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

John F. Bruno (/search?value1=John+F.+Bruno&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true)[1], Isabelle M. Côté (/search?value1=Isabelle+M.+C%C3%B4t%C3%A9&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true)[2] and Lauren T. Toth (/search?value1=Lauren+T.+Toth&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true)[3]

View Affiliations and Author Notes

Vol. 11:307-334 (Volume publication date January 2019)

Copyright © 2019 by Annual Reviews. All rights reserved

View Citation

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.

Keywords

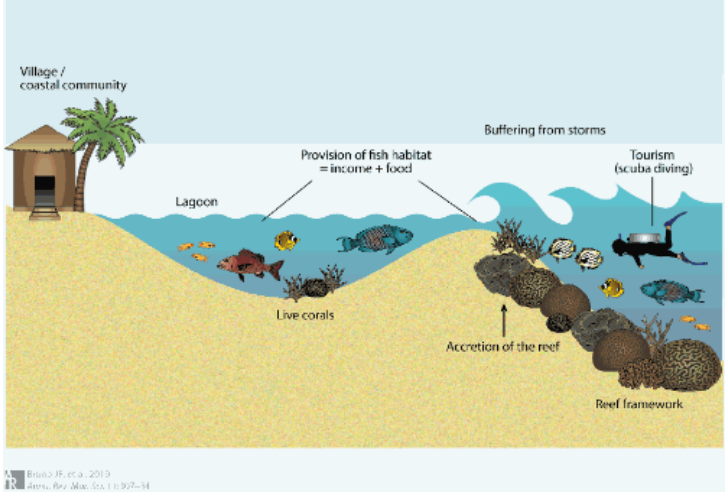
coral reef (/search?option1=pub_keyword&value1="coral reef"), **disturbance (/search?option1=pub_keyword&value1="disturbance")**, **parrotfish (/search?option1=pub_keyword&value1="parrotfish")**, **resilience (/search?option1=pub_keyword&value1="resilience")**, **resistance (/search?option1=pub_keyword&value1="resistance")**, **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 (**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.

Figure 1

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



Click to view

(/content/figure/10.1146/annurev-marine-010318-095300.f1) Download as PowerPoint

(/docserver/fulltext/marine/11/1/ma110307.f1.ppt?mimeType=application/vnd.ms-powerpoint)

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 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.

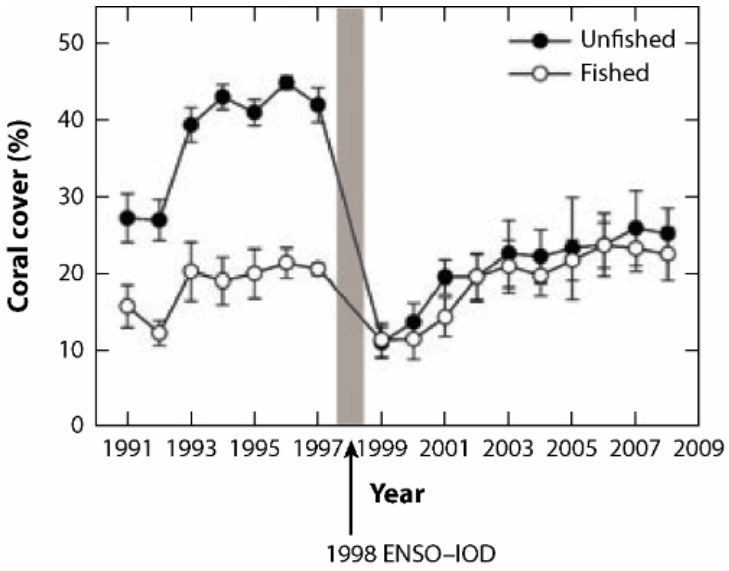
2. IS MANAGED RESILIENCE EFFECTIVE?

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**).

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)**.



Bruno JF, et al. 2019.
Annu. Rev. Mar. Sci. 11:307–34

Click to view

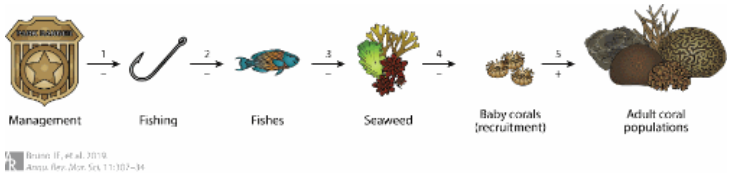
(/content/figure/10.1146/annurev-marine-010318-095300.f2) Download as PowerPoint

(/docserver/fulltext/marine/11/1/ma110307.f2.ppt?mimeType=application/vnd.ms-powerpoint)

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.



Click to view

(/content/figure/10.1146/annurev-marine-010318-095300.f3) Download as PowerPoint

(/docserver/fulltext/marine/11/1/ma110307.f3.ppt?mimeType=application/vnd.ms-powerpoint)

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**).

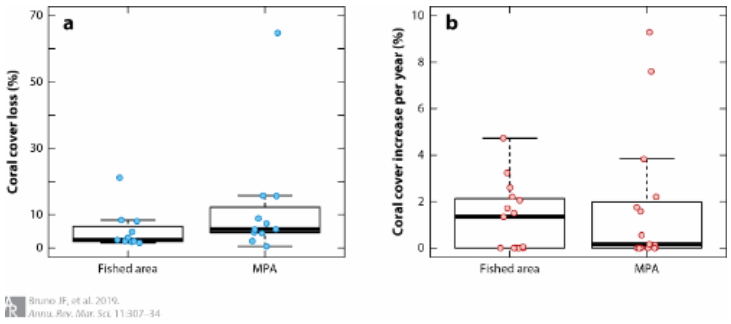
Table 1

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

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.



