

PERSPECTIVE

The deep ocean under climate change

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The deep ocean absorbs vast amounts of heat and carbon dioxide, providing a critical buffer to climate change but exposing vulnerable ecosystems to combined stresses of warming, ocean acidification, deoxygenation, and altered food inputs. Resulting changes may threaten biodiversity and compromise key ocean services that maintain a healthy planet and human livelihoods. There exist large gaps in understanding of the physical and ecological feedbacks that will occur. Explicit recognition of deep-ocean climate mitigation and inclusion in adaptation planning by the United Nations Framework Convention on Climate Change (UNFCCC) could help to expand deep-ocean research and observation and to protect the integrity and functions of deep-ocean ecosystems.

Most habitable space for life on Earth is not terrestrial. More than 90% of its livable volume is in the deep ocean, below water depths of 200 m. The diverse ecosystems in this vast realm play a key role in regulating Earth's climate by absorbing excess heat and CO₂ from the atmosphere. The deep ocean thus helps to buffer the greenhouse effect, but in the process it becomes warmer, more acidic, and less oxygenated (1) (Fig. 1). Such changes threaten ocean productivity, biodiversity, and provisioning of living resources (2). Potential loss of deep-sea biodiversity may suppress adaptation capacity and limit the living library of species, genes, and biomolecules available to future generations (3). The regulating capacity of the deep sea slows climate change while recycling nutrients for surface ecosystems, thus supporting food provision and providing economic and societal benefits (1, 2). However, because the deep ocean is vast and expensive to access, most of its species have not yet been described (4). Most climate change impacts in the deep ocean will remain unknown unless attention is directed to its vulnerable ecosystems.

Several features of deep-ocean ecosystems set them apart from those of the surface and coastal ocean and shape their response to climate change (4). Satellite mapping and robotic studies have shown the seafloor to be highly heterogeneous. Numerous deep-sea habitats, such as seamounts, canyons, hydrothermal vents, and methane seeps,

are hotspots of biodiversity and biomass, concentrating photosynthetic or chemosynthetic energy and sometimes providing essential commercial resources.

There are also vast abyssal habitats beneath low-nutrient (oligotrophic) waters. In these habitats, time almost stands still; potato-size Mn nodules form over millions of years, organisms grow slowly, and full recovery from human disturbances might require centuries or more. These ecosystems are all directly connected to climate change through the transport of heat, oxygen, CO₂, and particulate organic carbon (POC) from the ocean surface through ocean circulation and mixing (1). In these deep-sea settings, animals

can live for hundreds (fish) to thousands (colonial coral) of years. Great longevity and environmental stability may confer limited tolerance to change, limited adaptation ability, and possibly a long time lag between seafloor change and detectable change in fish production or carbon sequestration (5). For more than half of the ocean that lies beyond national jurisdictions, different regulators are responsible for the management of living resources in the water column and of the mineral resources on the seafloor, with biodiversity and its climate-change vulnerability existing in a policy vacuum (6).

Warming

Few long-term hydrographic or biodiversity data series exist for the deep ocean on climate-relevant time scales (typically several decades). Repeat hydrographic surveys have allowed estimates of decadal warming in deep basins, yielding an average temperature increase of up to 0.1°C per decade in the global ocean (7). The situation is, however, heterogeneous among and across deep-sea basins. Much higher warming rates are, for example, documented in the Arctic (8) and the southern Ocean (9).

