

REVIEW

Major impacts of climate change on deep-sea benthic ecosystems

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The deep sea encompasses the largest ecosystems on Earth. Although poorly known, deep seafloor ecosystems provide services that are vitally important to the entire ocean and biosphere. Rising atmospheric greenhouse gases are bringing about significant changes in the environmental properties of the ocean realm in terms of water column oxygenation, temperature, pH and food supply, with concomitant impacts on deep-sea ecosystems. Projections suggest that abyssal (3000–6000 m) ocean temperatures could increase by 1°C over the next 84 years, while abyssal seafloor habitats under areas of deep-water formation may experience reductions in water column oxygen concentrations by as much as 0.03 mL L⁻¹ by 2100. Bathyal depths (200–3000 m) worldwide will undergo the most significant reductions in pH in all oceans by the year 2100 (0.29 to 0.37 pH units). O₂ concentrations will also decline in the bathyal NE Pacific and Southern Oceans, with losses up to 3.7% or more, especially at intermediate depths. Another important environmental parameter, the flux of particulate organic matter to the seafloor, is likely to decline significantly in most oceans, most notably in the abyssal and bathyal Indian Ocean where it is predicted to decrease by 40–55% by the end of the century. Unfortunately, how these major changes will affect deep-seafloor ecosystems is, in some cases, very poorly understood. In this paper, we provide a detailed overview of the impacts of these changing environmental parameters on deep-seafloor ecosystems that will most likely be seen by 2100 in continental margin, abyssal and polar settings. We also consider how these changes may combine with other anthropogenic stressors (e.g., fishing, mineral mining, oil and gas extraction) to further impact deep-seafloor ecosystems and discuss the possible societal implications.

Keywords: deep-sea; climate change; ecosystem functioning; biodiversity; benthos

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Introduction

The oceans are a major sink for CO₂ produced by the burning of fossil fuels (Pauchauri et al., 2014) as well as for the heat produced by the greenhouse effect (Glecker et al., 2016). Oceans thus help to buffer multiple aspects of global climate change and their effects on marine and terrestrial ecosystems (Reid et al., 2009). Deep-sea ecological processes and characteristics, such as nutrient cycling, carbon sequestration, productivity, habitat provision, and trophic support, underlie the healthy functioning of ocean ecosystems and provide valuable ecosystem services to mankind (Thurber et al., 2014). For example, nutrients produced during the re-mineralization of organic matter at the deep seafloor are ultimately used by phytoplankton to produce organic matter that fuels secondary production. At the same time, organic-matter degradation and re-mineralisation contribute to carbon biogeochemical cycling in the ocean, and help to buffer the ocean against pH changes and the effects of ocean acidification (Berelson et al., 1997; Wenzhöfer et al., 2001; Cerrano et al., 2013). The health and sustainable functioning of the planet are therefore highly dependent on the deep sea (defined here as > 200 m), which accounts for more than 95% of the volume of the Earth's oceans.

Atmospheric CO₂ concentrations have risen from ~ 280 ppm during pre-industrial times to 407 ppm today as a result of the burning of fossil fuels, deforestation and the removal of other habitats that sequester carbon. Continued use of fossil fuels into the 21st century is predicted to lead to atmospheric CO₂ levels > 900 ppm by 2100 (under Representative Concentration Pathway (RCP) 8.5; Meinshausen et al., 2011), though the precise level is highly dependent on the emission scenario (Pachauri et al., 2014). These rising atmospheric greenhouse gas concentrations have led to an increase in global average temperatures of ~ 0.2°C decade⁻¹, much of which has been absorbed by the oceans, whilst the oceanic uptake of atmospheric CO₂ has led to major changes in surface ocean pH (Levitus et al., 2000, 2005; Feely et al., 2008; Hoegh-Guldberg and Bruno, 2010; Mora et al., 2013; Roemmich et al., 2015).

The deep sea has experienced dramatic changes in physical and chemical variables in the geological past. For example, major expansion and strengthening of oxygen minimum zones (OMZs; O₂ < 0.5 mL L⁻¹) are known to have occurred during abrupt, decadal–centennial-scale warming events during the last deglaciation (Moffitt et al., 2015b; Praetorius et al., 2015). Similar fluctuations in OMZ intensity have occurred during the Dansgaard-Oeschger (D-O) events (millennial-scale abrupt climate oscillations) during the last glacial period (Cannariato and Kennett, 1999; Schmittner et al., 2007). Bottom-water temperature and current velocities have also fluctuated in relation to decadal–millennial scale climatic changes during the last de-glaciation and Holocene (Bianchi and McCave, 1999; Marchitto and deMenocal, 2003; Farmer et al., 2011; Cronin et al., 2012). Finally, deep-sea bottom temperatures have also exhibited systematic glacial-low, interglacial-high patterns during the Plio-Pleistocene (Dwyer et al., 1995; Martin et al., 2002; Sosdian and Rosenthal, 2009; Elderfield et al., 2010).

These paleo-environmental changes significantly modified deep-sea biodiversity and probably ecosystem functioning (Thomas and Gooday, 1996; Yasuhara and Cronin, 2008; Yasuhara et al., 2008, 2016). For example, in the bathyal Santa Barbara Basin (California margin), rapid, alternated shifts in the seafloor ecosystem have occurred in response to changes in OMZ intensity associated with D-O and de-glacial abrupt warming events (Cannariato et al., 1999; Moffitt et al., 2015a). North Atlantic fossil records during the last de-glaciation showed abrupt changes in deep-sea biodiversity associated with a rapidly changing climate (specifically deep-water circulation and temperature) over decadal to centennial time-scales (Yasuhara et al., 2008, 2014). Longer time-scale paleo-ecological studies have also shown systematic changes in faunal structure and biodiversity related to glacial-interglacial climate cycles over the last three million years, and more specifically to climate-driven changes in bottom temperature or particulate organic carbon (POC) flux, depending on the ocean and taxonomic group (Cronin et al., 1996; Cronin and Raymo, 1997; Yasuhara and Cronin, 2008; Yasuhara et al., 2009, 2012a; Yasuhara and Danovaro, 2016). Paleoeecology (Yasuhara et al., 2015) has thus revealed the dynamic and sensitive nature of deep-sea ecosystem structure and biodiversity across a wide range of time scales in response to changing climatic conditions.

Many observational studies are showing that present-day climate change is already impacting deep-sea environments, as evidenced by increased deep-sea temperature (Purkey and Johnson, 2010), deoxygenation (Stramma et al., 2008, 2010, 2012; Keeling et al., 2010; Helm et al., 2011), lowered pH of intermediate deep-waters (Byrne et al., 2010), and altered POC flux to the seafloor (Ruhl and Smith, 2004; Smith et al., 2013). Despite emerging evidence that climate-driven changes in deep-sea environmental conditions may perturb the functioning of ocean-floor ecosystems (Danovaro et al., 2001; Smith et al., 2007, 2008; Dunlop et al., 2016; Yasuhara et al., 2016), our understanding of the extent to which projected physical and chemical changes will lead to deleterious ecological consequences is still very poor (Philippart et al., 2011). Given that deep-sea ecosystems are vitally important to the Earth system (Danovaro et al., 2014) and are at considerable risk from ongoing climate change (Mora et al., 2013; Jones et al., 2014; Levin and Le Bris, 2015), our goal in this paper is to understand and predict the nature and consequences of climate change at the deep seafloor until 2100. To this end, we describe the present status of four major environmental variables at the seabed that are likely to be altered by increased CO₂ emissions to the atmosphere: temperature, oxygenation, pH and food supply (or POC flux). We then explore how these conditions may change by 2100, and assess how these changes are likely to modify benthic biodiversity and ecosystem functioning especially along continental margins, in polar regions, and at the abyssal seafloor. Finally, we briefly address how additional pressures (e.g., from bottom fishing, deep-sea mining) may further impact deep-seafloor ecosystems, and identify the possible societal implications of these combined changes.

Methods

To identify the present and future state of deep-sea ecosystems, we used a combination of expert opinion, current literature, and the output of the IPCC (Intergovernmental Panel on Climate Change) Fifth Assessment Report (AR5) models. To generate maps of present-day ocean conditions at the seafloor we: (1) derived the annual climatological means of bottom temperature and dissolved O_2 based on the World Ocean Atlas 2013 (available from the NOAA National Oceanographic Data Center at http://www.nodc.noaa.gov/OC5/WOA09/pr_woa09.html); (2) calculated the current seafloor pH from total inorganic CO_2 , total alkalinity, temperature, salinity, and pressure using the program CO2SYS (data on seafloor carbon content and the program CO2SYS were available from the Global Ocean Data Analysis Project at <http://cdiac.ornl.gov/oceans/>; data on temperature, salinity and pressure were from the annual climatological mean from the World Ocean Atlas 2013); and (3) estimated POC flux to the global seafloor by first gathering data (from the portal www.science.oregonstate.edu/ocean.productivity) for global climatological monthly mean SeaWiFS (1998–2007) and MODIS (from 2008–2010) Level-3 chlorophyll-a concentration and Level-4 VGPM ocean primary productivity (Behrenfield and Falkowski, 1997). The export POC flux at the seafloor was then calculated using an equation from Lutz et al. (2007) based on the mean and seasonality (standard deviation/mean) of primary production, as well as the mean export depth below the euphotic zone over a 12-year period. The euphotic zone was calculated from the mean surface chlorophyll concentrations using the Case I model of Morel and Berthon (1989), while the export depth was calculated by subtracting the euphotic zone depth from the water depth. The ETOPO1 Global Relief Model from the NOAA National Geophysical Data Center (www.ngdc.noaa.gov/mgg/global/) was used for the global ocean depth.

