

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  $p\text{CO}_2$ . Studies at  $\text{CO}_2$  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  $p\text{CO}_2$  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  $\sim 0.002$  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 ( $p\text{CO}_2$ ) increases, the concentration of carbonate ions decreases. Figure 1 illustrates how  $p\text{CO}_2$  affects the saturation state ( $\Omega$ ) 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  $\Omega_{\text{arag}}$  is  $>3.3$  [5] and cold-water coralline algal maerl beds grow in areas with  $\Omega_{\text{arag}} > 2$  [6]. This is a concern because as seawater  $p\text{CO}_2$  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  $\text{CO}_2$  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].

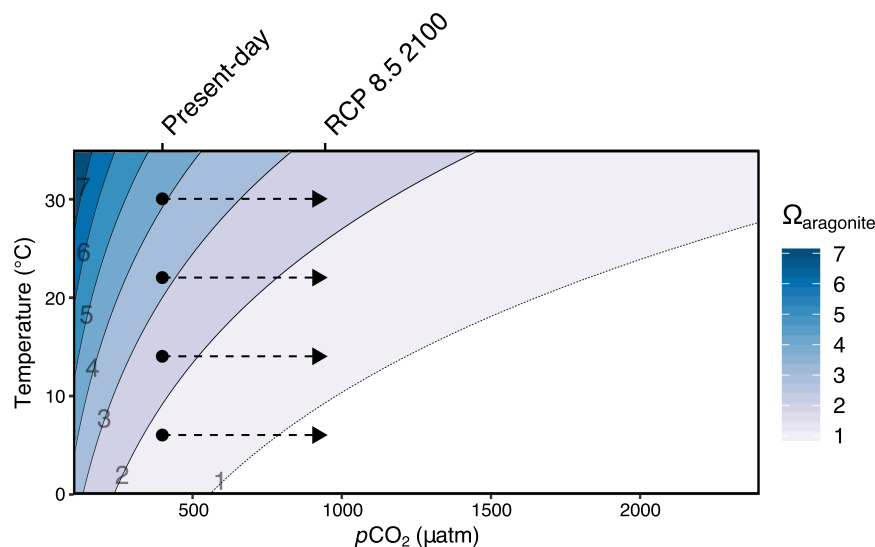
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**Figure 1. Aragonite saturation state ( $\Omega$ ) as a function of  $p\text{CO}_2$  and temperature.**

Carbonate chemistry calculated using ‘seacarb’ [58] at salinity 35 PSU and total alkalinity 2250  $\mu\text{mol/kg}$  seawater. The trajectories of  $\Omega$  are overlaid between present-day  $p\text{CO}_2$  (400 ppm) and IPCC RCP 8.5-year 2100  $p\text{CO}_2$  (~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  $p\text{CO}_2$ . 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.

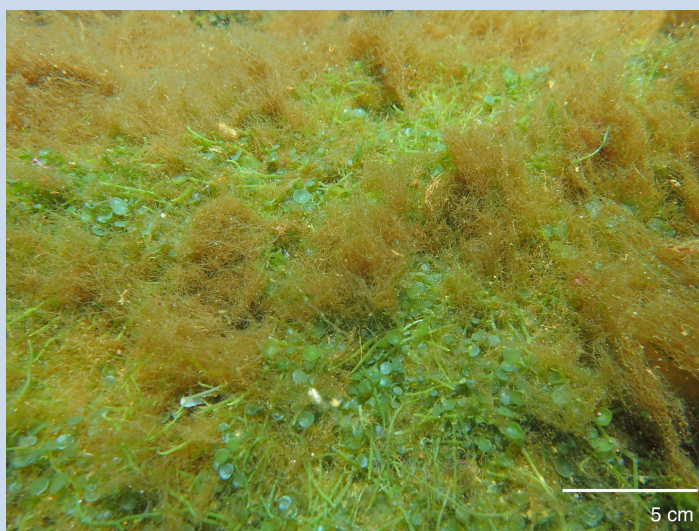
Marine waters near to volcanic seeps reveal ecological responses to acidification that retain natural pH variability [17,18]. Care is needed to avoid confounding effects caused by hydrogen sulfide or toxic metals that are usually present in volcanic seep fluids. Studies that focus on areas with realistic increases in  $p\text{CO}_2$  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  $p\text{CO}_2$  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<sub>2</sub> levels, they pose an emergent threat to aquaculture, fisheries and coastal communities.

