Review

Abyssal food limitation, ecosystem structure and climate change

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The abyssal seafloor covers more than 50% of the Earth and is postulated to be both a reservoir of biodiversity and a source of important ecosystem services. We show that ecosystem structure and function in the abyss are strongly modulated by the quantity and quality of detrital food material sinking from the surface ocean. Climate change and human activities (e.g. successful ocean fertilization) will alter patterns of sinking food flux to the deep ocean, substantially impacting the structure, function and biodiversity of abyssal ecosystems. Abyssal ecosystem response thus must be considered in assessments of the environmental impacts of global warming and ocean fertilization.

The nature of abyssal habitats

Based on faunal distributions and environmental characteristics, the abyssal seafloor occurs between ocean depths of 3000 and 6000 m [1,2]. Abyssal ecosystems are truly vast, covering 54% of the Earth's surface [3]; they are essentially a network of plains and rolling hills punctured by seamounts, and subdivided by mid-ocean ridges, island arcs and ocean trenches (Figure 1). Several ecological generalizations can be made about abyssal habitats [4,5]. The abyssal seafloor is mostly covered by fine sediments (medium sands to clays) (Figure 2). It is also characterized by an absence of *in situ* primary production (except at spatially rare hydrothermal vents and cold seeps), well-oxygenated waters and by low temperatures of -0.5–3.0°C [3,4]. Most of the abyssal seafloor experiences low current velocities and little sediment erosion; however, in some regions (e.g. beneath western boundary currents [3,6]), sediment erosion can be frequent. Much of the habitat structure of abyssal sediments is biogenic, consisting of the tests of giant protozoans and the burrows, mounds and tracks of megabenthos [3,4] (Figure 2). Hard substrates associated with manganese nodules and fault scarps occur in many parts of the abyss, and these substrates support faunal assemblages distinct from those in sediments [4,5,7] (Figure 2).

Probably the most important ecological characteristic of abyssal ecosystems is energy limitation; abyssal seafloor communities are considered to be 'food limited' because benthic production depends on the input of detrital organic material produced in the euphotic zone thousands of meters above [4]. Most of the organic flux arrives as an attenuated rain of small particles (typically, only 0.5–2% of net primary production in the euphotic zone), which decreases inversely with water depth [8] and varies regionally with levels of primary production in the upper ocean [9]. The small particle flux can be augmented by the fall of larger carcasses and downslope transport of organic material near continental margins [4,10].

Because of the size and remoteness of the abyss, ecosystem structure and function at the seafloor have historically been very poorly studied. For example, more than 80% of the hundreds of species of seafloor invertebrates collected at any abyssal station are new to science [11–13]. Nonetheless, it is recognized that local diversity (i.e. on

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Glossary

Abyssal: ocean floor depths from 3000 to 6000 m.
Bathyal: ocean floor depths from 200 to 3000 m.
Benthos: organisms living on or in the seafloor.
Bioturbation intensity (D_b): a parameter measuring the 'diffusive mixing' intensity of bioturbation, or reworking of sediment grains, by sediment-dwelling animals.
Bottom-up processes: controls on biotic community structure operating from lower to higher trophic levels, for example, control of features of detritus-based food webs (e.g. species structure, biomass, size distributions, etc.) by detritus availability.
Deposit feeder: an animal that ingests deposited, particulate material which primarily consists of inert sediments of low food value (mineral grains, refractory organic matter, etc.).
Export efficiency: the percentage of net primary production in the euphotic zones that sinks into the deep ocean (i.e. below depths of about 500 m).
Export production: the amount of organic matter produced in the ocean by primary production that sinks into the aphotic zone (i.e. below about 500 m).
Macrofauna: benthic animals passing through a 2 cm mesh, or not recognizable in bottom photographs, but retained on a 250–500 μm sieve.
Manganese nodules: rock concretions (typically 5–10 cm in diameter) on the seafloor formed of concentric layers of iron and manganese hydroxides.
Megafauna: animals recognizable in bottom photographs and video images, or collected in bottom trawls with mesh $\geq$ 2 cm.
Meiofauna: benthic animals passing through a 250–500 μm sieve and retained on a 41–63 μm sieve.
Particulate organic carbon (POC): organic carbon in particulate form (i.e. that can be filtered out of a sample), much of which sinks through the water column, providing a primary food source for abyssal ecosystems.
Pulse-chase experiments: experiments used to study ecosystem function by adding isotopically labeled phytoplankton detritus to intact sediment communities. The uptake and respiration of the phytodetritus is then tracked over time (e.g. [33]).
Sediment mixed-layer depth: the thickness of surface sediments actively reworked by benthic animals. The main agents of reworking are deposit-feeding and burrowing animals.
Working-species collections: collections of animals that have been sorted to the species level, but where the bulk of species have provisional identifications (species A, B, etc.) and remain undescribed.

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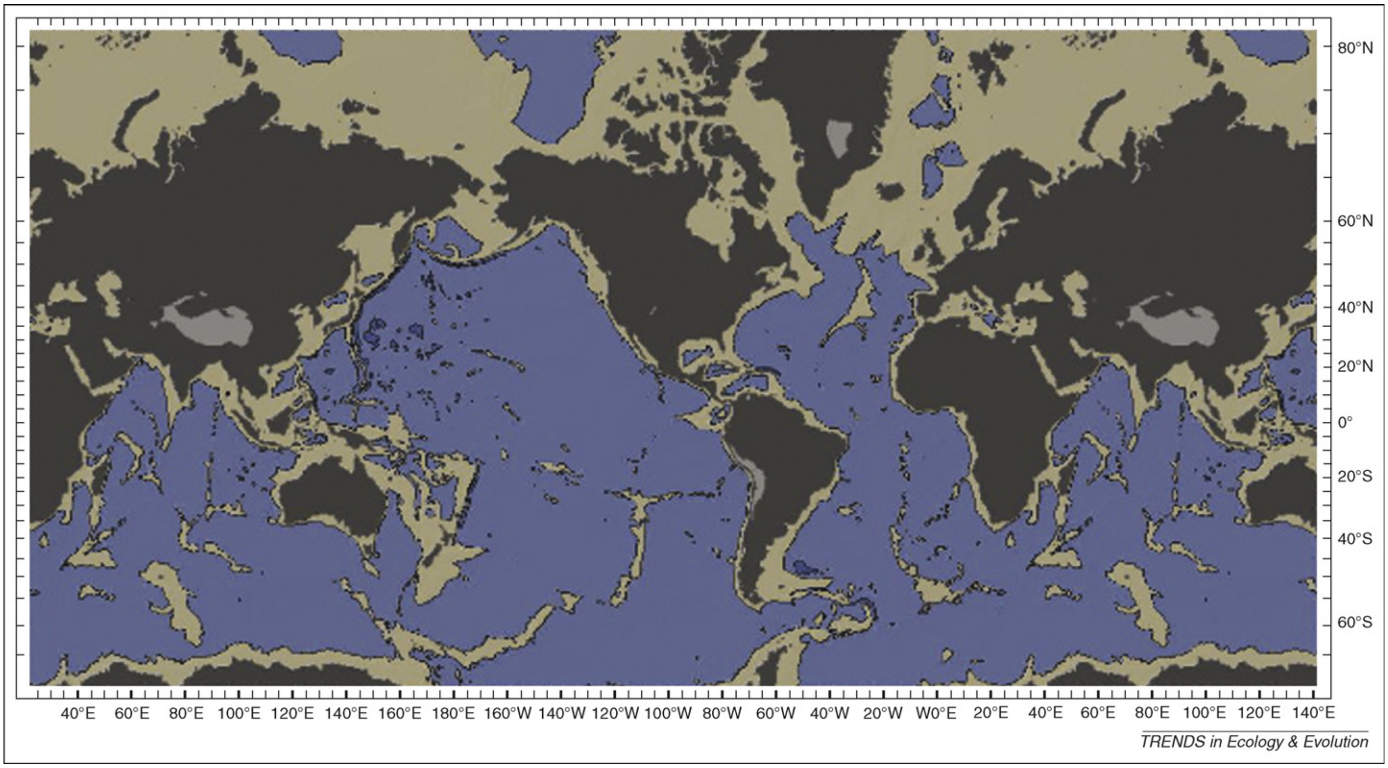