Future ocean projections for the year 2100 were compiled from all available data generated by Earth Systems Models as part of the Coupled Model Inter-comparison Project Phase 5 (CMIP5) to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (Taylor et al., 2012) as in Mora et al. (2013). A total of 31 Earth System Models from 18 centers in nine countries were collected and multi-model averages of temperature, pH, O_2 and POC flux to the seafloor were reported as the inter-annual mean projections between 2090 and 2100 (Mora et al., 2013). Detailed descriptions of the accuracy and precision of multi-model estimates can be found in Mora et al. (2013).

Characterization of present and future seafloor environmental conditions

Abyssal (water depth 3000–6000 m) and polar habitats can be characterized as cold, slightly alkaline, and well-oxygenated systems (**Table 1; Figure 1**). They are also quite dynamic environments with environmental conditions (e.g., temperature, POC flux) fluctuating over intra- and interannual timescales. At bathyal depths (200–3000 m) on continental margins, spatial gradients

in temperature, pH, O_2 and food supply can be much steeper (**Table 1; Figure 1**). One of the major differences between abyssal and bathyal regions is in terms of food supply to the seafloor, with abyssal regions being characterized by extreme food limitation over many thousands of kilometers (**Table 1; Figure 1**).

Temperature

Currently, temperatures at the abyssal seafloor at low to mid latitudes in the Atlantic, Indian and Pacific Oceans range between about 0.01 and 4°C (**Table 1; Figure 1**) (Yasuhara and Danovaro, 2016). Bathyal temperatures typically range from 2 to 8°C (**Figure 1**), though exceptionally warm seafloor temperatures can be found at upper bathyal depths, and in smaller enclosed seas such as the deep Red Sea (> 20°C; Roder et al., 2013), and bathyal and abyssal Mediterranean Sea (12–14°C). Sub-zero seafloor temperatures tend to occur only at high latitudes (**Table 1; Figure 1**).

Earth-system-model analyses suggest that some abyssal ecosystems are presently warming at rates of 0.01 to 0.1°C decade⁻¹ (e.g., the Southern Ocean; Purkey and Johnson, 2010). Approximately 19% of the ocean's heat uptake has gone into the deep ocean > 2000 m (Talley et al., 2015). Over the next 84 years, the highest temperature changes are likely to occur at the abyssal seafloor in the North Atlantic, Southern and Arctic Oceans (Mora et al., 2013) (**Table 2; Figure 2**). Bathyal depths are also likely to experience increasing temperatures (Soltwedel et al., 2005); Mora et al. (2013) modeled increases of 3.6, 4.4 and 3.7°C in the Pacific, Atlantic, and Arctic Oceans (e.g., Barents and Kara Sea), with lower temperature increases in the Indian and Southern Oceans (e.g., at sites of deep-water formation in the Weddell Sea) (**Table 2; Figure 2**) by 2100. These predictions of temperature change are in alignment with evidence that the deep Greenland Sea has warmed by 0.7°C since the 1950s (~ 0.01°C yr⁻¹; Somavilla et al., 2013). Bathyal waters off Antarctica are also warming by 0.005–0.01°C yr⁻¹ (Smith et al., 2007; Purkey and Johnson, 2010).

Oxygenation

Presently, much of the Atlantic Ocean is well oxygenated (**Figure 1**) relative to the North Indian and Pacific Oceans, where bottom water O_2 concentrations are lower because of the biological removal of O_2 as thermohaline circulation moves deep waters across ocean basins from the North and South Atlantic towards the North Pacific, in isolation from the surface ocean. Warming of the oceans will enhance thermal stratification and density gradients, which will reduce vertical mixing. Combined with a reduction in O_2 solubility in warmer water, increased thermal stratification is predicted to create widespread ocean deoxygenation (Keeling et al., 2010; Long et al., 2016), with the greatest effect in intermediate waters (100–1000 m; Stramma et al., 2012; Bopp et al., 2013). Already, distinct deep-water masses in the Southern Ocean (Helm et al., 2011), eastern North Atlantic (e.g., Sub-polar Mode Water, the Intermediate Water and the Mediterranean Outflow Water; Stendardo et al., 2015), and in the West Pacific

Table 1: Present-day ranges for temperature, dissolved oxygen, pH, and seafloor POC flux at abyssal and bathyal depths^a.
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| Ocean basin | Depth zone ^a | Temperature (°C) | Dissolved oxygen (mL L ⁻¹) | pH | Seafloor POC flux (mg C m ⁻² d ⁻¹) |
|-------------|-------------------------|------------------|--|-----------------|---|
| Atlantic | > 3 km | −0.07 to 4.39 | 4.6 to 6.92 | 7.98 to 8.11 | 0.69 to 10.41 |
| | 0.2–3 km | −1.23 to 27.83 | 1.48 to 7.54 | 7.71 to 8.25 | 1.4 to 108.05 |
| Pacific | > 3 km | 0.7 to 3.84 | 2.01 to 4.9 | 7.72 to 8 | 0.56 to 10.68 |
| | 0.2–3 km | −0.23 to 28.39 | 0.24 to 7.31 | 7.58 to 8.2 | 0.66 to 81.86 |
| Indian | > 3 km | 0.01 to 2.47 | 2.48 to 5.4 | 7.9 to 8.03 | 0.91 to 6.71 |
| | 0.2–3 km | 0.28 to 25.22 | 0.1 to 7.16 | 7.7 to 8.12 | 1.4 to 61.91 |
| Southern | > 3 km | −0.62 to 1.62 | 4.15 to 6.07 | 7.94 to 8.03 | 0.16 to 2.67 |
| | 0.2–3 km | −2.03 to 8.52 | 3.66 to 7.81 | 7.9 to 8.16 | 0.21 to 51.67 |
| Arctic | > 3 km | −1.05 to −0.25 | 5.79 to 7.18 | NA ^b | 0.26 to 4.34 |
| | 0.2–3 km | −1.77 to 7.87 | 2.67 to 8.13 | NA | 0.3 to 75.57 |

^aAbyssal depths are > 3 km; bathyal depths are 0.2–3 km.

^bData not available.

