

# Marine reserves can mitigate and promote adaptation to climate change

Callum M. Roberts<sup>a</sup>, Bethan C. O'Leary<sup>a</sup>, Douglas J. McCauley<sup>b,c</sup>, Philippe Maurice Cury<sup>d</sup>, Carlos M. Duarte<sup>e</sup>, Jane Lubchenco<sup>f</sup>, Daniel Pauly<sup>g</sup>, Andrea Sáenz-Arroyo<sup>h</sup>, Ussif Rashid Sumaila<sup>g</sup>, Rod W. Wilson<sup>i</sup>, Boris Worm<sup>j</sup>, and Juan Carlos Castilla<sup>k,l,m,1</sup>

Edited by B. L. Turner, Arizona State University, Tempe, AZ, and approved May 8, 2017 (received for review January 30, 2017)

**Strong decreases in greenhouse gas emissions are required to meet the reduction trajectory resolved within the 2015 Paris Agreement. However, even these decreases 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 the role of managed ecosystems in mitigating climate change by promoting carbon sequestration and storage and by buffering against uncertainty in management, environmental fluctuations, directional change, and extreme events. We highlight both strengths and limitations and conclude that marine reserves are a viable low-tech, cost-effective adaptation strategy that would yield multiple cobenefits from local to global scales, improving the outlook for the environment and people into the future.**

ecological insurance | marine protected areas | nature-based solution | MPA | global change

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 °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). These intensified impacts, in turn, will have significant consequences for wildlife (5, 6) and will put many of the benefits people receive from the environment at risk (7), with substantial repercussions for human health and well-being (8). Therefore, in addition to reducing greenhouse gas emissions aggressively, urgent steps are needed to boost the resilience of ecosystems, safeguard

their wildlife, and protect their capacity to supply vital goods and services. However, 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 (e.g., refs. 10 and 11) reveal that MPAs indeed serve these purposes, 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

<sup>a</sup>Environment Department, University of York, York, YO10 5NG, United Kingdom; <sup>b</sup>Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, CA 93106; <sup>c</sup>Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA 93106; <sup>d</sup>Research Institute for Development, Club of Associated Research Organizations-Marine Biodiversity, Exploitation, and Ecosystem Modeling, B-1210 Brussels, Belgium; <sup>e</sup>Red Sea Research Center, King Abdullah University of Science and Technology, Thuwal, 23955-6900, Saudi Arabia; <sup>f</sup>Department of Integrative Biology, Oregon State University, Corvallis, OR 97331; <sup>g</sup>Institute for the Oceans and Fisheries, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada; <sup>h</sup>Departamento de Conservación de la Biodiversidad, El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, CP 29290, Mexico; <sup>i</sup>Biosciences, College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4QD, United Kingdom; <sup>j</sup>Biology Department, Dalhousie University, Halifax, NS B3H 4R2, Canada; <sup>k</sup>Núcleo de Conservación Marina, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Alameda Bernardo O'Higgins 340, Santiago 8331150, Chile; <sup>l</sup>LincGlobal Project, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Alameda Bernardo O'Higgins 340, Santiago 8331150, Chile; and <sup>m</sup>Centro de Cambio Global, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Alameda Bernardo O'Higgins 340, Santiago 8331150, Chile  
Author contributions: C.M.R., J.L., U.R.S., and J.C.C. designed research; and C.M.R., B.C.O., D.J.M., P.M.C., C.M.D., J.L., D.P., A.S.-A., U.R.S., R.W.W., B.W., and J.C.C. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

<sup>1</sup>To whom correspondence should be addressed. Email: jcastilla@bio.puc.cl.

as “marine reserves,” produce the greatest conservation benefits (10, 12). Only recently, however, has there been interest in understanding the role that MPAs also may play in mitigating and adapting to the impacts of climate change. Most literature on this topic focuses on (i) 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., ref. 13); (ii) describing how existing MPAs perform under climate-related environmental stresses (e.g., ref. 14); and (iii), based on trajectories of environmental change, exploring how protected area networks may be designed best to accommodate the effects of climate change, i.e., how they can continue baseline functioning (e.g., ref. 15). Here we consider how the act of protection itself may enhance the biological processes that underpin adaptation and resilience, for the benefit of both the protected ecosystem and the people that depend on it. We also consider how the development of extensive MPA networks can help mitigate climate change through the multiplication of biological responses to protection.

Under the Convention on Biological Diversity and Sustainable Development Goal 14, coastal nations have committed to protecting 10% of their waters by 2020, 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 percentage). Nonetheless, if protection is weak or not enforced, the expected benefits will be fewer or may not materialize (10). Recent research also suggests that the target should be raised to at least 30% coverage for MPAs to safeguard marine ecosystems in the long term (17). Therefore there is an opportunity to accelerate the implementation of effective MPAs as part of an integrated strategy of climate change mitigation and adaptation, essentially aligning United Nations targets for biodiversity protection and emissions reduction.

Any discussion about the future application and expanded value of MPAs must recognize 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 instead should concentrate 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 such occurs (20); and insufficiencies in management scope (21). Such limitations are real and need to be acknowledged by managers contemplating the use of MPAs. However, there is also a counterbalancing literature (e.g., refs. 22 and 23) that explores approaches to increase success, because all these problems are all soluble. For MPAs to be an effective tool in addressing 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 also have 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 also have been raised about whether there are limitations in the marine systems that MPAs can best serve. Tropical coral reefs, for example, are

one of the most climate-vulnerable ecosystems on the planet because of 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 (e.g., from fishing or in the form of nutrient pollution reduction) can decrease the sensitivity of corals to warming (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 of 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: (i) 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 (ii) 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.

