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Climate Change, Coral Loss, and the Curious Case of the Parrotfish Paradigm: Why Don't Marine Protected Areas Improve Reef Resilience?

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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 to limit the effects of climate change on reef-building corals. However, in a literature review, we find little empirical support for the notion of managed resilience. We outline some 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 that the impacts of local stressors (e.g., pollution and fishing) are often swamped by the much greater effect of ocean warming on corals. Another is the sheer complexity (including numerous context dependencies) of the five cascading links assumed by the managed-resilience hypothesis. If reefs cannot be saved by local actions alone, then it is time to face reef degradation head-on, by directly addressing anthropogenic climate change—the root cause of global coral decline.

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 (**Figure 1**) (Spalding et al. 2017). The mean economic value of reefs with any tourism is $482,428 per square kilometer annually, and remarkably, the most valuable reefs generate more than $7 million per square kilometer annually (Spalding et al. 2017). Reefs also protect coastal communities from large waves generated by storms or tsunamis (Ferrario et al. 2014, Harris et al. 2018). However, these services and the continued existence of countless species that inhabit reefs depend on stable populations of reef-building corals, many of which have been declining globally.

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 & Selig 2007, Bruno et al. 2009, De'ath et al. 2012, Gardner et al. 2003, Hughes et al. 2018b, Jackson et al. 2014, Schutte et al. 2010). When coral cover declines, so does habitat complexity (Alvarez-Filip et al. 2009, 2011) and the diversity of reef inhabitants, including fishes and invertebrates (Idjadi & Edmunds 2006, Jones et al. 2004, Pratchett et al. 2008). Coral loss also leads to reduced fisheries production, tourism value, and coastal buffering (Moberg & Folke 1999). Moreover, the ability of reefs to continue to 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 only when the cover of fast-growing, framework-building species is relatively high (Kennedy et al. 2013; Perry et al. 2013, 2015).

Some putative localized factors causing coral population declines include increased water column turbidity, sedimentation, eutrophication and other forms of pollution, direct disturbances

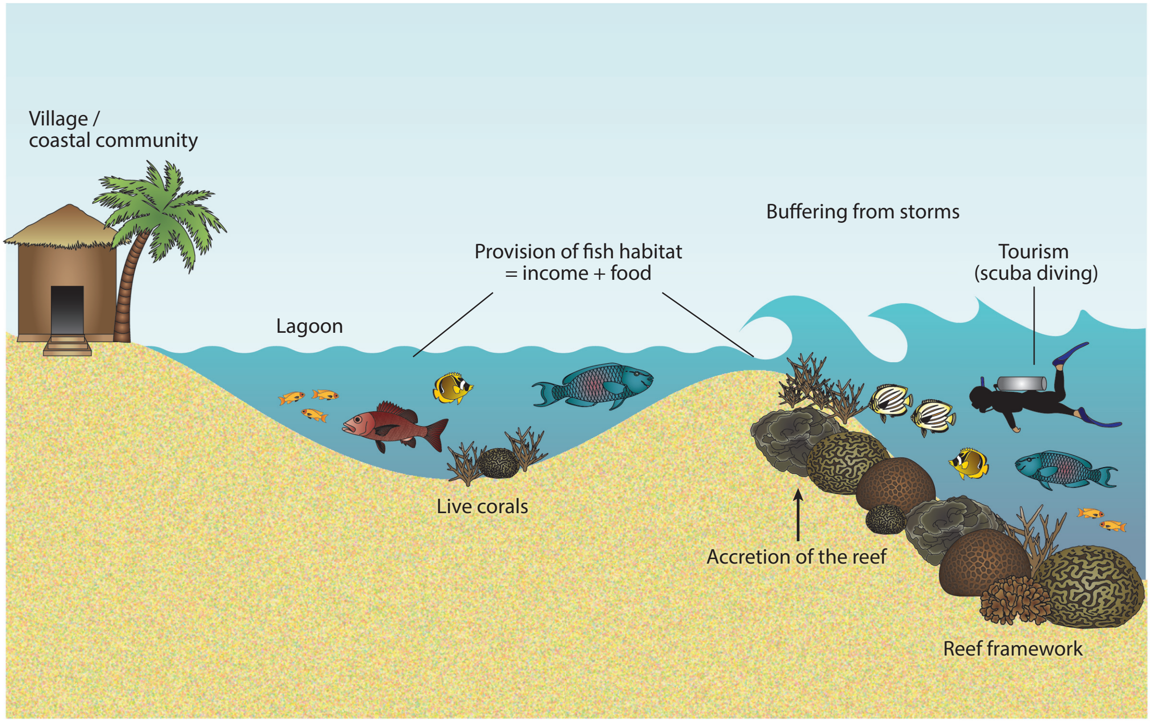

Figure 1
Ecosystem services provided by reefs and some of the geological and ecological features that support these benefits to people.

associated with fishing (e.g., the use of destructive gear), and the loss of fishes (including both predators and herbivores, especially parrotfishes). Disease 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. 2012), but the primary global factor of concern is ocean warming (Hughes et al. 2017a,b, 2018a,b). Related factors—including acidification, deoxygenation, and increased storm 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, reduce or eliminate other localized human disturbances, and increase or maintain biodiversity. MPAs and overall attenuations of local stressor intensity are also widely believed to indirectly confer resilience to reef ecosystems in general and coral populations in particular (i.e., the managed-resilience hypothesis) (Bellwood et al. 2004, Hughes et al. 2010, Mumby & Steneck 2008, Nyström et al. 2008, Roberts et al. 2017, West & Salm 2003). More specifically, controlling local stressors is thought to improve coral resistance to and recovery from disturbances such as storms, disease outbreaks, and mass bleaching caused by ocean warming. Increased resilience is believed to be conferred to corals via a range of physiological mechanisms, through stronger immunity and better health (Lamb et al. 2016), and ecological processes, e.g., by increasing grazing by herbivorous fish and thereby lowering competition with space-monopolizing macroalgae (Mumby & Steneck 2008). This idea is appealing because it implies that both local and global threats to reef ecosystems can be tackled with a single management action that can be taken by local governments.

MPAs and resilience management are the primary reef-conservation strategies for local, national, and international agencies and numerous nongovernmental organizations around the world. For example, the key policy recommendation of the recently released Coral Bleaching Recovery Plan for the US state of Hawaii (Soc. Sci. Res. Inst. 2017) was 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 fishes [e.g., Belize (Cox et al. 2013)], based on the idea that enhancing grazing will reduce macroalgae and restore coral populations. The managed-resilience hypothesis has remarkably broad acceptance among scientists. A survey of 82 international coral-bleaching experts found that 94% believed that no-take MPAs were somewhat or very effective in promoting coral-reef recovery and resilience (Rosinski & Walsh 2016). Three-quarters of respondents thought that parrotfish protection was effective at achieving these goals, while 0% and 1% (respectively) thought MPAs and parrotfish protection were ineffective (some respondents had no opinion). But does conserving herbivores through MPA establishment or fishing regulations really improve the resilience of coral populations and communities? If not, why not? And what are the negative ecological and 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 compile and analyze studies that conducted empirical field tests of the managed-resilience hypothesis by documenting changes in coral cover inside and outside of MPAs after major disturbances, including storms, disease outbreaks, and acute periods of ocean warming. Our results indicate that MPAs have no general effect on coral loss or postdisturbance recovery. We then explore possible explanations for the striking divergence between current thinking and empirical evidence. We also assess evidence for global (abiotic) 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 like managed resilience, including increasing bioerosion, which can accelerate the loss of the reef framework.