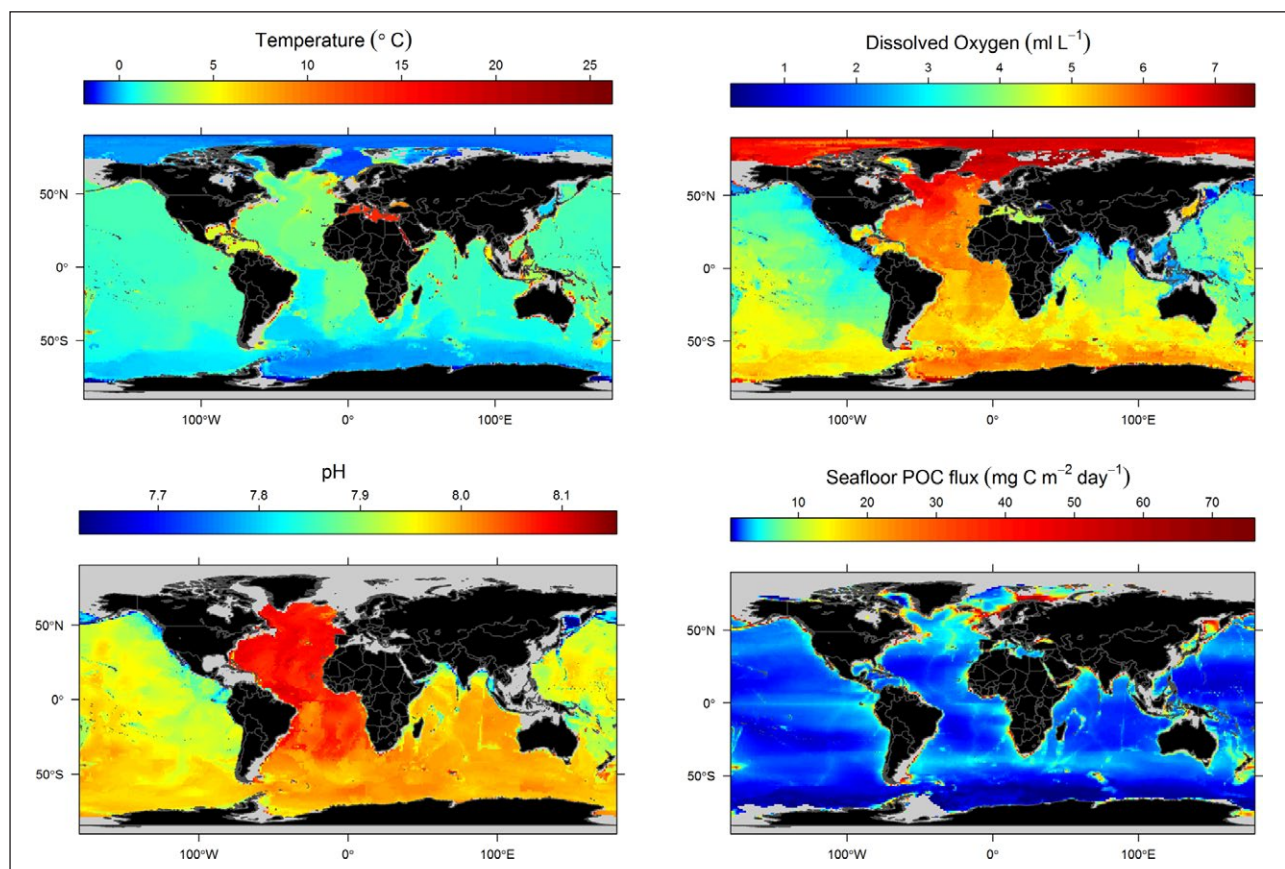
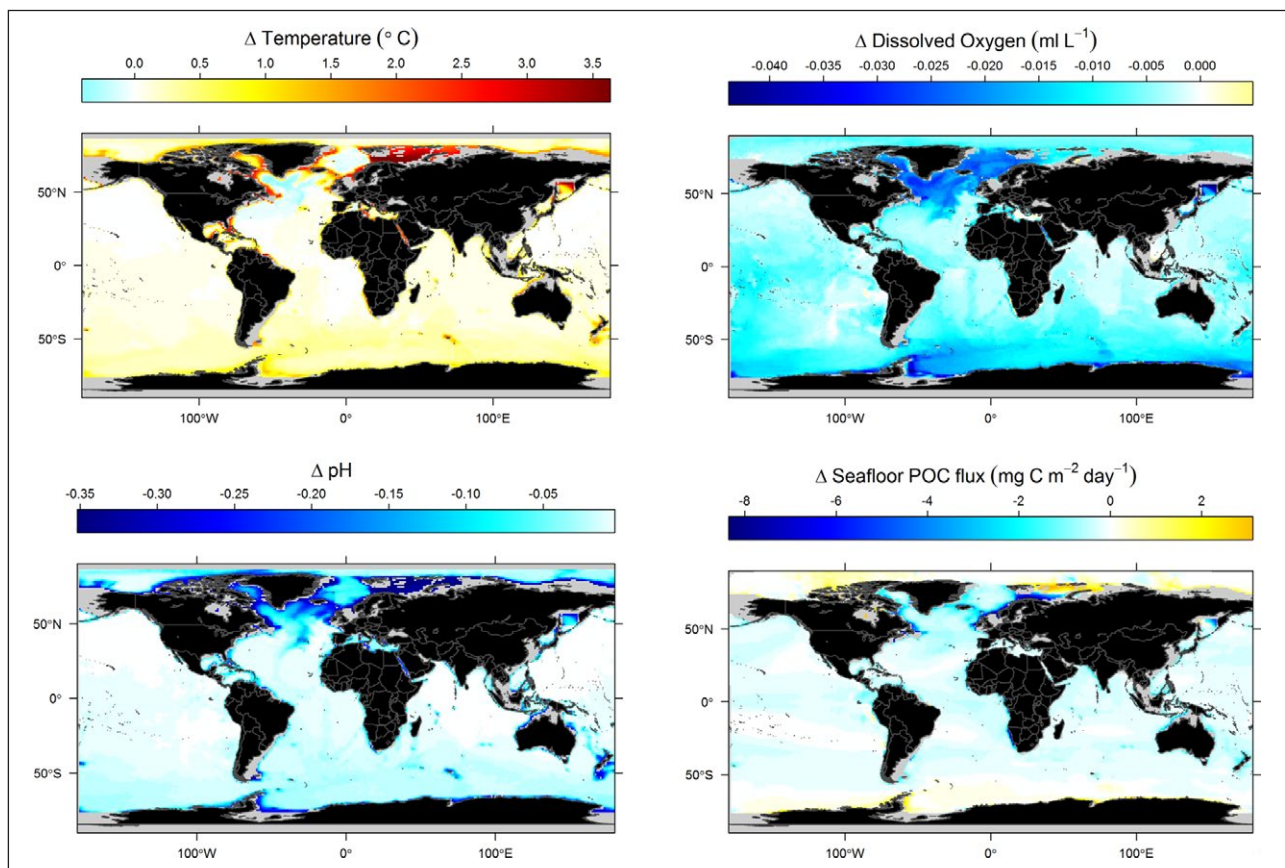


Figure 1: Present-day environmental conditions at the deep seafloor. Temperature (°C), dissolved oxygen (mL L⁻¹), pH, and seafloor POC flux (mg C m⁻² d⁻¹) conditions at the deep (> 200 m) seafloor. DOI: <https://doi.org/10.1525/elementa.203.f1>

Table 2: Modeled changes in temperature, dissolved oxygen, pH, and seafloor POC flux that could occur at the abyssal and bathyal seafloor^a by 2100 relative to present-day conditions. DOI: <https://doi.org/10.1525/elementa.203.t2>

| Ocean basin | Depth zone ^a | Temperature (°C) | Dissolved oxygen (mL L ⁻¹) | pH | Seafloor POC flux (mg C m ⁻² d ⁻¹) |
|-------------|-------------------------|------------------|--|----------------|---|
| Atlantic | > 3 km | -0.37 to 0.98 | -0.03 to 0 | -0.13 to 0 | -1.27 to -0.02 |
| | 0.2–3 km | -0.32 to 4.41 | -0.03 to 0.02 | -0.37 to -0.01 | -13.73 to 0.63 |
| Pacific | > 3 km | 0.02 to 0.47 | -0.01 to 0 | -0.06 to 0.01 | -1.27 to 0.51 |
| | 0.2–3 km | 0.03 to 3.63 | -0.05 to 0.01 | -0.31 to 0 | -5.19 to 2.37 |
| Indian | > 3 km | -0.01 to 0.45 | -0.01 to 0 | -0.06 to 0 | -0.64 to -0.04 |
| | 0.2–3 km | -0.01 to 2.17 | -0.01 to 0 | -0.29 to 0 | -3.7 to 0.4 |
| Southern | > 3 km | 0.09 to 0.74 | -0.03 to 0 | -0.09 to -0.01 | -0.31 to 0.48 |
| | 0.2–3 km | 0.08 to 1.71 | -0.04 to 0 | -0.33 to -0.01 | -1.95 to 4.78 |
| Arctic | > 3 km | -0.13 to 0.76 | -0.02 to 0 | -0.14 to -0.01 | -1.25 to 1.64 |
| | 0.2–3 km | -0.18 to 3.71 | -0.03 to 0.02 | -0.37 to -0.01 | -9.71 to 3.57 |

^aAbyssal depths are > 3 km; bathyal depths are 0.2–3 km.

**Figure 2:** Modelled environmental changes at the deep seafloor in the year 2100. Modeled changes in temperature (°C), dissolved oxygen (mL L⁻¹), pH, and seafloor POC flux (mg C m⁻² d⁻¹) conditions that could be seen at the at the deep (> 200 m) seafloor by 2100 relative to present-day conditions. DOI: <https://doi.org/10.1525/elementa.203.f2>

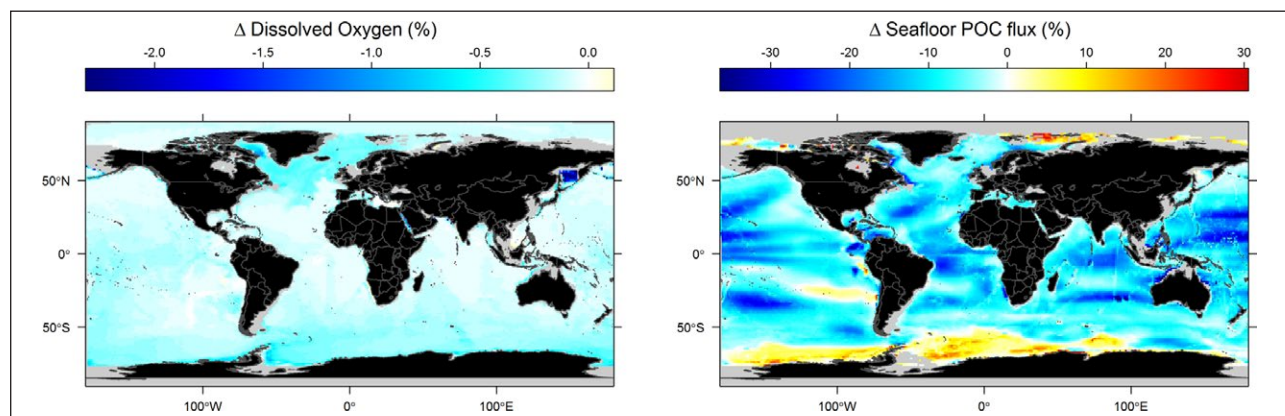
(North Pacific Subtropical mode water; Takatani et al., 2012) display long-term decreases in O₂ concentration. Bathyal seafloor habitats in the North Pacific, North Atlantic, Arctic and Southern Oceans could experience a reduction in bottom-water oxygenation by 0.03–0.05 mL L⁻¹ by the year 2100 (Table 2; Figure 2), which represents a

reduction in water column O₂ levels by 0.7%–3.7% (Table 3; Figure 3). Significant OMZs are presently found along the continental margins of the East Pacific, Southeast Atlantic, West Pacific and North Indian Oceans (Levin, 2003; Helly and Levin, 2004). Ecosystems within and on the fringes of OMZs could be particularly affected by the O₂ and warm-

