

OPINION

Anticipative management for coral reef ecosystem services in the 21st century

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Abstract

Under projections of global climate change and other stressors, significant changes in the ecology, structure and function of coral reefs are predicted. Current management strategies tend to look to the past to set goals, focusing on halting declines and restoring baseline conditions. Here, we explore a complementary approach to decision making that is based on the anticipation of future changes in ecosystem state, function and services. Reviewing the existing literature and utilizing a scenario planning approach, we explore how the structure of coral reef communities might change in the future in response to global climate change and overfishing. We incorporate uncertainties in our predictions by considering heterogeneity in reef types in relation to structural complexity and primary productivity. We examine 14 ecosystem services provided by reefs, and rate their sensitivity to a range of future scenarios and management options. Our predictions suggest that the efficacy of management is highly dependent on biophysical characteristics and reef state. Reserves are currently widely used and are predicted to remain effective for reefs with high structural complexity. However, when complexity is lost, maximizing service provision requires a broader portfolio of management approaches, including the provision of artificial complexity, coral restoration, fish aggregation devices and herbivore management. Increased use of such management tools will require capacity building and technique refinement and we therefore conclude that diversification of our management toolbox should be considered urgently to prepare for the challenges of managing reefs into the 21st century.

Keywords: coral reefs, degraded ecosystems, ecosystem function, ecosystem services, habitat complexity, marine reserve

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Introduction

A diverse suite of threats are modifying the structure and functioning of marine ecosystems, and very few now resemble their 'natural' state (Jackson *et al.*, 2001; Halpern *et al.*, 2008). Stressors that have localized impacts, such as overfishing and eutrophication can be addressed at small-scales, through management tools such as marine protected areas (MPAs; Halpern, 2003; Rodrigues *et al.*, 2004)

and land use modifications. However, global threats such as climate change cannot be managed directly at local scales and are likely to worsen into the future (Frieler *et al.*, 2012). Coral reefs are one of the most vulnerable marine ecosystems to local and global impacts; climate change and a host of localized threats are causing significant degradation, and future outlooks regarding reef health and function are pessimistic (e.g. Hoegh-Guldberg *et al.*, 2007; Kennedy *et al.*, 2013). However, managing for optimal reef health is important, not only because of the exceptionally high biodiversity of these systems but also because the ecosystem goods and services they provide are central to coastal economies and livelihoods (Moberg & Folke, 1999).

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It is increasingly recognised that the continuing pressure of human activities will lead to ecosystems that look and function very differently in the future (Hobbs *et al.*, 2006). Despite these inevitable changes and calls to reassess efforts (e.g. Seastedt *et al.*, 2008; Hobbs *et al.*, 2009; Graham *et al.*, 2014), coral reef management and research tends to orientate itself towards historic system states, with the aim being to restore or preserve 'natural' ecosystem states, functions and services (Pauly, 1995; Jackson *et al.*, 2001; Pitcher, 2001). There is nothing inherently wrong in this approach and it usually motivates important management goals such as protecting habitats from destructive activities, improving coral cover, recovering fisheries productivity and increasing the resilience of reefs to disturbance (Moberg & Folke, 1999; Pandolfi *et al.*, 2005; Mumby *et al.*, 2013). However, in the context of increasingly severe, global-scale stressors, it is questionable that local action can restore or maintain these baseline targets, based on either historic levels or some of the most desirable extant states. Future reefs that are either degraded, or represent novel ecosystems (Yakob & Mumby, 2011; Graham *et al.*, 2014), may not support the same level of ecosystem services as their historical counterparts, yet they will still provide many key services that should be maximized to sustain coastal economies and livelihoods. However, the efficacy of different management tools will likely change with the state of the ecosystem. Given that a suite of management tools exist for coral reefs it seems prudent to identify optimal portfolios of these tools that address emerging issues.

Here, we develop an anticipative approach to management that considers the future functioning of coral reefs, the services they provide, and their response to different management tools. We aim to identify portfolios of management approaches that maximize the delivery of ecosystem services in the future. To achieve this we adopt a scenario planning approach (Peterson *et al.*, 2003), which allows us to capture uncertainty about the structure and function of coral reefs ecosystems in the future. A range of potential scenarios allows for variability in the severity of local stressors, as well as heterogeneity in key biophysical characteristics such as structural complexity and productivity. By capturing uncertainty in future reef states we explore the potential for changes in the efficacy of different management approaches for different ecosystem services as we progress through the 21st century. Though our primary aim is to consider how management might need to adapt to suit future reef degradation, our approach and findings are also relevant for the management of the most heavily degraded coral reefs of today, when the goal is to maximize service provision.

Methods

The basis for our scenario planning framework was a conceptual coral reef food web that included 16 key functional groups and their interactions (Fig. 1). The groups and trophic links represented in the food web capture information from a broad range of key literature on the functional roles and predator-prey interactions of coral reef organisms (Opitz, 1996; Bascompte *et al.*, 2005, and see supplementary material for additional references). Future anticipated changes in the state of the ecosystem were described by relative changes in the abundance of these different functional groups. Changes in abundance were assessed in a semiquantitative manner, on a 7-point scale between -3 (much less) and 3 (much more, see Fig. 2).