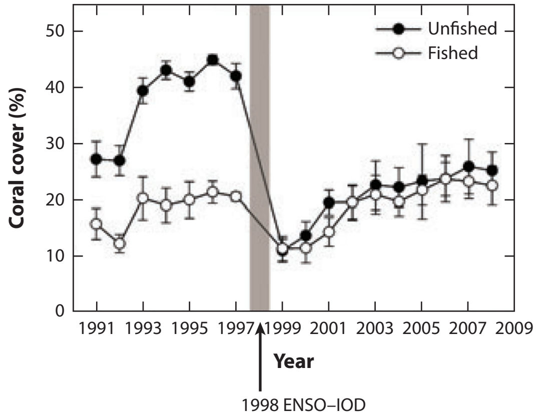

Figure 2

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. Figure adapted from Darling et al. (2010).

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 the degree of change (resistance) or rate of return to a similar predisturbance state (recovery) of a population or community. Multiple papers have developed and reviewed the application of resilience theory to coral-reef conservation (Bellwood et al. 2004, Hughes et al. 2010, Mumby & Steneck 2008, Nyström et al. 2008, Roberts et al. 2017, West & Salm 2003). In practical terms, resistance is measured as a change in ecological state (e.g., coral cover) in an experiment or monitoring study before and immediately after 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 rate, the greater the recovery) (**Figure 2**).

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. However, by far the most frequently discussed and promoted pathway is the protection of herbivorous fishes (e.g., parrotfishes and rabbitfishes) to suppress algal cover (Burkepile & Hay 2006, Burkepile et al. 2009, Mumby et al. 2006, Williams & Polunin 2001). Increased herbivory is assumed to decrease competition for space, chemical inhibition, disease transmission, and overgrowth of corals by macroalgae (Dixson et al. 2014, Hughes et al. 2007, Nugues et al. 2004, Smith et al. 2006), thereby theoretically increasing the postdisturbance recovery rate of coral populations. The hypothesized interaction chain leading from management to coral community resilience comprises five direct links (**Figure 3**): the effects of (1) management on fishing; (2) fishing on the abundance and size of parrotfishes and other herbivores; (3) parrotfishes (and other herbivores) on algae (primarily macroalgae); (4) algae on coral recruitment, growth, and survival; and (5) coral recruitment on rates of postdisturbance recovery of adult coral populations. It is also widely assumed that local stressors, which are presumably reduced in MPAs, increase the physiological sensitivity of corals to warming events and other acute disturbances (Shaver et al. 2017). Therefore, in theory, mitigating these local-scale stressors should increase the resilience of coral colonies and populations.

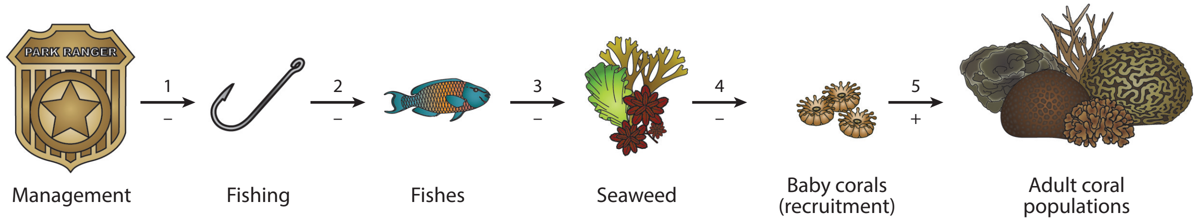

Figure 3

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 population resilience via the reduction of macroalgae, enhancement of coral recruitment, and adult population recovery following disturbances. The plus and minus symbols beneath the link arrows indicate the sign of the predicted interaction.

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 the managed-resilience hypothesis for coral reefs. We found 18 studies (not including prior synthetic studies and meta-analyses) that measured coral resistance to and/or recovery from large-scale disturbances in 66 MPAs and 89 unprotected control sites (**Table 1**). The study outcomes have been remarkably consistent: They found no significant effect of protection on total coral cover loss [11 out of 11 studies (**Table 1**)] or on the rate of postdisturbance coral cover gain (15 out of 16 studies). Critically, no study found that local protection benefited functionally important coral species (e.g., acroporids and massive, framework-building species), which provide a disproportionate amount of architectural complexity and carbonate accretion via their high growth rates (Alvarez-Filip et al. 2013, Kuffner & Toth 2016, Perry et al. 2015). The mean decline in absolute coral cover averaged across studies immediately after a disturbance tended to be greater, not smaller, inside MPAs [12.3% ± 5.5% (mean ± 1 SE)] than it was on unmanaged reefs (4.5% ± 2.0%; paired t-test, $t = -1.987$, d.f. $= 10$, $p = 0.08$) (**Figure 4**). There was no difference in coral recovery rates between control and managed sites (paired t-test, $t = -0.814$, d.f. $= 14$, $p = 0.43$) (**Figure 4**).

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 areas in the Florida Keys, the average coral cover in the no-take areas was greater than that in control sites, but 14 years later, the cover of coral and macroalgae did not differ between the 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 ecologically important boulder corals in the genus *Orbicella*. Coral recruitment rates were higher in the no-take reserves than in the fished sites, but the recruits were dominated by weedy taxa, and postsettlement survival appeared to be low (van Woesik et al. 2014). Significant coral loss occurred even though a previous study found that abundances of herbivorous fish (adult scarids, acanthurids, and pomacentrids) were higher in the no-take reserves (Kramer & Heck 2007). Surprisingly, large numbers of herbivores did not translate to higher grazing rates 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-enforced marine reserves in the Seychelles had no effect on coral loss or recovery in response to mass bleaching. Here, too, benthic communities in the reserves shifted from coral to 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 (2010) reported that coral

Table 1 Characteristics and outcomes of 18 tests of the managed-resilience concept

