

# Scientific frontiers in the management of coral reefs

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## Introduction

Coral reefs are an iconic marine ecosystem for their beauty and biodiversity, yet they also sustain a wealth of economic, cultural, and ecosystem services including livelihoods, tourism, coastal protection, and the provision of a secure food source for millions of people around the world ( [Richmond, 1993](#) ; [Reaka-Kulda, 1997](#) ). Despite their great importance, coral reefs face a long list of threats and are documented to be in a rapid decline in most regions ( [Gardner et al., 2003](#) ; [Bruno and Selig, 2007](#) ; [Ateweberhan et al., 2011](#) ; [De'ath et al., 2012](#) ). Local sources of anthropogenic disturbance such as overfishing, pollution, and sedimentation are widespread ( [McManus, 1997](#) ; [Newton et al., 2007](#) ; [Richmond et al., 2007](#) ; [Burke et al., 2011](#) ), and corals are exceptionally sensitive to rising sea temperatures and ocean acidification ( [Hoegh-Guldberg et al., 2007](#) ). From the perspective of marine ecosystem conservation and management, climate change is often seen as overwhelming. As a result, resource managers wonder whether their efforts are likely to be futile in the long-term. It is increasingly clear that reversing ongoing and future coral reef degradation will present significant challenges and take considerable efforts ( [Fenner, 2012](#) ; [Cinner et al., 2013](#) ; [Graham et al., 2013](#) ; [Rinkevich, 2014](#) ). Scientific knowledge can inform and guide the requisite decision-making process and offer practical solutions to the problem of coral reef protection in the face of climate change. The implementation of solutions, however, presently lags far behind the pace required to reverse global declines. Even in regions accepted to have the best management practices and enforcement capabilities, there is a need for an urgent and significant step-up in the extent and range of strategies being

implemented ( [Great Barrier Reef Marine Park Authority, 2013](#) ; [MacNeil et al., 2015](#) ).

Reef managers have a limited toolbox to mitigate threats and to intervene, including marine spatial planning, no-take reserves, watershed management, fisheries regulation, and reef restoration through top-down interventions, co-management, or community-based management activities. Reef health would improve markedly if these interventions were implemented more widely and more effectively. The inadequacy of much reef management has many causes but includes lack of corporate responsibility and social justice and ethics ( [Bundy et al., 2008](#) ), the implementation of poorly planned livelihood alternatives to reduce fishing pressure on reefs ( [Cinner, 2014](#) ), widespread poverty, poor governance at all levels, a lack of political will to protect reefs, and insufficient stakeholder engagement in management and conservation decisions. In this paper, we provide a systematic review of scientific frontiers in natural and social science research that can help build stronger support for reef management and improve the efficacy of interventions.

## **Enhancing the Case for Reef Conservation and Management**

### **Proving Causality Once a Stressor has been Identified**

Coral reefs are exposed to a variety of stressors, both natural and anthropogenic, often acting synergistically ( [Richmond, 1993](#) ; [Hoegh-Guldberg, 1999](#) ; [Hughes and Connell, 1999](#) ). Two of the greatest challenges to implementing effective coral reef management practices include our inability to clearly identify cause-and-effect relationships between stressor

exposure and coral responses and to determine the relative contributions when multiple stressors are involved. Managers are often trapped between different groups of stakeholders who finger-point at each other as being responsible for the observed diminished health of a coral reef and its related resources. Fishers are typically targeted even when overfishing is not the primary problem, and in response, they justifiably point to watershed discharges, pesticide-loaded agricultural and golf course runoff, sewage outfalls, diver-related damage, and climate change. Fishers are key stakeholders, and their constructive engagement is critical to meeting overall coral reef sustainability goals. For many agency-based managers with regulatory authority, in the absence of definitive data identifying the “smoking guns,” the default is inactivity, which is the least effective option for supporting coral reef persistence, resilience, and recovery.

Well-established and widely used coral reef monitoring and assessment protocols often rely on mortality as the key indicator of stress on an affected reef (the loss of individuals and species). While coral bleaching can be a visual sign of stress, the diagnostic value may be limited in multi-stressor situations, and eventual outcomes for bleached species can differ, including full recovery, partial mortality or complete mortality depending on species genotypes ( [Marshall and Baird, 2000](#) ; [Hueerkamp et al., 2001](#) ). Using a human health analogy, it is apparent that corals and coral reefs also demonstrate gradients of vigor and functionality. In order for management efforts to be more efficient, it is critical that stress be identified at sub-lethal levels. Thus, intervention at the local level can yield positive results and outcomes. Additionally, tools that can measure the effectiveness of

mitigation measures in real time (months vs. years) can help guide the allocation of limited human, financial, and institutional resources toward coral reef resource protection. Emerging tools in coral reef forensics (genomics and proteomics) are allowing researchers to address such issues in a more proactive and quantifiable manner.

Thus, new technologies in molecular biology are of high value to coral reef conservation efforts. The “-omics” (genomics, proteomics, and transcriptomics) provide tools and data that can be applied to identify specific cause-and-effect relationships between stressors and organismal responses, determine genotypic diversity within a population, levels of connectivity among reef populations, measure the effectiveness of mitigation and management efforts, and provide insight into the potential resilience of reef communities to both local and global level stressors. The genome or genetic makeup of an organism is fixed, and the range of genotypes within a population can be used as a key measure of important variability that may be responsible for some corals, populations, and reefs surviving exposure to a variety of stressors. Marginal habitats, such as harbors and bays that receive large amounts of runoff, pollutants, and sedimentation, are often assumed to be of lower conservation value than more pristine sites, yet it may be the more stressor resistant genotypes from these areas that survive to replenish downstream reefs and are better adapted to changing environments.

