Environmental Change in the Deep Ocean

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Abstract

Patterns of abundance, biomass, and species richness are reviewed for deep-sea ecosystems. Long-term monitoring studies have indicated that deep-sea ecosystems are sensitive to climatic variability through its influence on the quantity and quality of surface primary production. The potential impacts of climate change, through its effects on primary production and through changes in the temperature, pH, and oxygenation of the deep ocean are explored. It is concluded that deep-sea ecosystems are likely to be highly sensitive to changes in food supply and the physical environment driven by global climate change. As a result, ecosystem services will be negatively impacted with likely positive feedbacks to atmospheric CO_2 levels. It is a matter of urgency that baselines are established for diversity, abundance, and biomass of deep-sea ecosystems, particularly for the pelagic realm and that a mechanistic understanding is developed of how food supply and physical parameters affect community structure and function.

Contents

THE DEEP SEA

What Defines the Deep Sea?

The deep sea is defined here as the ocean lying below 200 m depth, generally beyond the depth of continental shelves and with insufficient light for net primary production by photosynthesis (**Figure 1**). It is the largest ecosystem on Earth, with a mean depth of 4.2 km, a volume of >1.19 billion km^3, and a seabed area of ~434,386,264 km^2 (1, 2). Life is found throughout the water column (the pelagic realm) and across the seabed (the benthic realm), down to the deepest ocean depths of nearly 11,000 m in the Challenger Deep, Marianas Trench (3). Microorganisms sustained through chemosynthesis have even been found as deep as >2,000 m *below* the seafloor (4). Despite the ubiquity of life, the deep sea may be viewed as an extreme environment, with an absence of sunlight below 1,000 m in depth, low temperatures (average <4°C), and high pressures (average >400 atmospheres) (1). In places where high surface productivity coincides with poor ocean circulation, conditions can be hypoxic or even anoxic [e.g., extreme oxygen minimum zones (eOMZs), such as the northern Arabian Sea and Black Sea] (5), whereas at deep-sea hydrothermal vents, fluids reach temperatures of >400°C with low pH and high concentrations of potentially toxic chemicals, such as hydrogen sulfide (H$_2$S) and heavy metals (6, 7). Life in the deep sea shows a range of physiological adaptations to the extreme physical parameters of these environments at the molecular level as well as behavioral adaptations. As can be seen in the sidebar Zonation of the Deep Sea, it can be divided into depth zones corresponding to changes in physical conditions, which form a gradient from shallow to deep and drive changes in biological communities.

Abundance, Biomass, and Diversity

Obtaining representative samples to ascertain patterns of spatial and temporal variation in deep-sea ecosystems is complicated by the enormous volume and area of the deep ocean, the distance from land, and the depth from the surface. As can be seen in the sidebar Sampling the Deep, much sampling is still undertaken using surface-deployed gears (**Figure 2a,b,d**), some of which are largely unchanged from the heroic age of deep-sea exploration of the nineteen century. There is a trend of increasing use of technologically advanced remotely operated vehicles (**Figure 2c**),
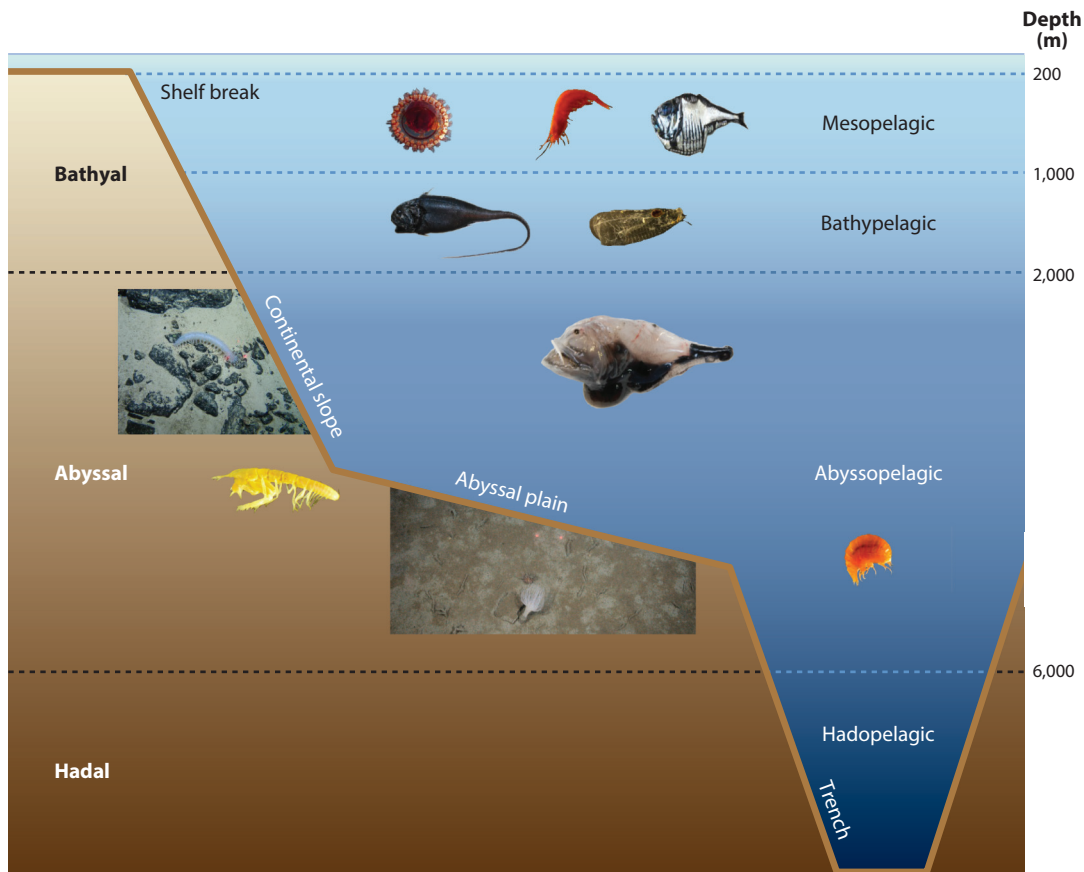
Figure 1

Division of deep-sea benthic and pelagic ecosystems. Note that different schemes are widely employed in the scientific literature, especially below 2,000 m. Photos © A.D. Rogers, International Union for Conservation of Nature Seamounts Project, **http://www.iucn.org/about/work/programmes/marine/marine_our_work/marine_governance/gmpp_ocean_governance_ projects/seamounts/**; O. Ashford, University of Oxford; P. Tyler, University of Southampton.

autonomous underwater vehicles, and cabled observatories. Here, current knowledge on the abundance, biomass, and diversity of deep-sea ecosystems is reviewed, but a recurring theme is the current lack of reliable baseline data.

Patterns with depth. Abundance and biomass of both pelagic and benthic communities tend to decline with depth in the ocean (10–13). This is a direct result of food limitation; deep-sea ecosystems are largely dependent on primary production in the epipelagic zone, and this organic material is rapidly consumed and recycled in upper water layers (10–13). Exceptions to this general pattern have been found, particularly in pelagic ecosystems. For example, sampling of the pelagic fauna over the Mid-Atlantic Ridge found a maximum fish biomass at depths of 1,500–2,300 m (14). Sampling of the deep-pelagic fauna of Monterey Canyon in the northeast Pacific also showed a peak in abundance between depths of 1,500 and 2,000 m (15). For the pelagic realm, understanding the distribution of the biota is severely hampered by inadequate sampling effort and sampling methodologies. As described in the sidebar The Deep Pelagic Fauna, animals are either highly

ZONATION OF THE DEEP SEA

The pelagic realm of the deep sea is divided into zones by depth (**Figure 1**). The mesopelagic zone lies between 200 m and 1,000 m depth, where sunlight is detectable but is insufficient for photosynthesis. Decreasing light with depth in this zone has driven the evolution of adaptations in vision, camouflage, and use of bioluminescence for defense or for prey capture. Below the mesopelagic zone is the bathyal zone, which extends down to about 2,000 m depth. Temperatures are low (4–10°C), food supply is poor, and the animals are slow growing with long life spans and slow reproductive cycles. The abyssopelagic zone is defined by the 4°C isotherm, and generally lies from 2,000 m to 6,000 m depth (8). Below 6,000 m depth is the hadopelagic zone, which lies in trenches that are semi-isolated bodies of water with a unique fauna. The benthic fauna is also classified vertically into the bathyal zone, from 200 m (the shelf break) to 2,000 m depth, the abyssal zone from 2,000 m to 6,000 m, and the hadal or ultra-abyssal zone within ocean trenches below 6,000 m depth (9). Both in the pelagic and benthic realms, these zones are not set by strict boundaries but reflect regional or local differences in marine ecosystems.

Infaunal animals: animals or communities of animals living in the sediment of the seabed

mobile (e.g., fish) or extremely delicate (e.g., gelatinous zooplankton); both present significant problems in quantitative studies. For example, the overall biomass of mesopelagic fish has been estimated at 1×10^9 tonnes (16). However, analysis of acoustic data collected simultaneously with net sampling indicates that this may have been underestimated by an order of magnitude because of avoidance of sampling gear by the fish (17). Nets are also unsuitable for sampling gelatinous animals and other delicate invertebrates in the deep water column, which may form the majority of organisms at bathypelagic or abyssopelagic depths numerically and up to a quarter of the biomass (18). The deep pelagic realm, therefore, is the largest part of the deep sea and yet is the most poorly sampled, with large tracts of this region lacking any biological records (19).

As can be seen in the sidebar Deep-Sea Benthos, the animals living on or in the seabed can be classified by size. Trends in body size also generally show a decrease with depth in infaunal communities of the benthic realm, although this pattern varies both regionally and with taxon in the macrofauna [animals retained in a sieve with a mesh size of 1 mm, but sieve sizes as small as 0.3 mm have been used (**Figure 5**)], and meiofauna (animals smaller than 1 mm but retained in sieve sizes down to 50 μm) (20). Exceptions have been observed with, for example, mollusks

SAMPLING THE DEEP

Sampling the deep seabed is achieved in a number of ways. Semiquantitative samples of the benthic megafauna and even the macrofauna can be obtained with trawls, epibenthic sledges, or dredges (**Figure 2b**). Quantitative sampling of the macrofauna or meiofauna is undertaken using spade box cores or tube-like multicorers (**Figure 2a**). The latter can be deployed from a ship or from an underwater vehicle. These are subsampled and sieved once returned. Remotely operated vehicles can undertake a wide range of sampling activities, including coring, suction sampling, image-based surveys (using video and still cameras), water sampling, and multibeam acoustic mapping (**Figure 2c**). Submersibles have a similar range of tools but tend to be less flexible for sampling. Free-fall baited camera traps or cameras can be used for surveying some elements of the fauna. The pelagic fauna is sampled using opening and closing nets (**Figure 2d**). These come in a variety of mesh sizes to target specific elements of the fauna. Multibeam acoustics can be used to survey the location and abundance/biomass of animals, which reflect acoustic energy (**Figure 2e**). Remotely operated vehicles are increasingly used to survey elements of the pelagic fauna that cannot be sampled using nets, such as the gelatinous zooplankton.
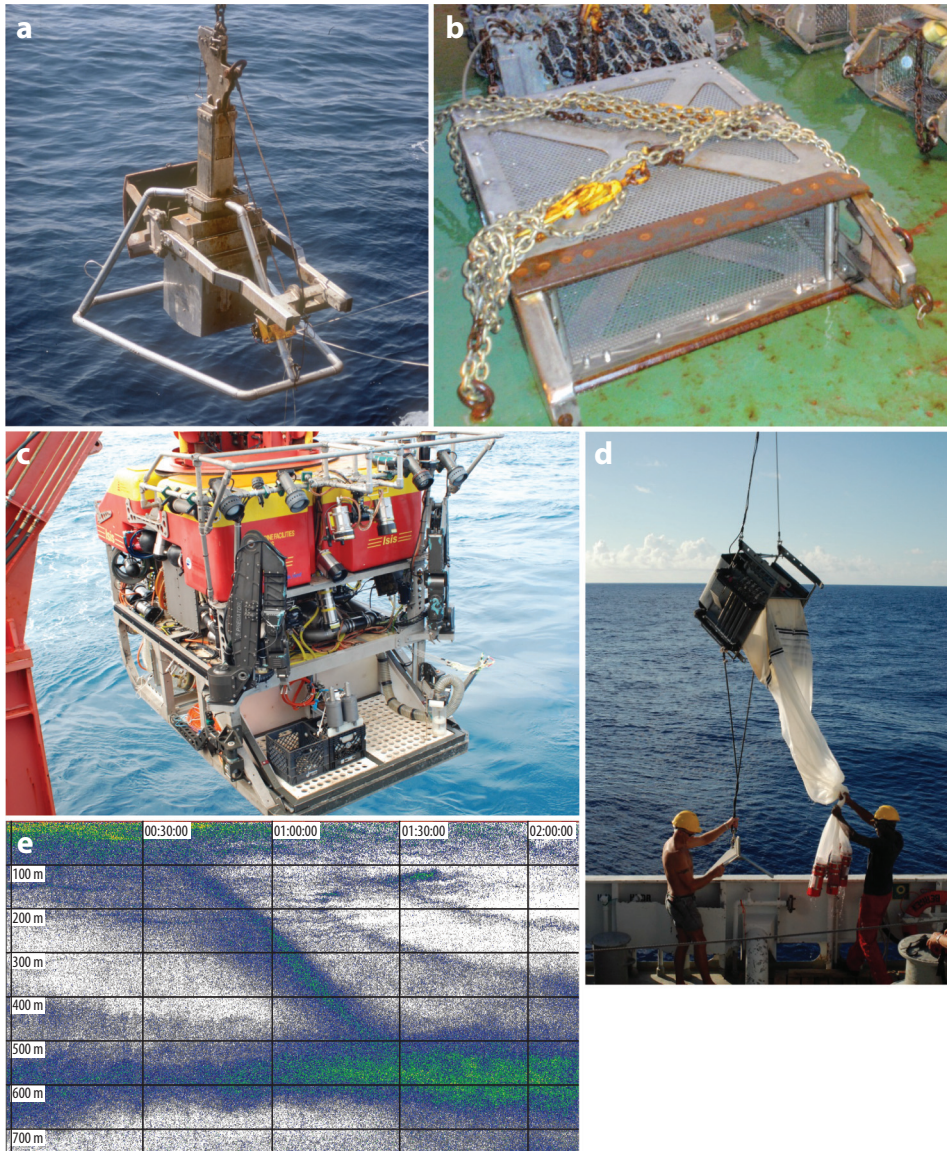
Figure 2

Sampling equipment employed for deep-sea research. (*a*) Spade box corer used for quantitative sampling of a set 50 × 50–cm area of soft sediment. (*b*) Epibenthic sledge, used for semiquantitative sampling of deep-sea macrofauna and megafauna. (*c*) Remotely operated vehicle *Isis*. The vehicle is capable of diving to 6,500 m and has two manipulators for sampling and undertaking experimental operations at depth. It also employs a suction sampler and carries water bottles and a range of high-definition video and still cameras. It can be used to map the seabed using multibeam bathymetry. (*d*) Macrozooplankton trawl. This is a multiple opening and closing net that can be used to sample the meso- and macrozooplankton at specific depths. The net is operated with acoustic signals. (*e*) Example of a trace during dawn of the upper ∼700 m of the water column taken with a multibeam scientific echo sounder. Increasing strength of acoustic signal return is denoted by color (*blue*, *green*, *yellow*, *red* from low to high; *white* is no return). The movement down into deep water of a layer of diel vertically migrating organisms can be seen in the trace. Photos © A.D. Rogers & M. Taylor, University of Oxford.