While we recognise that a range of human impacts, including poor water quality, can degrade coral reef ecosystems, we focused on climate change and overfishing as major drivers of degradation because they are ubiquitous (Bellwood *et al.*, 2004; Halpern *et al.*, 2008). To prepare for the worst consequences of stress, we assumed that global climate change will cause a uniform decline in the abundance of live coral to a level that is functionally limited. So in all of our potential future scenarios, coral cover is assumed to be lower than it is today (score of -2). We do not imply that this will definitely occur; it simply provides a pessimistic scenario for consideration, but one that is consistent with the downward trends of coral cover on many reefs (Baker *et al.*, 2008). We identified and explored two levels of fishing pressure: moderate and extreme overfishing. In scenarios with moderate overfishing, apex predators (large carnivores) are assumed to be

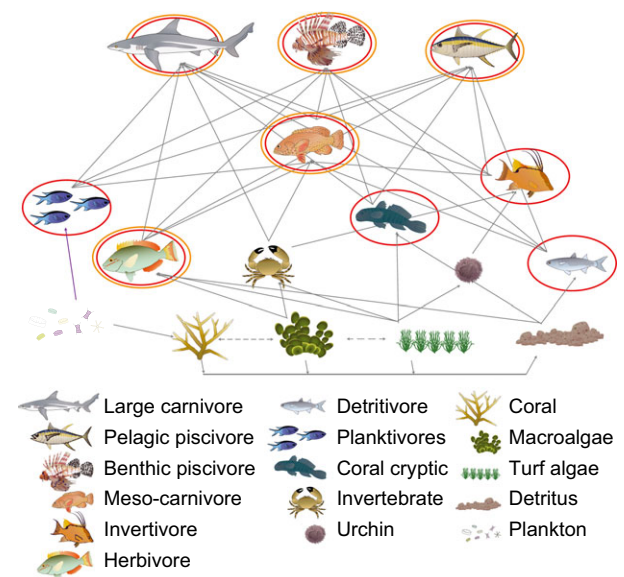


Fig. 1 Conceptual food web of a coral reef ecosystem identifying 16 key functional groups and the flow of energy between them as a result of predation or herbivory (solid lines). Dashed lines represent important competitive interactions between benthic groups. Orange and red circles denote groups that are affected by moderate and high overfishing respectively.