Molecular biomarkers of exposure such as specific proteins and enzymes produced by stressed corals can be utilized to diagnose the key classes of

stressors and their relative effect on individuals and populations ( [Downs et al., 2005](#), [2012](#) ; [Rougee et al., 2014](#) ). Just like the blood tests devised to assess the health of a person, some proteins that are either up or down-regulated can be used to identify which pollutants are both present and biologically relevant. Others can be used to detect temperature stress associated with climate change or oxidative stress associated with increases in fleshy algal abundance. In addition to such proteomic techniques, transcriptomic studies can provide valuable information on specific gene expression, which also varies with environmental conditions and the state of the coral. Measuring levels of protein and gene expression, and how they vary in response to management efforts can be used to guide the allocation of financial, human, and institutional resources to achieve desired outcomes. Such data can also be used in litigation, when needed, to identify the source(s) of stress and subsequently attribute responsibility accordingly ( [Downs et al., 2012](#) ). While scientists use the peer review process to validate the science, managers are often in need of data that will hold up in court. In sum, when used in conjunction with other physiological and ecological measures, molecular tools can provide essential information for use to managers. Progress in the development and application of such tools should include efforts at making them more broadly available including to developing areas where funding is limited.

### **Quantifying and Mapping Ecosystem Services**

A particular challenge for coral reef sustainability is reversing the widespread perception that reef protection is a trade-off with economic goals; positive economic and environmental outcomes are not mutually exclusive,

particularly in developed countries. For example, the Great Barrier Reef generates massive economic benefits to Australia, estimated at nearly &6 billion AUD for 2012, but this is dependent on a healthy ecosystem. Despite that, expenditures on protection of the ecosystem is a small fraction of the income generated ( [McCook et al., 2010](#) ). Further, many of the ecosystem services provided by reefs go unrecognized by stakeholders, primarily non-monetary values. Examples include the production and maintenance of beach sand, protection against wave damage and coastal erosion, and access to safe conditions for recreation such as calm lagoon environments. Here, much of the beach sediment is generated by living calcareous organisms ( [Perry et al., 2006](#) ), the reef provides a natural breakwater to reduce wave height in the lagoon ( [Sheppard et al., 2005](#) ), and the absence of urchin plagues reflects that their predators have not been overexploited ( [McClanahan and Kurtis, 1991](#) ). The general lack of awareness of natural assets is not confined to stakeholders; they are rarely included in national accounts and economic valuations ( [The World Bank, 2006](#) ).

Careful economic and social analysis of these biophysical services would strengthen local constituency and foster greater support for wise and equitable management of reef ecosystems. One challenge for scientists is to develop production functions that relate ecosystem state to function and services ( [Barbier et al., 2011](#) ). An example would be relating the complexity of a coral reef habitat (state) to the production of reef fish (function) to sustainable harvest by fishers (service). Once parameterized, such production functions can be integrated within scenario-support software such as InVEST ( [Daily et al., 2009](#) ) to help stakeholders consider the possible

consequences of a management issue. If an activity were proposed that will likely impact reef habitat complexity, then the cascading impacts and trade-offs on fishers and other ecosystem services would become apparent (e. g., [Daw et al., 2015](#)). Another challenge is to identify how management interventions will influence the future delivery of ecosystem services. Contrasting a business-as-usual scenario with a more pro-active management regime can provide compelling grounds for action.

## **Dealing with Local Stressors on Reefs**

### **Bottom-up Drivers of Reef Health**

Land-based sources of pollution including watershed discharges are a major contributor to the loss of coastal coral reefs, with influences typically extending hundreds of meters to a few km from discharge points, but extending up to 100 km from shore from the largest rivers ( [Andrefouet et al., 2002](#) ; [Wolanski et al., 2003](#) ; [Richmond et al., 2007](#) ). There are both physical and chemical effects of runoff and nutrients, which cause reductions in water and substratum quality. These translate into reduced fecundity of corals and other organisms, as well as decreases in reproductive success and subsequent recruitment. Effective watershed management requires an integrated approach, with targets of reducing erosion rates, the volumes and velocities of freshwater runoff, associated sediment loads, concentrations of toxicants, and distances over which the discharges have impacts. With such efforts, improvements in water quality can be achieved ( [Great Barrier Reef Report Card 2012 and 2013, 2014](#) ).



On-site retention of runoff through the use of ponding basins, underground cisterns, the incorporation of rain gardens into development projects, and “softening” of impervious surfaces can all lead to reductions in coastal impacts from watershed-based activities on smaller scales ( [Wolanski et al., 2004](#) ; [Brodie et al., 2012](#) ). Local and regional reductions in the application of pesticides and better practices to control the presence and disposal of hydrocarbons and household chemicals can substantially improve coastal water quality. Freshwater capture and containment is a very important approach which can be economically feasible, especially in tropical islands where freshwater may be in limited supply seasonally or during droughts, and in the future as climate change affects weather patterns.

### **Top-down Effects on Coral Reefs**

Although coral reefs are diverse and complex ecosystems, a few ecological processes have a disproportionately large impact on their structure and function. For example, the abundance of algae can control the recruitment of reef corals ( [Birrell et al., 2008](#) ). Any increase in benthic fleshy, filamentous, and turf algal cover reduces coral recruitment and even a small increase in diminutive turf algae mats from 2 to 4 mm can cause a 75% reduction in coral recruitment ( [Arnold et al., 2010](#) ). Larger algae can smother and out-compete adult coral ( [Lirman, 2001](#) ; [McCook et al., 2001](#) ; [Hughes et al., 2007](#) ). Recent studies have found allelochemicals from macroalgae poison reef corals ( [Rasher and Hay, 2010](#) ). Crustose coralline algae, on the other hand, can facilitate the settlement, metamorphosis, and recruitment of reef corals ( [Harrington et al., 2004](#) ), albeit coralline algae can also be overgrown and smothered by a carpet of macroalgae or thick turfs ( [Steneck, 1997](#) ).