Figure 1. Map of the abyssal seafloor, namely bottom depths of 3000–6000 m (light blue). Depths greater than 3000 m are dark blue, depths of 0–3000 m are gray and landmasses are black or off-white. (Map created with GeoMapApp.).

spatial scales 0.1–1 m^2) in abyssal sediments can be moderate to high (e.g. with ~50 species for every 150 individuals of polychaetes, and more than 100 macrofaunal species per 0.25 m^2 [4,13]). Very rough global extrapolations suggest, albeit controversially, that the vast size of the abyss could allow it to be a major reservoir of biodiversity [13,14]. The enormous abyss also provides important ecosystem services, exerting significant influence on ocean carbon cycling, calcium carbonate dissolution and atmospheric CO_2 concentrations over timescales of 100–1000 years [15–17].

Here we show that many aspects of ecosystem structure and function in the abyss are strongly modulated by the rate and nature of food flux to the seafloor. We then argue that climate change and successful ocean fertilization will substantially alter productivity patterns in the surface ocean and in turn the flux of food material to the abyss; this will profoundly affect abyssal ecosystem structure and function, altering patterns of diversity and ecosystem services.

Spatial patterns of food flux and abyssal ecosystem structure and function

It has long been postulated that an external factor, namely particulate-organic-carbon (POC) flux from the euphotic zone, controls spatial patterns of faunal biomass and abundance at the abyssal seafloor [18–20]. However, annual POC flux and benthic parameters have been measured concurrently at only a few sites in the abyssal ocean [10,21]; thus, most studies of the role of food limitation use proxies for POC flux, in particular water-column depth [22] and primary productivity in the overlying water column [23]. Nonetheless, recent data demonstrate a profound importance of food availability, in terms of annual POC flux, to abyssal ecosystems. For example, across regions where POC flux to the abyssal seafloor has been measured directly, there are strong linear relationships between POC flux and the abundance and biomass of specific biotic size classes such as bacteria, macrofauna and megafauna [4,24] (Figure 3). Key characteristics of community function, including the rates of sediment community respiration (i.e. organic-matter mineralization) [4] and the depth and intensity of bioturbation [21,24], decrease rapidly with declining POC flux to abyssal ecosystems (Figure 3). These community functions play important roles in the ecosystem services provided by the abyss, with organic-matter mineralization and bioturbation rates and depths affecting nutrient regeneration, carbon burial and rates of calcium carbonate dissolution at the seafloor. Thus, POC flux at the seafloor appears to control the rates and patterns by which abyssal ecosystems help to modulate atmospheric CO_2 levels and calcite saturation levels in the ocean [16,17,25].

Proxies for POC flux from the euphotic zone, in particular water depth, reveal that other fundamental characteristics of abyssal ecosystems also depend strongly on this external factor. For example, maximum body size within gastropods decreases substantially from 3000 to 5500 m in the northeast Atlantic, likely because diminishing food supply prevents growth to larger body sizes [26,27]. This pattern has led to new insights into the potential influence of food availability on body sizes in other habitats such as terrestrial islands, where extreme food limitation can also yield size reductions in a variety of taxa [27]. On a global scale, it has been shown that average biomass of the two largest size classes of benthos (the macrofauna and

