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Review Article

Ocean acidification impacts on coastal ecosystem services due to habitat degradation

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The oceanic uptake of anthropogenic carbon dioxide emissions is changing seawater chemistry in a process known as ocean acidification. The chemistry of this rapid change in surface waters is well understood and readily detectable in oceanic observations, yet there is uncertainty about the effects of ocean acidification on society since it is difficult to scale-up from laboratory and mesocosm tests. Here, we provide a synthesis of the likely effects of ocean acidification on ecosystem properties, functions and services based on observations along natural gradients in $p\mathrm{CO}_2$. Studies at CO_2 seeps worldwide show that biogenic habitats are particularly sensitive to ocean acidification and that their degradation results in less coastal protection and less habitat provisioning for fisheries. The risks to marine goods and services amplify with increasing acidification causing shifts to macroalgal dominance, habitat degradation and a loss of biodiversity at seep sites in the tropics, the sub-tropics and on temperate coasts. Based on this empirical evidence, we expect ocean acidification to have serious consequences for the millions of people who are dependent on coastal protection, fisheries and aquaculture. If humanity is able to make cuts in fossil fuel emissions, this will reduce costs to society and avoid the changes in coastal ecosystems seen in areas with projected $p\mathrm{CO}_2$ levels. A binding international agreement for the oceans should build on the United Nations Sustainable Development Goal to 'minimise and address the impacts of ocean acidification'.

Introduction

We are releasing around 1 million tons of carbon dioxide per hour into the Earth's atmosphere. About 25% of this gas is taken up by the ocean where it reacts with seawater to form a weak acid causing surface ocean pH to fall by ~0.002 units per year [1]. Geological weathering of alkaline rocks and dissolution of carbonate sediments is too slow to counter this rapid rate of acidification [2,3]. Changes in ocean carbonate chemistry are causing the depth at which seawater is corrosive to carbonate to shoal, threatening deep-water calcified habitats worldwide (e.g. deep-water coral reefs) through dissolution and intensified bioerosion [4]. In this paper, we focus on the impacts of ocean acidification in shallow coastal waters since this is where humanity gains most benefit from the oceans in terms of ecosystem services such as the provision of materials, food, recreation and coastal protection.

When the partial pressure of carbon dioxide in seawater ($p\mathrm{CO}_2$) increases, the concentration of carbonate ions decreases. Figure 1 illustrates how $p\mathrm{CO}_2$ affects the saturation state (Ω) of aragonite at different temperatures. Scleractinian corals use aragonite (a mineral form of calcium carbonate) to build reefs and this has about the same solubility as high-magnesium calcite, which coralline algae use to build their skeletons. Warm-water coral reefs form where Ω_{arag} is >3.3 [5] and cold-water coralline algal maerl beds grow in areas with $\Omega_{\mathrm{arag}} > 2$ [6]. This is a concern because as seawater $p\mathrm{CO}_2$ increases it causes the aragonite saturation state to fall below levels suitable for these globally important habitats. Even if humanity cuts present-day levels of emissions to the IPCC CO_2 emission representative concentration pathway (RCP) 8.5, aragonite saturation is expected to fall below 3 in tropical areas. In the Arctic, the area where surface seawater is corrosive to aragonite ($\Omega < 1$) is spreading rapidly because these cold waters already have naturally low levels of aragonite [1].

