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Marine reserves can mitigate and promote adaptation to climate change

(Short title) **Marine reserves and climate change**

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Abstract

Strong decreases in greenhouse gas emissions are required to meet the reduction trajectory resolved within the 2015 Paris Agreement. However, even this will not avert serious stress and damage to life on Earth and additional steps are needed to boost the resilience of ecosystems, safeguard their wildlife and protect their capacity to supply vital goods and services. We discuss how well-managed marine reserves may help marine ecosystems and people adapt to five prominent impacts of climate change: acidification, sea-level rise, intensification of storms, shifts in species distribution, and decreased productivity and oxygen availability, as well as their cumulative effects. We explore their role in mitigating climate change by promoting carbon sequestration and storage and by buffering against uncertainty in management, environmental fluctuations, directional change and extreme events. While highlighting both strengths and limitations, we conclude that marine reserves are a viable low-tech, cost-effective adaptation strategy that would yield multiple co-benefits from local to global scales, improving the outlook for the environment and people into the future.

Keywords

Ecological insurance; marine protected areas; nature-based solution; ocean acidification; social-ecological resilience

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Introduction

It is abundantly clear from successive Intergovernmental Panel on Climate Change (IPCC) reports that the impacts of greenhouse gas emissions on the planet are accelerating (1). Even the most extreme emissions reduction trajectory resolved within the Paris Agreement (Article 2) (2), to limit warming to 1.5^{o}C by 2100, will not avert serious stress and damage to life on Earth (3). Most scientific projections indicate that impacts will continue to intensify for at least another half century before the effects of emissions reductions may begin to be felt (4). This in turn will have significant consequences for wildlife (5, 6) and put many of the benefits people receive from the environment at risk (7) with substantial repercussions for human health and well-being (8). In addition to aggressively reducing greenhouse gas emissions, urgent steps are therefore needed to boost the resilience of ecosystems, safeguard their wildlife and protect their capacity to supply vital goods and services. Yet there is still serious underinvestment in environmental protection (9).

One of the most practical and cost-effective strategies in ocean conservation is the creation of marine protected areas (MPAs). MPAs were originally conceived as a nature-based tool for repairing damage to overexploited fish stocks and habitats, and for conserving biodiversity. Several decades of place-based research and meta-analyses reveal that MPAs indeed serve these purposes (e.g. 10, 11) although benefits are highly contingent on effective implementation and management (10). One key determinant is the level of protection given. Fully protected areas closed to all other extractive uses, and strongly protected areas that are closed to all but limited, low impact fishing methods, hereafter referred to as marine reserves, produce the greatest conservation benefits (10, 12). Only recently, however, has there been interest in understanding the role that MPAs may also play in mitigating and adapting to the impacts of climate change. Most literature on this topic focusses on: (1) identifying putative climate change refuges, where ecosystems may be less affected and, by inference, MPAs may be more successful in maintaining present habitats and biodiversity (e.g. 13), (2) describing how existing MPAs perform under climate-related environmental stresses (e.g. 14), and (3) based on trajectories of environmental change, exploring how protected area networks may be designed to best accommodate the effects of climate change, i.e. how they can continue baseline functioning (e.g. 15). Here we consider how the act of protection itself may enhance the biological processes that underpin adaptation and resilience, both for the benefit of the protected ecosystem and for the people that depend on it. We also consider how development of extensive MPA networks can help mitigate climate change, through multiplication of biological responses to protection.

Coastal nations have committed to protecting 10% of their waters by 2020 under the Convention on Biological Diversity and Sustainable Development Goal 14, but at the present rate, most will fall short of this target (16). As of 2015, only 3.5% of the oceans were afforded or promised some protection with 1.6% strongly or fully protected (12) although recent designations and promises for protection have increased this. Nonetheless, if protection is either weak or not enforced, the expected benefits will be fewer or may not materialise (10). Recent research also suggests the target should be raised to at least 30% coverage for MPAs to safeguard marine ecosystems in the long-term (17). There is therefore an opportunity to accelerate implementation of effective MPAs as part of an integrated climate change mitigation and adaptation strategy, essentially aligning UN targets for biodiversity protection and emissions reduction.

