The Present and Future Status of Ecosystem Services for Coral Reefs

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Abstract

Coral reef ecosystems are among the most imperiled globally from human impacts. They are also the most biodiverse marine ecosystems and play a vital role in the food and livelihood security of tens of millions of people. Although the ecological and socioeconomic importance of coral reefs has been relatively well-documented, the impacts of coral reef degradation on ecosystem service provisioning are less known. Here, we review the range of ecosystem services currently provided by reefs (provisioning, regulating, and cultural), the human activities that currently threaten these services, and the future prospects of reef ecosystem services given the projected combined effects of local human disturbances and climate change. We then propose promising policy and management interventions to promote the maintenance of key coral reef ecosystem services into the future.

Introduction

The concept of ecosystem services (ES) was developed to recognize and quantify the contribution of ecosystems to human well-being and is increasingly being used in the formulation of policies and management centered around sustainable development (IPBES, 2016). Recent research has focused on coastal marine habitats of particular importance to human well-being, including coral reefs (Culhane et al., 2018). Although coral reefs cover less than 1% of the ocean floor, they contain almost a third of marine fish species and one third of all marine species known while providing habitat for 10% of the fish consumed by people globally (Moberg and Folke, 1999; Fig. 1). However, coral reefs are in crisis due to overfishing, pollution, and climate change (Hughes et al., 2003; Burke et al., 2011), threatening the persistence of reef ecosystems, ES provisioning, and the well-being of tens of millions of people who depend on reefs for food and livelihood security (Moberg and Folke, 1999; Birkeland, 2017; Woodhead et al., 2019). To design strategies for maintaining coral reef ecosystem functioning and ES provisioning, it is necessary to identify the key services provided by reefs and the anthropogenic impacts on these services currently and into the future.

In this chapter, we discuss the present status and future prospects of ES provided by coral reefs. First, we explore the array of ecosystem services (provisioning, regulating, and cultural) historically provided by coral reefs, using as reference the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) framework. Second, we summarize the primary anthropogenic threats to coral reefs and how they alter reef ecosystem structure and functioning. Third, we present projected changes to ecosystem service provisioning as coral reefs continue to be altered by human activities. Finally, we propose promising policy and management interventions for maintaining coral reef services into the future.

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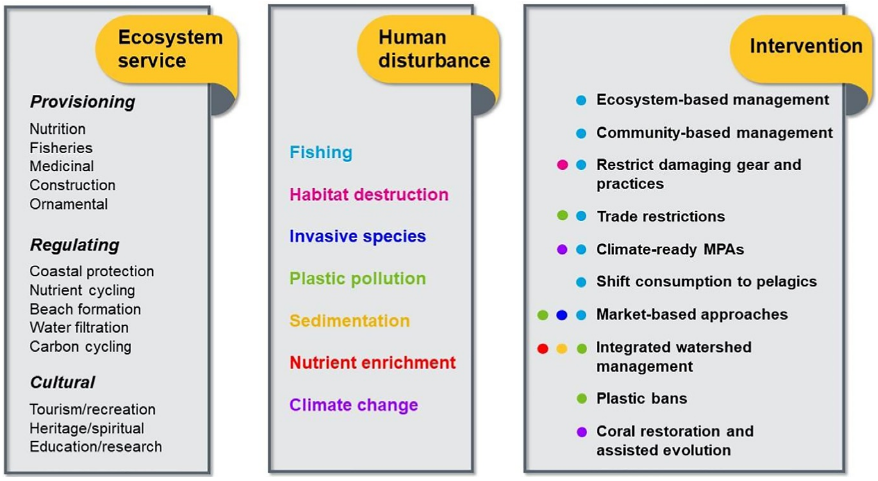

Fig. 1 Coral reef ecosystem services, human impacts to services, and promising interventions to maintain reef service provisioning. Reef ecosystem services are highly interconnected; each human impact, therefore, has the potential to affect the entire suite of ecosystem services.

Ecosystem services provided by coral reefs

Coral reefs are highly diverse and architecturally complex marine habitats formed primarily by the deposition of durable calcium carbonate skeletons by colonies of reef-building corals. Most reef-building corals contain symbiotic algae in their tissues that, via photosynthesis, provide the coral with sufficient energy to create their skeletons. Environmental stressors, including abnormally warm seawater, can disrupt this symbiosis and lead to declines in coral health or coral mortality. Coral reefs provide habitat for a diversity of marine life, including fish, turtles, marine mammals, and an enormous array of invertebrates, algae, and microbes; likely only a small fraction of the full diversity residing in reefs has been identified to date.

