In many of the tests of the managed-resilience hypothesis (Table 1), postdisturbance recruitment was low due to low coral settlement or because benthic grazing increased postsettlement mortality (i.e., link 4 in Figure 3 is weak and/or context dependent).


For more than a million years, Caribbean reefs were dominated by branching acroporid corals (*Acropora cervicornis* and *Acropora palmata*), massive boulder corals, and species has declined dramatically throughout the region, primarily due to coral disease and bleaching (Aronson & Precht 2006, Bruckner & Bruckner 2006). With rapid growth, these corals played a critical role in habitat provision and reef accretion (Alvarez-Filip et al. 2009, Kennedy et al. 2013) and thus in the primary production of these weedy corals may provide a living veneer that helps to shield reefs from erosion, their capacity for reef accretion and the long-term production of reef framework with encrusting or slow-growing massive corals in the genus *Porites* in the western Pacific and eastern Indian Oceans (Graham et al. 2006, Wilson et al. 2007). Successful, as existing strategies may not result in ecologically significant increases in the species that fill functional roles important to people and ecosystems.

2.3. Synthetic Tests of Managed Resilience

Four studies (Carassou et al. 2013, Graham et al. 2011, Selig & Bruno 2010, Selig et al. 2012) have used global survey databases to test the managed-resilience hypothesis that MPAs did not measurably reduce the effects of ocean warming (measured as the frequency of thermal stress anomalies) on coral cover loss (Selig et al. 2012). In the Great Barrier Reef, where bleaching was not lessened inside MPAs (Hughes et al. 2017b), Carassou et al. (2013) also found that coral losses immediately after climate change acute disturbances was not higher inside MPAs (Figure 5b,d). Combined, these studies include an enormous range of reef types, geographic locations, MPA types, and MPAs and regions. The fact that the results of both approaches are clear and concordant increases confidence in the conclusion that MPAs do not measurably reduce the effects of ocean warming on coral cover loss.

Table 2

Synthetic tests of the managed-resilience hypothesis for coral reefs

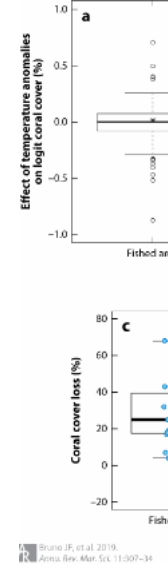
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Reference(s)	
Selig & Bruno 2010, Selig et al. 2012	4,456 sites, 310 MPAs, 83 countries
Graham et al. 2011	48 sites, 7 MPAs, 13 countries or US states
Carassou et al. 2013	36 sites, 17 MPAs, 15 countries

Abbreviation: MPA, marine protected area.

Figure 5

Results of published synthetic studies of the effect of local protection via the implementation of marine protected areas (MPAs) on the resilience of coral assemblages. (a) Effect of thermal stress anomalies on coral cover loss (measured as annual mean rate of change in absolute coral cover after disturbance), based on a meta-analysis of 22 studies (n = number of sites, error bars = 95% bootstrapped confidence interval); panel b is based on Graham et al. (2011); and panels c and d are based on values in appendix S2 from Carassou et al. (2013), which were extracted from 27 publications, including the Great Barrier Reef.



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3. WHY DOESN'T MANAGED RESILIENCE WORK?

Although countless opinion pieces, small-scale mechanistic experiments, and modeling studies support the managed-resilience hypothesis for coral reefs, the reality of coral-reef management. How did we get it so wrong? There are numerous non-mutually-exclusive explanations, which we explore below.

3.1. Marine Protected Areas Do Not Benefit Herbivores

First, it is possible that poor design, implementation, or enforcement of MPAs (Edgar et al. 2014) limits their effectiveness in promoting the components of resilience. Boundaries or because populations that could act as larval sources are being fished. This seems unlikely since many of the no-take reserves included in the marine reserves in the Florida Keys (Kramer & Heck 2007, Toth et al. 2014) and the Philippines (Russ et al. 2015) had higher parrotfish biomass, yet the effective restoration of fish communities in some protected areas could undermine efforts to manage macroalgae if replenished carnivores could reduce grazing by either consuming herbivores or altering their foraging behavior (Houk & Musburger 2018).