Most deep-sea species live in very stable thermal regimes; warming of 1°C or less may exert stress or cause shifts in depth or latitudinal distributions and alter species interactions. In the Palmer Deep near the Antarctic Peninsula, warming above a 1.4°C threshold has allowed invasion of lithodid crabs (Fig. 2A), voracious predators

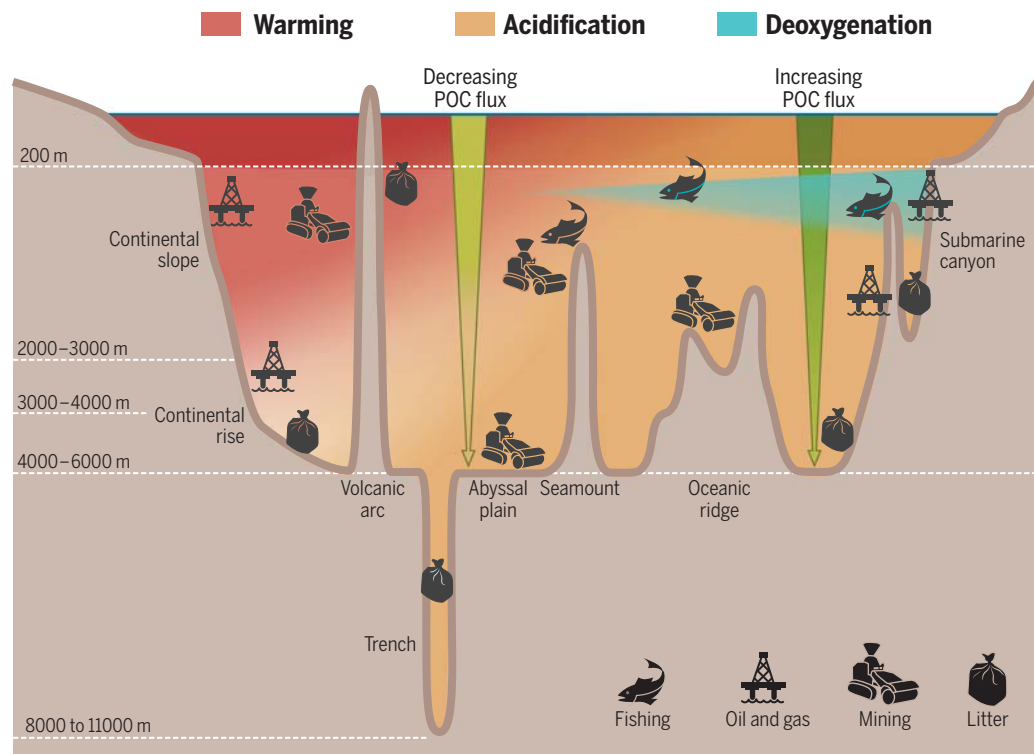


Fig. 1. Humans and climate change in the deep ocean. The schematic illustrates the depth-resolved confluence of current and proposed human exploitation activities and waste disposal with CO₂-induced change in the temperature, pH, and oxygenation of the deep ocean. Overlap of anthropogenic and climate stressors will be greatest along continental margins and at bathyal depths, but changes throughout the deep ocean will compromise ecosystem services globally.