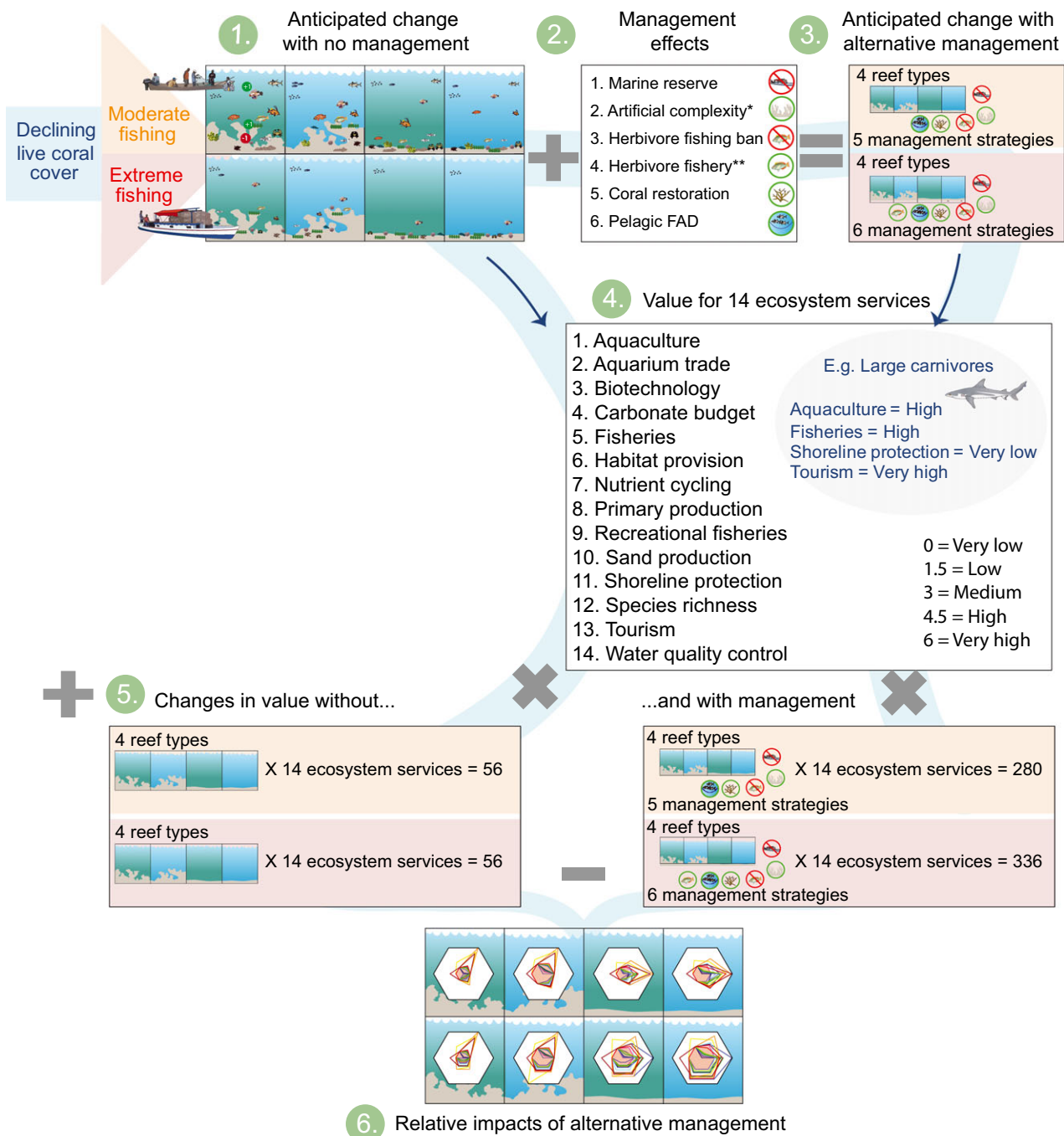


Fig. 2 Schematic showing the scenario planning framework to anticipate the impacts of alternative management strategies on the ecosystem services of future coral reef scenarios with varying levels of overfishing and different biophysical characteristics. Greener water depicts high productivity, rugose substrate depicts high complexity. Expert opinion and existing literature were used in steps 1, 2 and 4. *Applied only to habitats with low complexity and assumed to return functional groups to that of equivalent high complexity habitats. **Applied only to extreme fishing scenarios.

functionally absent (score of -3) and a number of other high to mid trophic level groups suffer moderate declines (Fig. 1). In scenarios with extreme overfishing, all high to mid trophic-level groups are functionally absent (score of -3), and smaller, more cryptic groups such as planktivores, detritivores and

coral reef cryptic species are also reduced in abundance (Fig. 1).

To capture heterogeneity in reef physical characteristics, we identified four types of reef habitat; (1) high habitat complexity with high primary productivity, (2) high habitat complexity

with low primary productivity, (3) low habitat complexity with high primary productivity and (4) low habitat complexity with low primary productivity (Fig. 2). Future reef types with high habitat complexity represent those that retain their topography in the absence of live coral, although this may be lost over longer timescales, whereas those with low complexity have largely lost their three-dimensional structure. Primary productivity refers predominantly to the relative abundance and growth rates of macroalgae and turf algae in future scenarios where free space becomes available due to reduced live coral cover.

To anticipate changes in the abundance of each functional group in response to stressors, reef type and different management strategies, the authors used an expert-knowledge approach (reviewed by Polasky *et al.*, 2011), based on a Delphi, or estimate-talk-estimate framework (Linstone & Turoff, 1975). Individuals decided on values for a matrix of change in each of the 16 functional groups under a given scenario of stress and reef type. A discussion was then facilitated that allowed all individuals to present their view and their reasoning. This was followed by a period of open discussion in light of differences in opinion, until a general consensus was reached by the whole group. By allowing estimation, discussion and re-estimation in this way, we minimized individual bias in our results. The expertise of the group is detailed in Table S1. This expertise includes 91 published papers and a further six in review on subjects highly relevant to managing future reefs, including empirical work on food web dynamics, reef management, and the effects of fishing and global climate change. Throughout the decision making processes, the authors drew upon their own knowledge and experiences as well as their understanding of a diverse range of existing scientific literature.

Figure 2 summarizes the steps involved in the scenario planning framework and expert-knowledge approach. In the first step, we predicted changes in the abundance of each functional group under each fishing and reef type scenario and in the absence of management (Fig. 2, step 1). We considered direct effects due to exploitation and climate change but also indirect effects associated with predator-prey interactions, resource availability and the biophysical characteristics of the reef. Table 1 provides a summary of the key predictions made, presenting only the general directions of change rather than their magnitude. Footnotes explain the assumptions that were made to capture uncertainty relating to differences in complexity and primary productivity. This table can be cross-referenced with Table S2 which is the complete matrix of anticipated change with no management. The eight reef scenarios that we anticipate in our study represent a spectrum of degradation of reef state. We consider these scenarios to represent future reefs, but acknowledge that contemporary examples of reefs with similar structure do exist.

The next step considered the effects of six different management strategies on the abundance of each functional group for each reef type (Fig. 2, step 2). The management strategies considered are by no means exhaustive but cover a broad range, including whole-ecosystem approaches and the protection of individual functional groups. A number of other important management strategies including gear and effort restrictions

for fisheries are not explicitly considered but their effects would not differ qualitatively from the effects of those tools that are. As in step one, both direct and indirect effects of management were considered. Table 2 summarizes the key predictions made for each management tool. This table can be cross-referenced with online supporting information, which provides the six resulting matrices of management effects (Tables S3–S7). Matrices of anticipated change with alternative management were calculated by adding management effect matrices to the matrix of anticipated change with no management (Fig. 2, step 3). Note that not all management effects were applied in all scenarios. Specifically, herbivore fisheries were only considered as a relevant tool for scenarios with extreme overfishing, and artificial complexity was applied only to reef types with low complexity. Where possible, when considering the effects of management in future scenarios we drew upon literature and individual knowledge of management effects in heavily degraded contemporary reefs most representative of anticipated future reef states.