Given the key role algae play, it becomes important to understand what drives algal abundance ( [McCook, 1999](#) ). For algae, herbivory is the key top-down process. Several studies have shown that as herbivore biomass increases, fleshy algal abundance declines ( [Bellwood and Choat, 1990](#) ; [Williams and Polunin, 2000](#) ; [Kramer et al., 2003](#) ). Herbivores capable of scraping the non-coral substrates of reefs have the greatest ability to denude the habitat of algae. Chief among the deep scraping herbivores are echinoids (sea urchins) and scarids (parrotfishes). Both of these herbivores have been shown to reduce fleshy algal biomass and increase the recruitment potential of coral reefs ( [Edmunds and Carpenter, 2001](#) ; [Mumby and Harborne, 2010](#) ). Nutrients can also be responsible for phase shifts to algal domination and can originate from agricultural and golf course runoff or sewage discharges.

If herbivory is identified as a key driver of reefs, then the current practice of confining herbivore management to no-take marine reserves should be overhauled, the Great Barrier Reef being a good example, where herbivore take is currently minimal ( [Great Barrier Reef Marine Park Authority, 2009](#) ). A focus on reserves does not maintain ecosystem function in exploited areas where it is necessary for maintaining fisheries production. Management should instead either protect some ecosystem processes throughout the entire seascape, as was recently done in Belize through a ban on parrotfish harvest ( [Mumby et al., 2012](#) ), or at least set national regulations for allowable catch and gear restrictions that do not undermine essential ecosystem processes. However, developing such policies is not straightforward because it requires study of how harvesting strategies alter

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reef fish community structure and how such changes cascade to influence ecological function ( [Adam et al., 2015](#) ). For example, it would be important to know how parrotfish populations respond to potential catch limits, how a change in population structure influences parrotfish grazing and corallivory, and how changes in these ecological processes affect the ability of reefs to produce a carbonate framework that underpins ecosystem function ( [Kennedy et al., 2013](#) ).

## **Dealing with Global Climate Change Impacts**

### **Genetic Intervention Strategies**

Current strategies for managing reefs in the face of climate change suggest that reefs should be managed for “resilience” by designing marine protected area networks that spread bleaching risk, maintain genetic and ecological connectivity, reinstate herbivores, and maximize ecological redundancy ( [Marshall and Schuttenberg, 2006](#) ). However, given the inevitability of future climate change impacts on reef ecosystems, there is growing interest in exploring direct intervention strategies to maximize the survival of reef corals over the next few decades. A number of intervention activities have been proposed that might help corals survive climate change over the coming century. These include (1) identifying, propagating, and restoring heat-tolerant corals on affected reefs; (2) translocating corals to local reefs from distant locations that are already adapted to warmer conditions; (3) inoculating corals with heat-tolerant symbiotic algae to boost their thermal tolerance; and (4) treating corals with probiotics (beneficial bacteria) or bacteriophages to combat pathogens, including some that may cause bleaching. All of these activities involve deliberate change in the

genetic distribution, abundance, or composition of the coral “ holobiont” (the combined genome that includes the coral animal, its symbiotic algae, and its bacterial and viral associates), and consequently need to be reviewed on the basis of their benefits, challenges, risks, and ethical basis ( [van Oppen et al., 2015](#) ). For some of these activities, such as the assisted migration of individuals to target areas from warmer locations, lessons from terrestrial systems may help inform best practices and likely risks ( [Hoegh-Guldberg et al., 2008](#) ). However, in most cases the application of these genetic interventions to restore marine species is in its infancy.

### **Manipulating Coral Symbioses to Increase Thermotolerance**

Corals engage in diverse mutualisms with microbial partners, including dinoflagellates ( *Symbiodinium* spp.), bacteria, archaea, and viruses. These microbes can impart different physiological properties to their coral hosts, including the ability to withstand environmental stress, such as higher temperatures ( [Baker, 2003](#) ; [Reshef et al., 2006](#) ). Therefore, they represent potential intervention points to enhance coral thermotolerance. For example, the genus *Symbiodinium* contains a number of genetically distinct clades, each containing numerous “ types” which can differ in their thermotolerance. Corals which shift their *Symbiodinium* communities in favor of these symbionts gain an immediate tolerance increase of 1. 0–1. 5°C compared to corals which do not, and this has resulted in less bleaching and higher recovery rates in response to bleaching events ( [Berkelmans and van Oppen, 2006](#) ; [Jones et al., 2009](#) ).

Corals hosting thermotolerant symbionts show higher resistance to

bleaching, and because these symbionts appear to be hosted in low  
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abundance by many (if not all) coral species ( [Silverstein et al., 2012](#) ), boosting the natural abundance of these symbionts by inoculating corals has been proposed as a means of helping corals survive climate change ( [Baker et al., 2008](#) ). However, before corals can be inoculated in the field, additional research into the response and trade-offs of corals hosting these symbionts must be conducted. For example, it has been shown that corals hosting thermotolerant symbionts grow more slowly than those which do not, both for juveniles ( [Little et al., 2004](#) ) and adults ( [Jones and Berkelmans, 2010](#) ), and this may be because these symbionts are less efficient at translocating photosynthates to their coral hosts ( [Cantin et al., 2009](#) ). Effects on reproduction should also be considered ( [Jones and Berkelmans, 2011](#) ). Consequently, it is clear that a variety of questions must be addressed regarding how thermotolerant symbionts influence coral life history and ecological dynamics ( [Ortiz et al., 2013](#) ) before field inoculations are attempted.