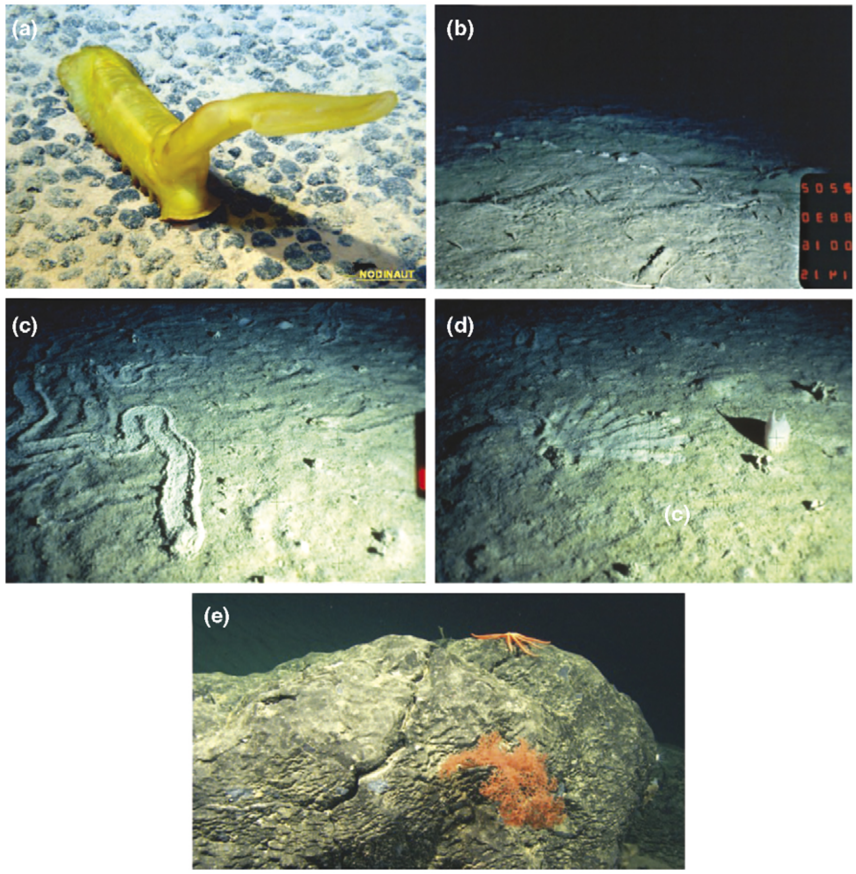

Figure 2. Representative views of abyssal seafloor habitats and abyssal megafauna. **(a)** Manganese nodule field at 4900 m between the Clipperton and Clarian Fracture Zones in the North Pacific. The yellow elasipod holothuroid, *Psychropotes longicauda*, is a widely distributed deposit feeder and uses its upright 'sail' to use current energy for transport along the seafloor. For scale, the body of the holothurians on the seafloor is ~50 cm long. (Photo credit: IFREMER.) **(b)** The seafloor at 4850 m in the Porcupine Abyssal Plain, northeast Atlantic. Three holothuroids, *Amperima rosea*, are visible lower center; each holothuroid is ~5 cm long. *A. rosea* is one of the species exhibiting dramatic increases in abundance on the Porcupine Abyssal Plain on decadal timescales, possibly as a consequence of changes in the quality of POC reaching the seafloor. Biogenic mounds, animal trails and a variety of other biogenic structures are also visible at the sediment surface. The compass (bottom) provides the orientation of the camera. (Photo credit: Lampitt and Burnham.) **(c,d)** The central equatorial Pacific seafloor at a depth of 4400 m showing calcareous sediments, greenish phytoplankton detritus deposited on the seafloor and a range of biogenic structures creating habitat heterogeneity. (Photo credit: Craig Smith.) In (c), a burrowing echinoid is creating a trail ~10 cm wide, removing and burying phytoplankton detritus. In (d), the feeding traces of an echiuran worm (center left), the mud tests of xenophyophore protozoans (irregular shapes at right) and a white elasipod holothuroid (center right) are visible. For scale, the bottom edges of (c) and (d) are ~80 cm across. **(e)** Basalt outcrop at the base of a seamount at ~3000 m in the northwest Atlantic. A large brisingid asteroid (*Freyella* sp., upper right) and black coral (*Stauropathes* sp., lower right) are visible. Brown spots on the rock face are tunicates. For scale, the image is ~1.5 m across. (Photo credit: Rhian Waller, DASS05_NOAAOE_URI_IFE.).

megafauna) decline dramatically with water depth (and hence POC flux), with the result that the smaller size classes (the bacteria and meiofauna) tend to dominate community biomass below water depths of 3000 m [22]. These data suggest that ecosystem function in much of the abyss could be fundamentally different from that in shelf and slope (i.e. bathyal) habitats, with diminutive microbes and meiofauna playing disproportionately large roles in abyssal energy flow. Based on the metabolic theory of ecology [28], this predominance by small organisms might be expected to reduce community-level production-to-biomass ratios, making abyssal ecosystems particularly inefficient at biomass production compared to bathyal systems. Such a reduction in ecosystem efficiency in food-poor abyssal regions has recently been documented [29]. Thus, not only is energy flux to some regions of the abyss very low but energy transfer to higher trophic levels might be relatively inefficient.

Pulse-chase experiments, in which isotopically labeled organic matter is tracked through sediment communities, have shed light on some details of energy flow in abyssal ecosystems. The results thus far are surprising, considering the predominance of microbial biomass in abyssal ecosystems mentioned above. In shallow-water experiments (intertidal to 140 m depths), added phytodetritus (labile organic material derived from fresh phytoplankton) was assimilated and respired rapidly, with bacteria dominating carbon cycling over timescales of days [30–32]. By contrast, at deep bathyal and abyssal depths, carbon uptake and respiration is approximately tenfold slower, and initial phytodetritus uptake (timescale of days) is dominated by the macrofauna and meiofauna, rather than by the relatively biomass-rich bacteria [33–35]. One possible explanation for initial faunal dominance in the abyss is suggested by optimal foraging theory; that is, very strong selection for efficient foraging behaviors in this food-poor environment [36] has caused functional responses of macrofauna and meiofauna to be less affected by the cold abyssal temperatures than the population responses of bacteria. Another possibility is that a significant