Matrices of change (both anticipated change with no management and with alternative management) were used to predict changes in the value of 14 ecosystem services by first assigning a value from low to high, of each functional group, to each service (Fig. 2, step 4; Table S9), and then multiplying the matrices of change by the matrices of value for ecosystem services (Fig. 2, step 5). Changes were summed across all 16 functional groups to obtain a predicted overall change in the value of reefs for a particular service, both in the absence of management and under different management strategies.

An important assumption was made regarding the effect that marine reserves, herbivore fishing bans and herbivore fisheries have on the value of the fisheries ecosystem service. It could be argued that these management tools should have a negative impact on fisheries due to losses of catch associated with fisheries closures. However, we do not implement such a direct effect in our scenarios. We envisage our scenarios to be occurring at relatively large scales, typically larger than the scale of marine reserves (e.g. the median reserve size in 2003 was 4.0 km², Halpern, 2003). While the establishment of marine reserves will lead to rebuilding populations of target species that are unavailable to fishers, we assume that fished areas will benefit because there are increased abundances of target species that become available due to adult and larval spill-over effects (Roberts *et al.*, 2001). Similarly, a herbivore fishing ban will have positive effects as a result of indirect increases in other target species. An additional, important assumption was made regarding the effect of marine reserves on coral abundance in future scenarios. We assume that global climate change causes not only a decreased abundance of living coral but also a reduction in its health and capacity to recover from disturbance (Anthony *et al.*, 2011). Hence, we assume that marine reserves do not have a positive impact on coral abundance or structural complexity. The only management tool that allowed for increased coral abundance in our scenarios was active coral restoration. Our conclusions regarding best management practices are therefore really most relevant for future reefs whose function as well as structure is

Table 1 Summary of direct and indirect changes in the abundance of coral reef functional groups in response to global climate change and two levels of overfishing threat. Arrows represent the direction of change in each functional group

Current status	Direct future effects	Indirect future effects
Moderate fishing pressure	↓ Corals* ↓ Large carnivores ↓ Benthic piscivores, Pelagic piscivores, Meso carnivores, Invertivores, Herbivores†	↑ Macroalgae, Mobile invertebrates‡, Detritus§¶ ↓↑ Turfs ¶** ↓ Live coral cryptic species ↑ Benthic piscivores, Pelagic piscivores, Meso carnivores, Invertivores, Herbivores†† ↓ Planktivores† ↓↑ Detritivores††† ↓↑ Urchins†††
Extreme fishing pressure	↓ Corals* ↓ Large carnivores, Benthic piscivores, Pelagic piscivores, Meso carnivores, ↓ Invertivores, Herbivores, Planktivores, Detritivores†	↓ Macroalgae ↓ Detritus§ ↑ Turfs ↓ Live coral cryptic species ↑ Urchins

*Change in coral is associated with global climate change.

†Declines occur more, or only when complexity is lost because of increased fishing efficiency or predation risk in low complexity habitats (Hixon & Beets, 1993).

‡Invertebrate abundance responds to macroalgal abundance, with the assumption that invertebrates are macroalgal-associated (Roff *et al.*, 2013).

§Detritus abundance responds to macroalgal abundance with the assumption that indigestible macroalgae contribute to the detrital pool (Alongi, 1988).

¶In high productivity systems, lost corals are replaced by macroalgae but in low productivity systems, they are replaced by turfs (Roff & Mumby, 2012).

**Algae increase less in high complexity habitats because grazing intensity remains constant due to increases in herbivore abundance associated with available refugia from predation and fishing.

††When high complexity persists, refugia from fishing or predation allow for increases in abundance when there are associated increases in prey, or resource availability.

degraded. Some insights can be drawn from our conclusions for contemporary reefs that are highly degraded, but this should be done with an understanding that some management tools have a greater potential to recover present day reefs than those we anticipate in the future.

The final step in the scenario planning process was to calculate the relative impacts of different management tools, which were defined as the difference in the change in ecosystem service value with, and without management (Fig. 2, step 6).

Loss of services in the absence of management

Without management, anticipated changes in the structure of coral reefs resulted in decreases in the value of almost all 14 ecosystem services considered (Fig. 3), though the magnitude of decrease varied among ecosystem services, and with fishing pressure and biophysical context. On average, tourism, carbonate budgets and fisheries appeared to be most vulnerable, whereas primary productivity, water quality control and biotechnology were predicted to lose less value, and in some instances increase. Increases were predicted to occur because some functional groups, such as macroalgae, turfs and detritivores, have a high value for some services, and their abundance is anticipated to increase in future scenarios where live coral, predatory fish and herbivores decline (Gardner *et al.*, 2003; Hughes *et al.*, 2010). With respect to fishing pressure and

reef type (Fig. 3), losses in value of services appeared to be significantly greater for all scenarios with extreme vs. moderate overfishing. Within a fishing regime, locations that maintained structural complexity lost less value than those that became less complex.

