# Scientific frontiers in the management of coral reefs

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Coral reefs are subjected globally to a variety of natural and anthropogenic stressors that often act synergistically. Today, reversing ongoing and future coral reef degradation presents significant challenges and countering this negative trend will take considerable efforts and investments. Scientific knowledge can inform and guide the requisite decision-making process and offer practical solutions to the problem of protection as the effects of climate change exacerbate. However, implementation of solutions presently lags far behind the pace required to reverse global declines, and there is a need for an urgent and significant step-up in the extent and range of strategies being implemented. In this paper, we consider scientific frontiers in natural and social science research that can help build stronger support for reef management and improve the efficacy of interventions. We cover various areas including: (1) enhancing the case for reef conservation and management, (2) dealing with local stressors on reefs, (3) addressing global climate change impacts, (4) and reviewing various approaches to the governance of coral reefs. In sum, we consider scientific frontiers in natural and social science that will require further attention in coming years as managers work toward building stronger support for reef management and improve the efficacy of local interventions.

Keywords: coral reefs, management, social science, natural science, scientific frontiers

## 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 functionally. 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 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 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 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, refugee 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 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 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 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 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 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 comparitive 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.

## 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 fedback to reef managers as well as local authorities and communities in an

understanble 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 succesfully 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.

## References

Abernethy, K. E., Aswani, S., Albert, S., Hoddy, E. T., Vaccaro, I., Beare, D. J., et al. (in press). Differential perceptions of environmental change among coastal communities of western Solomon Islands. *Ecol. Soc.*

Acheson, J. M. (1988). *The Lobster Gangs of Maine.* Durham, NH: University Press of New England.

Adam, T. C., Burkepile, D. E., Ruttenberg, B. I., and Paddack, M. J. (2015). Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. *Mar. Ecol. Prog. Ser.* 520, 1–20. doi: 10.3354/meps11170

Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Cote, I. M., and Watkinson, A. R. (2009). Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 276, 3019–3025. doi: 10.1098/rspb.2009.0339

Andrefouet, S., Mumby, P. J., McField, M., Hu, C., and Muller-Karger, F. E. (2002). Revisiting coral reef connectivity. *Coral Reefs* 21, 43–48. doi: 10.1007/s00338-001-0199-0

Anthony, K. R. N., Diaz-Pulido, G., Verlinden, N., Tilbrook, B., and Andersson, A. J. (2013). Benthic buffers and boosters of ocean acidification on coral reefs. *Biogeoscie. Disc.* 10, 1–35. doi: 10.5194/bgd-10-1831-2013

Arnold, S. N., Steneck, R. S., and Mumby, P. J. (2010). Running the gauntlet: inhibitory effects of algal turfs on the process of coral recruitment. *Mar. Ecol. Prog. Ser.* 414, 91–105 doi: 10.3354/meps08724

Aswani, S., Christie, P., Muthiga, N., Mahon, R., Primavera, J. H., Cramer, L. A., et al. (2012). The way forward with ecosystem-based management in tropical contexts: reconciling with existing management systems. *Mar. Pol.* 36, 1–10. doi: 10.1016/j.marpol.2011.02.014

Aswani, S., and Ruddle, K. (2013). The design of realistic hybrid marine resource management programs in Oceania. *Pac. Sci.* 67, 461–476. doi: 10.2984/67.3.11

Atad, A., Zvuloni, A., Loya, Y., and Rosenberg, E. (2012). Phage therapy of the white plague- like disease of *Favia favus* in the Red Sea. *Coarl Reefs* 31, 665–670. doi: 10.1007/s00338-012-0900-5

Ateweberhan, M., McClanahan, T. R., Graham, N. A. J., and Sheppard, C. R. C. (2011). Episodic heterogeneous decline and recovery of coral cover in the Indian Ocean. *Coral Reefs* 30, 739–752. doi: 10.1007/s00338-011-0775-x

Baker, A. C. (2003). Flexibility and specificity in coral-algal symbiosis: diversity, ecology and biogeography of *Symbiodinium. Ann. Rev. Ecol. Syst.* 34, 661–689. doi: 10.1146/annurev.ecolsys.34.011802.132417

Baker, A. C., Glynn, P. W., and Riegl, B. (2008). Climate change and coral reef bleaching: an ecological assessment of the long-term impacts, recovery trends and future outlooks. *Estua. Coa. Shelf Sci.* 80, 435–471. doi: 10.1016/j.ecss.2008.09.003

Ball, I. R., Possingham, H. P., and Watts, M. (2009). "Marxan and relatives: Software for spatial conservation prioritisation," in *Spatial Conservation Prioritisation: Quantitative Methods and Computational Tools,* eds A. Moilanen, K. A. Wilson, and H. P. Possingham (Oxford: Oxford University Press), 185–195.