Microbial symbionts have short generation times and have large population sizes, characteristics that facilitate rapid adaptation. As the symbionts reproduce primarily via asexual means, adaptive genotypes can proliferate quickly within and among host corals. Therefore, the potential exists for microbial symbionts to acquire thermotolerant traits over ecologically relevant time scales. It has been predicted that these phenomena may encourage the spread of microbial “ disaster taxa ” that may be significant in understanding the long-term persistence of mutualistic hosts such as corals ( [Correa and Baker, 2009](#) ). Recent work has shown that this may already be occurring, and it has been demonstrated that symbionts isolated from the <https://assignbuster.com/scientific-frontiers-in-the-management-of-coral-reefs/>

same host species, but taken from reefs with different temperature regimes, had heritable differences in thermotolerance ( [Howells et al., 2012](#) ). Moreover, experimental evolution of *Symbiodinium* in the lab, using a “ratchet” approach to growing symbionts at progressively higher temperatures, has found that thermal tolerance can be selected for within months. Therefore, *Symbiodinium* could be isolated from a host coral, cultured at higher temperatures in the lab to select for thermal tolerance, and then reintroduced to the coral. This approach would minimize histocompatibility issues and potential adverse effects on growth, reproduction, and/or disease resistance. However, it is unlikely that thermotolerance will be maintained as a trait once the selection pressure is removed, and widespread application would still require an efficient inoculation technique and scaling up of culture facilities.

In addition to inoculation of algae, coral “ probiotics” (beneficial bacteria) have also been proposed as a means of treating coral disease, as well as bacteriophages (viruses that attack bacteria), which have recently been engineered as a therapy for white plague disease of corals in the Red Sea ( [Atad et al., 2012](#) ). Bacteriophages have the advantage of host specificity and self-replication and have already been used to treat bacterial infections in aquacultured fish ( [Nakai and Park, 2002](#) ). Because the phage only attacks specific pathogens, the beneficial bacterial community is believed to be unaffected. After testing phage in controlled lab settings, [Atad et al. \(2012\)](#) examined the phage therapy in the field and found that it inhibited the spread of white plague disease, as well as transmission of illness to other corals. They suggest that, for phage therapy to be used as a viable

treatment for coral disease outbreaks, it would be necessary to (1) develop a large scale delivery technique, (2) demonstrate it is environmentally safe, and (3) scale-up production of phage. Assuming that these issues could be addressed, phages could be developed to treat a variety of unidentified bacterial diseases elsewhere, e. g., the Caribbean. However, the deliberate introduction of a virus into the marine environment to treat disease needs further consideration from the perspective of ethics and biosafety.

### **Restoration of Thermotolerant and Disease-resistant Corals from Local Source Colonies**

In addition to manipulating coral symbioses by inoculation with microbial and viral associates of corals, populations of severely depleted coral species are also being farmed in nurseries for replanting on local reefs. For example, Caribbean staghorn and elkhorn corals became the first corals to be listed as threatened under the Endangered Species Act (2006) after disease, bleaching, and environmental stress caused rapid loss of these corals (> 90%) over the last three decades ( [Bythell and Sheppard, 1993](#) ). The loss of these species on Caribbean reefs has resulted in a decline in reef structure and function ( [Alvarez-Filip et al., 2009](#) ; [Kennedy et al., 2013](#) ). Currently, a coral “ gardening” approach is being employed in Florida to restore these dwindling populations ( [Lirman et al., 2010](#) ), and efforts are underway to identify and selectively propagate the coral and symbiont genotypes that are most likely to survive future stresses. For example, white band disease (WBD) devastated these coral species, but some coral genotypes have been found to be resistant to the WBD pathogen ( [Vollmer and Kline, 2008](#) ). Similarly, different coral genotypes can vary widely in their tolerance to

thermal stress ( [Fitt et al., 2009](#) ; [Barshis et al., 2010](#) ). Therefore, attempts to propagate selectively these genotypes could be used to replant reefs with corals expected to be better able to survive projected future conditions.

Moreover, the use of high-resolution molecular tools could lead to the discovery of genotypes with other important properties, such as increased reproductive output. The high cost and labor-intensive nature of restoration techniques indicate that maximizing success using these approaches would be attractive to managers, assuming appropriate local genotypes can be identified.

### **Translocation of Corals from Distant Source Reefs Adapted to Higher Temperatures**

Translocation of individuals has been proposed as a method of bolstering the population sizes of rare species ( [Griffith et al., 1989](#) ), and this approach has been recently adopted in Florida as a strategy to restore formerly abundant populations of *Acropora cervicornis* . Current restoration efforts in Florida have been confined to propagating only coral genotypes found on local reefs, and no corals are yet being introduced to reefs more than a few kilometers distant from their original collection locations. However, in Australia, pilot projects involving long-distance transplantation (100 s of km) of juvenile corals from warm areas to cooler areas that are expected to warm are already being undertaken ( [van Oppen et al., 2011](#) ), and similar activities have been proposed for the Caribbean. A recent study ( [D'Angelo et al., 2015](#) ) found the algal symbiont *Symbiodinium thermophilum* allowed host colonies of *Porites* to survive temperatures up to 36°C in the Persian/Arabian Gulf, but the survival advantage was lost at the lower salinities common on



other reef systems, raising concerns about the practicality of translocation programs. The Irish Potato Famine was attributed to the loss of genetic variation within the crop population, where a single genotype was planted due to its notable growth under the local, harsh conditions, but unfortunately, the subsequent lack of resistance to a pathogen resulted in catastrophic crop failure. While the emerging technologies to test the value of adaptive genotypes of both corals and algal symbionts is a fertile area of research, underlying issues of maintaining genetic variability within populations as a hedge against other threats is critical. Likewise, logistical challenges including balancing the costs vs. benefits and the potential for unintended consequences (e. g., introduced pathogens) must also be considered.