Table 3: Relative (%) changes in dissolved oxygen and POC flux that could occur at the abyssal and bathyal seafloor^a by 2100 relative to present-day conditions. DOI: <https://doi.org/10.1525/elementa.203.t3>

| Ocean basin | Depth zone ^a | Dissolved oxygen | Seafloor POC flux |
|-------------|-------------------------|------------------|-------------------|
| Atlantic | > 3 km | −0.44 to −0.02 | −27.12 to −1.26 |
| | 0.2–3 km | −0.68 to 2.05 | −36.27 to 4.79 |
| Pacific | > 3 km | −0.37 to 0.03 | −31.8 to 9.8 |
| | 0.2–3 km | −3.71 to 0.25 | −50.4 to 6.54 |
| Indian | > 3 km | −0.22 to −0.02 | −39.65 to −1.27 |
| | 0.2–3 km | −2.36 to 0.72 | −54.61 to 3.87 |
| Southern | > 3 km | −0.46 to −0.06 | −18.81 to 21.2 |
| | 0.2–3 km | −0.84 to −0.03 | −14.63 to 53.16 |
| Arctic | > 3 km | −0.31 to −0.03 | −15.21 to 37.76 |
| | 0.2–3 km | −1.08 to 0.24 | −34.58 to 59.73 |

^aAbyssal depths are > 3 km; bathyal depths are 0.2–3 km.

**Figure 3:** Relative environmental changes at the deep seafloor in the year 2100. Relative change (%) in dissolved oxygen (mL L^{-1}) and seafloor POC flux ($\text{mg C m}^{-2} \text{d}^{-1}$) conditions that could be seen at the deep (> 200 m) seafloor by 2100 relative to present-day conditions. DOI: <https://doi.org/10.1525/elementa.203.f3>

ing changes predicted for bathyal environments (**Table 3**; **Figures 2, 3**; Keeling et al., 2010; Sperling et al., 2016). Though not resolved at the grid resolution shown in **Figure 1**, tropical and subtropical bathyal waters between 200 and 700 m, including those bathyal margins of all major eastern boundaries, have already lost considerable amounts of O_2 over the last half-century, and many OMZs have expanded in volume (Stramma et al., 2008, 2010, 2012; Gilly et al., 2013; Deutsch et al., 2014).

In the abyssal realm, seafloor habitats under areas of deep-water formation (e.g., those in the North Atlantic and Southern Oceans) could experience a maximum decline in O_2 concentration of 0.03 mL L^{-1} by 2100 (i.e., a 0.5% drop from current levels; **Tables 2, 3**; **Figures 2, 3**). Greenhouse warming may also exert an effect on abyssal O_2 levels (as well as pH and temperature) by changing thermohaline circulation (Rahmstorf et al., 2015; Yamamoto et al., 2015). Reduced Atlantic Ocean overturning circulation will initially lead to lower O_2 levels at the deep seafloor, and may alter the intensity of Pacific and Indian Ocean OMZs (Schmittner et al., 2007). However,

over longer terms, deep-water oxygenation may also increase even if Atlantic meridional overturning circulation becomes weaker, as deep convection in the Weddell Sea and Antarctic Bottom Water becomes enhanced (Yamamoto et al., 2015).

pH

The North Atlantic Ocean is currently the most alkaline in terms of seafloor pH, while the pH of the deep North Pacific Ocean is lower (**Figure 1**). This spatial gradient in pH reflects the age and isolation of the water masses, which accumulate CO_2 released by biological respiration as they move through the ocean basins. There is also a contribution of excess atmospheric CO_2 absorption introduced to deep-water masses from dense, cold CO_2 -rich surface waters at downwelling sites (e.g., North Atlantic), which then move through the oceans via meridional overturning circulation. Presently, studies in the Pacific Ocean have revealed that intermediate waters down to 500 m depth have experienced a decline in pH of 0.06 units between 1991 and 2006, with the greatest changes

occurring around 25°N (Byrne et al., 2010). Model predictions from the North Atlantic have revealed that over 17% of the seafloor area below 500 m depth will experience pH reductions exceeding 0.2 units by 2100 because of subduction of high-CO₂ waters by thermohaline circulation (Gehlen et al., 2014). These major pH reductions are projected to occur over important deep-sea features, such as seamounts and canyons (Gehlen et al., 2014). Bathyal seafloor habitats in other areas of the world's oceans will also experience significant reductions in pH by the year 2100 (e.g., a decrease of 0.29 to 0.37 pH units) as a result of the entrainment of CO₂-rich seawater to the seafloor at sites of bottom-water formation (**Table 2; Figure 2**). Since it is estimated to take 1000 years for water entrained at deep-water formation sites to circulate throughout the abyssal ocean basins, vast areas of the abyssal Indian and North Pacific Oceans will experience a lesser shift in pH by 2100 (maximum decrease in pH = 0.06; **Table 2; Figure 2**).

POC flux or food supply

With the exception of certain continental margin habitats (e.g., OMZs, some canyons and seamounts) and chemosynthetic ecosystems, most of the deep sea, and particularly the abyss, is characterized by severe food limitation (POC flux of 1–2 g C m⁻² yr⁻¹; Watling et al., 2013) (**Table 1; Figure 1**). Currently, regions with the highest POC export lie at high latitudes, although transfer efficiency (the proportion of POC exported that arrives at the seafloor) is lowest here compared to lower latitudes. At lower latitudes, extensive mineralization takes place in the upper water column leading to less export from the euphotic zone, but transfer efficiency is higher, as most of the exported carbon tends to be refractory (Henson et al., 2012). Enhanced warming of the upper ocean is predicted to enhance stratification, reducing nutrient input to the upper euphotic zone and causing a shift in phytoplankton assemblages from large, fast-sinking diatoms (with low surface area:volume [SA:V] ratios) to slow-sinking picoplankton (with high SA:V ratios; Bopp et al., 2005). This shift is likely to reduce export flux to the seafloor, as well as transfer efficiency (Buesseler et al., 2007; Morán et al., 2010, 2015; Steinacher et al., 2010). Furthermore, freshening of Arctic regions by sea-ice melt-water and episodic input of large river runoff have been shown to reduce phytoplankton size and, by inference, export flux, a trend that has been projected to continue into the future (Li et al., 2009, 2013). The areas likely to be impacted by significant declines in POC flux owing to enhanced water column stratification lie in the North and South Pacific, North and South Atlantic, and North and South Indian Oceans (**Tables 2, 3; Figures 2, 3**). The abyssal and bathyal regions of the Indian Ocean are predicted to experience declines in POC flux by as much as 40% and 55%, respectively (**Tables 2, 3; Figures 2, 3**) by 2100. For abyssal seafloor habitats, these changes could be severe, as they are some of the most food-limited regions on the planet (Berelson et al., 1997; Danovaro et al., 2001; Smith et al., 1997, 2008). In contrast, the polar oceans are areas where POC flux is likely to rise. Vast abyssal and bathyal areas of the Arctic and Southern Oceans are predicted

to experience a POC flux increase of up to 60 and 53%, respectively (**Tables 2, 3; Figures 2, 3**) as a result of longer ice-free periods (Comiso, 2010), though accounting for future shifts in phytoplankton size and their nutrient supply could modify this expectation (Tremblay et al., 2012; Arrigo, 2013). Localized increases in POC are also predicted for upwelling regions, such as coastal Chile and the west coast of the United States (**Figures 2, 3**) (Jones et al., 2014). These regions have already seen an increase in primary production and frequency of high POC flux to the deep seafloor because of increased wind stress and nutrient upwelling.