Reference	Location	MPA effect?	Sites (MPA/control)	Duration (years)	Disturbance[a]
Bégin et al. 2016	Saint Lucia, Caribbean	No	6/6	10	S
Bood 2006	Belize, Caribbean	No	3/3	8	B, C
Coelho & Manfrino 2007	Little Cayman, Caribbean	No	2/5	6	B, C, D
Darling et al. 2010	Kenya	No	3/4	21	B
Graham et al. 2008	Indian Ocean	No	9/10	10	B
Graham et al. 2015	Seychelles	No	4/12	17	B
Halpern et al. 2013	Solomon Islands	No	3/3	5	S
Harris et al. 2014	Seychelles	No	6/15	6	B
Huntington et al. 2011	Belize, Caribbean	No	1/1	10	B, C, D
Jones et al. 2004	Papua New Guinea	No	4/4	7	B, S
Manfrino et al. 2013	Little Cayman, Caribbean	No	2/4	13	B, S
McClanahan 2008	Kenya	No	3/4	12	B
McClanahan et al. 2001	Kenya	No	4/4	1	B
Miller et al. 2009	US Virgin Islands, Caribbean	No	5/1	2	B, D
Mumby & Harborne 2010	Bahamas, Caribbean	Yes	4/6	3	B, C
Muthiga 2009	Kenya	No	2/2	12	B
Russ et al. 2015	Philippines	No	2/2	30	B
Toth et al. 2014	Florida Keys	No	3/3	15	B, C, D

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. We searched for articles using the terms "coral reef + resilience OR recovery OR resistance" via Web of Science. The tests measured resistance to (as change in coral cover before versus immediately after a disturbance) and/or recovery from (as rate of coral cover 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 realms. The average study duration was 10 years. One study (Bood 2006) was an unpublished MS thesis.

[a]B, bleaching or warming event; C, cyclone or hurricane; D, disease; S, sediment.

cover recovered from mass bleaching and hurricane impacts slightly faster inside the Exuma Cays Land and Sea Park in the Bahamas than it did outside the reserve. 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 still only 9% [~7% below the Caribbean average, and ~30–40% below the healthiest reefs in the region (Jackson et al. 2014)]. This recovery rate is substantially below the global average 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 protected and unmanaged reefs) analyzed in this review. Moreover, the two species for which cover increased significantly (*Porites astreoides* and *Agaricia agaricites*) are weedy, brooding 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 function (Alvarez-Filip et al. 2013). In the Caribbean, these are the only species that appear to be facilitated by the top-down control of

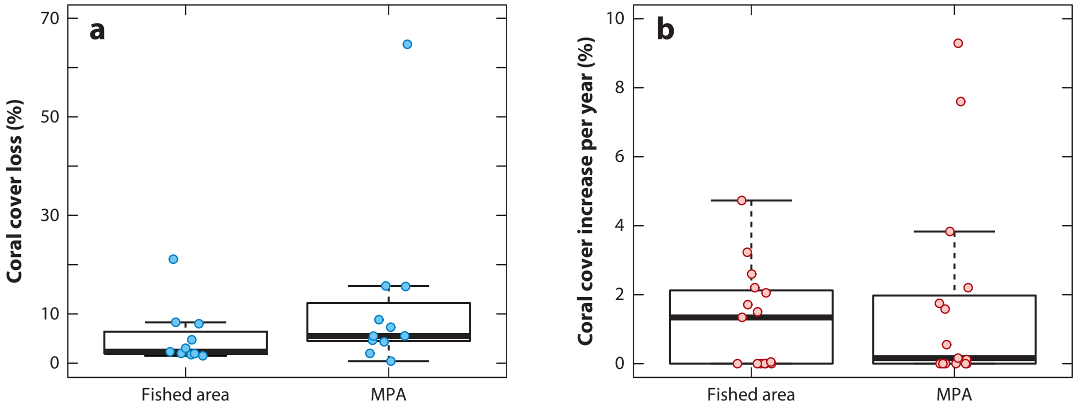

Figure 4

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, based on predisturbance coral cover minus postdisturbance cover (i.e., resistance), and (*b*) the postdisturbance increase in absolute coral cover (i.e., recovery rate). **Table 1** lists and describes the component studies. From 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 or in the text) using the ImageJ tool developed by the National Institutes of Health. All analyses were performed in R.

macroalgae. It has been assumed that eventually 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 management, but this assumption is unfounded if other factors (changing environmental conditions, reduced larval production caused by Allee effects, etc.) cause limited settlement and recruitment of these framework-building species. In many of the tests of the managed-resilience hypothesis (**Table 1**), postdisturbance recruitment was low despite intense grazing, abundant bare space, and little macroalgae (Harris et al. 2014, Russ et al. 2015, Toth et al. 2014, van Woesik et al. 2014), perhaps because other factors limited 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 in the genus *Orbicella*, and to a lesser extent massive brain corals (Kuffner & Toth 2016, Pandolfi & Jackson 2006). In the last several decades, the abundance of these foundation species has declined dramatically throughout the region, primarily due to coral disease and bleaching (Aronson & Precht 2006, Bruckner & Bruckner 2006, Weil et al. 2009), both of which are linked to ocean warming (Bruno et al. 2007, Harvell et al. 2009, Randall & van Woesik 2015). Due to their large size, complex colony architecture, and 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 ecosystem services people derive from reefs (**Figure 1**). These species have been replaced by smaller, slower-growing corals that generally do not fill the vacated functional roles. Although 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 frameworks is limited (Kuffner & Toth 2016, Perry et al. 2015). Similar compositional shifts are being observed in other regions, such as the replacement of plating and branching acroporids 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. 2012). The strong link between species growth morphology and functional role suggests that coral-reef

Table 2 Synthetic tests of the managed-resilience hypothesis for coral reefs

Reference(s)	Replication/extent	Findings
Selig & Bruno 2010, Selig et al. 2012	4,456 sites, 310 MPAs, 83 countries	MPAs reduce coral loss but not in response to ocean warming.
Graham et al. 2011	48 sites, 7 MPAs, 13 countries or US states/territories	Recovery from disturbance was slower in marine reserves.
Carassou et al. 2013	36 sites, 17 MPAs, 15 countries	MPAs have no effect on coral recovery from bleaching and storms.

Abbreviation: MPA, marine protected area.

conservationists may need to narrow their criteria for classifying management actions as successful, as existing strategies may not result in ecologically significant increases in the species that fill functional roles important to people and ecosystems (**Figure 1**).

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 for coral reefs (**Table 2**). Selig & Bruno (2010) found that, on average, coral loss was reduced in MPAs compared with unprotected sites; however, a follow-up study indicated 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)—i.e., MPAs did not increase coral resistance to high temperatures (**Figure 5*a***). This result is supported by recently observed patterns of bleaching intensity across Australia's 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 climatic disturbances were similar in MPAs and fished sites (**Figure 5*c***). Moreover, both Graham et al. (2011) and Carassou et al. (2013) found that the recovery rate of total coral cover from acute disturbances was not higher inside MPAs (**Figure 5*b*,*d***). Combined, these studies include an enormous range of reef types, geographic locations, MPA designs, coral species diversity, and disturbance characteristics. This meta-analytic approach complements the more localized studies (**Table 1**) performed by scientists familiar with specific 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 improve either aspect of coral resilience.