There are a number of risks that should be considered before these activities are implemented further, however. The introduction of novel genotypes has the potential to result in outbreeding depression—the hybridization of maladapted genotypes with local populations ( [Crémieux et al., 2010](#) ).

Moreover, translocation of corals from distant areas may facilitate the spread of accompanying diseases or pathogens that are endemic to the source area, but new to the relocation site. Translocated corals will not only bring with them a community of microbial and viral associates, but also a variety of metazoan organisms whose population structure must be considered. In some cases, the potential risks may be outweighed by the benefits of habitat construction because target coral species (such as staghorn and elkhorn corals) already have low levels of sexual recruitment ( [Williams et al., 2008](#) ).

Finally, previous transplantation efforts have demonstrated logistical

challenges exist, with typical levels of mortality of 30% just due to handling. Regardless, the likely disruption of local genetic structure and the potential for outbreeding depression illustrates the importance of population genetics to coral reef conservation ( [Baums, 2008](#) ). In short, it is important to review the ethical considerations of assisted migration as a matter of urgency.

### **Building Resilience and Prioritizing Where to Intervene**

Most management interventions attempt to increase the resilience of reefs either by reducing the exposure of reefs to a stressor, such as pollution, or restoring natural ecosystem processes, like herbivory, that can decrease the abundance of algae and increase coral recruitment and growth ( [McCook et al., 2007](#) ; [Great Barrier Reef Marine Park Authority, 2013](#) ). However, with limited resources, managers must often prioritize the locations and timing of interventions. In the context of climate change, it is prudent to consider the level of stress reefs face, and this has primarily focused on thermal stress but will increasingly need to include ocean acidification as data become available ( [Gledhill et al., 2008](#) ; [Anthony et al., 2013](#) ; [McLeod et al., 2013](#) ). It is also worth noting that corals from marginal habitats may already have populations and genotypes that have elevated resilience and resistance to stressors. Following the 1998 mass coral bleaching event in Palau, refuge populations were found in areas previously exposed to temperature stress (reefs experiencing sub-aerial exposure during spring tides) and other physical stressors such as sedimentation and reduced salinities at the mouths of estuaries. Corals found growing within harbors, routinely subjected to a variety of heavy metals, hydrocarbons, turbidity, and widely ranging temperatures also exhibit higher levels of resilience than corals from

areas of reduced levels of stress. While there is the temptation for establishing and enforcing protection of reefs in pristine areas, the value of corals in marginal habitats should not be ignored. Such corals may end up making sizable contributions to the reefs of the future.

Satellite data on sea surface temperature reveal that no two reefs experience the same physical environment. Some, for example, usually experience relatively cool conditions but appear to warm up dramatically during a bleaching episode. Others experience relatively high levels of stress most of the time. Reefs that experience high-temperature variability have been shown to be more resistant to bleaching than reefs characterized by low-temperature variability ( [McClanahan et al., 2007](#) ), suggesting that acclimatization mechanisms employed by the reef coral holobiont to cope with chronic stress also offer some protection to acute stress. In principle, heterogeneity in the stress experienced by corals can be used to prioritize management interventions, perhaps placing greater emphasis on more benign physical environments ( [Mumby et al., 2011](#) ). However, interpreting the response of corals, both today and in the future, remains a daunting challenge. Similarly, consideration is needed to prioritize management actions depending on the vulnerability of reefs ( [Game et al., 2008](#) ) and the overarching objectives of management. For example, prioritization will differ if conservation funds are invested to ensure that some relatively “pristine” locations remain natural, to minimize the overall loss of reef health in general, or to promote recovery in heavily impacted sites.

Building resilience of reefs is also better achieved by understanding larval dispersal, as connectivity has long been recognized as an important process to consider in the design of marine reserves ( [Sale et al., 2005](#) ), albeit this has been difficult to operationalize ( [McCook et al., 2009](#) ). However, oceanographic simulation models of larval dispersal are only now becoming available publically (e. g., BlueLink from Australia's Commonwealth Scientific Industrial Research Organization). Genetic studies have found the predictions of such models to be robust, at least for resolving connectivity at the scale of gene flow ( [Galindo et al., 2006](#) ; [Foster et al., 2012](#) ). Also, optimization methods for conservation planning, such as Marxan ( [Ball et al., 2009](#) ), have now been extended to incorporate asymmetric dispersal among reefs ( [Beger et al., 2010](#) ). Finally, other more localized approaches include incorporation of seascape connectivity and surrogate species ecology to improve the ability of reserves to promote the abundance of multiple species of fish ( [Olds et al., 2014](#) ). Thus, the tools are now available to operationalize connectivity in conservation planning, including the importance of self-seeding in some reef systems vs. larval input over greater distances for others ( [Golbuu et al., 2012](#) ; [Green et al., 2014](#) ). However, the application of such methods is still confounded by one of the oldest questions in ecology: at what point are reefs recruitment limited ( [Caley et al., 1996](#) )? There is an inevitable temptation to assume that sites predicted to receive greater larval supply will in fact experience greater recruitment. The validity of this depends on the level of post-settlement mortality and density-dependent population regulation ( [Doherty et al., 2004](#) ; [van Woesik et al., 2014](#) ). There is a need, therefore, to “ connect” studies of dispersal

and larval supply with those of settlement and post-settlement mortality. Failure to do so could see management prioritizing sites on the grounds of high predicted larval supply whereas an inhospitable recruitment habitat might render such abundant supply irrelevant because of high post-settlement mortality.