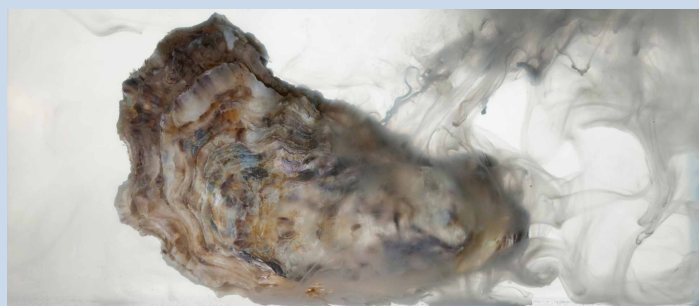


We illustrate this ‘Winner’ box with the benthic macroalgae *Caulerpa chemnitzia* var. *peltata* and a turf of the diatom *Bidulphia biddulphiana* (photo by Ben P. Harvey) as these are common at CO<sub>2</sub> seeps off Shikine Island in Japan. *Caulerpa* spp. are highly invasive and have been dubbed ‘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<sub>2</sub> 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<sub>2</sub> 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].

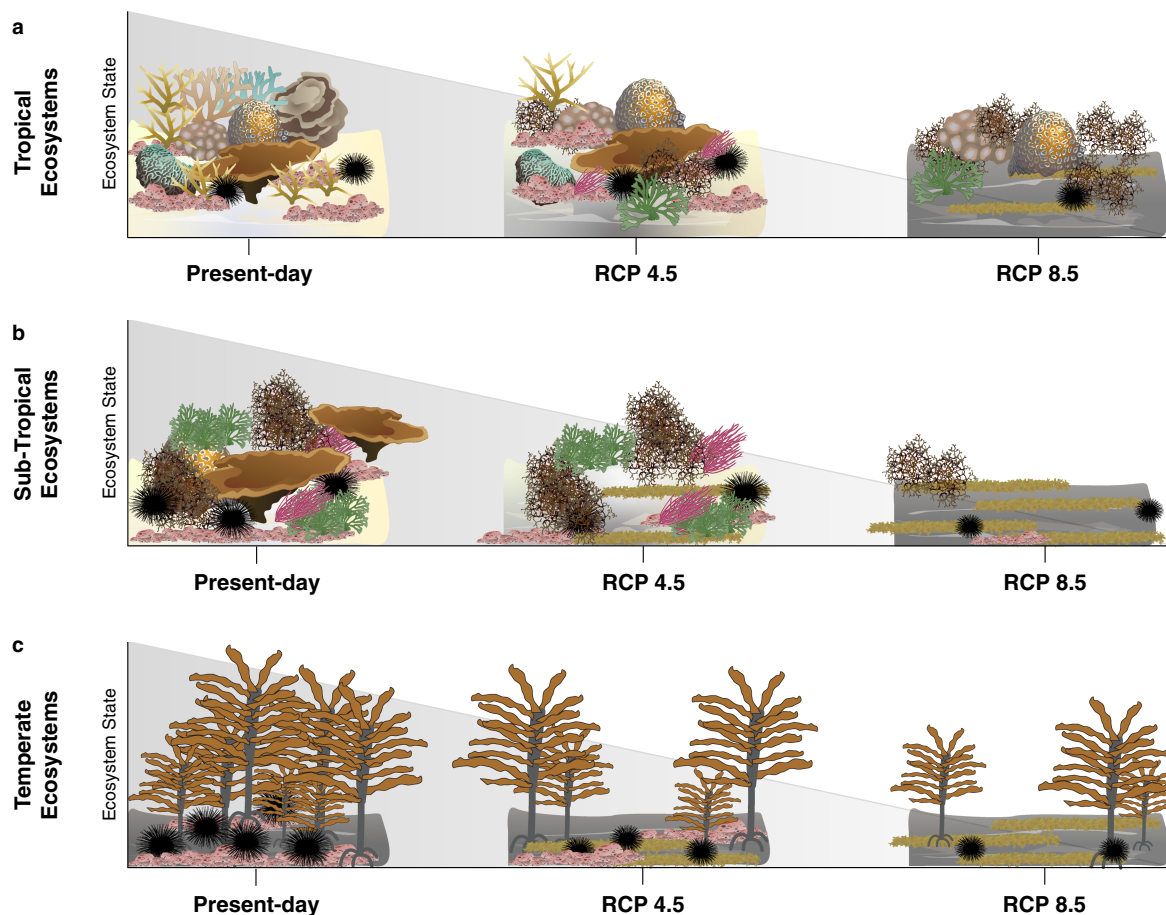
## Effects of ocean acidification on ecosystem state