Any discussion about the future application and expanded value of MPAs must be had recognising the rich, constructive, and fast growing literature examining the weaknesses and limitations of MPAs. These dialogues have gone so far as to ask whether even the best MPAs can deliver benefits under climate change, or whether they are a distraction and managers should concentrate instead on promoting human adaptation to rapidly changing conditions. There is considerable disquiet in parts of the scientific community on this point. Potential shortcomings of MPAs include, prominently, lack of staff, equipment and funding (18), inadequate consultation with and support from local communities (19), concerns about managing displaced fishing effort if it occurs (20), and insufficiencies in management scope (21). Such limitations are real and need to be acknowledged by managers contemplating use of MPAs. However, there is also a counterbalancing literature that explores approaches to increase success, as these are all soluble problems (e.g. 22, 23). For MPAs to be an effective tool to address the impacts of climate change, it is clear we must get better at consistently creating effective, well-managed, socially conscious, and sustainably resourced sites.

Marine managers and scientists have also opened a healthy dialogue pointing out that MPAs alone cannot meet global targets for marine biodiversity management and that sound fisheries management practices will also be required in the 70-90% of ocean that is likely to remain open to fishing in the medium term (20). As anthropogenic stresses increase, such portfolio approaches to management are prudent. Questions have also been raised as to whether there are limitations as to which marine systems MPAs can best serve. Tropical coral reefs, for example, are one of the most climate vulnerable ecosystems on the planet due to the extreme sensitivity of the coral-zooxanthellae symbiosis (6, 24). Corals inside marine reserves have received scant protection from extreme seawater-warming events (25, 26). Even for coral reefs, however, there is substantial evidence that protection, such as from fishing or in the form of nutrient pollution reduction, can decrease warming sensitivity of corals (27), facilitate recovery following climate-related disturbance such as floods or bleaching (28-30), and promote larger fish stocks that can help sustain fisheries as conditions change (10, 11). In the case of vulnerable seagrass meadows, such as the Mediterranean *Posidonia oceanica*, which are projected to decline with warming (31), protection from anthropogenic pressures such as anchoring disturbance and nutrient inputs should slow decline (32). It is likely however, that only climate change mitigation consistent with the more ambitious goals of the Paris agreement will safeguard this key habitat-forming species (31).

While maintaining a constructive and clear view of these limitations to MPAs, in the remainder of this paper, we explore the potential strengths and weaknesses of well-managed marine reserves in climate change adaptation and mitigation based on documented responses of marine ecosystems to protection. We also examine how such values may influence the well-being of coastal human populations. We divide our discussion into two major parts: 1) an examination of the role of marine reserves in helping marine ecosystems and people adapt to five key predicted impacts of climate change: acidification, sea-level rise, intensification of storms, shifts in species distribution, and decreased productivity and oxygen availability, as well as the cumulative effects of these stressors, and 2) an evaluation of how marine reserves may help reduce or slow (mitigate) the advance of climate change by promoting carbon sequestration and storage and acting as an insurance policy against climate change (Fig. 1). Finally, we briefly discuss marine reserve size and coverage, and the broader context of marine management.

Climate change adaptation

Acidification

Oceans have absorbed approximately one-third of human CO_2 emissions (1), with the result that surface layers have become 26% more acidic, on average, since pre-industrial times (5). Acidity is expected to increase by 100% or more by 2100 under a business-as-usual scenario (5). Experimental, theoretical and geological evidence indicates that acidification is a major threat to marine ecosystems (32, 33). Field evidence for changes in calcification as a result of acidification is still limited but variable responses are likely as a result of interactions between temperature and acidification (34). Nonetheless, declines have been measured in planktonic and reef-building taxa such as molluscs, coccolithophores, corals and some calcareous algae (35).

Coastal wetlands (mangroves, seagrasses, salt marshes) contain marine plants with high photosynthetic rates which engineer localised reductions in CO_2 concentrations, thereby raising pH and offering daytime refugia to vulnerable calcifying organisms (e.g. 36, 37). These ecosystems are highly threatened and have undergone rapid losses (38). Wetland protection is a major aim of many marine reserves and their establishment has gone a long way to protect these systems from human activities such as coastal development or conversion to aquaculture (e.g. 39).