Because almost 40% of the world's human population lives in coastal areas (Burke et al., 2011), much of humanity depends directly on the ES provided by marine ecosystems such as coral reefs. Identifying and understanding the full array of coral reef ES provides an additional incentive for implementing sustainable reef management (Spalding et al., 2017). The major ES provided by coral reefs have been identified by IPBES (2016), Moberg and Folke (1999), and Woodhead et al. (2019) and are summarized in Fig. 1.

Provisioning services are usually associated with extractive activities that yield a direct benefit for humans. Coral reefs provide broad economic and social benefits, especially for the fishing sector. Reefs provide job opportunities and act as an important food source as they are home to several fish and invertebrate species consumed by humans (Spalding et al., 2017). Additional provisioning services include, but are not limited to, medicinal, biochemical and genetic resources, construction materials, and ornamental uses.

Cultural services provided by ecosystems provide opportunities for learning and education, support identities, and facilitate physical and psychological experiences including for recreation. Travelers from over 100 countries and territories travel to coral reef sites across the globe, making tourism an important cultural service derived from this ecosystem (Spalding et al., 2017). Approximately 30% of the world's reefs are valuable for the tourism sector, representing an estimated value of nearly US$36 billion (Spalding et al., 2017).

Regulating services include habitat processes and interactions that directly contribute to the supply of other service categories and indirectly contribute to human well-being (Woodhead et al., 2019). Due to their durable geobiological structure, coral reefs provide coastal protection from currents and waves and supply the raw materials for beach and sand formation. They can also create favorable conditions for the formation of habitats such as sea grasses or mangroves that store carbon and filter pollutants and sediments from coastal runoff (Moberg and Folke, 1999). Reefs also play an important role in the cycling of nutrients and carbon, increasing the productivity and regulating the pH of coastal waters (Moberg and Folke, 1999; Woodhead et al., 2019).

As it has developed, the ecosystem services approach has evolved to become more comprehensive and interdisciplinary. The application of ES to environmental management and conservation has traditionally focused on data from the natural sciences and economics. In contrast, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), the most recent framework, developed an approach that recognizes the importance of considering the numerous linkages and feedbacks between human and natural systems and indigenous and local knowledge in the environmental decision-making process (IPBES, 2016).

Anthropogenic threats to reef ecosystems

Many reef-building corals are sensitive to altered environmental conditions, making coral reefs particularly vulnerable to anthropogenic stressors. Human population growth in tropical and subtropical regions has resulted in increased coastal development and marine resource use in reef-bearing countries. These stressors, compounded by climate change, have made coral reefs one of the most imperiled ecosystems in the world. The abundance of reef-building corals has been halved over the last 40 years and continues to decline (Fig. 2; Bruno and Selig, 2007; Jackson et al., 2014). In the following sections, we outline the key anthropogenic stressors driving the decline of these ecosystems.

Climate change

Climate change is a global and chronic anthropogenic stressor affecting coral reef ecosystems around the world. Climate change is causing an array of environmental changes that can weaken coral health and survival, including increased seawater temperature, sea level, seawater acidity, and storm frequency and intensity. Many of these changes are occurring simultaneously, making reef environments less hospitable to many corals and other coral reef inhabitants (Hoegh-Guldberg, 2011; Ban et al., 2014).

Rising ocean temperatures pose a serious threat to coral reef ecosystems globally. When sea surface temperatures become abnormally high for extended periods of time, reef-building corals may expel their symbiotic algae ("zooxanthellae") as a stress response known as coral bleaching. Corals will not take up new zooxanthellae from surrounding waters while stressful environmental conditions persist, leading to more severe bleaching and increased rates of disease and mortality. As sea surface temperatures continue to rise, mass bleaching events are occurring more frequently and for longer durations, leading to mass die offs of reef-building corals around the world (Hoegh-Guldberg, 2011; Ban et al., 2014).