Anticipating future impacts of management

Three generalities emerged from the analysis of management impacts on future ecosystem services (Fig. 4). Firstly, there were marked differences in the relative impacts of management strategies on reefs with high vs. low structural complexity. These differences are broadly attributable to the widely acknowledged functional importance of habitat structure on coral reefs (Graham & Nash, 2012). Crevices and holes provide locations for settlement, foraging (Feary *et al.*, 2007) and nesting (Karino & Nakazono, 1993) and mediate predator-prey interactions through the provision of refugia (Hixon & Beets, 1993; Holbrook & Schmitt, 2002; Almany, 2004). Therefore, low complexity reefs are likely to function differently to high complexity reefs, and require different management strategies to maximize the ecosystem services that they can provide. Secondly, the diversity of management strategies that had high positive impacts on services increased as the projected state of ecosystems became more degraded. Thirdly, trade-offs emerged among services associated with

Table 2 Summary of direct and indirect changes in the abundance of coral reef functional groups in response to six alternative management strategies. Arrows represent the direction of change in abundance in each functional group

Management tool	Scenario applied to	Direct effects	Indirect effects
Marine Reserve	All	↑ Large carnivores, Benthic piscivores, Pelagic piscivores, Mesocarnivores, Invertivores, Herbivores*	↓ Detritivores, Planktivores, Live coral cryptics, Urchins† ↓ Macroalgae, Mobile invertebrates, Detritus ↑ Turf
Pelagic FAD	All	↑ Pelagic piscivores	
Live Coral Restoration	All	↑ Corals	↑ Large carnivores, Planktivores* ↑ Benthic piscivores, Mesocarnivores, Invertivores, ↑ Herbivores*‡ ↓ Urchins† ↓ Macroalgae, mobile invertebrates, detritus ↑ Turfs ↓ Urchins
Herbivore Fishery	Extreme fishing scenarios	↑ Herbivores§	
Herbivore Fishing Ban	All	↑ Herbivores	↓ Urchins ↓ Macroalgae, mobile invertebrates

*Has more positive impacts in habitats with high complexity because target fishery species have a greater potential for population growth due to the presence of refugia and settlement habitat (Harborne *et al.*, 2008).

†Increases in predator species cause trophic cascades, effects of which can be greater in habitats with low complexity due to lack of refugia.

‡Increase less in low productivity systems due to less food increase.

§Assumes that a fishery for herbivores will manage stocks effectively improving population abundance in comparison to extreme overfishing.

different management strategies. Application of a particular management tool increased the value of some ecosystem services, but simultaneously decreased the value of others, for example marine reserves improved fisheries and tourism but reduced sand production. It has been acknowledged previously that ecosystem services are not always positively correlated, and that management will often have unintended, or unanticipated negative effects (Tallis & Polasky, 2009). In practice, management strategies including those considered here are often used in combination (e.g. artificial structure and coral restoration inside marine reserves; Edwards, 2010), and this may mitigate some trade-offs. However, our approach and results provide a response to calls for tools to help managers explore trade-offs associated with particular management tools for the delivery of particular ecosystem services (Tallis & Polasky, 2009).

Managing future reefs with high habitat complexity. For high complexity reefs of the future, the anticipated significance of marine reserves as a management tool is striking (Fig. 4). As demonstrated in a large body of empirical literature, reserves were predicted to have clear positive impacts on tourism, fisheries and recreational fisheries and few other management tools came close to promoting any other ecosystem service value to the same extent. However, reserves also appear to lead to trade-offs, whereby they reduced the value of some ecosystem services. Large-bodied predators benefit significantly from the implementation of marine reserves (Russ, 2002) and hold high value for fisheries and tourism

(Newman *et al.*, 2006), but strengthening of the trophic structure within a reserve can reduce the services provided by groups at lower trophic levels. Our predictions suggest, for example, that services such as sand production and biotechnology, which place a high value on macroalgae (Nuemann & Land, 1975; Wefer, 1980) and invertebrates (Hunter, 1977; Bak, 1994; De Vries & Beart, 1995; Langer, 2008) could lose value on a degraded future reef when a reserve is implemented, compared to when no management is applied. These services may however continue to be available elsewhere in the seascape, outside of the marine reserve. But, in light of these results, it is important that the use of MPAs be carefully considered to ensure that they meet requirements, and promote the value of the ecosystem services that are in the highest demand.