Click to view

(/content/figure/10.1146/annurev-marine-010318-095300.f4) Download as PowerPoint

(/docserver/fulltext/marine/11/1/ma110307.f4.ppt?mimeType=application/vnd.ms-powerpoint)

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 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 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 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

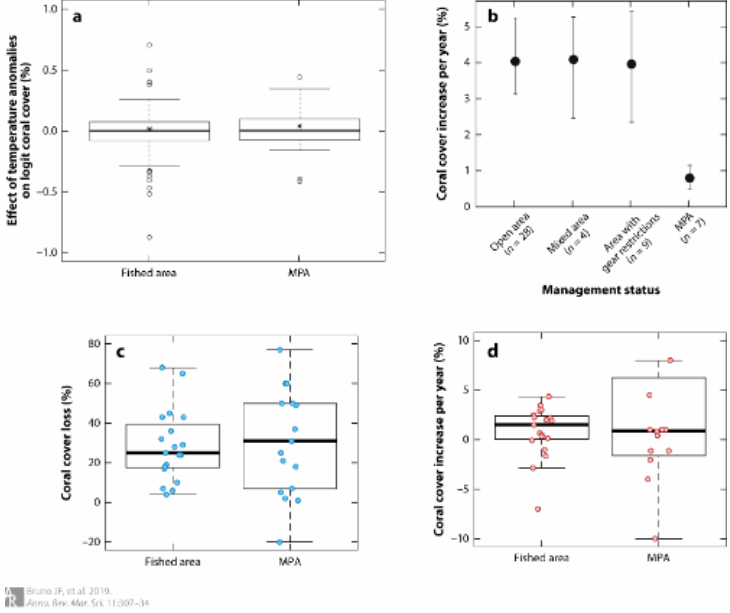
Four studies (**Carassou et al. 2013**, **Graham et al. 2011**, **Selig & Bruno 2010**, **Selig et al. 2012**) have used global survey databases to test the managed-resilience hypothesis for coral reefs (**Table 2**). **Selig & Bruno (2010)** found that, on average, coral loss was reduced in MPAs compared 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.

Table 2

Synthetic tests of the managed-resilience hypothesis for coral reefs

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.



Click to view

(/content/figure/10.1146/annurev-marine-010318-095300.f5) Download as PowerPoint

(/docserver/fulltext/marine/11/1/ma110307.f5.ppt?mimeType=application/vnd.ms-powerpoint)

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. 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).

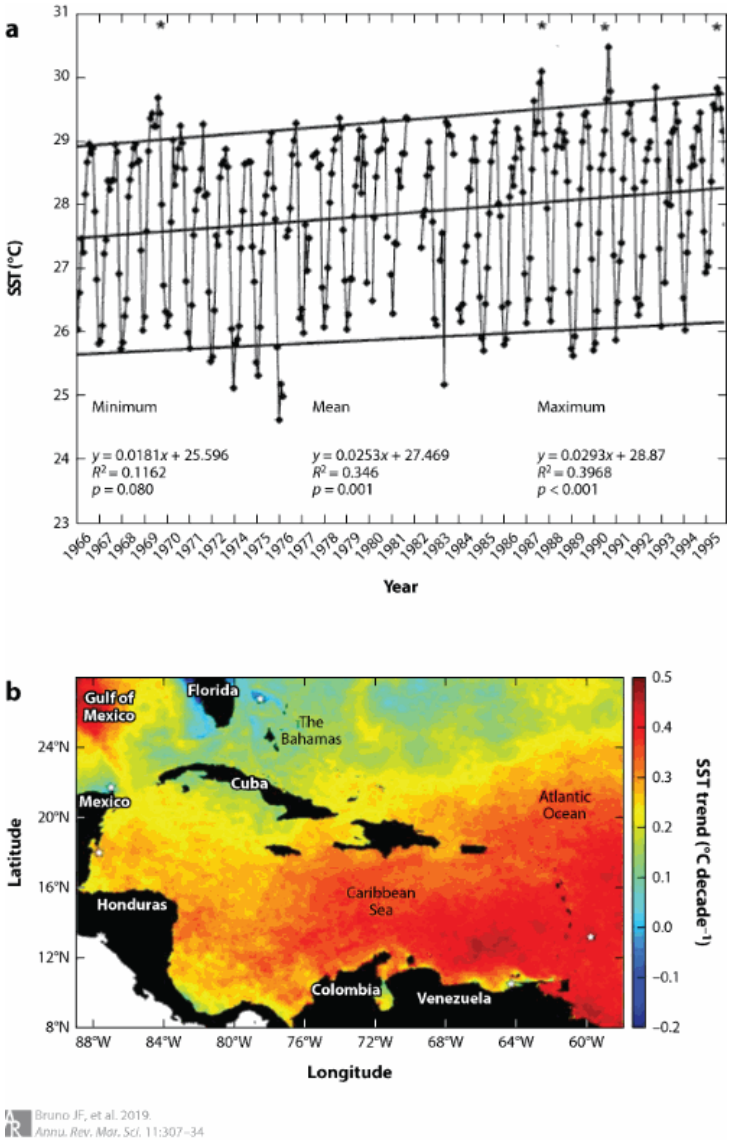
4.1. Evidence That Ocean Warming Causes Coral Loss

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 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.

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)**.



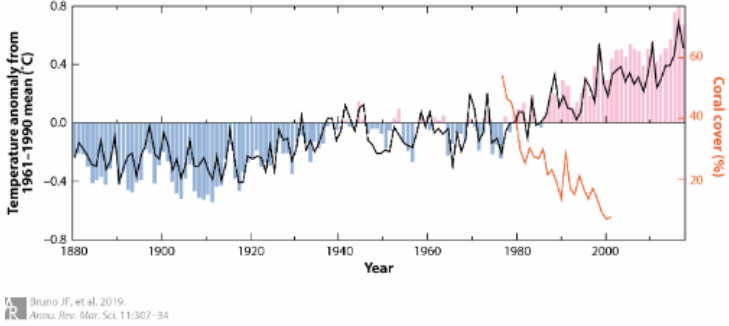
Click to view

(/content/figure/10.1146/annurev-marine-010318-095300.f6) Download as PowerPoint

(/docserver/fulltext/marine/11/1/ma110307.f6.ppt?mimeType=application/vnd.ms-powerpoint)

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)**.



Click to view

(/content/figure/10.1146/annurev-marine-010318-095300.f7) Download as PowerPoint

(/docserver/fulltext/marine/11/1/ma110307.f7.ppt?mimeType=application/vnd.ms-powerpoint)

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**).

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

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 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.

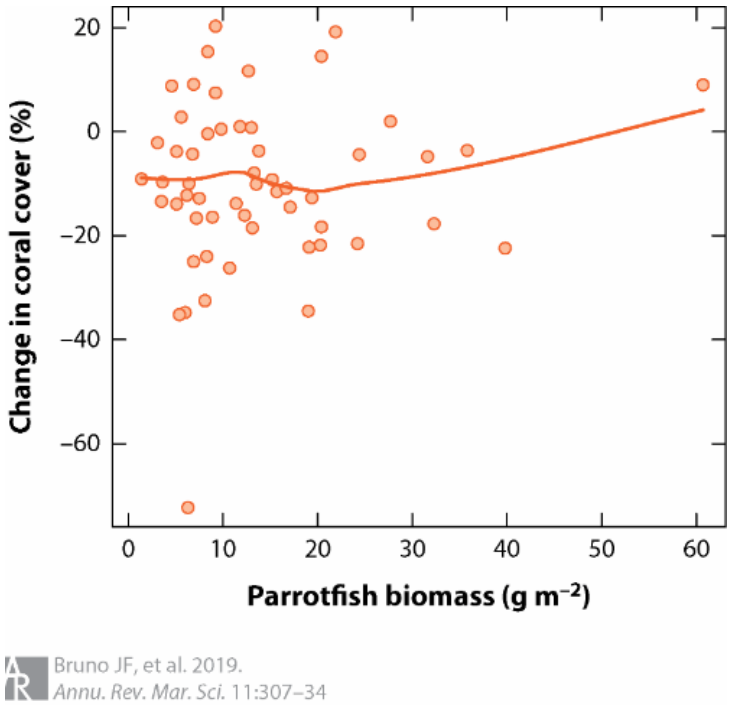
Fishing is thought to cause coral mortality directly through the use of destructive fishing practices (e.g., **Fox & Caldwell 2006**) and indirectly by reducing the biomass and/or density of herbivorous fishes. As described above, decreases in the abundance of herbivorous fishes, primarily parrotfishes, 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 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**).