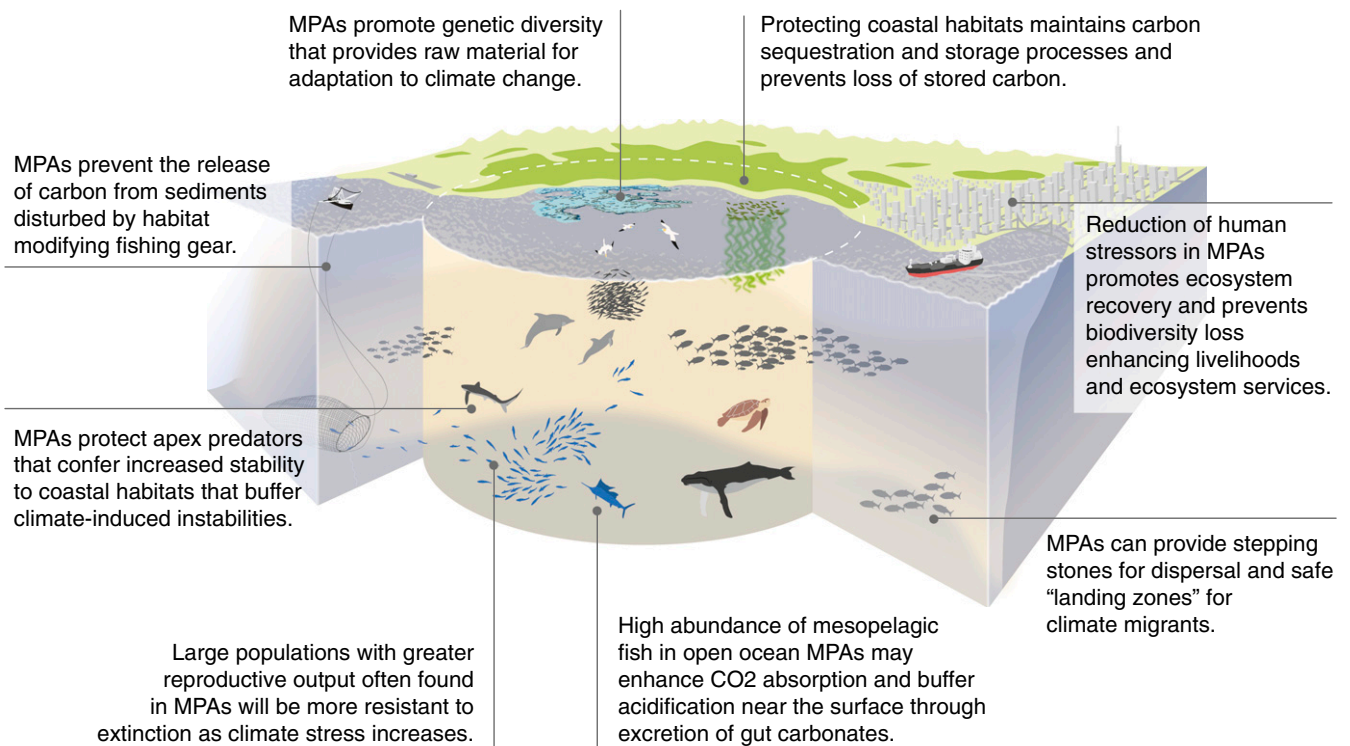
### Climate Change Adaptation

**Acidification.** Oceans have absorbed approximately one-third of human CO<sub>2</sub> emissions (1), with the result that surface layers have become 26% more acidic, on average, since preindustrial 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 localized reductions in CO<sub>2</sub> concentrations, thereby raising pH and offering daytime refugia to vulnerable calcifying organisms (e.g., refs. 36 and 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., ref. 39).

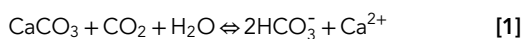
Marine reserves can also help rebuild to high abundance teleost fish populations that play a significant role in the marine inorganic carbon cycle. Teleost fish drink seawater for osmoregulation and precipitate almost all the ingested calcium and some ingested

**Marine Protected Areas** | Help the oceans to mitigate and adapt to climate change by promoting intact and complex ecosystems with high diversity and abundance of species.



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

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 the calcite and aragonite produced by marine calcifiers such as coccolithophores, foraminifera, and corals (41). Near-surface dissolution of fish carbonates raises alkalinity



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 [a large proportion of which derives from fish (e.g., ref. 42)] could act as a first line of defense against 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, vertical daily migrations provide a potentially important scenario in which their gut carbonates are produced mainly during their time at greater depths but may be released primarily near the surface. Their rapid dissolution therefore would contribute to the net removal of CO<sub>2</sub> from and the addition of HCO<sub>3</sub><sup>-</sup> to the surface ocean (Eq. 1). We speculate that mesopelagic fish may drive an upward alkalinity pump that is currently acting to counter surface ocean acidification. With dwindling stocks of more accessible fish, there is increased interest in fishing mesopelagic species (45), and this fishing could have significant ecological and biogeochemical effects. Open-ocean marine reserves, including reserves on the high seas, will

help maintain this large migratory fish biomass and facilitate the continued role of these fish in biogeochemical cycles.

