Coral Reefs Under Climate Change and Ocean Acidification: Challenges and Opportunities for Management and Policy

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Abstract

Carbon emissions in an industrialized world have created two problems for coral reefs: climate change and ocean acidification. Climate change drives ocean warming, which impacts biological and ecological reef processes, triggers large-scale coral bleaching events, and fuels tropical storms. Ocean acidification slows reef growth, alters competitive interactions, and impairs population replenishment. For managers and policymakers, ocean warming and acidification represent an almost paradoxical challenge by eroding reef resilience and simultaneously increasing the demand for reef resilience. Here, I address this problem in the context of challenges and potential solutions. Management efforts can compensate for reduced coral reef resilience in the face of global change, but to a limited extent and over a limited time frame. Critically, a realistic perspective on what sustainability measures can be achieved for coral reefs in the face of ocean warming and acidification is important to avoid setting unachievable goals for regional and local-scale management programs.

Contents

1. INTRODUCTION

1.1. Purpose of the Review

The purpose of this article is twofold. One is to bring clarity around the complex issue of how climate change and ocean acidification are likely to impact tropical coral reefs in the near and medium-term future. Another is to identify the challenges and opportunities for environmental managers and policymakers in sustaining reef ecosystems in the face of those global pressures. Tropical coral reefs are only one of many ecosystems threatened by global environmental change (1). However, they are one of the most sensitive systems to ocean warming and acidification as their existence hinges on the health and performance of a key group of ecosystem engineers, reef-building corals, which have narrow thermal and chemical tolerance limits (2, 3). Also, coral reefs are valuable from multiple perspectives. Although they cover only approximately 1% of the ocean floor, they are likely to be home to more than one-quarter of the species in the ocean (4). Furthermore, coral reefs support the livelihoods of tens of millions of people in tropical coastal regions in both developing and developed countries. In monetary terms, the value of the bundle of ecosystem services that coral reefs provide (i.e., provisioning, regulating, habitat, and cultural services) range from Int$40,000 to $2 million ha^{-1} $year^{-1}$; this is two and three orders of magnitude more than tropical forests and the open ocean, respectively (5).

Coral reef managers and policymakers face growing decision challenges around which interventions at local, regional, and global scales will sustain coral reefs and their dependent social and economic dimensions (6). Solutions to coral reef sustainability in the long run will need to balance multiple objectives. This review provides a framework that can help simplify the issues and provide a transparent and realistic view of the challenges and opportunities for management and policy as climate change and ocean acidification unfold.

1.2. The Ocean Environment Is Changing

A decade ago, the general narrative was that coral reefs face an uncertain future under climate change and ocean acidification (7–10). Now, as evidence from observational and experimental research is mounting, providing more signal to the noise, the narrative focuses increasingly on the changes we expect coral reefs to undergo (11), the consequences for society (12), and potential solutions (13). The expected ecological change will be a shift away from structurally diverse and species-rich seascapes toward more depauperate systems composed of fewer but more stress-resistant species (14, 15). These predictions are consistent with multiple lines of evidence.

First, global observations indicate a trend consistent with predictions for an atmosphere increasingly enriched with carbon dioxide (CO_2) and to an extent that has been unprecedented for the past 800,000 years (16, 17). A key summary point of the latest report by the IPCC is that "Warming of the climate system is unequivocal, and since the 1950s, many of the observed changes are unprecedented over decades to millennia (17, p. 2)." At the time of writing, the Australian Bureau of Meteorology recently released a report stating that 2015 is estimated to be the warmest year globally since 1880 (see **http://www.bom.gov.au/climate/current/annual/aus/2015**). Also, the National Oceanic and Atmospheric Administration's (NOAA's) National Centers for Environmental Information (NOAA NCEI 2016) released their annual global analysis (**https://www.ncdc.noaa.gov/sotc/global/201513**) stating that 2015 and 2014 were 0.90 and 0.74°C warmer than the global average for the twentieth century. The warming trend of the upper ocean, which is Earth's primary heat sink (18, 19), reflects largely the global warming trend.

Second, since the beginning of the industrial era, the ocean has taken up approximately one-third of the CO_2 released from human activity (20). This uptake has resulted in a decline in the pH of surface ocean waters by approximately 0.1 units, corresponding to a more than 25% increase in the concentration of hydrogen ions (21). Whereas Earth's climate is associated with substantial interannual and interdecadal variability driven by large-scale drivers including the El Niño Southern Oscillation (ENSO; 17, 22), ocean acidification is a chemical process with relatively fewer factors implicated (23; but see 24). Ocean acidification hence elicits a clearer cause-and-effect relationship with the atmospheric concentration of CO_2 and global carbon emissions (3).

Third, a growing body of experimental work demonstrates that ocean acidification projected for the middle to end of this century (25, 26) will lead to variable but predominantly adverse biological and ecological responses for key species of coral reef organisms (27). Reef areas exposed to clean CO_2 from underground seepage provide windows to the future of coral reefs under ocean acidification. Those studies report a suite of adverse effects including substantial loss of species (16), loss of ecological functions (28), and physiological impairment of invertebrates (29) and fish (30). Conservative model predictions building on observations and experimental research indicate that if carbon emissions continue to follow a business-as-usual path, tropical coral reef environments are likely to shift toward conditions that are marginal for reef growth during this century (3, 31, 32).

Fourth, in addition to climate change and ocean acidification, many coral reefs are also exposed to a suite of pressures of local or regional origin. Examples of such local-scale stressors are overfishing (33); pollution from urban and coastal developments (34); and the runoff of sediment, nutrients, and pesticides from agricultural land (35, 36). In these areas, stresses from global- and local-scale stressors are compounding each other, leading to the problem of cumulative impacts and compromised resilience (37).

In this article, I review and synthesize the consequences of climate change and ocean acidification for the sustainability of coral reefs. I ask two related questions. First, what are the likely consequences of climate change and ocean acidification for coral reef vulnerability and resilience? Second, what are the practical solutions to the problem at the local, regional, and global scales?

With the 21st Conference of the Parties to the United Nations Framework Convention on Climate Change (in Paris) just completed, will a global carbon emissions policy now be an effective part of the solution for coral reefs, or will management and adaptation measures at the local and regional scales be facing an uphill battle? Before reviewing consequences and discussing solutions, I present an overview of the warming and acidification observations and predictions under different global carbon emissions scenarios. This overview provides a basis for understanding the risks to reefs associated with carbon emissions and their timelines.