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)**.



Click to view

(/content/figure/10.1146/annurev-marine-010318-095300.f8) Download as PowerPoint

(/docserver/fulltext/marine/11/1/ma110307.f8.ppt?mimeType=application/vnd.ms-powerpoint)

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.

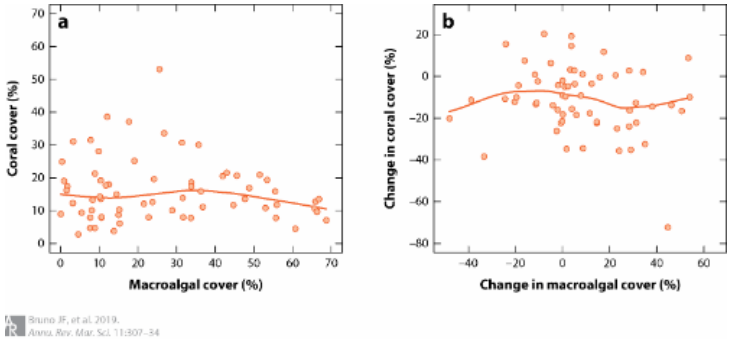
Countless studies have documented increases in benthic macroalgae at individual sites around the world, and several meta-analyses have quantified regional increases (e.g., **Côté et al. 2005**, **Jackson et al. 2014**, and **Schutte et al. 2010** for the Caribbean region). The question is whether the 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 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.

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)**.



Click to view

(/content/figure/10.1146/annurev-marine-010318-095300.f9) Download as PowerPoint

(/docserver/fulltext/marine/11/1/ma110307.f9.ppt?mimeType=application/vnd.ms-powerpoint)

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.

ACKNOWLEDGMENTS

ACKNOWLEDGMENTS

We thank Logan Gin, Olivia Gorman, Rachel Snider, and Allison VanSant for assistance in evaluating the literature, and Richard Aronson, Les Kaufman, Steven Miller, William Precht, and Abel Valdivia for countless discussions about the role of MPAs in coral-reef conservation. J.F.B.'s contribution to this review was funded in part by a grant from the US National Science Foundation (OCE-1737071). I.M.C. is funded by the

Natural Sciences and Engineering Research Council of Canada. L.T.T. is funded by the US Geological Survey's Coastal and Marine Geology Program and Climate and Land Use Research and Development Program and by the US National Science Foundation (OCE-1535007). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

LITERATURE CITED

1. AdamTC BurkepileDE RuttenbergBI PaddackMJ 2015 Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management Mar. Ecol. Prog. Ser. **520** 1 20
2. AltieriAH HarrisonSB SeemannJ CollinR DiazRJ KnowltonN 2017 Tropical dead zones and mass mortalities on coral reefs PNAS **114** 3660 65
3. Alvarez-FilipL Carricart-GanivetJP Horta-PugaG Iglesias-PrietoR 2013 Shifts in coral-assemblage composition do not ensure persistence of reef functionality Sci. Rep. **3** 3486
4. Alvarez-FilipL DulvyNK GillJA CôtéIM WatkinsonAR 2009 Flattening of Caribbean coral reefs: region-wide declines in architectural complexity Proc. R. Soc. B **276** 3019 25
5. Alvarez-FilipL GillJA DulvyNK PerryAL WatkinsonAR CôtéIM 2011 Drivers of region-wide declines in architectural complexity on Caribbean reefs Coral Reefs **30** 1051 60
6. AronsonA PrechtWF ToscanoM KoltesK 2002 The 1998 bleaching event and its aftermath on a coral reef in Belize Mar. Biol. **141** 435 47
7. AronsonRB PrechtWF 2001 a White band diseases and the changing face of Caribbean coral reefs Hydrobiologia **460** 25 38
8. AronsonRB PrechtWF 2001 b Evolutionary paleoecology of Caribbean coral reefs Evolutionary Paleoecology: The Ecological Context of Macroevolutionary Change WD Allmon, DJ Bottjer 171 223 New York Columbia Univ. Press
9. AronsonRB PrechtWF 2006 Conservation, precaution, and Caribbean reefs Coral Reefs **25** 441 50
10. AronsonRB PrechtWF MacIntyreIG TothLT 2012 Catastrophe and the life span of coral reefs Ecology **93** 303 13
11. BakerAC GlynnPW RieglB 2008 Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook Estuar. Coast. Shelf Sci. **80** 435 71
12. BeethamE KenchPS PopinetS 2017 Future reef growth can mitigate physical impacts of sea-level rise on atoll islands Earth's Future **5** 1002 14
13. BéginC ScheltenCK NuguesMM HawkinsJ RobertsC CôtéIM 2016 Effects of protection and sediment stress on coral reefs in Saint Lucia PLOS ONE **11** e0146855
14. BellwoodDR HughesTP FolkeC NystroM 2004 Confronting the coral reef crisis Nature **429** 827 33
15. BellwoodDR HughesTP HoeyAS 2006 Sleeping functional group drives coral-reef recovery Curr. Biol. **16** 2434 39
16. BonaldoRM BellwoodDR 2008 Size-dependent variation in the functional role of the parrotfish *Scarus rivulatus* on the Great Barrier Reef, Australia Mar. Ecol. Prog. Ser. **360** 237 44
17. BonaldoRM KrajewskiJP BellwoodDR 2011 Relative impact of parrotfish grazing scars on massive *Porites* corals at Lizard Island, Great Barrier Reef Mar. Ecol. Prog. Ser. **423** 223 33
18. BoodN 2006 Recovery and resilience of coral assemblages on managed and unmanaged reefs in Belize: a long-term study MS Thesis, Univ. South Ala., Mobile
19. BrainardRE OliverT McPhadenMJ CohenA VenegasR et al. 2018 Ecological impacts of the 2015/16 El Niño in the Central Equatorial Pacific Bull. Am. Meteorol. Soc. **99** 21 26
20. BrownBE 1997 Coral bleaching: causes and consequences Coral Reefs **16** Suppl. 1 S129 38
21. BrucknerA BrucknerR 2006 Consequences of yellow band disease (YBD) on *Montastraea annularis* (species complex) populations on remote reefs off Mona Island, Puerto Rico Dis. Aquat. Org. **69** 67 73
22. BrunoJF CarrLA O'ConnorMI 2015 Marine metabolic ecology: exploring the role of temperature in the ocean through metabolic scaling Ecology **96** 3126 40