Ban, N. C., Adams, V. M., Almany, G. R., Ban, S., Cinner, J. E., McCook, L. J., et al. (2011). Designing, implementing and managing marine protected areas: emerging trends and opportunities for coral reefs nations. *Exp. Mar. Biol. Ecol.* 408, 21–31. doi: 10.1016/j.jembe.2011.07.023

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., and Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecol. Mono.* 81, 169–193. doi: 10.1890/10-1510.1

Barshis, D. J., Stillman, J. H., Gates, R. D., Toonen, R. J., Smith, L. W., and Birkelands, C. (2010). Protein expression and genetic structure of the coral *Porites lobata* in an environmentally extreme Samoan back reef: does host genotype limit phenotypic plasticity? *Mol. Ecol.* 19, 1705–1720. doi: 10.1111/j.1365-294X.2010.04574.x

Baums, I. B. (2008). A restoration genetics guide for coral reef conservation. *Mol. Ecol.* 17, 2796–2811. doi: 10.1111/j.1365-294X.2008.03787.x

Beger, M., Linke, S., Watts, M., Game, E. T., Treml, E., Ball, I., et al. (2010). Incorporating asymmetric connectivity into spatial decision making for conservation. *Cons. Lett.* 3, 359–368. doi: 10.1111/j.1755-263X.2010.00123.x

Bellwood, D. R., and Choat, J. H. (1990). A functional-analysis of the grazing in parrotfishes (Family Scaridae): the ecological implications. *Environ. Biol. Fish.* 28, 189–214. doi: 10.1007/BF00751035

Berkelmans, R., and van Oppen, M. J. H. (2006). The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. *Proc. Biol. Sci.* 273, 2305-2312. doi: 10.1098/rspb.2006.3567

Birrell, C. L., McCook, L. J., Willis, B. L., and Diaz-Pulido, G. A. (2008). Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. *Oceano. Mar. Bio. Ann. Rev.* 46, 25–64. doi: 10.1201/9781420065756.ch2

Blythe, J. L. (2014). Resilience and social thresholds in small-scale fishing communities Sustain. *Sust. Sci.* 10, 157–165. doi: 10.1007/s11625-014-0253-9

Brodie, J. E., Kroon, F. J., Schaffelke, B., Wolanski, E., Lewis, S. E., Devlin, M. J., et al. (2012). Terrestrial pollutant runoff to the Great Barrier Reef: an update of issues, priorities and management responses. *Mar. Poll. Bull* 65, 81–100. doi: 10.1016/j.marpolbul.2011.12.012

Bruno, J. F., and Selig, E. R. (2007). Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE* 8:e711. doi: 10.1371/journal.pone.0000711

Bundy, A., Chuenpagdee, R., Jentoft, S., and Mahon, R. (2008). If science is not the answer, what is? An alternative governance model for the world's fisheries. *Front. Ecol. Environ.* 6, 152–155. doi: 10.1890/060112

Burke, L., Reytar, K., Spalding, M., and Perry, A. (2011). *Reefs at Risk Revisited.* Washington, DC: World Resources Institute.

Bythell, J., and Sheppard, C. (1993). Mass mortality of Caribbean shallow corals. *Mar. Poll. Bull.* 26, 296–297.

Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P., and Menge, B. A. (1996). Recruitment and the local dynamics of open marine populations. *Ann. Rev. Ecol. Syst.* 27, 477–500. doi: 10.1146/annurev.ecolsys.27.1.477

Cantin, N. E., van Oppen, M. J. H., Willis, B. L., Mieog, J. C., and Negri, A. P. (2009). Juvenile corals can acquire more carbon from high-performance algal symbionts. *Coral Reefs* 28, 405-414. doi: 10.1007/s00338-009-0478-8

Christie, P. (2011). Creating space for interdisciplinary marine and coastal research: five dilemmas and suggested resolutions. *Environ. Cons.* 38, 172–186. doi: 10.1017/S0376892911000129

Christie, P., Pollnac, R. B., Fluharty, D. L., Hixon, M. A., Lowry, G. K., Mahon, R., et al. (2009b). Tropical marine EBM feasibility: a synthesis of case studies and comparative analyses. *Coast. Manag.* 37, 374–385. doi: 10.1080/08920750902937994