Ecosystem state is degraded as we move from areas of the seabed with present-day levels of  $p\text{CO}_2$  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  $p\text{CO}_2$  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  $p\text{CO}_2$  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  $p\text{CO}_2$  levels projected under RCP8.5 (Figure 2b; [19]). In temperate systems, there are again fewer crustose coralline algae on rock surfaces as  $p\text{CO}_2$  levels increase; in sheltered conditions, habitat-forming kelps and fucoids benefit from the increased availability





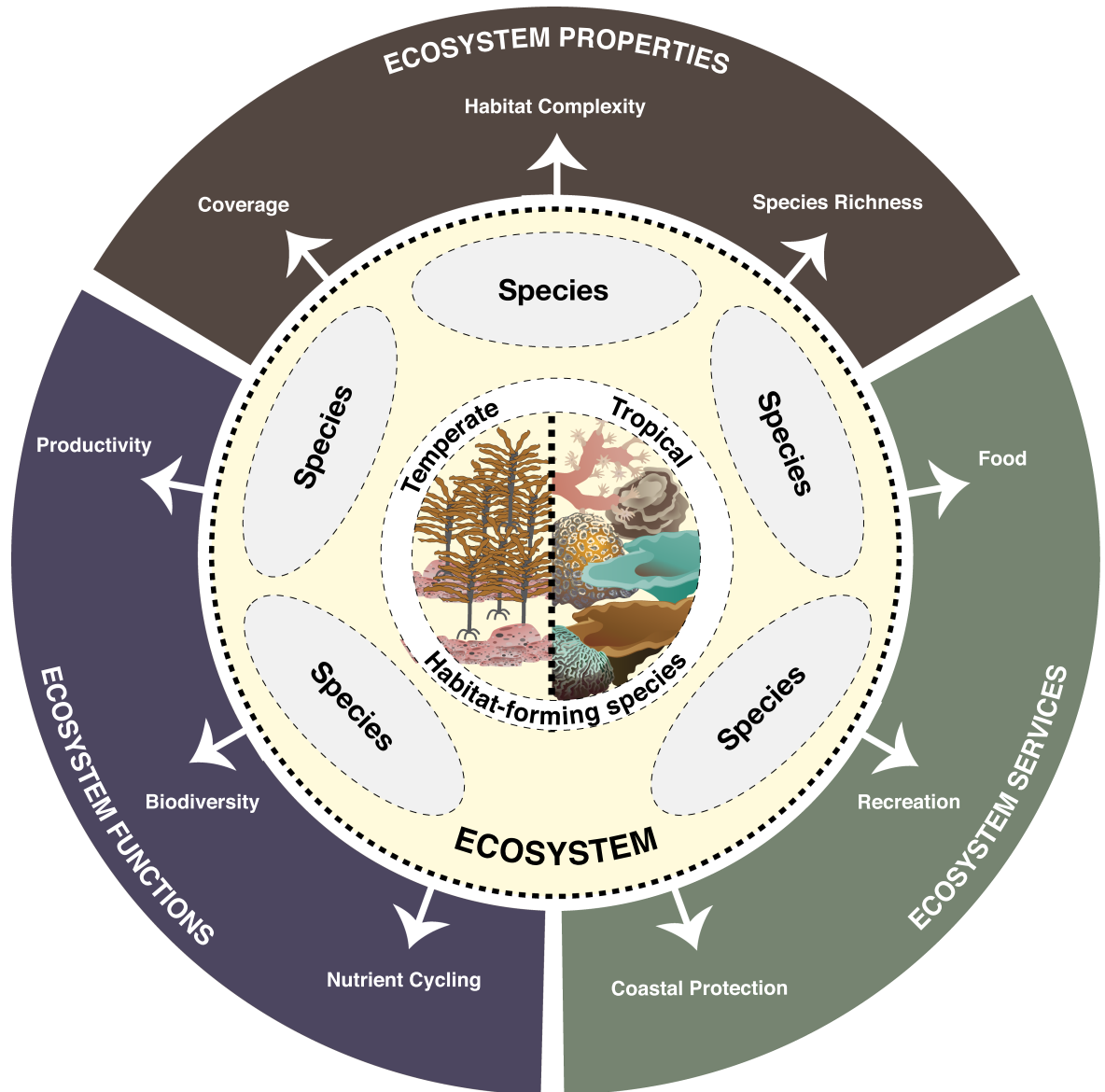
**Figure 2. Changes in ecosystem state and benthic community composition in areas with present-day (400  $\mu\text{atm}$ ), and elevated levels of  $p\text{CO}_2$  at volcanic seep sites (corresponding to IPCC emissions scenarios RCP 4.5 = 550  $\mu\text{atm}$  and RCP 8.5 = 950  $\mu\text{atm}$ ).**