Marine reserves can also help rebuild to high abundance teleost fish populations that play a significant role in the marine inorganic carbon cycle. Teleost fish drink seawater for osmoregulation and precipitate almost all the ingested calcium, and some ingested magnesium, as carbonate minerals in their alkaline intestine, excreting 'high magnesium calcite' crystals from their gut (40). Such fish carbonates dissolve at shallower depths than calcite and aragonite produced by marine calcifiers like coccolithophores, foraminifera and corals (41). Near-surface dissolution of fish carbonates raises alkalinity

$$CaCO_3 + CO_2 + H_2O \Leftrightarrow 2HCO_3^- + Ca^{2+} \qquad (1)$$

and has a more immediate impact on surface pH and buffering of seawater than calcite or aragonite. The accumulation of high magnesium calcite in shelf sediments (of which a large proportion derives from fish [e.g. 42]) could act as a 'first line of defence' to the reduced saturation state caused by acidification (43).

Mesopelagic fish are the most abundant vertebrates on Earth (44) and play a significant role in the active flux of organic carbon from the ocean surface to the deep-sea (45, 46). Their large, daily vertical migrations provide a potentially important scenario, whereby their gut carbonates are mainly produced during their time at greater depths, but may be primarily released near the surface. Here, their rapid dissolution would therefore contribute to the net removal of CO_2 from, and addition of HCO_3^- to, the surface ocean (equation 1). We speculate that mesopelagic fish could drive an 'upward alkalinity pump' which is currently acting to counter surface ocean acidification. With dwindling stocks of more accessible fish, there is increased interest in fishing mesopelagic species (45), which could have significant ecological and biogeochemical effects. Open-ocean marine reserves, including on the high seas, will help maintain this large migratory fish biomass and facilitate their continued role in biogeochemical cycles.

Sea-level rise

Thermal expansion, increased meltwater and discharged ice from terrestrial ice caps have increased ocean volume and sea-level (6). Average global sea level has risen by 19 cm since 1900, and the IPCC predicts further rises of up to 82 cm by 2100 (5) with multiple associated impacts on coastal people (47).

Intact coastal wetlands, mudflats and biogenic reefs offer protection against rises in sea-level (38), leading to increasing momentum for ecosystem-based adaptation to safeguard people, infrastructure and property against adverse climate change impacts (e.g. 48). Marine reserves protect these ecosystems from threats such as overharvesting, dredging, and coastal development helping safeguard their function as coastal defences. These habitats have the added advantage over engineered coastal defences in that they increase in elevation over time and may 'keep pace' with predicted sea-level rise (49-51). Their ability to offer long-term, dynamic protection to vulnerable coastal communities, is dependent on an adequate supply of sediment from either land-derived sources or in-situ carbonate production (e.g. 38, 52), and landward migration not constrained by steep topography or human infrastructure such as seawalls (51).

Intensification of storms

Warmer oceans will drive more intense storm systems (53) and extend their latitudinal range (54). Well-protected coastal ecosystems reduce risks from storms and coastal flooding (38). Large wetland habitats with dense and productive vegetation attenuate wave energy, stabilise shorelines and accrete sediment more effectively than degraded or fragmented wetlands (e.g. 55). Marine reserves can reduce loss, damage and degradation, thereby promoting more intact habitats that offer coastal defence (40), recover after extreme events (e.g. 50, 56, 57) and enhance human livelihoods (e.g. 58). Large-scale habitat restoration efforts around the world are ongoing, often prompted by a disaster, such as the 2004 Indian Ocean tsunami or Typhoon Haiyan in the Philippines in 2013, for which impacts could have been lessened if wetlands and biogenic reefs had not been cleared or degraded (61). The protection of coastal habitats in marine reserves often offers a more cost-effective solution than habitat restoration or engineering solutions (50).

Shifts in species distribution

Climate change is expected to create a global diaspora of wildlife. Uneven and more intense heating and changes in the salinity of polar oceans due to ice melt will affect ocean currents (6) and influence the distribution of taxa and marine ecosystems (34, 60). Redistribution of species towards more temperate waters ('tropicalization') may reduce diversity in tropical and sub-tropical regions (61). Average measured expansions of the leading edge of the distributions of marine organisms are 72.0 ± 13.5 km per decade, generally towards polar regions (60). Phytoplankton communities are also changing in response to warming, acidifying and stratifying ocean conditions (62).