1.3. Ocean Warming and Acidification Under Carbon Emissions Scenarios

Global warming has a near-linear relationship with carbon accumulated in the atmosphere (e.g., 38). Although warming trends vary geographically (39), ocean warming largely follows the global trend (18). The heat content of the global upper ocean (0–700 m depth) has increased steadily since circa 1990 (40; see also **Figure 1*a***), with the mean thermal anomaly for 2015 reaching

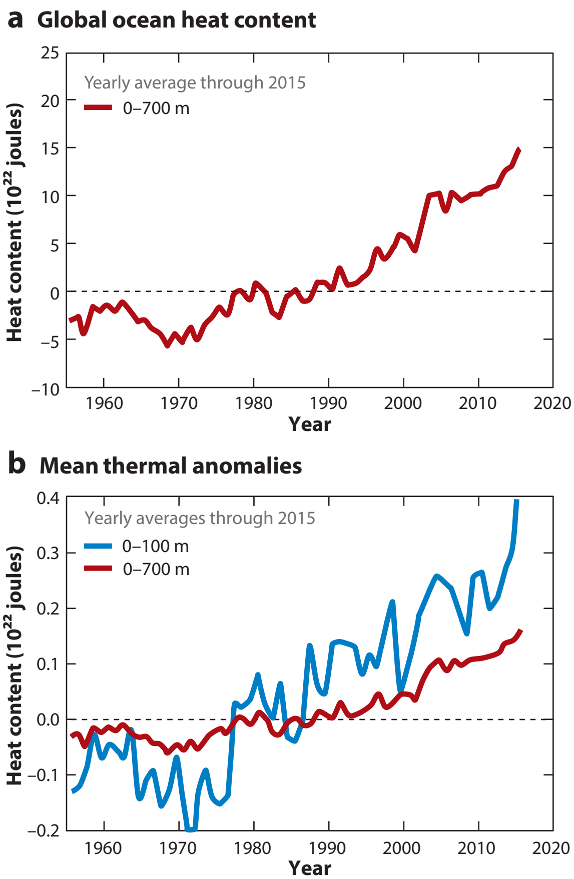

Figure 1

Estimated (*a*) mean global heat content of the upper ocean (0–700 m) based on multiple data sources (40) and (*b*) mean annual thermal anomalies for two global ocean layers. Figure compiled and redrawn with permission from the NOAA/NESDIS/NODC Ocean Climate Laboratory (**https://www.nodc.noaa.gov/OC5/3M_HEAT_CONTENT/**).

approximately 0.15°C for the 0–700-m layer and 0.4°C for the 0–100-m layer (**Figure 1*b***). The rate of warming of tropical ocean surface waters is on average 70% of the global warming rate (41).

In parallel with the warming trend, the accumulated atmospheric carbon will drive ocean acidification along a predictable trajectory (26). Therefore, projections for ocean warming and acidification in the coming decades will in part depend on which carbon emissions scenario and mitigation measures play out on a global scale.

The climate research community has recently established a process for developing such scenarios referred to as Representative Concentration Pathways (RCPs). These RCPs capture the carbon consequences of different societal behaviors across the globe, including policies, changes in vegetation land cover, technological trends, and attempts at mitigation through shifts to renewable and alternative energy sources (42). Among the four key pathways, the business-as-usual scenario (RCP8.5) represents a fossil-fuel intensive world with little or no shifts to renewable energy sources and an outlook to 4°C warming by year 2100 relative to 2005 (**Figure 2*a***). The predicted consequence of RCP8.5 for the carbon chemistry of ocean surface waters is a decline in

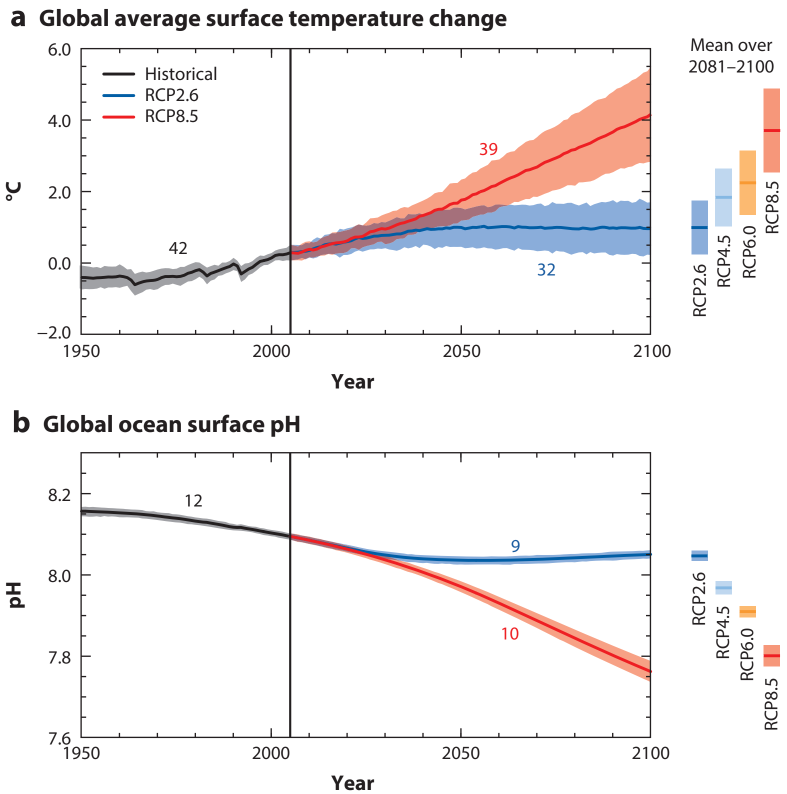

Figure 2

Model projections of (*a*) changes in global annual mean surface temperature (air) and (*b*) ocean surface pH for Representative Concentration Pathway (RCP)2.6 (*blue*) and RCP8.5 (*red*). Shaded envelopes indicate uncertainties. Temperature projections are relative to years 1986–2005. Projections are based on multiple models (numbers indicated) under the Coupled Model Intercomparison Project Phase 5 (**http://cmip-pcmdi.llnl.gov/cmip5/**). The black line is the modeled historical evolution based on reconstructed forcings (*gray* shading indicates uncertainty). The mean and associated uncertainties averaged over 2081– 2100 are given for all RCPs to the right of the graphs. Reproduced with permission from Reference 47, figures 7a,c.

pH to less than 7.8 by year 2100 (**Figure 2*b***). This corresponds to a drop in the seawater aragonite saturation state to approximately 2 (43), well below the optimum for sustained coral reef growth of approximately 3.5–4.5 (3, 44, 45). Other predicted consequences of a strong warming scenario for the oceans are risks of changing ocean circulation and significant sea level rise due to thermal expansion and the melting of polar ice caps (17).