Seafloor ecosystem changes under future climate change scenarios

The continental margins

The continental margins of the world's ocean are among the most heterogeneous and diverse of the ocean's environments (Levin and Sibuet, 2012). Hydrographic, topographic and biotic influences create a multitude of seabed habitats and biomass/biodiversity hotspots, and can influence biodiversity–ecosystem functioning relationships (Zeppilli et al., 2016). These include broad expanses of organic-rich sediment, low O₂ zones and OMZs, seamounts, banks, ridges, fjords, canyons, basins, coral and sponge reefs, organic falls, and areas of methane seepage. This heterogeneity supports the biodiversity responsible for a whole host of ecosystem functions and services (Levin and Dayton, 2009; Thurber et al., 2014). Because of the shallower depth of continental margin habitats and closer connections with land compared to abyssal habitats, continental margin ecosystems are likely to experience a greater degree of change in all environmental parameters compared to the abyssal seafloor (**Tables 2, 3**).

While few continental margin systems have been investigated directly in terms of the consequences of climate change, their strong gradients and regional variations have allowed significant understanding of the effects of temperature, pH, O₂ and POC flux on deep-sea benthic ecosystems. Warming of surface waters along continental margins, and increased thermal stratification and reduced nutrient supply to the surface are likely to reduce both productivity and phytoplankton type and size (Smith et al., 2008; Morán et al., 2010, 2015), yielding reduced phytodetrital flux to the seabed (Bopp et al., 2005; Buesseler et al., 2008; Smith et al., 2008). Model outputs suggest that bathyal areas particularly prone to declining POC flux lie in the Norwegian and Caribbean Seas, NW and NE Atlantic, the eastern tropical Pacific, and bathyal Indian and Southern Oceans, which could experience as much as a 55% decline in POC flux by 2100 (**Tables 2, 3; Figures 2, 3**). Elevated seafloor temperatures at northerly latitudes (**Figure 2**) will lead to warming boundary currents and may trigger massive release of methane from gas hydrates buried on margins (Phrampus and Hornbach, 2012; Johnson et al., 2015) especially in the Arctic, with simultaneous effects on global climate, aerobic methane oxidation, water column de-oxygenation and ocean acidification (Biaosoch et al., 2011; Boetius and Wenzhöfer, 2013). Along canyon-cut margins (e.g., the western Mediterranean), warming may

additionally reduce density-driven cascading events, leading to decreased organic matter transport to the seafloor (Canals et al., 2006), though this very process is also likely to reduce physical disturbance at the seafloor. Greenhouse warming will also increase temperature differentials between land and oceans, and intensify wind-driven upwelling in eastern boundary currents, stimulating photosynthetic production at the surface (Bakun, 1990; Bakun et al., 2015; Wang et al., 2015). However, this new production will ultimately start to decay as it sinks and increase biogeochemical drawdown of O_2 . Upwelling will also bring low- O_2 , high- CO_2 water onto the shelf and upper slope (Bakun, 1990; Feely et al., 2008; Bakun et al., 2010; Sydeman et al., 2014; Wang et al., 2015). Increased levels of precipitation on land will also alter terrestrial inputs, including sediments and organic debris, nutrients, and contaminants (Jaedicke et al., 2009; Caroletti and Barstad, 2010) that may smother seafloor sediments, and alter the trophic ecology of deep-sea habitats situated close to land (McLeod and Wing, 2007; McLeod et al., 2010).

Margin habitats are noted for dense, high biomass aggregations of structure-forming species, such as cold-water coral (CWC) reefs and coral 'garden' habitats

(Coleman and Williams, 2002; Roberts et al., 2006; Levin and Dayton, 2009; Buhl-Mortensen et al., 2010; De Leo et al., 2010). CWC structures provide shelter from predation for a variety of fauna and, as such, can act as nursery grounds for commercially important species (Koslow et al., 2000; Baillon et al., 2012; Henry et al., 2013). The habitat complexity of these biogenic reefs also leads to high levels of biodiversity on the reefs (Henry et al., 2007). By altering internal currents, CWCs can also act as ecosystem engineers boosting organic matter deposition at the seafloor (van Oevelen et al., 2009; Soetaert et al., 2016). CWCs and other calcifying taxa (e.g., bivalves and echinoderms) may be susceptible to ocean acidification leading to brittle structures, enhanced susceptibility to predation and a loss of habitat as a result of lowered aragonite and calcite saturation states (Figures 2, 4C).

To date, studies of aragonitic, scleractinian CWC responses to ocean acidification have frequently examined short-term acclimation, with effects on coral bio-mineralization, growth, and skeletal strength only becoming evident in experiments run for periods of a year or more (e.g., Tittensor et al., 2010). Intriguingly, aragonitic CWC species are found close to and even below the aragonite

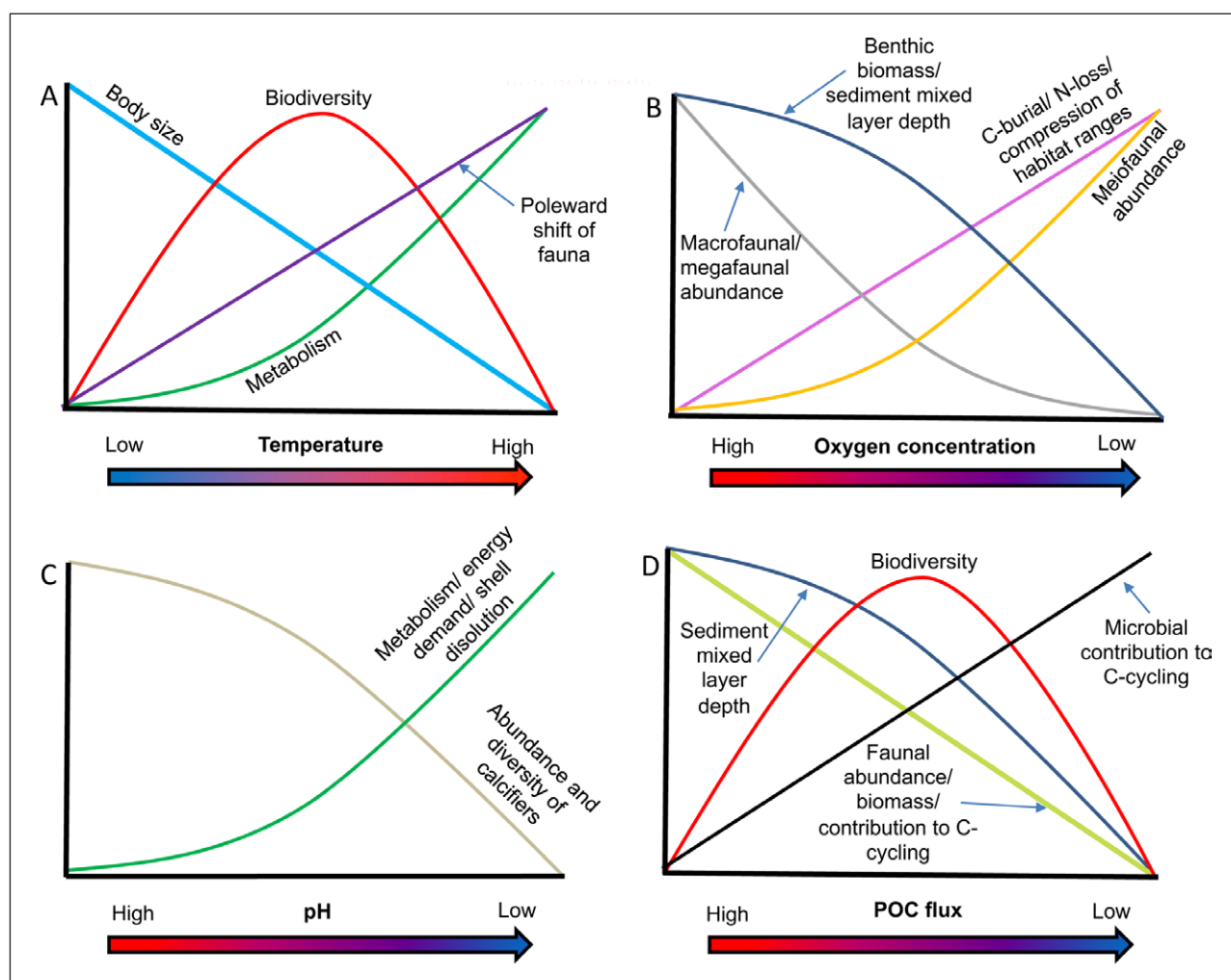


Figure 4: Predicted effects of climate change on deep-sea benthic ecosystems. Concept depictions showing how changes in temperature (A), oxygen (B), pH (C), and POC flux (D) may alter specific ecosystem properties of deep-sea benthic ecosystems. DOI: <https://doi.org/10.1525/elementa.203.f4>

saturation horizon (Roberts et al., 2009a; Findlay et al., 2014), raising the question of whether species adapted to lower saturation states may have inherent adaptations to future lower pH ocean conditions. However, with many of the known CWC reefs projected to be bathed in under-saturated water by the end of the century (Guinotte et al., 2006; Roberts et al., 2006) the accumulated biogenic reef structures will degrade over time, even if living corals persist (Hennige et al., 2015). This degradation could have implications for habitat provision with consequent effects on fish populations and fisheries production. Likely major impact zones include CWC reefs found in the northern Atlantic and Arctic Oceans, the Southern Ocean, and around New Zealand (Guinotte et al., 2006; Yesson et al., 2012) where deep-water pH could decrease by approximately 0.3–0.4 pH units by 2100 relative to current day values. Reduced food supply owing to lower POC fluxes could exacerbate these impacts because the metabolic cost of increased rates of calcification become greater as pH declines (Wood et al., 2008). Calcareous reef habitats in the northern Atlantic could therefore be especially hard-hit (**Figure 2**).