THE DEEP PELAGIC FAUNA

The pelagic fauna comprises a diversity of groups, including Protozoa, Cnidaria, Ctenophora, Chaetognatha, Polychaeta, Mollusca, Crustacea, Urochordata, and fish (**Figures 3** and **4**). They are divided into classes by mobility, plankton, drifters with poor locomotor ability, and nekton swimmers. They are also divided by size: femtoplankton (0.02–0.2 μm), picoplankton (0.2–2.0 μm), nanoplankton (2.0–20 μm), microplankton (20–200 μm), mesoplankton (0.2–20 mm), macroplankton (2–20 cm), megaplankton (20–200 cm), micronekton (2–10 cm), and nekton (>10 cm). As with the benthic fauna, the deep-sea pelagic fauna is food limited. However, many groups of micronekton, nekton, and plankton in the mesopelagic and upper bathypelagic zones undergo diel vertical migration, moving up to shallow depths in the ocean to feed at night and migrating down at dawn to avoid visual predators (**Figure 2e**). This may explain the difference in patterns of biomass and abundance with increased depth compared to elements of the benthic fauna. The gradients in light intensity and spectral range between 200 and 1,000 m depth have required a wide range of adaptations to increase vision sensitivity and for camouflage (cryptic coloration, transparency, silvering, bioluminescent countershading) (**Figures 3** and **4**). Many of these species use bioluminescence for prey capture or for defense. A significant element of the pelagic fauna comprises gelatinous zooplankton groups, including medusae, siphonophores, ctenophores, salps, and chaetognaths (**Figure 3**).

from the northwest Atlantic showing a parabolic pattern of body size with depth or no trend being detectable at all (21). Pelagic organisms show an increase in body size to at least 1,000 m depth (22); however, it may be that they show a parabolic pattern if the depth of sampling is increased. Decreasing body size and environmental temperature with depth would be consistent with a reduction in metabolic rate as it scales with the former parameters (metabolic theory of ecology) (23) and may be adaptive to reducing food supplies moving from the shelf break to abyssal depths. However, for some groups of organisms, competing selective factors may shift groups of organisms away from size optima predicted solely on the basis of energy supply (21). For example, in fish with a scavenging life style where individuals rely on encountering food falls, such as the carcasses of organisms or algal or plant debris from shallow water or the land, there is a trend of increasing body size with depth (24). This is thought to be an adaptation to the decreasing density of food falls with increasing depth meaning that a scavenger must store increasing amounts of food to survive from one meal to the next (24).

The species richness of deep-sea benthic ecosystems has been found to be extremely high, particularly in the infaunal macrofauna and meiofauna. For example, in a seminal study on the species richness of macrofaunal communities of the northwest Atlantic slope at 1,500–2,500 m depth, on average 100 species were found in a 0.09 m^2 area represented by the nine central subcores of a 0.25 m^2 box core, comprising on average 400 individual animals (25). A total of 798 species were identified from 90,677 individuals from 233 box cores (25). Extrapolation of the species accumulation curve generated by this study suggested that conservatively there may be 10^7 species in the deep ocean (25). It was soon realized that such extrapolations were not realistic and that local species richness was driven by processes at multiple temporal and spatial scales (26, 27). Small-scale habitat heterogeneity, especially given the small size of deep-sea infaunal organisms, resulting from periodic physical and biological disturbance of the seabed might generate a mosaic of patches whose successional stages are temporally chaotic. Over time, evolution may have promoted complementarity among the deep-sea fauna allowing partitioning of seabed resources (27). This may explain why, for example, the diversity of sediment grain size in the deep sea is positively correlated with species diversity (27). Food limitation might assist the occurrence of high diversity,
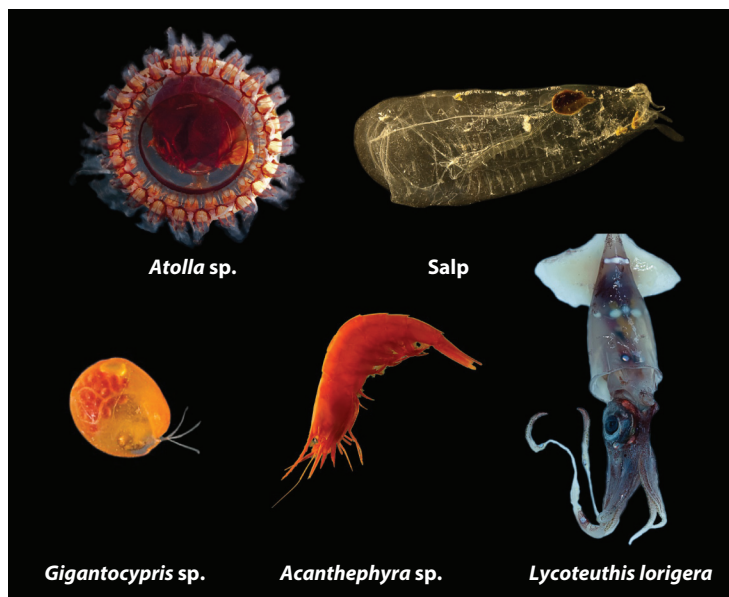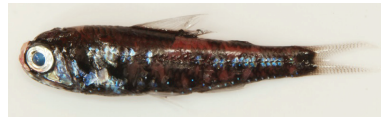
Figure 3

Examples of the mesopelagic fauna, including Scyphozoa (*Atolla*), Urochordata (salp), Ostracoda (*Gigantocypris*), Decapoda (*Acanthephyra*), and Cephalopoda (*Lycoteuthis*). Examples of the use of transparency and red-cryptic coloration (appears black in deep water) can be seen. *Atolla* can produce startling defensive bioluminescent displays. The large photophores (bioluminescent organs) are visible on *Lycoteuthis*. Photos © International Union for Conservation of Nature Seamounts Project, **http://www.iucn.org/about/work/ programmes/marine/marine_our_work/marine_governance/gmpp_ocean_governance_projects/ seamounts/**.

coupled with the slow rate of processes in the deep sea, by reducing opportunities for competitive exclusion. At larger scales, larval dispersal for small species, which have limited fecundity as a result of food limitation, may also contribute to source-sink dynamics and may explain why so many singletons occur in deep-sea samples (25, 27). The neutral theory of species diversity may also come into play if many species are functionally equivalent (27). Over geological timescales, continental margins might accumulate high numbers of species if patterns of species origin and extinction are different from those in shallow water (27).

Deep-sea communities generally show a parabolic pattern of species richness with depth, especially in the benthic realm (9, 27) but also in pelagic communities (12). In some cases, for example, with deep-sea fish, a trend of continual decrease in species richness has been detected with increasing depth, attributed to increasing food limitation (28). The unimodal pattern of diversity with depth may be largely explained by the macroecological relationship between productivity (in this case availability of food) and species richness (27). As overall primary production decreases, as can be seen in comparing different ocean regions, the peak of the unimodal relationship shifts to the left (peak diversity occurs in shallower water) until diversity simply declines with depth in the most food-limited conditions (27). Other factors also shape this relationship, including sediment heterogeneity and levels of hydrodynamic disturbance (27). Sediment heterogeneity has a positive relationship with diversity, whereas increasing current strength or exposure to benthic storms depresses diversity probably through homogenization of sediment as well as direct disturbance
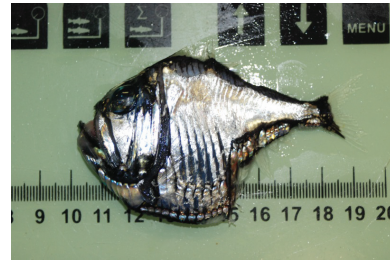
Diaphus effulgens

Astronesthes sp.

Cryptopsaras couesii

Argyropelecus aculeatus

Figure 4

Mesopelagic fish. Adaptations to the twilight zone include silvering (*Diaphus* and *Argyropelecus*) or use of black pigmentation (*Cryptopsaras*, *Astronesthes*). Both of the latter species also use a bioluminescent lure to attract prey. Note *Argyropelecus* has light-sensitive upwardly pointing tubular camera eyes used for hunting prey by detecting silhouettes in downwelling sunlight. Photos © A.D. Rogers & International Union for Conservation of Nature Seamounts Project, **http://www.iucn.org/about/work/programmes/marine/ marine_our_work/marine_governance/gmpp_ocean_governance_projects/seamounts/**.

Allee effect: a decline in individual fitness at low-population size/density; in the deep-sea context, reproductive failure at low-population densities

and burial (27). The decline in diversity for many macrofaunal groups from midbathyal depths to the abyssal plain has been explained as resulting from diminishing food and decreasing population densities. As populations thin out, Allee effects come into play, and abyssal populations may effectively become sink populations (27). Evidence for this comes from studies that indicate that ranges of a subset of bathyal species do extend into the abyssal zone (27), and recent analysis of nestedness (29) in benthic communities along the depth gradient suggest that this increases with greater depth, supporting the bathyal source and abyssal sink hypothesis (30). Not all taxonomic

DEEP-SEA BENTHOS

The benthic fauna is divided by size into the meiofauna (animals retained in a 50-μm sieve), macrofauna (animals retained in a 1-mm sieve) (**Figure 5**), and megafauna (animals big enough to see in a camera; **Figure 6**). The fauna can be sessile, attached to the seabed, or mobile. They are also classed into the infauna, animals living in sediments, or epifauna, animals living on the surface of the deep seabed. The meiofauna are diverse with the nematodes and harpacticoid copepods being the most diverse and abundant groups. Many other phyla are represented, but the polychaetes, bivalve mollusks, and groups of crustaceans, such as tanaids and cumaceans, can also be common. The macrofauna are dominated by the polychaete worms, peracarid crustaceans (amphipods and isopods), and mollusks (**Figure 5**). The benthic megafauna is also very varied and includes echinoderms, cnidarians (sea anemones, corals, sea pens, hydroids), sponges, ascidians, and fish, along with more exotic groups, such as giant foraminiferans and xenophyophores (**Figure 6**). Some of these animals can form biogenic structures on the seabed, which may be associated with a high diversity of associated species (e.g., stony corals) (**Figure 6**).
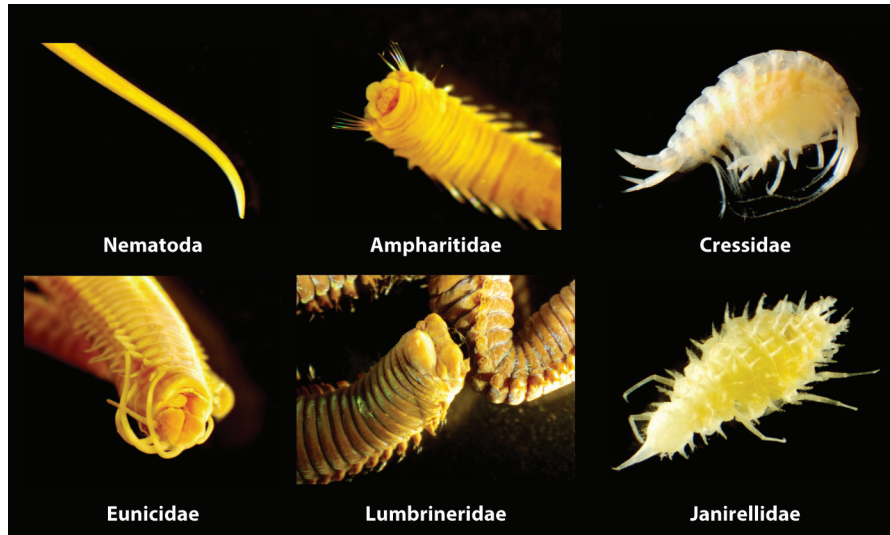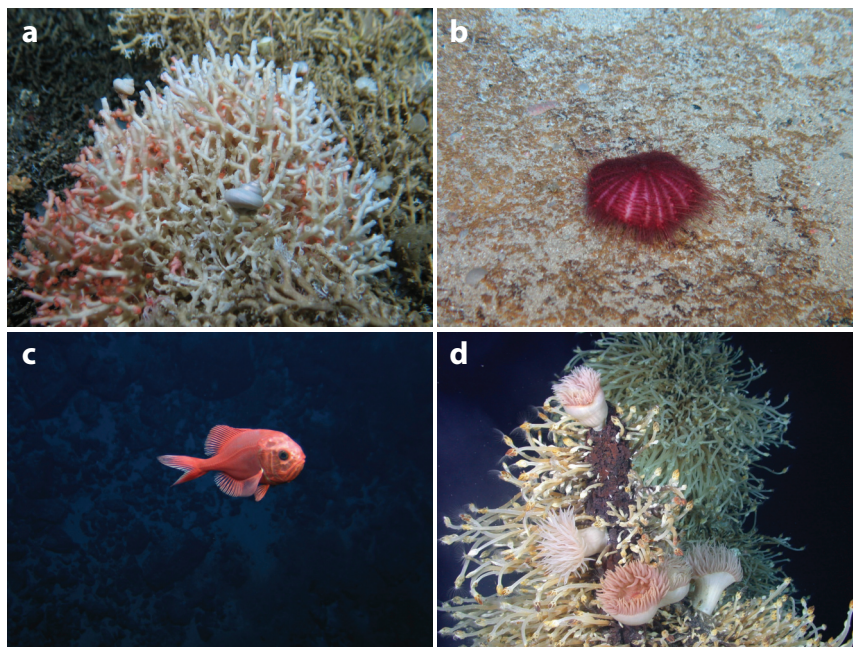
Figure 5

Examples of deep-sea macrofauna. Note the nematodes are usually meiofaunal and are the most abundant and diverse group in deep-sea meiofaunal communities. Polychaete worms and peracarid crustaceans (amphipods, isopods, tanaids, and others). Photos © O. Ashford & J. van der Grient, University of Oxford.

groups show low diversity in the abyss; some, such as holothurians (sea cucumbers), appear well adapted to the conditions at these depths (27). Modeling of larval dispersal suggests that the bathyal source and abyssal sink hypothesis are unlikely to solely explain how abyssal macrofaunal populations are sustained (31). Instead, macrofaunal populations in abyssal areas with higher organic input probably also act as larval sources for more food-limited sink populations (31). The combination of these hypotheses offers a more plausible explanation of how abyssal populations are structured by food supply.

Hot spot ecosystems. The deep sea does not simply consist of the continental slopes and abyssal plains. There are a variety of large-scale geological features that may be hot spots of faunal abundance and/or diversity or endemism. These include canyons, which occur on the continental slope or slopes of oceanic islands; seamounts; submerged plateaus; trenches; and chemosynthetic ecosystems.