Ecosystem state degrades because habitat complexity and biodiversity decline along gradients of increasing  $p\text{CO}_2$ . 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  $p\text{CO}_2$  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  $\text{CO}_2$  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,  $\text{CO}_2$  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



**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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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

$p\text{CO}_2$ , 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.

## References

- IPCC. (2013) *Climate Change 2013 – The Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the IPCC*, pp. 1535, Cambridge University Press, Cambridge, UK and New York, USA, Report No.: 0521880092
- Sabine, C.L., Feely, R.A., Gruber, N., Key, R.M., Lee, K., Bullister, J.L. et al. (2004) The oceanic sink for anthropogenic  $\text{CO}_2$ . *Science* **305**, 367–371 <https://doi.org/10.1126/science.1097403>
- Figueres, C., Le Quéré, C., Mahindra, A., Bäte, O., Whiteman, G., Peters, G. et al. (2018) Emissions are still rising: ramp up the cuts. *Nature* **564**, 27–30 <https://doi.org/10.1038/d41586-018-07585-6>
- Gómez, C.E., Wickes, L., Deegan, D., Etnoyer, P.J. and Cordes, E.E. (2018) Growth and feeding of deep-sea coral *Lophelia pertusa* from the California margin under simulated ocean acidification conditions. *PeerJ* **6**, e5671 <https://doi.org/10.7717/peerj.5671>
- Albright, R., Takeshita, Y., Koweek, D.A., Ninokawa, A., Wolfe, K., Rivlin, T. et al. (2018) Carbon dioxide addition to coral reef waters suppresses net community calcification. *Nature* **555**, 516 <https://doi.org/10.1038/nature25968>
- Brodie, J., Williamson, C.J., Smale, D.A., Kamenos, N.A., Mieszkowska, N., Santos, R. et al. (2014) The future of the northeast Atlantic benthic flora in a high  $\text{CO}_2$  world. *Ecol. Evol.* **4**, 2787–2798 <https://doi.org/10.1002/ece3.1105>
- Harvey, B.P., Gwynn-Jones, D. and Moore, P.J. (2013) Meta-analysis reveals complex marine biological responses to the interactive effects of ocean acidification and warming. *Ecol. Evol.* **3**, 1016–1030 <https://doi.org/10.1002/ece3.516>
- Cattano, C., Claudet, J., Domenici, P. and Milazzo, M. (2018) Living in a high  $\text{CO}_2$  world: a global meta-analysis shows multiple trait-mediated fish responses to ocean acidification. *Ecol. Monogr.* **88**, 320–335 <https://doi.org/10.1002/ecm.1297>
- Evans, T.G. and Hofmann, G.E. (2012) Defining the limits of physiological plasticity: how gene expression can assess and predict the consequences of ocean change. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 1733–1745 <https://doi.org/10.1098/rstb.2012.0019>
- Byrne, M. (2011) Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean. *Ocean. Mar. Biol.* **49**, 1–42
- Riebesell, U. and Gattuso, J.-P. (2015) Lessons learned from ocean acidification research. *Nat. Clim. Change* **5**, 12–14 <https://doi.org/10.1038/nclimate2456>