As oceans continue to absorb a large proportion of the greenhouse gases emitted from the burning of fossil fuels, seawater is becoming more acidic. Ocean acidification threatens corals and many of the marine invertebrates critical to coral reef ecosystems by reducing the availability of carbonate ions. The calcium carbonate skeletons formed by reef-building corals create the physical structure of the reef ecosystem, providing habitat for the immense diversity of species that live and/or forage within the reef. Other important coral reef invertebrates such as clams, snails, and urchins contain calcium carbonate shells or skeletons that are critical for their structural integrity and protection. As carbonate ions are less available, it becomes more difficult for these organisms to form their protective structures. Extreme acidification can result in the dissolution of calcium carbonate altogether, threatening the health and survival of coral reef invertebrates and the very foundation of the coral reef itself (Hoegh-Guldberg, 2011; Ban et al., 2014).

Water depth is an important environmental factor for many coral species. Reef-building corals containing zooxanthellae must reside within water depths with sufficient light for photosynthesis but that are deep enough to receive some protection from UV radiation. Historically, coral growth rates have been able to keep up with the rate of sea level rise, allowing corals to maintain their ideal water depth (Hoegh-Guldberg, 2011). However, because sea level rise is expected to increase rapidly over the next century and coral growth rates are being depressed by an array of human disturbances, corals may not be able to keep up (Hoegh-Guldberg, 2011). For coral species that are highly specialized to a specific depth range, this may increase mortality rates, as the acceleration of sea level rise may make repeated recolonization in appropriate depths difficult (Hoegh-Guldberg, 2011).

Warmer ocean temperatures will also increase the intensity and frequency of storm events. Intense storms can cause physical damage to coral colonies via high swell events and can reduce coastal water quality via high precipitation events. Increased storm intensity and frequency will also increase nutrient and sediment loads onto reefs. Because corals thrive in nutrient-poor, clear waters and are susceptible to smothering by sediments, elevated runoff negatively affects coral health in several ways. Increased sediment loads may also be exacerbated by changing coastal vegetation from the higher temperatures and drought events caused by climate change, which can cause soil destabilization (Hoegh-Guldberg, 2011).

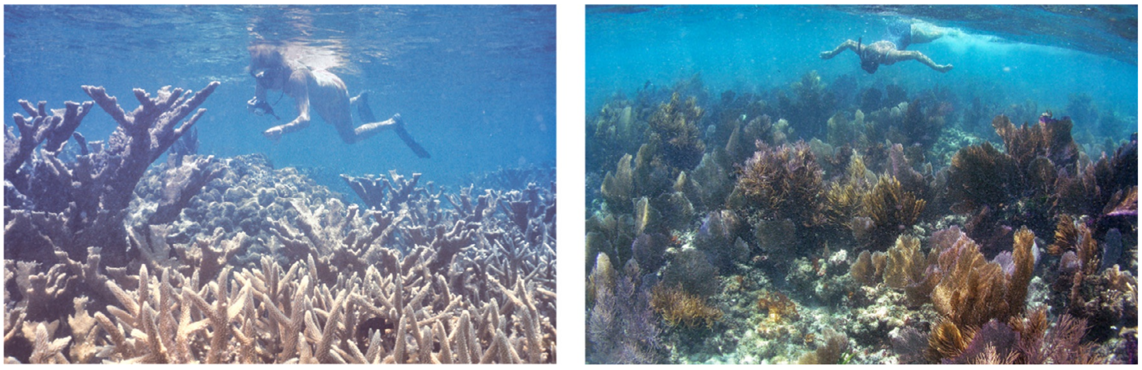

Fig. 2 The worldwide loss of reef-building corals, the architects of coral reef habitats, threatens the persistence of coral reef ecosystems and the services they provide to people. This reef site in the Florida Keys transitioned from dominance of tall, branching reef-building corals in 1971 (left) to dominance of non-reef building organisms by 2004 (right), a pattern occurring on many reefs due to local and global human stressors. Photos taken by Gene Shinn, United States Geological Survey (https://coastal.er.usgs.gov/data-release/doi-F7S46QWR/).

Coastal development

The direct and indirect impacts of coastal development can be detrimental to the health of adjacent coral reefs. With over 40% of the world's population living within 100 km of the coast, the alteration of coastal watersheds for development exerts tremendous pressures on the coastal marine ecosystems downstream (Burke et al., 2011). While intact coastal vegetation and soils regulate the amount and quality of freshwater that enters reef ecosystems and serve as filters or barriers for nutrients, sediments, and contaminants that would otherwise flow onto reefs, the removal of these natural buffers compromises coral reef water quality.

Direct impacts of coastal development include dredging, construction, and mining. These activities, such as the construction of piers, often require the destruction and removal of coral reefs. Additionally, these activities have indirect effects on reef health by reducing water quality and altering habitats that are essential breeding and foraging grounds for key fish species (e.g. mangroves or sea grasses).