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 vast majority of field tests do not. The fact that the empirical evidence for and opinions about managed resilience are diametrically opposed (Rosinski & Walsh 2016) is a critical issue for 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 underlying effective managed resilience.

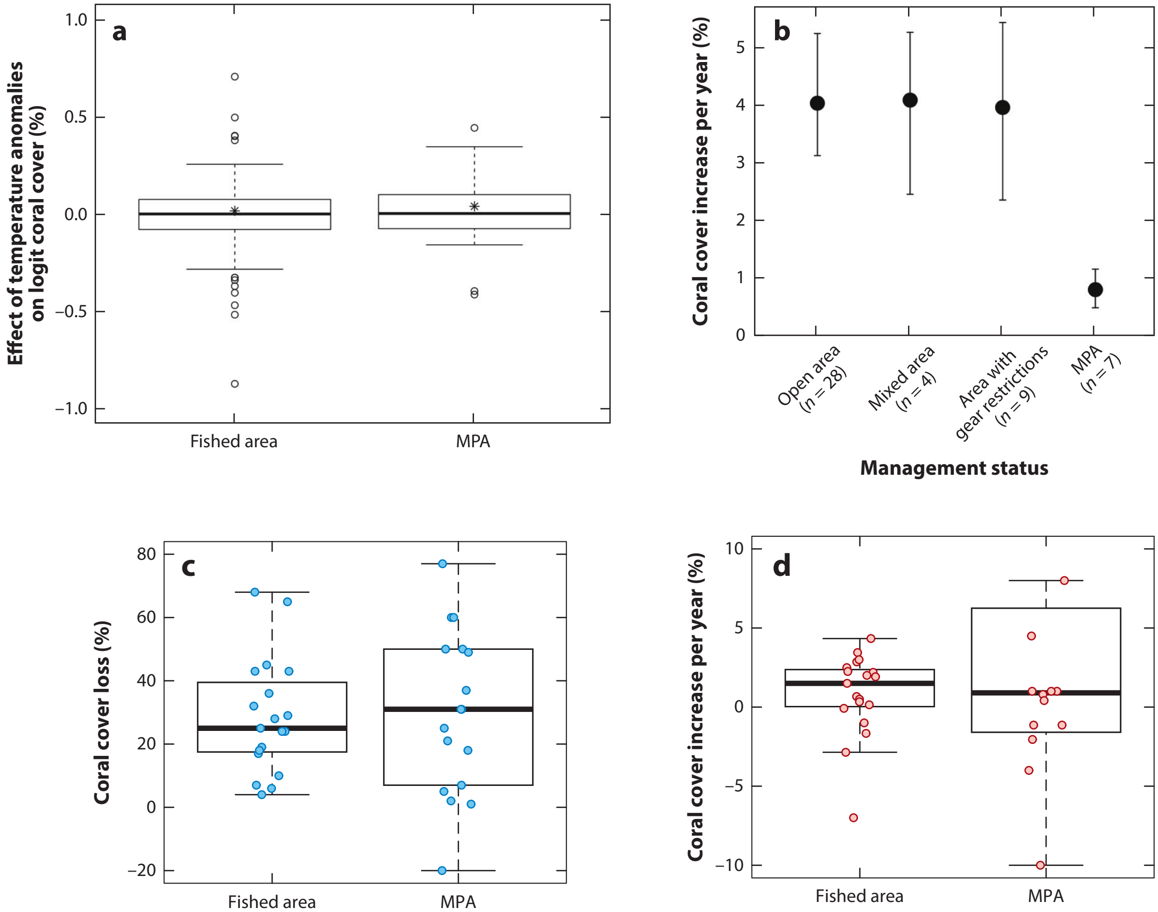

Figure 5

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 the change in absolute coral cover on reefs in MPAs and fished areas. Positive values indicate an increase and negative values a decline in absolute coral cover. (*b*) Effect of management status on the recovery of coral communities from large-scale disturbances (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). (*c*) Loss in absolute coral cover based on predisturbance coral cover minus postdisturbance cover (i.e., resistance) ($t = 1.18$, d.f. = 23.8, $p = 0.25$). (*d*) Recovery rate of coral cover after a disturbance ($t = 0.40$, d.f. = 23.5, $p = 0.70$). Panel *a* is based on Selig et al. (2012); 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 36 case studies.

Therefore, MPAs might not measurably increase parrotfish abundance and/or biomass (links 1 and 2 in **Figure 3**) because fishing occurs within protected 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 various analyses have demonstrated effectiveness in protecting herbivore populations and high overall fish biomass but have not demonstrated an effect on coral resilience. For example, no-take 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 there was no difference in macroalgal cover or dynamics between no-take reserves and fished sites.

Ironically, the effective restoration of fish communities in some protected areas could undermine efforts to manage macroalgae if replenished carnivores consume or alter the grazing behavior of herbivores (Dill et al. 2003). The strength and ubiquity of carnivore–herbivore–macroalgae trophic cascades on reefs are unknown, but there is growing evidence that sharks and other large predators can reduce grazing by either consuming herbivores or altering their foraging behavior (Houk & Musburger 2013, Madin et al. 2010). If this is true, then management could reduce fishing (link 1 in **Figure 3**) but fail to increase herbivore biomass (link 2) or grazing (link 3).

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 appears to depend on both algal and fish composition and richness due to differences in macroalgal defenses and herbivore dietary preferences (Adam et al. 2015; Burkepile & Hay 2010, 2011). The size of herbivores also significantly affects their per capita effects, with larger parrotfishes often consuming more and different algae than smaller congeners or conspecifics do (Bonaldo & Bellwood 2008, Lokrantz et al. 2008). Finally, the grazing rate of ectotherms is often positively related to temperature due to their strongly temperature-dependent metabolism (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 pressure to keep algal cover low (Williams et al. 2001, McClanahan et al. 2002). Nutrient pollution and natural variability in nutrient flux also influence primary production and 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, then the probability that the context that enables all five is present for a meaningful amount of time (years to decades) at any given site is obviously very low.

There might be ecological contexts in which herbivorous fishes—or, more specifically, parrotfishes—do not play a major role in grazing pressure. For example, the fish species that grazed down the lush macroalgae growing in fish exclosures on the Great Barrier Reef, once the cages were removed, were neither parrotfishes nor surgeonfishes, as had been expected, but batfish (family Ephippidae) (Bellwood et al. 2006). Fishes are also sometimes not the main herbivores. In the Caribbean, for instance, herbivorous urchins have at times been the dominant grazers on shallow-water reefs (Carpenter 1986), but their role is less marked on deeper reefs (Morrison 1988). The increase in coral cover that 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 (Carpenter & Edmunds 2006, Edmunds & Carpenter 2001) suggests that *Diadema* provides a different grazing function than parrotfishes.