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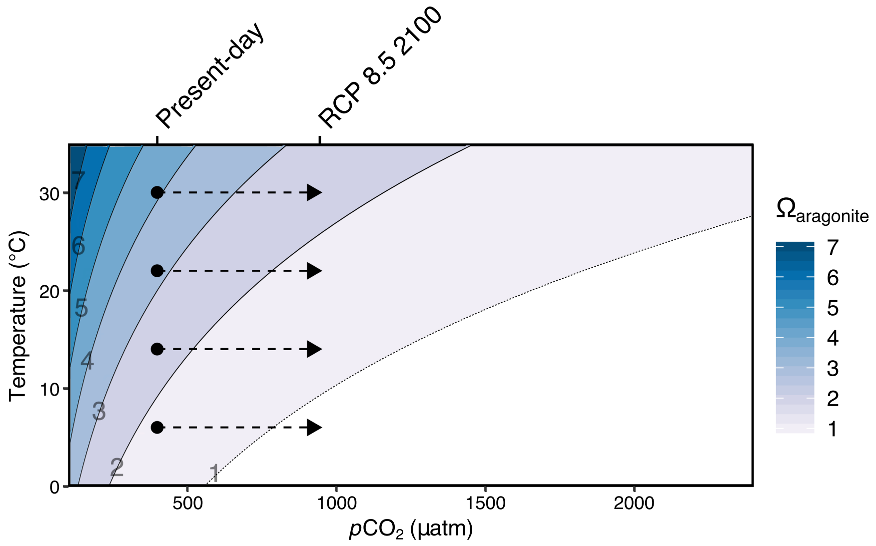


Figure 1. Aragonite saturation state (Ω) as a function of pCO$_2$ and temperature.

Carbonate chemistry calculated using 'seacarb' [58] at salinity 35 PSU and total alkalinity 2250 µmol/kg seawater. The trajectories of Ω are overlaid between present-day pCO$_2$ (400 ppm) and IPCC RCP 8.5-year 2100 pCO$_2$ (~950 ppm) for four temperatures, spanning tropical to polar regions.

The chemistry of ocean acidification is well understood scientifically and is readily detectable in oceanic observations, yet there is uncertainty about the ecosystem effects of this change. Laboratory and mesocosm experiments show that ocean acidification may affect all marine life, for example, through changes in gene expression, physiology, reproduction and behaviour [7–10]. However, such experiments are usually conducted on single or small groups of species that are isolated from their natural environment, so it is difficult to scale-up from these results to the ecosystem scale [11]. In recent years, alternative approaches have increasingly been used, including *in situ* and long-term mesocosm experiments [12–16] and the use of natural gradients in pCO$_2$. Here, we focus on the latter and provide a synthesis of the likely effects of ocean acidification on ecosystem properties, functions and services based on observations at a range of temperatures.

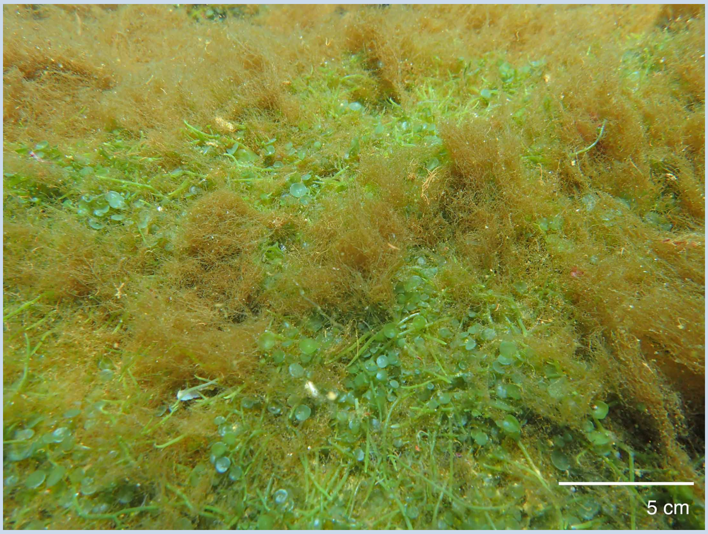
Marine waters near to volcanic seeps reveal ecological responses to acidification that retain natural pH variability [17,18]. Care is needed to avoid confounding effects caused by hydrogen sulfide or toxic metals that are usually present in volcanic seep fluids. Studies that focus on areas with realistic increases in pCO$_2$ that are away from the seeps themselves reveal the consequences of long-term exposure to acidified waters and the ecological effects of more frequent low pH excursions [17–19]. Observations along gradients of falling pH and aragonite saturation levels reveal 'winners', organisms that tend to do well in the acidified conditions (Box 1), and 'losers' that tend to do badly (Box 2) [20]. There are no perfect proxies for the global effects of ocean acidification; a drawback of carbon dioxide seeps is that they are open systems that allow recruitment from outside. This hinders genetic adaptation [20] and so these systems show which marine organisms are resilient today, but not which will evolve resilience in the future.