Christie, P., Pollnac, R. B., Oracion, E. G., Sabonsolin, A., Diaz, R., and Pietri, D. (2009a). Back to basics: an empirical study demonstrating the importance of local-level dynamics for the success of tropical marine ecosystem-based management. *Coast Manag.* 37, 349–373. doi: 10.1080/08920750902851740

Cinner, J. E. (2014). Coral reef livelihoods. *Curr. Opin. Environ. Sust.* 7, 65–71. doi: 10.1016/j.cosust.2013.11.025

Cinner, J. E., Huchery, C., Darling, E. S., Humphries, A. T., Graham, N. A. J., Hicks, C. C., et al. (2013). Evaluating social and ecological vulnerability of coral Reef fisheries to climate change. *PLoS ONE* 8:e74321. doi: 10.1371/journal.pone.0074321

Cinner, J. E., McClanahan, T. R., Graham, N. A. J., Daw, T. M., Maina, J., Stead, S. M., et al. (2012). Vulnerability of coastal communities to key impacts of climate change on coral reef fisheries. *Glob. Environ. Chan.* 22, 12–20. doi: 10.1016/j.gloenvcha.2011.09.018

Clark, J. R. (1995). *Coastal Zone Management Handbook*. Boca Raton, FL: Lewis Publishers, Inc.

Cornu, E. L., Kittinger, J. N., Koehn, J. Z., Finkbeiner, E. M., and Crowder, L. B. (2014). Current practice and future prospects for social data in coastal and ocean planning. *Cons. Biol.* 28, 902–911. doi: 10.1111/cobi.12310

Correa, A. M. S., and Baker, A. C. (2009). Understanding diversity in coral-algal symbiosis: a cluster-based approach to interpreting fine-scale genetic variation in the genus *Symbiodinium*. *Coral Reefs* 28, 81–93. doi: 10.1007/s00338-008-0456-6

Crémieux, L., Bischoff, A., Müller-Schärer, H., and Steinger, T. (2010). Gene flow from foreign provenances into local plant populations: fitness consequences and implications for biodiversity restoration. *Am. J. Bot.* 97, 94–100. doi: 10.3732/ajb.0900103

Daily, G. C., Polasky, S., Goldstein, J., Kareiva, P. M., Mooney, H. A., Pejchar, L., et al. (2009). Ecosystem services in decision making: time to deliver. *Front. Ecol. Environ.* 7, 21–28. doi: 10.1890/080025

D'Angelo, C., Hume, B. C. C., Burt, J., Smith, E. G., Achterberg, E. P., and Wiedenmann, J. (2015). Local adaptation constrains the distribution potential of heat-tolerant *Symbiodinium* from the Persian/Arabian Gulf. *ISME J.* doi: 10.1038/ismej.2015.80. [Epub ahead of print].

Daw, T. M., Coulthardc, S., Cheungd, W. W. L., Brown, K., Abunge, C., Galafassi, D., et al. (2015). Evaluating taboo trade-offs in ecosystems services and human well-being. *Proc. Natl. Acad. Sci. U.S.A.* 112, 6949–6954. doi: 10.1073/pnas.1414900112

De'ath, G., Fabricius, K. E., Sweatman, H., and Puotinen, M. (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc. Natl. Acad. Sci. U.S.A.* 109, 17995–17999. doi: 10.1073/pnas.1208909109

Doherty, P. J., Dufour, V., Galzin, R., Hixon, M., Meekan, M. G., and Planes, S. (2004). High mortality during settlement as a population bottleneck for a tropical surgeonfish. *Ecology* 85, 2422–2428. doi: 10.1890/04-0366

Downs, C. A., Ostrander, G. K., Rougee, L., Rongo, T., Knutson, S., Williams, D. E., et al. (2012). The use of cellular diagnostics for identifying sub-lethal stress in reef corals. *Ecotoxicology* 21, 768–782. doi: 10.1007/s10646-011-0837-4

Downs, C. A., Woodley, C. M., Richmond, R. H., Lanning, L. L. and, Owen, R. (2005). Shifting the paradigm for coral-reef 'health' assessment. *Mar. Poll. Bull.* 51, 486–494. doi: 10.1016/j.marpolbul.2005.06.028

Dumas, P., Jimenez, H., Leopold, M., Petro, G., and Jimmy, R. (2010). Effectiveness of village-based marine reserves on reef invertebrates in Emau, Vanuatu. *Environ. Cons.* 37, 364–372. doi: 10.1017/S0376892910000536

Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., et al. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506, 216–220. doi: 10.1038/nature13022