3.2. Context Dependency

The context dependency of the component links in Figure 3 could also explain the ineffectiveness of managed resilience. For example, grazing intensity depends on the size of herbivores also significantly affects their per capita effects, with larger parrotfishes often consuming more and different algae than smaller congeners (Bruno et al. 2015). Therefore, effectively protecting herbivores in general may not guarantee increased top-down control of algae.

Another important contingency is the rate and bulk amount of primary production. Coral mortality opens up new space for algae, subsequently requiring higher grazing rates, thus the grazing rate required to control macroalgae. If most or all of the managed-resilience links (Figure 3) are context dependent, which seems likely, the effectiveness of managed resilience will be highly variable.

There might be ecological contexts in which herbivorous fishes—or, more specifically, parrotfishes—do not play a major role in grazing pressure. For example, batfish (family Ephyraeidae) (Bellwood et al. 2006). Fishes are also sometimes not the main herbivores. In the Caribbean, for instance, the decline of parrotfishes coincided with the return of the urchin *Diadema antillarum*, which was decimated by disease in the early 1980s, to some Caribbean reefs with healthy parrotfish populations.

Finally, Harborne & Mumby (2018) argued that parrotfishes can increase coral resilience only in the absence of disturbances like warming-induced disease and temperature anomalies (Oliver et al. 2018) and mass coral-bleaching events (Hughes et al. 2018a) are increasing globally. The average return time of several disturbances, resistance is clearly the more important component of resilience for reef conservation and the maintenance of ecosystem services. Yet nearly all models assume a disturbance during the recovery phase, and more realistic models that include disturbance come to very different conclusions. For example, Representative Concentration Pathway 8.5, parrotfish conservation delayed degradation by only approximately 10 years.

3.3. Macroalgal Dominance Is Uncommon

If seaweed is not the dominant benthic space holder, then promoting herbivory will do little to increase coral settlement and recruitment. Even across the globe (Jackson et al. 2013, Jackson et al. 2014, Schutte et al. 2010). Vroom (2011) found that relatively high levels of macroalgal cover can be natural even on pristine, isolated reefs. Vroom et al. (2011) found that the extreme dominance of macroalgae across reefs in Jamaica—widely viewed as the poster child for phase shifts in the region—is actually a global phenomenon (Loh et al. 2015, Norström et al. 2009), or simply by bare substrate covered in turf or crustose coralline algae (Toth et al. 2014). Management designed to reduce macroalgal cover may be ineffective.

3.4. Interactions Between Stressors Are Antagonistic

The effective mitigation of local ecological stressors could, paradoxically, increase community sensitivity to large-scale disturbances (Côté & Darling 2010). Antagonisms between stressors (where one factor reduces the effect of another) were as common as synergies. On coral reefs, fast-growing and competitive mechanism of observed antagonisms among stressors on reefs (Darling & Côté 2008, Darling et al. 2010).

Cosensitivity and its corollary, cotolerance, could explain why the negative effect of large-scale disturbances (natural or anthropogenic) on coral cover depends on the density of coral species (Côté & Darling 2010, Selig et al. 2012, Zhang et al. 2014; but see Carassou et al. 2013). This is likely due to the relationship between total coral cover and coral species cover. From a conservation perspective, such density dependence is obviously good news for conservationists; it suggests that a negative feedback, such as an increase in the relative cover of coral species, could increase community sensitivity to disturbance (Côté & Darling 2010, Darling et al. 2010). Likewise, even if the mitigation of local stressors increases coral cover, it could also increase community sensitivity to disturbance.