At the other end of the scenario spectrum, the RCP2.6 represents strong mitigations with immediate transition to alternative renewable energy sources and associated technologies (17). The warming projections for RCP2.6 is a peak at approximately 1.5°C above preindustrial levels by the middle of this century (0.5°C above 1986–2005; see **Figure 1*a***), thereafter cooling gradually toward 1°C above preindustrial levels by 2300 (46). Importantly, warming patterns driven by RCP8.5 and RCP2.6 scenarios do not diverge significantly until around year 2030 due to the inertia of technology and infrastructure changes, and the residence time of carbon in the atmosphere (47). RCP4.5 and RCP6 are intermediate scenarios with projected end-of-century warming of 1.8°C and 2.2°C mean increases above the 1986–2005 mean global temperature (**Figure 1*a***). Importantly, although projected ocean acidification under RCP4.5 and RCP6 presents an improved outlook compared to RCP8.5, RCP6 will lead to a significant drop in ocean surface pH below 8 (~7.9; see **Figure 1*b***), signifying potentially damaging carbon chemical conditions for coral reef builders and other marine calcifiers (48). Recent analyses indicate that current global carbon emissions are tracking the RCP8.5 scenario (49).

In the following section, I discuss more specifically the predicted consequences of different severities of ocean warming and acidification for coral reefs. Importantly, other consequences of severe climate change, such as changing ocean circulation and sea level rise, may also have significant impacts on coral reefs (9). Specifically, modern coral reefs are keeping up with current sea level rise and may continue to do so under RCP2.6 and RCP4.5 (50). However, risks of rapid sea level rise in combination with suppressed net rates of coral calcification due to warming and acidification under the RCP8.5 scenario might see some coral reefs drowning in a high-CO_2 world. This is likely to be most prevalent in coastal environments where increased sediment resuspension (turbidity) due to altered flows combine with reduced light in deeper turbid water, hence potentially pushing corals into a zone where coral's energy expenditure exceeds intake (51).

2. GLOBAL CHANGE AND CORAL REEFS—IN A NUTSHELL

Tropical coral reefs are found between latitudes 20–30° N and S, depending on region (52), and predominantly within the euphotic depth zone (53). The formation and growth of tropical reefs hinge on the symbiotic relationship between corals and unicellular algae (zooxanthellae) of the genus *Symbiodinium*. Photosynthesis by the symbiotic algae accounts for more than 90% of the coral's energy budget (54) needed for calcification (55), tissue growth (56), and reproduction (57). This symbiotic relationship is possible and productive within only a range of environmental conditions, technically within reef-building coral's fundamental (physiological) niche. At the scale of oceans, the main dimensions of coral's fundamental niche are seawater temperature, light, and carbon chemical conditions; they are the first-order environmental determinants of reef distributions at the global scale (2).

Corals like it hot, but not too hot. In more technical terms, tropical reef-building corals live close to their upper thermal limits (58). For example, the rate of calcification increases with temperature up to a point (the thermal optimum) and then declines (59, 60). When summer temperatures get hotter than optimal, i.e., they exceed the long-term summer average that corals have become acclimated or adapted to (61), the risk of coral bleaching increases. Due to the relatively narrow environmental envelopes that tropical coral reef organisms have typically occupied historically, they are sensitive to departures beyond those envelopes (2, 3).

2.1. Bleaching: A Modern Stressor on Coral Reefs

Bleaching is a popular term for a process whereby the relationship between the coral host and its endosymbiotic algae breaks down (62). More specifically, under supraoptimal light and temperature conditions, the zooxanthellae release free oxygen radicals that are toxic to the coral host (63, 64). In response, the host cells expel the dysfunctional algal cells, leaving the coral colony to appear white. The loss of zooxanthellae, when severe, starves the coral of energy from photosynthesis and can lead to mortality unless temperatures return to normal and symbiont densities are restored before the coral exhausts its energy reserves (65). Prolonged coral bleaching can lead to extensive coral mortality with devastating consequences for the associated reef fauna (66, 67).

The earliest severe coral bleaching event at the scale of oceans was in 1982–1983 during a strong El Niño event (68). Earlier reports were of a local nature or were mostly attributed to factors other than warming (69). The summer of 1998 saw the most severe mass coral bleaching, spanning all ocean basins (62, 70–74). Although the 1998 pantropical mass bleaching episode was associated with another El Niño event, its scale and intensity were unprecedented and were potentially a harbinger of what is to come for coral reefs in a warming world. Another warming event in the western Pacific in 2002 led to a subsequent extensive bleaching episode on Australia's Great Barrier Reef (GBR; 75). In 2005, the Caribbean saw its warmest summer on record, resulting in severe coral bleaching throughout the region (76). A region-wide warming event occurred in Southeast Asia and North West Australia in 2010, leading to extensive coral bleaching in Southeast Asia (77) and unprecedented levels of bleaching in North West Australia (78). At the time of writing, the GBR and other coral reefs in the Pacific and Indian Oceans are in the early recovery phase following another El Niño–driven mass bleaching event, and the worst to date, where more than 90% of reefs on the GBR were affected (79). ENSO is expected to remain a dominant driver of the interannual climate variability in the Pacific (17, 22). Under global warming, however, risks of mass coral bleaching are likely to increase under both El Niño and La Niña conditions. Specifically, bleaching models for this century predict that coral reefs may bleach on an annual basis by year 2030–2060, depending on carbon emissions scenarios, coral species, and geographic locations (14, 80).

Because different coral taxa have different susceptibilities (81, 82), bleaching risks and consequences are likely to be more variable than previously assumed (11). Also, there is evidence for thermal adaptation via mechanisms ranging from selective mortality (77, 83) to symbiont adaptation (84) to heritability of acquired thermal resistance (85). Despite such capacity, however, rates of adaptation are unlikely to keep pace with the rate of warming under a business-as-usual emissions scenario (86), and adaptation via selective mortality may come at the cost of reduced genotypic variation (83). Results of a recent study indicate that seasonal trajectories of ocean summer heating under progressed climate change will prevent corals from preacclimating to the main summer warming event, potentially lowering overall thermal tolerance and increasing coral mortality risk (87).