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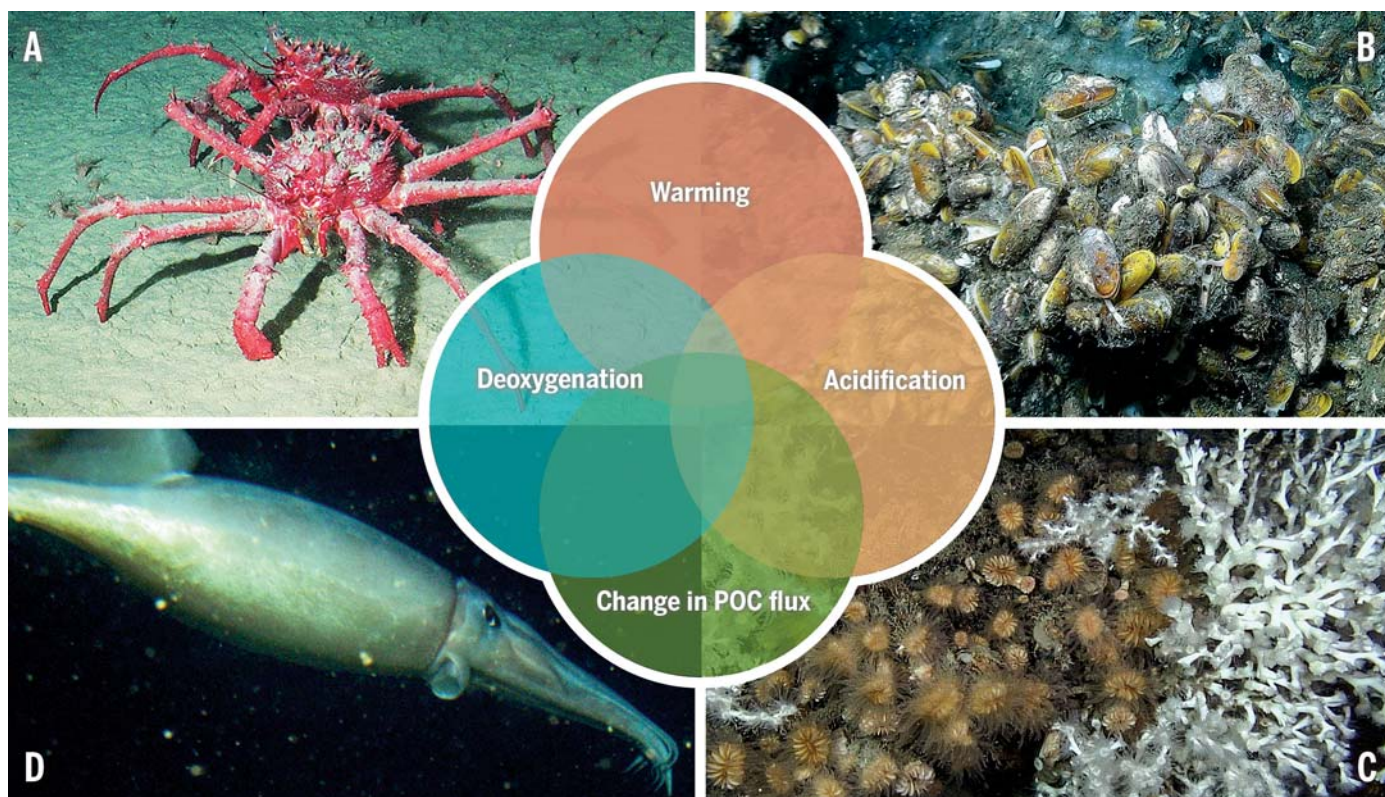


Fig. 2. Winners and losers from exposure to interacting climate stressors.

(A) King crabs invading Palmer Deep in Antarctica enabled by warming (9). (B) Cold seep fauna may expand as warming promotes methane release from the seafloor (12), such as occurs at sites recently discovered along the Atlantic coast. (C) Cold-water coral reefs vulnerable to warming and acidification in Mediterranean canyons. (D) Hypoxia-tolerant Humboldt squid (*Dosidicus gigas*) have extended their distribution in concert with expanding oxygen minima along the East Pacific margin

(20). [Photo credits: (A) Image courtesy of K. Heirman and C. Smith, NSF LARISSA and Ghent University HOLANT projects. (B) Image courtesy of Deepwater Canyons 2013–Pathways to the Abyss, National Oceanic and Atmospheric Administration (NOAA)–Office of Exploration and Research, Bureau of Ocean Energy Management, and U.S. Geological Survey. (C) Image courtesy of N. Le Bris, Laboratoire d'Ecogéochimie des Environnements Benthiques (LECOB), Fondation Total–UPMC. (D) Image courtesy of R. Starr, NOAA–Cordell Bank National Marine Sanctuary]

that appear to have decimated benthic invertebrates (9). In the Mediterranean Sea, naturally warm deep waters (13° to 14°C) place deep-water coral species close to their tolerance threshold (4). In such semi-enclosed ocean basins, ecosystem responses may be rapid and difficult to predict, because warming is not only faster but also discontinuous as a result of intense deep-water convection events (10, 11).