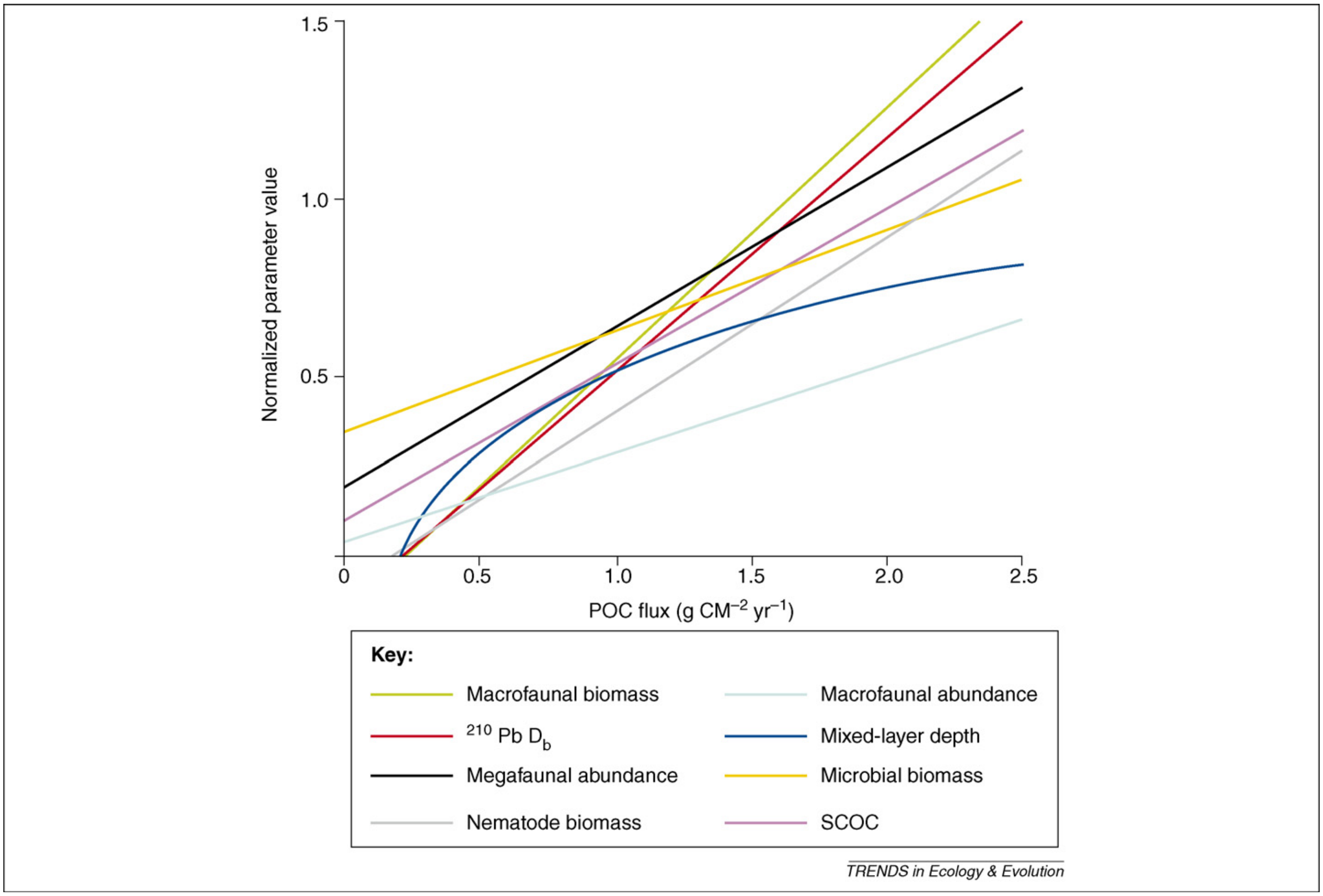

Figure 3. Regression relationships demonstrating the strong dependence of abyssal benthic ecosystem structure and function on POC flux to the seafloor. For all but macrofaunal abundance, POC flux was measured with sediment traps at 500–800 m above the seafloor integrated over 4 month timescales (for microbial and nematode biomass) or over annual timescales (the remaining parameters). For macrofaunal biomass, abyssal seafloor POC flux was estimated based on satellite ocean-color data and modeling of POC export to the abyss [23]. All relationships are statistically significant ($p < 0.05$). Benthic parameters are normalized by their maximum value to allow plotting on a single *y* axis. Macrofaunal biomass (mg C m^{-2}/59), $r^2 = 0.96$, n = 7, data from the North Pacific and North Atlantic [4]. Bioturbation intensity, based on $^{210}Pb\ D_b$ ($cm^2\ yr^{-1}$/0.345), $r^2 = 0.88$, n = 5, data from the North Pacific [24]. Megafaunal abundance (number per 1000 m^2/250), $r^2 = 0.94$, n = 5, data from the North Pacific [24]. SCOC (sediment community oxygen consumption) (mmol C $m^{-2}\ d^{-1}$), $r^2 = 0.605$, n = 7, data from the equatorial Pacific [24]. Nematode biomass (μg 100 cm^2), $r^2 = 0.921$, n = 5, data from the North Pacific [84]. Microbial biomass (μg C cm^{-2}/32), $r^2 = 0.58$, n = 7, data from the North Pacific [24]. Sediment mixed-layer depth (cm/10.769), $r^2 = 0.87$, n = 21, data from the Atlantic, Pacific and Indian Oceans [21]. Macrofaunal abundance (individuals m^{-2}/4630), $r^2 = 0.672$, n = 127, data from the North Atlantic [23].

proportion of the bacterial biomass in abyssal sediments consists of cells that have fallen out on sinking particles from the shallower, warmer water column above and are thus poorly adapted to grow in the high-pressure, low-temperature conditions of the abyss. Whatever the explanation, these pulse-chase experiments suggest that the macrofauna and meiofauna play important roles in the initial processing and redistribution of fresh food material reaching the abyssal seafloor [37]. The rapid removal of phytodetritus by holothurians feeding at the sediment surface in the North Atlantic and Pacific [38,39] also suggests that larger organisms might play important functional roles in the flow of energy through food-limited abyssal ecosystems, even if the community biomass is dominated by bacteria [23].

Although the details of organic-matter recycling can vary from shallow bathyal to abyssal habitats, a recent global study suggests that functional diversity and ecosystem function might be similarly exponentially related across all deep-sea depth zones [29]. Specifically, as food availability and nematode trophic diversity (considered a proxy for functional diversity in the whole benthic community) decline into the abyss, key ecosystem functions such as the rate of organic-matter recycling and biomass production decline exponentially [29]. Similar positive relationships between diversity and ecosystem functions (e.g. community respiration, productivity, nutrient recycling) have been documented in terrestrial and shallow aquatic ecosystems (reviewed in Ref. [40]). Because the massive abyss plays key roles in ecological and biochemical processes on a global scale [15,29], declines in abyssal functional diversity driven by reductions in POC flux, or large-scale anthropogenic disturbances such as seafloor mining [41,42], could influence the provision of ecosystem services from the ocean [29], especially over 1000 year timescales.

Abyssal biodiversity: sinks and hotspots controlled by food availability

The food-poor nature of some abyssal habitats can cause benthic population densities to be very low [22]. For example, abyssal community abundance under oligotrophic central gyres is only ~1% of that on continental slopes, where greater overlying productivity and a shallower water column allow a much greater flux of POC to reach the seafloor [4,22]. For many taxa in the North Atlantic (and for polychaetes in the northeast Pacific), the decline in benthic abundance from slope to abyssal depths is correlated with a decline in local diversity, which often peaks at depths of 2000–3000 m [43–45]. Within the abyss itself, local diversity appears to be correlated with energy availability, much as it is in many terrestrial and shallow marine ecosystems [46]. For example, along a POC flux gradient in the equatorial Pacific from low to moderate food availability, the diversity of the polychaetes and nematodes rises substantially [11,47]. However, like in other ecosystems [46], the mechanisms behind this diversity–energy relationship are not obvious.

The abyss as a diversity sink

For some invertebrate taxa, extreme food limitation in parts of the abyss might approach adaptive limits, causing regional declines in species diversity. In particular, a recent study [48] in the North Atlantic found that most of the bivalves (80%) and roughly half of the gastropod species found below 4000 m in the North Atlantic had depth ranges extending up to bathyal depths of less than 3000 m, where population densities (and food availability) are substantially higher. In addition, most of the gastropods and bivalves in the abyssal North Atlantic have planktonic larvae which might be capable of long-distance dispersal from bathyal continental slopes to the abyss. This study [48] suggests that food limitation could force abyssal North Atlantic mollusks to population densities too low for successful sexual reproduction; that is, many populations might consist of nonreproductive individuals transported as larvae from the bathyal zone. In this scenario, the bathyal and abyssal North Atlantic populations could form source-sink systems in which abyssal population densities (and species diversity) are regulated by a balance between chronic extinction in the abyss from Allee effects (i.e. density-dependent reproductive failure) and immigration from bathyal source populations.