4. THE RELATIVE AND REALIZED EFFECTS OF LOCAL AND GLOBAL STRESSORS

Another possible explanation for the general failure of the managed resilience of coral assemblages is that the effects of localized stressors are simply insignificant. Whether in the laboratory or the field—to be invaluable tools in applied reef ecology. Experiments enable controlled tests of the effects of putative biotic and abiotic stressors. However, field studies are often needed to make a strong inference about cause and effect from an observed relationship in a mensurative study. But experiments usually cannot be conducted on coral disease severity, but that result did not indicate that nutrient pollution was actually affecting coral–disease dynamics or how important it might be relative to other factors.

Descriptive survey data, usually replicated across space and time [i.e., through a monitoring study, ideally with a BACI (before–after, control–impact) design], can provide evidence. For example, if fishing and parrotfish abundance are important drivers of coral loss, reefs with the greatest parrotfish biomass should have reduced (or no) coral loss. (a) the effect size of fishing or fish biomass was small relative to that of other factors or (b) fishing and parrotfishes were important, but their effect depends on other factors. Field studies that enabled tests of these predicted associations. Although spatiotemporal relationships alone do not prove the importance of a putative cause, they are a necessary condition. A factor could cause coral mortality or population declines, (b) experimental evidence of such an effect in a controlled setting, (c) evidence that the factor had the predicted effect in the field in the predicted manner (e.g., coral cover decreased most rapidly where and when the magnitude of the factor was greatest).

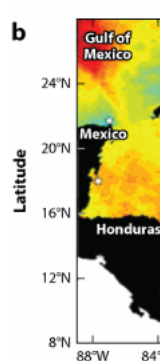
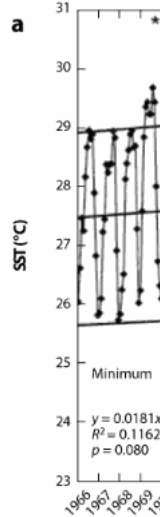
4.1. Evidence That Ocean Warming Causes Coral Loss

The experimental and observational evidence that anomalously high temperatures (often only 0.5–2°C beyond typical summer highs) are stressful (and lethal) to coral is growing. This is supported by Baker et al. (2008). Countless laboratory experiments have documented the strong effect of temperature on coral survival, calcification, and even reproduction.

Satellite records and direct temperature measurements indicate that nearshore seawater temperatures increased significantly during the period of global climate change. The regional average warming rate across the Greater Caribbean region from 1985 to 2009 was 0.27°C per decade, with some regions, such as the southwestern Caribbean, warming at rates of 0.4–0.5°C per decade. Warming in these regions in general (Lough et al. 2018) but nearly four times greater than the observed rate of global ocean-surface warming since 1960 [0.07°C per decade (IPCC 2007)] beginning of the twentieth century) began roughly five decades ago and that the average temperature of many reefs has already increased by approximately 0.5°C since the

Figure 6

Recent warming of the Greater Caribbean region. (a) Trends in monthly mean sea-surface temperature (SST) from La Parguera, Puerto Rico, based on in situ measurements. Asterisks indicate years of severe

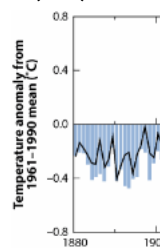


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Figure 7

Temporal relationships between ocean warming and coral cover decline. The blue and pink bars show the average annual temperature anomalies for land and sea from a 1961–1990 baseline [based on the dataset]. The orange line shows the temporal trend in absolute mean Caribbean coral cover (based on a regional meta-analysis). Figure adapted from **Gardner et al. (2003)** and **Lough et al. (2018)**.



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Hundreds of field studies have documented the strong positive association between anomalously high ocean temperatures and coral bleaching and subsequent mortality (e.g., **Harvell et al. 2009**), which takes into account the magnitude and duration of anomalously high temperatures during a 12-week period at a given site. Degree heating weeks (DHW) is a metric that quantifies the general association (global, across decades) also exists between ocean temperature anomalies and coral loss (**Selig et al. 2012**). Coral mortality during these events is often linked to the **Harvell et al. 2009, Randall & van Woiesik 2015**). The final smoking gun is the long-term association between coral loss and the gradual warming of reefs (e.g., **Harvell et al. 2009, Randall & van Woiesik 2015**). The evidentiary components are present: a biological explanation, experimental evidence, evidence for an increase in frequency and magnitude, and the prediction of future coral loss.