- Pansch, C. and Hiebenthal, C. (2019) A new mesocosm system to study the effects of environmental variability on marine species and communities. *Limnol. Oceanogr. Methods* **17**, 145–162 <https://doi.org/10.1002/lom3.10306>
- Pansch, A., Winde, V., Asmus, R. and Asmus, H. (2016) Tidal benthic mesocosms simulating future climate change scenarios in the field of marine ecology. *Limnol. Oceanogr. Methods* **14**, 257–267 <https://doi.org/10.1002/lom3.10086>
- Wahl, M., Buchholz, B., Winde, V., Golomb, D., Guy-Haim, T., Müller, J. et al. (2015) A mesocosm concept for the simulation of near-natural shallow underwater climates: the Kiel Outdoor Benthocosms (KOB). *Limnol. Oceanogr. Methods* **13**, 651–663 <https://doi.org/10.1002/lom3.10055>
- Riebesell, U., Aberle-Malzahn, N., Achterberg, E.P., Algueró-Muñiz, M., Alvarez-Fernandez, S., Aristegui, J. et al. (2018) Toxic algal bloom induced by ocean acidification disrupts the pelagic food web. *Nat. Clim. Change* **8**, 1082–1086 <https://doi.org/10.1038/s41558-018-0344-1>
- Taucher, J., Bach, L.T., Boxhammer, T., Nauendorf, A., The Gran Canaria KOSMOS Consortium, Achterberg, E.P. et al. (2017) Influence of ocean acidification and deep water upwelling on oligotrophic plankton communities in the subtropical North Atlantic: insights from an in situ mesocosm study. *Front. Mar. Sci.* **4**, 85 <https://doi.org/10.3389/fmars.2017.00085>
- Foo, S.A., Byrne, M., Ricevuto, E. and Gambi, M.C. (2018) The carbon dioxide vents of Ischia, Italy, a natural system to assess impacts of ocean acidification on marine ecosystems: an overview of research and comparisons with other vent systems. *Oceanogr. Mar. Biol. Annu. Rev.* **56**, 237–310 <https://doi.org/10.1201/9780429454455-9>
- González-Delgado, S. and Hernández, J.C. (2018) The importance of natural acidified systems in the study of ocean acidification: what have we learned? *Adv. Mar. Biol.* **80**, 57–99 <https://doi.org/10.1016/bs.amb.2018.08.001>
- Agostini, S., Harvey, B.P., Wada, S., Kon, K., Milazzo, M., Inaba, K. et al. (2018) Ocean acidification drives community shifts towards simplified non-calcified habitats in a subtropical-temperate transition zone. *Sci. Rep.* **8**, 11354 <https://doi.org/10.1038/s41598-018-29251-7>
- Fabrizius, K.E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G. et al. (2011) Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nat. Clim. Change* **1**, 165–169 <https://doi.org/10.1038/nclimate1122>
- Gunderson, A.R., Armstrong, E.J. and Stillman, J.H. (2016) Multiple stressors in a changing world: the need for an improved perspective on physiological responses to the dynamic marine environment. *Annu. Rev. Mar. Sci.* **8**, 357–378 <https://doi.org/10.1146/annurev-marine-122414-033953>
- Cornwall, C.E., Revill, A.T., Hall-Spencer, J.M., Milazzo, M., Raven, J.A. and Hurd, C.L. (2017) Inorganic carbon physiology underpins macroalgal responses to elevated  $\text{CO}_2$ . *Sci. Rep.* **7**, 46297 <https://doi.org/10.1038/srep46297>