Edmunds, P. J., and Carpenter, R. C. (2001). Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proc. Natl. Acad. Sci. U.S.A.* 98, 5067–5071. doi: 10.1073/pnas.071524598

Fenner, D., 2012. Challenges for managing fisheries on diverse coral reefs. *Diversity* 4, 105-160. doi: 10.2305/IUCN.CH.2004.PAPS.1.en

Finkbeiner, E., and Basurto, X. (2015). Re-defining co-management to facilitate small-scale fisheries reform: an illustration from Northwest Mexico. *Mar. Pol.* 51, 433–441. doi: 10.1016/j.marpol.2014.10.010

Fitt, W. K., Gates, R. D., Hoegh-Guldberg, O., Bythell, J. C., Jatkard, A., Grottoli, A. G., et al. (2009). Response of two species of Indo-Pacific corals, *Porites cylindrica* and *Stylophora pistillata*, to short-term thermal stress: the host does matter in determining the tolerance of corals to bleaching. *Exp. Mar. Biol. Ecol.* 373, 102-110. doi: 10.1016/j.jembe.2009.03.011

Folke, C., Hahn, T., Olsson, P., and Norberg, J. (2005). Adaptive governance of social-ecological systems. *Ann. Rev. Environ. Res.* 30, 441–473. doi: 10.1146/annurev.energy.30.050504.144511

Foster, N. L., Paris, C. B., Kool, J. T., Baums, I. B., Stevens, J. R., Sanchez J. A., et al. (2012). Connectivity of Caribbean coral populations: complementary insights from empirical and modelled gene flow. *Mol. Ecol.* 21, 1143–1157. doi: 10.1111/j.1365-294X.2012.05455.x

Galindo, H. M., Olson, D. B., and Palumbi, S. R. (2006). Seascape genetics: a coupled oceanographic-genetic model predicts population structure of Caribbean corals. *Curr. Biol.* 16, 1622–1626. doi: 10.1016/j.cub.2006.06.052

Game, E. T., McDonald-Madden, E., Puotinen, M. L., and Possingham, H. P. (2008). Should we protect the strong or the weak? Risk, resilience, and the selection of marine protected areas. *Cons. Biol.* 22, 1619–1629. doi: 10.1111/j.1523-1739.2008.01037.x

Gardner, T. A., Cote, I. M., Gill, J. A., Grant, A., and Watkinson, A. R. (2003). Long-term region-wide declines in Caribbean corals. *Science* 301, 958–960. doi: 10.1126/science.1086050

Gledhill, D. K., Wanninkhof, R., Millero, F. J., and Eakin, C. M. (2008). Ocean acidification of the Greater Caribbean Region 1996–2006. *J. Geophys. Res.* 113:C10031. doi: 10.1029/2007jc004629

Golbuu, Y., Wolanski, E., Idechong, J. W., Victor, S., Isechal, A. L., Oldiais, N. W., et al. (2012). Predicting coral recruitment in a complex reef archipelago, Palau. *PLoS ONE* 7:e50998. doi: 10.1371/journal.pone.0050998

Graham, N. A. J., Bellwood, D. R., Cinner, J. E., Hughes, T. P., Norström, A. V., and Nyström, M. (2013). Managing resilience to reverse phase shifts in coral reefs. *Front. Ecol. Environ.* 11, 541–548. doi: 10.1890/120305

Great Barrier Reef Marine Park Authority. (2009). *Great Barrier Reef Region Strategic Assessment*, Townsville, QLD: Program Report.

Great Barrier Reef Marine Park Authority. (2013). *Great Barrier Reef Region Strategic Assessment: Program Report. Draft for Public Comment.* Townsville, QLD: GBRMPA. Available online at: http://ptedocs.gbrmpa.gov.au/ptRefWorks/2011-20/2013/GBRMPA_2013_GB RRegion-StrategicAssessmentDraftProgramReport.pdf

Great Barrier Reef Report Card 2012 and 2013. (2014). *Reef Water Quality Protection Plan.* Available online at: http://www.reefplan.qld.gov.au/ measuring-success/report-cards/assets/report-card-2012-2013.pdf

Green, A. L., Fernandes, L., Almany, G., Abesamis, R., McLeod, E., Aliño, P. M., et al. (2014). Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. *Coast. Manag.* 42, 143–159. doi: 10.1080/08920753.2014.877763

Griffith, B., Scott, J. M., Carpenter, J. W., and Reed, C. (1989). Translocation as a species conservation tool: status and strategy. *Science* 245, 477–480. doi: 10.1126/science.245.4917.477