If generally true for the abyssal fauna, the 'slope-abyss source-sink' (SASS) hypothesis has profound implications for marine evolution, biodiversity and conservation. It suggests that the food-poor conditions of at least some abyssal regions severely constrain evolutionary potential for diversification [48] and that 'the abyssal ecosystem, despite its disproportionately huge area, might not contribute appreciably to global marine diversity' [48]. If generally correct, this hypothesis also suggests that large-scale disturbance of abyssal ecosystems, such as from manganese nodule mining or iron fertilization [4,41], might have little chance of causing species extinctions simply because conspecific source populations would persist on distant continental margins.

Whereas the SASS hypothesis could apply to bivalves and gastropods with planktonic larvae, it is not clear whether the hypothesis is tenable for the other invertebrates (e.g. crustaceans, polychaetes, echinoderms and nematodes [12]) that make up >90% of abyssal species richness and frequently lack dispersing planktonic larvae [13,49,50]. Furthermore, the SASS hypothesis appears difficult to apply in the vast Pacific Ocean, which contains more than half of the Earth's abyssal seafloor and where larval transport distances from the slope are very large (up to 3000–5000 km). The intriguing SASS hypothesis merits serious consideration for mollusks in the North Atlantic, but it needs substantially more testing before it can be invoked to explain abundance and diversity patterns for most abyssal invertebrate taxa, especially in the vast plains of the Pacific which constitute most of the abyss.

Hotspots of abyssal diversity

Is the abyss a relatively homogeneous system populated by cosmopolitan species, or are there hotspots of biodiversity related to energy availability? Knowledge of large-scale distribution patterns of individual species and levels of regional biodiversity is essential to evaluate the size of the biodiversity 'reservoir' in the abyss, and to predict the impacts to biodiversity (e.g. species extinctions) and loss of ecosystem function likely to result from large-scale human activities in the ocean (e.g. deep-sea mining, CO_2 sequestration [11,42]). Although the picture of global abyssal diversity is still extremely fragmentary, patterns are beginning to emerge from global programs such as the Census of Diversity of Abyssal Marine Life (CeDAMar; http://www.cedamar.org).

Inferences about regional diversity in the abyss are possible because local and regional diversity are frequently positively correlated in both terrestrial and marine ecosystems [46]. Isopod crustaceans typically exhibit high local species diversity in the abyss, and there is strong evidence that abyssal habitats have supported adaptive radiation in this taxon [49,51–53]. Thus, isopod biogeography reflects patterns of evolution in the abyss for at least one successful invertebrate group. Cosmopolitan species of abyssal isopods are known, but constitute only a few percent of the 100 or more species found within single abyssal regions [49,51]. The Atlantic sector of the Southern Ocean appears to be an abyssal biodiversity hotspot for isopods [51] and the North Atlantic appears to be a coldspot [49,51,54,55]. Another hotspot appears to lie in the equatorial Pacific, where the diversity of polychaete and nematode worms (and probably isopods and holothurians) is high relative to other regions in the abyssal Pacific and in the North Atlantic [1,11,13,47,53,56,57]. The equatorial Pacific and the Southern Ocean are both very large abyssal regions that sustain relatively high food input for the open ocean from overlying zones of elevated surface-ocean productivity [4,9,51]; such a combination of large area with high productivity is often correlated with high local and regional species diversity in terrestrial and aquatic ecosystems [46]. Thus, the general ecological and evolutionary processes balancing speciation, immigration and extinction in other ecosystems [46] appear to operate in the abyss as well. The North Atlantic abyss is very small compared to other basins (i.e. ~25% the size of the abyssal Pacific) so, based on general biogeographic theory [46], abyssal diversity in this region might be expected to be low.

Species distribution patterns

Do the distribution patterns of individual species match productivity patterns in the abyss, or are many species found throughout the oceans below depths of 3000 m? Although species distribution data are still limited, there clearly is no general abyssal distribution pattern: some benthic species are very widely distributed whereas others appear to be restricted to regions or basins. For example, the foraminiferan *Epistominella exigua* has been found from bathyal to abyssal depths in both the Weddell Sea and the Arctic Ocean, and molecular genetic studies suggest substantial gene flow from Antarctic to Arctic populations [51]. Several abyssal polychaetes also exhibit very wide distribution patterns in the abyss [55]. By contrast, some foraminiferans (including locally very abundant species) and many species of isopods and polychaetes have only been found in single relatively productive abyssal regions such as the Southern Ocean, the eastern equatorial Pacific or the Angola Basin, suggesting substantial regional endemism related to patterns of food availability [11,49,51,58]. As in shallow-water ecosystems, differences in biogeographic patterns appear to be linked to differences in larval dispersal abilities, with high dispersal abilities and wide distributions found for some foraminiferans, and brooding of young correlated with relatively narrow distributions in isopods. However, the poor sampling and the high species richness and evenness of most abyssal basins [50] make it very difficult to resolve rarity from endemism; that is, a rare species might appear to be absent from a region (and species richness depressed) simply because the regional species pool remains incompletely sampled [11,51,58]. More intensive sampling and modeling studies are needed to help distinguish actual levels of regional endemism from 'pseudo-endemism' in the abyss, and to better resolve the relationship between environmental parameters, especially food availability, and species distribution patterns.