Managing future degraded reefs with low structural complexity. Reefs with low structural complexity benefit from a wider diversity of management strategies than complex habitats. For complex habitats, the 'best' management strategy is relatively clear (marine reserves) but when complexity is lost, a broad suite of tools can have equally positive impacts on a range of ecosystem services (Fig. 4). Note that low complexity reefs might occur both on uniformly degraded seascapes in the future and also in unprotected parts of a seascape that includes reserves. They are also not unique to the future and exist both naturally, and in response to severe degradation today. Consequently, managers may have to increasingly consider managing high and low complexity reefs simultaneously

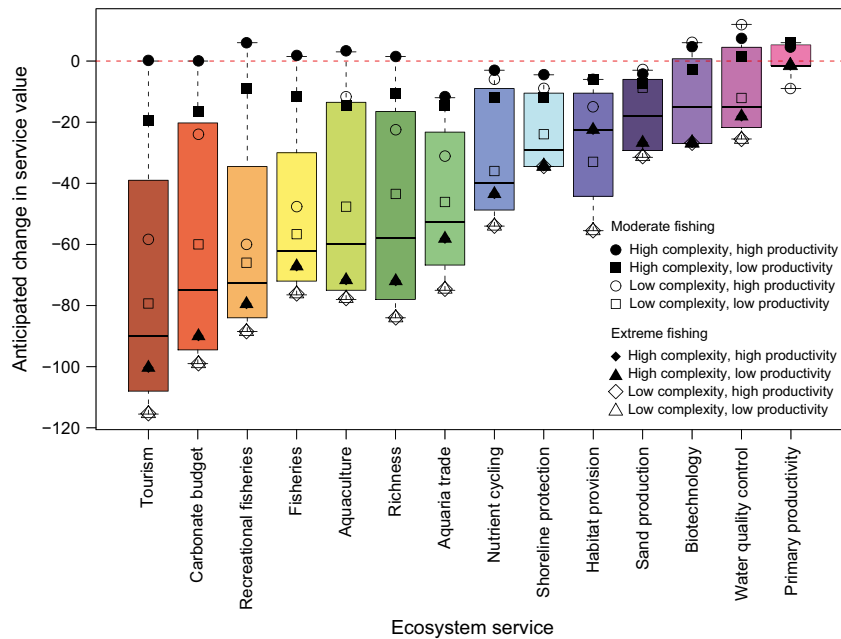


Fig. 3 Anticipated losses in the value of 14 ecosystem services under a projected decline in live coral cover due to global climate change, and either moderate or extreme overfishing. For each fishing scenario, habitats with high or low structural complexity and high or low productivity are shown, where symbol filling represents complexity, and symbol shapes depict productivity. Ecosystem services are ordered from high to low based on the median change in value depicted by the horizontal lines on bars. Boxes represent the interquartile range and whiskers extend to minimum and maximum data points.

within a single seascape. Here, we consider the efficacy of different management strategies for degraded reefs with low structural complexity.

Artificial complexity—We predict that the greatest benefit to low complexity reefs accrues from the provision of artificial complexity (Fig. 4). We defined artificial complexity as the

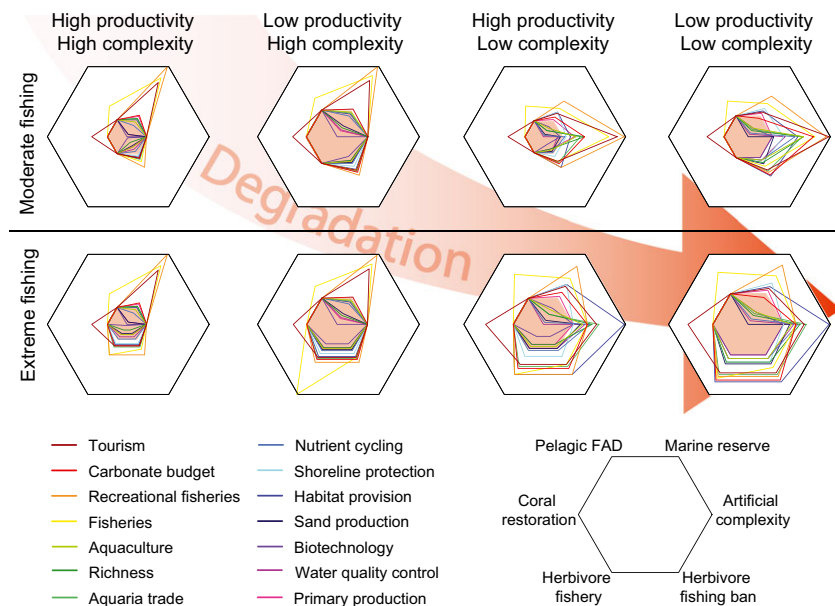


Fig. 4 Relative impacts of alternative management strategies on future coral reefs with moderate or high overfishing, and with high or low habitat complexity and productivity. Each spider diagram represents a distinct reef type with alternative levels of stress. Management impacts are scaled and comparable within plots. The further a line extends to the edge of the web, the more positive (relative to all other strategies) the impact of that management strategy on that ecosystem service. Shaded pink areas represent negative impacts of management.

replacement of structure that has been lost due to degradation, and therefore does not necessarily mean replacing the corals themselves. As a result, an artificial reef is considered to be identical in structure to a complex reef that has similar levels of productivity and fishing pressure. It remains to be seen whether this assumption holds true. A wide range of approaches to artificial habitat provision have been explored (see Bohnsack & Sutherland, 1985; Broughton, 2012 for reviews) and in certain areas artificial reefs have been shown to support healthy assemblages of fish (Abelson & Shlesinger, 2002). However, there remains debate about the role of artificial reefs as sources of new production vs. aggregation devices for fish from neighbouring natural reefs (Pickering & Whitmarsh, 1997; Brickhill *et al.*, 2005). Other persistent problems with artificial complexity include limited stability and longevity, toxin-leaching, high cost and public opposition (Broughton, 2012), along with whether the spatial scales and locations are appropriate. Most existing, 'successful' artificial reefs are much smaller than their natural counterparts (e.g. Ambrose & Swarbrick, 1989) and located far from natural reef systems. Yet for degraded reefs of the future, artificial structure would need to be located where reefs currently exist, and the economics of doing so at ecologically meaningful scales are uncertain.