Canyons. Globally there are estimated to be 5,849 ocean canyons, and these can be divided into three types: shelf incising connected to a river, shelf-incising and blind canyons manifesting only on the continental slope (32). River-connected incising canyons are more common on active continental margins where oceanic and continental plates are colliding and shelves are narrow, but such canyons are absent from Australia and Antarctica (32). Shelf-incising canyons are most common on the shelves of Antarctica and Southeast Asia, whereas blind canyons, the most common type, form the highest proportion of canyons in Australia on island slopes and submarine plateaus (32). Canyons are extremely heterogenous and so generalizations regarding their ecology are difficult given the level of study to which they have been subjected. They interact with current flows, generating upwelling, downwelling, internal waves, and strong cascading flows from the shelf into the deep sea (33). The mixing of the water column as well as the trapping of organic material

Figure 6

(*a*) *Solenosmilia variabilis*, a deep-sea reef-forming coral. Here a cold-water coral reef is located at 1,000 m on the Coral Seamount, Southwest Indian Ridge. Such habitats are likely to show a contraction in their vertical and geographic range as a result of acidification and other effects of climate change. (*b*) Echinoid on the summit of Atlantis Bank Seamount on the Southwest Indian Ridge. Echnoids and holothurians are common deposit-feeding megafauna in deep-sea ecosystems. (*c*) Orange roughy, *H. atlanticus*. This species is associated with seamounts where it spawns. It lives to ∼150 years old and is highly vulnerable to overexploitation through fishing. (*d*) Part of a hydrothermal vent chimney on the East Scotia Ridge, Southern Ocean. Visible is *Vulcanolepas scotiaensis*, a barnacle with episymbiotic bacteria on its feeding appendages. The actiniarians are predatory and not yet described. Photos are from the Natural Environment Research Council (NERC) Royal Research Ship *James Cook* Cruise JC66 (*a–c*) and JC42 (*d*), © A.D. Rogers NERC NE/F005504/1 and NERC NE/D010470/1.

from continental shelves, coupled with the presence of hard substrata and habitat heterogeneity at <10 m scales, all act to enhance biological activity at canyons for both benthic and pelagic communities (34, 35). The benthic fauna can occur at very high densities and biomass, orders of magnitude higher than surrounding continental slope environments at similar depths (34). Cetaceans have been found to associate with canyons probably because they are zones of enhanced primary production (as a result of water mixing) and aggregation of prey because of elevated food and hydrodynamic and topographic phenomena (35).

Seamounts and plateaus. Seamounts are another surprisingly ubiquitous habitat in the deep ocean, but as with canyons, they are poorly studied with only 0.4–4% having been sampled (36). They are mainly associated with mid-ocean ridges, island arcs, and intraplate hot spots where chains of seamounts may be generated (e.g., Hawaii). Data based on ship soundings and satellite gravity mapping indicate that there are >33,000 large seamounts (elevation >1,000 m, 4.7% of the seafloor) and >138,000 smaller features (16.3% of the seafloor) in the ocean (37). Aggregations of

pelagic predators are associated with these features, including whales, sharks, seabirds, seals, and large predatory teleosts such as tuna (38–40). Seamounts are also associated with aggregations of benthopelagic or demersal fish species such as orange roughy (*Hoplostethus atlanticus*) (**Figure 6c**), alphonsino (*Beryx* spp.), and oreos (Oreosomatidae) (41). Aggregations of pelagic and demersal fish around seamounts are thought to relate to the concentration and trapping of prey or to the availability of prey advected over elevated topography by the prevailing current (36, 41, 42). Mesopelagic migratory micronekton (fish and crustaceans) (**Figures 3** and **4**) may become trapped by the elevated topography of seamounts, preventing these organisms from completing their daily migration into deep water as the sun rises (42). Other hydrodynamic mechanisms may also act to concentrate prey (42). Benthic communities on seamounts can exhibit a higher biomass than those of the surrounding deep sea or nearest slope (seamount oasis hypothesis) (43) and a high species richness (44). Communities can show an inventory of species similar to nearby continental slopes, although they may be structured very differently with a high prevalence of sessile suspension feeding taxa, such as corals, some of which can form an extensive biogenic habitat with high diversity (**Figure 6a**) (43, 44). Elevated topography receives a higher supply of food per unit area by virtue of being closer to the epipelagic zone where primary production takes place. However, topographically induced current acceleration brings higher supplies of particulate organic material for the benthos, and strong benthopelagic coupling through other mechanisms (e.g., forays into the water column by benthic organisms, trapping of pelagic fauna, etc.) is also likely to enhance food supplies. Submarine plateaus occur in several parts of the global deep ocean and are a particular feature of the Indian Ocean (e.g., the Mascarene Plateau). These have not received much research attention but are likely to share ecological attributes with seamounts.

Trenches. The ultra-abyssal or hadal zone is defined by depths greater than 6,000 m and mostly comprises trenches, located on active continental margins (e.g., Peru Trench) or next to island arcs associated with subduction zones (e.g., South Sandwich Trench). Like the habitats described above, trenches suffer from a lack of investigation but perhaps more so because their extreme depth has severely limited opportunities for sampling using modern equipment (45). Trenches are much like other abyssal environments with the exception that they are subject to greater pressure. Temperatures, like elsewhere in the deep ocean, are low, although adiabatic heating causes a reversal of the usual trend of declining temperature with depth after about 4,000 m (45). Food limitation is likely to play an important role in the ecology of trench systems, even though there is some suggestion that food may actually accumulate, thus increasing in concentration, along the axis of the deepest parts of these features (45). The fauna includes fish, holothurians, polychaetes, bivalves, gastropods, isopods, amphipods, and actiniarians, and gigantism occurs among some of these groups possibly as a result of relying on sporadic food supply or as a response to other ecological drivers (45). It is estimated that ~56% of the trench fauna is endemic, but 95% of these are restricted in their distribution to a single trench (46). The non-endemic fauna mainly resembles that of the surrounding abyssal zone and suggests that trench faunas generally evolve in situ (46). Such figures must be treated with caution as sampling has been limited (45).

Chemosynthetic ecosystems. Most primary production in the oceans comes from oxygenic photosynthesis in the epipelagic zone, whereby light is used as an energy source for the fixation of inorganic carbon (CO_2) through the Calvin-Benson-Bassham (CBB) cycle (47, 48). However, different groups of microorganisms fix carbon in the oceans using a range of alternative energy sources and biochemical pathways (47, 48). This complexity has only been fully appreciated in the past 10 years or so (47), and it has been realized that chemoautotrophy and chemoheterotrophy

Demersal fish: fish that live and feed on or near the seabed

Micronekton: animals that lie between plankton (passive drifters) and nekton (powerful swimmers) in terms of their size and locomotor power

Adiabatic heating: a thermodynamic process whereby pressure causes compression of the seawater volume, raising its temperature as heat cannot escape

have greater importance in the carbon and other nutrient cycles than formerly understood. There are several alternative carbon fixation pathways:

- The CBB cycle uses energy obtained from the oxidation of reduced chemicals or geofuels (e.g., from oxidation of H_2S) instead of light.
- The reductive tricarboxylic acid (rTCA) cycle synthesizes acetyl coenzyme A from two CO_2 molecules through a reverse Krebs cycle.
- The reductive acetyl coenzyme A pathway, or Wood-Ljungdahl pathway, generates acetyl coenzyme A by direct combination of two CO_2 molecules.
- The 3-hydroxyproprionate (3-HP) bicycle for CO_2 fixation involves two cycles, one whereby two molecules of bicarbonate are fixed and glyoxalate is formed and the other whereby glyoxalate and propionyl coenzyme A are disproportionated to pyruvate and acetyl coenzyme A.
- The 3-HP/4-hydroxybutyrate cycle bears similarities to the 3-HP bicycle but involves different steps involving different enzymes and is likely to have evolved independently.
- The dicarboxylate/4-hydroxybutyrate (DC/4-HB) cycle (48) utilizes enzymes/steps from both the rTCA cycle and the 4-HB part of the DC/4-HB cycle, but additional enzymes are used to convert acetyl coenzyme A to oxaloacetate.

These chemosynthetic pathways form the basis of primary production at several hot spot ecosystems in the deep ocean, including hydrothermal vents, seeps and large food falls (wood, whale carcasses). Their phylogenetic distribution is different with the CBB and rTCA cycles occurring in various groups of Bacteria; the Wood-Ljungdahl pathway is found in various groups of Bacteria and Archaea; the 3-HP cycle takes place in Chloroflexaceae; the 3-HP/4-hydroxybutyrate cycle occurs in the Sulfolobales with variants possibly occurring in the Crenarcheota; and the DC/4-HB cycle is found in the Crenarcheota (48).

Hydrothermal vents. Hydrothermal vents form along ocean spreading centers or mid-ocean ridges, places where new oceanic crust is formed by the upwelling of magma from the mantle (49, 50). They also occur at subduction zones associated with submarine volcanic arcs, back-arc spreading centers, and mantle hot spots, such as the Hawaiian Islands and associated seamounts (49, 50). In these settings, seawater penetrates the crust and usually comes into contact with hot basalt associated with a magma chamber. The water is heated, and a complex chemical exchange occurs with the rock, stripping the seawater of oxygen, magnesium, and sulfate, usually making it acidic and enriching it with hydrogen sulfide, methane, hydrogen, CO_2, and various metals (49). Heated water is buoyant and as a result rushes upward through the crust toward the seabed, where it exits the seafloor as high-temperature black smokers (>300°C and as high as ~500°C) (6, 49), as lower-temperature white smokers (100–300°C), or as lower-temperature diffuse flow. The appearance of black smokers is a result of the hot chemical-rich clear vent fluid coming into contact with cold seawater, and at this point metal sulfides precipitate, forming dense black clouds of particles. White smokers have a different chemistry because of their lower temperatures and precipitate silica, anhydrite ($CaSO_4$), and barite ($BaSO_4$) (49). Chimneys (**Figure 6d**) form rapidly around black smokers, initially by the high-temperature precipitation of anhydrite, which then insulates hydrothermal fluids from seawater, allowing the deposition of chalcopyrite ($CaFeS_2$) and other metal sulfides including zinc, copper, iron, lead, cadmium, and silver, as well as other minerals. Black smoker chimneys can be large (up to >40 m high) (51) and very complex. The largest known vent chimneys (>60 m) are formed of carbonates as a result of unusual chemistry (the reaction of seawater with peridotite rather than basalt) at a site, located on the flanks of the Mid-Atlantic Ridge, called the Lost City (52).

Hydrothermal vents provide a rich source of reduced chemical energy (49, 50), which is exploited by chemoautotrophic bacteria and archaea to fix carbon. The most energetic reaction fueling chemoautotrophy is the oxidation of hydrogen sulfide, followed by iron oxidation and methanotrophy, with sulfate reduction and methanogenesis occurring at higher temperatures. The dominant pathways for carbon fixation are the CBB cycle and the rCBB cycle with other pathways also present (48). Microbial primary production at vent sites is locally very high, and there can be spectacular abundances (up to >6,000 individuals m^{-2}) (53) and biomass (up to 70 kg m^{-2}) (54) of megafauna specially adapted to life in such ecosystems, either grazing or suspension feeding on bacteria and other microorganisms, harboring internal endosymbiotic or external episymbiotic chemoautotrophic bacteria, or living as predators (**Figure 6d**) (e.g., 55). Vent species must be able to tolerate extremes of temperature, pH (generally acidic), hypoxia, the presence of toxic chemicals (such as H_2S) and heavy metals, as well as the usual high pressures associated with the deep sea. Their tolerance of such conditions generally determines their vertical and horizontal distribution around hydrothermal vent chimneys and other areas where fluids are emanating, leading to a distinct zonation along the steep environmental gradients present (53). Because the extreme conditions of these environments have driven the evolution of a highly adapted biota, communities comprise species with a high level of endemism (>70% species are not found outside of vent ecosystems). Thus, they are significant in terms of biodiversity and are sources of unique genetic diversity.

At regional and global scales, it is largely the interaction of the physiology and life history of the vent biota and the physicochemical manifestation of hydrothermal venting that determines patterns of distribution and community structure. Vents show a great deal of heterogeneity in terms of their physical manifestations, temperatures, and chemistry that reflect underlying geology. For example, vents associated with island back arcs in subduction zones can be subject to high levels of volcanic disturbance, and vent fluids tend to be rich in volatiles [e.g., H_2S, SO_2, H_2O, CO_2, hydrogen chloride (HCl), and hydrogen fluoride (HF)] (56). Along mid-ocean ridges, the longevity and distribution of individual hydrothermal vent fields and their chemistry depend on their underlying geology (57). On ridges with fast-spreading rates, the vents occur every few dozen kilometers along the ridge, and they may have a relatively short life, perhaps only tens of years before the flow of vent fluid shuts off or volcanic eruptions occur that obliterate a hydrothermal vent site (58). They are also basalt hosted; in other words, hydrothermalism is associated with magmatic injection into the underlying ridge, and vent fluids, as a result, are generally rich in H_2S and metals (59, 60). Vents on slow-spreading ridges tend to be much longer lived, are physically larger, and are a further distance apart along the ridge, perhaps separated by hundreds or thousands of kilometers (58). They also originate from a more diverse underlying geology, with vents either hosted in basaltic rock or in ultramafic rock associated with an uplift of the mantle. The latter may be associated with vent fluids that have relatively high concentrations of methane (CH_4) and H_2 and low concentrations of metals (59, 60). The differences in vent chemistry influence the composition of microbial communities at the vents as well as the major metabolic pathways for energy generation and carbon fixation (60). This, in turn, coupled with physiological tolerance for such conditions, determines what megafauna can survive at a particular set of vents. The dispersal abilities of the vent fauna, largely determined by their life history, interact with the spatial distribution and longevity of vents to determine their community structure and dynamics (58).

Individual vent sites cover a relatively small area of the seabed, so carbon production at deep-sea vents has been estimated at only 0.005 gigatonnes C year^{-1} (48). Since these figures were published, it has been estimated that globally there may be as many as 1,000 active deep-sea hydrothermal vents (57, 61). However, the discovery of vents in off-axis ridge locations and/or on slow- and ultraslow-spreading ridges means that this number may be considerably underestimated (6). Even

taking this into account, it is unlikely that carbon fixation directly associated with hydrothermal vents is more than a minor contribution to ocean primary production.

Cold seeps. Cold seeps are areas of the seabed where fluids rich in methane, CO_2, H_2S, nitrogen, and other hydrocarbons, such as oil or asphalt, leak from beneath the surface (50). They are often associated with specific geological structures on the seabed, including mud volcanoes, pockmarks, gas chimneys, hydrate mounds, and carbonate slabs, sometimes with gas actively bubbling out of sediment (62, 63). Significant deposits of gas hydrates may lie under these structures, zones where the low temperature and high pressures associated with deep-sea environments cause the formation of frozen methane. Seep sites are associated with active and passive continental margins from 15 m to 7,400 m deep (62). Although they are generally associated with the continental slope, they have also been found near trenches, ridges, and seamounts, especially where the latter are associated with subduction zones. Mass wasting associated with seismic activity, tsunamis, or other forms of large-scale disturbances may also expose reducing sediments and be close to seepage (62).