**Sea-Level Rise.** Thermal expansion and increased meltwater and discharged ice from terrestrial ice caps have increased the ocean volume and sea level (6). The 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., ref. 48). Marine reserves protect these ecosystems from threats such as overharvesting, dredging, and coastal development, helping safeguard their function as coastal defenses. These habitats have an added advantage over engineered coastal defenses 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., refs. 38, 52) and on 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 will 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, stabilize shorelines, and accrete

sediment more effectively than degraded or fragmented wetlands (e.g., ref. 55). Marine reserves can reduce loss, damage, and degradation, thereby promoting more intact habitats that offer coastal defense (40), recover after extreme events (e.g., refs. 50, 56, and 57), and enhance human livelihoods (e.g., ref. 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 (59), the impacts of which could have been lessened if wetlands and biogenic reefs had not been cleared or degraded (60). 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 because of ice melt will affect ocean currents (6) and will influence the distribution of taxa and marine ecosystems (34, 61). Redistribution of species toward more temperate waters (“tropicalization”) may reduce diversity in tropical and subtropical regions (60). Average measured expansions of the leading edge of the distributions of marine organisms are  $72.0 \pm 13.5$  km per decade, generally toward the polar regions (61). 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, safe “landing zones” for colonizing 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, because constraints on migration, such as acidification, the 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., ref. 71), thereby promoting adaptability and resilience (72–75). The best way to design reserve networks to accommodate shifting species ranges and connectivity patterns under climate change is currently uncertain and is 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 to 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 the extent of nutrient-poor “ocean deserts” increased 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 effect 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 (60), and acidification (81). These changes may alter developmental times and create mismatches between developmental stages and food sources (82). They also may 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 the 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 kilometers (85), and the export of eggs and larvae extends for tens to more than 100 kilometers (68). Protection of coastal wetland nurseries can facilitate the 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, which 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 four- to fivefold compared with unfished sites (90). Thus, marine reserves could also stimulate primary productivity, and therefore CO<sub>2</sub> 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., ref. 96). By protecting areas from damage and degradation and allowing the 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) and are further complicated by interactions with other impacts such as overfishing, habitat modification, and eutrophication (14, 98, 99). Marine reserves limit direct anthropogenic stressors, thus enabling species to recover abundance (11), biomass (11), diversity (11), age structure (100), and reproductive output (67) and enabling 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 (103, 104) 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., ref. 105) and dampen explosive prey growth (e.g., ref. 104). Moreover, by protecting natural habitats that 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 and thereby reducing susceptibility, marine reserves may also help reduce the extent or severity of disease outbreaks (106, 107). Nonetheless, direct stressors that marine reserves cannot alleviate, such as poor water quality, will likely undermine the benefits associated with restricting activities that damage habitats (107). This limitation emphasizes that MPAs are only one 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., ref. 108). Mobile marine apex predators that increasingly occur in high abundance only within reserves provide links between different ecosystems (e.g., between reefs and pelagic systems [109] or between shallow reefs and mesophotic reefs [110]) and consequently can increase whole-ecosystem stability (104); such stability 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). Because wetlands hold 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., ref. 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., ref. 114). Marine reserves are not the only means of protecting 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); therefore 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 reduced predation on herbivores leads to large-scale declines in algal communities (116) and even to complete habitat loss (117). Restoring predators reduces the effects of overgrazing on primary productivity (116), thereby potentially benefitting carbon sequestration and storage (115, 118, 119). In this way marine reserves may promote ecosystems that act as more vigorous carbon sinks, despite higher turnover rates for primary production (120).

Although calcification in the guts of teleost fish is a quantitatively important component of the marine inorganic carbon cycle (40, 121), the contribution of this calcification to long-term removal or

addition of atmospheric CO<sub>2</sub>, and therefore the potential influence of marine reserves, is currently difficult to ascertain. This difficulty arises from lack of information about factors such as (i) the influence of inorganic calcium carbonate on the sinking rate of organic fecal carbon; (ii) the rate of separation of inorganic and organic carbon within fecal pellets; (iii) the subsequent rates of carbonate dissolution and consumption/respiration of organic fecal carbon; and (iv) phase heterogeneity in the type of carbonate produced by fish guts, which strongly affects their dissolution (120). However, marine reserves (in concert with other fishery-rebuilding tools) may play an important role in carbon sequestration and storage by rebuilding fish and shellfish populations that then stimulate primary productivity via their role in excreting bioavailable nitrogen. This topic is an emerging field in need of further research.

Trawling and other mobile fishing gear alter biogeochemical cycles by resuspending sediments, releasing carbon that is otherwise buried (122), and shifting the composition of benthic communities, including reduced numbers of suspension feeders (123). In sufficient abundance, these animals exert a strong influence on overlying waters, enriching underlying sediments with nutrients and improving light penetration, thereby boosting 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., ref. 125). Protecting against mobile fishing gear will facilitate the 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, although commercial seabed mining has not yet begun, more than 1 million square kilometers 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 zone and manage these impacts constructively.