Gurney, G. G., Cinner, J. E., Ban, N. C., Pressey, R. L., Pollnac, R., Campbell, S. J., et al. (2014). Poverty and protected areas: an evaluation of a marine integrated conservation and development project in Indonesia. *Glob. Environ. Change* 26, 98–107. doi: 10.1016/j.gloenvcha.2014.04.003

Harrington, L., Fabricius, K., De'Ath, G., and Negri, A. (2004). Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* 85, 3428–3437. doi: 10.1890/04-0298

Hicks, C. C., and Cinner, J. E. (2014). Social, institutional, and knowledge mechanisms mediate diverse ecosystem service benefits from coral reefs. *PNAS* 111, 17791–17796. doi: 10.1073/pnas.1413473111

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Fresh. Res.* 50, 839–866. doi: 10.1071/MF99078

Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D. B., Parmesan, C., Possingham, H. P., et al. (2008). Assisted colonization and rapid climate change. *Science* 321, 345–346. doi: 10.1126/science.1157897

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., et al. (2007). Coral reefs under rapid climate change and ocean acidification. *Science* 318, 1737–1742. doi: 10.1126/science.1152509

Howells, E. J., Beltran, V. H., Larsen, N. W., Bay, L. K., Willis, B. L., and van Oppen, M. J. H. (2012). Coral thermal tolerance shaped by local adaptation of photosymbionts. *Nat. Clim. Change* 2, 116–120. doi: 10.1038/nclimate1330

Hueerkamp, C., Glynn, P. W., D'Croz, L., Maté, J. L., and Colley, S. B. (2001). Bleaching and recovery of five eastern Pacific corals in an El Nino-related temperature experiment. *Bull. Mar Sci.* 69, 215–236.

Hughes, T. P., and Connell, J. H. (1999). Multiple stressors on coral reefs: a long-term perspective. *Limnol. Oceanogr.* 44, 932–940. doi: 10.4319/lo.1999.44.3_part_2.0932

Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L. J., et al. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* 17, 360–365. doi: 10.1016/j.cub.2006.12.049

Jones, A. M., and Berkelmans, R. (2010). Potential costs of acclimatization to a warmer climate: growth of a reef coral with heat tolerant vs. sensitive symbiont types. *PLoS ONE* 5:e10437. doi: 10.1371/journal.pone.0010437

Jones, A. M., and Berkelmans, R. (2011). Tradeoffs to thermal acclimation: energetics and reproduction of a reef coral with heat tolerant *Symbiodinium* type D. *J. Mar. Biol.* 2011, 885-890. doi: 10.1155/2011/185890

Jones, G. P., Almany, G. R., Russ, G. R., Sale, P. F., Steneck, R. S., van Oppen, M. J. H., et al. (2009). Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* 28, 307–325. doi: 10.1007/s00338-009-0469-9

Juda, L. (1999.). Considerations in the development of a functional approach to the governance of large marine ecosystems. *Ocean Dev. Int. Law.* 30, 89–125. doi: 10.1080/009083299276203

Kennedy, E. V., Perry, C. T., Halloran, P. R., Iglesias-Prieto, R., Schonberg, C. H., Wisshak, M., et al. (2013). Avoiding coral reef functional collapse requires local and global action. *Curr. Biol.* 23, 912–918. doi: 10.1016/j.cub.2013.04.020

Kittinger, J. N., Finkbeiner, E. M., Ban, N. C., Broad, K., Carr, M. H., Cinner, J. E., et al. (2013). Emerging frontiers in social-ecological systems research for sustainability of small-scale fisheries. *Curr. Opin. Environ. Sust.* 5, 352–357. doi: 10.1016/j.cosust.2013.06.008

Kramer, P. A., Kramer, P. R., and Ginsburg, R. N. (2003). Assessment of the andros island reef system, bahamas (part 1: stony corals and algae). *Atoll. Res. Bull.* 496, 77–100. doi: 10.5479/si.00775630.496-5.76

Lirman, D. (2001). Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19, 392–399. doi: 10.1007/s003380000125

Lirman, D., Thyberg, T., Herlan, J., Hill, C., Young-Lahiff, C., Schopmeyer, S., et al. (2010). Propagation of the threatened staghorn coral *Acropora cervicornis*: methods to minimize the impacts of fragment collection and maximize production. *Coral Reefs* 29, 729–735. doi: 10.1007/s00338-010-0621-6

Little, A. F., van Oppen, M. J. H., and Willis, B. L. (2004). Flexibility in algal endosymbioses shapes growth in reef corals. *Science* 304, 1492–1494. doi: 10.1126/science.1095733

MacNeil, M. A., Graham, N. A. J., Cinner, J. E., Wilson, S. K., Williams, I. D., Maina, J., et al. (2015). Recovery potential of the world's coral reef fishes. *Nature* 520, 341–344. doi: 10.1038/nature14358

Margoluis, R. A., and Salafsky, N. (1998). *Measures of Success: Designing, Managing, and Monitoring Conservation and Development Projects*. Washington, DC: Island Press.