Table 3
 Summary of the evidence supporting the putative effect of four drivers of adult coral mortality and/or coral population dynamics, leading to observed declines in coral cover and reef health.

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Evidence component**Nutrients**

Biological explanation	Yes	Yes
Experimental evidence	Mixed	Yes ^a
Increase in prevalence or magnitude	Unknown	Yes
Predicted spatiotemporal relationship	No	Mixed

^aEvidence of an effect on coral recruitment but not on adult mortality, changes in coral cover, absolute coral cover, etc.

4.2. Evidence That Localized Stressors Cause Coral Loss

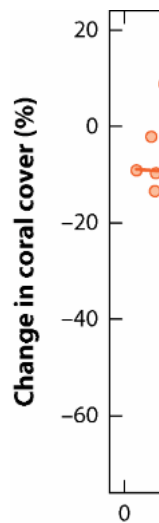
Numerous reviews and meta-analyses of evidence have linked various putative local anthropogenic drivers with coral mortality, including sedimentation (F) coral reefs—fishing and nutrient pollution—are important drivers of regional- to global-scale coral loss. We also assess evidence for the role of macroalgae in focus on these local factors and not others because they are widely believed to interact synergistically with ocean warming, an assumption that underlies the

4.2.1. Fishing and herbivore biomass.

Fishing is thought to cause coral mortality directly through the use of destructive fishing practices (e.g., **Fox & Caldwell 2006**) and indirectly by reducing the macroalgae, and a large number of experiments (generally based on exclusion cages) have demonstrated the strong top-down effects of parrotfish grazing on benthic communities dominated by crustose coralline algae and filamentous turfs (**Steneck 1988; Hay 1991, 1997**), thereby promoting the settlement, growth, and reported negative associations between the cover of macroalgae and the biomass of herbivorous fishes (**Mora 2008, Newman et al. 2006, Williams & Polunin 2008**) as a result they attributed to an increase in nutrient pollution. Similarly, **Russ et al. (2015)** argued that macroalgal cover at six sites monitored over 30 years ago. There is clear evidence of widespread and striking declines in fish biomass on coral reefs, including general declines in parrotfish biomass (**Paddack et al. 2015**). Tests for mechanistic links between coral and fish assemblages have focused on how coral mortality affects the composition and diversity of fishes via habitat loss. In the Caribbean was unrelated to coral loss (**Figure 8**).

Figure 8

Relationship between change in coral cover and parrotfish biomass. Each point represents a location average based on surveys performed between 1965 and 2012 of 1–17 reefs per location. This relationship



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Why are there no large-scale-pattern data to corroborate results from fish exclusion experiments? One explanation is that the studies just have not been done up to the seascape and regional scales to which they have been widely applied. Moreover, the treatments in many of these experiments are unrepresentative (fishes and animals larger than a few centimeters) and therefore may not predict the outcome of management actions. It is also possible that the effects of experiments are context-specific, influenced by environmental context, larval connectivity, or other factors that influence coral resistance and recovery. Strong effects at all five links are necessary for effective management (**2015**).

4.2.2. Nutrient pollution.

Excess nutrients (nitrogen and phosphorus) could harm corals directly or indirectly by facilitating the growth of benthic macroalgae. The hypothesized role of nutrient pollution in coral loss and concluded,

Critical examination of both experimental laboratory and field studies of nutrient effects on corals and coral reefs, including the Elevated N documented at anthropogenically-enriched sites can affect the physiology of corals in a harmful way, or for most cases, be the sole or major cause of coral mortality. (p. 743)

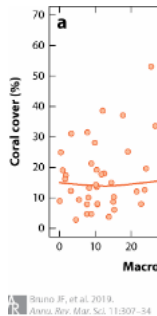
The more recent science has not substantially changed this broad evaluation (e.g., **Humanes et al. 2017**), although there is a growing appreciation for the potential that multisite nutrient monitoring makes it almost impossible to assess whether and (if so) where nutrient concentrations on reefs are increasing. There are certainly challenges in testing whether nutrient pollution is related to macroalgal growth and cover or to coral cover or mortality at large scales and on reefs tens or hundreds of kilometers apart.