**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 defense, 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 in the recovery of diversity and ecosystem services (129) and can 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. Although reefs experienced >90% coral mortality during the 1998 bleaching event, communities within the marine reserve recovered rapidly on the whole, with coral cover restored to 1996 levels by 2010, and in 2015 the average carbonate production recorded in Chagos was 28% higher than in post-disturbance sites across the Caribbean (50). (Note, however, that 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 that reserves have a beneficial role in coral protection is

equivocal. In some cases corals have fared better inside than outside protected areas (29, 101), but in other well-studied cases protected corals fared as badly or worse during bleaching events, perhaps because the protected 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 the 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 protective mechanism is direct protection from mechanical disturbance, such as the elimination of bottom trawling, dredging, blast fishing, or conversion to aquaculture. However habitat recovery also occurs through reestablishment 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 such as rabbitfish have stripped kelp canopies as they spread to higher latitudes (134), although these patterns may be regional (135). This adverse effect reemphasizes the general points 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 recolonized once the 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 understand better 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, well-established ( $\geq 10$  y old), large ( $\geq 100$  km<sup>2</sup>), 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 fishery-management tools such as territorial user rights (138, 139) and comanagement mechanisms (138, 140), and can jointly contribute to climate change adaptation and mitigation.

Many of the benefits we have outlined are delivered locally. Hence, the proactive creation of small reserves by local people offers a practical pathway to manage the reserves' natural resources

sustainably while improving their potential adaptation to climate change, irrespective of global, national, or regional targets. Combining such bottom-up approaches within large partially protected MPAs that 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 commitments regarding climate change adaptation and mitigation.

The establishment of 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 fishery management, such as effort limitation, and ancillary conservation initiatives (20, 138, 139), ideally implemented in a comanagement framework (141). In light of the evidence presented here, we think marine reserves can provide an essential foundation of the management portfolio, delivering benefits that other tools cannot, such as protection for vulnerable species and habitats. They also serve as buffers against uncertainty in fishery management, 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 a monumental ecological upheaval is underway. There is much still to be learned about the benefits, costs, and limits of MPA protection, what complementary management measures are needed, and alternative strategies to minimize 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 suggests that MPAs can serve as a powerful tool to help ameliorate some problems resulting from 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 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 realization of what we have lost. Ultimately, by helping 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 for appropriate land and water

management, e.g., to reduce nutrient and sediment inputs from coastal catchments. Moreover, some of the benefits that marine reserves offer can be achieved through other tools, such as fishing effort limitation (20). However, marine reserves offer a relatively simple nature-based solution that bundles many potential benefits. Given their many dimensions of influence, it is hard to conceive of any circumstances in our fast-changing world in which 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 the widespread establishment of MPAs can, in a 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.

### Acknowledgments

We thank Ivan Gromicho, King Abdullah University of Science and Technology, for drawing Fig. 1. We also thank the editors and reviewers for their helpful comments which much improved the manuscript. B.C.O. and C.M.R. are supported by The Pew Charitable Trusts. D.J.M. is supported by the Benioff Ocean Initiative. J.C.C. received support from Project CCM RC 130004 of the Iniciativa Científica Milenio, Ministerio de Economía, Chile. C.M.D. was supported by the Baseline Fund of King Abdullah University of Science and Technology. D.P. receives support from the Paul G. Allen Family Foundation through the Sea Around Us Project of the University of British Columbia. U.R.S. is Project Director of the OceanCanada Partnership, which receives support from the Social Science and Humanities Research Council of Canada. R.W.W. is supported by the Natural Environment Research Council and Biotechnology and Biological Sciences Research Council in the United Kingdom.