Effects on habitat-forming organisms

Most macroalgae can tolerate the effects of ocean acidification, with only around a 5% loss in species diversity at levels projected under RCP 8.5 [30]. However, ocean acidification causes marked shifts in algal community composition that greatly alter coastal habitats [30,31]. At tropical, sub-tropical and temperate seep sites, periods of carbonate undersaturation reduce the thickness of coralline algae; these normally form a pavement on rock in the photic zone, upon which other life settles and grows [20,32]. Increased availability of bicarbonate and pCO$_2$ stimulates primary production and in areas sheltered from wave action, this increases carbon fixation and the standing stock of large seaweeds and seagrasses [22,33–35]. In wave-exposed areas, acidification lowers coastal ecosystem resilience such that only microalgal biofilm and small turf algae persist after storms (e.g. sub-tropical regions [19], temperate regions [36]).

Box 1. Winners: some species benefit from ocean acidification

Sensitivity to ocean acidification is dependent upon the amount of exposure to acidified conditions. For example, animals that vertically migrate and commonly encounter low pH conditions are more able to withstand lower pH conditions, as are those that are naturally exposed to upwelling waters [21]. Overall, photosynthetic organisms are set to benefit from acidification, particularly those phytoplankton, macroalgae and seagrasses that are currently carbon limited [22]. Opportunistic species typically have the molecular and physiological machinery needed to withstand the effects of acidification. Considering the role of toxic phytoplankton in fish kills, and their proliferation at high CO_2 levels, they pose an emergent threat to aquaculture, fisheries and coastal communities.



We illustrate this ‘Winner’ box with the benthic macroalgae *Caulerpa chemnitzia* var. *peltata* and a turf of the diatom *Biddulphia biddulphiana* (photo by Ben P. Harvey) as these are common at CO_2 seeps off Shikine Island in Japan. *Caulerpa* spp. are highly invasive and have been dubbed ‘killer algae’ since they compete strongly for space and contain toxic compounds that grazers in the invaded habitats avoid. Invasive species that are able to tolerate wide changes in physicochemical conditions in ballast water or attached to ships have inbuilt resilience to ocean acidification [23].

Many macrofauna are susceptible to the effects of ocean acidification, with around a 30% fall in animal biodiversity as average pH declines from 8.1 to 7.8 at CO_2 seeps [19,20,32]. This is due to a mixture of direct and indirect effects, such as increased metabolic costs of coping with hypercapnia [37], or increased susceptibility to predation [38]. Corals are the most famous habitat-forming marine animals, but a diverse range of other groups build calcareous seabed habitats such as sponges, serpulids, vermetids, oysters, mussels and bryozoans. Along natural gradients of decreasing carbonate saturation such reefs are degraded, due to increased metabolic costs of calcification, chemical dissolution, enhanced bioerosion and intolerance of many reef-forming organisms to hypercapnia [20,31,39]. Some reef-building corals can up-regulate calcification in an adaptive response to acidification [40], although this does not combat reef dissolution. On the whole, ocean acidification reduces the complexity, extent and species richness of biogenic reefs in all the biogeographic regions that CO_2 seep studies have taken place.

Box 2. Losers: many species are vulnerable to ocean acidification

Many shellfish are sensitive to ocean acidification, particularly at the larval stage. Physiological responses include decreased aerobic scope for growth, suppressed immune defence against parasites and pathogens, disruption of iono- and osmoregulation and reduced reproductive success [24]. Thermal stress associated with heat waves exacerbates the effects of ocean acidification on shellfish, particularly if the organisms have insufficient food to meet increased metabolic costs [25,26].

We illustrate this 'Loser' box with an oyster *Magallana gigas* that is spawning (photo by David Liittschwager). Oysters and mussels decline markedly in abundance along gradients of falling carbonate saturation [19]. Ocean acidification has the potential to reduce the abundance of oysters and the ecosystem services they provide in the wild; it can also impair their quality as seafood [27,28]. Consequently, people who depend on aquaculture may experience substantial declines in income unless they adapt, e.g. by selecting and breeding resistant stock or altering seawater carbonate chemistry to improve yield [29].