2.2. Tropical Storms in a Warmer Atmosphere

Storms are a natural part of tropical environments and have historically been the primary acute disturbance agent on coral reefs (88). The high species diversity often seen on reefs reflects a nonequilibrial state (89) and are, in part, shaped by acute disturbances fully or partly resetting the system after 5–20 year-long interludes of succession (90). The effect of tropical storms (cyclones, hurricanes) on coral reefs is that of physical, structural damage, where the degree of damage scales with storm intensity—or more specifically, wave impact (91). Recurrent questions are (*a*) whether storms will increase in intensity and/or frequency in a warmer climate and (*b*) whether storms in combination with mass bleaching events will overwhelm the ability of coral reefs to recover and restore ecological function, diversity, and ecosystem services between disturbances. For the first question, analyses of storm history in the North Atlantic and western North Pacific indicate a doubling of the power dissipation from storms in the period 1970–2000 (92). Also, high-resolution dynamical models predict that the average intensity of tropical storms will shift toward stronger storms in a warmer climate (93). Lastly, recent analyses using downscaled global simulation models predict an increase in tropical storm frequency and intensity in most locations (94). For the second question, a series of severe cyclones in the past decade and two mass bleaching events in 1998 and 2002 on the GBR provide a tentative answer. Since 2005, eight severe cyclones (category 3 or above) affected the GBR, including one of the largest and most powerful tropical storms to have made landfall in Queensland in modern history (95). Cyclones account for approximately half of the coral mortality that has led to the 50% decline of coral cover on the GBR in recent decades (96).

Importantly, a strong storm regime does not reduce reef resilience per se, but increases the demand for resilience (6). That is, frequent and/or severe impacts on coral mortality and reef structure places greater demand on recovery processes; but if these are intact, then resilience is retained. Warming and bleaching events, however, lower resilience by reducing coral growth rates (97) and reproduction (98, 99). Therefore, although bleaching events have been attributed to only 10% of the observed coral mortality on the GBR (100), the prolonged loss of calcification rate and reproductive output of heat-affected corals following the 1998 and 2002 bleaching events is likely to have affected coral resilience to both bleaching and cyclones.

2.3. Ocean Acidification: A Creeping Invisible Challenge

Like climate change, ocean acidification is a global problem. In essence, ocean acidification is the chemical consequence in the ocean of increasing CO_2 in the atmosphere. Briefly, as the CO_2 partial pressure in the atmosphere increases, more CO_2 is taken up by surface waters of the ocean (101). There, the dissolution of CO_2 produces carbonic acid, which lowers pH and shifts the carbonate system toward reduced concentrations of carbonate ions (20, 24), which are the building blocks of marine biogenic calcium carbonate structures. Unlike climate variability (such as ENSO extremes) and climate change, which episodically mark their presence with strong thermal anomalies and large-scale bleaching events, ocean acidification is a creeping stressor that gradually compromises a suite of biological functions on coral reefs. One of the most critical functions affected by ocean acidification is marine calcification (44). The shift in the seawater carbonate system under ocean acidification lowers the capacity of calcifying organisms, including corals, to build skeletons (48). Reduced coral calcification under acidification means slower coral growth (102), more fragile structures (103), and potentially a shift from net accretion to net dissolution (45, 104). This implies greater susceptibility to storm damage, slower recovery rates between disturbances, less habitat-forming structures, and overall reduced reef resilience (32). Other biological and ecological functions affected by ocean acidification are reduced abundance of crustose coralline algae (105), which play a key role as substrates for invertebrate larval recruitment (106); shifts in competitive hierarchies between corals and macroalgae (107); and potentially increased bleaching susceptibility of corals to warming (31). However, biological effects of ocean acidification extend beyond the sessile fauna. Experimental work with larval reef fish demonstrates that carbon chemical conditions representative of a late-century business-as-usual carbon emissions scenario lead to impairment of behavioral responses critical for fish recruitment (30, 108). As yet, there is no evidence that coral reef organisms can adapt or acclimate to ocean acidification.

Laboratory and field experiments provide key insights into the likely combined impacts of ocean acidification and warming on coral reef processes under different future carbon emissions scenarios. For example, Dove et al. (109) showed that the calcification rate of small experimental patch reefs in tanks subjected to projected end-of-century conditions for the business-as-usual carbon emissions scenario (~RCP8.5) dropped by approximately 130% relative to the present-day control—i.e., from net accretion to net dissolution. This result is largely consistent with predictions (45, 110). Conversely, experimental reef calcification under conditions representative of an intermediate emissions scenario (RCP4.5) was approximately 50% of controls, i.e., suppressed but positive net accretion. Interestingly, experimental reef calcification under present-day control conditions was approximately 25% lower than under preindustrial conditions (109). A recent field experiment manipulating the carbon chemistry of seawater flowing over a natural reef community (111) demonstrated a 6.9% increase in net calcification at aragonite saturation states representative of preindustrial levels. Both studies (109, 111) provide evidence that coral reefs have already lost significant calcification capacity due to ocean acidification.

3. CUMULATIVE IMPACTS AND RESILIENCE UNDER GLOBAL AND LOCAL STRESSORS

The highly dynamic nature of coral reefs, combined with examples of reef communities undergoing succession from barrens to climax coral assemblages in less than a decade (90, 112), indicate that coral reefs are inherently resilient (113). Climate change and ocean acidification, however, are now adding increasingly to the natural stress regimes on coral reefs with both press-type (chronic) and pulse-type (acute) disturbances (3, 6, 7), and some authors argue that this decline started centuries ago (114). These unprecedented cumulative impacts of global and local stressors may increasingly overwhelm the resilience of coral reefs by compromising their capacity for resistance, repair, replenishment, and recovery. With key resilience processes compromised, the sustainability of coral reefs will be a challenge.

I address this management challenge in Section 4. In preparation for that discussion, I first review the issue of cumulative impacts and ecosystem resilience under multiple stressors that occur at different scales in time and space, and with different root causes. Understanding cumulative impacts on coral reefs can provide critical insight into factors affecting the system's resilience. In turn, an understanding of factors driving resilience can inform what management and policy initiatives can be achieved, and equally important, what cannot be achieved, through efforts to sustain coral reefs in a high-CO_2 world.