23. BrunoJF PetesLE HarvellCD HettingerA 2003 Nutrient enrichment can increase the severity of coral diseases Ecol. Lett. **6** 1056 61

24. BrunoJF PrechtWF VroomPS AronsonRB 2014 Coral reef baselines: How much macroalgae is natural Mar. Pollut. Bull. **80** 24 29

25. BrunoJF SeligER 2007 Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons PLOS ONE **2** e711

26. BrunoJF SeligER CaseyKS PageCA WillisBL et al. 2007 Thermal stress and coral cover as drivers of coral disease outbreaks PLOS Biol **5** e124

27. BrunoJF SweatmanH PrechtWF SeligER SchutteVGW 2009 Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs Ecology **90** 1478 84

28. BrunoJF ValdiviaA 2016 Coral reef degradation is not correlated with local human population density Sci. Rep. **6** 29778

29. BurkeL ReytarK SpaldingM PerryA 2011 Reefs at risk revisited Rep., World Resour. Inst Washington, DC

30. BurkepileDE 2011 Context-dependent corallivory by parrotfishes in a Caribbean reef ecosystem Coral Reefs **31** 111 20

31. BurkepileDE HayME 2006 Herbivore versus nutrient control of marine primary producers: context-dependent effects Ecology **87** 3128 39

32. BurkepileDE HayME 2008 Herbivore species richness and feeding complementarity affect community structure and function on a coral reef PNAS **105** 16201 6

33. BurkepileDE HayME 2009 Nutrient versus herbivore control of macroalgal community development and coral growth on a Caribbean reef Mar. Ecol. Prog. Ser. **389** 71 84

34. BurkepileDE HayME 2010 Impact of herbivore identity on algal succession and coral growth on a Caribbean reef PLOS ONE **5** e8963

35. BurkepileDE HayME 2011 Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef Coral Reefs **30** 351 62

36. BurkepileDE HayME MiamiN 2009 Nutrient versus herbivore control of macroalgal community development and coral growth on a Caribbean reef Mar. Ecol. Prog. Ser. **389** 71 84

37. BurrowsMT SchoemanDS BuckleyLB MooreP PoloczanskaES et al. 2011 The pace of shifting climate in marine and terrestrial ecosystems Science **334** 652 55

38. CarassouL LéopoldM GuillemotN WantiezL KulbickiM 2013 Does herbivorous fish protection really improve coral reef resilience? A case study from New Caledonia (South Pacific) PLOS ONE **8** e60564

39. CarpenterRC 1986 Partitioning herbivory and its effects on coral-reef algal communities Ecol. Monogr. **56** 345 63

40. CarpenterRC 1990 Mass mortality of *Diadema antillarum* I. Long-term effects on sea urchin population-dynamics and coral reef algal communities Mar. Biol. **104** 67 77

41. CarpenterRC EdmundsPJ 2006 Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals Ecol. Lett. **9** 271 80

42. ChollettI Müller-KargerFE HeronSF SkirvingW MumbyPJ 2012 Seasonal and spatial heterogeneity of recent sea surface temperature trends in the Caribbean Sea and southeast Gulf of Mexico Mar. Pollut. Bull. **64** 956 65

43. CoelhoVR ManfrinoC 2007 Coral community decline at a remote Caribbean island: Marine no-take reserves are not enough Aquat. Conserv. Mar. Freshw. Ecosyst. **17** 666 85

44. ColvardNB EdmundsPJ 2011 Decadal-scale changes in abundance of non-scleractinian invertebrates on a Caribbean coral reef J. Exp. Mar. Bio. Ecol. **397** 153 60

45. CôtéIM DarlingES 2010 Rethinking ecosystem resilience in the face of climate change PLOS Biol **8** e1000438

46. CôtéIM GillJA GardnerTA WatkinsonAR 2005 Measuring coral reef decline through meta-analyses Philos. Trans. R. Soc. Lond. B **360** 385 95

47. CôtéIM PrechtWF AronsonRB GardnerTA 2013 Is Jamaica a good model for understanding Caribbean coral reef dynamics Mar. Pollut. Bull. **76** 28 31

48. CoxCE JonesCD WaresJP CastilloKD BrunoJF 2013 Fish mislabeling in Belize: implications for coral reef conservation Conserv. Lett. **6** 132 40

49. DarlingES CôtéIM 2008 Quantifying the evidence for ecological synergies Ecol. Lett. **11** 1278 86

50. DarlingES McClanahanTR CôtéIM 2010 Combined effects of two stressors on Kenyan coral reefs are additive or antagonistic, not synergistic Conserv. Lett. **3** 122 30

51. De'athG FabriciusKE SweatmanH PuotinenM 2012 The 27-year decline of coral cover on the Great Barrier Reef and its causes PNAS **109** 17995 99

52. DillLM HeithausMR WaltersCJ 2003 Behaviorally mediated indirect interactions in marine communities and their conservation Ecology **84** 1151 57

53. DixsonDL AbregoD HayME 2014 Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery Science **345** 892 97

54. EakinCM MorganJA HeronSF SmithTB LiuG et al. 2010 Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005 PLOS ONE **5** e13969

55. EdgarGJ Stuart-SmithRD WillisTJ KininmonthS BakerSC et al. 2014 Global conservation outcomes depend on marine protected areas with five key features Nature **506** 216 20

56. EdmundsPJ 2013 Decadal-scale changes in the community structure of coral reefs of St. John, US Virgin Islands Mar. Ecol. Prog. Ser. **489** 107 23

57. EdmundsPJ CarpenterRC 2001 Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef PNAS **98** 5067 71

58. EdwardsHJ ElliottIA EakinCM IrikawaA MadinJS et al. 2011 How much time can herbivore protection buy for coral reefs under realistic regimes of hurricanes and coral bleaching? Glob. Change Biol. **17** 2033 48

59. FabriciusKE 2005 Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis Mar. Pollut. Bull. **50** 125 46

60. FerrarioF BeckMW StorlazziCD MicheliF ShepardCC AiroldiL 2014 The effectiveness of coral reefs for coastal hazard risk reduction and adaptation Nat. Commun. **5** 3794