The most conspicuous faunas of cold-seep ecosystems are large symbiont-hosting vesicomyid clams, bathymodiolid mussels, siboglinid tubeworms, and cladorhizid and hymedesmiid sponges (62, 64). As with hydrothermal vents, the abundance and biomass of megafaunal communities may be very high for the deep sea (e.g., >1,000 individuals m^{-2} for seep clams and 10–30 kg m^{-2} biomass) (62). Additionally, like vents, a concentric zonation in the distribution of the fauna around seep sites may be observed, again reflecting steep gradients in environmental conditions (62). Many species appear restricted in distribution to one or two seep sites, although at higher taxonomic levels, genera and families are widely distributed. The biological diversity of seeps is in general more poorly understood than that of deep-sea hydrothermal vents, although they are probably more species rich than hydrothermal vents (62, 64). Some general trends in the diversity of seep habitats have been identified, but the lack of knowledge concerning these systems means that generalizations are difficult. The occurrence of symbiont-hosting species tends to decrease with increasing depth, and the endemicity of the fauna increases (62, 64). In general, higher species diversity is encountered in sediment seep systems rather than those with a high cover of hard substrata (64). The diversity of seep communities is generally thought to reflect the age of a seep site, with continual seepage in some regions going back >10,000 years (e.g., Gulf of Mexico) (65). The meiofauna of seeps is very poorly studied, whereas different patterns of community responses to seepage have been found in the macrofauna, with the density of individuals either enhanced or impoverished compared to surrounding deep-sea sediments (62). Deeper communities, and those associated with elevated H_2S, appear to have higher densities compared to surrounding sediments (62). In some cases, sulfidic sediments may be associated with a reduced diversity (62).

Organic food falls. When large carcasses of whales sink into the ocean, they are stripped of flesh very quickly, but the skeleton is left behind (66). This is lipid rich and can lead to the development of a chemosynthetic community. The decomposition of whale bones generates H_2S through anaerobic sulfate reduction (oxidation of the lipids). This provides nutrition for mats of bacteria and for megafauna associated with chemosynthetic environments, such as the clam *Vesicomya* and gastropods, e.g., *Provanna*, some of which are also found on vents or seeps. A group of siboglinid worms, known as zombie worms (*Osedax* spp.), specifically inhabit whale bones. These have a ramifying set of tubes that penetrate the marrow of the whale bones and contain bacteriocytes. The bacteria are known as a group involved in the heterotrophic breakdown of complex organic molecules, and they sustain the zombie worms as endosymbionts (67). Wood falls also generate chemosynthetic communities in a similar manner.

Biogeography of the Deep-Sea Biota

As with understanding local patterns of biodiversity, describing and explaining regional and global biogeography are hampered by the lack of data. At the largest scales, studies of components of the deep-sea fauna indicate a latitudinal gradient in estimated species richness, with higher diversity at low latitudes and reduced diversity at the poles (e.g., in the gastropods, isopods, cumaceans, and foraminiferans of the Northern Hemisphere) (27) as in shallow-water marine organisms (68). This pattern, however, is much less obvious in the Southern Hemisphere, where there is greater regional variation than in the Northern (27). For some groups of organisms, a statistically significant gradient of species richness with latitude appears absent in the Southern Hemisphere (e.g., isopods) (27). Such patterns reflect the integration of environmental influences on species distribution [temperature, particulate organic carbon (POC) flux, seasonality] with the historical processes of speciation and extinction. For example, an explanation of the depressed diversity of mollusks in polar regions has been a higher species origination rate in the tropics since the end-Cretaceous extinction (68).
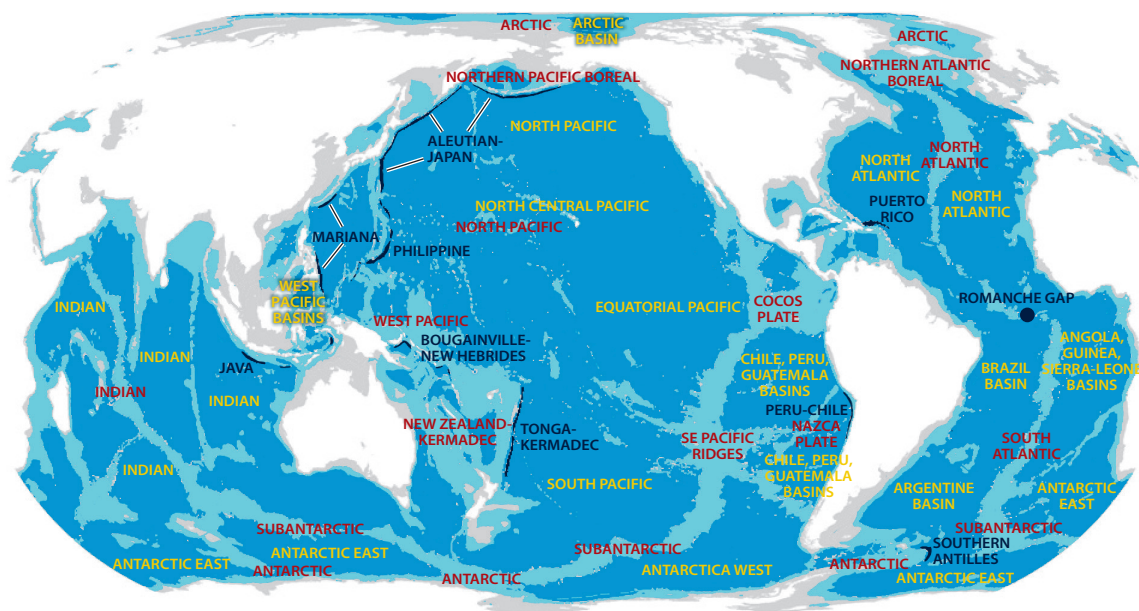
Understanding regional patterns of biogeography in the deep sea has been subject to study for at least a century (69). In general, it has been considered that the deep-ocean fauna is not cosmopolitan but varies at least between the major oceans and also regionally (69). In some cases, it has been proposed that the deep-sea fauna becomes more homogenous with depth, reflecting greater homogeneity of physical conditions, whereas in others, it has been suggested that the fauna tends toward more regional endemicity with increasing depth as the ocean basins become more divided up by mid-ocean ridges and other topographic features (69). The latest efforts to derive a biogeography for the deep ocean (below 800 m depth) have been based on a characterization of the deep sea on the basis of depth, temperature, and POC, with verification based on existing knowledge of faunal distribution (69). This suggests 14 lower bathyal provinces (800–3,500 m depth), 14 abyssal provinces (3,501–6,500 m depth), and 10 hadal provinces (>6,501 m depth) (**Figure 7**) (69). This scheme largely replicates an earlier bioregionalization effort (70) with a few minor differences in the Pacific. Because, the upper bathyal provinces were thought to likely resemble those of the continental shelf, these are not specifically analyzed in this study. The study provinces are divided approximately along latitudes, with high latitudes in the Southern Hemisphere showing the broadest provinces by longitude, and provinces becoming divided by the continents and mid-ocean ridges further north.

Such a scheme fits well with recent observations on the distribution of elements of the deep-sea fauna. For example, the deep-sea ophiuroids off of Australia and New Zealand appear to form latitudinal bands of similar fauna, fitting well with the bathyal scheme suggested (71). Whether the scheme is generally applicable needs much more verification.

Deep-sea hydrothermal vent analyses of faunal records of vent biota, using multivariate regression trees, suggested that a model comprising 11 faunal provinces best fit the data (55). These include Atlantic, Indian, and Southern Ocean provinces, with the Pacific Ocean divided roughly by latitude into four eastern provinces and into four western provinces (55). These appear to fit quite well with the scheme for deep bathyal bioregionalization (69, 70). No such classification has been attempted for seep environments.

Environmental Variation in the Deep Sea

Visual observations of the rapid arrival at the deep seabed of phytodetritus from the surface in the 1980s provided the first evidence that seasonality in primary production may lead to intra-annual variation in food supply and biological activity at bathyal and abyssal depths (72). Long-term

Lower bathyal
(800–3,500 m)

Arctic
Northern Atlantic boreal
Northern Pacific boreal
North Atlantic
SE Pacific ridges
New Zealand-Kermadec
Cocos Plate
Nazca Plate
Antarctic
Subantarctic
Indian
West Pacific
South Atlantic
North Pacific

Abyssal
(3,500–6,500 m)

Arctic basin
North Atlantic
Brazil basin
Angola, Guinea, Sierra Leone basins
Argentine basin
Antarctic East
Antarctica West
Indian
Chile, Peru, Guatemala basins
South Pacific
Equatorial Pacific
North Central Pacific
North Pacific
West Pacific basins

Hadal
(>6,500 m)

Aleutian-Japan
Philippine
Mariana
Bougainville-New Hebrides
Tonga-Kermadec
Peru-Chile
Java
Romanche
Puerto Rico
Southern Antilles (includes South Sandwich and South Orkneys trenches)

Figure 7

Map showing biogeographic regions of the deep sea after Watling et al. (69). Lower bathyal biogeographic regions (800–3,500 m depth) are denoted in red text. Abyssal biogeographic regions are denoted in yellow text (3,500–6,500 m depth). Hadal biogeographic regions are denoted in dark blue text (6,500 m depth and deeper). Note we have renamed the Romanche hadal region as the Romanche Gap and moved it further south than indicated by Watling et al. (69). The depth zones are different from those given in **Figure 1** because this scheme used physical oceanographic proxies to delineate depth zones along with some biological information on species distributions. As stated in the caption for **Figure 1**, different schemes are employed across different studies. Modified with permission from Watling et al. (69).

monitoring studies of deep-sea benthic communities, coupled with analysis of surface primary production in the northeast Atlantic and northwest Pacific, have conclusively demonstrated that interannual variation in surface primary production can have a dramatic effect on the diversity and abundance of abyssal communities at depths >4,000 m (73, 74). Changes to the food supply to the seabed have been detected in terms of periodic increases in the quantity and possibly quality of phytodetritus (73, 74) as well as in amounts of other organic material, including dead gelatinous zooplankton, such as salps (74), known to rapidly sink through the water column (75). In the northwest Pacific, changes in organic flux have been followed by complete changes in communities from sessile suspension-feeding-dominated to mobile-fauna-dominated states with increases in faunal density but decreases in diversity (74). In the northeast Atlantic, changes have included large increases in the density of several holothurian species (thought to result from large-scale recruitment events) (73) as well as changes in the macrofauna (polychaetes) (76) and meiofauna (metazoan and protozoan components) (77, 78). In both cases, the rate of processing of organic material on the seabed by the benthic fauna changed with increases in flux along with changes in levels of bioturbation and probably burial of organic material (73, 74). Changes in the POC flux that drive alterations in diversity and abundance of these deep-sea communities have been correlated with decadal-scale climatic variations in the northwest Pacific. This has clearly demonstrated the linking of environmental variation, primary production, and upper-ocean processes with the diversity, abundance, and ecological functions of deep-sea communities (79, 80).

Given that climate change associated with CO_2 and other greenhouse gas emissions is likely to affect the patterns and magnitude of surface primary production, it would seem reasonable to assume significant changes will also take place in deep-sea biota (80). Looking back in the geological record suggests that past episodes of global climate change have led to significant changes in marine ecosystems, including the deep sea. Over millennial timescales, switches between cool ocean states, where the global thermohaline circulation maintains an oxygenated deep ocean, and warm ocean states, where salinity-induced sinking of water at low latitudes leads to warm and saline deep water with poor circulation and lower concentrations of oxygen (halothermal ocean) (81, 82), appear important in the context of the deep sea. A warmer ocean has been associated with widespread ocean hypoxia or even anoxia in deep waters as well as ocean acidification and euxinia (release of H_2S into shallow water). Such conditions have been linked to major extinction events affecting shallow and also deep-water ecosystems [e.g., end Cambrian (83), end Ordovician (84), end Permian (85), early Jurassic (86), and Paleocene-Eocene thermal maximum (87)]. The latest of these events, the Paleocene-Eocene thermal maximum, was specifically associated with an extinction of deep-water foraminifera (87, 88). In addition to its association with extinctions, climate change has also been involved in creating the conditions for invasion by various groups of animals and radiation into the deep ocean, mainly during the onset of cool conditions that drive the thermohaline circulation. For example, there is evidence of the invasion by octopuses of the deep seas of the Atlantic, Indian, and Pacific oceans following the strengthening of the thermohaline circulation from the Antarctic after the establishment of the circumpolar current (89). Furthermore, there is evidence that significant elements of the deep-sea hydrothermal vent fauna arose after the Mesozoic following the establishment of oxygenated conditions in the deep sea (e.g., 90–92). Although there is evidence that some deep-sea groups may have survived in refugia (93) or that there may have been shifts to anoxia-resistant taxa (86), there is surprising evidence that a significant component of the deep-sea fauna is relatively young (tens of millions of years old), probably as a result of past climate-driven episodes of extinction followed by invasion by groups of animals of the deep sea when conditions ameliorated. Even over shorter timescales of tens to thousands of years, there is evidence of climatically driven changes in deep-ocean

circulation, leading to changes in the distribution of deep-sea species (e.g., invasion of the North Atlantic by deep-sea corals following the strengthening of the Atlantic meridional overturning circulation following the last glaciation) (94). Given this, it is interesting to speculate how future climate change may influence primary production and food delivery to the deep ocean or directly influence the deep-sea fauna.