3.1. Cumulative Impacts: Sources of Stress and Management Levers

Stress can accumulate in time and space from single and multiple sources (115). If stress exceeds resistance and/or recovery is low between disturbance events, these influences will give rise to cumulative consequences or impacts. For example, frequent warming events or a cluster of cyclones can become dependent stressors over time if the system state resulting from one impact influences the resistance to, or recovery from, the subsequent event (116, 117). Where multiple stressors coincide in time and space, the degree to which they influence the system individually and through interactions will determine the nature and severity of cumulative impacts. Examples of such cumulative influences are increased coral bleaching susceptibility under nutrient enrichment (118, 119), the role of herbivore loss in preventing the control of macroalgae that compete with corals for space (120), and the role of ocean acidification in lowering resistance to storm damage (103) and in increasing coral bleaching susceptibility (31). The type of cumulative impacts that cause the greatest concern are activities that lead to the crossing of ecological thresholds, i.e., the triggering of ecosystem shifts to undesirable states (121, 122). Under cumulative stress regimes where global ocean warming and acidification unfold and lower the resilience of coral reefs (32), the additional influence of seemingly innocuous stressors from local and regional disturbances may increasingly lead to risks of threshold exceedance.

Managing cumulative impacts requires insight into (*a*) the drivers and activities that result in stress on the system, (*b*) what scales they operate on (115), and (*c*) in what way these influences interact (123, 124). Such insight helps identify stress pathways as well as management actions that can alleviate stress on the system, i.e., via effective management "levers." A useful approach to assist in this process is the drivers-pressures-state-impacts-responses framework (125) combined with models of the linked social-ecological system (6, 126, 127). This approach maps the pathways of stress from sources to impacts on ecosystem goods and services and enables analysis of possible options for impact avoidance or mitigation by closing the loop back to stressors via management responses (**Figure 3**). By facilitating the exploration of (*a*) possible scenarios that can lead to

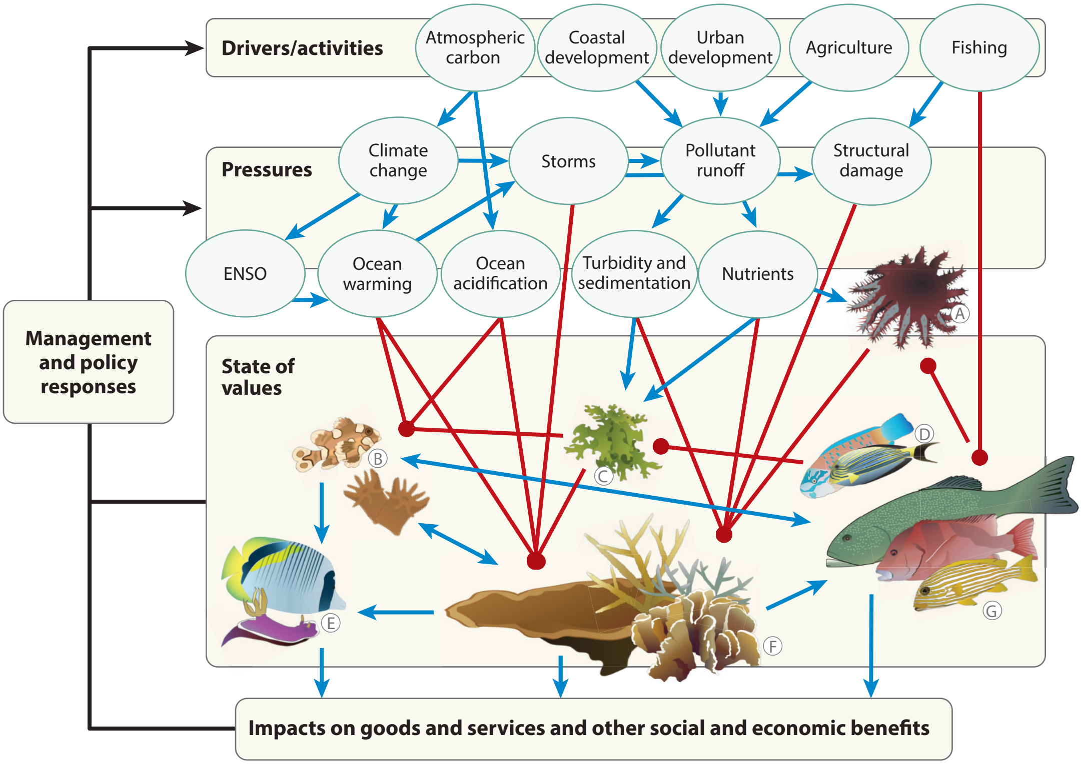

Figure 3

Simplified conceptual model of global and local environmental influences on key functional groups on coral reefs. The model is structured within a drivers-pressures-state-impacts-responses framework. Sharp (*blue*) and blunt (*red*) arrows indicate positive and negative influences, respectively. Organisms shown: (A) Crown-of-thorns-starfish, (B) juvenile corals and fish, (C) macroalgae, (D) herbivorous fish, (E) coral-associated fish and invertebrates, (F) corals, and (G) predatory fish. Fauna and flora images by T. Saxby, C. Collier, and D. Tracey, Integration and Application Network, University of Maryland Center for Environmental Science (**http://www.ian.umces.edu/imagelibrary/**). ENSO, El Niño Southern Oscillation.

cumulative impacts at global and local scales (e.g., carbon emission paths, regional development trends, political and socio-economic changes) and (*b*) tangible alternatives for intervention, the approach can help guide effective management and policy decisions.