The expansion of low O_2 zones will affect many aspects of deep-sea ecosystem structure and function (Gooday et al., 2010). Biodiversity declines as O_2 levels decline, which can be manifested in multiple ways. Many species of octocorals (including gorgonians and pennatulaceans) provide habitat for a diverse array of associated invertebrates, but octocorals often decrease in abundance as O_2 levels decline (e.g., Etnoyer and Morgan, 2005; Roberts et al., 2009b; Buhl-Mortensen et al., 2010). Reductions in octocoral abundance from de-oxygenation could significantly impact hard substratum availability, habitat complexity and benthic biodiversity (Roberts et al., 2009b; Hennige et al., 2015). Sediment-burrowing fauna will probably be increasingly excluded as water column O_2 levels decline leading to a reduction in the mixed layer depth, and altered bioturbation rates and C-sequestration in sediments (Smith et al., 1997; Smith et al., 2000; Levin et al., 2009; Sperling et al., 2016; **Figure 4B**). This cascade of effects is highly likely at depths of 500–1000 m in parts of the Eastern Pacific, where OMZ expansion is projected to exceed thresholds for biodiversity (Sperling et al., 2016; **Figures 2, 3**).

Intolerant pelagic, demersal and benthic fish and invertebrate species that are mobile will experience habitat compression into shallower depths (McClatchie et al., 2010; Koslow et al., 2011; Sato et al., 2016), or adapt by migrating horizontally along continental slopes into higher- O_2 environments. Hypoxia expansion over methane seeps may inhibit oxidizing symbionts that support dense mussel and tubeworm aggregations. These chemosynthetic aggregations typically enhance production and biodiversity on margins (Levin and Dayton, 2009; Cordes et al., 2010), and can provide critical nursery habitats (Treude et al., 2011). In contrast, hypoxia-tolerant taxa (e.g., squid and jellyfish) may expand their population sizes and distributions with consequences for food-web structure and pelagic-benthic coupling (Gilly et al., 2013; Lebrato et al., 2013; Sweetman et al., 2014a).

Single stressors like warming will limit tolerance windows for other stressors such as low O_2 or low pH (Pörtner and Knust, 2007; Pörtner, 2012). Reductions in food supply and warming together with expansion of low O_2 and pH zones, will increase the vulnerability of key habitats (e.g., CWC reefs) to anthropogenic disturbance (e.g., benthic trawling) and retard recovery of these fragile habitats from physical damage. Heavily-fished areas off the northern coast of Norway, which are also home to abundant CWC reefs (Fosså et al., 2002), could be especially sensitive, as they are predicted to experience an increase in temperature of 2–3°C and pH changes of –0.3 to –0.35 units, while also being subject to declining O_2 (0.03 mL L^{-1} ; **Figures 2, 3**).

Benthic organisms inhabiting sediments along continental margins are responsible for most nitrogen cycling, while over 50% of carbon burial in the ocean occurs in continental margin sediments. In eastern current boundary systems (e.g., off the coast of Namibia), where O_2 is already at sub-oxic levels, these regulating services (e.g., nitrogen removal, carbon sequestration) are currently, and will continue to be highly sensitive to small changes in oxygenation (Deutsch et al., 2011). For example, expansion of low O_2 waters could easily shift carbon-processing pathways by favoring chemosynthesis and by increasing the relative importance of bacteria, protozoa (e.g., foraminifera) and metazoan meiofauna in biogeochemical cycling relative to larger taxa (Levin et al., 2003; Diaz and Rosenberg, 2008; Woulds et al., 2009; Sweetman et al., 2016), which would impact energy flow to upper trophic levels (**Figure 4B**).

The abyssal zone

Major changes in the upper ocean resulting from global warming are likely to include increased sea-surface temperatures and thermal stratification, and reduced nutrient upwelling over vast areas of the open ocean (Bopp et al., 2001; Gregg et al., 2003; Fischlin et al., 2007; Smith et al., 2008). Ocean acidification is also predicted to reduce microbial production of nitrate from ammonium (Beman et al., 2011), which could have major consequences for oceanic primary production because a significant fraction of the nitrate used by phytoplankton is generated by nitrification at the ocean surface (Yool et al., 2007). Major consequences of such changes over regional scales will probably include (1) reductions in primary production combined with (2) shifts from diatom-dominated (low SA:V ratio) phytoplankton assemblages with high POC-export efficiencies to picoplankton communities (high SA:V ratio) characterized by low export efficiencies (Smith et al., 2008; Morán et al., 2010; Morán et al., 2015). In addition, reductions in calcification from lowered pH in surface waters could reduce phytoplankton sinking rates through loss of ballast (Hofmann and Schellnhuber, 2009), though this effect will depend on the ratio of the fraction of ballasted vs. un-ballasted fractions of the sinking POC. Our model outputs suggest that seafloor POC flux will decline in most oceanic areas with exceptions off Peru, the northern coast of Chile, and the Southern and Arctic Oceans (**Tables 2, 3; Figures 2, 3**). The continued

reduction in the extent of sea ice in the Arctic is expected to lead to increased photosynthetic primary production and POC flux there (Jones et al., 2014), which could benefit fauna whose energetic demands increase as a result of ocean acidification (e.g., calcifying taxa). Reductions in seafloor POC flux will be most drastic, on a percentage basis, in the oceanic gyres and equatorial upwelling zones, with the northern and southern Pacific Ocean and southern Indian Ocean gyres experiencing as much as a 32–40% decline in POC flux (**Tables 2, 3; Figures 2, 3**). Recent studies have suggested that the NE Atlantic Ocean could also undergo similar reductions in POC flux (Jones et al., 2014). Because the quantity and quality of POC flux is an important ecological forcing factor in the abyss, abyssal ecosystems will be highly sensitive to such changes (Smith et al. 2008, 2009; Tittensor et al., 2011). For example, 3-fold reductions in POC flux (e.g., from 1.5 to 0.5 g C m⁻² yr⁻¹), which might occur in the equatorial Pacific (Laws et al., 2000), are predicted to halve benthic microbial and nematode biomass (**Figure 4D**). These POC flux changes could also lead to a 5-fold decline in macrofaunal biomass, and cause dramatic reductions in the sediment mixed-layer depth, benthic respiration, and bioturbation intensity (Smith et al., 2008; Jones et al., 2014; **Figure 4D**). Such a decrease in POC flux would also mean a decline in the diversity of nematodes and macrofauna, which are thought to be key functional components of abyssal seafloor ecosystems. This decline in diversity is particularly likely as these groups of organisms tend to rely heavily on detrital matter sinking to the seafloor for their energy requirements (Danovaro et al., 2008; Smith et al., 2008; Jones et al., 2014).

Holothurians are often the prominent abyssal benthic megafauna (Lauerman and Kaufmann, 1998) and play an important role in organic carbon processing and bioturbation. Holothurian population dynamics have been linked to POC flux (Smith et al., 2008) and are considered indicators of climate change impacts on abyssal ecosystems (Glover et al., 2010). Holothurian community dynamics have been examined in detail at long-term time-series sites in relation to shifts in surface phytodetritus input linked to the North Atlantic Oscillation (Porcupine Abyssal Plain, NE Atlantic; Billett et al., 2001) and to the Northern Oscillation Index and Bakun Upwelling Index (Station M, NE Pacific; Ruhl et al., 2014). At both sites, variation in these climate indices were correlated with increased pulses of POC, which resulted in significant increases in abundance of holothurian species, particularly those species able to rapidly use phytodetrital material and successfully reproduce and recruit (Billett et al., 2001; Smith et al., 2006, 2009; Huffard et al., 2016). These studies confirm the predictions of basic macro-ecology and spatial-gradient studies that climate change fluctuations can cause temporal changes in food inputs leading to changes in overall macro- and megafaunal biomass and community structure in terms of size distributions and dominance (Ruhl et al., 2008, 2014). Thus, it is a reasonable expectation that macro- and megafaunal communities will shift in relation to future climatically linked changes in POC flux to the abyssal seafloor (**Figure 4D**). Episodic pulses

provide food supply to sustain benthic communities over periods of deficit (Smith et al., 2013, 2014); the predicted reduction in POC input over large abyssal areas will likely increase these deficits with a significant impact on faunal communities and their role in ecosystem functioning (**Figure 4D**).