Temporal coupling between food flux and community structure

Abyssal ecosystems have traditionally been viewed as largely decoupled from the dynamism of the surface ocean, with ecosystem structure and function stable over long periods. However, monitoring of megafaunal community structure in both the North Atlantic and North Pacific over 10–15 years reveals surprisingly abrupt shifts in the species composition of deposit-feeding echinoderms. These shifts appear to be driven, in part, by changes in the quantity and quality of POC flux to the abyssal seafloor. For example, on the Porcupine Abyssal Plain in the North Atlantic, *Amperima rosea* and several other deposit-feeding holothurians increased dramatically in abundance (up to 1000-fold) between 1994 and 1996 while other species declined [39,59]; this change in abyssal community structure has been correlated with climatic forcing by the North Atlantic Oscillation to yield increased iron input to the upper ocean, which in turn has altered phytoplankton community structure and the nutritional quality of POC arriving at the abyssal seafloor [60]. In particular, iron deposition appears to increase the flux of cyanobacteria, whose pigments are selectively ingested by *A. rosea* and serve as important nutrients enhancing reproductive and recruitment success in this holothurian [61]. Similar large changes in megafaunal community structure have been observed in the abyssal North Pacific and again appear to be driven by climate forcing, such as El Niño/La Niña events altering upper-ocean biogeochemistry, phytoplankton community structure and the quantity and quality of sinking food flux [62–65]. Concentrations of sterols and carotenoids in depositing food material appear to be particularly important drivers of echinoderm abundance patterns, with some species gaining a reproductive advantage and others becoming disadvantaged, as plankton community structure is altered in the waters above [60,61,66,67]. These time-series studies elegantly demonstrate that contemporary climate-induced changes in upper-ocean biogeochemistry (e.g. increased iron input) and phytoplankton community structure can have profound ecosystem effects on underlying abyssal community structure with time lags as short as 6–23 months [62,63,65].

Climate change and iron fertilization

Climate-induced changes in ocean biogeochemistry (e.g. upwelling of nutrients, iron input from the atmosphere) will alter the quantity and quality of POC flux from the euphotic zone to the abyssal seafloor. Such changes will in turn alter the structure and function of abyssal ecosystems. Biogeochemical changes in the upper ocean resulting from global warming will include increased sea-surface temperatures and thermal stratification, as well as reductions in nutrient upwelling [68–70]. The net effects of such changes over regional scales are likely to be reductions in primary production as well as a shift from diatom-based phytoplankton assemblages with high export efficiencies to picoplankton assemblages characterized by low POC export to the abyss (Figure 4) [8]. The magnitude of such climate-change effects are likely to be substantial because ocean warming to date appears to have caused a 6% decline in global ocean primary production [70], and climate models predict major reductions in ocean productivity over large regions within this century, especially in the tropical ocean [71]. Furthermore, the impacts of rising sea-surface temperatures and declining net primary production on deep POC flux are nonlinear. For example, a halving of net primary production alone can cause export efficiency and abyssal POC flux to decline by two-thirds [72]. Ocean acidification [73] has the potential to further reduce the efficiency at which phytoplankton production is exported to the deep ocean, enhancing the nonlinear response of abyssal food flux to climate change.

The equatorial Pacific, a large upwelling region characterized by relatively high POC flux and abyssal biodiversity, is predicted to be especially impacted by increasing stratification and consequent reductions in productivity [71]. The net effects of climate warming are likely to mimic or exceed those of intense El Niño events [71] in which POC flux to the equatorial abyss can be reduced by at least 50% [74]. The Pacific zone of high productivity and POC flux within 5–20° of the equator can be expected to decline substantially in area. Climate warming might also enhance primary productivity and deep POC flux in some regions, especially at high latitudes in the Southern Ocean [71].

How will abyssal ecosystems respond to long-term, regional changes in the quantity and quality of POC flux? We can gain quantitative insights from the response of