Regionally networked marine reserves can provide stepping stones for dispersal and safe 'landing zones' for colonising species (63), and possible refugia for those unable to move (64, 65). For example, the Papahānaumokuākea Marine National Monument in the Pacific covers the northwest Hawaiian Islands and represents a strategic refuge for coral reef ecosystems that may be forced poleward, as constraints on migration such as acidification, availability of suitable bottom habitat, and dispersal are few here (66). By increasing reproductive output (67), marine reserves increase ecologically meaningful dispersal distances improving population connectivity (68, 69), while reducing risks of population extirpation and increasing resilience to stress (15), as well as supporting populations outside reserve boundaries (70). Reserves also promote genetic diversity by increasing population sizes and broadening the selective environment (e.g. 71), thereby promoting adaptability and resilience (72-75). The question of how best to design reserve networks to accommodate shifting species ranges and connectivity patterns under climate change is currently uncertain and an area of active research (15, 64, 65).

Decreased productivity and oxygen availability

The average temperature of the surface ocean increased by 0.9°C between 1901 and 2012 (1). Metabolic rates and photosynthesis are strongly influenced by temperature and warmer oceans are likely to affect processes such as predator-prey interactions and reduce the ratio of plant to animal biomass (6), with substantial implications for food web dynamics (76). Surface warming increases stratification and can reduce mixing, nutrient availability and primary production (6). Effects are already visible in the Pacific and Atlantic where nutrient-poor 'ocean deserts' increased in extent by 15% between 1998 and 2006 (6). Global ocean primary productivity has decreased by at least 6% since the early 1980s (6). Increasing stratification is expected to decrease oxygen content in the upper ocean and changes consistent with this have been detected (77), with increased incidences of hypoxic and anoxic events and associated mass mortalities (6, 78). An interesting example of the role of marine reserves in buffering this change is seen in Baja California, Mexico which is experiencing more frequent putatively climate-driven hypoxic episodes. Here, the high egg production of larger abalone found inside a marine reserve appears to have permitted faster recovery of protected populations which in turn yielded spillover benefits to regions bordering the reserve (58).

Fisheries productivity is predicted to decline as a result of warming and reduced dissolved oxygen (79), lower surface nutrients and phytoplankton biomass (80), shifts in range and species abundance patterns (61) and acidification (81). These changes may alter developmental times and create mismatches between developmental stages and food sources (82). They may also reduce body size (79) and have already compromised recruitment capacity for a given fish biomass (83).

Humans have already depressed ocean secondary productivity well below its potential by reducing abundances of marine species. Effectively managed marine reserves play well-understood roles in supporting fishery management, rebuilding exploited stocks and degraded habitats, increasing reproduction and facilitating replenishment of fishing grounds (67). By extending population age structures, they reduce the spatial and temporal variability of population replenishment and increase resilience (84). Spillover of juvenile and adult animals emigrating from reserves typically extends for several kilometres (85) while export of eggs and larvae extends tens to more than 100 kilometres (68). Protection of coastal wetland nurseries can facilitate completion of life cycles that require multiple habitats and enhance fisheries (86). These effects can increase food security and prosperity, especially in developing countries (87), and may offset predicted declines in ocean and fisheries productivity (88).

Another relatively unexplored role of fish is in nutrient recycling that is vital in sustaining marine primary productivity. Fish continuously excrete, via their gills, ammonia/ammonium, the most bioavailable forms of nitrogen, at very high rates (e.g. 100-fold greater than benthic bivalves [89]). Overfishing reduced nitrogen recycling by an abundant fish species in the Bahamas (gray snapper, *Lutjanus griseus*) by 4 to 5-fold compared to unfished sites (90). Thus marine reserves could also stimulate primary productivity and therefore CO_2 removal, as an indirect result of boosting nutrient recycling by enhanced fish stocks.

Cumulative effects

Most of the ocean is already experiencing multiple anthropogenic drivers (91), the effects of which can be seen in all ecosystems from coasts to the open ocean and deep-sea (38, 92-95). Organisms and ecosystems already under multiple anthropogenic stresses are more vulnerable to further pressures, including impacts arising from climate change (e.g. 96). By protecting areas from damage and degradation and allowing recovery of ecosystems, marine reserves will help wildlife and coastal societies adapt to climate change by reducing its effects.

The effects of climate change may be additive, antagonistic or synergistic (35, 97), further complicated by interactions with other impacts such as overfishing, habitat modification and eutrophication (14, 98, 99). Marine reserves limit direct anthropogenic stressors enabling species to recover abundance (11), biomass (11), diversity (11), age structure (100) and reproductive output (67), and habitats to recover complexity (101). Larger populations are more resistant to extinction on local, regional and global scales because there is a greater buffer against decline and higher reproductive output, factors that beget resilience (102). Marine reserves enhance the potential of species to respond to both changing conditions and sudden mass mortalities by increasing the chance of survival as a consequence of more diverse populations (105), and by protecting larger, more fecund animals (56, 100) thereby promoting recovery.