## **Governance of Coral Reefs**

### **Local Governance Principles for Successful Management Implementation**

Coral reefs are found largely in tropical, developing countries, yet they are appreciated globally for their high biodiversity, ecosystem services, and cultural importance amongst other relevant provisions. The ecological crisis of coral reefs is paralleled by a social crisis in which food security, cultural systems, and other essential societal relations with reefs are being lost. More troubling is that the corporate responsibility, social justice, and environmental ethics necessary for the better stewardship of coral reefs, and more generally for a reversal in the decline of world fisheries ( [Bundy et al., 2008](#) ; [Cinner, 2014](#) ), are for the most part lacking from local to international governance levels. To begin addressing this crisis, not only is a genuine transformation of policy and politics required, but whatever combination of management tools selected to address this crisis, like hybrid systems ( [Aswani and Ruddle, 2013](#) ) or marine spatial planning ( [Cornu et al., 2014](#) ), need to be implemented with sufficient flexibility to accommodate existing variations in governance ( [Sale et al., 2014](#) ) and knowledge systems at a local scale.

Governance is best thought of as “ formal and informal arrangements, institutions, and mores which determine how resources or an environment are utilized; how problems and opportunities are evaluated and analyzed, what behavior is deemed acceptable or forbidden, and what rules and sanctions are applied to affect the pattern of resource and environmental use” ( [Juda, 1999](#), p. 89). Thus, policy makers and conservation practitioners need to tailor coral reef management to local contexts in a way that acknowledges the importance of, for instance, local peer-to-peer social networks ( [Christie et al., 2009a](#) ), cultural ecosystems services ( [Satz et al., 2013](#) ), customary management, and local forms of territoriality ( [Acheson, 1988](#) ) among other local processes. In addition, forcing coastal populations to appreciate the esthetic or ecological value of coral reefs to conserve natural resources may work for a short period of time, but it is not a good long-term strategy. Officials in most tropical countries are incapable or unwilling to enforce existing legislation (weak governance), and most coral reef management (or lack thereof) is carried out by local communities. The latter may have a complete different cultural understanding of the meaning of “ management,” which often means control or ownership of resources rather than good stewardship. Policy that is designed and experimented with locally and is informed by social and ecological science, if successful, can assist in scaling up to a more realistic management and conservation policy that can be applied regionally, nationally, and internationally.

National and international plans for protecting coral reefs are important (particularly in developed nations), but effective management needs to be accomplished at the local level (particularly in developing nations). Working

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with communities presents a number of political, economic, and social challenges, but it also can offer many opportunities for hands-on, realistic, and on the ground effective management of coral reefs. Numerous coastal communities across the tropics (particularly in Oceania and SE Asia) have or have had customary or local management systems that can be revived, re-adapted, or hybridized with current systems (e. g., with EBM) to achieve modern management ( [Christie et al., 2009b](#) ). Such strategy, however, may not work in cases where local customary management systems are completely defunct or irreconcilable with modern prescriptions ( [Aswani et al., 2012](#) ), or in densely populated and highly urbanized centers ( [Ban et al., 2011](#) ; [Cinner et al., 2013](#) ). But even in those cases, stakeholder involvement will be crucial for the creation of new or transformed governance structures that are locally managed. In short, coral reef management and conservation needs to be both top-down (e. g., institutional support and enforcement, environmental protection legislation, etc.) and bottom-up (e. g., proactive inclusion of community governance systems, tenurial rights, local ecological knowledge, etc.). As [Finkbeiner and Basurto \(2015\)](#) suggest, it needs to be a form of “ multi-level” co-management that incorporates the values of power devolution, peer-to-peer/governance networks, and truly democratic participatory involvement in the creation of hybrid co-management systems that are tailored to particular historical and cultural contexts.

Governance initiatives that couple government or non-government organizations (NGOs) sponsored resource management plans with local needs and concerns can be successful, among other things, at meeting

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ecological and social objectives such as sustaining ecological function and local livelihoods ( [Pollnac et al., 2010](#) ; [Mora et al., 2011](#) ; [Gurney et al., 2014](#) ). Establishing any co-managerial scheme in most developing coral reef nations, however, will require an understanding and the integration of customary management (CM) (whether informal or formal) and existing Integrated Coastal Management (ICM) schemes with any external prescription. As detailed in [Christie et al. \(2009b\)](#) , [Christie \(2011\)](#) and [Aswani et al. \(2012\)](#) , working with customary management or ICM systems is challenging and a number of conceptual hurdles need to be crossed including, for instance, reconciling the dynamism of CM systems with more formal structures of formal management before effective hybridization can be established. As argued by [Ruddle \(1994\)](#) , any policy and program decisions regarding the effectiveness of local management and knowledge systems (for hybridization) must be based on a cogent and genuine evaluation of the moral authority, social motives, local political interests, and cultural constructions underlying them. Hybridized management programs may not be a cure-all for daunting coral reef management problems everywhere, as often community interest and participation in conservation does not ensure a positive outcome, and global-level change can undermine local commitment ( [Sale et al., 2014](#) ). Nevertheless, they offer innovative opportunities for managing these ecosystems in a cost-effective, equitable, and realistic fashion, as well as for building on effective practices of existing management systems locally.