Nutrient pollution and sedimentation stress coral reefs by reducing water quality. Nutrient pollution, primarily due to agricultural runoff and wastewater treatment, poses serious risks to coral reef ecosystems. Coral-dominated systems are nutrient poor and nutrient pollution promotes the growth of benthic algae which actively compete with corals for space. When exposed to chronic levels of nutrient input, coral-dominated ecosystems can shift to algal-dominated systems which cannot support the same reef-dependent species. Sedimentation threatens coral reefs by inhibiting photosynthesis and smothering corals. Agriculture, dredging, construction, and land development are major sources of sedimentation and other pollutants including fertilizers and pesticides. Sewage effluent is a common source of pollution in the Caribbean, Southeast Asia, and the Pacific Islands. Sewage contains a variety of pollutants including sediments, toxins, pathogens, nutrients, and pharmaceuticals that can cause disease, hinder growth and reproduction, and increase mortality rates of coral reef organisms. As a result, coral reef ecosystems near sewage outflows are often markedly degraded (Burke et al., 2011).

Marine resource use

Marine resource can affect the ecological balance of coral reef ecosystems in several ways. The unsustainable removal of coral reef fish and invertebrates (overfishing) is one of the main stressors to coral reef ecosystems, affecting over 55% of reefs worldwide (Burke et al., 2011). The overfishing of herbivorous fish such as parrotfish can lead to replacement of corals with benthic macroalgae due to decreased grazing. In addition to overfishing, destructive fishing practices (e.g., blast fishing, poison fishing, capture of juvenile fish) intensify the negative impacts of fishing to coral reef habitats (Goldberg and Wilkinson, 2004).

Marine resource use can also have indirect impacts on coral reef ecosystems. Shipping and the marine aquairum trade have increased the risk of introduction of invasive species onto reefs. These species often have ecological advantages that allow them to outcompete local species for resources and, as a result, cause damage to the native ecosystem (Goldberg and Wilkinson, 2004). Common invasive species in coral reef ecosystems include algae, invertebrates, and fishes (Goldberg and Wilkinson, 2004). One of the most iconic examples of the introduction of an invasive species on coral reefs is the lionfish in the Northwest Atlantic and Caribbean. Outside of their native Indo-Pacific waters, lionfish have few predators. They are effective predators themselves, consuming fish such as groupers and snappers that provide food and economic security for local communities. Lionfish also consume herbivorous fish, further reducing herbivory on reefs and increasing the likelihood of reefs shifting from coral- to algal-dominated systems (Kindinger and Albins, 2017).

Changing environmental quality and ecosystem function due to increased nutrient inputs and overfishing can allow some native species to disrupt reef ecosystem functioning. Crown-of-thorns starfish (COTS) are natural coral predators in Indo-Pacific reefs. However, unprecedented spikes in their populations (possibly due to removal of their natural predators and/or more favorable conditions for COTS larvae caused by increased nutrients) have devastated coral reef ecosystems, dramatically decreasing coral cover and changing community structure (Goldberg and Wilkinson, 2004).

Concurrent stressors

Coral reefs are often impacted by multiple human stressors simultaneously. Co-occurring stressors can have synergistic (i.e., their joint impact is greater than the sum of their independent impacts), additive (i.e., their joint impact is equal to the sum of their independent impacts), and antagonistic effects (i.e., their joint impact is less than the sum of their independent impacts; Ban et al., 2014). Synergistic effects are the dominant type of interaction between stressors. Often the presence of one stressor, such as decreased water quality, makes a reef less resilient to other stressors (Burke et al., 2011). For instance, if coral health is degraded by nutrient-rich water, then the reef may be more susceptible to disease or bleaching.

Stressors that have the greatest influence on other stressors are temperature, storms, and sedimentation (Ban et al., 2014). This is concerning because almost every reef in the world is experiencing increased water temperature due to climate change. Increased temperature can also cause increased storm frequency. Storms cause physical damage to reefs, but may also dampen coral bleaching intensity by decreasing water temperature and solar irradiance. Similarly, sedimentation heightens the impacts of nutrient loading, pollution, and disease on corals, but can lessen the impacts of irradiance and ultraviolet exposure by reducing water clarity and shading corals.