By protecting predator populations, marine reserves can, in certain contexts, help prevent disease outbreaks (e.g. 104) and dampen explosive prey growth (e.g. 105). Moreover, by protecting natural habitats which reduce anthropogenic stressors known to affect disease (e.g. healthy mangroves and seagrasses improve water quality and remove nutrients [106]), and by preventing damage to habitats, which reduces susceptibility, marine reserves may also help reduce the extent or severity of disease outbreaks (106, 107). Nonetheless, direct stressors marine reserves cannot alleviate, such as poor water quality, will likely undermine benefits associated with restricting activities that damage habitats (107). This emphasises that MPAs are only one out of several components in the climate-mitigation and adaptation toolkit.

Highly mobile and migratory species can play key functional roles in marine ecosystems, for example through effects on prey populations (see above) and influences on nutrient cycles (e.g. 108). Mobile marine apex predators that increasingly occur in high abundance only within reserves provide links between different ecosystems (e.g. reefs and pelagic systems [109], or shallow reefs to mesophotic reefs [110]) and consequently can increase whole-ecosystem stability (105) – stability that may be critically important in systems stressed by climate change.

Climate change mitigation

Carbon sequestration and storage

The oceans play a fundamental role in climate regulation and have already mitigated the effects of climate change by serving as a major sink for carbon (111). Changes in biogeochemical cycles are expected under climate change, with the likelihood that the carbon capture and storage potential of the oceans may decline (112). Coastal wetlands store organic carbon in underlying sediments for millennia and account for almost 50% of carbon storage in ocean sediments despite occupying only 0.2% of ocean area (38). Holding some of the largest organic carbon stocks in the biosphere (38), even small disturbances can significantly perturb carbon fluxes and vegetation clearance exposes stored carbon to loss (e.g. 113). Furthermore, mangroves, seagrasses and salt marshes often form a spatially-linked continuum of intertidal habitats with unvegetated mudflats and sandbars, habitats that may sequester and store large amounts of organic carbon (e.g. 114). Marine reserves are not the only means to protect these habitats, but they can maintain and enhance these spatially connected ecosystems preventing the release of carbon stored in sediments and perturbations from direct anthropogenic disturbance.

Animals can indirectly mediate biogeochemical processes (115) and consequently protecting animals that play important roles in carbon cycling will become more important. Trophic downgrading (i.e.

removal of predators), which has proceeded rapidly in many regions outside marine reserves, affects carbon uptake, storage and release in vegetated ecosystems because of reduced predation on herbivores leads to large-scale declines in algal communities (116) and even complete habitat loss (117). Restoring predators reduces overgrazing effects on primary productivity (116), thereby potentially benefitting carbon sequestration and storage (115, 118). In this way marine reserves may promote ecosystems that act as more vigorous carbon sinks, despite higher turnover rates for primary production (121).

Although calcification in the guts of teleost fish is a quantitatively important component of the marine inorganic carbon cycle (40, 120) the contribution this makes to long-term removal or addition of atmospheric CO_2, and therefore the potential influence of marine reserves, is currently difficult to ascertain. This is due to lack of information such as (1) the influence of inorganic calcium carbonate on the sinking rate of organic fecal carbon, (2) the rate of separation of inorganic and organic carbon within fecal pellets, (3) the subsequent rates of carbonate dissolution and consumption/respiration of organic fecal carbon, and (4) phase heterogeneity in the type of carbonate produced by fish guts which strongly affects their dissolution (121). However, marine reserves (in concert with other fisheries rebuilding tools) may play an important role in carbon sequestration and storage by rebuilding fish and shellfish populations which then stimulate primary productivity via their role in excreting bioavailable nitrogen. This is an emerging field in need of further research.