Marshall, P. A., and Baird, A. H. (2000). Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* 19, 155–163. doi: 10.1007/s003380000086

Marshall, P. A., and Schuttenberg, H. Z. (2006). *A Reef Manager's Guide to Coral Bleaching*. Townsville, QLD: Great Barrier Reef Marine Park Authority.

McClanahan, T. R., Ateweberhan, M., Muhando, C. A., Maina, J., and Mohammed, M. S. (2007). Effects of climate and seawater temperature variation on coral bleaching and mortality. *Ecol. Monogr.* 77, 503-525 doi: 10.1890/06-1182.1

McClanahan, T. R., and Kurtis, J. D. (1991). Population regulation of the rock-boring sea urchin *Echinometra mathaei* (de Blainville). *J. Exp. Mar. Biol. Ecol.* 147, 121–146. doi: 10.1016/0022-0981(91)90041-T

McCook, L. J. (1999). Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18, 357–367. doi: 10.1007/s003380050213

McCook, L. J., Almany, G. R., Berumen, M. L., Day, J. C., Green, A. L., Jones, G. P., et al. (2009). Management under uncertainty: guidelines for incorporating connectivity into the protection of coral reefs. *Coral Reefs* 28, 353–366. doi: 10.1007/s00338-008-0463-7

McCook, L. J., Ayling, T., Cappo, M., Choat, J. H., Evans, R. D., De Freitas, D. M., et al. (2010). Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. *Proc. Natl. Acad. Sci. U.S.A.* 107, 18278–18285 doi: 10.1073/pnas.0909335107

McCook, L. J., Folke, C., Hughes, T., Nyström, M., Obura, D., and Salm, R. (2007). *Ecological Resilience, Climate Change and the Great Barrier Reef, in Climate Change and the Great Barrier Reef: A vulnerability assessment*. Townsville, QLD: Great Barrier Reef Marine Park Authority.

McCook, L. J., Jompa, J., and Diaz-Pulido, G. (2001). Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19, 400–417. doi: 10.1007/s003380000129

McLeod, E., Anthony, K. R. N., Andersson, A., Beeden, R., Golbuu, Y., Kleypas, J., et al. (2013). Preparing to manage coral reefs for ocean acidification: lessons from coral bleaching. *Front. Ecol. Environ.* 11, 20–27. doi: 10.1890/110240

McManus, J. W. (1997). Tropical marine fisheries and the future of coral reefs: a brief review with emphasis on Southeast Asia. *Coral Reefs* 16, S121–S127. doi: 10.1007/s003380050248

McMillen, H. L., Ticktin, T., Friedlander, A., Jupiter, S. D., Thaman, R., Campbell, J., et al. (2014). Small islands, valuable insights: systems of customary resource use and resilience to climate change in the Pacific. *Ecol. Soc.* 19:44. doi: 10.5751/ES-06937-190444

Moon, K., and Blackman, D. (2014). A guide to understanding social science research for natural scientists. *Cons. Biol.* 28, 1167–1177. doi: 10.1111/cobi.12326

Mora, C., Aburto-Oropeza, O., Ayala, A., Ayotte, P. M., Banks, S., et al. (2011). Global human footprint on the linkage between diversity and ecosystem functioning in reef fishes. *PLoS Biol.* 9:e1000606. doi: 10.1371/journal.pbio.1000606

Mumby, P. J., Elliott, I. A., Eakin, C. M., Skirving, W., Paris, C. B., Edwards, H. J., et al. (2011). Reserve design for uncertain responses of coral reefs to climate change. *Ecol. Lett.* 14, 132–140. doi: 10.1111/j.1461-0248.2010.01562.x

Mumby, P. J., and Harborne, A. R. (2010). Marine reserves enhance the recovery of corals on Caribbean reefs. *PLoS ONE* 5:e8657. doi: 10.1371/journal.pone.0008657

Mumby, P. J., Steneck, R. S., Edwards, A. J., Ferrari, R., Coleman, R., Harborne, A. R., et al. (2012). Fishing down a Caribbean food web relaxes trophic cascades. *Mar. Ecol. Prog. Ser.* 445, 13–24. doi: 10.3354/meps09450