Emerging stressors

There are several emerging anthropogenic stressors that scientists expect will further influence coral reef ecosystems and their ability to provide services, despite these being newer areas of research. Two emerging stressors likely having significant effects on coral reef ecosystems are plastic pollution and endocrine disruptors (pollutants that mimic naturally occurring hormones). For instance, an initial study of plastic pollution found that contact with plastics significantly increased coral disease and mortality rates (Lamb et al., 2018). Additionally, research indicates that more than 900 marine species have been negatively affected by marine plastic pollution, suggesting major impacts to reef ecosystem functioning (Kühn et al., 2015).

Endocrine disruptors are introduced to marine ecosystems via agricultural runoff, sewage outflows, and vessel pollution (e.g., anti-fouling agents). Endocrine disruptors such as pesticides and steroids have been shown to mimic estrogen, testosterone, and other natural hormones, leading to reduced reproductive success, altered sex ratios, delayed maturation, and altered hormone levels. This is best documented in marine invertebrates (Fernandez, 2019). Though the ecosystem-level effects of these stressors have not yet been well documented, their extensive impacts on marine organisms suggest that more research is necessary. With increased levels of human activity in the coastal zone for the foreseeable future, reefs will likely continue to be subjected to novel human disturbances.

The future of coral reef ecosystem services

Due to the imperiled status of coral reef ecosystems, ES tied to coral reefs face particular risk. As global temperatures continue to climb, climate change and ocean acidification will be especially harmful for reef systems. Around the world, population trends and percent area coverage of most known coral species are declining (Hughes et al., 2003; Carpenter et al., 2008). While many reefs will have the capacity to adapt to shifting oceanic conditions, the likelihood of continued ecosystem functioning will be diminished as anthropogenic stressors become more severe and numerous. Future reefs, both new and degraded, will be unable to sustain current levels of services, potentially causing both local and global socio-economic disruptions (Rogers et al., 2015). As the effects of climate change increase, there is evidence to suggest poleward shifts in both coral species and other marine organisms (Weatherdon et al., 2016). As a result, tropical regions that currently depend heavily on ES provided by reefs may experience both cultural and economic upheavals. For coastal communities to develop more effective decision-support tools to help mitigate these risks, future research must quantify the impact of specific anthropogenic stressors on reef ES. This will require a more complete framework for estimating the value of the various ecosystem services provided by reefs, how values will change given different levels and types of human disturbance, and which services may be the most impacted by specific human activities.

Major ecosystem service shifts

As the rate of climate change and other anthropogenic disturbances continue to increase, it is likely that many of the services provided by reefs will face accelerated declines. The localized services most likely to experience major shifts in their capacity to benefit communities and nations are tourism, fisheries, and aquaculture. Additionally, at a global level, reefs will be increasingly compromised in their ability to secrete and maintain the carbonate structures required to form and repair reefs, further exacerbating the negative effects of greenhouse gas emissions (Rogers et al., 2015).

As reef ecosystem health is diminished, there will be a significant decrease in the level of biological diversity that these systems can support, particularly for larger organisms (e.g., sharks, sea turtles) which are more reliant on larger areas of intact reef structures. Compromised reefs have a reduced capacity to be sources of refuge, food, and breeding grounds for a variety of marine organisms, potentially impacting food webs beyond the edges of the reef itself. As climate change increases, the rate of ocean acidification and coral bleaching events will also accelerate, impacting the survival rate of other calcifiers on reefs beyond reef-building corals. This may cause many species to adapt to changing environmental conditions by exhibiting drastic shifts in their ranges due to declines in living coral cover. Major shifts in economically valuable species could be problematic for fisheries and aquaculture industries, particularly for smaller, more localized operations. This will be further exacerbated by the degradation of other habitats that are ecologically connected with reefs. For example, mangrove forests provide vital nursery habitat to many important reef species and are particularly sensitive to impacts from temperature and CO_2 changes. The loss of coral will also leave mangrove habitat even more vulnerable to sea level rise and storm damage, further threatening coastlines and their associated human communities.

Coral reefs also attract large numbers of tourists and any reduction in the extent of reef habitat will almost certainly have serious socio-economic consequences. A shift in the quality and quantity of reef biodiversity will likely result in changes in tourists' preferences and potential abandonment of previously popular attractions. Hotspots for marine tourism are likely to mimic shifts in marine biodiversity, as species' ranges are forced to adapt to climate change (Weatherdon et al., 2016). Marine-based tourism may no longer be a viable industry in many regions where reef loss results in a severe reduction in biodiversity. This would be especially problematic in countries where tourism functions as a major component of local or national economies. Most of the value that reef habitat generates through tourism is a result of the recreational, spiritual, and or esthetic values associated with coral reefs, all of which are directly linked to biodiversity and structural complexity (Rogers et al., 2015; Fig. 1).