- 23 Hall-Spencer, J.M. and Allen, R. (2015) The impact of CO<sub>2</sub> emissions on 'nuisance' marine species. *Res. Rep. Biodivers. Stud.* **4**, 33–46 <https://doi.org/10.2147/RRBS.S70357>
- 24 Gattuso, J.-P., Magnan, A., Billé, R., Cheung, W.W.L., Howes, E.L., Joos, F. et al. (2015) Contrasting futures for ocean and society from different anthropogenic CO<sub>2</sub> emissions scenarios. *Science* **349**, aac4722 <https://doi.org/10.1126/science.aac4722>
- 25 Rodolfo-Metalpa, R., Houlbrèque, F., Tambutté, É., Boisson, F., Baggini, C., Patti, F.P. et al. (2011) Coral and mollusc resistance to ocean acidification adversely affected by warming. *Nat. Clim. Change* **1**, 308–312 <https://doi.org/10.1038/nclimate1200>
- 26 Rodolfo-Metalpa, R., Montagna, P., Aliani, S., Borghini, M., Canese, S., Hall-Spencer, J.M. et al. (2015) Calcification is not the Achilles' heel of cold-water corals in an acidifying ocean. *Glob. Change Biol.* **21**, 2238–2248 <https://doi.org/10.1111/gcb.12867>
- 27 Lemasson, A.J., Fletcher, S., Hall-Spencer, J.M. and Knights, A.M. (2017) Linking the biological impacts of ocean acidification on oysters to changes in ecosystem services: a review. *J. Exp. Mar. Biol. Ecol.* **492**, 49–62 <https://doi.org/10.1016/j.jembe.2017.01.019>
- 28 Lemasson, A.J., Hall-Spencer, J.M., Kuri, V. and Knights, A.M. (2019) Changes in the biochemical and nutrient composition of seafood due to ocean acidification and warming. *Mar. Environ. Res.* **143**, 82–92 <https://doi.org/10.1016/j.marenvres.2018.11.006>
- 29 Cooley, S.R., Ono, C.R., Melcer, S. and Roberson, J. (2016) Community-level actions that can address ocean acidification. *Front. Mar. Sci.* **2**, 128 <https://doi.org/10.3389/fmars.2015.00128>
- 30 Porzio, L., Buia, M.C. and Hall-Spencer, J.M. (2011) Effects of ocean acidification on macroalgal communities. *J. Exp. Mar. Biol. Ecol.* **400**, 278–287 <https://doi.org/10.1016/j.jembe.2011.02.011>
- 31 Enochs, I.C., Manzello, D.P., Donham, E.M., Kolodziej, G., Okano, R., Johnston, L. et al. (2015) Shift from coral to macroalgae dominance on a volcanically acidified reef. *Nat. Clim. Change* **5**, 1083–1088 <https://doi.org/10.1038/nclimate2758>
- 32 Hall-Spencer, J.M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.M. et al. (2008) Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* **454**, 96–99 <https://doi.org/10.1038/nature07051>
- 33 Russell, B.D., Connell, S.D., Uthicke, S., Muehllehner, N., Fabricius, K.E. and Hall-Spencer, J.M. (2013) Future seagrass beds: can increased productivity lead to increased carbon storage? *Mar. Pollut. Bull.* **73**, 463–469 <https://doi.org/10.1016/j.marpolbul.2013.01.031>
- 34 Sunday, J.M., Fabricius, K.E., Kroeker, K.J., Anderson, K.M., Brown, N.E., Barry, J.P. et al. (2017) Ocean acidification can mediate biodiversity shifts by changing biogenic habitat. *Nat. Clim. Change* **7**, 81–85 <https://doi.org/10.1038/nclimate3161>
- 35 Linares, C., Vidal, M., Canals, M., Kersting, D.K., Ambias, D., Aspillaga, E. et al. (2015) Persistent natural acidification drives major distribution shifts in marine benthic ecosystems. *Proc. R. Soc. B Biol. Sci.* **282**, 20150587 <https://doi.org/10.1098/rspb.2015.0587>
- 36 Connell, S.D., Doubleday, Z.A., Foster, N.R., Hamlyn, S.B., Harley, C.D.G., Helmuth, B. et al. (2018) The duality of ocean acidification as a resource and a stressor. *Ecology* **99**, 1005–1010 <https://doi.org/10.1002/ecy.2209>
- 37 Garilli, V., Rodolfo-Metalpa, R., Scuderi, D., Brusca, L., Parrinello, D., Rastrick, S.P.S. et al. (2015) Physiological advantages of dwarfing in surviving extinctions in high-CO<sub>2</sub> oceans. *Nat. Clim. Change* **5**, 678–682 <https://doi.org/10.1038/nclimate2616>