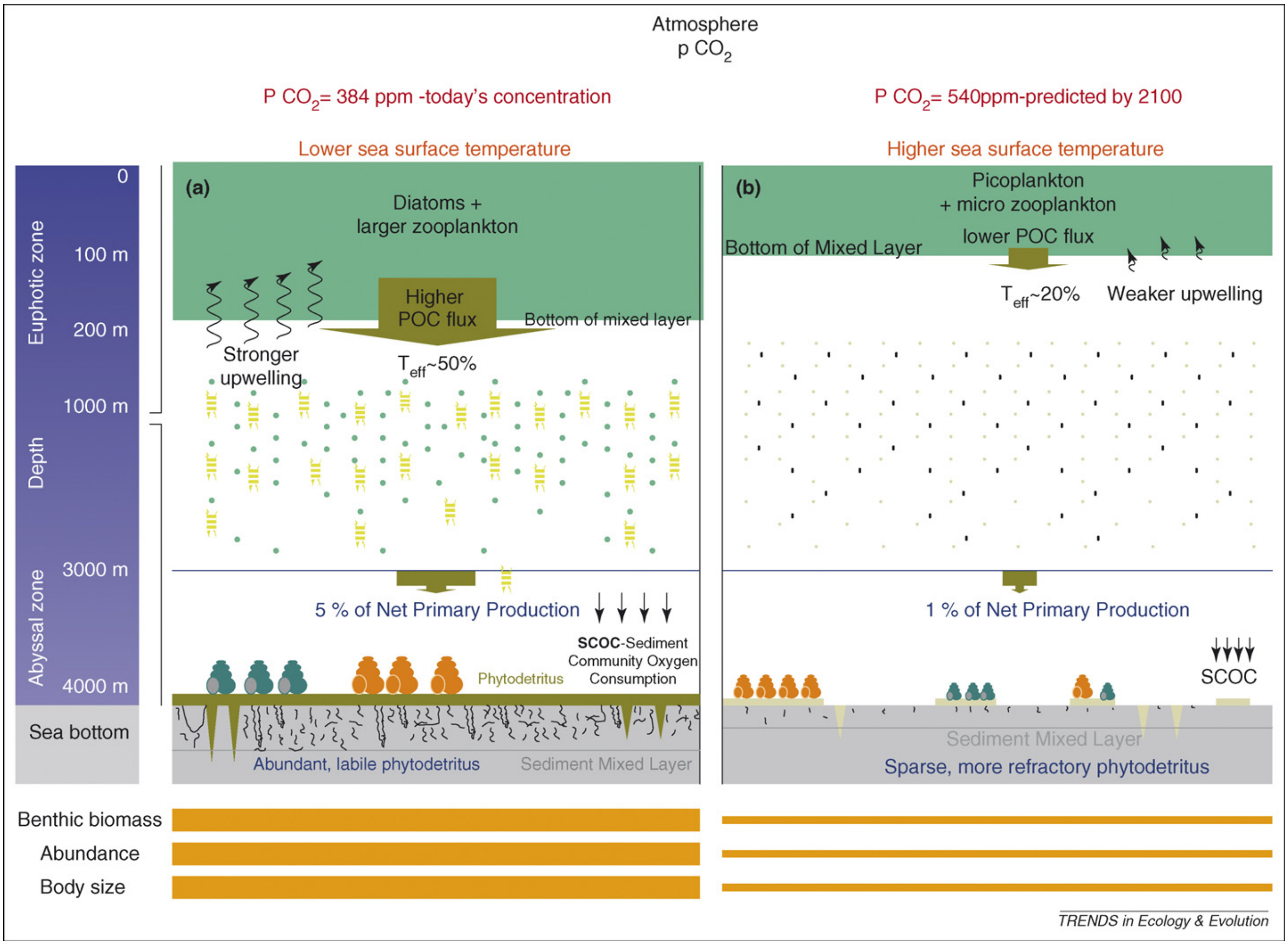

Figure 4. Predictions of the effects of rising atmospheric pCO_2 and climate change on abyssal benthic ecosystems. By increasing mean sea-surface temperature (SST) and ocean stratification, and by reducing upwelling, global warming has the potential to shift pelagic ecosystems from **(a)** diatom- and large zooplankton-dominated assemblages with higher export efficiencies to **(b)** picoplankton- and microzooplankton-dominated assemblages with lower export efficiencies. Such pelagic community shifts will reduce overall primary production and the efficiency of organic-carbon export from the euphotic zone into the deep ocean, and thus will substantially reduce POC flux to large areas of the abyssal seafloor. Reductions in POC flux will in turn reduce sediment community oxygen consumption (SCOC), bioturbation intensities, sediment mixed-layer depths, faunal biomass and body sizes of invertebrate taxa (e.g. gastropods), and alter a variety of other abyssal ecosystem parameters (see Figure 3). Shifts in the quality of sinking POC, for example in fatty acid composition, caused by changes from diatoms to picoplankton, will alter the nutritional quality of this food material, favoring reproductive success of some abyssal species and reducing reproductive success of others (e.g. [66]). Scenario (a) depicts the northeast Pacific subarctic gyre at Station K whereas scenario (b) depicts the oligotrophic North Pacific gyre at Station Aloha [8], which represent distinct biogeochemical conditions over large areas of the open ocean. The term T_{eff} (mesopelagic transfer efficiency) is the ratio of POC flux entering the deep ocean at a depth of 500 m relative to POC flux at 150 m. Note: the figure depicts end-member POC flux regimes; climate-induced changes are likely to yield a gradual transition from regime (a) to regime (b) in many parts of the ocean (e.g. equatorial upwelling zones) as pCO_2 increases in the atmosphere.

open-ocean abyssal ecosystems to regional variations in POC flux shown in Figure 3. For example, a threefold reduction in POC flux (e.g. from 1.5 to 0.5 $g\,C\,m^{-2}\,y^{-1}$), which might result in the equatorial Pacific from moderate changes in net primary production and sea-surface temperature [72], is likely to yield a halving of microbial, nematode and megafaunal standing stocks, a fivefold reduction in macrofaunal biomass and two- to fourfold reductions in sediment mixed-layer depth, sediment community oxygen consumption and bioturbation intensity. In other words, fundamental properties of ecosystem structure and function in the abyss are likely to be highly sensitive to climate-driven changes in biogeochemistry of the upper ocean. These changes will alter the provision of ecosystem services by the abyss because nutrient regeneration, carbon burial and dissolution of calcium carbonate at the deep-sea floor are all influenced by sediment community respiration as well as the rates and depths of bioturbation [25]. Long-term declines in POC flux, such as are expected in the equatorial abyss, are also likely to yield reductions in species diversity and body size [11,47,26], as well as basic shifts in the taxonomic composition of abyssal assemblages. In particular, echinoderms, which dominate the more productive regions of the abyss [65], might decline relative to other megafaunal invertebrates. In addition, shifts in phytoplankton community structure from diatoms to picoplankton can alter the nutritional characteristics of settling POC [61,66], yielding dramatic shifts in reproductive success and species composition of echinoderm deposit feeders [59,60,62,66,67]. Declines of productivity over large areas, such as the equatorial Pacific biodiversity hotspot, have the potential to cause regional extinctions as populations decline below reproductively viable levels [48], shrinking major hotspots of biodiversity. Increased productivity in other regions, for example the Southern Ocean, might expand abyssal diversity hotspots and increase the rates of certain ecosystem services (e.g. carbon burial and calcium carbonate dissolution). Overall, climate change is predicted over the next century to significantly reduce marine export production and POC flux to the deep ocean [71], enhancing stress in already food-poor abyssal ecosystems.

To help mitigate CO_2 buildup in the atmosphere, ocean iron fertilization, in which iron is released into the ocean to stimulate net phytoplankton growth, has been proposed (Box 1). The underlying reasoning is that major regions of the open ocean are thought to be 'iron limited,' that is, phytoplankton production slows because of an inadequate input of the micronutrient iron from atmospheric dust or upwelling (Box 1). Although the efficacy of iron fertilization to sequester carbon in the deep ocean remains controversial [75,76], it is clear that if iron fertilization were successful on scales necessary to affect climate change, it would substantially change the quantity and quality of deep POC flux over large areas [75,77]. If we assume conservatively that POC export is doubled by successful iron fertilization [78] and that this occurs for decades over large spatial scales, we would expect marked changes in the structure and function of the underlying abyssal ecosystem, including a doubling of microbial biomass and bioturbation intensity (Figure 3), and a significant increase in carbon burial [79]. Large shifts in megafaunal species composition are also likely to result from changes in phytoplankton community structure [80] and the quality of POC flux to the seafloor [61,62,65]. In some very extreme scenarios of large-scale iron fertilization, for example involving complete drawdown of excess macronutrients in the Southern Ocean, there appears to be the potential for anoxia to develop over substantial areas of the abyssal seafloor [77], which would yield benthic ecosystem collapse and could cause species extinctions. In some ways, iron fertilization might mitigate the losses of primary productivity and deep POC flux associated with climate warming [71]. However, because abyssal communities appear to be highly sensitive to both the quality (e.g. floristic composition) as well as quantity of sinking phytodetritus [61,66,67], and phytoplankton community structure varies with water-column properties in addition to iron availability (e.g. with sea-surface temperature, wind-driven mixing intensity, etc.; Figure 4), there is no guarantee that iron fertilization will maintain underlying abyssal community structure in areas where climate change is otherwise reducing primary productivity. Because abyssal ecosystems are highly sensitive to the quantity and quality of export production, impacts on the abyss must be considered in evaluating ocean fertilization as an environmentally acceptable strategy for mitigating anthropogenic climate warming.

Box 1. Iron fertilization and food export to the abyss

Oceanic primary production constitutes ~50% of global photosynthesis and produces ~60 Gt of carbon/year [85]. Roughly 50–80% of this organic material is respired as CO_2 in the upper ocean (Figure 4). Consequently, a small proportion (<5%) of oceanic net primary production sinks to the abyssal seafloor as particulate organic carbon (POC) [8].