Provisioning services such as biochemical pharmaceuticals, genetic resources, and the trade in marine ornamentals (species for the aquarium, jewelry, and curios trades) will also be directly impacted by reef loss. However, the magnitude of change in these services and the full extent of associated impacts to local human communities remains unknown. Low-value species and functional groups (plankton-eating and detritus-eating invertebrates and fishes) may increase in value following major ecological shifts that reduce more commercially desirable species, especially within reefs with low biological diversity and structural complexity (Rogers et al., 2015). The trajectories of such value changes require further research to ensure sustainable management and service use into the future.

Regulating services including water filtration, shoreline protection, and nutrient and carbon cycling are also expected to change as reefs are further degraded by local and global human stressors. As coral species lose their ability to successfully reproduce and grow new colonies, photosynthetic organisms such as benthic algae and seagrasses, as well as sponges, are taking their place and altering the nutrient and carbon dynamics on reefs (Rogers et al., 2015). Future ecosystem transitions are possible given the ability of marine algae and seagrasses to withstand increasingly acidic conditions and the ability of sponges to withstand high-nutrient conditions (Weatherdon et al., 2016). Although collapsed reefs leave behind calcium carbonate skeletal structures which can provide a diminished level of storm mitigation for coasts and shelter for marine species while still intact, these structures will eventually give way due to physical and biological erosion and will not regenerate in the absence of living coral.

Regions at risk

It is important to note that not all regions of the world will experience the same decline in reef ecosystem service benefits as the distribution of coral reefs continues to shift. Most reef systems occur in tropical waters, therefore any reduction in the capacity of reefs to provide essential services will have the highest impact within low-latitude nations. As species' ranges shift toward warming waters in higher latitudes, equatorial nations will likely see a reduction in the number of resident marine species, whereas other nations could see an increase (Weatherdon et al., 2016).

The net revenue of reef fisheries is expected to decrease globally, but more so in the tropics than elsewhere (Weatherdon et al., 2016). These regions house shallow tropical water and coastal mangrove habitats which provide important nursery habitat for many fish species. Mangrove habitats are predicted to experience a poleward habitat shift in response to higher global temperatures, though southern and eastward expansions have also been observed. Mangrove loss will impact reef biodiversity and population levels, as many key reef species use mangroves as nursery habitat, thereby impacting the number of fish available for harvest by fisheries.

Reductions in reef fisheries yields will be especially harmful for small islands, indigenous communities, and Southeast Asian countries, which are all expected to experience severe food insecurity due to reduced nutritional access (Weatherdon et al., 2016). Indigenous communities, which often maintain traditional fishing practices of spiritual and cultural significance, already face restricted access to marine resources likely to become less accessible with reduced coral cover. Small island communities are expected to show the earliest signs of large-scale socioeconomic impacts of reef declines due to their heavy dependence on marine services such as fisheries and tourism (Weatherdon et al., 2016).

Management interventions for maintaining reef ecosystem services

Strategies for managing anthropogenic impacts to coral reef ecosystems are primarily focused on restricting the harvest of reef organisms and the input of land-based sediments and pollutants. The primary regulatory approaches for coral reef fisheries include management controls in the form of seasonal fisheries closures, creation of marine protected areas, establishment of catch quotas, delineation of access rights, and restrictions on highly efficient or damaging gear (Friedlander, 2015). However, due to the lack of scientific information and fisheries management infrastructure in many reef-bearing countries, and the high reliance of local communities on reef species for food security, regulatory approaches are typically more difficult to implement and enforce for coral reef fisheries (Friedlander, 2015). Nevertheless, additional interventions are urgently needed to improve the sustainability of coral reef fisheries: over three-quarters of reef fisheries are currently being fished at unsustainable levels (MacNeil et al., 2015) and fishing has been identified as a major threat to coral reef ecosystem resilience and ES provisioning (Burke et al., 2011). The sustainability of reef fisheries is further threatened by projected increased demand, coastal development and ocean pollution, invasive species, and the mass die-off of reef-building corals due to local human stressors and climate change (Carpenter et al., 2008; Friedlander, 2015).