By exploring the stress paths resulting from different combinations of drivers in **Figure 3**, the problem of cumulative consequences for ecosystem values can be illustrated conceptually for a coral reef in a coastal zone area. For example, more carbon in the atmosphere drives climate change, which drives ocean warming and storm regimes (94). By affecting storm regimes (and thereby in part rainfall and flood risks), climate change also influences pollutant runoff from the land; this is the case particularly if flood events are preceded by deeper droughts (128) and/or if the land has been cleared (129). Thus, some of the cumulative consequences of climate change are (*a*) impacts of ocean warming on corals, e.g., as bleaching and reduced growth; (*b*) reduced recruitment, e.g., as a consequence of reduced reproduction; (*c*) direct storm impacts on coral reef structures; and (*d*) secondary impacts on corals, fish, and other reef-dependent species via enhanced runoff of sediment, nutrients, and toxins (**Figure 3**). The interaction between climate change, climate variability, and land use on the consequences for coral reefs can be used to illustrate the potential for management actions that can alleviate cumulative impacts. For example, land use practices that make water sheds less exposed to soil erosion following floods may reduce coral reef vulnerability to this indirect impact of climate change via storms. Also, management of reef fisheries that prevent loss of herbivores can alleviate risks of reef-community shifts from corals to macroalgae under nutrient enrichment, potentially compensating for some lost competitive ability of corals over macroalgae under climate change and ocean acidification (**Figure 3**).

3.2. Reef Resilience: Management Opportunities and Limitations

Ecological resilience is broadly defined as the capacity of a system to absorb stress, reorganize and recover from disturbances, and over time retain the same function, structure, and identity (113, 130). The concept of managing for resilience is the optimistic angle on managing against vulnerability (131) and builds on the premise that smart actions on the ground can provide some level of protection against decline caused by climate change (132). Although this premise works in some situations, an important limitation is that resilience lost to one pressure might not be replaceable by mitigation of another pressure. In the following, I first review how different environmental pressures affect coral reef resilience and then discuss situations where management interventions at local scales can build resilience, and also where these are unlikely to be effective in the face of global environmental change.

From a management and policy perspective, ocean warming and acidification represent an almost paradoxical problem by eroding reef resilience and simultaneously increasing the demand for resilience (32). Specifically, press-type (chronic) stresses from ocean acidification and warming reduce coral growth and productivity (31, 133), scope for recruitment (108, 134), resistance to storm damage (103), and competitive strength of corals over algae (107, 135). Weakening of these processes translates to a weakening of the cornerstones of coral reef resilience (113). This effectively means that ocean warming and acidification will act as a ceiling on the scope for resilience-based management, lowered in pace with the increase in atmospheric carbon (**Figure 4**). In parallel, pulse-type (acute) disturbances in the form of coral bleaching events (80), tropical cyclones (94), and ENSO extremes (136, 137) are predicted to become more severe and frequent, thereby increasing mortality risks associated with each disturbance event as well as shortening the time frame available for recovery between events.

On reefs where multiple stressors from local, regional, and global stressors accumulate on the processes that underpin resilience (e.g., recruitment, recovery, resistance to bleaching and

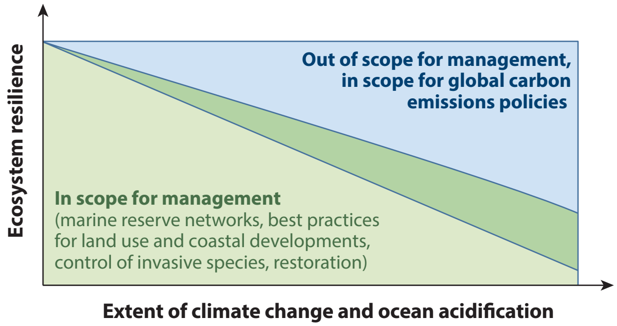

Figure 4

Scope for the enhancement of natural ecosystem resilience by local- and regional-scale management actions (*green*) and global carbon emissions policies (*blue*). The model builds on the premise that resilience has an upper limit, defined by the rates and strengths of processes that lead to succession and recovery, population replenishment, competitive hierarchies between species, trophic relations, and community reassembly. As ocean warming and acidification compromise most or all of these processes, the scope for local- and regional-scale management efforts to restore resilience to preindustrial levels is expected to decline. The dark green wedge represents the potential opportunity for management actions to compensate for lost resilience due to climate change and ocean acidification, for example, by intensified control of natural stressors such as crown-of-thorns starfish, assisted evolution, and effective and sustainable measures of reef restoration.

disease), well-designed management strategies can help increase reef resilience, albeit not beyond the ceiling imposed by ocean warming and acidification. Examples of such strategies are the establishment of networks of marine park areas or no-take fishing reserves, especially in countries where herbivorous fish are overfished (120). A recent study on the GBR showed that no-take zones on the GBR built resilience in coral trout populations to cyclone damage as larger fish were less vulnerable to storms and had higher reproductive output that could help replenish the population (138). Another study demonstrated analytically that reserve networks on the GBR confer enhanced resilience to disturbances for coral and fish communities (139). The mechanisms by which fisheries management enhances reef resilience are unknown but are likely to include indirect impacts on herbivory, trophic cascades, and maintenance of key ecological functions.

In the following section, I explore situations where management actions can be effective in increasing resilience for coral reefs in the face of global change. I also present a reality check on the extent to which such management actions can be a solution to a global problem. Management programs are expensive, so a clear understanding of the scope and effectiveness of different actions can facilitate more informed decision-making and better returns on investments in management and policy.

4. LOCAL MANAGEMENT SOLUTIONS TO A GLOBAL PROBLEM?

A question often raised in the context of climate change effects on coral reefs is: Can local or regional management actions support reef resilience and thereby reduce the threat of climate change and ocean acidification? The question has given rise to numerous papers proposing that intensified management at the local scale can help offset the global problem or buy reefs some time until carbon emissions can be stabilized. Examples include improved spatial planning (140–143), improved land use practices to enhance water quality in coastal zones (144–146), protection of herbivorous fish to promote top-down control of macroalgae (132), and intensified control of coral-eating crown-of-thorns starfish (CoTS) (6). There are two challenges associated with the local-scale approach to alleviating stress from global pressures. One is that there are limits to resilience (i.e., the maximum resilience potential), and another is that local-scale actions have limited geographical reach.

4.1. Limits to Resilience-Based Management

Resilience is the result of a suite of biological and ecological processes that enable stress resistance, survival, recovery, trophic and competitive hierarchies in favor of key functional groups, population replenishment, and community reassembly (147). Resilience-based management hence refers to the management or policy interventions or strategies that can support these processes (6). For example, management actions that alleviate algal overgrowth of corals by protecting herbivorous fish (148), reduce coral disease risks by alleviating nutrient or sediment stress (149), or strengthen source-sink relationships by establishing networks of marine reserves (142) all help build resilience. In particular, if the local stressor (e.g., poor water quality) interacts with a climate change variable (121), efforts to reduce the local stressor can to some extent counteract climate change impacts at that local scale (124). However, impairment of resilience caused by ocean acidification and warming cannot directly be restored by protecting more herbivores, improving water quality even further, or establishing bigger reserves. Reduced coral calcification (102), recruitment (134), and competitive strength of corals over macroalgae (107) caused by acidification will be a resilience handicap that can only be addressed by reversal of changes in ocean carbon chemistry through carbon mitigation strategies or potentially via geoengineering (13).