Effects of ocean acidification on ecosystem state

Ecosystem state is degraded as we move from areas of the seabed with present-day levels of $p\mathrm{CO}_2$ to those that are increasingly acidified (Figure 2). At tropical, sub-tropical and temperate seep sites, there is a shift towards less ecosystem diversity, less species richness and lower spatial heterogeneity as $p\mathrm{CO}_2$ levels increase [34]. This is empirical evidence that if humanity is able to make major cuts in fossil fuel emissions then coastal ecosystems will remain in a far better state than if seabed habitats are altered to the extent seen in areas with $p\mathrm{CO}_2$ levels projected under the Intergovernmental Panel on Climate Change's emissions scenario RCP8.5.

Carbon dioxide seep studies show that acidification leads to greater dominance by non-calcified species; turf algae over coralline algae [19], soft corals and anemones over hard corals [41,42]. It also alters competitive interactions between organisms, favouring opportunistic organisms that can more easily adapt to the change in environmental conditions [43,44]. In the tropics, some coral species are able to grow well in acidified conditions, but the habitats they form lack complexity and the reef itself is eroded by increased dissolution and bioerosion [20]. These degraded reefs have more fleshy macroalgae, less calcified algae and tend to harbour fewer invertebrates [31,45] (Figure 2a).

In the sub-tropics, the effects are similar — with fewer crustose coralline algae, a reduction in the size and abundance of calcified animals (such as sea urchins) and a proliferation of turf algae (Figure 2b; [19,38]). In these cooler waters, hermatypic corals are living on the edge of their biogeographic distribution and so they are especially vulnerable; they disappear from areas around seeps with the $p\mathrm{CO}_2$ levels projected under RCP8.5 (Figure 2b; [19]). In temperate systems, there are again fewer crustose coralline algae on rock surfaces as $p\mathrm{CO}_2$ levels increase; in sheltered conditions, habitat-forming kelps and fucoids benefit from the increased availability