Although the major role of land-based pollution in coral loss is increasingly being recognized, it largely remains unmanaged (Richmond et al., 2007). This management gap stems from a lack of policies and practices to account for and mitigate the downstream effects of coastal land use (e.g., farming of plants and livestock, urban and industrial development) on coral reef ecosystems. As land-based sediments and pollutants have been shown to weaken coral resilience to climate change (Kroon et al., 2014), the mitigation of these impacts is critical for coral reef persistence.

To maintain the variety of ecosystem services provided by coral reefs, there is a clear need for management strategies that promote reef ecosystem resilience to local and global human impacts. It is critical that these strategies account for the full range of human activities affecting reefs, the synergistic effects of multiple stressors, the projected increase in global and regional (e.g., climate change, plastic pollution, and invasive species) as well as local (e.g., fishing and land clearing) human impacts, and the characteristics and feedbacks of coupled social-ecological coral reef systems. Promising strategies are outlined below and summarized in Fig. 1.

Fishing

To maintain the ecosystem functioning and service provisioning of reefs, the most successful fisheries management strategies will be those that are ecosystem-based (i.e., consider the interdependency of reef organisms) and optimize reef resilience (i.e., encourage reef ecosystems to maintain the same structure despite environmental perturbations) (Moberg and Folke, 1999). For example, restrictions on the take (or harvesting) of ecologically important herbivorous fishes (e.g., parrotfishes) can facilitate higher rates of coral recovery from bleaching due to climate change (Steneck et al., 2019). Fishing regulations that recognize traditional management practices and are tailored to the realities of most coral reef social-ecological systems (e.g., weak fisheries governance, monitoring, and enforcement, strong cultural attachment to reef fishing, and high dependence on reefs for food security and livelihoods) will have the greatest chance of success. In places with a recent history of customary governance, traditional approaches such as Customary Marine Tenure, co-management or participatory management, and community- based individual transferable quotas have shown promise (Cramer and Kittinger, 2021). In contrast to catch restrictions, restrictions on highly efficient or damaging gear (including cyanide, dynamite, SCUBA, gillnets, traps) may be more socially acceptable and relatively easier to implement and enforce (Cramer and Kittinger, 2021).

For intensive, high-value, export-oriented coral reef fisheries that have inherently unsustainable elements such as the live reef food fish, aquarium, and dried sea cucumber (*beche-de-mer*) trades, trade policies such as moratoria on commercial sale, export limits or bans, import bans, and tariffs are most appropriate due to the threatened status of fished species and the relatively greater management and governance focus placed on these fisheries (Cramer and Kittinger, 2021). However, because many reef fishers are reliant on fishing as their sole source of income, the restriction or banning of one fishing activity may result in shifts to unsustainable or illegal fishing on other reef resources (Cramer and Kittinger, 2021). Therefore, while export restrictions may allow for the recovery of one reef resource, these actions can increase pressure on other reef resources if not carefully designed and implemented.

'Climate-ready' Marine Protected Areas (MPAs) address local human stressors and climate change impacts and also hold promise for sustaining reef ecosystem service provisioning. Design principles for climate- ready MPAs include: (1) protecting key areas (e.g., climate refugia, fish spawning aggregations, and resilient regions with high fish biomass/low siltation stress), (2) protecting degraded reefs in addition to healthy reefs as reef degradation becomes more widespread, and (3) creating networks of ecologically-connected MPAs at a seascape scale to facilitate dispersal and settlement of fishes and corals and account for climate-related species migrations (Harvey et al., 2018). Finally, to increase the chances of enforcement and compliance, climate-ready MPAs should be planned, designed, and implemented via participatory processes to involve local stakeholders (Harvey et al., 2018).

Because coral reef environments are characterized by low primary productivity, tightly integrated ecosystem components, and species with irregular and slow recruitment, coral reef fisheries are easily overexploited (Birkeland, 2017). To account for this reality and the projected impacts to reefs from increased human populations and climate change, several countries are implementing policies to shift consumption from reef species to more productive pelagic fish stocks (Birkeland, 2017). The expansion of this policy to additional reef-bearing countries could help maintain reef ecosystem functioning and local food security in the face of climate impacts.