Finally, Harborne & Mumby (2018) argued that parrotfishes can increase coral resilience only in the absence of disturbances like warming-induced disease outbreaks. Unfortunately, a regime of frequent bleaching and coral disease has become the new reality for nearly all coral reefs (Hughes et al. 2017a). In fact, the frequencies of high-ocean-temperature anomalies (Oliver et al. 2018) and mass coral-bleaching events (Hughes et al. 2018a) are increasing globally. The average return time of severe bleaching is now only six years (Hughes et al. 2018a), while the time for full coral assemblage recovery is decades to centuries. Thus, under the current context of increasingly frequent disturbances, resistance is clearly the more important component of resilience for reef conservation and the maintenance of ecosystem services. Yet nearly all hypothesized mechanisms and interventions are based on improving recovery. Nearly all resilience models based on parrotfish conservation assume plentiful coral settlement and infrequent (or no) disturbance during the recovery phase, and more realistic models that include disturbance come to very different conclusions. For example, Kennedy et al. (2013) modeled reef accretion rates with and without local protection (MPAs) under different ocean warming scenarios, and under the business-as-usual emissions scenario (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 Greater Caribbean, considered to be the hot spot of coral-to-macroalgal phase shifts (Jackson et al. 2014), the regional average macroalgal cover is below 20% (Bruno et al. 2009, Côté 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. Moreover, the baseline cover for macroalgae is far from clear, and thus it is also unclear how much (if at all) the macroalgal cover has increased (Bruno et al. 2014). Côté et al. (2013) 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 globally unique outcome of multiple causes of mass coral mortality. More often, corals are replaced by other invertebrates, such as sponges, soft corals, and corallimorphs (Aronson et al. 2002, 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 macroalgae could just as easily facilitate the establishment of these alternative space monopolizers, thereby maintaining or increasing the competitive landscape for settling corals.

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). It is generally assumed that multiple stressors have additive or synergistic effects at the individual or community level. However, Darling & Côté (2008) found that in multifactor experiments, antagonisms between stressors (where one factor reduces the effect of another) were as common as synergies. On coral reefs, fast-growing and competitively dominant taxa (e.g., acroporid corals) are often especially sensitive to multiple forms of disturbance (storms, predators, disease, warming, etc.). This cosensitivity is likely an underlying 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 strongly on predisturbance cover. Sites with high initial coral cover have substantially greater coral loss from bleaching, disease, storms, and probably other disturbances (Darling et al. 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 composition: High-cover reefs tend to be dominated by branching and plating acroporid corals and other competitively dominant species that are highly sensitive to disturbance. From one 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 more disturbance-tolerant species as cover declines, could limit loss at low levels of coral cover. On the other hand, it also suggests (perversely) that effectively promoting coral recovery could increase community sensitivity to disturbance (Côté & Darling 2010, Darling et al. 2010). Likewise, even if the mitigation of local stressors increased the resilience of individual colonies to acute warming events, it could still reduce community resilience by selecting for thermally sensitive taxa.

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 relative to the impact of global stressors like ocean warming. To test this hypothesis, we assessed evidence for global- versus local-scale drivers of coral loss. We consider experiments—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 factors on coral fitness and other response variables related to reef functioning. Experiments also allow tests of mechanistic explanations for observed effects. Finally, experimental 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 test whether a given factor is affecting coral health or mortality—only whether it could do so. For example, Bruno et al. (2003) found that experimental nutrient enrichment increased 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], are generally needed to assess whether the effects of a putative factor are realized and detectable (over the background noise inherent in most ecological systems) in the real world. 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 and/or higher coral cover (assuming that other factors, such as the disturbance regime, do not covary with parrotfish biomass). The absence of such a pattern would indicate that either (*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 another factor, such as coral cover or primary production. We based our assessments of whether a given factor was affecting coral loss at regional to global scales on descriptive survey data that enabled tests of these predicted associations. Although spatiotemporal relationships alone do not prove the importance of a putative cause, they are a critical component of impact assessment. Strong evidence in support of a given factor's role in coral decline would include four components: (*a*) a theory or biological explanation of how the 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 increased in prevalence or magnitude over time, and (*d*) evidence that the presence or magnitude of the factor was spatiotemporally related to concordant changes in coral cover 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 beyond species-specific thresholds) to reef-building corals (and essentially all ectotherms) is unequivocal. The mechanisms through which thermal stress is harmful to corals were reviewed by Baker et al. (2008). Countless laboratory experiments have documented the strong effect of temperature on coral survival, calcification, and even reproductive output, as well as the underlying mechanisms of bleaching (reviewed in Baker et al. 2008, Brown 1997).

Satellite records and direct temperature measurements indicate that nearshore seawater temperatures increased significantly during the period of global coral loss that appears to have begun in the 1970s (Gardner et al. 2003). Based on an analysis of satellite-derived sea-surface

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**

Evidence component	Nutrients	Fishing	Algae	Warming
Biological explanation	Yes	Yes	Yes	Yes
Experimental evidence	Mixed	Yes[a]	Yes[a]	Yes
Increase in prevalence or magnitude	Unknown	Yes	Yes	Yes
Predicted spatiotemporal relationship	No	Mixed[a]	Mixed[a]	Yes

[a]Evidence of an effect on coral recruitment but not on adult mortality, changes in coral cover, absolute coral cover, etc.

temperature data, Chollett et al. (2012) estimated that 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 faster, at more than 0.4°C per decade (**Figure 6**). This rate is generally concordant with other estimates for the Caribbean (Glenn et al. 2015, Jury 2011) and for coral-reef 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 (Burrows et al. 2011)] (**Figure 7**). An important finding of these and many similar studies of trends in tropical sea-surface temperature is that recent warming (excluding warming during the beginning of the twentieth century) began roughly five decades ago and that the average temperature of many reefs has already increased by approximately 1°C.

Hundreds of field studies have documented the strong positive association between anomalously high ocean temperatures and coral bleaching and subsequent mortality (Baker et al. 2008; Brown 1997; Eakin et al. 2010; Hughes et al. 2017b, 2018b). One widely used metric of accumulated thermal stress is degree heating weeks (Eakin et al. 2010), which takes into account the magnitude and duration of anomalously high temperatures during a 12-week period at a given site. Degree heating week values of 6–8 generally cause mass coral bleaching and mortality, although the precise impact depends on coral composition and cover (Hughes et al. 2018a, Selig et al. 2012). A strong general association (global, across decades) also exists between ocean temperature anomalies and coral loss (Selig et al. 2012). Coral mortality during these extreme events is due primarily to bleaching but also to disease outbreaks, which large-scale epidemiological studies have linked to temperature extremes and warming (Bruno et al. 2007, Harvell et al. 2009, Randall & van Woesik 2015). The final smoking gun is the long-term association between coral loss and the gradual warming of reefs (**Figure 7**)—a key pattern predicted by the hypothesis that ocean warming is a primary driver of the decline of coral populations and overall coral cover. In summary, for ocean warming, all four evidentiary components are present: a biological explanation, experimental evidence, evidence for an increase in frequency and magnitude, and the predicted spatiotemporal associations (**Table 3**).