- 1 Intergovernmental Panel on Climate Change (2013) Climate change 2013: The physical science basis. *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, eds Stocker TF, et al. (Cambridge Univ Press, Cambridge, UK).
- 2 United Nations Framework Convention on Climate Change (2015) *Adoption of the Paris Agreement. Proposal by the President. UNFCCC. Conference of the Parties (COP)* (United Nations, Geneva).
- 3 Magnan AK, et al. (2016) Implications of the Paris agreement for the ocean. *Nat Clim Chang* 6:732–735.
- 4 Kintisch E (2015) Climate crossroads. *Science* 350:1016–1017.
- 5 Intergovernmental Panel on Climate Change (2014) *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, eds Field CB, et al. (Cambridge Univ Press, Cambridge, UK).
- 6 Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. *Science* 328:1523–1528.
- 7 Rockström J, et al. (2009) Planetary boundaries: Exploring the safe operating space for humanity. *Ecol Soc* 14:32.
- 8 McMichael AJ (2013) Globalization, climate change, and human health. *N Engl J Med* 368:1335–1343.
- 9 Watson JEM, Dudley N, Segan DB, Hockings M (2014) The performance and potential of protected areas. *Nature* 515:67–73.
- 10 Edgar GJ, et al. (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506:216–220.
- 11 Lester SE, et al. (2009) Biological effects within no-take marine reserves: A global synthesis. *Mar Ecol Prog Ser* 384:33–46.
- 12 Lubchenco J, Grorud-Colvert K (2015) OCEAN. Making waves: The science and politics of ocean protection. *Science* 350:382–383.
- 13 Chollett I, Mumby PJ, Cortés J (2010) Upwelling areas do not guarantee refuge for coral reefs in a warming ocean. *Mar Ecol Prog Ser* 416:47–56.
- 14 Darling ES, McClanahan TR, Côte IM (2010) Combined effects of two stressors on Kenyan coral reefs are additive or antagonistic, not synergistic. *Conserv Lett* 3:122–130.
- 15 McLeod E, Salm R, Green A, Almany J (2009) Designing marine protected area networks to address the impacts of climate change. *Front Ecol Environ* 7:362–370.
- 16 Tittensor DP, et al. (2014) A mid-term analysis of progress toward international biodiversity targets. *Science* 346:241–244.
- 17 O'Leary BC, et al. (2016) Effective coverage targets for ocean protection. *Conserv Lett* 9:398–404.
- 18 Gill DA, et al. (2017) Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* 543:665–669.
- 19 McClanahan TR, Marnane MJ, Cinner JE, Kiene WE (2006) A comparison of marine protected areas and alternative approaches to coral-reef management. *Curr Biol* 16:1408–1413.
- 20 Hilborn R (2016) Policy: Marine biodiversity needs more than protection. *Nature* 535:224–226.
- 21 Plumeridge AA, Roberts CM (2017) Conservation targets in marine protected area management suffer from shifting baseline syndrome: A case study on the Dogger Bank. *Mar Pollut Bull* 116:395–404.
- 22 Christie P, White AT (2007) Best practices for improved governance of coral reef marine protected areas. *Coral Reefs* 26:1047–1056.
- 23 Ban NC, et al. (2011) Designing, implementing and managing marine protected areas: Emerging trends and opportunities for coral reef nations. *J Exp Mar Biol Ecol* 408:21–31.
- 24 Hoegh-Guldberg O, et al. (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742.
- 25 Graham NAJ, et al. (2008) Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. *PLoS One* 3:e3039.
- 26 McClanahan TR, Ateweberhan M, Muhando CA, Maina J, Mohammed MS (2007) Effects of climate and seawater temperature variation on coral bleaching and mortality. *Ecol Monogr* 77:503–525.
- 27 Wooldridge SA (2009) Water quality and coral bleaching thresholds: Formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. *Mar Pollut Bull* 58:745–751.
- 28 Olds AD, et al. (2014) Marine reserves help coastal ecosystems cope with extreme weather. *Glob Change Biol* 20:3050–3058.
- 29 Mumby PJ, et al. (2007) Trophic cascade facilitates coral recruitment in a marine reserve. *Proc Natl Acad Sci USA* 104:8362–8367.
- 30 Mumby PJ, Harborne AR (2010) Marine reserves enhance the recovery of corals on Caribbean reefs. *PLoS One* 5:e8657.
- 31 Jordà G, Marbà N, Duarte CM (2012) Mediterranean seagrass vulnerable to regional climate warming. *Nat Clim Chang* 2:821–824.
- 32 Gattuso J-P, et al. (2015) OCEANOGRAPHY. Contrasting futures for ocean and society from different anthropogenic CO<sub>2</sub> emissions scenarios. *Science* 349:aac4722.
- 33 Hönisch B, et al. (2012) The geological record of ocean acidification. *Science* 335:1058–1063.
- 34 Poloczanska ES, et al. (2016) Responses of marine organisms to climate change across oceans. *Front Mater Sci* 3:62.
- 35 Nagelkerken I, Connell SD (2015) Global alteration of ocean ecosystem functioning due to increasing human CO<sub>2</sub> emissions. *Proc Natl Acad Sci USA* 112:13272–13277.
- 36 Unsworth RKF, Collier CJ, Henderson GM, McKenzie LJ (2012) Tropical seagrass meadows modify seawater carbon chemistry: Implications for coral reefs impacted by ocean acidification. *Environ Res Lett* 7:024026.
- 37 Sippo JZ, Maher DT, Tait DR, Holloway C, Santos IR (2016) Are mangroves drivers or buffers of coastal acidification? Insights from alkalinity and dissolved inorganic carbon export estimates across a latitudinal transect. *Global Biogeochem Cycles* 30:753–766.