HUMAN IMPACTS ON THE DEEP OCEAN

Here the direct impacts of human activities on the deep sea are summarized, and readers are referred to previous studies that cover several of these areas in more detail (e.g., 95, 96). The deep sea has a legacy of human inputs with ships being lost at sea from ancient times to the more recent introduction of pollution from the dumping of dredge spoil and sewage to radioactive materials (96). Impacts are summarized as follows:

- Introduction of hard substrata into soft-sediment ecosystems (shipwrecks, clinkers, trash, cables, pipelines, submarine structures)
- Organic enrichment (sewage dumping, organic cargo on sunken vessels, dumping of bycatch)
- Chemical pollution (oil, drilling muds and other oil/gas production chemicals, industrial chemicals, pharmaceuticals, munitions including chemical weapons)
- Radiochemical pollution
- Biomass removal (fishing, bioprospecting, scientific research)
- Mechanical disturbance (bottom fishing, cable laying, submarine pipelines, scientific research)
- Light pollution (industrial activity, scientific research)
- Acoustic disturbance (oil and gas exploration, military activity, scientific research)

Of these, the most serious present impacts arise from deep-sea bottom fisheries that target low-productivity species. Low-productivity species are those characterized by slow growth rates, high longevity, and sporadic reproduction when they have accumulated sufficient energy for producing offspring. Examples include orange roughy (*H. atlanticus*), oreos (Oreosomatidae), cardinal fish (*Epigonus* spp.), and grenadiers (Macrouridae) (97). Some seamount species, such as orange roughy, pelagic armorhead (*Pseudopentaceros wheeleri*), and alfonsinos (*Beryx splendens, B. decadactylus*), aggregate over submarine features, such as seamounts, to reproduce or to feed, and fishing intensity can be very high, also leading to rapid depletion of stocks (98, 99). A result of this has been a boom-bust cycle of fishing with stocks of these species rapidly being depleted after targeted fishing has commenced. For seamounts, fishing fleets have moved from feature to feature, leading to serial depletion (99, 100). As well as severely impacting target species, bycatch can include other low-productivity species, such as sharks, rays, and finfish, which also become depleted (101). Deep-sea bottom trawling, especially where it has been targeted at hot spot ecosystems, such as seamounts, has also resulted in the destruction of fragile benthic ecosystems, such as cold-water coral reefs, coral gardens, and sponge beds. Such ecosystems have a low capacity for recovery because structural species are extremely slow growing, have a high longevity (thousands of years for some coral species) (102), and probably low levels of recruitment. Observations indicate that removal of these vulnerable marine ecosystems (VMEs) results in a significant reduction of species richness as a result of loss of habitat complexity (e.g., 103). The broader ecosystem impacts of removal of large quantities of biomass from the deep sea through trophic linkages or the effects of removal of complex habitats are not understood. The latter may form important habitat for some species of fish and crustaceans as juveniles or adults, so there is a potential for feedback on stocks of commercial species (e.g., 104, 105).

International concern regarding the impacts of deep-sea bottom fisheries on the high seas to both target and bycatch species as well as VMEs led to several United Nations General Assembly Resolutions calling for improved management (106). This has led to improvements in the management of these fisheries by regional fisheries management organizations, as well as those in the exclusive economic zone of states including the freezing of fishing effort, banning of some destructive fishing methods or restricting their use, establishment of closed areas where VMEs are known to be present, and the development of rules to cease fishing and move on when VMEs are encountered and to undertake environmental impact assessments for exploratory or ongoing deep-sea fisheries. There has also been an effort to assess stock size in deep-sea fisheries and to move catches to levels where they are sustainable (e.g., 106, 107). Although these developments can be seen as progress, many deep-sea fisheries remain depleted or overexploited, and environmental impacts from bottom fishing, especially trawling, continue.

Another area of human influence on the deep sea, which has recently come to light, is the widespread contamination by plastic. Several studies have documented the occurrence of plastic trash (including lost fishing nets), microplastic particles, and fibers in deep-sea ecosystems (108–110). Lost fishing nets have been observed encrusted with marine organisms and entangling marine animals, such as fish, crustaceans, and coral (ghost fishing) (109). Microplastic particles or fibers have been found in deep-sea sediments and even on sessile organisms, such as corals. At present, it is largely unknown whether there are harmful effects from these microplastics, such as leaching of toxic chemicals or interference with feeding. The quantities of these materials are substantial, with potentially tens of millions of items of trash on seamounts of the Mid-Atlantic Ridge and South West Indian Ridge (110) and an abundance of microfibers in deep-sea sediments similar to those in intertidal or shallow subtidal sediments (109). This suggests the deep sea may be a major sink of plastics entering the ocean (109).

A growing human population, rising living standards, and technological developments are all leading to increased demand for resources. This is driving both existing and new forms of resource extraction into the deep sea. Oil exploration and production is increasingly focused on deep water (111), with extraction taking place in depths as great as nearly 3,000 m. It is estimated that deepwater continental margins contain about 40% of the world's future oil reserves (111). Other forms of energy, including gas hydrates on continental margins, hydrogen from deep-sea hydrothermal vents, and renewables from deep-sea turbines, are being assessed for commercial use. States are exploring the possibility of deep-sea mining, focusing on several types of deposits including seabed massive sulfides (SMSs), manganese or polymetallic nodules, cobalt crusts, metalliferous muds, and phosphate deposits. These are potential sources of copper, nickel, zinc, manganese, cobalt, gold, silver, platinum, tellurium, titanium, tungsten, lithium, molybdenum, yttrium, zirconium, bismuth, niobium, arsenic, cadmium, gallium, germanium, indium, tin selenium, rare earth elements (112), and phosphate, the latter for use as fertilizer (113). Such deposits occur within the exclusive economic zones of states or in areas beyond national jurisdictions, where mining is regulated by the UN International Seabed Authority. At present one deep-sea mining operation is in an advanced stage of preparation for extraction of SMS deposits from the waters of Papua New Guinea. The UN International Seabed Authority has granted 21 licenses for exploration of mineral deposits, 14 for manganese nodules (13 in the Clarion-Clipperton Fracture Zone in the Pacific Ocean and 1 in the basin of the Central Indian Ocean); 4 for SMS deposits on the Mid-Atlantic Ridge, Southwest Indian Ridge, and Central Indian Ridge; and 3 for cobalt crusts on seamounts in the western Pacific (114). These mineral deposits lie in very different environments, with varied levels of biodiversity and endemism, and require different approaches for extraction, meaning that management of the environmental impacts for different mining operations are likely to vary substantially.

Ghost fishing: the mortality of marine life associated with becoming entrapped in lost fishing gear

There is a strong potential for new direct impacts to influence the deep sea in the near future. Governance structures are evolving to attempt to manage existing and future direct impacts on the deep sea. For example, negotiations over a new implementing agreement for the United Nations Convention on the Law of the Sea, which lays out the rights and responsibilities of States with respect to the oceans, will commence in 2016, focusing on establishing a legal framework for spatial conservation measures, environmental impact assessments, and benefit sharing for marine genetic resources in the high seas (115). Scientific knowledge of environmental baselines associated with deep-sea ecosystems also needs to advance to facilitate knowledge-based decision making with respect to assessment and monitoring of environmental impacts from new activities.

THE IMPACTS OF CLIMATE CHANGE ON THE DEEP OCEAN

The overall impact of increased atmospheric CO_2 on the ocean primary production and delivery of POC to the deep sea largely occurs through its influences on the biological carbon pump. Although there are significant feedback effects to atmospheric CO_2 levels through the physical carbon pump of the oceans, the effects are less direct on the deep-sea biota (other than to exacerbate changes in the biological carbon pump as well as warming and acidification).

Effects of Increased Temperature

Evidence suggests that between 1971 and 2013, 93% of the excess heat in Earth's energy inventory, resulting from global warming, was taken up by the ocean (116). Temperature is a major driver of the distribution of marine organisms and has been positively correlated to species richness in shallow waters (117). Direct effects of changes in ocean temperature to the distribution and diversity of deep-sea species are expected. However, because of the coupling between surface and deep-sea ecosystems through processes, such as primary production, other indirect effects are also expected.

Increased stratification. The thermal stratification of the upper ocean affects nutrient availability and primary productivity (118). Whether overall trends of primary production in the oceans are increasing or decreasing as a result of increased stratification has been controversial. Some observations suggest that annual primary productivity has decreased (119, 120), whereas others suggest that it has increased and is tightly coupled with climate variability occurring interannually or over multidecadal timescales (121, 122). Likewise, future projections of changes on global oceanic primary production have also produced mixed results, with some predicting a global decrease in primary production (e.g., 123) and others predicting an increase (e.g., 124). The latest model projections of future change in global primary production, based on coupled carbon cycle-climate models that incorporate marine biogeochemical-ecosystem models of different complexity and, critically, that explicitly consider the cycling of nutrients and nutrient availability, suggest an overall decrease in global primary production and export of POC (125). A common causative mechanism in models predicting such declines of global primary and export production is the increased stratification of the ocean in low to mid-latitudes and a slowing of the thermohaline circulation, reducing nutrient availability in surface water layers (125). The decrease in nutrients is offset to some degree (but not completely) by the reduction in duration and coverage of polar sea ice, leading to higher primary production at high latitudes. In the context of the deep sea, this implies that at low to mid-latitudes the flux of POC will decrease, and at high latitudes, it may increase along with alterations in seasonality. The situation is broadly consistent with recent models of export flux to the deep ocean that suggest that, although flux and deep-sea

benthic biomass may increase in polar regions, it will decline elsewhere (by up to 38% in parts of the northeast Atlantic under Representative Concentration Pathway 8.5 (126). This will have maximal impact at abyssal and hadal depths because of the spatial pattern of changes in export flux and because these are already the most food-stressed environments. Changes in biomass will also result in changes in the size structure of affected deep-sea communities (126).

An alteration in the balance between autotrophic carbon fixation and heterotrophic re-mineralization resulting from increased sea surface temperatures. Mesocosm studies have suggested that CO_2 fixation by phytoplankton increases with increased CO_2 concentration (127). However, increased temperature has the potential effect of increasing metabolic rates and thus respiration rates of both phytoplankton and heterotrophic bacteria. In a mesocosm experiment examining the consequences of elevated temperature on natural phytoplankton communities, evidence of such an increase in community respiration rates, an enhancement of channeling of primary production through the microbial loop, and an increase in dissolved organic carbon production were found (128). This experiment suggests that the drawdown of CO_2 via the biological pump may decrease by up to 31% over a range of temperature increases of 2 to 6°C and that transfer of primary production to higher trophic levels may also significantly decrease (128). Similar mesocosm experiments have given different results of an increasing net primary production with temperature, possibly as a result of community differences in phytoplankton species (129). The results of Wohlers et al. (128) appear to be confirmed by a global meta-analysis of community respiration and gross primary production rates across 1,156 measurements from natural communities. Here, it was shown that again community respiration rates increase faster than rates of primary production (130). This study includes various effects of temperature on phytoplankton and bacterioplankton communities, such as changes in the size class of primary producers, as the findings are based on global observations of natural communities. Overall, the report predicts a decline of the ratio of photosynthetic primary production to respiration of 25% for a 4°C increase in temperature (130). In comparison, some biogeochemical models show that the effects of temperature on net primary production are inconsistent (e.g., 131). However, this study notes a general consistency in a negative relationship between temperature and export production as a result of enhanced recycling via the microbial loop across models (131). Overall, these changes suggest that a reduction in POC flux to the deep sea may be expected with increased temperature as a result of increased metabolic rates.

Changes in marine community structure as a result of increased temperature. Regardless of whether primary productivity of a given ocean basin changes, the composition of the phytoplankton may well change, a phenomenon, reported from many regions, associated with already warming sea surface temperatures (e.g., North Sea) (132–134). This in itself can alter the ratio of primary production to community respiration (130) and can also propagate through ecosystems via trophic interactions (134). As stated above, it is suspected that changes in the quality of phytodetritus arriving at the deep seabed may drive changes in benthic communities.

Habitat suitability modeling has also suggested that the latitudinal distribution of marine finfish and shellfish will move poleward and retreat from the equator (135). A recent meta-analysis of 1,735 responses for marine ecosystems—for which regional or global climate changes were considered a driver—found 81–83% were consistent with the expected range of responses, including poleward shifts in distribution as well as changes in community composition and abundance of species (136). The mean rate of latitudinal shift at the leading (poleward) edge of the range expansion was estimated at 72 +/− 13.5 km decade^{-1}, an order of magnitude faster than for terrestrial species. The fastest range shifts detected were for phytoplankton (469.9 +/− 115.3 km decade^{-1})

followed by finfish (277.5 +/− 76.9 km decade^{-1}) (136). The overall impacts of such complex and multifaceted changes on the operation of marine food webs are extremely difficult to predict given current knowledge. Their influence on the flux of food to deep-sea ecosystems is almost unstudied. It is important to recognize that food does not only sink into the deep sea as POC, but a proportion is actively transported through vertical migration of animals, especially between the surface and mesopelagic zone.

For the deep-sea communities themselves, there is surprisingly little information on the influence of temperatures on benthic or pelagic communities other than a broad acceptance that temperature influences biogeography at large scales (69). At the scale of community, studies have suggested that species diversity in benthic ecosystems may have a unimodal relationship with temperature (137). This effect is a relatively weak one with changes only at low temperatures ($<5°C$) and high temperatures ($\sim>15°C$) showing changes in diversity (137). The relationship may reflect oxygen- and capacity-limited thermal tolerance (see Impacts of Declining Oxygen Levels on Ocean Life and Feedbacks on Climate Change below). Biomass may also be significantly influenced by temperature, although macroecological studies suggest the effect is small (138).

Effects of Acidification on Primary Production and Particulate Organic Carbon Flux

Feedback effects on primary producers and calcifiers. Ocean acidification results from the absorption of CO_2 by seawater and its conversion to carbonic acid:

$$CO_{2(atmos)} \leftrightarrow CO_{2(aq)} + H_2O \leftrightarrow HCO_3 \leftrightarrow H^+ \, HCO_3^- \leftrightarrow 2H^+ + CO_3{}^{2-}.$$

At equilibrium, seawater with a pH of 8.1 contains $\sim90\%$ of the inorganic carbon as bicarbonate, 9% as carbonate, and 1% as CO_2. Adding CO_2 to seawater increases CO_2, bicarbonate, and hydrogen ions (the latter reducing pH) and reduces carbonate ions (139). To date, pH has declined by approximately 0.1, representing a 30% increase of hydrogen ions in seawater (140). If atmospheric CO_2 concentrations continue to increase as current trends suggest, then we will reach ~500 ppm CO_2 by the middle of the century and ~800 ppm by 2100 (139, 141). This corresponds to a decrease in pH in the surface oceans of 0.3–0.4 and an increase in hydrogen ions of 100–150% (139, 142, 143).

The operation of the biological carbon pump is partially driven by ballasting of phytodetritus and other organic matter with calcium carbonate structures derived from planktonic organisms, the most important of which are liths (calcareous scales) from coccolithophorids, an ecologically important group of unicellular algae. It has been experimentally demonstrated that many planktonic organisms show marked responses to declines in the calcium carbonate saturation state of seawater. This often manifests as decreased rates of calcification or an imbalance in calcium carbonate accretion with dissolution, although experimental results have been contradictory. For the ecologically important coccolithophore *Emiliania huxleyi*, for example, many studies have shown a decline in calcification rates with decreasing carbonate saturation of seawater (see review in 144). However, these studies were contradicted by some studies showing increased calcification with lowered pH and carbonate saturation states (most notably 145). These intraspecific differences have been attributed to both genetic and physiological differences between strains (in fact *E. huxleyi* is now regarded as a complex of several species) (144). Also, studies based on mesocosms or environmental samples of coccolithophores tend to show a more unified decrease in calcification of communities probably because strains or species that show lower levels of calcification grow faster than those that accrete heavier calcium carbonate scales under conditions of acidification (144). This is supported by the finding that *E. huxleyi* strains characterized by increased

calcification under reduced carbonate saturation show lower growth rates than those that show decreased calcification (e.g., 144, 145). For other organisms, such as pelagic foraminifera, experiments simulating low-pH waters also suggest a negative impact on calcification rates (146, 147). At present, there is insufficient understanding of the effects of reduced carbonate saturation on calcification in coccolithophorids and other important planktonic calcifiers to fully understand what the impact of this may be on POC flux to parts of the deep sea, especially in areas where calcareous phytoplankton form a significant component of communities of primary producers (e.g., 144).