Trawling and other mobile fishing gears alter biogeochemical cycles by re-suspending sediments, releasing carbon otherwise buried (122), and shifting the composition of benthic communities, including reduced numbers of suspension feeders (123). In great enough abundance, these animals exert a strong influence on overlying waters, enriching underlying sediments with nutrients and improving light penetration which boosts plant growth and productivity (124). Suspension feeders are also a pathway for the flux of organic carbon from the water column to sea floor (e.g. 125). Protecting against mobile gears will facilitate recovery of these species and could promote carbon uptake by seabed ecosystems as well as prevent further loss of organic carbon stored in sediments. Moreover, while commercial seabed mining, has not yet begun, over 1 million square kilometres of high seas have been included in seabed mining contracts (126). Seabed mining will further remobilize carbon with uncertain consequences for carbon dynamics in the ocean (127). Marine reserves, particularly in the high seas, could become a tool to constructively zone and manage these impacts.

An insurance policy

The trajectories of anthropogenic change in our rapidly shifting oceans and seas are difficult to predict and harder to control. We contend that because marine reserves limit direct pressures, they will give ecological communities the best chance to develop and adapt to changing conditions in ways that maintain ecological function and structure. Complex ecosystems with high abundances and diversity of species promote the processes that govern provision of goods and ecosystem services such as carbon sequestration and storage, coastal defence, food, pollution sinks, and recreational and aesthetic benefits (128, 129), while avoiding regime shifts with severe and unexpected consequences (130). Removing anthropogenic stressors can help recover diversity and ecosystem services (129) and build resilience enabling faster recovery from the effects of climate change (50, 56, 57). For example, evidence from the remote Indian Ocean Chagos Marine Protected Area show that reefs free from many human stresses and disturbance have remarkable recovery capacity. While reefs experienced >90% coral mortality during the 1998 bleaching event, on the whole communities within the marine reserve recovered rapidly with coral cover restored to 1996 levels by 2010, and in 2015 28% higher average carbonate production was recorded in Chagos than in post-disturbance sites across the Caribbean (50); although the fallout from the widespread coral bleaching event in 2016 is yet to be reported. If reserves promote coral recovery they will enhance coastal protection and livelihoods, recreation and tourism potential, and may restore carbon uptake and storage (30, 50). However, as noted earlier, evidence for a beneficial role of reserves in coral protection is equivocal. In some cases corals have fared better inside protected areas compared to outside (29, 101), but in other well-studied cases, protected corals fared as badly or worse during bleaching events, perhaps because communities had a greater fraction of sensitive species (25, 26, 99) or had depressed levels of genetic diversity (74).

Biodiversity and the abundance of life are essential for the provision of ecosystem services and loss of either may erode resilience to future environmental perturbations (131). For example, more diverse reef systems have greater and more stable fish biomass production, and more diverse communities may be less affected by rising and variable temperatures (132). By protecting areas from damage and degradation, marine reserves facilitate habitat recovery, especially of fragile, vulnerable, highly diverse and three dimensionally complex habitats (101). One mechanism is direct protection from mechanical disturbance, such as elimination of bottom trawling, dredging, blast fishing, or conversion to aquaculture. But habitat recovery also occurs through re-establishment of the upper levels of food webs, reversing cascading effects of fishing and transforming one habitat type (e.g. urchin barrens) to another (e.g. kelp forest) (133). On a cautionary note, there is evidence that for some kelp forests, such a beneficial effect may be reversed by warming. In eastern Australia and Japan tropical herbivores like rabbitfish have stripped kelp canopies as they spread to higher latitudes (134), although these patterns may be regional (135). This re-emphasises the general point that rapid warming can override at least some of the effects of marine protection, and that marine reserves are only part of a wider climate mitigation and adaptation strategy. On the other hand, even as conditions and habitats change, marine reserves will continue to relieve anthropogenic stresses and offer a refuge to vulnerable species, whatever they may be.

Extensive marine reserve networks, especially those with very large reserves, may act as wildlife refugia as planetary conditions change, preventing extinctions and forming a basis from which other areas can be recolonised once mechanisms for reduction of human stresses become effective. This role is akin to that played by ice-free Pleistocene refugia during glaciations (136). Furthermore, reserves increase knowledge by providing ecological reference points to better understand the structure and dynamics of marine systems in a rapidly changing world (137), and provide controls to tease apart the often correlated impacts of climate change from those of other anthropogenic stressors.