Nakai, T., and Park, S. C. (2002). Bacteriophage therapy of infectious diseases in aquaculture. *Res. Microbiol.* 153, 13–18. doi: 10.1016/S0923-2508(01)01280-3

Newton, K., Cote, I. M., Pilling, G. M., Jennings, S., and Dulvy, N. K. (2007). Current and future sustainability of island coral reef fisheries. *Curr. Biol.* 17, 655–658. doi: 10.1016/j.cub.2007.02.054

Olds, A., Connolly, R. M., Pitti, K. A., Maxwell, P. S., Aswani, S., and Albert, S. (2014). Incorporating seascape species and connectivity to improve marine conservation outcomes. *Cons. Biol.* 28, 982–991. doi: 10.1111/cobi.12242

Ortiz, J. C., Gonzalez-Rivero, M., and Mumby, P. J. (2013). Can a thermally tolerant symbiont improve the future of Caribbean coral reefs? *Glob. Change Biol.* 19, 273–281. doi: 10.1111/gcb.12027

Ostrom, E. (2007). A diagnostic approach for going beyond panaceas. *Proc. Natl. Acad. Sci. U.S.A.* 104, 15181–15187. doi: 10.1073/pnas.0702288104

Ostrom, E. (2009). A general framework for analyzing sustainability of social-ecological systems. *Science* 325, 419–422. doi: 10.1126/science.1172133

Perry, C. T., Taylor, K. G., and Machent, P. G. (2006). Temporal shifts in reef lagoon sediment composition, Discovery Bay, Jamaica. *Estu. Coas. Shelf Sci.* 67, 133–144. doi: 10.1016/j.ecss.2005.11.031

Pollnac, R., Christie, P., Cinner, J. E., Dalton, T., Daw, T. M., Forrester, G. E., et al. (2010). Marine reserves as linked social–ecological systems. *Proc. Natl. Acad. Sci. U.S.A.* 107, 18262–18265. doi: 10.1073/pnas.0908266107

Pomeroy, R. S., Parks, J. E., and Watson, L. M. (2004). *How's Your MPA Doing? A Guidebook for Natural and Social Indicators for Evaluating Marine Protected Area Management Effectiveness*. Gland; Cambridge: IUCN.

Rasher, D. B., and Hay, M. E. (2010). Chemically rich seaweeds poison corals when not controlled by herbivores. *Proc. Natl. Acad. Sci. U.S.A.* 107, 9683–9688. doi: 10.1073/pnas.0912095107

Reaka-Kulda, M. L. (1997). "The global biodiversity of coral reefs: a comparison with rainforests," in *Biodiversity II: Understanding and Protecting our Natural Resources,* eds M. L. Reaka-Kulda, D. E. Wilson, and O. E. Wilson (Washington, DC: Joseph Henry/National Academy Press), 83–108.

Renken, H., and Mumby, P. J. (2009). Modelling the dynamics of coral reef macroalgae using a Bayesian belief network approach. *Ecol. Model.* 200, 1305–1314. doi: 10.1016/j.ecolmodel.2009.02.022

Reshef, L., Koren, O., Loya, Y., Zilber-Rosenberg, I., and Rosenberg, E. (2006). The coral probiotic hypothesis. *Environ. Microbiol.* 8, 2068–2073. doi: 10.1111/j.1462-2920.2006.01148.x

Richmond, R. H. (1993). Coral reefs: present problems and future concerns resulting from anthropogenic disturbance. *Coral Reefs* 33, 524–536. doi: 10.1093/icb/33.6.524

Richmond, R. H., Rongo, T., Golbuu, Y., Victor, S., Idechong, N., Davis, G., et al. (2007). Watersheds and coral reefs: conservation science, policy, and implementation. *Bioscience* 57, 598–607. doi: 10.1641/B570710

Rinkevich, B. (2014). Rebuilding coral reefs: does active reef restoration lead *to* sustainable reefs? *Curr. Opin. Env. Sust.* 7, 28–36. doi: 10.1016/j.cosust.2013.11.018

Rougee, L. R. A., Richmond, R. H., and Collier, A. C. (2014). Natural variations in xenobiotic-metabolizing enzymes: developing tools for coral monitoring. *Coral Reefs* 33, 523–535. doi: 10.1007/s00338-014-1136-3

Ruddle, K. (1994). External forces and change in traditional community-based fishery management systems in the Asia-Pacific region. *Mar. Anthropol. Stud.* 6, 1–37.