- 38 Duarte CM, Losada IJ, Hendriks IE, Mazarrasa I, Marbà N (2013) The role of coastal plant communities for climate change mitigation and adaptation. *Nat Clim Chang* 3:961–968.
- 39 Miteva DA, Murray BC, Pattanayak SK (2015) Do protected areas reduce blue carbon emissions? A quasi-experimental evaluation of mangroves in Indonesia. *Ecol Econ* 119:127–135.
- 40 Wilson RW, et al. (2009) Contribution of fish to the marine inorganic carbon cycle. *Science* 323:359–362.
- 41 Woosley RJ, Millero FJ, Grosell M (2012) The solubility of fish-produced high magnesium calcite in seawater. *J Geophys Res* 117:C04018.
- 42 Perry CT, et al. (2011) Fish as major carbonate mud producers and missing components of the tropical carbonate factory. *Proc Natl Acad Sci USA* 108:3865–3869.
- 43 Morse JW, Andersson AJ, Mackenzie FT (2006) Initial responses of carbonate-rich shelf sediments to rising atmospheric  $pCO_2$  and “ocean acidification”: Role of high Mg-calcites. *Geochim Cosmochim Acta* 70:5814–5830.
- 44 Irigoien X, et al. (2014) Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nat Commun* 5:3271.
- 45 St John MA, et al. (2016) A dark hole in our understanding of marine ecosystems and their services: Perspectives from the mesopelagic community. *Front Mater Sci* 3:31.
- 46 Davison PC, Checkley DM, Koslow JA, Barlow J (2013) Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. *Prog Oceanogr* 116:14–30.
- 47 Hauer ME, Evans JM, Mishra DR (2016) Millions projected to be at risk from sea-level rise in the continental United States. *Nat Clim Chang* 6:691–695.
- 48 Narayan S, et al. (2016) The effectiveness, costs and coastal protection benefits of natural and nature-based defences. *PLoS One* 11:e0154735.
- 49 Rodriguez AB, et al. (2014) Oyster reefs can outpace sea-level rise. *Nat Clim Chang* 4:493–497.
- 50 Perry CT, et al. (2015) Remote coral reefs can sustain high growth potential and may match future sea-level trends. *Sci Rep* 5:18289.
- 51 Spalding MD, et al. (2014) The role of ecosystems in coastal protection: Adapting to climate change and coastal hazards. *Ocean Coast Manage* 90:50–57.
- 52 Mazarrasa I, et al. (2012) Seagrass meadows as a globally significant carbonate reservoir. *Biogeosciences* 12:4993–5003.
- 53 Kang N-Y, Elsner JB (2015) Trade-off between intensity and frequency of global tropical cyclones. *Nat Clim Chang* 5:661–664.
- 54 Kossin JP, Emanuel KA, Vecchi GA (2014) The poleward migration of the location of tropical cyclone maximum intensity. *Nature* 509:349–352.
- 55 Shepard CC, Crain CM, Beck MW (2011) The protective role of coastal marshes: A systematic review and meta-analysis. *PLoS One* 6:e27374.
- 56 Micheli F, et al. (2012) Evidence that marine reserves enhance resilience to climatic impacts. *PLoS One* 7:e40832.
- 57 Mellin C, Aaron MacNeil M, Cheal AJ, Emslie MJ, Julian Caley M (2016) Marine protected areas increase resilience among coral reef communities. *Ecol Lett* 19:629–637.
- 58 Aburto-Oropeza O, et al. (2008) Mangroves in the Gulf of California increase fishery yields. *Proc Natl Acad Sci USA* 105:10456–10459.
- 59 Marois DE, Mitsch WJ (2015) Coastal protection from tsunamis and cyclones provided by mangrove wetlands – a review. *Int J Biodivers Sci Ecosyst Serv Manage* 11:71–83.
- 60 Cheung WWL, et al. (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Glob Change Biol* 16:24–35.
- 61 Poloczanska ES, et al. (2013) Global imprint of climate change on marine life. *Nat Clim Chang* 3:919–925.
- 62 Beaugrand G, Luczak C, Edwards M (2009) Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob Change Biol* 15:1790–1803.
- 63 Saura S, Bodin Ö, Fortin M-J (2014) Stepping stones are crucial for species’ long-distance dispersal and range expansion through habitat networks. *J Anim Ecol* 83:171–182.
- 64 Green AL, et al. (2014) Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. *Coast Manage* 42:143–159.