We can still learn more from today's living reefs about the attributes that they possess that support healthy food webs, high productivity and high fish abundance. The more knowledge we can gain now, the better equipped we will be to carefully design artificial habitats that are able to increase local productivity and support ecosystem services (Sale & Hixon, 2014). Investing more time and effort now into acquisition of this knowledge and perhaps less into the creation of ineffectual artificial reefs will better prepare us to manage low complexity habitats in the future.

Coral restoration—Many coral restoration projects, in particular coral transplantation, occur in response to chronic, devastating disturbances such as ship groundings and hurricanes, particularly in the Florida Keys (Jaap, 2000; Rinkevich, 2005; Precht, 2006). However, restoration strategies only tend to be successful at small spatial scales (Edwards & Gomez, 2007; Edwards, 2010) and currently achievable increases in live coral abundance do not represent fully functioning reefs (Edwards & Gomez, 2007). Therefore, in our scenarios, we restrict the positive impacts of coral restoration to tourism, capturing for example, the provision of 'house reefs' at dive resorts and hotels. Our scenarios predict that coral restoration as a management strategy is, relative to other strategies, much more effective for low complexity future reefs. If the management goal was to improve tourism on a heavily degraded reef, coral restoration is predicted to be the most effective tool available, particularly if the system has also been heavily overfished (Fig. 4). Heavily impacted habitats like those created by ship groundings and hurricane damage may be some of the best contemporary representatives of degraded future reef scenarios. More rigorous monitoring and reporting of the success of small-scale coral restoration efforts in these locations, alongside well-planned experiments and continued efforts to improve techniques, would greatly improve our capacity to

expand the use of this tool in the future. Stakeholders and scientists might benefit from collaboration to determine the benefits and costs of reef restoration (Guest *et al.*, 2013).

Marine reserves—Marine reserves are predicted to have relatively weak positive impacts on fisheries and tourism if placed on low complexity reefs of the future. Contemporary examples of marine reserve efficacy on low complexity reefs are limited because most reserves are placed in 'the best' reef locations with high structural complexity (Russ 1985, Russ *et al.* 2005). However, comparative studies of reserve vs. structural complexity effects provide evidence that structure is as strong if not a stronger driver of the abundance and size structure of reef fish (Chapman & Kramer 1999, Wilson *et al.*, 2010). Furthermore, when variation in habitat structure is accounted for, the positive impacts of reserves are weaker than when the effects of complexity are ignored (Chapman & Kramer 1999, Russ *et al.* 2005). Without habitat refugia, postsettlement survival and recovery of species released from fishing pressure is likely to be reduced (Tupper & Boutilier, 1997; Wilson *et al.*, 2010). One contemporary study that explicitly considers reserve effects on low complexity reefs, showed that a well-established marine reserve in The Bahamas successfully increased the abundance of predators in complex habitats, but had no significant effect on their abundance in habitats that naturally lacked structure (Harborne *et al.*, 2008). These studies and our model results underscore the need to consider the characteristics of reefs before assessing whether reserves are the most appropriate management tool. Although the data are limited, we suggest that marine reserves may not be the optimum tool for heavily degraded, low complexity reefs now, or in the future.

Fish aggregation devices—In the context presented here, fish aggregation devices (FADs) are used to aggregate pelagic fish species close to the shore so that they can be accessed by fishermen in coastal communities. When effective, the devices not only improve food supplies, local economies and jobs but can also reduce fishing pressure on nearby coral reefs (Bell *et al.*, 2013). When compared to other management strategies, we predict that the relative impact of FADs for fisheries will be greater on low complexity reefs because they will supplement coral reef fisheries value. In fact, FADs become a highly effective management strategy, second only to artificial complexity when overfishing pressure is moderate, and the most effective strategy when overfishing is extreme on nearby reefs. However, the implementation of FADs comes with a broad suite of logistical, political and social issues. To aggregate pelagic species, FADs need to be anchored in deep water which can incur high costs and is logistically challenging. To avoid such costs, FADs are sometimes deployed in lagoons closer to the reef where they have the potential to aggregate nearby reef fish rather than pelagics, compromising their positive impact on reef ecosystems. There are also issues regarding management and access rights, and conflicts can occur between the use of FADs for providing local food and livelihoods vs. commercial exports (Andrew *et al.*, 2007). Furthermore, issues can arise when individuals feel that there is inequitable access to the

resource, and cases have been reported where FADs have been wilfully removed, at high cost. While there is evidence of adaptive management strategies that have allowed for the effective use of FADs in locations in the Eastern Pacific (Bell *et al.*, 2013), their widespread use in the future is likely to require major changes in societal priorities and values.