Indirect impacts via reduction in calcification. Sea butterflies make a less important contribution to the generation of biogenic calcium carbonate. Studies of their responses to acidification also suggest a variable impact on sea butterfly species, but observations from experiments suggest that in many cases (but not all) their shells are subject to dissolution in water of reduced saturation or undersaturation of calcium carbonate (e.g., 142, 148, 149). These experimental results are consistent with observations of corroded sea butterfly shells in the natural environment, where the pH has been reduced through high respiratory CO_2 levels (150) or by the upwelling of deep water mixing with surface waters with lowered pH as a result of anthropogenic acidification (151). In both of these cases, aragonite saturation had been reduced to around or just below 1.0 (the point below which water is undersaturated with calcium carbonate and becomes corrosive to aragonite). Polar waters naturally have lower carbonate saturation than waters at middle and low latitudes because CO_2 is more soluble at lower temperatures and thus causes carbonate saturation to be lower (50). Models of the effect of atmospheric CO_2 on the carbonate saturation state of the oceans indicate that, even at atmospheric CO_2 concentrations of 450 ppm, parts of the Southern Ocean will be undersaturated with carbonate at the surface. By 550 ppm, half the ocean south of 60°S will be undersaturated and by 750 ppm, 95% of the Antarctic Southern Ocean will be undersaturated with calcium carbonate (140). Sea butterflies are important members of zooplankton communities in polar and subpolar waters, where they are prey for a variety of other zooplankton and fish (139). They are unlikely to adapt to such rapid acidification effects on carbonate saturation at high latitudes, and their range will therefore contract to shallower waters and lower latitudes, potentially leading to impacts via trophic links in polar and subpolar food webs (139), which may ultimately impact deep pelagic and benthic ecosystems.

Other indirect impacts of ocean acidification on marine ecosystems. Ocean acidification interacts with so many aspects of the physiology of marine organisms that it is not possible to give an exhaustive account of likely or speculative ecosystem impacts here. However, a number of notable studies indicate some important areas where acidification may have large-scale impacts on ecosystem functions.

One effect of the change in ocean chemistry with decreasing pH is a decrease in the bioavailability of iron. Iron is an important micronutrient that can limit primary production if in short supply. High-nutrient low-chlorophyll regions, such as the Southern Ocean, have their primary production largely limited by iron availability. As pH declines, it has significant impacts on iron chemistry, affecting its speciation in seawater and reducing its availability to phytoplankton (152). Experiments indicate a decrease in iron uptake by phytoplankton in seawater in which pH is reduced (152). The implications of this discovery are not entirely clear, although they may indicate a positive feedback process (i.e., a weakening of the biological carbon pump as a result of acidification). However, iron also becomes less likely to absorb to surfaces under such conditions, one of the major sinks for iron in the surface oceans (153).

The effect of acidification on the chemistry of the boundary layer around phytoplankton cells has also been raised as a potential issue impacting primary production. The boundary layer is the

layer of fluid immediately around a phytoplankton cell where a chemical microenvironment is maintained through the physical effects of a particle lying in a fluid. The effect of anthropogenic acidification combined with the impacts on pH around phytoplankton cells, resulting from normal metabolic processes, may cause stress to these organisms, especially in species that rely on a high pH to maintain calcium carbonate shells (154). Whether large pH changes in the boundary layer around phytoplankton cells are significant in terms of the biological carbon pump is unknown at present (155).

Acidification is likely to have significant impacts on the nitrogen cycle in the oceans through biologically mediated effects. Marine cyanobacteria are likely to increase their growth rates and their rate of nitrogen fixation in a high-CO_2 world (156). However, the process of nitrification by ammonia-oxidizing bacteria has been shown as negatively impacted by decreasing pH by 0.05– 0.14 units (157). It is suggested that ammonia oxidation may decline by as much as 3–44% for a 0.1 pH unit decrease over the next few decades. This nitrification generates nitrate at the base of the euphotic zone, which is estimated to support 32% of global primary production with a further 26% supported by upwelled previously generated NO_3^- from deep water (157). A decrease in the generation of nitrate may lead to depletion of this important form of nitrogen in the euphotic zone, causing a major shift from NO_3^- to NH_4, the remineralized product of nitrate (157). Such a shift may favor small-celled primary producers and disadvantage large-celled organisms, such as diatoms (157), with knock-on effects on the biological carbon pump and on the operation of deep-ocean food webs.

Many experiments indicate responses in the development of marine species from acidification. Studies of marine fish indicate a range of effects that may be viewed as negative or positive or unclear in significance (158). Antarctic krill are the keystone species in the Southern Ocean, mediating the flow of energy from primary producers to predators. Experiments indicate that this species shows no effect on development at the equivalent of 1,000 microatmospheres (µatm) pCO_2 (pressure of carbon dioxide) in the atmosphere, but at 1,250 µatm pCO_2 development is slowed down, and larval survival is reduced (159). The effects of acidification progressively become more severe, until at 1,750 to 2,000 µatm pCO_2 development completely ceases. Krill eggs sink after release, and the larvae hatch and sink further to depths of $\sim$1,000 m before ascending toward the surface as they go through successive growth stages (159). Deeper waters are less saturated or undersaturated with calcium carbonate and have higher pCO_2 levels than the surface. Models suggest that krill development may be impacted to some degree in parts of the Southern Ocean by as early as the end of the twenty-second century, depending on the CO_2 emissions scenario that humankind follows (159). Such effects would have large implications for Southern Ocean food webs, especially when other climate change–associated changes may be already having negative impacts on krill abundance (e.g., 160, 161). This would inevitably affect deep-sea communities, which probably have many direct and indirect trophic linkages to this important species in the Southern Ocean.

Acidification may also interact with ocean hypoxia (see the section Impacts of Climate Change on Oxygenation below). A further consequence of the reduced ballasting and sinking of POC is increased remineralization of primary production in the upper water column. This may manifest as increased utilization of oxygen through respiration most markedly at depths between 200 and 800 m (162). Such an effect would be synergistic with hypoxia already occurring in the oceans through expansion of oxygen minimum zones, an effect of weakening ocean ventilation and a decline in oxygen solubility with increasing temperatures (162).

Direct effects on deep-ocean biota. It is already understood that the calcium carbonate concentration in the deep sea acts as a significant control on the distribution of both scleractinian

corals and octocorals and the habitats they form (163–165). Modeling studies of changes in calcium carbonate concentrations resulting from climate change indicate that the shallowing of the carbonate compensation depth would likely have a significant impact on habitat suitability for these groups of organisms (166). Similarly, other deep-sea species with calcareous skeletons may be vulnerable to changes in the carbonate compensation depth and would also suffer reduction in available habitat. Other effects of changes in ocean chemistry associated with acidification on shallow water species, such as negative impacts on chemosensory systems (e.g., 167), have not been investigated in deep-sea species.

Climate Change Effects on Oxygenation of the Ocean

The dissolution of oxygen in seawater is directly dependent on temperature. and therefore, it should be of no surprise that ocean warming resulting from increasing atmospheric CO_2 levels alters ocean oxygenation. However, the levels of oxygen in seawater are sensitive to both biological processes, such as photosynthesis and respiration, and physical processes, such as ocean circulation and mixing. Because climate change effects both types of processes, its effects on oxygenation are complex.

Patterns of oxygenation in the global ocean. The oxygen levels of the ocean are maintained through the air-sea interface, especially at high latitudes where low temperatures lead to greater oxygen solubility in seawater (168). Oxygen is also generated in the euphotic zone of the ocean by photosynthesis and approximately tracks patterns of primary production at the surface (168). Oxygen is mainly used by microorganisms using organic matter as it sinks down from the surface layers of the ocean. This microbial activity decreases rapidly with depth, declining by a factor of 10–50 between the surface and 1,000 m depth (168). This bacterial utilization of oxygen is balanced by ocean ventilation and the uptake of oxygen at high latitudes, and approximates the time any given parcel of water was in contact with the surface. In the upper ocean, between ∼400 m and 1,200 m, oxygen levels reach a minimum because of weak ventilation of water at this depth and bacterial respiration. Where ocean circulation is weak and ventilation times are longest, eOMZs develop (169) generally between ∼200 m and 1,000 m depth (170). The term eOMZ is used here to define waters where oxygen levels fall below 60 μmol kg^{-1} (∼1.34 ml l^{-1}) (171), the level at which many higher organisms cannot survive. This has also been defined as the oxygen-limited zone (172). However, for many organisms, such as some fish and crustaceans, oxygen levels well above 2 milliliters per liter (ml l^{-1}) (∼89 μmol kg^{-1}) may be lethal, and there is great variation in sensitivity to hypoxia among different taxa (173). Furthermore, tolerance to low-oxygen concentrations also depends on temperature and CO_2 concentrations.

When oxygen levels fall below 5 μmol kg^{-1}, nitrate becomes important in respiration, progressively replacing oxygen as an electron acceptor as levels of the latter decrease (168). Thus, denitrification becomes increasingly important in severely hypoxic waters until nitrate is depleted when microbial sulfate reduction takes over as the dominant process metabolizing organic fuel (168).

The North Pacific gyre comprises the world's largest eOMZ, with smaller eOMZs in the Atlantic gyres. In the North Pacific, there is relatively poor ventilation at high latitudes (168). The Southern Hemisphere tends to be quite well ventilated owing to efficient oxygenation of deeper waters by the Antarctic Circumpolar Current (168). The northern Indian Ocean has no connection to subpolar waters because it is landlocked from the north, and here the largest eOMZ is found outside of the Pacific (168). Suboxic waters are shallow to less than 200 m depth across

large areas of the equatorial and north Pacific and the northern Indian Ocean, most notably in the Arabian Sea and Bay of Bengal (168).

Impacts of climate change on oxygenation. Climate change has two main physical impacts on oxygen concentrations in the oceans. First, oxygen is less soluble in warmer water, and second, stratification reduces the mixing of surface waters with deeper water layers, reducing ventilation of the ocean (168). The latter is potentially offset to some degree by the reduction of injection of nutrients from deep water to the euphotic zone as a result of stratification. This reduces primary production and the rate of sinking of POC below the euphotic zone. Models suggest that the physical effects of stratification on ventilation are larger than the offset from reduced primary production (168). Also, alteration in the relative rates of autotrophic carbon fixation versus heterotrophy in the upper ocean as a result of temperature increases (see An Alteration in the Balance Between Autotrophic Carbon Fixation and Heterotrophic Remineralization Resulting from Increased Sea Surface Temperatures above) may lead to increased relative oxygen demand by microbial communities, acting to reduce oxygen concentrations.

Models predict a decline in the oxygenation of the oceans of 1–7% by 2100 (reviewed in 168). Time-series observations in the Atlantic, Pacific, and Indian oceans have shown declining oxygen levels since the 1950s (168, 172). Decreasing oxygen has been most intense in eOMZs, with a shoaling of hypoxic waters in some cases, an increase in the depth of hypoxic waters, and a horizontal increase in hypoxic waters, in other words expansion of eOMZs (172). Since the 1960s, the maximum rate of declining oxygen levels at 200 m depth has been $\sim$0.5 μmol kg^{-1} year^{-1} in the Atlantic and tropical Pacific eOMZs (174). Locally, rates have been three to four times higher in the California Current region (specifically in the California Bight between 1984 and 2006). Long-term oxygen measurements in the midwater depths of the Gulf of Alaska and in the Oyashio Current off Japan, both in the northern Pacific, have shown a decrease of $\sim$7 μmol kg^{-1} decade^{-1} oxygen over the last 50 years (reviewed in 168). Similar declines have been detected elsewhere in the subarctic Pacific. These changes are thought to result from reduced ocean ventilation rather than from increased oxygen utilization, possibly linked to freshening of subarctic waters and warming in northeast Asia (168). The upper boundary of waters >60 μmol kg^{-1} of oxygen shallowed by $\sim$100 m in the Gulf of Alaska and $\sim$70 m in the California Bight over similar time periods (172). Declines in oxygen have also been detected in the tropical Atlantic and Pacific of between 0.9 and 3.4 μmol kg^{-1} decade^{-1} in the 300–700 m depth layer, including an expansion of the eOMZ with oxygen below 60 μmol kg^{-1} rising from 245–170 m depth in the eastern Pacific (reviewed in 168). Overall, these changes illustrate the extreme sensitivity to climate change of ocean oxygen levels. Beyond eOMZs, levels of oxygen have declined at rates $\sim$10% of those cited for eOMZs (172).

Impacts of declining oxygen levels on ocean life and feedbacks on climate change. The expansion of eOMZs increases the volume of water in which microbial denitrification and anaerobic ammonium oxidation are taking place. These processes convert biologically available nitrogen, as ammonium or nitrates, to nitrogen gas and nitrous oxide (N_2O), which is a powerful greenhouse gas (172). Thus, there is a potential positive feedback in terms of global warming. However, the reduction of biologically accessible nitrogen, in the form of nitrates, also potentially reduces primary production, reducing the microbial consumption of oxygen and progressive hypoxia in the water column (172). However, this reduction in primary production is a further positive feedback on the rate of CO_2 increase because of the reduced uptake of CO_2 via the biological carbon pump. To some extent, these effects may be offset by an increase in nitrogen-fixing cyanobacteria with increasing CO_2 levels (see section, Other Indirect Impacts of Ocean Acidification on Marine

Ecosystems, above), but please note that this is also associated with reduced nitrification. Iron may become more available from sediments under low-oxygen conditions, potentially enhancing primary production as it is a micronutrient (168). However, a decrease in the ballasting of phytodetritus because of reduced calcification by primary producers as well as rising temperatures may also lead to further reductions in water column oxygen levels because of increased remineralization in the euphotic zone (see section, Other Indirect Impacts of Ocean Acidification on Marine Ecosystems, above).

In addition, it has been found that sulfate reduction may be occurring within eOMZs, generating sulfides (see section, Patterns of Oxygenation in the Global Ocean, above). These compounds are toxic, although they are generally oxidized by sulfur-oxidizing bacteria (175). However, how sulfur oxidizers respond to decreasing oxygen levels is unclear. At least some sulfur oxidizers appear to use nitrate and/or nitrite as an electron acceptor through chemoautotrophic denitrification, thus linking the nitrogen and sulfur cycles (172). Shoaling OMZs may also generate new forms of habitat, where suboxic waters are found in the lower reaches of the euphotic zone, particularly in regions such as the California Current. The influence of such zones on biogeochemical cycling is difficult to predict but gives rise to the possibility of changing major groups of photosynthesizing organisms, including the increased occurrence of anoxygenic photosynthesizers (172).