61. FoxHE CaldwellRL 2006 Recovery from blast fishing on coral reefs: a tale of two scales Ecol. Appl. **16** 1631 35

62. GardnerTA CôtéIM GillJA GrantA WatkinsonAR 2003 Long-term region-wide declines in Caribbean corals Science **301** 958 60

63. GilMA GoldenbergSU Ly Thai BachA MillsSC ClaudetJ 2016 a Interactive effects of three pervasive marine stressors in a post-disturbance coral reef Coral Reefs **35** 1281 93

64. GilMA JiaoJ OsenbergCW 2016 b Enrichment scale determines herbivore control of primary producers Oecologia **180** 833 40

65. GlennE ComarazamyD GonzálezJE SmithT 2015 Detection of recent regional sea surface temperature warming in the Caribbean and surrounding region Geophys. Res. Lett. **42** 6785 92

66. GrahamNAJ JenningsS MacNeilMA MouillotD WilsonSK 2015 Predicting climate-driven regime shifts versus rebound potential in coral reefs Nature **518** 94 97

67. GrahamNAJ McClanahanTR MacNeilMA WilsonSK PoluninNVC et al. 2008 Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems PLOS ONE **3** e3039

68. GrahamNAJ NashKL KoolJT 2011 Coral reef recovery dynamics in a changing world Coral Reefs **30** 283 94

69. GrahamNAJ WilsonSK JenningsS PoluninNVC BijouxJP RobinsonJ 2006 Dynamic fragility of oceanic coral reef ecosystems PNAS **103** 8425 29

70. GreenDH EdmundsPJ CarpenterRC 2008 Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in coral cover Mar. Ecol. Prog. Ser. **359** 1 10

71. HalpernBS SelkoeKA WhiteC AlbertS AswaniS LauerM 2013 Marine protected areas and resilience to sedimentation in the Solomon Islands Coral Reefs **32** 61 69

72. HarborneAR MumbyPJ 2018 FAQs about Caribbean parrotfish management and their role in reef resilience Biology of Parrotfishes, AS Hoey, RM Bonaldo 383 405 Boca Raton, FL CRC

73. HarrisA WilsonS GrahamN SheppardC 2014 Scleractinian coral communities of the inner Seychelles 10 years after the 1998 mortality event Aquat. Conserv. Mar. Freshw. Ecosyst. **24** 667 79

74. HarrisDL RovereA CasellaE PowerH CanavesioR et al. 2018 Coral reef structural complexity provides important coastal protection from waves under rising sea levels Sci. Adv. **4** eaao4350

75. HarvellD AltizerS CattadoriIM HarringtonL WeilE 2009 Climate change and wildlife diseases: When does the host matter the most? Ecology **90** 912 20

76. HayME 1991 Fish–seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey The Ecology of Fishes on Coral Reefs PF Sale 96 119 San Diego, CA Academic

77. HayME 1997 The ecology and evolution of seaweed–herbivore interactions on coral reefs Coral Reefs **16** S67 77

78. HollingCS 1973 Resilience and stability of ecological systems Annu. Rev. Ecol. Syst. **4** 1 23

79. HoukP MusburgerC 2013 Trophic interactions and ecological stability across coral reefs in the Marshall Islands Mar. Ecol. Prog. Ser. **488** 23 34

80. HughesTP AndersonKD ConnollySR HeronSF KerryJT et al. 2018 a Spatial and temporal patterns of mass bleaching of corals in the Anthropocene Science **359** 80 83

81. HughesTP BarnesML BellwoodDR CinnerJE CummingGS et al. 2017 a Coral reefs in the Anthropocene Nature **546** 82 90

82. HughesTP BellwoodDR FolkeCS McCookLJ PandolfiJM 2007 No-take areas, herbivory and coral reef resilience Trends Ecol. Evol. **22** 1 3

83. HughesTP GrahamNAJ JacksonJBC MumbyPJ SteneckRS 2010 Rising to the challenge of sustaining coral reef resilience Trends Ecol. Evol. **25** 633 42

84. HughesTP KerryJ Álvarez-NoriegaM Álvarez-RomeroJ AndersonK et al. 2017 b Global warming and recurrent mass bleaching of corals Nature **543** 373 77

85. HughesTP KerryJT BairdAH ConnollySR DietzelA et al. 2018 b Global warming transforms coral reef assemblages Nature **556** 492 96

86. HumanesA FinkA WillisBL FabriciusKE de BeerD NegriAP 2017 Effects of suspended sediments and nutrient enrichment on juvenile corals Mar. Pollut. Bull. **125** 166 75

87. HuntingtonBE KarnauskasM LirmanD 2011 Corals fail to recover at a Caribbean marine reserve despite ten years of reserve designation Coral Reefs **30** 1077 85

88. IdjadiJA EdmundsPJ 2006 Scleractinian corals as facilitators for other invertebrates on a Caribbean reef Mar. Ecol. Prog. Ser. **319** 117 27

89. JacksonJ DonovanM CramerK LamV 2014 Status and Trends of Caribbean Coral Reefs: 1970–2012 Gland, Switz Glob. Coral Reef Monit. Netw

90. JonesGP McCormickMI SrinivasanM EagleJV 2004 Coral decline threatens fish biodiversity in marine reserves PNAS **101** 8251 53

91. JuryMR 2011 Long-term variability and trends in the Caribbean Sea Int. J. Oceanogr. **2011** 465810

92. KennedyEV PerryCT HalloranPR Iglesias-PrietoR SchönbergCHL et al. 2013 Avoiding coral reef functional collapse requires local and global action Curr. Biol. **23** 912 18

93. KnowltonN JacksonJBC 2008 Shifting baselines, local impacts, and global change on coral reefs PLOS Biol **6** e54

94. KramerK HeckK 2007 Top-down trophic shifts in Florida Keys patch reef marine protected areas Mar. Ecol. Prog. Ser. **349** 111 23

95. KuffnerIB TothLT 2016 A geological perspective on the degradation and conservation of western Atlantic coral reefs Conserv. Biol. **30** 706 15

96. LambJB WengerAS DevlinMJ CeccarelliDM WilliamsonDH WillisBL 2016 Reserves as tools for alleviating impacts of marine disease Philos. Trans. R. Soc. B **371** 20150210

97. LessiosHA 2016 The great *Diadema antillarum* die-off: 30 years later Annu. Rev. Mar. Sci. **8** 267 83

98. LewisA 1997 Effects of experimental coral disturbance on the structure of fish communities on large patch reefs Mar. Ecol. Prog. Ser. **161** 37 50