POC flux to the seafloor, and its degree of seasonality, also strongly influence benthic foraminiferal abundance, diversity and assemblage composition (Altenbach et al., 1999; Sun et al., 2006; Corliss et al., 2009; Gooday et al., 2012). There are well-established decreases in the relative abundance of calcareous taxa (as well as calcite saturation) compared to agglutinated taxa, and in labile organic matter flux, with increasing water depth. Thus, one consequence of reduced POC flux may be enhanced abundances of agglutinated relative to calcareous foraminifera (Gooday, 2003; Cornelius and Gooday, 2004). Shoaling of the carbonate compensation depth (CCD) over time as a result of increased CO₂ levels would also have important consequences for the diversity of abyssal benthic foraminifera, especially in regions where the depth of the seafloor lies close to the present depth of the CCD (e.g., the eastern Clarion Clipperton Zone, Pacific Ocean). This is an area where foraminifera are overwhelmingly dominated by agglutinated taxa already (Saidova, 1965; Nozawa et al., 2006). A shift from calcareous to agglutinated foraminifera would likely impact deep-sea function (e.g., deep-sea carbon cycling) in addition to altering the biogeographical distribution of fauna (Gooday et al., 2012). Agglutinated foraminifera, particularly forms such as komokiaceans, which are a dominant faunal component in the abyssal deep sea (Tendal and Hessler, 1977), are believed to have a lower metabolic rate and to be less active in carbon processing than calcareous foraminifera (Gooday et al., 2008).

All of these changes predicted for the abyssal zone are likely to fundamentally alter the structure of abyssal ecosystems, as well as the functions that they provide. Changes to microbial and faunal biomass, as well as shifts in biodiversity resulting from changes in POC flux (**Figure 4D**), and the complex interactions among benthic organisms, have the potential to feed back over long time-scales to a range of intertwined functions, such as carbon cycling, which is highly dependent on benthic biomass and diversity (Thurber et al., 2014).

The polar deep seas

The Arctic Ocean and Antarctic coastal seas have particular characteristics in common, notably seasonality in solar radiation, sea-ice cover and temperature, that can modulate surface primary production. Despite these commonalities, the oceanographic and physiographic settings and the geological histories of the Arctic and Antarctic regions are very different. There are also major differences in their faunal characteristics (Dayton, 1990; Clarke and Johnston, 2003), as well as contrasting macro-ecological patterns (Brandt et al., 2009; Yasuhara et al., 2012b). For example, the Arctic seafloor has many more surface-burrowing species, such as echinurans, polychaetes, echinoderms and crustaceans, relative to the Antarctic (Dayton, 1990), but deep-sea diversity is generally much lower in the Arctic

(Culver and Buzas, 2000). This difference is thought to reflect more glacial disturbance and insufficient time for recolonization in the Arctic, as well as fluctuations in surface productivity and reduced circulation during glacial episodes (Culver and Buzas, 2000).

The Arctic and many areas of the Antarctic (e.g., western Antarctic Peninsula or WAP) are predicted to undergo more surface-water warming than other parts of the Earth over the next century, which will affect surface production, sea-ice cover, and hence food availability and quality for deep-sea benthic organisms (see Ingels et al., 2012, for Antarctic coastal to deep-sea ecosystems). Parts of the Antarctic Peninsula, including the WAP, are already experiencing the greatest increase in mean annual atmospheric temperature on Earth (Chapman and Walsh, 2007; Clarke et al., 2007; Solomon et al., 2007; Smale and Barnes, 2008), and temperatures at the seafloor in the Southern Ocean are predicted to rise by as much as 0.7°C at abyssal depths and 1.7°C at bathyal depths by 2100 (**Table 2**). Field and modeling studies have also revealed rapid atmospheric and surface-water warming in the Arctic Ocean during recent decades (Overland et al., 2004; Spielhagen et al., 2011). Bathyal Arctic waters are following this rapid warming trend (Soltwedel et al., 2005), and temperatures at both bathyal and abyssal depths could increase by as much as 0.1–3.7°C relative to present-day temperatures by 2100 (**Table 2**; **Figure 2**). A recent study has shown that deep-sea benthic Archaea can be more sensitive to temperature shifts than their bacterial counterparts; changes in deep-water temperature may thus alter the relative importance of Archaea in benthic ecosystem processes at polar latitudes (Danovaro et al., 2016). Warming at polar latitudes will also open up new habitat for invasive species (**Figure 4A**). For example, in the Arctic, the commercially important snow crab has extended its range to the north (Alvsvåg et al., 2009; Bluhm et al., 2009), and warming appears to have led to the appearance of highly predacious, temperature-sensitive king crabs (*Lithodidae*) in waters of the WAP (Smith et al., 2011). These invasive top predators can threaten the diversity of epi- and infaunal communities, as well as physically disturb large areas of soft sediment (Smith et al., 2007). On the other hand, warming-induced extensions of the ranges of temperate–subpolar benthic species into polar oceans (Bluhm et al., 2011) may increase benthic diversity, both in the short-term (Węśławski et al., 2011) and the long-term (Rasmussen et al., 2003; Yasuhara and Danovaro, 2016), although these invasive species are likely to displace less competitive, endemic species unable to cope with increased temperatures (**Figure 4A**).

Although open ocean polar regions are likely to experience increased primary productivity and POC flux, the production and transport of organic matter to the seafloor will probably initially decline in deep-sea habitats located close to land. As polar and sub-polar regions become warmer, glacial meltwater and erosion of melting tundra (Węśławski et al., 2011) will enhance water column turbidity in coastal zones (Grange and Smith, 2013; Sahade et al., 2015), reducing water column light levels and phytoplankton production, which could affect near-shore

deep-sea systems. The increased sedimentation in deep coastal areas, particularly fjords, may also smother or clog the breathing and feeding apparatus of sessile suspension-feeding fauna. Ophiuroids, capitellid polychaetes and other opportunists may be favored by increased sediment inputs. In deep Arctic fjords, high sediment fluxes already create large areas of burial disturbance, which can negatively impact trophic complexity, diversity and productivity of benthic assemblages while also inducing O₂ stress (Syvitski, 1989; Włodarska-Kowalczyk et al., 2005; Renaud et al., 2007). In time, continued warming will reduce sediment fluxes into many high-latitude fjords as a result of glacial retreat onto land, potentially increasing benthic productivity and biodiversity (Syvitski et al., 1989).

Changing ice regimes will impact glacial and ice-sheet calving, with ramifications for physical disturbance in the deep sea. Large icebergs can scour the sediment down to 400 m on the Antarctic shelf. This disturbance leads to scale-dependent recolonization of scoured areas and an increased input of dropstones (Smale and Barnes, 2008). These processes will enhance seafloor heterogeneity and create hard substrates for sessile megafauna (Schulz et al., 2010; Meyer et al. 2015, 2016). Dropstones also create diverse microhabitats for meiofauna, allowing for greater trophic and functional diversity around stones (Hasemann et al., 2013; Gooday et al., 2015). In the longer term, iceberg scouring and dropstone deposition will tend to elevate diversity on regional scales through (re)colonization processes, although the immediate effect of scouring will be local elimination of many species (Gutt et al., 1996; Gutt and Piepenburg, 2003). In addition, recent evidence suggests that iceberg production followed by melting might significantly elevate local nutrient levels, driving greater primary production and POC flux to the seafloor in deeper waters (Smith et al., 2007), though this will probably decline after initial increases under continued warming. Thus, the immediate direct impacts on seafloor communities will be relatively short-lived, but the wider effects may be longer lasting. Finally, melting of icebergs and glacial ice may lead to freshening of surface waters leading to enhanced stratification of the upper water column and the release of essential nutrients and trace metals such as iron (Wang et al., 2014). Together with decreased sea-ice cover these factors may act to increase primary production and POC flux. However, increased respiration (owing to increased temperatures) might result in local hypoxia, especially in isolated intra-shelf basins and fjords such as those found along the WAP.

Changes in the quantity and the quality of POC flux to the seafloor will have impacts on ecosystem structure and function (**Figure 4D**). Present-day reductions in sea-ice and ice-shelf cover (Comiso, 2010) are leading to changes in upper-ocean pelagic dynamics (e.g., increasing surface primary production, and generating shifts from krill to salps; Loeb et al., 1997; Arrigo et al., 2008, 2013; Arrigo and van Dijken, 2011). Under high O₂ conditions at shallow depths, metazoans tend to outcompete bacteria in terms of organic matter processing when carbon input to the seafloor increases (van Nugteren et al., 2009; Sweetman et al., 2014b). If the same holds true for the deep seafloor,

then elevated POC fluxes caused by reduced sea-ice cover could trigger a switch from dominance of benthic organic matter processing by bacteria to dominance by metazoans with consequences for energy flow to upper-trophic levels (**Figure 4D**). Increases in the abundance, biomass and diversity of benthic communities, the depth of bioturbation, the prevalence of large, habitat-forming taxa (sponges, benthic cnidarians), and the extension of species ranges downslope into deeper water (De Rijk et al., 2000) are other likely consequences of enhanced POC flux (**Figure 4D**). However, minor increases in temperature will also increase overall metabolic rates of benthic and pelagic communities. In Antarctic regions, one of the key processes that is thought to govern the deep-water soft sediment communities is captured in the FOODBANCS hypothesis (Smith and DeMaster, 2008), according to which concentrated summer food pulses and slow microbial enzymatic activity caused by the cold temperatures provide a long-lasting food bank that supports benthic metazoan communities (Mincks et al., 2005). With increasing temperatures, bacterial recycling will be enhanced, potentially leading to a non-linear increase in the overall metabolism of the benthic community and increased food limitation in deeper seas (**Figure 4A**). This effect could explain why some groups like meiofauna may prefer to feed on bacterial food sources in polar areas (Ingels et al., 2010).