The export of POC to depths is particularly efficient during phytoplankton blooms when primary production is enhanced and larger algal cells – especially diatoms – aggregate and sink rapidly [8]. Phytoplankton blooms can occur when concentrations of macronutrients (nitrate and phosphate) and necessary trace metals (especially Fe) are sufficient, and when physical conditions (i.e. available sunlight, depth of the surface mixed layer) allow the buildup of phytoplankton biomass [86]. In large areas of the ocean termed high-nutrient low-chlorophyll (HNLC) regions, surface waters are replete with macronutrients owing to upwelling, but are deficient in Fe because of limited dust input from the atmosphere [86]. Large-scale Fe-addition experiments have demonstrated that primary production, especially by diatoms, in these HNLC regions (including the Southern Ocean and the equatorial and subarctic Pacific) is limited by Fe availability [80]. Iron-addition experiments have yielded substantial increases in primary production and changes in phytoplankton community structure (including a shift to diatoms), although enhanced POC export to the deep ocean has not been widely demonstrated [80]. Nonetheless, Fe enrichment of HNLC regions over large spatial scales has been proposed to sequester large amounts of POC in the deep ocean to mitigate anthropogenic emissions of CO_2 into the atmosphere [75]. The ability of artificial Fe enrichment of HNLC regions to sequester large amounts of carbon in the deep ocean for long periods of time (e.g. centuries) remains unsubstantiated and highly controversial [75,78].

Intense algal blooms, such as those created by Fe-enrichment experiments [80], are expected both to increase POC export and to alter the quality of organic material reaching the abyssal seafloor [87]. Diatoms contain different concentrations of essential nutrients from other phytoplankton taxa [87], and the postbloom aggregation and rapid sinking of diatoms facilitates rapid transport of labile organic material to the abyss [66]. Thus, diatom blooms resulting from successful large-scale Fe enrichment are expected to enhance the flux of labile food material and to alter the input of essential nutrients to the seafloor [66,87], causing substantial change in abyssal ecosystem structure and function (see main text).

Conclusions, unknowns and future directions

The structure and function of the vast abyssal ecosystem are heavily modulated by a single extrinsic factor, POC flux from the euphotic zone. Ecosystem characteristics controlled, or heavily influenced, by regional variations in POC flux include the biomass of all biotic size classes, body sizes of benthos, rates of key ecosystem processes (e.g. community respiration, rates and depths of bioturbation, biomass-to-production ratios) and the provision of ecosystem services (e.g. carbon burial and calcium carbonate dissolution) (Figure 3). Food availability is also postulated to regulate biodiversity in the abyss: for example, high POC flux over large areas of the Southern Ocean and the equatorial Pacific appears to create biodiversity hotspots, whereas extreme food limitation in other regions might cause diversity sinks for some taxa (e.g. the North Atlantic for mollusks) [48]. Abyssal ecosystems are also responsive to temporal variations in the quantity and quality of export production from the euphotic zone, with the consequence that biogeochemical changes in the upper ocean can restructure abyssal communities over timescales of months to years.

The abyssal seafloor differs from other ecosystems in the overwhelming importance of a single extrinsic factor (POC flux) to ecosystem structure and function. For example, in many terrestrial ecosystems, multiple extrinsic factors, in particular temperature and precipitation, interact to control key ecosystem functions such as levels of productivity

[81]. The prominence of POC flux as a forcing factor in the abyss also leads to a predominance of 'bottom-up control' [64]; that is, many aspects of ecosystem structure and function in the abyss are controlled by nutrient input at the base of the food web rather than by the 'top-down' effects of grazers or predators. This contrasts with grasslands, coral reefs and some stream and lake ecosystems in which ecosystem structure and productivity can be heavily influenced by higher trophic levels [81]. This suggests that abyssal ecosystems will be much more sensitive than many other ecosystems to changes in the input of nutrients (i.e. the influx of organic detritus) at the base of the food web.

Climate change and successful ocean iron fertilization will substantially alter the biogeochemistry of the upper ocean, yielding major, regional changes in the quantity and quality of food material sinking to the abyssal seafloor. Such changes in the flux of detritus are likely to cause dramatic shifts in the structure and function of abyssal communities, altering patterns of biodiversity and the provision of ecosystem services. Some hotspots of abyssal biodiversity, for example in the equatorial Pacific, are likely to shrink with climate-driven reductions in export production [71], whereas other hotspots (in particular in the Southern Ocean) will be sustained or could even expand.

Although it is clear that changes in upper-ocean biogeochemistry can substantially alter abyssal ecosystems, major unknowns prevent us from making explicit predictions of the effects of climate change, or iron fertilization, on species composition and patterns of biodiversity. For example, we know too little about resource utilization and population dynamics to identify which species will be abyssal winners or losers from particular changes in the quantity and quality of POC flux. In addition, it is still unclear for many taxa whether the abyss is simply an evolutionary dead end or whether regions such as the Southern Ocean and equatorial Pacific have fostered adaptive radiation and serve as reservoirs of unique biodiversity. Knowledge of the distribution and richness of biodiversity hotspots is, of course, fundamental to predicting the response of biodiversity to climate change [82]. It is also uncertain what proportion of the abyssal fauna is so widely distributed across ocean basins and productivity zones that it will be protected from extinctions as climate change (or iron fertilization) alters regional patterns of POC flux.

Progress toward resolving these unknowns requires advances in several areas. First, much better sampling of many abyssal regions is needed to fully assess patterns of biodiversity. Vast, largely unsampled regions such as the abyssal South Pacific merit special attention. For some 'representative' abyssal regions (including hotspots and coldspots of biodiversity), very intensive sampling is desirable to illuminate the relationship between local and regional species richness in the abyss; this will facilitate estimation of diversity reservoirs in more poorly sampled regions. Time-series studies of abyssal habitats must be continued, and *in situ* experimental studies initiated, to develop any predictive understanding of how climate-driven changes in POC flux will alter abyssal community structure. To elucidate the role of the abyss as a cradle of unique biodiversity, substantial progress must also be made in the description and phylogenetic analysis of novel abyssal taxa from a range of size classes, life histories and functional groups; combined use of molecular and morphological approaches is essential in this effort [51]. In addition, because the many thousands of new species from the abyss (e.g. ~600 species of isopods from the deep Southern Ocean alone [51]) will require decades for formal description, intercalibration of working-species collections from disparate sampling efforts is critical for biogeographic syntheses (e.g. to evaluate species ranges) across ocean regions and basins. Finally, modeling efforts are needed to assess the errors in estimating abyssal endemism from various levels of sampling intensity. Such efforts are crucial for placing confidence limits on estimates of regional endemism (e.g. [83]), which are necessary to evaluate the likelihood of species extinctions from regional shifts in abyssal food availability engendered by climate change.

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