- 38 Harvey, B.P., Agostini, S., Wada, S., Inaba, K. and Hall-Spencer, J.M. (2018) Dissolution: the Achilles' heel of the triton shell in an acidifying ocean. *Front. Mar. Sci.* **5**, 371 <https://doi.org/10.3389/fmars.2018.00371>
- 39 Milazzo, M., Rodolfo-Metalpa, R., Chan, V.B.S., Fine, M., Alessi, C., Thiagarajan, V. et al. (2014) Ocean acidification impairs vermetid reef recruitment. *Sci. Rep.* **4**, 4189 <https://doi.org/10.1038/srep04189>
- 40 Schoepf, V., Jury, C.P., Toonen, R.J. and McCulloch, M.T. (2017) Coral calcification mechanisms facilitate adaptive responses to ocean acidification. *Proc. R. Soc. B Biol. Sci.* **284**, 20172117 <https://doi.org/10.1098/rspb.2017.2117>
- 41 Inoue, S., Kayanne, H., Yamamoto, S. and Kurihara, H. (2013) Spatial community shift from hard to soft corals in acidified water. *Nat. Clim. Change* **3**, 683–687 <https://doi.org/10.1038/nclimate1855>
- 42 Suggett, D.J., Hall-Spencer, J.M., Rodolfo-Metalpa, R., Boatman, T.G., Payton, R., Tye Pettay, D. et al. (2012) Sea anemones may thrive in a high CO<sub>2</sub> world. *Glob. Change Biol.* **18**, 3015–3025 <https://doi.org/10.1111/j.1365-2486.2012.02767.x>
- 43 Brown, N.E.M., Milazzo, M., Rastrick, S.P.S., Hall-Spencer, J.M., Theriault, T.W. and Harley, C.D.G. (2018) Natural acidification changes the timing and rate of succession, alters community structure, and increases homogeneity in marine biofouling communities. *Glob. Change Biol.* **24**, e112–e127 <https://doi.org/10.1111/gcb.13856>
- 44 Kroeker, K.J., Micheli, F., Gambi, M.C. and Martz, T.R. (2011) Divergent ecosystem responses within a benthic marine community to ocean acidification. *Proc. Natl Acad. Sci. U.S.A.* **108**, 14515–14520 <https://doi.org/10.1073/pnas.1107789108>
- 45 Smith, J.N., De'ath, G., Richter, C., Cornils, A., Hall-Spencer, J.M. and Fabricius, K.E. (2016) Ocean acidification reduces demersal zooplankton that reside in tropical coral reefs. *Nat. Clim. Change* **6**, 1124 <https://doi.org/10.1038/nclimate3122>
- 46 Baggini, C., Issaris, Y., Salomidi, M. and Hall-Spencer, J. (2015) Herbivore diversity improves benthic community resilience to ocean acidification. *J. Exp. Mar. Biol. Ecol.* **469**, 98–104 <https://doi.org/10.1016/j.jembe.2015.04.019>
- 47 Vizzini, S., Martínez-Crego, B., Andolina, C., Massa-Gallucci, A., Connell, S.D. and Gambi, M.C. (2017) Ocean acidification as a driver of community simplification via the collapse of higher-order and rise of lower-order consumers. *Sci. Rep.* **7**, 4018 <https://doi.org/10.1038/s41598-017-03802-w>
- 48 Teixidó, N., Gambi, M.C., Parravacini, V., Kroeker, K., Micheli, F., Villéger, S. et al. (2018) Functional biodiversity loss along natural CO<sub>2</sub> gradients. *Nat. Commun.* **9**, 5149 <https://doi.org/10.1038/s41467-018-07592-1>
- 49 Nagelkerken, I. and Connell, S.D. (2015) Global alteration of ocean ecosystem functioning due to increasing human CO<sub>2</sub> emissions. *Proc. Natl Acad. Sci. U.S.A.* **112**, 13272–13277 <https://doi.org/10.1073/pnas.1510856112>
- 50 Ekstrom, J.A., Suatoni, L., Cooley, S.R., Pendleton, L.H., Waldbusser, G.G., Cinner, J.E. et al. (2015) Vulnerability and adaptation of US shellfisheries to ocean acidification. *Nat. Clim. Change* **5**, 207 <https://doi.org/10.1038/nclimate2508>
- 51 Côté, I.M., Darling, E.S. and Brown, C.J. (2016) Interactions among ecosystem stressors and their importance in conservation. *Proc. Biol. Sci.* **283**, 20152592 <https://doi.org/10.1098/rspb.2015.2592>
- 52 Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C. et al. (2008) A global map of human impact on marine ecosystems. *Science* **319**, 948–952 <https://doi.org/10.1126/science.1149345>
- 53 Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S. et al. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* **314**, 787 <https://doi.org/10.1126/science.1132294>