Another important stressor, ocean acidification (OA), will be enhanced at high latitudes because of the higher capacity of seawater to absorb CO_2 at low temperatures (Orr et al., 2005; **Table 2**; **Figure 2**). While some areas will experience increased POC flux resulting from a loss of sea-ice cover that could help alleviate some OA effects (Wood et al., 2008), the additional carbon deposited will increase respiratory CO_2 production with impacts on carbonate dissolution. Carbonate dissolution is an issue of particular concern around the Antarctic continent, where it exerts a strong influence on the distributions of benthic foraminifera and other calcareous fauna. Here, the CCD is currently 'multi-bathic', ranging from a few hundred meters in intra-shelf basins to several thousand meters over abyssal plains. The depression of the CCD will increase the energy required for organism calcification (Wood et al., 2008), impacting many of the archetypal Antarctic fauna (e.g., molluscs, echinoderms, foraminifera and ostracods). The exact nature of these effects, however, needs detailed examination because, as with all of these factors, there will be synergies that could either exacerbate or ameliorate the stress induced by another perturbation.

Many of the changes outlined above could affect both Arctic and Antarctic seafloor ecosystems, although their intensity will probably vary between the poles and among areas within polar regions that are warming at different rates (e.g., WAP versus the eastern Ross Sea). Moreover, different organism groups (e.g., bacteria versus metazoans), and different life stages of the same species (e.g., larvae versus adults), may respond differently and display different degrees of sensitivity to environmental changes (Ingels et al., 2012).

Implications of climate forcing on societal uses and values of the deep sea

Climate mitigation by the deep ocean may ultimately compromise many of the ecosystem services we value. The large fraction of the planet covered in deep waters guarantees that most carbon sequestration and significant nitrogen cycling in the ocean occurs here. Presently the ocean absorbs approximately 25% of industrial area CO_2 emissions, and 93% of the heat; much of this absorption occurs in deep waters below 200 m (Levin and Le Bris, 2015). Non-market supporting services are provided by deep-sea ecosystems in the form of habitat provision, nursery grounds, trophic support, refugia, and biodiversity functions provided by assemblages on seamounts, coral and sponge reefs, banks, canyons, slopes, fjords and other settings (Armstrong et al., 2012; Mengerink et al., 2014; Thurber et al., 2014; Levin and Le Bris, 2015). The extensive species, genetic, enzymatic, and biogeochemical diversity hosted by the deep ocean also holds the potential for new pharmaceutical and industrial applications, as well as keys to adaptation to environmental change. Because huge expanses of the deep ocean will be exposed to changing environmental conditions as a result of climate change (Mora et al., 2013; this study), the societal impacts of climate change in the deep sea will undoubtedly be widespread, complex and dynamic. Some effects will be direct; for example, we expect alterations in the distributions and health of open-ocean and deep-sea fish populations and commercially exploited stocks. This impact will result from warming-induced changes in metabolism (Deutsch et al., 2015) and body size (Cheung et al., 2013) linked to latitudinal or depth shifts in species distributions, in addition to vertical habitat compression from OMZ expansions (Prince and Goodyear, 2006; Stramma et al., 2010, 2012; Yasuhara and Danovaro, 2016). Less clear are the impacts of acidification stress and multiple stressors on deep-sea fish populations and fisheries production (Rosa and Seibel, 2008). These effects can be indirect, via shifts in food availability or species interactions (e.g., predation and competition). Direct effects from depletion of O_2 levels and rising water temperatures over the next century may also impact embryonic survival rates of vulnerable deep-sea oviparous (egg-laying) elasmobranchs that currently deposit their capsules at the seafloor in very narrow oceanographic niches with distinct O_2 , salinity and temperature conditions (Henry et al., 2016).

At the same time, the deep sea is fast becoming a target area for increased exploitation of key resources and the dumping of pollutants (Mengerink et al., 2014). For example, oil and gas are currently being extracted to depths > 3000 m on continental margins, with increasing risk for leakage and spills (Cordes et al., 2016). Pressure from fishing has also increased since the mid-20th century on seamounts and along continental margins, and there is now strong evidence that many deepwater fish species (e.g., rockfish, Greenland halibut, lingcod and tusks, orange roughy, sablefish and blue grenadier) have been severely exploited through trawling and longlining, with some species having been fished to commercial extinction (e.g., pelagic armourhead; Koslow et al. 2000). There

is also extensive interest in mineral mining at hydrothermal vent systems along mid ocean ridges and back arc basins, bathyal seamounts and polymetallic nodule areas at abyssal depths, as well as for phosphorites on margins (Mengerink et al., 2014; Thurber et al., 2014; Wedding et al., 2015; Amon et al., 2016; Levin et al., 2016; Vanreusel et al., 2016). Deep-sea sediments and organisms are also sinks for a variety of chemical pollutants, including persistent organochlorine pollutants (e.g., PCBs), which may have toxic effects for a variety of fauna at high concentrations (Froescheis et al., 2000; Looser et al., 2000; Ramirez Llodra et al., 2011).

Many of the areas that will be targeted for resource extraction lie in areas that will be most heavily impacted by climate change (e.g., the Arctic for oil, gas and fisheries, the equatorial open ocean for nodule mining, upwelling margins for phosphorites, and the North Atlantic for fishing). Although some animals (e.g., fishes) may be able to adapt to a limited degree to these anthropogenic stressors, for example, by accelerating their growth and reaching maturity at earlier ages (Koslow et al., 2000), the slow population growth rates and long generation times that characterize the evolution of many deep-sea organisms will ultimately limit their adaptation to stress. Additional stresses imposed by low O_2 , low pH, elevated temperature and reduced food supply are likely to further reduce the resilience of individual species and ecosystems to anthropogenic stressors, and slow rates of recovery. For example, slowed growth of carbonate skeletons in the face of acidification will reduce recovery of biogenic habitats from bottom fishing disturbance, and delayed development under hypoxic conditions and nutritional stress with declining food availability could impact communities recovering from oil pollution and mining impacts, which will further compromise ecosystem structure and function in the deep sea. Thus, a key challenge going forward is to understand the synergies between different stressors associated with climate change and those linked to direct human impacts, such as physical disturbance from bottom trawling or mining plumes, overfishing, oil spills and more.

There is a growing need for multi-sector ocean governance in the deep sea. Efforts to reform the single-sector approach to marine spatial management should incorporate expected climate-induced changes in temperature, oxygenation, pH, and POC flux to the seabed in the development of regional and international management scenarios. By the end of the 21st century, managers will also need to account for background changes in ecosystem functions and services that may not relate to anthropogenic climate change. Naturally occurring interannual and multidecadal shifts in regional ocean regimes such as the Pacific El Niño-Southern Oscillation, the North Atlantic Oscillation, and the Atlantic Multidecadal Oscillation, for example, are bimodal oscillations that cycle between phases of warmer and cooler sea surface temperatures. These oscillations can produce effects that mimic CO_2 -induced changes (e.g., altered upwelling regimes of deep nutrient-rich waters with effects on POC flux; Merino and Monreal-Gomez, 2009). Observations of climate variables underpin much of the knowledge and modeling described

here. However, these observations are decidedly sparse in the deep sea and need to be enhanced, through sustained deep-ocean observing (e.g., via Deep Argo). Meeting this need will require enhanced international co-operation across disciplines as enshrined by the Global Ocean Observing System, and the associated, nascent Deep Ocean Observing Strategy. An integrated approach would allow policy-makers to react to changing distributions and resilience of marine resources, and would underpin adaptive multi-sectoral marine spatial plans to help safeguard deep-sea ecosystems.

The deep sea provides our global society a diversity of ecological and ecosystem services, which are likely to expand in the coming decades. At the same time, a number of co-occurring stressors are likely to impact the ecology of deep-sea communities and the ways in which these communities influence the long-term carbon cycle. As society makes critical decisions about the use and conservation of deep-ocean ecosystems, it is important that we recognize the vulnerability of life on the ocean floor to climate-related stressors, and the direct influence that the surface climate can exert on the world's largest biome.

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Competing interests

The authors have no competing interests to declare.

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- Generated research funding: AKS, ART, LAL, CRS
- Developed methods and carried out analysis: AKS, ART, LAL, CRS, CM, CLW, DOBJ
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