Herbivore fishing bans and fisheries—The herbivore fisheries considered in our scenarios are envisaged as well-managed, sustainable fisheries, where herbivore populations maintain their functional role. Bans on fishing are only considered where management has failed to maintain adequate herbivore function. We predict that herbivorous fish management can have a positive impact on a broad range of ecosystem services on low complexity reefs, and may even be more effective than marine reserves (Fig. 3). This is due to the important functional role of herbivory on coral reefs, and its indirect impacts on other functional groups (Steneck, 1988; Mumby *et al.*, 2006; Hughes *et al.*, 2007). Herbivorous fish management appeared to have few, if any negative trade-off impacts on ecosystem services, with the exception of biotechnology, which places a high value on macroalgae (De Vries & Beart, 1995).

Despite their potential benefits, herbivore fishing bans and herbivore fisheries are not currently widespread management tools. There has been a recent ban on the fishing of parrotfish in Belize (Cox *et al.*, 2013), and the IUCN Red List states that all parrotfish species are protected in Bonaire, Bermuda and the Turks and Caicos, as well as a number of species being given protected status in Puerto Rico and the United States Virgin islands (Choat *et al.*, 2012; also see Kahekili marine reserve, Hawaii). The question of moratoria on the exploitation of herbivorous fish is often complex however, in part because of the high dependency on such species, or a cultural legacy of preferentially exploiting herbivores (Bejarano *et al.*, 2013). Furthermore, the importance of grazing in controlling algal blooms, and hence affecting reef resilience, may be fundamentally different between Caribbean and Indo-Pacific reefs (Roff & Mumby, 2012), meaning that this strategy may be more effective in some biogeographical regions.

Conclusions

Resource management increasingly considers the effects of management options on the delivery of ecosystem functions and services (MEA, 2005; Daily *et al.*, 2009; Nelson *et al.*, 2009). Formal models linking ecosystem function to services are lacking for many services, so we attempt to bridge this gap using semiquantitative models based on expert opinion and literature review. We found that the strategies employed on reefs today may not necessarily be the optimal solutions to maximize ecosystem services on some reefs of the future, and by proxy, some of the most heavily degraded reefs now. Commonly used tools like marine reserves will be effective where high structural complexity is preserved, but when complexity is lost their efficacy will decline. Such a loss of complexity is highly

likely following coral mortality (Alvarez-Filip *et al.*, 2009). For degraded reefs, tools such as artificial complexity, FADs, coral restoration and herbivorous fish management will all become relatively more effective. As systems decline, achieving high levels of ecosystem service provision will therefore require a diversity of complementary management approaches. Although a number of the management tools that we consider here have been used in combination in contemporary settings, they are rarely used in combinations of more than two (e.g. active restoration inside reserves; Edwards, 2010 and FADs alongside marine reserves; Bell *et al.*, 2011). In addition, the efficacy of such combined management use for the provision of ecosystem services and the synergies among them is not well monitored or reported. Moreover, there are no direct comparisons of multiple tool use vs. single tool use in equivalent reef settings, and multiple tool use is rarely effectively coordinated to maximize the provision of particular ecosystem services. In the future, we suggest management frameworks will need to consider the challenges and opportunities for diversifying interventions in the same seascape. Increased use of novel, understudied and underrefined tools will be necessary to gain maximum provisions from future reef ecosystems. In short, we will need to diversify our standard management toolbox.

Another consideration that is not addressed explicitly here but should be considered in a framework of anticipative management is that the perceived value of some functional groups, for some services has the potential to change in the future. For example, groups such as planktivores and detritivores that may not be highly valued fishery targets today may be perceived with increased value in the future on a reef that has low fish diversity and abundance. Such changes in value should also be monitored and anticipated to ensure that management tools respond to maximize ecosystem service provision.

The use of some of the tools we consider (e.g. FADs) are in their infancy in terms of technology, governance and policy. Further research is required to maximize efficacy of their use and resolve potential conflicts and trade-offs. The literature review required to prepare this article also highlighted the lack of data related to low complexity reefs, and filling this gap will be increasingly important as physical and biological erosion reduce the complexity of degraded reefs. Similarly, additional current research to understand, monitor and report on the impacts of alternative management tools in the most degraded contemporary reef settings would allow us to test some of the conclusions of this study and continually improve the model to reduce uncertainty. Our conclusions suggest that it will take time to build capacity, refine technologies and adapt policies to

meet the challenges of ensuring maximum service provision from degraded future reef systems. It is critical, therefore, to start preparing for these management changes today.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of authors' expertise and publication history to support their ability to use expert opinion for scenario predictions for future coral reef degradation and management efficacy.

Table S2. Matrix of anticipated change with no management.

Table S3. Management effects matrix: Marine Reserves.

Table S4. Management effects matrix: Artificial habitat complexity.

Table S5. Management effects matrix: Herbivore fishing ban.

Table S6. Management effects matrix: Herbivore fishery.

Table S7. Management effects matrix: Coral restoration.

Table S8. Management effects matrix: Pelagic fish aggregation device (FAD).

Table S9. Matrix of value for 14 ecosystem services.