Moreover, in areas where multiple stressors of global and local origin lead to cumulative impacts, management of the local stressors can promote local resilience as discussed above. Importantly, however, understanding the spatial and temporal scope of such actions is critical to set realistic expectations for what can be achieved through management actions in the face of global change. Two useful concepts here are (*a*) the zone of impact of different stressors and (*b*) the zone of influence of management and policy. The latter can be identified by examining the consequences of pulling a management or policy lever on one or more drivers or activities causing adverse impacts. This is illustrated nonspatially in **Figure 4** where, for example, improved land use and lowered risk of floods (following droughts on cleared land) associated with storms can reduce the risk of pollutant runoff to reef waters in coastal regions.

4.2. Example from the Great Barrier Reef

To provide spatial context, consider the example of outbreaks of coral-eating CoTS on the GBR. Briefly, CoTS are one of the most damaging disturbances on the GBR (96). Contrary to cyclones and bleaching, however, CoTS are amenable to local and regional management intervention through at least three paths. First, CoTS occur in outbreak waves, starting in the narrow northern part of the GBR close to the Queensland coast, likely triggered by nutrient pulses flowing into reef waters following major floods, which improves the survival of CoTS larvae in the plankton (150). Hence, one tangible management handle is improved land use practices to reduce nutrient runoff (**Figure 5**). Second, build-up of CoTS densities in the primary outbreak area leads to subsequent spread to southern reefs via larval connectivity between reefs (151). Once an outbreak is underway, efforts to contain or stabilize the growing starfish population using manual control techniques have limited effect. However, targeted CoTS control efforts on key source reefs in the early stage of the outbreak can prevent population spread (152)—i.e., a local management action can here potentially alleviate CoTS risks to the entire reef system (**Figure 5**). Third, CoTS numbers appear to be suppressed in areas closed to fishing, potentially due to increased fish predation on juvenile CoTS (153).

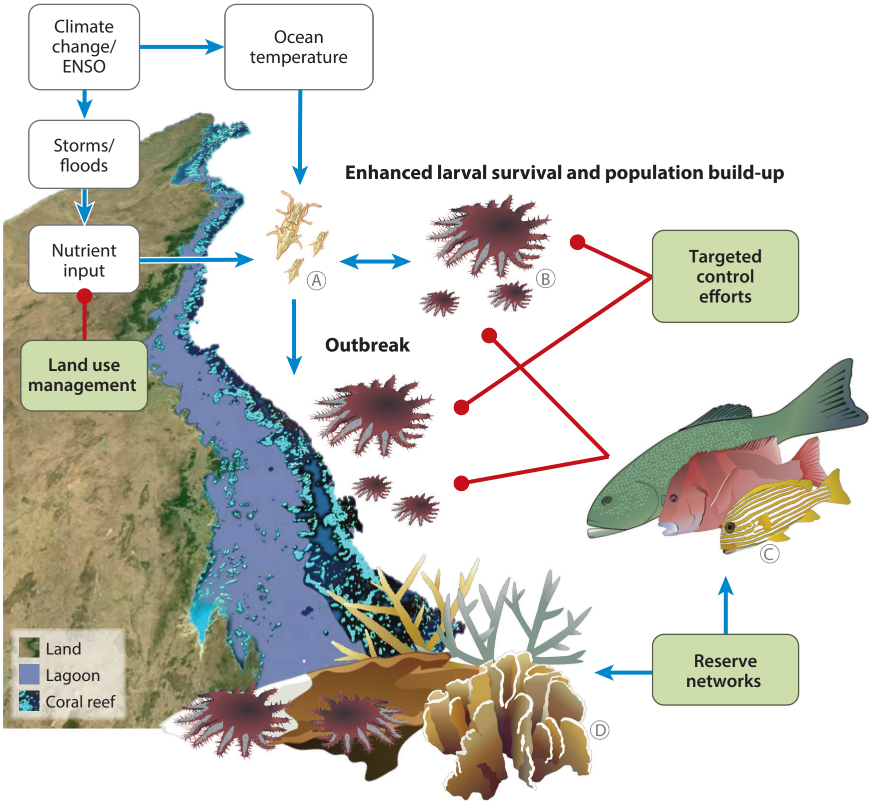

Figure 5

Schematic representation of the drivers (*white boxes*) influencing outbreaks of crown-of-thorns starfish on Australia's Great Barrier Reef and three potential avenues for management (*green boxes*). The example illustrates that intensified management of a natural, but major, stressor on coral reefs can to a limited extent compensate for loss of resilience due to climate change. Sharp (*blue*) and blunt (*red*) arrows indicate positive and negative influences, respectively. Organisms shown: (A) crown-of-thorns starfish larvae, (B) starfish juveniles and adults, (C) predatory fish, (D) corals. Fauna and flora images by T. Saxby, C. Collier, and D. Tracey, Integration and Application Network, University of Maryland Center for Environmental Science (**http://ian.umces.edu/imagelibrary/**). ENSO, El Niño Southern Oscillation.

This example illustrates that alleviation of a major stressor (CoTS) can potentially, and to some extent, compensate for the increased pressure of climate change on the world's largest coral reef system via a three-pronged management strategy. Historically, CoTS outbreaks were major disturbances on the GBR and other Pacific reefs before climate change had become an issue (154), but the natural resilience of coral reefs was then sufficiently high to absorb and recover from CoTS outbreaks. Although the example demonstrates the potential for targeted management to compensate for some resilience loss due to global pressures (see the dark wedge in **Figure 4**), it is not a long-term insurance policy against progressed climate change and ocean acidification. If or when coral bleaching events become annual events (79) combined with reef dissolution rates exceeding calcification (45) and increased intensity and/or frequency of cyclones, then the system's capacity for recovery, replenishment, and reassembly is likely to be overwhelmed, regardless of the effectiveness of CoTS control, amount of investment into water quality management, and the extent of marine spatial planning. By then the problem of resilience enhancement moves beyond the scope of local and regional management. Solutions to the medium-to-long-term problem of protecting coral reefs under climate change and ocean acidification will ultimately have to come from both global and local solutions to the carbon emissions problem.