Warming at upper bathyal depths (200 to 2000 m) also threatens to release more methane from deep continental margins through gas hydrate dissociation. A climate-induced shift in warm currents such as the Gulf Stream may be sufficient to release many gigatons of frozen methane from the seafloor (12) (Fig. 2B), surpassing the buffering capacity of the seep microbial and animal biota that routinely oxidize methane (13).

Acidification

Both excess atmospheric CO₂ absorption and the oxidation of organic matter in the water column are causing acidification of intermediate-depth waters globally (14); subsequent subduction of high-CO₂ waters via thermohaline circulation is contributing to rapid acidification in the North Atlantic (15). Direct observation of biological consequences is lacking for the modern deep sea,

and laboratory studies on deep-sea organisms are still rare, constrained by the capacity to maintain them alive. Elevated CO₂ is predicted to reduce the suitable habitat range for calcifying species over multiple life stages, because the depth limit at which water becomes corrosive (undersaturated) for aragonite or calcite will move upward. Effects on deep-water corals (Fig. 2C) are of particular concern, because their three-dimensional aragonite structures form vast gardens that support highly diverse communities and provide key nursery habitat to commercial fishes. The limited occurrence of deep-sea corals in waters naturally undersaturated in aragonite suggests that the energetic cost for these foundation species to grow in these conditions is high (16).

Deoxygenation

A warming ocean holds less oxygen. A warmer ocean is also more stratified because warm water is less dense than cold water, and strong density gradients reduce vertical mixing. The combined effects of reduced oxygen solubility in warmer water and increased thermal stratification create widespread oxygen reduction, termed deoxygenation (17). The effects are greatest at depths of 200 to 700 m and, over the past 50 years, have affected large swaths of naturally hypoxic trop-

ical and subtropical waters in the Eastern Pacific and the Indian Ocean (18). Expansion of the world's naturally occurring low oxygen zones (oxygen minimum zones or OMZs) has led to habitat compression for intolerant demersal, mesopelagic, and bill fishes and habitat expansion of hypoxia-tolerant species such as the Humboldt squid (19, 20) (Fig. 2D). Oxygen exerts tremendous control on marine biodiversity through effects on evolution, physiology, reproduction, behavior, and species interactions (18, 20, 21), as illustrated by El Niño–Southern Oscillation (ENSO)–induced changes in oxygenation. Except for historical core data (22), there are few long-term studies that link oxygen reduction to shifts in extant ecosystems on the deep-sea floor.

Organic flux and hydrodynamics

Increased stratification not only limits deep-water ventilation but also reduces nutrient supply to surface waters from the deeper ocean, where organic matter is recycled. Predicted reduction of phytoplankton production will result in lower POC fluxes to the deep ocean, particularly at mid to low latitudes (23). Below large oligotrophic areas, already food-poor abyssal plains may be further deprived of organic matter supply, resulting in lower benthic biomass and altered respiration

and bioturbation rates (5). Globally, predictions suggest a similar trend affecting 80% of biodiversity hotspots, such as canyons or seamounts, on decadal to century time scales (23). But regional variation is evident, and the deep sea beneath some upwelling regions such as the Northeast Pacific is seeing increasing POC fluxes on decadal time scales (24). Furthermore, short-term events that accelerate exchange between surface and deep waters are regulated by atmospheric processes (storm-induced convection, mesoscale eddies, and dense water cascading) and, hence, are climate sensitive. These events can affect deep-sea benthos through habitat disturbance and enhanced POC fluxes (25), governing the capacity of deep-sea ecosystems to sustain fisheries and provide major regulating services (26).