- 54 Mcleod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M. et al. (2011) A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO<sub>2</sub>. *Front. Ecol. Environ.* **9**, 552–560 <https://doi.org/10.1890/110004>
- 55 Brander, L.M., Rehdanz, K., Tol, R.S. and Van Beukering, P.J. (2012) The economic impact of ocean acidification on coral reefs. *Clim. Change Econ.* **3**, 1250002 <https://doi.org/10.1142/S2010007812500029>
- 56 Mathis, J.T., Cooley, S.R., Lucey, N., Colt, S., Ekstrom, J., Hurst, T. et al. (2015) Ocean acidification risk assessment for Alaska's fishery sector. *Prog. Oceanogr.* **136**, 71–91 <https://doi.org/10.1016/j.pocean.2014.07.001>
- 57 Gattuso, J.-P., Hoegh-Guldberg, O. and Portner, H.O. (2014) Cross-chapter box on coral reefs. In *Climate Change 2014: Impacts Adaptation Vulnerability Part A: Global and Sectoral Aspects Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E. et al., eds), pp. 97–100, Cambridge University Press, Cambridge, UK and New York, USA
- 58 Gattuso, J.-P., Epitalon, J.-M., Lavigne, H. and Orr, J. (2019) *seacarb: Seawater Carbonate Chemistry. R package. Version 3.2.11 [Internet]*. <https://CRAN.R-project.org/package=seacarb>