The effects of expansion of eOMZs on larger organisms are very difficult to predict. In zones where eOMZs exist, diurnal vertically migrating mesopelagic organisms may enter the upper reaches of eOMZs during the day as a refuge from predation. These organisms have a range of physiological adaptations to survive in low-oxygen conditions, including specific physiological adaptations to extract oxygen in seawater when it is at low-oxygen partial pressure, the ability to store oxygen, increased capacity for anaerobic metabolism, and metabolic suppression resulting in lower oxygen requirements (176). Many active predators, such as tuna and marlin, have high metabolic rates and oxygen requirements of at least 150 μmol kg^{-1} (177) and thus cannot enter eOMZ waters (176). The effects of eOMZ expansion are to compress habitat for animals that can tolerate some level of hypoxia and that may enter the eOMZ boundary or upper layers by day, and also for fast-swimming predators that live above the eOMZ, such as marlin. For diurnal vertical migrators, this is potentially a double squeeze on habitat with climate change. This is because, in addition to shoaling of the eOMZ, the oxygen concentration of surface waters declines; rising CO_2 levels potentially lead to abnormally high levels of CO_2 in the body fluids (hypercapnia), interfering with the exchange of oxygen between organisms and the environment; and the metabolic rate of such species increases with temperature (e.g., jumbo squid in the California Current system) (176, 178). The overall effect of this is to potentially restrict the depth of species both from below (maximum depth of occurrence) and above (shallowest depth of occurrence) (176). An analogous situation has been proposed for oceans during the Permian-Triassic extinction, suggesting a refuge zone lying beneath very warm surface layers and anoxic deep layers in the water column (179). For marlin in the eastern tropical Atlantic between 1960 and 2010, it has been estimated that shoaling of eOMZ has reduced the volume of available habitat by 15% (180). This result is supported by tagging studies recording the diving depth of marlin within this geographic region (180). The consequences of habitat compression on deep pelagic species living in regions associated with eOMZs are currently not understood.

For benthic communities, low-oxygen environments are inevitably associated with reduced species diversity. For protozoans and meiofauna, densities are generally elevated within OMZs because of abundant organic material and possibly because they are protected from predation (170). Macrofauna and megafauna often exhibit depressed densities at the OMZ core but aggregate at the oxyclines, forming the boundaries of such zones (170). Fauna associated with OMZs tend to be specially adapted to life at low-oxygen concentrations, with thin bodies, relatively large respiratory
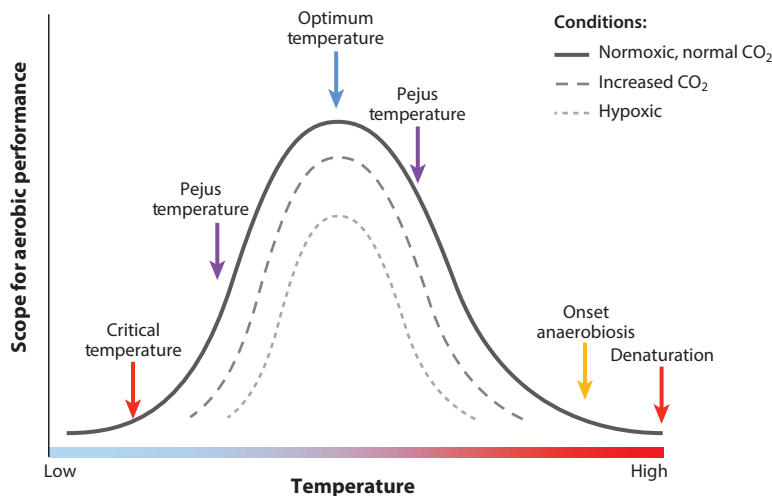
Figure 8

The window of optimal performance of an organism is affected by temperature, ocean carbonate chemistry, and hypoxia (the three direct symptoms of climate change in the ocean). For animals, the concept of oxygen- and capacity-limited thermal tolerance provides explanations for the specialization of animals across limited temperature ranges and their sensitivity to temperature extremes. Furthermore, it allows integration of other stressors on a thermal matrix of performance. The critical temperature is where there is an onset of anaerobic metabolism. The pejus temperature is the temperature above and below which oxygen supplies to tissues become suboptimal. The optimal temperature is the temperature at which the organism has maximum aerobic capacity for growth, reproduction, and activity. The denaturation temperature is where molecules, such as enzymes, lose integrity, leading eventually to death (adapted from 158). As CO_2 concentrations rise and/or oxygen supply decreases, the scope for aerobic performance decreases across a range of temperatures. Likewise there is evidence that tolerance to high pressure may also decline (161). Figure redrawn from Bijma et al. (181).

surfaces, and respiratory pigments, as well as having the ability to produce biogenic structures, allowing them to inhabit very soft sediments (170). Thus, the expansion of OMZs impacts the benthic ecosystems where they are located.

It is important to note that temperature, oxygen concentration, CO_2 concentration, and pressure tolerance may all be linked in the physiological determination of the environmental niche of a species (see **Figure 8**). The theory of oxygen- and capacity-limited thermal tolerance indicates that the scope for aerobic performance is affected by temperature and the concentrations of oxygen and CO_2 (181). Recent work suggests that pressure tolerance may also be limited by availability of oxygen (182). The implications of this for the deep-sea fauna, especially in regions where OMZs may be expanding, is currently not understood.

FINAL REMARKS

The deep sea is already under stress from a variety of human activities, but dumping of waste and deep-sea fisheries have probably been the most damaging (96). In some cases, impacts are widely distributed (e.g., marine litter); in others, they predominantly affect specific parts of deep-sea ecosystems, such as deep-sea trawling, which is generally restricted to the upper bathyal of the continental slope and seamounts and canyons (96). The magnitude of human influence on the deep

ocean is only just being recognized in some places, and its consequences are not fully understood, for example, the widespread occurrence of microplastics (108). Although the deep sea is largely out of sight, it should be of concern because it is the largest ecosystem on Earth and provides important ecosystem services for humankind (183). Correlative studies of the effects of spatial environmental variation on communities as well as long-term monitoring of a few sites in the Atlantic and Pacific provide evidence as to the influence of physical parameters and food supply on the abundance, biomass, and diversity of the deep-sea benthos and pelagic realms. These show that deep-ocean ecosystems are likely to be highly sensitive to climate-driven changes, which affect the quantity and quality of primary production and how production is processed in upper-water column food webs. Furthermore, direct impacts of temperature rise, acidification, and hypoxia are also likely to cause significant changes in the distribution and diversity of deep-sea communities. Major changes in ocean circulation have not been considered here but also have the potential to change these parameters where they occur. Geological history tells us that, if the process of global climate change is allowed to continue unchecked, the results of the phenomena described may be severe, leading to wide-scale horizontal and vertical range contraction in deep-ocean species and local or even global extinction, especially in species that inhabit relatively rare hot spot ecosystems. Many of these systems are already under stress from anthropogenic activities, and additive or negatively synergistic effects might be expected between direct impacts and the pervasive effects of climate change. One result will be a reduction in ecosystem services. The reduced services include positive feedbacks to atmospheric CO_2 levels through a weakening biological carbon pump, although this is likely small compared to feedbacks in atmospheric CO_2 related to changes in the physical carbon pump.

SUMMARY POINTS

1. General patterns in the abundance, biomass, body size, and diversity of deep-sea benthic communities are now known, although regional and taxonomic variations are insufficiently sampled or understood. Plausible explanations for these patterns have developed over recent years, but many remain to be tested experimentally.

2. Some general patterns have also been observed for the deep pelagic fauna, but the reliability of these patterns is poor because of extreme difficulties with sampling, and there is low confidence in even basic community parameters. The pelagic realm remains the most inadequately sampled ecosystem on Earth.

3. Long-term observations have indicated the sensitivity of deep-sea ecosystems to changes in food supply, resulting from the effects of environmental variation on the quantity and quality of primary production at the surface.

4. Climate change is likely to lead to significant changes in patterns of primary production in the surface ocean, with low and temperate latitudes likely to show a reduction in food supply to deep-sea communities, resulting in negative impacts on biomass, body size, and diversity changes at the level of community.

5. The direct impacts of climate change, including rising temperatures, increasing hypoxia, and acidification, are not well understood for deep-sea organisms.

6. Overall it is expected that climate change will lead to significant impacts on deep-sea ecosystems with negative impacts on ecosystem functions and services.

FUTURE ISSUES

1. Patterns of abundance, biomass, and diversity are known for some areas of the deep sea, but more sampling is required, especially in the Southern Hemisphere. The distribution of the deep pelagic fauna is not well understood.

2. Although hypotheses have been put forward to explain patterns of abundance, biomass, body size, and diversity, experimental approaches are required to fully understand the drivers of community structure in deep-sea ecosystems.

3. The functions of deep-sea food webs, particularly in relation to flows of carbon from the surface ocean to the deep sea, are poorly understood. Deep pelagic communities are barely understood even in terms of basic data, such as community composition, biomass, and the trophic roles of faunal groups.

4. There is clear evidence of the changes in range, phenology, and community structure in shallow-water marine communities, but similar data are almost absent for the deep sea. Historical data sets and sample collections are available for some regions and may be suitable for comparison with modern samples.

5. There is an urgent need to undertake observational and experimental approaches to better understand the effects of changes in food supply, temperature, oxygen, and pH on the deep-sea fauna.

DISCLOSURE STATEMENT

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LITERATURE CITED

1. Danovaro R, Snelgrove PVR, Tyler PA. 2014. Challenging the paradigms of deep-sea ecology. *Trends Ecol. Evol.* 29:465–75
2. Costello MJ, Cheung A, De Hauwere N. 2010. Surface area and the seabed area, volume, depth, slope, and topographic variation for the world's seas, oceans, and countries. *Environ. Sci. Technol.* 44:8821–28
3. Glud RN, Wenzhöfer F, Middelboe M, Oguri K, Turnewitsch R, et al. 2013. High rates of microbial carbon turnover in sediments in the deepest oceanic trench on Earth. *Nat. Geosci.* 6:284–88

4. Taira A, Toczko S, Eguchi N, Kuramoto S, Kubo Y, Azuma W. 2014. Recent scientific and operational achievements of D/V *Chikyu*. *Geosci. Lett.* 1:2

5. Paulmier A, Ruiz-Pino D. 2009. Oxygen minimum zones (OMZs) in the modern ocean. *Prog. Oceanogr.* 80:113–28

6. Connelly DP, Copley JT, Murton BJ, Stansfield K, Tyler PA, et al. 2012. Hydrothermal vent fields and chemosynthetic biota on the world's deepest seafloor spreading centre. *Nat. Commun.* 3:620

7. Van Dover C. 2000. *The Ecology of Hydrothermal Vents*. Princeton, NJ: Princeton Univ. Press

8. Bruun A. 1956. The abyssal fauna: its ecology, distribution and origin. *Nature* 177:1105–8

9. Gage JD, Tyler PA. 1992. *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor*. Cambridge, UK: Cambridge Univ. Press

10. Rex MA, Etter RJ, Morris JS, Crouse J, McClain CR, et al. 2006. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Mar. Ecol. Prog. Ser.* 317:1–8

11. Wei C-L, Rowe GT, Escobar-Briones E, Boetius A, Soltwedel T, et al. 2010. Global patterns and predictions of seafloor biomass using random forests. *PLOS ONE* 5(12):e15323

12. Angel MV, de Baker AC. 1982. Vertical standing crop of plankton and micronekton at three stations in the northeast Atlantic. *Biol. Oceanogr.* 2:1–30

13. Sutton TT, Wiebe PH, Madin L, Bucklin A. 2010. Diversity and community structure of pelagic fishes to 5000 m depth in the Sargasso Sea. *Deep-Sea Res. II* 57:2220–33

14. Sutton TT, Porteiro FM, Heino M, Byrkjedal I, Langhelle G, et al. 2008. Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. *Deep-Sea Res. II* 55:161–84

15. Robison BH, Sherlock RE, Reisenbichler KR. 2010. The bathypelagic community of Monterey Canyon. *Deep-Sea Res II* 57:1551–56

16. Gjøsæter J, Kawaguchi K. 1980. *A review of the world resources of mesopelagic fish*. FAO Fisheries Tech. Pap. No. 193 FIRM/T193, UN Food Agric. Organ., Rome

17. Kaartvedt S, Staby A, Aksnes D. 2012. Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. *Mar. Ecol. Prog. Ser.* 456:1–6

18. Robison BH. 2004. Deep pelagic biology. *J. Exp. Mar. Biol. Ecol.* 300:253–72

19. Webb TJ, Vanden Berghe E, O'Dor R. 2010. Biodiversity's big wet secret: The global distribution of marine biological records reveals chronic under-exploration of the deep pelagic ocean. *PLOS ONE* 5:e10223

20. van der Grient J, Rogers AD. 2015. Body size versus depth: regional and taxonomical variation in deep-sea meio- and macrofaunal organisms. *Adv. Marine Biol.* 71:71–108

21. McClain CR, Rex MA, Jabbour R. 2005. Deconstructing bathymetric body size patterns in deep-sea gastropods. *Mar. Ecol. Prog. Ser.* 297:181–87

22. Angel MV. 1989. Does mesopelagic biology affect the vertical flux? In *Productivity of the Oceans: Past and Present*, ed. WH Berger, VS Smetacek, G Wefer, pp. 155–73. Chichester, UK: Wiley

23. Beaugrand G. 2015. *Marine Biodiversity, Climatic Variability and Global Change*. Abingdon, Oxon., UK: Routledge

24. Collins MA, Bailey DM, Ruxton GD, Priede IG. 2005. Trends in body size across an environmental gradient: a differential response in scavenging and non-scavenging demersal deep-sea fish. *Proc. R. Soc. B* 272:2051–57

25. Grassle JF, Maciolek NJ. 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *Am. Nat.* 139:313–41

26. Lambshead PJD, Boucher G. 2003. Marine nematode deep-sea biodiversity—hyperdiversity or hype? *J. Biogeogr.* 30:475–85

27. Rex MA, Etter RJ. 2010. *Deep-Sea Biodiversity: Pattern and Scale*. Cambridge, MA: Harvard Univ. Press

28. Priede IG, Froese R. 2013. Colonization of the deep sea by fishes. *J. Fish. Biol.* 83:1528–50

29. Baselga A. 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Glob. Ecol. Biogeogr.* 21:1223–32

30. Brault S, Stuart CT, Wagstaff MC, Rex MA. 2013. Global evidence for source-sink dynamics in deep-sea neogastropods of the eastern North Atlantic: an approach using nested analysis. *Glob. Ecol. Biogeogr.* 22:433–39

31. Hardy SM, Smith CR, Thurnerr AM. 2015. Can the source-sink hypothesis explain macrofaunal abundance patterns in the abyss? A modelling test. *Proc. R. Soc. B* 282: In press. doi: 10.1098/rspb.2015.0193

32. Harris PT, Whiteway T. 2011. Global distribution of large submarine canyons: geomorphic differences between active and passive continental margins. *Mar. Geol.* 285:69–86

33. Allen SE, Durrieu de Madron X. 2009. A review of the role of submarine canyons in deep-ocean exchange with the shelf. *Ocean Sci.* 5:607–20

34. De Leo FC, Smith CR, Rowden AA, Bowden DA, Clark MR. 2010. Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. *Proc. R. Soc. B* 277:2783–92

35. Moors-Murphy HB. 2014. Submarine canyons as important habitat for cetaceans, with special reference to the Gully: a review. *Deep-Sea Res. II* 104:6–19

36. Kvile KO, Taranto GH, Pitcher TJ, Morato T. 2014. A global assessment of seamount ecosystems knowledge using an ecosystem evaluation framework. *Biol. Conserv.* 173:108–20

37. Yesson C, Clark MR, Taylor ML, Rogers AD. 2011. *The global distribution of seamounts based on 30 arc seconds bathymetry data*. Deep Sea Res. Part I, Oceanogr. Res. Pap. 58:442–53, JPI Oceans, Brussels, Belg.