99. LewisSM 1986 The role of herbivorous fishes in the organization of a Caribbean reef community Ecol. Monogr. **56** 183 200

100. LirmanD FongP 2007 Is proximity to land-based sources of coral stressors an appropriate measure of risk to coral reefs? An example from the Florida Reef Tract Mar. Pollut. Bull. **54** 779 91

101. LittlerMM LittlerDS BrooksBL 2006 Harmful algae on tropical coral reefs: bottom-up eutrophication and top-down herbivory Harmful Algae **5** 565 85

102. LohT-L McMurraySE HenkelTP VicenteJ PawlikJR 2015 Indirect effects of overfishing on Caribbean reefs: sponges overgrow reef-building corals PeerJ **3** e901

103. LokrantzJ NyströmM ThyressonM JohanssonC 2008 The non-linear relationship between body size and function in parrotfishes Coral Reefs **27** 967 74

104. LoughJM AndersonKD HughesTP 2018 Increasing thermal stress for tropical coral reefs: 1871–2017 Sci. Rep. **8** 6079

105. MadinEMP GainesSD MadinJS WarnerRR 2010 Fishing indirectly structures macroalgal assemblages by altering herbivore behavior Am. Nat. **176** 785 801

106. ManfrinoC JacobyCA CampE FrazerTK 2013 A positive trajectory for corals at Little Cayman Island PLOS ONE **8** e75432

107. McClanahanTR 2008 Response of the coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance Oecologia **155** 169 77

108. McClanahanTR CokosBA SalaE 2002 Algal growth and species composition under experimental control of herbivory, phosphorus and coral abundance in Glovers Reef, Belize Mar. Pollut. Bull. **44** 441 51

109. McClanahanTR MuthigaNA NinE 2001 Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs Coral Reefs **19** 380 91

110. McCookLJ JompaJ Diaz-PulidoG 2001 Competition between corals and algae on coral reefs: a review of evidence and mechanisms Coral Reefs **19** 400 17

111. MillerJ MullerE RogersC WaaraR AtkinsonA et al. 2009 Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands Coral Reefs **28** 925 37

112. MillerMW HayME MillerSL MaloneD SotkaEE SzmantAM 1999 Effects of nutrients versus herbivores on reef algae: a new method for manipulating nutrients on coral reefs Limnol. Oceanogr. **44** 1847 61

113. MobergF FolkeC 1999 Ecological goods and services of coral reef ecosystems Ecol. Econ. **29** 215 33

114. MoraC 2008 A clear human footprint in the coral reefs of the Caribbean Proc. R. Soc. B **275** 767 73

115. MorrisonD 1988 Comparing fish and urchin grazing in shallow and deeper coral reef algal communities Ecology **69** 1367 82

116. MumbyPJ 2009 Herbivory versus corallivory: Are parrotfish good or bad for Caribbean coral reefs Coral Reefs **28** 683 90

117. MumbyPJ DahlgrenCP HarborneAR KappelCV MicheliF et al. 2006 Process of grazing on coral reefs Science **311** 98 101

118. MumbyPJ HarborneAR 2010 Marine reserves enhance the recovery of corals on Caribbean reefs PLOS ONE **5** e8657

119. MumbyPJ SteneckRS 2008 Coral reef management and conservation in light of rapidly evolving ecological paradigms Trends Ecol. Evol. **23** 555 63

120. MuthigaNA 2009 Evaluating the effectiveness of management of the Malindi-Watamu marine protected area complex in Kenya Ocean Coast. Manag. **52** 417 23

121. MuthukrishnanR FongP 2014 Multiple anthropogenic stressors exert complex, interactive effects on a coral reef community Coral Reefs **33** 911 21

122. NadonMO BaumJK WilliamsID McphersonJM ZgliczynskiBJ et al. 2012 Re-creating missing population baselines for Pacific reef sharks Conserv. Biol. **26** 493 503

123. NewmanMJH ParedesGA SalaE JacksonJBC 2006 Structure of Caribbean coral reef communities across a large gradient of fish biomass Ecol. Lett. **9** 1216 27

124. NorströmAV NyströmM LokrantzJ FolkeC 2009 Alternative states on coral reefs: beyond coral–macroalgal phase shifts Mar. Ecol. Prog. Ser. **376** 295 306

125. NuguesMM SmithGW HooidonkRJ SeabraMI BakRPM 2004 Algal contact as a trigger for coral disease Ecol. Lett. **7** 919 23

126. NyströmM FolkeC MobergF 2000 Coral reef disturbance and resilience in a human-dominated environment Trends. Ecol. Evol. **15** 413 17

127. NyströmM GrahamNAJ LokrantzJ NorströmAV 2008 Capturing the cornerstones of coral reef resilience: linking theory to practice Coral Reefs **27** 795 809

128. OliverECJ DonatMG BurrowsMT MoorePJ SmaleDA et al. 2018 Longer and more frequent marine heatwaves over the past century Nat. Commun. **9** 1324

129. PaddackMJ ReynoldsJD AguilarC AppeldoornRS BeetsJ et al. 2009 Recent region-wide declines in Caribbean reef fish abundance Curr. Biol. **19** 590 95

130. PandolfiJM JacksonJBC 2006 Ecological persistence interrupted in Caribbean coral reefs Ecol. Lett. **9** 818 26

131. PerryCT Alvarez-FilipL GrahamNA MumbyPJ WilsonSK et al. 2018 Loss of coral reef growth capacity to track future increases in sea level Nature **558** 396 400

132. PerryCT MurphyGN KenchPS EdingerEN SmithersSG et al. 2014 Changing dynamics of Caribbean reef carbonate budgets: emergence of reef bioeroders as critical controls on present and future reef growth potential Proc. R. Soc. Lond. B **281** 20142018

133. PerryCT MurphyGN KenchPS SmithersSG EdingerEN et al. 2013 Caribbean-wide decline in carbonate production threatens coral reef growth Nat. Commun. **4** 1402

134. PerryCT SteneckRS MurphyGN KenchPS EdingerEN et al. 2015 Regional-scale dominance of non-framework building coral on Caribbean reefs affects carbonate production and future reef growth Glob. Change Biol. **21** 1153 64

135. PratchettM MundayP WilsonS GrahamN CinnerJ et al. 2008 Effects of climate-induced coral bleaching on coral-reef fishes – ecological and economic consequences Oceanogr. Mar. Biol. Annu. Rev. **46** 251 96

136. RandallCJ van WoesikR 2015 Contemporary white-band disease in Caribbean corals driven by climate change Nat. Clim. Change **5** 375 79

137. RasherDB StoutEP EngelS KubanekJ HayME 2011 Macroalgal terpenes function as allelopathic agents against reef corals PNAS **108** 17726 31