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 (Fabricius 2005) and nutrient pollution (Szmant 2002). Here, we summarize the evidence available to test the hypotheses that the two most well-studied local issues that are putatively affecting coral reefs—fishing and nutrient pollution—are important drivers of regional- to global-scale coral loss. We also assess evidence for the role

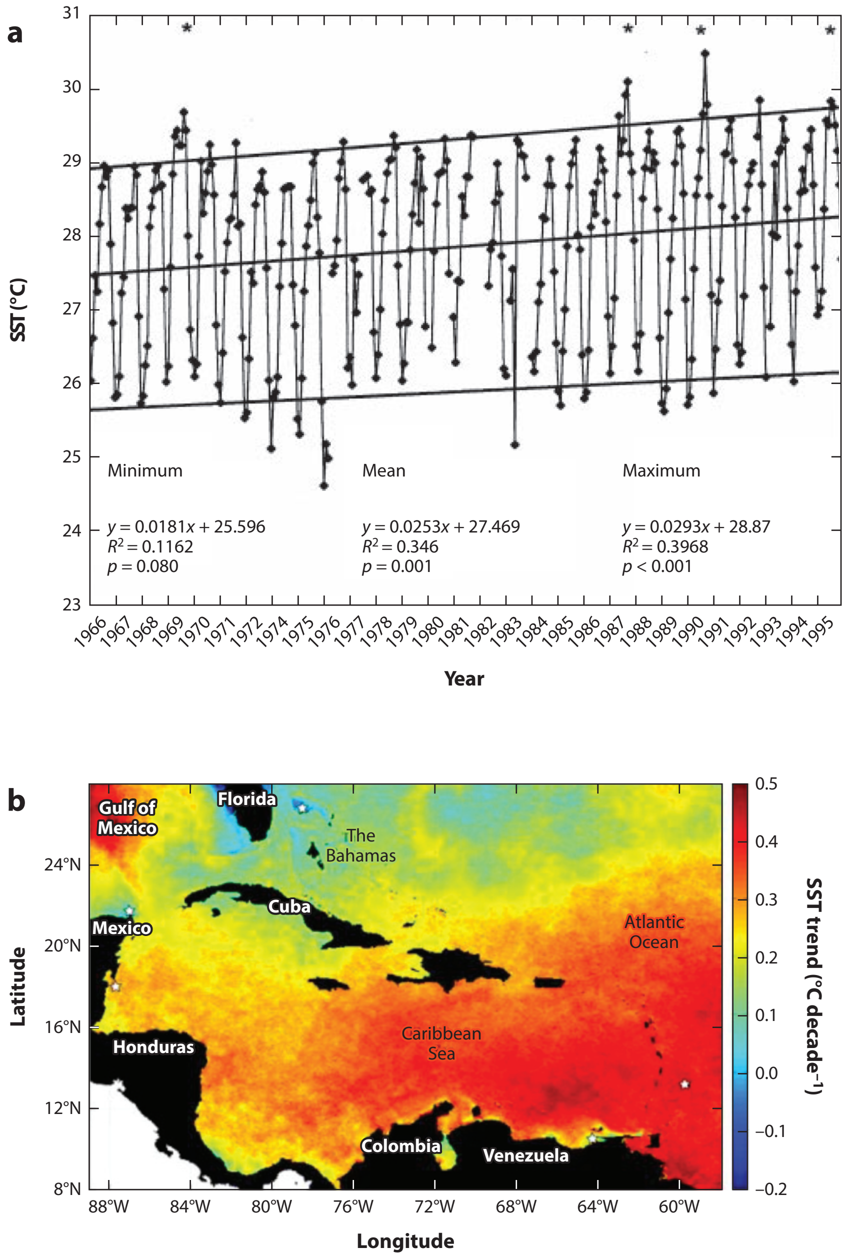

Figure 6

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 coral bleaching. (*b*) Decadal trends in average SST based on NOAA Pathfinder v5.0 satellite SST data (1985–2009). Panel *a* adapted from Winter et al. (1998); panel *b* adapted from Chollett et al. (2012).

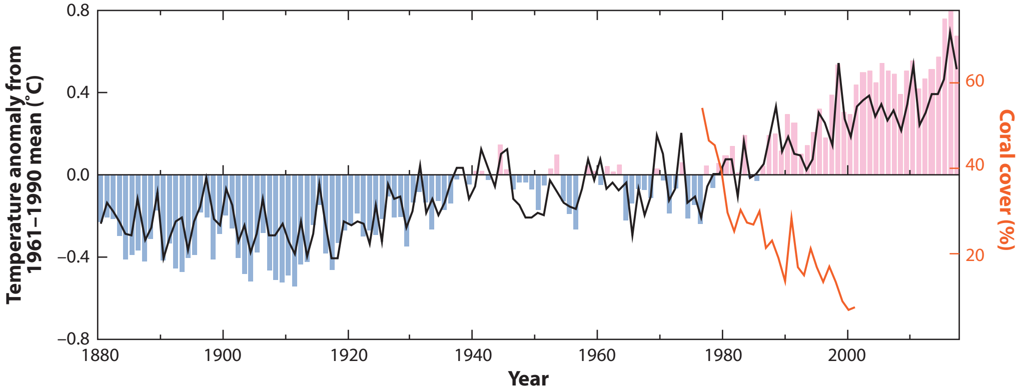

Figure 7

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 Hadley Centre Climatic Research Unit Temperature 4 (HadCRUT4) data set], and the black line shows the average annual coral-reef sea-surface temperature [from the Hadley Centre Global Sea Ice and Sea Surface Temperature 1 (HadISST1) data set]. 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).

of macroalgae in coral declines (a proximate driver, rather than an ultimate driver like fishing), which is a potential outcome of nutrient pollution and the reduction of herbivore populations via fishing. We focus on these local factors and not others because they are widely believed to interact synergistically with ocean warming, an assumption that underlies the managed-resilience paradigm.

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 biomass and/or density of herbivorous fishes. As described above, decreases in the abundance of herbivorous fishes, primarily parrotfishes, are thought to reduce grazing pressure on macroalgae, and a large number of experiments (generally based on exclusion cages) have demonstrated the strong top-down effects of parrotfish grazing on macroalgal cover, biomass, and composition (Burkepile & Hay 2009, Burkepile et al. 2009, Lewis 1997, Miller et al. 1999, Steneck et al. 2014). The suppression of macroalgae facilitates benthic communities dominated by crustose coralline algae and filamentous turfs (Steneck 1988; Hay 1991, 1997), thereby promoting the settlement, growth, and survivorship of corals (e.g., Burkepile & Hay 2008, Hughes et al. 2007, Lewis 1986). These experimental results are corroborated by some large-scale mensurative studies that reported negative associations between the cover of macroalgae and the biomass of herbivorous fishes (Mora 2008, Newman et al. 2006, Williams & Polunin 2001) but not by others. For example, Suchley et al. (2016) observed a gradual increase in macroalgae across the Mesoamerican Barrier Reef while parrotfish biomass was also increasing, 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 appeared to be driven by coral loss and external disturbances rather than by fishing or herbivory.