Market-based interventions, which include a variety of approaches focused on generating incentives along the seafood supply chain that favor sustainability, are increasingly utilized in non-reef fisheries and hold promise for increasing the sustainability of some coral reef fisheries. Appropriate interventions that could be applied to a subset of reef fisheries include eco-certification schemes (particularly appropriate for invasive species such as lionfish in the Caribbean), fisheries improvement projects, seafood ratings systems, and consumer awareness campaigns. In addition, fisher empowerment efforts such as measures that provide access to real-time market information, training in improved handling and processing methods, and facilitate formation of direct marketing ventures have the potential to improve fisher incomes and reduce the economic imperative to overfish (Cramer and Kittinger, 2021).

Coastal development and pollution

Because coral reef ecosystem service provisioning is directly tied to the health of reef habitat (i.e., reef-building corals), it is imperative to decrease the input of land-based sediments, nutrients, and other pollutants that threaten coral survival. Strategies for mitigating land-based runoff include coastal and marine spatial planning, designating reef water quality targets, and defining and implementing best practices for coastal watershed management. Coastal and marine spatial planning involves the explicit zoning of various uses of a coastal area with the overarching goals of maintaining ecosystem processes, biological diversity, and multiple uses that support human well-being. Effective spatial planning requires regulatory frameworks that (1) integrate the management bodies responsible for the uses of various coastal resources and habitats and (2) account for the hydrological connectivity between land and sea in coastal zones (Richmond et al., 2007). Unfortunately, effective coastal spatial planning has not been implemented in most of the tropical coastal zones that house coral reefs.

To protect the integrity of reef habitats and ecosystem services, it is critical to increase the number of reef regions incorporating integrated watershed management practices into coastal planning frameworks. Templates for success include the "ridge-to-reef" indigenous watershed management practices used within many Pacific Island Nations. These recognize the potential impact of land use on marine coastal habitats and have effectively protected corals from siltation and land-based pollution (Richmond et al., 2007). Additional locations can, and should, adopt these practices via efforts to (1) empower community-based conservation,

(2) enact regulations that set water quality targets for reefs, (3) manage point sources of pollution such as wastewater treatment plans, mines, and livestock farming, (4) provide financial incentives to induce landowners and municipalities to adopt soil conservation and other sustainable land-use practices, (5) implement control measures for the application of agrochemicals and other pollutants, (6) restore wetlands that enhance sediment and nutrient retention, (7) reduce government subsidies for agrochemicals and other pollutants, (8) establish terrestrial protected areas in tandem with MPAs to create effective coastal resource protection areas, and (9) establish long-term monitoring programs to ascertain the ecological impacts of management changes (Richmond et al., 2007; Kroon et al., 2014).

Promising strategies for reducing the input of plastic pollution to reefs include a combination of approaches applicable to fisheries and coastal land management such as (1) improving waste management infrastructure, (2) a binding international agreement that requires countries to regulate, reduce, and monitor plastic waste via implementation of comprehensive national programs, (3) enforcing existing international law to strengthen management of plastic and other pollution from fishing vessels, and (4) market based interventions including taxes/levies on waste sent to landfills, trade restrictions, bans, and fees on single use plastics, consumer awareness campaigns, and ecolabelling schemes for biodegradable packaging (Kühn et al., 2015; Lamb et al., 2018).

Emerging interventions

As coral mortality rates continue to increase, efforts within the academic, conservation, non-profit, and private sectors are shifting toward more active interventions to conserve reef habitats. These efforts include coral restoration efforts such as direct transplantation of coral fragments from a donor reef to a recipient reef (often to offset planned construction activities), coral gardening (coral fragments are raised in intermediate nurseries and then placed in reef habitat), creation of artificial reefs to increase coral habitat (often in areas destroyed by destructive fishing techniques), and seeding reefs with coral embryos and larvae (created from coral gametes collected from reefs then fertilized in holding tanks on-reef or in aquaria before being released back on to reefs). Future restoration efforts may also involve assisted evolution (selecting for resilient coral genotypes by crossing gametes from coral colonies that are resistant to bleaching, for example) and possibly the design of novel genotypes via gene editing. The potential for meaningful ecological improvement and the myriad ethical issues surrounding these interventions are being actively debated within the scientific community (Boström-Einarsson et al., 2020).

Conclusion

The ecological importance of coral reefs has been widely recognized (Burke et al., 2011), but the full value of coral reefs to humans is less documented. Here, we provide a general framework for describing the various ecosystem service values of coral reefs. Our review of the present status and future of reef ecosystem services provides a departure point to devising policy and management interventions for maintaining these essential services for years to come. Considering this plurality of values - not only for nature, but also for people - is essential to a future that includes coral reefs.

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