138. RobertsCM O'LearyBC McCauleyDJ CuryPM DuarteCM et al. 2017 Marine reserves can mitigate and promote adaptation to climate change PNAS **114** 6167 75

139. RosinskiA WalshW 2016 Prioritized management strategies for promoting post-bleaching coral recovery in Hawai'i: survey results Rep., Div. Aquat. Resour Dep. Land Nat. Resour Honolulu, HI

140. RotjanRD DimondJL ThornhillDJ LeichterJJ HelmuthB et al. 2006 Chronic parrotfish grazing impedes coral recovery after bleaching Coral Reefs **25** 361 68

141. RotjanRD LewisS 2008 Impact of coral predators on tropical reefs Mar. Ecol. Prog. Ser. **367** 73 91

142. RussGR QuestelSLA RizzariJR AlcalaAC 2015 The parrotfish-coral relationship: refuting the ubiquity of a prevailing paradigm Mar. Biol. **162** 2029 45

143. SandinSA SmithJE DemartiniEE DinsdaleEA DonnerSD et al. 2008 Baselines and degradation of coral reefs in the Northern Line Islands PLOS ONE **3** e1548

144. SchutteV SeligE BrunoJ 2010 Regional spatio-temporal trends in Caribbean coral reef benthic communities Mar. Ecol. Prog. Ser. **402** 115 22

145. ScoffinTP StearnCW BoucherD FrydlP HawkinsCM et al. 1980 Calcium carbonate budget of a fringing reef on the west coast of Barbados: part II. Erosion, sediments and internal structure Bull. Mar. Sci. **30** 475 508

146. SeligER BrunoJF 2010 A global analysis of the effectiveness of marine protected areas in preventing coral loss PLOS ONE **5** e9278

147. SeligER CaseyKS BrunoJF 2012 Temperature-driven coral decline: the role of marine protected areas Glob. Change Biol. **18** 1561 70

148. ShaverEC ShantzAA McMindsR BurkepileDE ThurberRLV SillimanBR 2017 Effects of predation and nutrient enrichment on the success and microbiome of a foundational coral Ecology **98** 830 39

149. SheppardC SheppardA MoggA BayleyD DempseyAC et al. 2017 Coral bleaching and mortality in the Chagos Archipelago to 2017 Atoll Res. Bull. 613, Smithson. Inst Washington, DC

150. SmithJE ShawM EdwardsRA OburaD PantosO et al. 2006 Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality Ecol. Lett. **9** 835 45

151. Soc. Sci. Res. Inst. 2017 Coral Bleaching Recovery Plan: identifying management responses to promote coral recovery in Hawai'i. Rep., Div Aquat. Resour., Dep. Land Nat. Resour Honolulu, HI https://dlnr.hawaii.gov/reefresponse/current-rapid-responses/coral-bleaching-recovery-plan

152. SpaldingM BurkeL WoodSA AshpoleJ HutchisonJ zu ErmgassenP 2017 Mapping the global value and distribution of coral reef tourism Mar. Policy **82** 104 13

153. StallingsCD 2009 Fishery-independent data reveal negative effect of human population density on Caribbean predatory fish communities PLOS ONE **4** e5333

154. SteneckRS 1988 Herbivory on coral reefs: a synthesis Proceedings of the 6th International Coral Reef Symposium, Vol. 1: Plenary Addresses and Status Review JH Choat, D Barnes, MA Borowitzka, JC Coll, PJ Davies et al. 37 49 Townsville, Aust Sixth Int. Coral Reef Symp. Exec. Comm

155. SteneckRS ArnoldSN MumbyPJ 2014 Experiment mimics fishing on parrotfish: insights on coral reef recovery and alternative attractors Mar. Ecol. Prog. Ser. **506** 115 27

156. SteneckRS MumbyPJ MacDonaldC RasherDB StoyleG 2018 Attenuating effects of ecosystem management on coral reefs Sci. Adv. **4** eaao5493

157. StoddartDR 1969 Post-hurricane changes on the British Honduras reefs: re-survey of 1965 Atoll Res. Bull. 131, Smithson. Inst Washington, DC

158. StorlazziCD EliasE FieldME PrestoMK 2011 Numerical modeling of the impact of sea-level rise on fringing coral reef hydrodynamics and sediment transport Coral Reefs **30** 83 96

159. Stuart-SmithRD BrownCJ CeccarelliDM EdgarGJ 2018 Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching Nature **560** 92 96

160. SuchleyA McFieldMD Alvarez-FilipL 2016 Rapidly increasing macroalgal cover not related to herbivorous fishes on Mesoamerican reefs PeerJ **4** e2084

161. SzmantAM 2002 Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries **25** 743 66

162. TothLT KuffnerIB StathakopoulosA ShinnEA 2018 A 3,000-year lag between the geological and ecological shutdown of Florida's coral reefs Glob. Change Biol. **24** 5471 83

163. TothLT van WoesikR MurdochTJT SmithSR OgdenJC et al. 2014 Do no-take reserves benefit Florida's corals? 14 years of change and stasis in the Florida Keys National Marine Sanctuary Coral Reefs **33** 565 77

164. ValdiviaA CoxCE BrunoJF 2017 Predatory fish depletion and recovery potential on Caribbean reefs Sci. Adv. **3** e1601303

165. van WoesikR ScottWJ AronsonRB 2014 Lost opportunities: Coral recruitment does not translate to reef recovery in the Florida Keys Mar. Pollut. Bull. **88** 110 17

166. VeronJEN 2011 Ocean acidification and coral reefs: an emerging big picture Diversity **3** 262 74

167. VroomPS 2011 “Coral dominance”: a dangerous ecosystem misnomer? J. Mar. Biol. **2011** 164127

168. VuI SmelickG HarrisS LeeSC WeilE et al. 2009 Macroalgae has no effect on the severity and dynamics of Caribbean yellow band disease PLOS ONE **4** e4514

169. WebsterPJ HollandGJ CurryJA ChangHR 2005 Changes in tropical cyclone number, duration, and intensity in a warming environment Science **309** 1844 46

170. WeilE CroquerA UrreiztietaI 2009 Temporal variability and impact of coral diseases and bleaching in La Parguera, Puerto Rico from 2003–2007 Caribb. J. Sci. **45** 221 46

171. WestJM SalmRV 2003 Resistance and resilience to coral bleaching: implications for coral reef conservation and management Conserv. Biol. **17** 956 67

172. WilliamsDE MillerMW 2005 Coral disease outbreak: pattern, prevalence and transmission in *Acropora cervicornis* Mar. Ecol. Prog. Ser. **301** 119 28