4.2.3. Macroalgae.

Increases in macroalgae could result from fishing, nutrient pollution, or even ocean warming via coral mortality. Although macroalgae have been shown to inhibit the growth of juvenile corals via shading and abrasion (reviewed in **McCook et al. 2001**), which might, in theory, affect coral population recovery (**Steneck et al. 2002**), the transmission or severity of coral diseases, e.g., by harboring pathogens or facilitating them through the release of dissolved organic carbon (**Smith et al. 2006**), and that several species of macroalgae, placed in close proximity to juvenile and adult corals, had no effect on among-colony disease transmission rates or withstanding mortality. Countless studies have documented increases in benthic macroalgae at individual sites around the world, and several meta-analyses have quantified regional-scale, widespread cause of coral loss. The increase in macroalgae across the Caribbean is often invoked as evidence that macroalgae caused the observed decline in coral cover (**Schutte et al. 2010**). A more parsimonious explanation is that the increased cover of macroalgae was due to reduced competition with corals and, in shallow reefs, rapidly after mass coral mortality events, presumably due to the reduction in competition for space (**Aronson & Precht 2001b, Stoddart 1969**). The common view is that numerous studies have reported that the large-scale spatiotemporal dynamics of coral and macroalgal cover appear to be unrelated. In a regional-scale assessment, other long-term monitoring studies have documented this apparent decoupling of coral and macroalgal community dynamics (**Aronson et al. 2012, Colvill et al. 2012**).

Figure 9

Relationships between (a) coral cover and macroalgal cover and (b) change in coral cover and change in macroalgal cover across the Caribbean region. Each point represents a location average based on



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4.3. Isolated Reefs as Indicators of Coral State in the Absence of Local Stressors

One way to test the relative and interactive effects of putative local and global drivers of coral decline is to compare coral loss across a gradient of human population density from any human settlement or activities (**Sandin et al. 2008**). For example, nutrient pollution on reefs should be associated with the coastal human footprint. In some communities, the intensity of fishing on reefs is still strongly related to proximity to ports and people (**Nadon et al. 2012, Stallings 2009**). A decrease in coral cover could be either (a) their effects are synergistic or (b) the effects of local factors are greater.

In one of the first applications of this approach, **Lirman & Fong (2007)** found that live coral cover on 84 patch reefs in the Florida Keys was strongly negatively related to human population density (and lower partial mortality rates). **Sandin et al. (2008)** found lower coral cover adjacent to islands with more people in a limited comparison of four central Pacific Islands. Macroalgal cover was also not related to human population density. These findings suggest that either (c) local stressors have only a small effect on these reefs, or with the hypothesis that the effects of local and global factors are multiplicative—a critical assumption of the managed-resilience paradigm.

During the marine heat wave of 2016 [which coincided with a strong El Niño event but was caused by anthropogenic ocean warming, via the gradual increase in sea surface temperatures], thermally sensitive species—experienced mass bleaching and coral loss. Some of the hardest hit included the world's most isolated and well-protected reefs. This has been a wake-up call, forcing scientists to reevaluate assumptions about the inherent resilience of these reefs. In retrospect, the recent high coral cover on these reefs (despite extreme spatial isolation and effective management) did not prevent striking ecosystem change in response to a heat wave, the magnitude of which is predicted to increase.

4.4. Evidence Summary

The warming of the near-surface portions of tropical seas has been unambiguously and mechanistically linked with coral loss. By contrast, evidence that local-scale management actions are limited or absent or suggest that the realized effect size is small or even undetectable. For example, **Steneck et al. (2018)** found that a mere 8% of the variance in coral cover among authors argued that the realized effects of management on fish communities were attenuated by the complexity of the linkages between fishing and coral populations. The effects caused by greenhouse gas emissions, especially given the compositional mismatch between the functionally important species being lost and those being protected.