There is clear evidence of widespread and striking declines in fish biomass on coral reefs, including general declines in parrotfish biomass (Paddack et al. 2009, Valdivia et al. 2017, Williams et al. 2011). Yet there is no broad-scale evidence that these changes have had any effect on coral mortality or declines in coral cover. Most studies that have tested for mechanistic links between

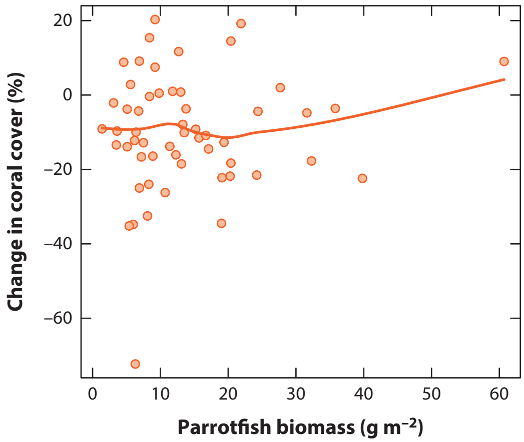

Figure 8

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 was not statistically significant ($p > 0.05$), and the line represents the smoothed curve fitted by loess. Data are from table 2 of Jackson et al. (2014).

coral and fish assemblages have focused on how coral mortality affects the composition and diversity of fishes via habitat loss (Jones et al. 2004, Pratchett et al. 2008, Wilson et al. 2006). Jackson et al. (2014) asked the inverse question and found that spatial variation in parrotfish biomass across the Caribbean was unrelated to coral loss (**Figure 8**).

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. Another is that some of the inferences from the experiments are invalid. The scale of these experiments is usually small (<1.0 m^2 and often far smaller), and the results may simply not scale up to the seascape and regional scales to which they have been widely applied. Moreover, the treatments in many of these experiments are unrepresentative of anything in nature. For example, the complete exclusion of fishes (i.e., via exclusion cages) is not representative of fishing (which reduces fish biomass but does not literally eliminate all 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 on the links between fishes and algae (link 3 in **Figure 3**) and between algae and coral recruitment (link 4 in **Figure 3**) are real but small in magnitude relative to the effects of disturbances, environmental context, larval connectivity, or other factors that influence coral resistance and recovery. Strong effects at all five links are necessary for effective managed resilience. The sheer complexity of the cascade underlying managed reef resilience may be its Achilles' heel and the most likely explanation for its general failure (Russ et al. 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 nutrients in structuring reef communities (interactively with herbivory) is outlined in several conceptual models (e.g., Littler et al. 2006). Szmant (2002) thoroughly evaluated the potential 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 Nutrient on Coral Reefs Experiment (ENCORE) enrichment

> experiment conducted on the Great Barrier Reef, does not support the idea that the levels of nutrient enrichment 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 shifts in coral-algal abundance. Over-enrichment can be and has been the cause of localized coral reef degradation, but the case for widespread effects is not substantiated. (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 interactions between nutrient enrichment and other anthropogenic stressors of corals (Gil et al. 2016a, Muthukrishnan & Fong 2014, Zaneveld et al. 2016). The general absence of multisite nutrient monitoring makes it almost impossible to assess whether and (if so) where nutrient concentrations on reefs are increasing. There are certainly well-documented, highly localized examples, but most available nutrient monitoring suggests that enrichment on offshore reefs is rare (Szmant 2002). This data limitation also precludes 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 from potential sources of nutrient pollution (see also Gil et al. 2016b).

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 overgrow adult corals only in a few extreme cases, numerous studies have found that benthic algae, including macroalgae and algal turfs, can reduce coral settlement and the survival and 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. 2014). Some macroalgae produce chemicals that can have negative effects on small corals (Dixson et al. 2014, Rasher et al. 2011). It has also been suggested that macroalgae can increase 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), but the evidence is mixed. For example, while Nugues et al. (2004) reported that contact with the calcifying alga *Halimeda opuntia* triggered disease in corals, Vu et al. (2009) found that several species of macroalgae, placed in close proximity to juvenile and adult corals, had no effect on among-colony disease transmission rates or within-colony spread.

Countless studies have documented increases in benthic macroalgae at individual sites around the world, and several meta-analyses have quantified regional increases (e.g., Côté et al. 2005, Jackson et al. 2014, and Schutte et al. 2010 for the Caribbean region). The question is whether the observed increase in macroalgae is an important or 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. However, macroalgal cover increased several years after the beginning of the regional coral die-off caused by white band disease (Aronson & Precht 2006, Jackson et al. 2014, 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 water, the regional die-off of the important herbivorous urchin *Diadema antillarum* (Carpenter 1990). Reef ecologists have known for decades that macroalgal cover frequently increases rapidly after mass coral mortality events, presumably due to the reduction in competition for space (Aronson & Precht 2001b, Stoddart 1969). The common lag of months to years between coral mortality events and a subsequent increase in benthic algal cover strongly suggests that algae are responding to, rather than the cause of, coral loss.

Numerous studies have reported that the large-scale spatiotemporal dynamics of coral and macroalgal cover appear to be unrelated. In a regional-scale assessment of the patterns and causes of Caribbean reef degradation, Jackson et al. (2014) found that macroalgal cover was unrelated to

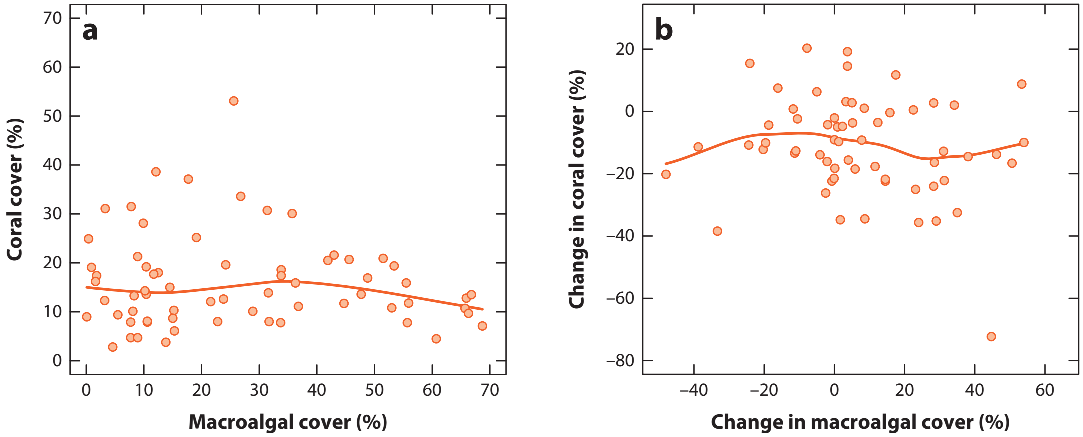

Figure 9

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 surveys performed between 1965 and 2012 of 1–17 reefs per location. This relationship was not statistically significant ($p > 0.05$), and the line represents the smoothed curve fitted by loess. Data are from table 2 of Jackson et al. (2014).

coral loss across the Caribbean (**Figure 9**). Numerous other long-term monitoring studies have documented this apparent decoupling of coral and macroalgal community dynamics (Aronson et al. 2012, Colvard & Edmunds 2011, Edmunds 2013, Russ et al. 2015, Toth et al. 2014), suggesting that they are not mechanistically linked and are likely responding to different drivers.