173. WilliamsID PoluninNVC 2001 Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean Coral Reefs **19** 358 66

174. WilliamsID PoluninNVC HendrickVJ 2001 Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize Mar. Ecol. Prog. Ser. **222** 187 96

175. WilliamsID RichardsBL SandinSA BaumJK SchroederRE et al. 2011 Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and western Pacific J. Mar. Biol. **2011** 826234

176. WillisBL PageCA DinsdaleEA 2002 Coral disease on the Great Barrier Reef Coral Health and Disease E Rosenberg, Y Loya 69 104 Berlin Springer

177. WilsonSK GrahamNAJ FisherR RobinsonJ NashK et al. 2012 Effect of macroalgal expansion and marine protected areas on coral recovery following a climatic disturbance Conserv. Biol. **26** 995 1004

178. WilsonSK GrahamNAJ PratchettMS JonesGP PoluninNVC 2006 Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient Glob. Change Biol. **12** 2220 34

179. WinterA AppeldoornRS BrucknerA WilliamsEHJr GoenagaC 1998 Sea surface temperatures and coral reef bleaching off La Parguera, Puerto Rico (northeastern Caribbean Sea) Coral Reefs **17** 377 82

180. YatesKK ZawadaDG SmileyNA Tiling-RangeG 2017 Divergence of seafloor elevation and sea level rise in coral reef ecosystems Biogeosciences **14** 1739 72

181. ZaneveldJR BurkepileDE ShantzAA PritchardCE McMindsR et al. 2016 Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales Nat. Commun. **7** 11833

182. ZhangSY SpeareKE LongZT McKeeverKA GyoerkoeM 2014 Is coral richness related to community resistance to and recovery from disturbance? PeerJ **2** e308

Most Read This Month

Hidden Threat: The Influence of Sea-Level Rise on Coastal Groundwater and the Convergence of Impacts on Municipal Infrastructure (/content/journals/10.1146/annurev-marine-020923-120737)

Shellie Habel, Charles H. Fletcher, Matthew M. Barbee and Kyrstin L. Fornace
pp. 81–103 (23)

The Impact of Fine-Scale Currents on Biogeochemical Cycles in a Changing Ocean (/content/journals/10.1146/annurev-marine-020723-020531)

Marina Lévy, Damien Couespel, Clément Haëck, M.G. Keerthi, Inès Mangolte and Channing J. Prend
pp. 191–215 (25)

The Physical Oceanography of Ice-Covered Moons (/content/journals/10.1146/annurev-marine-040323-101355)

Krista M. Soderlund, Marc Rovira-Navarro, Michael Le Bars, Britney E. Schmidt and Theo Gerkema
pp. 25–53 (29)

Aquatic Eddy Covariance: The Method and Its Contributions to Defining Oxygen and Carbon Fluxes in Marine Environments (/content/journals/10.1146/annurev-marine-042121-012329)

Peter Berg, Markus Huettel, Ronnie N. Glud, Clare E. Reimers and Karl M. Attard
pp. 431–455 (25)

Modeling the Morphodynamics of Coastal Responses to Extreme Events: What Shape Are We In? (/content/journals/10.1146/annurev-marine-032221-090215)

Christopher R. Sherwood, Ap van Dongeren, James Doyle, Christie A. Hegermiller, Tian-Jian Hsu, Tarandeep S. Kalra, Maitane Olabarrieta, Allison M. Penko, Yashar Rafati, Dano Roelvink, Marlies van der Lugt, Jay Veeramony and John C. Warner
pp. 457–492 (36)

Most Cited

(/rss/content/journals/marine/mostcitedarticles?fmt=rss)

Ocean Acidification: The Other CO_2 Problem (/content/journals/10.1146/annurev.marine.010908.163834)

Scott C. Doney (/search?value1=Scott+C.+Doney&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), Victoria J. Fabry (/search?value1=Victoria+J.+Fabry&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), Richard A. Feely (/search?value1=Richard+A.+Feely&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true) and Joan A. Kleypas (/search?value1=Joan+A.+Kleypas&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true)
Vol. 1 (2009), pp. 169–192

Climate Change Impacts on Marine Ecosystems (/content/journals/10.1146/annurev-marine-041911-111611)

Scott C. Doney (/search?value1=Scott+C.+Doney&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), Mary Ruckelshaus (/search?value1=Mary+Ruckelshaus&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), J. Emmett Duffy (/search?value1=J.+Emmett+Duffy&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), James P. Barry (/search?value1=James+P.+Barry&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), Francis Chan (/search?value1=Francis+Chan&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), Chad A. English (/search?value1=Chad+A.+English&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), Heather M. Galindo (/search?value1=Heather+M.+Galindo&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), Jacqueline M. Grebmeier (/search?value1=Jacqueline+M.+Grebmeier&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), Anne B. Hollowed (/search?value1=Anne+B.+Hollowed&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), Nancy Knowlton (/search?value1=Nancy+Knowlton&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), Jeffrey Polovina (/search?value1=Jeffrey+Polovina&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), Nancy N. Rabalais (/search?value1=Nancy+N.+Rabalais&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), William J. Sydeman (/search?value1=William+J.+Sydeman&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true) and Lynne D. Talley (/search?value1=Lynne+D.+Talley&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true)
Vol. 4 (2012), pp. 11–37

Larval Dispersal and Marine Population Connectivity (/content/journals/10.1146/annurev.marine.010908.163757)

Robert K. Cowen (/search?value1=Robert+K.+Cowen&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true) and Su Sponaugle (/search?value1=Su+Sponaugle&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true)
Vol. 1 (2009), pp. 443–466

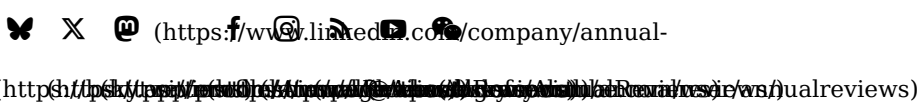
Carbon Cycling and Storage in Mangrove Forests (/content/journals/10.1146/annurev-marine-010213-135020)

Daniel M. Alongi (/search?value1=Daniel+M.+Alongi&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true)
Vol. 6 (2014), pp. 195–219

Ocean Deoxygenation in a Warming World (/content/journals/10.1146/annurev.marine.010908.163855)

Ralph F. Keeling (/search?value1=Ralph+F.+Keeling&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true), Arne Körtzinger (/search?value1=Arne+K%C3%B6rtzinger&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true) and Nicolas Gruber (/search?value1=Nicolas+Gruber&option1=author&noRedirect=true&sortField=prism_publicationDate&sortDescending=true)
Vol. 2 (2010), pp. 199–229

+ More


(https://www.linkedin.com/company/annual-
(https://www.annualreviews)