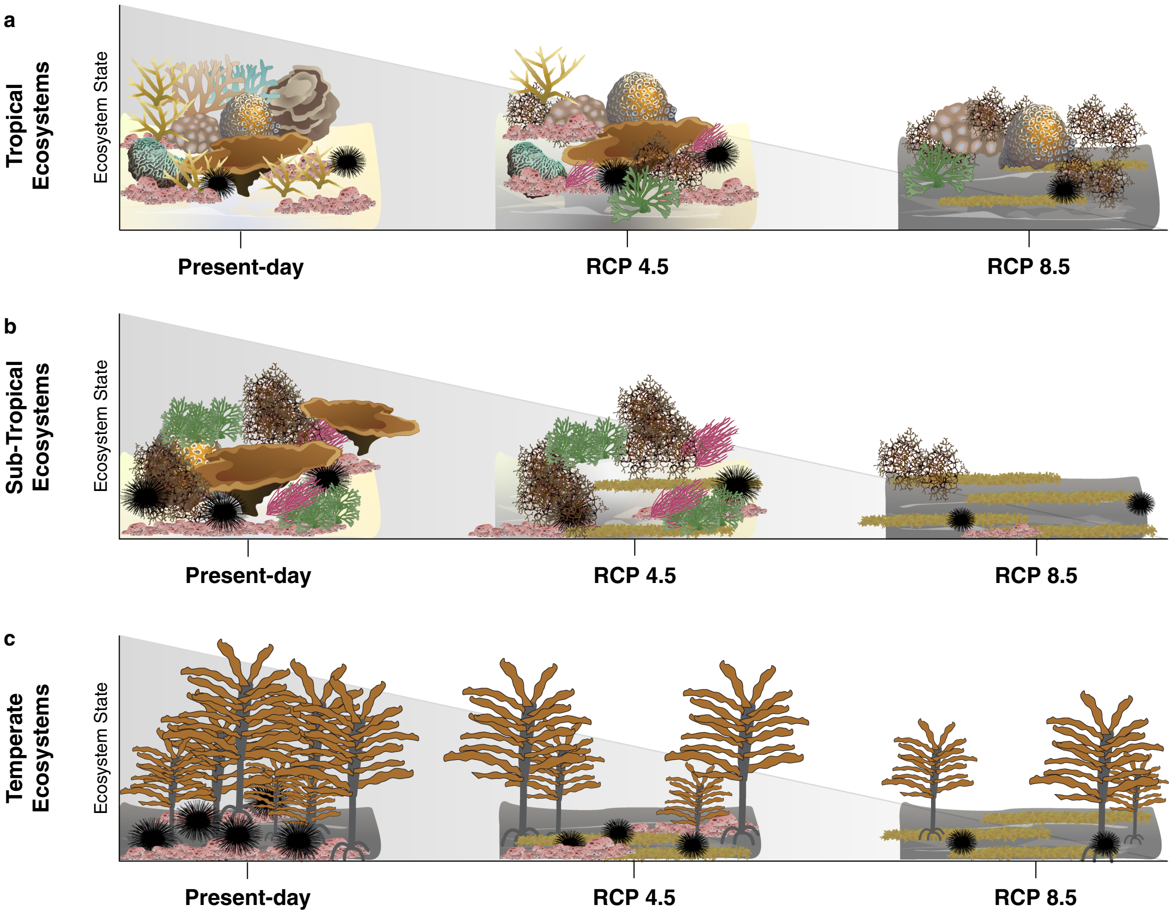


Figure 2. Changes in ecosystem state and benthic community composition in areas with present-day (400 μatm), and elevated levels of pCO_2 at volcanic seep sites (corresponding to IPCC emissions scenarios RCP 4.5 = 550 μatm and RCP 8.5 = 950 μatm).

Ecosystem state degrades because habitat complexity and biodiversity decline along gradients of increasing pCO_2. At tropical seeps, dead reef substratum (yellow) is eroded, structural complexity of living corals declines and algae proliferate. In the sub-tropics, there is a loss of hard coral and coralline algal cover (shown in pink); diverse macroalgal communities are replaced by turf algae. On exposed temperate coasts, coralline algae also decline as turf algae proliferate, with a loss of brown algal canopy cover. In each case, calcified invertebrates (represented here by black-spined sea urchins) become fewer and smaller as pCO_2 increases. For more information, see text in section 'Effects of ocean acidification on ecosystem state'.

of dissolved inorganic carbon [32] but at exposed sites turf algae dominate in acidified conditions (Figure 2c; [36]). The dual effects of increased CO_2 and decreased carbonate alter trophic interactions. Reductions in the abundance and size of calcareous herbivores such as sea urchins, that normally create space for rare and competitively inferior organisms, contributes to the overgrowth of weedy turf algae and a simplification of food webs [44,46–48], with losses in functional diversity [48] (Figure 2b,c). Overall, CO_2 seep sites demonstrate similarities in their broad patterns whereby (regardless of species composition) the ecosystem state is simplified by acidification with reductions in the diversity, abundances and complexity of habitat-forming organisms, loss of some associated organisms, and altered interactions between taxa.

Ocean acidification impacts on coastal ecosystem services

Coastal ecosystem services depend on which basic biotic functions are maintained [49], which ecosystem engineers and keystone species are retained [34], and whether the spread of nuisance species is avoided [23]. Figure 3 illustrates the fact that the capacity of marine ecosystems to provide functions and services is