- 65 Jones KR, Watson JEM, Possingham HP, Klein C (2016) Incorporating climate change into spatial conservation prioritisation: A review. *Biol Conserv* 194:121–130.
- 66 Couce E, Ridgwell A, Hendy EJ (2013) Future habitat suitability for coral reef ecosystems under global warming and ocean acidification. *Glob Change Biol* 19:3592–3606.
- 67 Roberts CM, Hawkins JP (2012) Establishment of fish stock recovery areas (European Parliament, Brussels, Belgium), IP/B/PECH/IC/2012-053.
- 68 Roberts CM, et al. (2010) Guidance on the size and spacing of Marine Protected Areas in England (Natural England, Peterborough, UK), Commissioned Report NECR037.
- 69 Castilla JC, Campo MA, Bustamante RH (2007) Recovery of *Durvillaea antarctica* (Durvilliales) inside and outside Las Cruces Marine Reserve, Chile. *Ecol Appl* 17:1511–1522.
- 70 Harrison HB, et al. (2012) Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Curr Biol* 22:1023–1028.
- 71 Munguía-Vega A, et al. (2015) Marine reserves help preserve genetic diversity after impacts derived from climate variability: Lessons from the pink abalone in Baja California. *Glob Ecol Conserv* 4:264–276.
- 72 Reusch TBH, Ehlers A, Hämmerli A, Worm B (2005) Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc Natl Acad Sci USA* 102:2826–2831.
- 73 Ehlers A, Worm B, Reusch TBH (2008) Importance of genetic diversity in eelgrass *Zostera marina* for its resilience to global warming. *Mar Ecol Prog Ser* 355:1–7.
- 74 Selkoe KA, et al. (2016) The DNA of coral reef biodiversity: Predicting and protecting genetic diversity of reef assemblages. *Proc Royal Soc B* 283:20160354.
- 75 Mee JA, Otto SP, Pauly D (2017) Evolution of movement rate increases the effectiveness of marine reserves for the conservation of pelagic fishes. *Evol Appl* 10:444–461.
- 76 Brown CJ, et al. (2010) Effects of climate-driven primary production change on marine food webs: Implications for fisheries and conservation. *Glob Change Biol* 16:1194–1212.
- 77 Helm KP, Bindoff NL, Church JA (2011) Observed decreases in oxygen content of the global ocean. *Geophys Res Lett* 38:L23602.
- 78 Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. *Science* 321:926–929.
- 79 Cheung WWL, et al. (2012) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nat Clim Chang* 3:254–258.
- 80 Boyce DG, Lewis MR, Worm B (2010) Global phytoplankton decline over the past century. *Nature* 466:591–596.
- 81 Doney SC, Fabry VJ, Feely RA, Kleydas JA (2009) Ocean acidification: The other  $CO_2$  problem. *Annu Rev Mar Sci* 1:169–192.
- 82 Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. *Clim Res* 33:271–283.
- 83 Britten GL, Dowd M, Worm B (2016) Changing recruitment capacity in global fish stocks. *Proc Natl Acad Sci USA* 113:134–139.
- 84 Hsieh CH, et al. (2006) Fishing elevates variability in the abundance of exploited species. *Nature* 443:859–862.
- 85 Halpern BS, Lester SE, Kellner JB (2009) Spillover from marine reserves and the replenishment of fished stocks. *Environ Conserv* 36:268–276.
- 86 Beger M, et al. (2010) Conservation planning for connectivity across marine, freshwater, and terrestrial realms. *Biol Conserv* 143:565–575.
- 87 Mascia MB, Claus CA, Naidoo R (2010) Impacts of marine protected areas on fishing communities. *Conserv Biol* 24:1424–1429.
- 88 Cheung WWL, et al. (2016) Transform high seas management to build climate-resilience in marine seafood capacity. *Fish Fish* 18:254–263.
- 89 Villéger S, Ferraton F, Mouillot D, de Wit R (2012) Nutrient recycling by coastal macrofauna: Intra- versus interspecific differences. *Mar Ecol Prog Ser* 452:297–303.
- 90 Layman CA, Allgeier JE, Rosemond AD, Dahlgren CP, Yeager LA (2011) Marine fisheries declines viewed upside down: Human impacts on consumer-driven nutrient recycling. *Ecol Appl* 21:343–349.
- 91 Halpern BS, et al. (2015) Spatial and temporal changes in cumulative human impacts on the world’s ocean. *Nat Commun* 6:7615.