Size, coverage and management matter

MPAs with five key characteristics (no-take, well-enforced, old (≥10 years), large (≥100 km^2), and isolated) have been shown to produce the greatest conservation benefits (10) and the effectiveness of MPAs in supporting climate change mitigation and adaptation will be contingent, in part, on these factors. However, very large marine reserves will not be appropriate in all instances, for example near coasts populated by those who rely on fishing for subsistence. In such instances, networks of smaller, well-connected reserves will be important to prevent subpopulations from being extirpated and to enable recovery of local populations (64). Such small marine reserves can produce tangible benefits to local people, particularly when combined with other fisheries management tools such as territorial user rights (138, 139) and co-management mechanisms (138, 140), and jointly contribute to climate change adaptation and mitigation.

Many of the benefits we have outlined are delivered locally. Hence, proactive creation of small reserves by local people offers a practical pathway to sustainably manage their natural resources while improving their adaptation potential to climate change, irrespective of global, national or regional targets. Combining such bottom-up approaches within large partially protected MPAs which exclude the most damaging activities and are designed with local communities offers an opportunity to merge local and global benefits. One example is the Palauan National Marine Sanctuary which is designed to help ensure local food security as ecosystems adapt to climate change, while meeting global marine conservation goals and supporting large-scale efforts to mitigate climate change. To scale up effects to achieve regional and global impacts, such approaches need encouragement and support from governments and development agencies, using appropriate legal, financial and social incentives, and should be considered part of national and international climate change adaptation and mitigation commitments.

Establishing well-managed marine reserves removes direct anthropogenic disturbances within their boundaries, but cannot protect them from all sources of harm, including those posed by warming and acidifying waters. We have made a case for how protection could enhance the biological processes that bolster resilience to the effects of greenhouse gas emissions. However, the oceans form an ecologically connected continuum of ecosystems. Negative effects experienced in surrounding waters will also affect protected ecosystems. Effective management in the matrix surrounding marine reserves will be required using both traditional forms of fisheries management such as effort limitation and ancillary conservation initiatives (20, 138, 139), ideally implemented in a co-management framework (141). On the balance of the evidence presented here, we think marine reserves can provide an essential foundation of the management portfolio, delivering benefits other tools cannot, such as protection for vulnerable species and habitats. They also buffer against uncertainty in fisheries management as well as environmental fluctuations, directional change, and extreme events.

Conclusion

Significant progress has been made in our understanding of the effects of climate change on marine ecosystems and it is clear there is a monumental ecological upheaval underway. There is much still to be learned about the benefits, costs and limits of MPA protection, what complementary management measures are needed, as well as alternative strategies to minimise disruption to ecosystems and human societies from climate change. Marine reserves will not halt change or stop many of the threats associated with climate change affecting communities within their boundaries. We contend, however, that existing and emerging evidence suggest they can serve as a powerful tool to help ameliorate some problems of climate change, slow the development of others, and improve the outlook for continued ecosystem functioning and delivery of ecosystem services. This edge may matter more than ever as the stress that climate change places on marine ecosystems and biodiversity continues to mount.

Marine reserves will also help to insure against inadequate management both in national waters (137, 142) and beyond national jurisdiction (88, 143). They extend the precautionary principle to management and ensure that we do not make scientific advances through the belated realisation of what we have lost. Ultimately, by helping to mitigate and promote adaptation to climate change, reserves would protect the many economic and social benefits we derive from marine ecosystems (144).

Marine reserves are not a substitute for rapid reductions in greenhouse gas emissions, or appropriate land and water management to reduce, for example, nutrient and sediment inputs from coastal catchments. Moreover, some of the benefits marine reserves offer can be achieved through other tools, like fishing effort limitation (20). However, marine reserves offer a relatively simple nature-based solution that bundles a lot of potential benefits**.** Taken across their many dimensions of influence, it is hard to conceive of any circumstances in our fast-changing world where well-designed networks of strongly and fully protected reserves would not lead to a net increase in environmental and human wellbeing, particularly when coupled with effective management of human activities outside reserves. The evidence indicates that their widespread establishment can, in cost-effective fashion (145), help slow climate change, alleviate some of its expected hardships (e.g. reduced food security, sea level rise), reduce biodiversity loss, help safeguard critical ecological processes underpinning the planetary life support system, and improve the outlook for recovery after greenhouse gas emissions have been brought under control. We suggest that further quantification of these effects, and a comprehensive assessment of climate mitigation and adaptation priorities should form a cornerstone in future marine reserve planning.

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Figure Legends

Figure 1. Eight illustrative pathways by which MPAs can mitigate and promote adaptation to the effects of climate change in the oceans.