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Stressor interactions

As in shallow waters, interactions among climate stressors in deep-sea ecosystems are complex (Fig. 1) (27). For example, warming combined with acidification is predicted to deprive deep-water corals now abundant on the South Australia margin of suitable habitat (28). In OMZs that are expanding at bathyal depths, acidification from anthropogenic CO₂ is further enhanced, because the same process that draws down the oxygen (respiration) releases carbon dioxide. The combination of expanding midwater deoxygenation from below with surface warming and acidification from above reduces habitability of pelagic waters for species such as vertically migrating fish and krill. They are squeezed into a narrow-depth layer as they migrate to the surface at night to feed and recoup depleted oxygen, increasing their vulnerability to predators (20). The likelihood that oxygen stress narrows thermal and pH/CO₂ tolerances or reduces calcification rates has yet to be examined for most deep-water species, but recent studies suggest notable threats for the ecosystem engineer *Lophelia pertusa*, a deep-water coral that forms a habitat for many other species (29).

Adaptations to combined climate stressors have occurred in the past over evolutionary time and are exhibited by stress-tolerant organisms in today's ocean (20, 22). For most deep-water species, there are no data on the range shifts, physiological changes, life-history alterations, or rapid evolution necessary to adapt to deep-ocean climate change.

Fueled by a growing demand for food, energy, and raw materials, continental margins and many seamounts are increasingly subject to overfishing

and seascape alteration (30), oil and gas extraction (31), waste disposal (31), and proposed minerals mining (32). Many areas expected to experience the greatest temperature rise, pH drop, and oxygen loss also experience increasing anthropogenic pressure (Fig. 1). Deep-water coral habitat in the North Atlantic, the Mediterranean Sea, and the sea off southern Australia may be particularly vulnerable, because effects of climate change and direct impact from deep-sea bottom fishing may coincide in these regions (16, 28). As climate and human disturbance converge, the accumulation of impacts may alter the state and functions of deep-ocean ecosystems and reduce the important benefits they provide.

Mitigation and adaptation

How can climate change be mitigated in the deep ocean? Reduction and halting of CO₂ emissions are unquestionably the first line of defense; but in coming years the deep ocean will continue to experience the effects of accumulated emissions. Using the deep ocean for mitigation through geoengineering—for example, by surface fertilization with iron, ocean alkalization (the addition of limestone to surface waters in upwelling regions to reduce CO₂ outgassing), or injection of CO₂ at depth—carries many uncontrolled risks. There can be no changes in deep- or surface-ocean properties without major effects on deep-sea animal densities and trophic guilds (23). Geoengineering outcomes would be superimposed on an already changing food supply to the abyss (24).

Options to mitigate the effects of climate change in the deep sea are decidedly limited. Spatial planning to restrict direct human disturbance—for example, by creating networks of deep-water marine protected areas—may help to establish refugia for endangered species and habitats and can reduce cumulative stresses. Protections to reduce physical and chemical disturbances from bottom trawling, mine tailings disposal, oil and gas extraction, or even seabed mining in areas subject to the greatest stress of warming, acidification, or deoxygenation will lessen chances of habitat loss and extinction of species and the ecological functions they support.

To address future climate change, the deep ocean must be recognized by the United Nations Framework Convention on Climate Change (UNFCCC). Such recognition should entail greater attention to predicting and reporting the role of the deep ocean in mitigation and the resulting impacts, acknowledgment of the vulnerability and importance of the deep ocean in negotiation text, and the application of adaptation funding to costly deep-ocean observation and ecosystem studies. Investigations of deep-sea processes, functions, and services should inform planetary carbon budgets and feedback modeling, as well as decisions about resource exploitation in the deep ocean. However, 64% of the ocean is beyond national jurisdiction and would thus not automatically be covered by the UNFCCC, which is an agreement among nation states (33). Nobody is explicitly responsible for protecting the mitigation potential or resilience of ecosystems in these vast re-

gions. Legal instruments currently being negotiated for climate, biodiversity, and sustainable development could help build global capacity for long-term observation and monitoring of deep-sea ecosystems, both within and beyond national jurisdiction, that are subject to climate-induced change. Such observations will be critical to decision-makers and the health of most of the planet's biosphere in coming decades.

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