5. NEGATIVE CONSEQUENCES OF HERBIVORE PROTECTION

The coral-reef structures built over thousands of years provide the foundation for marine biodiversity, fisheries, and local economies in tropical and subtropical regions. The provision of ecosystem services depends on the ability of reefs to maintain a structurally complex surface and vertical accretion (**Kennedy et al. 2013, Kuffner & Toth 2016**). The loss of herbivorous corals over the last several decades has begun to tip the balance from reef accretion to reef erosion (**Kennedy et al. 2013; Kuffner & Toth 2016; Perry et al. 2014**). Effective management on promoting reef accretion and mitigating reef erosion may be crucial to preventing the remaining reef structure from being lost (**Kuffner & Toth 2016**).

Paradoxically, the policies enacted to promote reef resilience by protecting herbivorous fishes may actually exacerbate the problems of declining coral health. For example, the loss of herbivorous corals, i.e., the *Orbicella* spp. complex in the Caribbean and *Porites* spp. in the Pacific (**Bonaldo et al. 2011, Rotjan et al. 2006**). Although their preferred prey are corals, the impacts of corallivory can also reduce the resilience of coral colonies to acute disturbances like coral bleaching (**Rotjan et al. 2006**) and may provide a vector for disease. If coral cover was high, the reduction in coral abundance has focused predation on remaining colonies, making it a greater threat to the coral populations that remain.

A larger threat is the bioerosion of dead coral skeletons and the reef framework by scraping and excavating parrotfishes. Although some researchers have supported this claim. Indeed, one of the most dominant parrotfishes in the Caribbean, the stoplight parrotfish *Sparisoma viride*, is also the most destructive bioeroder. It has become the dominant contributor to reef bioerosion in this region (**Perry et al. 2014**). In a survey of the contemporary carbonate budget throughout the Caribbean, budgets are likely relatively low compared with historic levels due to the region-wide decline in herbivorous fish populations and the loss of *Diadema antillarum* (**Perry et al. 2014**). Destroying the reef structures that remain, and carbonate budget deficits on reefs are predicted to worsen as reef communities shift to slower-calcifying taxa.

6. IF NOT MANAGED RESILIENCE, THEN WHAT?

The persistence of coral reefs and the valuable ecosystem services they provide (**Figure 1**) may require a paradigm shift in management. It is clear that the current paradigm is not justified under most conditions encountered on today's reefs. This is not to say that promoting the recovery of herbivore populations cannot ever help. However, herbivores are increasingly rare on modern coral reefs (**Hughes et al. 2017a**). More realistic simulation models of coral-reef dynamics affected by climate disturbances suggest that herbivore populations are unlikely to recover to historic levels (**Edwards et al. 2011, Kennedy et al. 2013**). The inconvenient truth is that herbivorous fish management, on its own, is ineffective. It is clearly time that aggressive mitigation of greenhouse gas emissions is necessary to give coral reefs a chance to persist long into the future.

SUMMARY POINTS

1. The managed-resilience paradigm has virtually no empirical support. Marine protected areas (MPAs) do not measurably increase the resilience of coral communities to global climate change.
2. Among other possible explanations, managed resilience for coral reefs may be ineffective because of the complexity of the five-step cascade of ecological effects that underlie the managed-resilience paradigm.
3. It is plausible that MPAs and parrotfish protection could promote coral population resilience under some very narrow set of environmental conditions—high coral cover, low herbivory, and low ocean warming, which are increasingly uncommon on today's reefs.
4. The protection of herbivorous fishes, especially parrotfishes, which is a focus of managed resilience, is not ecologically benign. In large numbers, some parrotfishes can be destructive to coral reefs.
5. The empirical evidence linking coral loss to ocean warming is strong. By contrast, the roles of putative drivers of coral mortality that act on more local scales, such as fish herbivory, are less clear.
6. The many threats to coral populations must be tackled directly and independently. This is particularly true for ocean warming and other aspects of anthropogenic climate change that threaten the persistence of reefs and the critical ecosystem services they provide.

DISCLOSURE STATEMENT

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