4.3. Solutions via Adaptation

The amount of ocean warming and acidification expected for the near future under the RCP2.6 and RCP4.5 (committed ocean warming and acidification due in part to the inertia of transitions to renewable energy sources and the retirement of fossil-fuel-dependent infrastructure; see 17, 47) raises questions around what adaptation measures can be pursued to protect coral reef ecosystem services in the face of climate change. One approach that is gaining interest is that of human-assisted evolution, centered on the proposal to explant manipulated (i.e., more climate resistant) stock onto coral reefs (155). In theory, the approach could help coral reef managers break through the resilience ceiling imposed by climate change and ocean acidification, as enhanced physiological capacity for stress resistance and improved performance of selected species could help maintain ecosystem function and goods and services. Genetically engineered or genetically modified organisms are not yet a tangible management solution, but assisted evolution approaches (e.g., artificial selection and heritable acclimation via epigenetics) are an area of active research with a view to management application in the near future (155). Briefly, the approach explores four avenues: (*a*) stress exposure and acclimatization of natural stock within and between generations (i.e., via epigenetic mechanisms), (*b*) the modification of the microbial community associated with corals to afford increased stress resistance and risk of disease, (*c*) selective breeding for stress resistance, and (*d*) manipulation of the strains of algal symbionts (zooxanthellae).

Although the approach has merits, it also has risks and limitations. The obvious merits are the possibility that the conservation of keystone species that function as ecosystem engineers (i.e., corals) and underpin coral reef fisheries and tourism industries (e.g., fish and invertebrates) may continue in the face of climate change and ocean acidification. This may help sustain at least some of the goods and services of coral reefs and may support some dependent societies and livelihoods. Obvious risks are the spread and eventual monopolization by a few species that outcompete others and that in the process become invasive pests. A counterargument here might be that, with climate change and coral reef decline on the horizon, the spread and dominance of selected keystone species may be a better outcome than total decline. An obvious limitation is the practical limitation on the number of species that can be enhanced for the purpose of maintaining or restoring coral reef biodiversity and function. Coral reefs are home to hundreds of species of reef-building corals, thousands of species of fish, and tens of thousands of species of invertebrates. More broadly, coral reefs are the rainforests of the sea and may be home to around 25% of the species in the ocean (156). With that perspective in mind the question is: Will the selection of a small subset of those species for assisted evolution and resilience enhancement be an adequate surrogate for coral reef function and ecosystem services in the future?

In addition to supporting livelihoods and industries, an increasingly important service provided by coral reefs in the face of climate change and sea level rise is coastal protection; and here coral reefs provide more cost-effective solutions than artificial ones (157). More than 100 million people live in low-lying areas within 10 km from coral reefs, and their future depends on the future of coral reefs in multiple ways (156, 157). Given the significant global value of coral reefs from social, economic, environmental/ecological, and conservation perspectives, efforts to sustain reefs and reef-dependent people in a high-CO_2 world are likely to involve trade-offs between the protection of broad-scale biodiversity and key ecosystem services—i.e., between ecological and social objectives. Because coral reefs and dependent societies make up a linked social-ecological system (6), management and policy solutions that deliver the best chance of long-term success are likely those that maintain or strengthen reef–people synergies at the local, regional, and global levels. Future climate and ocean acidification risk trajectories will be a function of global carbon emission behavior (17, 47), and additional stressors on coral reefs and other marine ecosystems will be driven by a suite of local and regional anthropogenic drivers (158). Therefore, solutions that offer the best long-term prospects for coral reefs and dependent people will be those that build on an integrated strategy of rapid reductions in global carbon emissions, climate adaptation, and targeted local and regional management actions.

5. SUMMARY

Climate change is the physical consequence of increasing greenhouse gasses in the atmosphere. It drives ocean warming, fuels tropical storms, and leads to sea level rise. Ocean warming drives coral bleaching and leads to reduced coral growth and reproduction. In addition to causing physical damage, stronger storms may also enhance the intensity of floods. Sea level rise may further compromise reef growth, especially in coastal environments.

Ocean acidification is the chemical consequence of increasing CO_2 in the atmosphere. It lowers marine calcification, and thereby lowers reef growth and reduces the capacity for population replenishment. Under fossil-fuel intensive scenarios (RCP8.5 and RCP6), ocean acidification and warming may in combination shift coral reefs from a state of net accretion to net erosion during this century.

Climate change and ocean acidification are jointly the greatest challenge facing coral reef managers and policymakers globally. Predicted ocean warming and acidification will lower ecosystem resilience (**Figure 4**) by impacting biological and ecological processes that underpin stress resistance, recovery, replenishment, reorganization, and reassembly. Such resilience loss makes coral reefs more vulnerable to other stressors, including poor water quality, overfishing, and invasive species.

Although these global pressures place a ceiling on the effectiveness of local management actions in sustaining reef health, some opportunities exist to compensate for lost resilience by strategic management of local- and regional-scale stressors. A specific example is the management of crown-of-thorns starfish on the GBR (**Figure 5**). Importantly, although local- and regional-scale management strategies may build resilience in the short term, and within defined geographical zones of influence, the investment in such resilience gain will give medium- to long-term returns only if accompanied by a shift to a low-emissions scenario, e.g., RCP2.6 or RCP4.5, where ocean warming and acidification are expected to peak during the middle of this century. Under the business-as-usual scenario (RCP8.5), global climate change and ocean acidification will eventually overwhelm the processes that underpin coral reef resilience, regardless of investments into local or regional management plans.

Innovative measures of adaptation are being explored to break through the resilience ceiling for coral reefs imposed by climate change and ocean acidification. Of these, the concept of assisted evolution via mechanisms of acclimation, adaptation, and artificial selection may increase the resilience of a subset of keystone species on coral reefs, providing for some continued goods and services in the face of global change. Assisted sustainability of a subset of chosen coral reef species may support continued livelihoods in a high-CO_2 world, but in a relatively species-poor system with unknown feedbacks, tipping points, and vulnerabilities.

Coral reefs support the livelihoods of millions, and threats to coral reefs are ultimately threats to people. Solutions that will carry healthy coral reefs into the next century will be those that tackle the global carbon emissions challenge and the local management problems, involving reefs and people, as two sides of the same coin.

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