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 and presumably local disturbance (Knowlton & Jackson 2008). Most local impacts should be absent, or at least minimized, on reefs that are tens or hundreds of kilometers from any human settlement or activities (Sandin et al. 2008). For example, nutrient pollution on reefs should be associated with the coastal human footprint through development, agriculture, and sewage—all of which stem from and increase with coastal human populations. Although fishing is global and few reefs have near-intact fish 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 with decreasing isolation from people and local human impacts would suggest that both local and global factors are important and that, depending on the shape of the relationship, 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 their distance from shore. That is, reefs closer to shore, where nutrient concentrations were greatest, had substantially higher coral cover (inshore corals also grew faster and had 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. However, Bruno & Valdivia (2016), using survey data from 1,708 reefs around the world, found no meaningful relationship between live coral cover and reef isolation from people. 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 measures of reef health (in other words, they are swamped by the larger effect of warming) or (*d*) local and global factors have antagonistic effects. Either way, these results are not consistent 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 of the baseline around which the natural El Niño–Southern Oscillation phenomenon cycles (Hughes et al. 2018a)], countless reefs—at least those with enough remaining coral cover and thermally sensitive species—experienced mass bleaching and coral loss. Some of the hardest hit included the world's most isolated and well-protected reefs, e.g., the northern Great Barrier Reef, the Chagos Archipelago, and even remote Jarvis Island (Brainard et al. 2018, Hughes et al. 2017b, Sheppard et al. 2017, Stuart-Smith et al. 2018). 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 was more likely due to prolonged periods with little disturbance than an indication of their resistance to ocean warming. The near absence of local human impacts (due to 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 be commonplace within a few decades.

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 factors are an important cause of regional and global coral loss is mixed. For some factors, there is strong experimental evidence pointing to a possible role, but the field-pattern data 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 recruitment could be explained by parrotfishes, and only 17% by local fisheries restrictions (based on an analysis of one-time surveys of reefs adjacent to 12 Caribbean islands). The authors argued that the realized effects of management on fish communities were attenuated by the complexity of the linkages between fishing and coral populations. Even if measurable and statistically significant, such modest outcomes are not likely to meaningfully improve reef condition and functioning in the face of climatic disturbances caused by greenhouse gas emissions, especially given the compositional mismatch between the functionally important species being lost and those being facilitated by fisheries restrictions and herbivory.

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 around the world. Reefs also promote coastal protection by buffering nearby shorelines from wave energy during storms (Ferrario et al. 2014). The persistence of these key ecosystem services depends on the ability of reefs to maintain a structurally complex surface and vertical accretion (Kennedy et al. 2013, Kuffner & Toth 2016), particularly as sea-level rise accelerates in the future (Perry et al. 2018, Storlazzi et al. 2011). For many reefs around the world, however, the rapid decline in the cover of reef-building 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. 2013, 2015). With significant declines in structural complexity (Alvarez-Filip et al. 2009) and reductions of reef elevation (Yates et al. 2017) already occurring on many reefs, focusing management on promoting reef accretion and mitigating reef erosion may be crucial to preventing the remaining reef structure from being lost (Kuffner & Toth 2016, Toth et al. 2018).

Paradoxically, the policies enacted to promote reef resilience by protecting herbivorous fishes may actually exacerbate the problems of declining coral health and reef erosion. In addition to their role as grazers, many parrotfishes are active corallivores (Rotjan & Lewis 2008) and preferentially feed on some of the most important reef-building 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 have become less abundant in many locations, the intensity of corallivory on the weedy corals that remain may actually increase as coral cover declines (Burkepile 2011). The chronic 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 coral disease transmission (Rotjan & Lewis 2008, Williams & Miller 2005). Although corallivory was likely not a significant source of coral morbidity or mortality in the past when 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 (Rotjan & Lewis 2008).

A larger threat is the bioerosion of dead coral skeletons and the reef framework by scraping and excavating parrotfishes. Although some researchers have suggested that the role of parrotfishes as bioeroders is negligible relative to their putative benefits as grazers (Harborne & Mumby 2018, Mumby 2009), there is no quantitative evidence to support this claim. Indeed, one of the most dominant parrotfishes in the Caribbean, the stoplight parrotfish *Sparisoma viride*, is also the most destructive bioeroder (Harborne & Mumby 2018, Scoffin et al. 1980). Since the loss of the urchin *Diadema antillarum* throughout the western Atlantic in the mid-1980s (Lessios 2016), parrotfishes have 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, Perry et al. (2013) found that nearly half of the reefs included in the study were already eroding faster than they were accreting, even though the current rates of parrotfish bioerosion 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). While reef-conservation efforts have focused on fishery management as the solution to coral-reef degradation, the parrotfishes we have been protecting have been steadily destroying the reef structures that remain, and carbonate budget deficits on reefs are predicted to worsen as reef communities shift to slower-calcifying taxa (Perry et al. 2014).

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 evidence base supporting the effectiveness of managed resilience of coral reefs is poor. The enthusiasm for a management focus on herbivores, and on parrotfishes in particular, is therefore 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. Models suggest that it can, in the long term, but only under a very restricted set of conditions (e.g., at relatively high levels of coral cover and a low frequency of disturbances), which 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 increased grazing pressure resulting from parrotfish protection can only briefly delay the inevitable degradation of coral reefs that stems from coral loss and negative carbonate budgets (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 to lay the parrotfish paradigm to rest. Where proven to be important, local stressors obviously need to be addressed, but the devastating impacts of recent thermal stress events demonstrate 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 stressors, although there are numerous other demonstrated benefits of MPAs, such as the protection and restoration of biodiversity.
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 underpin it, because the effects of localized stressors are swamped by ocean warming, because macroalgal dominance is in fact rare, and/or because interactions between local and global stressors are often antagonistic.
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 algal productivity, infrequent disturbance, sufficient coral settlement, etc. However, these conditions were not met in any of 18 field tests of the managed-resilience hypothesis across 66 MPAs, and they 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 consume corals, increase bioerosion, and reduce coral accretion rates.
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 fishing and nutrient enhancement (and the resulting increases in macroalgal abundance), are less certain.
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. Climate change has and will continue to be the most significant threat to the future of coral reefs, suggesting that it must mitigated through direct and aggressive action to reduce carbon emissions to ensure the persistence of reefs and the critical ecosystem services they provide.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Contents

Errata

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