Sale, P. F., Agardy, T., Ainsworth, C. H., Feist, B. E., Bell, J. D., Christie, P., et al. (2014). Transforming management of tropical coastal seas to cope with challenges of the 21st century. *Mar. Poll. Bull.* 85, 8–23. doi: 10.1016/j.marpolbul.2014.06.005

Sale, P. F., Cowen, R. K., Danilowicz, B. S., Jones, G. P., Kritzer, J. P., Lindeman, K. C., et al. (2005). Critical science gaps impede use of no-take fishery reserves. *Tren. Ecol. Evol.* 20, 74–80. doi: 10.1016/j.tree.2004.11.007

Satz, D., Gould, R. K., Chan, K. M., Guerry, A., Norton, B., Satterfield, T., et al. (2013). The challenges of incorporating cultural ecosystem services into environmental assessment. *Ambio* 42, 675–684. doi: 10.1007/s13280-013-0386-6

Sheppard, C., Dixon, D. J., Gourlay, M., Sheppard, A., and Payet, R. (2005). Coral mortality increases wave energy reaching shores protected by reef flats: examples from the Seychelles. *Estu. Coas. Shelf Sci.* 64, 223–234. doi: 10.1016/j.ecss.2005.02.016

Silverstein, R. N., Correa, A. M. S., and Baker, A. C. (2012). Specificity is rarely absolute in coral-algal symbiosis: implications for coral response to climate change. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 279, 2609–2618. doi: 10.1098/rspb.2012.0055

Smith, E. A. (1991). *Inujjuamiut Foraging Strategies: Evolutionary Ecology of an Arctic Hunting Economy.* New York, NY: Aldine de Gruyter.

Steneck, R. S. (1997). Crustose corallines, other algal functional groups, herbivores and sediments: complex interactions along reef productivity gradients. *Proc. Int. Coral Reef Symp.* 1, 695–700.

The World Bank. (2006). *Where is the Wealth of Nations?* Washington, DC: The World Bank.

van Oppen, M. J. H., Oliver, J. K., Putnam, H. M., and Gates, R. D. (2015). Building coral reef resilience through assisted evolution. *Proc. Natl. Acad. Sci. U.S.A.* 112, 2307–2313. doi: 10.1073/pnas.1422301112

van Oppen, M. J. H., Souter, P., Howells, E. J., Heyward, A. J., and Berkelmans, R. (2011). Novel genetic diversity through somatic mutations: fuel for adaptation of reef corals? *Diversity* 3, 405–423. doi: 10.3390/d3030405

van Putten, I., Lalancette, A., Bayliss, P., Dennis, D., Hutton, T., Norman-López, A., et al. (2013). A Bayesian model of factors influencing indigenous participation in the Torres Strait tropical rocklobster fishery. *Mar Pol.* 37, 96–105. doi: 10.1016/j.marpol.2012.04.001

van Woesik, R., Scott, W. J., and Aronson, R. B. (2014). Lost opportunities: coral recruitment does not translate to reef recovery in the Florida Keys. *Mar. Poll. Bull.* 88, 110–117. doi: 10.1016/j.marpolbul.2014.09.017

Vollmer, S. V., and Kline, D. K. (2008). Natural disease resistance in threatened Staghorn Corals. *PLoS ONE* 3:e3718. doi: 10.1371/journal.pone.0003718

Williams, G. J., Aeby, G. S., and Davy, S. K. (2008). Coral disease at Palmyra Atoll, a remote reef system in the Central Pacific. *Coral Reefs* 27, 207–207. doi: 10.1007/s00338-007-0314-y

Williams, I. D., and Polunin, N. V. C. (2000). Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* 19, 358–366. doi: 10.1007/s003380000121

Wolanski, E., Richmond, R. H., and McCook, L. (2004). A model of the effects of land-based human activities on the health of coral reefs in the Great Barrier Reef and in Fouha Bay, Guam, Micronesia. *J. Mar. Syst.* 46, 133–144. doi: 10.1016/j.jmarsys.2003.11.018

Wolanski, E., Richmond, R. H., McCook, L., and Sweatman, H. (2003). Mud, marine snow and coral reefs. *Am. Sci.* 91, 44–51. doi: 10.1511/2003.1.44

Wooldridge, S., and Done, T. J. (2004). Learning to predict large-scale coral bleaching from past events: a Bayesian approach using remotely sensed data, *in-situ* data, and environmental proxies. *Coral Reefs* 23, 96–108. doi: 10.1007/s00338-003-0361-y