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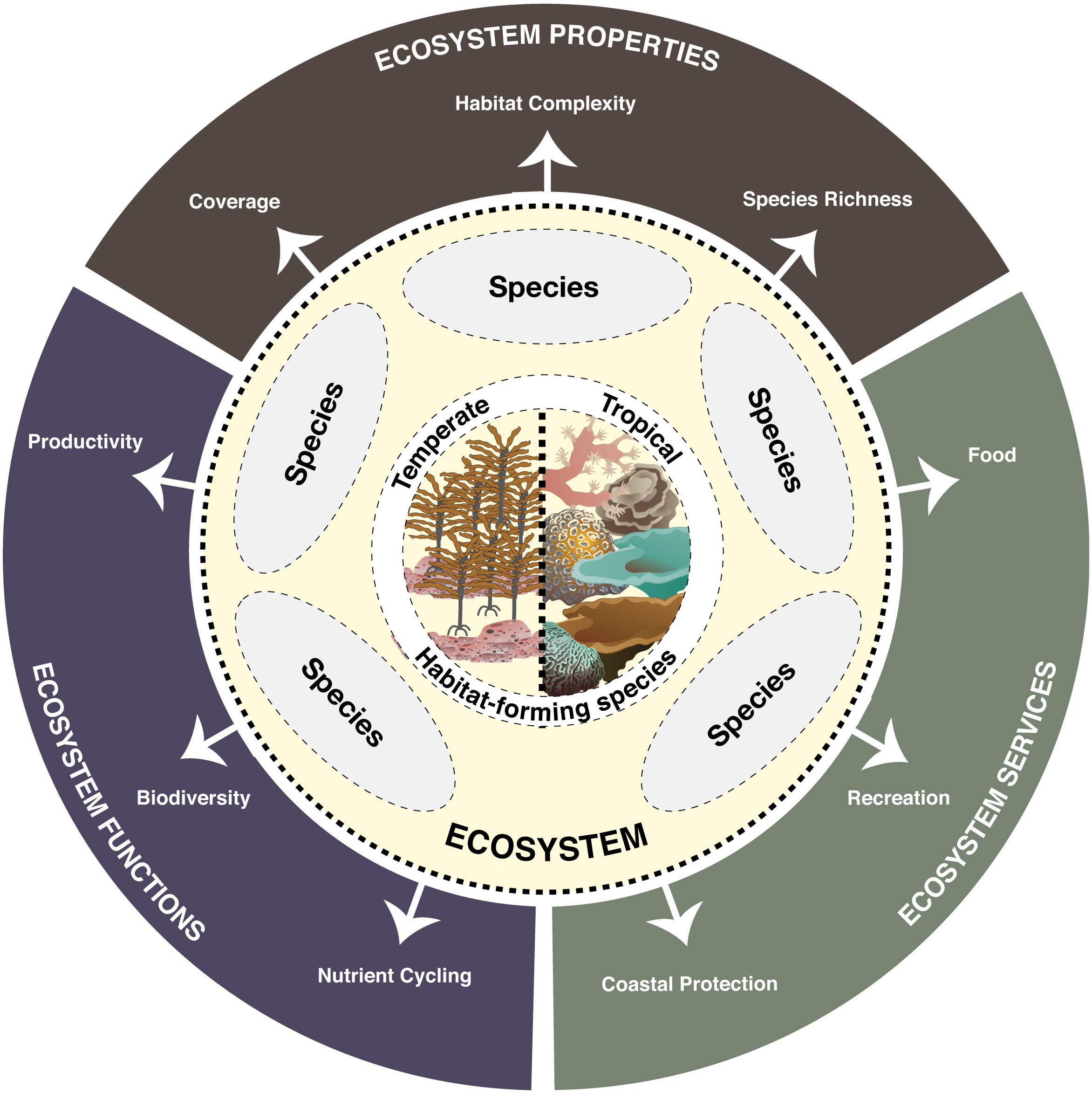

Figure 3. Ecosystem properties, functions and services provided by coastal habitat-forming species and the communities that they support.

The loss of habitat-forming organisms and degradation of ecosystem state diminishes ecosystem services. Observations at CO_2 seeps worldwide show that ocean acidification results in reductions in habitat complexity, species richness and habitat coverage. This impairs ecosystem function and the goods and services available to society, such as coastal protection, recreation and food provision.

dependent on the habitat-forming organisms and the species they maintain. Regardless of the biogeographic region that they are located in, loss of habitat-forming organisms and degradation of ecosystem state (as highlighted in the previous sections) diminishes coastal ecosystem services (Figure 3). Human activities have already eroded the capacity of marine ecosystems to provide services (e.g. coastal protection, fisheries and aquaculture) are already negatively affected by fossil fuel emissions [24,50], and this is expected to worsen in the future [24]. Observations at CO_2 seeps worldwide show that shallow biogenic reefs are particularly sensitive to ocean acidification, the degradation of these habitats results in less coastal protection and less habitat provisioning for biodiversity and fisheries, as well as having a knock-on effect for the other ecosystem services

(Figure 3). These natural gradients in seawater CO_2 show that risks to marine goods and services amplify with increasing carbon emissions.