Achieving any form of co-management hybrid plan at any given location will require local resolve to protect coral reefs from political corruption and



concomitant capital resource extraction (e. g., watershed protection from logging and mining). It will also require sustained institutional governance and financial and educational support (training in hybrid local-Western science to ensure understanding of local social and biological processes) from government agencies and non-government organizations. Simply put, there is really no alternative to existing governance and management systems locally (even if highly eroded). These may offer an institutional context that under the right circumstances and with the right legislative/policing support can be effective at fostering coral reef protection while upholding the interests and rights of coastal communities across the tropics. Comparative research and practical experiences have revealed recurring mechanisms that underpin coral reef management in tropical developing nations' contexts ( [Christie et al., 2009b](#) ; [Edgar et al., 2014](#) ; [Sale et al., 2014](#) ). These lessons need to be considered in future plans for combining local and introduced management systems.

As described in detail previously ( [Christie, 2011](#) ; [Aswani et al., 2012](#) ) and expanded here, management systems that are designed locally or nationally, will need to have a series of attributes for their success. First, *simplicity* is the rule. Management plans need to be understood by policy makers and resource users (who are frequent *de facto* decision makers) alike. [Ostrom \(2007\)](#) has argued that successful common pool resource management regimes often have simple and clear rules. As prescriptions grow harder to understand, people grow more likely to not conform, to interlope, and to free-ride. The objectives of management should be transparent and should accurately identify ecosystem health problems that impinge on people's

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livelihoods locally and which local populations can conform to and identify with. Second, *experimentation* is necessary. Managers need to observe and learn from local histories, customary practices, and human-environment interactions. An effective manager will learn from these experiences and assimilate these local processes into their experience toolbox to better design and implement future adaptive management interventions. Third, a clear *strategy* that is informed from early successes and failures is fundamental for successful management. Managers need to listen to resource users, integrate different kinds of existing information, and create long-lasting partnerships at local, national, and international scales to solve the often intractable problems affecting coral reef management and conservation.

Fourth, coral reef management need to be context *appropriate* . One-size-fits-all solutions are likely to fail and successful management is often designed by teams of people who understand local problems and concerns, and who are aware of prescriptions that are likely to be rejected locally, regardless of their managerial effectiveness elsewhere. Fifth, effective *evaluation* can close the loop to not only design and implementation, but support adaptive management by adjusting efforts appropriately. The traditional metrics of fish and coral recruitment take longer time periods to show effectiveness, but the “-omics” can be applied to show a different set of metrics and how they change over short time periods. Finally, coral reef management has to be *multi-disciplinary* . Coral reef managers cannot ignore the social, cultural, and economic needs and interests of people living in tropical contexts and focus on immediate conservation priorities over the

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long-term well-being of existing communities. The reality is that trade-offs between long-term conservation and short-term development will have to be considered by managers in locations where impoverished people are struggling to survive ( [Christie et al., 2009a](#) ; [Moon and Blackman, 2014](#) ). In sum, understanding these local socio-economic concerns and limitations, which are necessary for designing effective management systems (hybrid or otherwise), will require clever and systematic social and ecological science research.

### **Coupled Social and Ecological Research for Disentangling Governance Institutions**

If effective coral reef management is best accomplished at the local scale, particularly in developing nations, then scaling-down in the study of human-environmental interrelations is essential for identifying the drivers of resource cognition and governance in any one location. Indeed, coral reefs are best thought of as coupled social and ecological systems (SES) ( [Pollnac et al., 2010](#) ; [Cinner et al., 2013](#) ) that are increasingly shaped by individual and collective human behavior. Coral reef ecological change shapes human behavior and *vice versa* . While socio-ecological case studies (e. g., [Blythe, 2014](#) ) and synthesis papers ( [Folke et al., 2005](#) ; [Kittinger et al., 2013](#) ; [McMillen et al., 2014](#) ) are central for understanding social and ecological interrelations (drivers, SES traps, knowledge systems, etc.) in small-scale fisheries, researchers are widely relying on interview data at the regional and community-scale to explain drivers of change.

Perception data could be better coupled with other individual-scale data (e. g., human foraging, human-prey/resource interactions, time allocation,

economic and cooperative behavior, etc.) to analyze the specific drivers (i. e., proximate causation) in human-environmental relationships (both perceptual and behavioral) at any one location before scaling up the system boundaries. Socio-ecological studies can overlook actor-based scenarios, i. e., the role of individual cognition and behavior at finer spatial and temporal scales in shaping, and driving, social, and ecological interactions and change. Thus, a return to more systematic research traditions in human ecology, environmental economics, and human geography (e. g., [Smith, 1991](#)) is needed to complement and expand current approaches. New research will require more fine-grained empirical and longitudinal data to test hypotheses related to social and natural interactions, vulnerability, and resilience. This effort will improve cross-scale linkages in analyses regarding ongoing social and ecological feedbacks in coupled human-natural systems (such as small-scale fisheries in coral reefs).

Different methodologies can be used for this task, and [Ostrom's \(2009\)](#) diagnostic framework for analyzing social-ecological systems is a useful theoretical framework ( [Cinner et al., 2012](#) ) for understanding the conditions that cause problems or create opportunities in the governance of small-scale coral reef fisheries. Coupling this framework with the study of human-environmental interactions from the perspective of human ecology, as mentioned, can help us identify fine-grained local processes that may not be apparent from regional or national studies. Various focal areas can be explored for comprehending local resource use and governance systems for the purpose of understanding local human-environment dynamics—research that can assist in the design of hybrid management schemes. Research can

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examine human cooperative strategies, human foraging behavior, sustainable and non-sustainable livelihoods, environmental perceptions and concomitant environmental action, conflict and conflict resolution, and so forth.