- 92 Beck MW, et al. (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience* 61:107–116.
- 93 Smith JE, et al. (2016) Re-evaluating the health of coral reef communities: Baselines and evidence for human impacts across the central Pacific. *Proc Royal Soc B* 283:20151985.
- 94 Lotze HK, Worm B (2009) Historical baselines for large marine animals. *Trends Ecol Evol* 24:254–262.
- 95 Ramirez-Llodra E, et al. (2011) Man and the last great wilderness: Human impact on the deep sea. *PLoS One* 6:e22588.
- 96 Zaneveld JR, et al. (2016) Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nat Commun* 7:11833.
- 97 Seabra R, Wethey DS, Santos AM, Lima FP (2015) Understanding complex biogeographic responses to climate change. *Sci Rep* 5:12930.
- 98 Hewitt JE, Ellis JI, Thrush SF (2016) Multiple stressors, nonlinear effects and the implications of climate change impacts on marine coastal ecosystems. *Glob Change Biol* 22:2665–2675.
- 99 Côté IM, Darling ES (2010) Rethinking ecosystem resilience in the face of climate change. *PLoS Biol* 8:e1000438.
- 100 Hixon MA, Johnson DW, Sogard SM (2014) BOFFFFs: On the importance of conserving old-growth age structure in fishery populations. *ICES J Mar Sci* 71:2171–2185.
- 101 Selig ER, Bruno JF (2010) A global analysis of the effectiveness of marine protected areas in preventing coral loss. *PLoS One* 5:e9278.
- 102 Anderson CNK, et al. (2008) Why fishing magnifies fluctuations in fish abundance. *Nature* 452:835–839.
- 103 Bernhardt JR, Leslie HM (2013) Resilience to climate change in coastal marine ecosystems. *Annu Rev Mar Sci* 5:371–392.
- 104 Rooney N, McCann K, Gellner G, Moore JC (2006) Structural asymmetry and the stability of diverse food webs. *Nature* 442:265–269.
- 105 Lafferty KD (2004) Fishing for lobsters indirectly increases epidemics in sea urchins. *Ecol Appl* 14:1566–1573.
- 106 Groner ML, et al. (2016) Managing marine disease emergencies in an era of rapid change. *Phil Trans R Soc B* 371:20150364.
- 107 Lamb JB, et al. (2016) Reserves as tools for alleviating impacts of marine disease. *Phil Trans R Soc B* 371:20150210.
- 108 Lavery TJ, et al. (2010) Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. *Proc Royal Soc B* 277:3527–3531.
- 109 McCauley DJ, et al. (2012) Assessing the effects of large mobile predators on ecosystem connectivity. *Ecol Appl* 22:1711–1717.
- 110 Papastamatiou YP, Meyer CG, Kosaki RK, Wallsgrove NJ, Popp B (2015) Movements and foraging of predators associated with mesophotic coral reefs and their potential for linking ecological habitats. *Mar Ecol Prog Ser* 521:155–170.
- 111 Le Quéré C, et al. (2015) Global carbon budget 2014. *Earth Syst Sci Data* 7:47–85.
- 112 Gruber N (2011) Warming up, turning sour, losing breath: Ocean biogeochemistry under global change. *Phil Trans R Soc B* 369:1980–1996.
- 113 Lang'at JKS, et al. (2014) Rapid losses of surface elevation following tree girdling and cutting in tropical mangroves. *PLoS One* 9:e107868.
- 114 Phang VXH, Chou M, Friess DA (2015) Ecosystem carbon stocks across a tropical intertidal habitat mosaic of mangrove forest, seagrass meadow, mudflat and sandbar. *Earth Surf Process Landf* 40:1387–1400.
- 115 Schmitz OF, et al. (2014) Animating the carbon cycle. *Ecosystems (N Y)* 17:344–359.
- 116 Wilmers CC, Estes JA, Edwards M, Lairde KL, Konar B (2012) Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis for sea otters and kelp forests. *Front Ecol Environ* 10:409–415.
- 117 Silliman BR, van de Koppel J, Bertness MD, Stanton LE, Mendelssohn IA (2005) Drought, snails, and large-scale die-off of southern U.S. salt marshes. *Science* 310:1803–1806.
- 118 Atwood TB, et al. (2015) Predators help protect carbon stocks in blue carbon ecosystems. *Nat Clim Chang* 5:1038–1045.
- 119 Lewis SL, et al. (2009) Increasing carbon storage in intact African tropical forests. *Nature* 457:1003–1006.
- 120 Salter MA, Harborne AR, Perry CT, Wilson RW (2017) Phase heterogeneity in carbonate production by marine fish influences their roles in sediment generation and the inorganic carbon cycle. *Sci Rep* 7:765.
- 121 Howard J, et al. (2017) Clarifying the role of coastal and marine systems in climate mitigation. *Front Ecol Environ* 15:42–50.
- 122 Pusceddu A, et al. (2014) Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. *Proc Natl Acad Sci USA* 111:8861–8866.
- 123 Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar Ecol Prog Ser* 318:31–45.
- 124 Wall CC, Peterson BJ, Gobler CJ (2008) Facilitation of seagrass *Zostera marina* productivity by suspension-feeding bivalves. *Mar Ecol Prog Ser* 357:165–174.
- 125 Kahn AS, Yahel G, Chu JWV, Tunnicliffe V, Leys SP (2015) Benthic grazing and carbon sequestration by deep-water glass sponge reefs. *Limnol Oceanogr* 60:78–88.
- 126 McCauley DJ, et al. (2015) Marine defaunation: Animal loss in the global ocean. *Science* 347:1255641.
- 127 Thurber AR, et al. (2014) Ecosystem function and services provided by the deep sea. *Biogeosciences* 11:3941–3963.
- 128 Gamfeldt L, et al. (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat Commun* 4:1340.
- 129 Worm B, et al. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787–790.
- 130 Travis J, et al. (2014) Integrating the invisible fabric of nature into fisheries management. *Proc Natl Acad Sci USA* 111:581–584.
- 131 Oliver TH, et al. (2015) Biodiversity and resilience of ecosystem functions. *Trends Ecol Evol* 30:673–684.
- 132 Duffy JE, Lefcheck JS, Stuart-Smith RD, Navarrete SA, Edgar GJ (2016) Biodiversity enhances reef fish biomass and resistance to climate change. *Proc Natl Acad Sci USA* 113:6230–6235.
- 133 Steneck RS, et al. (2002) Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environ Conserv* 29:436–459.
- 134 Vergés A, et al. (2016) Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proc Natl Acad Sci USA* 113:13791–13796.
- 135 Reed D, et al. (2016) Extreme warming challenges sentinel status of kelp forests as indicators of climate change. *Nat Commun* 7:13757.
- 136 Pellissier L, et al. (2014) Quaternary coral reef refugia preserved fish diversity. *Science* 344:1016–1019.
- 137 Lauck T, Clark CW, Mangel M, Munro GR (1998) Implementing the precautionary principle in fisheries management through marine reserves. *Ecol Appl* 8:S71–S78.
- 138 Gelcich S, et al. (2015) Alternative strategies for scaling up marine coastal biodiversity conservation in Chile. *Maritime Studies* 14:5.
- 139 Gelcich S, Godoy N, Prado L, Castilla JC (2008) Add-on conservation benefits of marine territorial user rights fishery policies in central Chile. *Ecol Appl* 18:273–281.
- 140 Cinner JE, Aswani S (2007) Integrating customary management into marine conservation. *Biol Conserv* 140:201–216.
- 141 Gutiérrez NL, Hilborn R, Defeo O (2011) Leadership, social capital and incentives promote successful fisheries. *Nature* 470:386–389.
- 142 Carpenter S, Kleinjans R, Villasante S, O'Leary BC (2016) Landing the blame: The influence of EU Member States on quota setting. *Mar Policy* 64:9–15.
- 143 Cullis-Suzuki S, Pauly D (2010) Failing the high seas: A global evaluation of regional fisheries management organisations. *Mar Policy* 34:1036–1042.
- 144 Sumaila UR, Cheung WWL, Lam WWY, Pauly D, Herrick S (2011) Climate change impacts on the biophysics and economics of world fisheries. *Nat Clim Chang* 1:449–456.
- 145 McCrea-Strub A, et al. (2011) Understanding the cost of establishing marine protected areas. *Mar Policy* 35:1–9.