Ocean acidification and warming have synergistic effects that exacerbate the risk of population declines in sensitive species [7,25], and synergistic interactions between other anthropogenic stressors threaten biological processes, functions and biodiversity [51]. Important areas for fisheries and recreation are already subject to increasing levels of anthropogenic stress [52], with the loss of coastal biodiversity estimated to have caused a 33% decline in viable fisheries, and a 69% decline in the provision of nursery functions [53]. It is estimated that 25–50% of coastal ecosystems (by area), such as mangroves, seagrass and saltmarshes, were lost during the 20th century [54]. When combined with rising temperatures, sea-level rise and increasing extreme events, ocean acidification further threatens the goods and services provided by coastal ecosystems [24]. This is particularly important for those people that are heavily reliant on marine resources for protection, nutrition, employment and tourism [55,56]. It is estimated, for example, that coral reefs currently provide ecosystem goods and services worth ∼$375 billion annually to 500 million people worldwide [57].

Proposed actions to lessen the impacts of ocean acidification include reduction in pollution and other stressors (to strengthen resilience); seaweed cultivation and seagrass restoration, water treatment (e.g. for high-value aquaculture); adapting human activities such as fishing and repairing damage [48]. It is likely that the societal costs of ocean acidification will be greatest in regions that have limited options for alternative employment or nutrition [41,47]. The Paris Agreement on climate change is welcome but it does not mention ocean acidification — nor the fact that this rapid change in surface ocean chemistry undermines the social, economic and environmental pillars of sustainable development. The time is ripe for a 'Paris Agreement for the oceans', one that builds on the non-binding United Nations Sustainable Development Goal 14 to 'conserve and sustainably use the oceans, seas and marine resources for sustainable development' with the specific target (Sustainable Development Goal 14.3) to 'minimise and address the impacts of ocean acidification, including through enhanced scientific cooperation at all levels'.

Conclusion

Studies in areas with naturally high levels of carbon dioxide show that coastal ecosystems are susceptible to ocean acidification. Very similar patterns are seen in tropical, sub-tropical and temperate coastal systems, with macroalgal dominance, habitat degradation and loss of biodiversity in acidified areas. This lowers the resilience of these coastal habitats to a cluster of other drivers associated with climate change (global warming, sea-level rise, increased storminess) increasing the risk of marine regime shifts and the loss of critical ecosystem functions and services. The impacts of ocean acidification on coastal ecosystems will have less serious consequences for the millions of people who are dependent on coastal protection, fisheries and aquaculture if cuts in emissions align with the Intergovernmental Panel on Climate Change RCP 4.5 scenario.

Summary

- Studies in areas with naturally high levels of carbon dioxide dissolved in seawater show that coastal ecosystems are susceptible to ocean acidification.
- Very similar patterns are seen in tropical, sub-tropical and temperate coastal systems, with macroalgal dominance, habitat simplification and loss of biodiversity in acidified conditions.
- Ocean acidification lowers the resilience of coastal habitats to a cluster of other drivers associated with climate change (global warming, sea-level rise, increased storminess) increasing the risk of marine regime shifts and the loss of critical ecosystem functions and services.
- The impacts of ocean acidification on coastal ecosystems will have less serious consequences for the millions of people who are dependent on coastal protection, fisheries and aquaculture if cuts in emissions align with the Intergovernmental Panel on Climate Change RCP 4.5 scenario.

Abbreviations

pCO$_2$, partial pressure of carbon dioxide; RCP, representative concentration pathway.

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Competing Interests

The Authors declare that there are no competing interests associated with the manuscript.

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