Particular case studies and comparative analysis can provide a window into differential perceptions of change within and between communities, which are often produced by existing asymmetries of how individuals perceive change according to gender, education, age, economic status, and distance to markets among other factors. Researchers have used approaches such as Bayesian network analysis to understand what contributes to the probability of attributing change to a particular cause, which can include the demographic, social, and economic characteristics of the respondents as well as other internal and external variables. Such approaches are also developing conceptual models of the variables and relationships that help drive/influence adaptation action (or conception of) to perceive future changes ( [van Putten et al., 2013](#) ). Many other promising socio-ecological approaches are being developed to analyze human interactions with coral reefs, including understanding the social and economic factors that lead to asymmetries in people's perceptions of ecosystem services ( [Hicks and Cinner, 2014](#) ), using participatory modeling and scenarios approaches to evaluate “taboo” trade-offs (or trade-offs between morally incommensurable values) in tropical fisheries ( [Daw et al., 2015](#), p. 1), and approaches to better understand human perceptions of environmental and climatic changes, their causes, and adaptation actions taken by people to locally cope with these transformations (Abernethy et al., in press) among others.

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## **Resolving the Crisis of Motivation for Social and Ecological Reef Monitoring**

Monitoring and evaluation of management success is a core part of any good management program ( [Clark, 1995](#) ). Today many successful conservation initiatives have mainstreamed regular multi-disciplinary evaluation into their monitoring protocols. Notably, participatory programs allow conservation practitioners as well as stakeholders to learn from mistakes and successes and adapt such learning into ongoing adaptive management processes ( [Margoluis and Salafsky, 1998](#) ; [Pomeroy et al., 2004](#) ; [Christie et al., 2009b](#) ; [Christie, 2011](#) ). Unfortunately, however, reef monitoring is often undertaken sporadically, inconsistently, or not at all. There are many reasons for this, including the unattractiveness of investing in a long-term activity that offers modest and mundane rewards in the short-term. But other constraints to monitoring can be overcome with better science and closer engagement with communities.

A common complaint of staff tasked with monitoring is the lack of feedback or benefit from having added another dataset. Imagine that an updated dataset finds that coral cover has increased by 2%. So what? Is that better than expected and does that mean that management is working? Answering these questions requires an understanding of how ecosystems behave. Thus, in tandem with participatory research, a useful approach to modeling ecosystems from individual case histories is the parameterization of Bayesian belief networks, BBNs ( [Wooldridge and Done, 2004](#) ; [Renken and Mumby, 2009](#) ). If monitoring programmes contributed their data to a regional BBN, the information would measurably improve understanding of reef dynamics, and the model would provide a simple interface with which

users can manipulate the ecosystem, run management scenarios, and interpret their results within a wider context. This information can then be fed back to reef managers as well as local authorities and communities in an understandable format for possible adjustment of management plans.

Any ecological monitoring should be balanced by social monitoring that provides insights into how society relates to coral reefs and opportunities for improved management. Such information can be invaluable in countering assumptions of negative impacts on communities. For example, on the Great Barrier Reef, implementation of significant increases in no-take reserves were asserted to threaten recreational fishing investment, yet monitoring of vessel registrations indicates no impact at all ( [McCook et al., 2010](#) ).

Management primarily focuses on changing human behaviors, institutions, and other human constructs (recognizing interventions on reefs can also yield positive results). Barriers exist to balance social-ecological monitoring, including disciplinary biases, disciplinary training, and worldviews, which are fortunately being overcome ( [Christie, 2011](#) ). In sum, attempts to improve coral reef management should also be systematically studied. New insights can be gained by establishing program assessments that utilize a social and ecological framework to determine which policies had the desired outcomes. This goes beyond basic reef monitoring in that such program evaluations “test” program and policy assumptions or “theories of change.”

## **Conclusion**

In this paper, we have considered various scientific frontiers in natural and social science that will require further attention in coming years as we work

toward building stronger support for reef management and improve the efficacy of local interventions. While coral reef management and conservation will require both top-down and bottom-up interventions—and governments have a serious challenge in creating effective and genuine legislation to protect coral reefs—much work remains to be done to engage properly and communicate with those closer to coral reefs, i. e., those who are the significant drivers of change (often negative) and who have a real stake in ensuring their future survival. Engaging coastal communities and local authorities in coral reef protection will require conservation practitioners to work within the framework of contextualized hybrid governance systems. Such arrangements should be able to successfully implement marine spatial planning, no-take reserves, watershed management, fisheries regulation, protection of functional groups, reef restoration through top-down interventions (as detailed in this paper), and co-management or community-based management, among other activities. It is likely that a combination of coral reef management approaches will be necessary for success, particularly in sites where the implementation of no-take marine reserves is difficult ( [MacNeil et al., 2015](#) ). These engagements will often require patience and the willingness to accept trade-offs, particularly in developing nations, between community livelihood needs and conservation and management goals (e. g., in some cases, particularly for fecund invertebrates, allowing the periodic harvest of resources within management areas, [Dumas et al., 2010](#) ). It will also require a strong emphasis on cross-generational environmental education and awareness



while training local users and officials in reef monitoring and peer-to-peer enforcement frameworks. Much work remains to be done.

## **Author Contributions**

SA and PM are Joint Senior Authors and wrote the paper. All the other authors also contributed equally to this work.

## **Conflict of Interest Statement**

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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