38. Young JW, Hunt BPV, Cook TR, Llopiz JK, Hazen EL, et al. 2014. The trophodynamics of marine top predators: current knowledge, recent advances and challenges. *Deep-Sea Res. II* 113:170–87

39. Kaschner K. 2007. Air-breathing visitors to seamounts, section A: marine mammals. In *Seamounts: Ecology, Fisheries & Conservation*, *Fisheries and Aquatic Resource Series*, ed. TJ Pitcher, T Morato, PJB Hart, MR Clark, N Haggan, RS Santos, pp. 230–38. Oxford, UK: Blackwell

40. Maxwell SM, Frank JJ, Breed GA, Robinson PW, Simmons SE, et al. 2012. Benthic foraging on seamounts: a specialized foraging behavior in a deep-diving pinniped. *Mar. Mammal Sci.* 28:E333–44

41. Koslow JA. 1996. Energetic and life-history patterns of deep-sea benthic, benthopelagic and seamount-associated fish. *J. Fish. Biol.* 49:54–74

42. Genin A. 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *J. Mar. Syst.* 50:3–20

43. Rowden AA, Schlacher TA, Williams A, Clark MR, Stewart R, et al. 2010. A test of the seamount oasis hypothesis: seamounts support higher epibenthic megafaunal biomass than adjacent slopes. *Mar. Ecol.* 31(Suppl. 1):95–106

44. McClain CR, Lundsten L, Ream M, Barry J, DeVogelaere A. 2009. Endemicity, biogeography, composition, and community structure on a Northeast Pacific seamount. *PLOS ONE* 4(1):e4141

45. Jamieson AJ, Fujii T, Mayor DJ, Solan M, Priede IG. 2010. Hadal trenches: the ecology of the deepest places on Earth. *Trends Ecol. Evol.* 25:190–97

46. Belyaev GM. 1989. *Deep sea ocean trenches and their fauna*. Scripps Inst. Oceanogr. Tech. Rep., Univ. Calif. San Diego. **http://escholarship.org/uc/item/46n6148x#page-1**

47. Raven JA. 2009. Contributions of anoxygenic and oxygenic phototrophy and chemolithotrophy to carbon and oxygen fluxes in aquatic environments. *Aquat. Microb. Ecol.* 56:177–92

48. Hügler M, Sievert SM. 2011. Beyond the Calvin Cycle: autotrophic carbon fixation in the ocean. *Annu. Rev. Mar. Sci.* 3:261–89

49. Van Dover CL. 2000. *The Ecology of Deep-Sea Hydrothermal Vents*. Princeton, NJ: Princeton Univ. Press

50. Libes SM. 2009. *Introduction to Marine Biogeochemistry*. Burlington, MA: Academic. 2nd ed.

51. Devey CW, Fisher CR, Scott SC. 2007. Responsible science at hydrothermal vents. *Oceanography* 20:162–71

52. Kelley DS, Karson JA, Früh-Green GL, Yoerger DR, Shank TM, et al. 2005. A serpentinite-hosted ecosystem: the Lost City hydrothermal field. *Science* 307:1428–34

53. Marsh L, Copley JT, Huvenne VAI, Linse K, Reid WDK, et al. 2012. Microdistribution of faunal assemblages at deep-sea hydrothermal vents in the Southern Ocean. *PLOS ONE* 7:e48348

54. Gebruk AV, Chevaldonné P, Shank T, Lutz RA, Vrijenhoek RC. 2000. Deep-sea hydrothermal vent communities of the Logatchev area (14°45′N, Mid-Atlantic Ridge): diverse biotopes and high biomass. *J. Mar. Biol. Assoc. UK* 80:383–93

55. Rogers AD, Tyler PA, Connelly DP, Copley JT, James R, et al. 2012. The discovery of new deep-sea hydrothermal vent communities in the Southern Ocean and implications for biogeography. *PLOS Biol.* 10:e1001234

56. Cole CS, James RH, Conelly DP, Hathorne EC. 2014. Rare earth elements as indicators of hydrothermal processes within the East Scotia subduction zone system. *Geochim. Cosmochim. Acta* 140:20–38

57. Hannington M, Jamieson J, Monecke T, Petersen S, Beaulieu S. 2011. The abundance of seafloor massive sulfide deposits. *Geology* 39:1155–58

58. Vrijenhoek RC. 2010. Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations. *Mol. Ecol.* 19:4391–411

59. Marbler H, Koschinsky A, Pape T, Seifert R, Weber S, et al. 2010. Geochemical and physical structure of the hydrothermal plume at the ultramafic-hosted Logatchev hydrothermal field at 14°45′N on the Mid-Atlantic Ridge. *Mar. Geol.* 271:187–97

60. Perner M, Hansen M, Seifert R, Strauss H, Koschinsky A, et al. 2013. Linking geology, fluid chemistry, and microbial activity of basalt- and ultramafic-hosted deep-sea hydrothermal vent environments. *Geobiology* 11:340–55

61. Hoagland P, Beaulieu S, Tivey MA, Eggert RG, German C, et al. 2010. Deep-sea mining of seafloor massive sulfides. *Mar. Policy* 34:728–32

62. Levin LA. 2005. Ecology of cold seep sediments: interactions of fauna with flow, chemistry and microbes. *Oceanogr. Mar. Biol. Annu. Rev.* 43:1–46

63. Boetius A, Wenzhöfer F. 2013. Seafloor oxygen consumption fuelled by methane from cold seeps. *Nat. Geosci.* 6:725–34

64. Sibuet M, Olu K. 1998. Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep-Sea Res. II* 45:517–67

65. Feng D, Roberts HH, Cheng H, Peckmann J, Bohrmann G, et al. 2010. U/Th dating of cold-seep carbonates: an initial comparison. *Deep-Sea Res. II* 57:2055–60

66. Smith CR, Baco A. 2003. Ecology of whale falls at the deep-sea floor. *Oceanogr. Mar. Biol. Annu. Rev.* 41:311–54

67. Rouse GW, Goffredi SK, Vrijenhoek RC. 2004. *Osedax*: bone-eating marine worms with dwarf males. *Science* 305:668–71

68. Clarke A, Crame JA. 2010. Evolutionary dynamics at high latitudes: speciation and extinction in polar marine faunas. *Philos. Trans. R. Soc. Lond. B* 365:3655–66

69. Watling L, Guinotte J, Clark MR, Smith CR. 2013. A proposed biogeography of the deep ocean floor. *Prog. Oceanogr.* 111:91–112

70. Vierros M, Cresswell I, Escobar Briones E, Rice J, Ardron J, eds. 2009. *Global open oceans and deep seabed (GOODS): biogeographic classification*. IOC Tech. Ser. 84, Intergov. Oceanogr. Comm. (IOC)/UN Educ. Sci. Cult. Organ. (UNESCO), Paris

71. O'Hara TD, Rowden AA, Bax NJ. 2011. A Southern Hemisphere bathyal fauna is distributed in latitudinal bands. *Curr. Biol.* 21:226–30

72. Billett DSM, Lampitt RS, Rice AL, Mantoura RFC. 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* 302:520–22

73. Billett DSM, Bett BJ, Reid WDK, Boorman B, Priede IG. 2010. Long-term change in the abyssal NE Atlantic: the '*Amperima* event' revisited. *Deep-Sea Res. II* 57:1406–17

74. Kuhnz LA, Ruhl HA, Huffard CL, Smith KL Jr. 2014. Rapid changes and long-term cycles in the benthic megafaunal community observed over 24 years in the abyssal northeast Pacific. *Prog. Oceanogr.* 124:1–11

75. Lebrato M, de Jesus Mendes P, Steinberg DK, Cartes JE, Jones BM, et al. 2013. Jelly biomass sinking speed reveals a fast carbon export mechanism. *Limnol. Oceanogr.* 58:1113–22

76. Soto EH, Patterson GLJ, Billett DSM, Hawkins LE, Galéron J, et al. 2010. Temporal variability in polychaete assemblages of the abyssal NE Atlantic Ocean. *Deep-Sea Res. II* 57:1936–405

77. Gooday AJ, Malzone MG, Bett BJ, Lamont PA. 2010. Decadal scale changes in shallow-infaunal foraminiferal assemblages at the Porcupine Abyssal Plain, NE Atlantic. *Deep-Sea Res. II* 57:1362–82

78. Kalogeropoulou V, Bett BJ, Gooday AJ, Lampadariou N, Martinez Arbizu P, Vanreusel A. 2010. Temporal changes (1989–1999) in deep-sea metazoan meiofaunal assemblages on the Porcupine Abyssal Plain, NE Atlantic. *Deep-Sea Res. II* 57:1383–95

79. Smith KL Jr, Ruhl HA, Bett BJ, Billett DSM, Lampitt RS, Kaufmann RS. 2009. Climate, carbon cycling, and deep-ocean ecosystems. *PNAS* 106:19211–18

80. Smith KL Jr, Ruhl HA, Kahru M, Huffard CL, Sherman AD. 2013. Deep ocean communities impacted by changing climate over 24 y in the abyssal northeast Pacific Ocean. *PNAS* 110:19838–41

81. Rogers AD. 2000. The role of the oceanic oxygen minima in generating biodiversity in the deep sea. *Deep-Sea Res. II* 47:119–48

82. McClain CR, Hardy SM. 2010. The dynamics of biogeographic ranges in the deep sea. *Proc. R. Soc. B* 277:3533–56

83. Gill BC, Lyons TW, Young SA, Kump LR, Knoll AH, Saltzman MR. 2011. Geochemical evidence for widespread euxinia in the later Cambrian ocean. *Nature* 469:80–83

84. Harper DAT, Hammarlund EU, Rasmussen CMØ. 2014. End Ordovician extinctions: a coincidence of causes. *Gondwana Res.* 25:1294–1307

85. Brennecka GA, Herrmann AD, Algeo TJ, Anbar AD. 2011. Rapid expansion of oceanic anoxia immediately before the end-Permian mass extinction. *PNAS* 108:17631–34

86. Ullman CV, Thibault N, Ruhl M, Hesselbo SP, Korte C. 2014. Effect of a Jurassic oceanic anoxic event on belemnite ecology and evolution. *PNAS* 111:10073–76

87. Dickson AJ, Rees-Owen RL, März C, Coe AL, Cohen AS, et al. 2014. The spread of marine anoxia on the northern Tethys margin during the Paleocene-Eocene thermal maximum. *Paleoceanography* 29:471–88

88. Winguth AME, Thomas E, Winguth C. 2012. Global decline in ocean ventilation, oxygenation and productivity during the Paleocene-Eocene thermal maximum: implications for benthic extinction. *Geology* 40:263–66

89. Strugnell JM, Rogers AD, Prodöhl PA, Collins MA, Allcock AL. 2008. The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. *Cladistics* 24:1–8

90. Little CTS, Vrijenhoek RC. 2003. Are hydrothermal vent animals living fossils? *Trends Ecol. Evol.* 18:582–88

91. Roterman CN, Copley JT, Linse KT, Tyler PA, Rogers AD. 2013. The biogeography of the yeti crabs (Kiwaidae) with notes on the phylogeny of the Chirostyloidea (Decapoda: Anomura). *Proc. R. Soc. B* 280:1764

92. Yang J-S, Lu B, Chen D-F, Yu Y-Q, Yang F. 2014. When did decapods invade hydrothermal vents? Clues from the western Pacific and Indian oceans. *Mol. Biol. Evol.* 30:305–9

93. Thuy B, Kiel S, Dulai A, Gale AS, Kroh A, et al. 2014. First glimpse into Lower Jurassic deep-sea biodiversity: in situ diversification and resilience against extinction. *Proc. R. Soc. B* 281:20132624

94. Henry L-A, Frank N, Hebbeln D, Wienberg C, Robinson L. 2014. Global ocean conveyor lowers extinction risk in the deep sea. *Deep-Sea Res. I* 88:8–16

95. Glover AG, Smith CR. 2003. The deep-seafloor ecosystem: current status and prospects of anthropogenic change by the year 2025. *Environ. Conserv.* 30:219–41

96. Ramirez-Llodra E, Tyler PA, Baker MC, Bergstad OA, Clark MR, et al. 2011. Man and the last great wilderness: human impact on the deep sea. *PLOS ONE* 6:e22588

97. Norse EA, Brooke S, Cheung WWL, Clark MR, Ekeland I, et al. 2012. Sustainability of deep-sea fisheries. *Mar. Policy.* 36:307–20

98. Rogers AD. 1994. The biology of seamounts. *Adv. Mar. Biol.* 30:305–50

99. Clark MR, Rowden AA, Schlacher T, Williams A, Consalvey M, et al. 2010. The ecology of seamounts: structure, function and human impacts. *Annu. Rev. Mar. Sci.* 2:253–78

100. Clark MR. 2009. Deep-seamount fisheries: a review of global status and future prospects. *Lat. Am. J. Aquat. Sci.* 37:501–12

101. Devine JA, Baker KD, Haedrich RL. 2006. Fisheries: deep-sea fishes qualify as endangered. *Nature* 439:29

102. Robinson LF, Adkins JF, Frank N, Gagnon AC, Prouty NC, et al. 2014. The geochemistry of deep-sea coral skeletons: a review of vital effects and applications to palaeoceanography. *Deep-Sea Res. II* 99:184–98

103. Althaus F, Williams A, Schlacher TA, Kloser RJ, Green MA, et al. 2009. Impacts of bottom trawling on deep-coral ecosystems of seamounts are long lasting. *Mar. Ecol. Prog. Ser.* 397:279–94

104. Stone RP. 2006. Coral habitats in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations and fisheries interactions. *Coral Reefs* 25:229–38

105. Pham CK, Vandeperre F, Menezes G, Porteiro F, Isidro E, et al. 2015. The importance of deep-sea vulnerable marine ecosystems for demersal fish in the Azores. *Deep-Sea Res. I* 96:80–88

106. Rogers AD, Gianni M. 2010. *The implementation of UNGA Resolutions 61/105 and 64/72 in the management of deep-sea fisheries on the high seas*. Rep. prepared for Deep-Sea Conserv. Coalit., Int. Program. State Ocean, London, UK

107. Large PA, Agnew DJ, Pérez PAA, Froján CB, Cloete R, et al. 2013. Strengths and weaknesses of the management and monitoring of deep-water stocks, fisheries, and ecosystems in various areas of the world—a roadmap toward sustainable deep-water fisheries in the Northeast Atlantic? *Rev. Fish. Sci.* 21:157–80

108. Van Cauwenberghe L, Vanreusel A, Mees J, Janssen CR. 2013. Microplastic pollution in deep-sea sediments. *Environ. Pollut.* 182:495–99

109. Woodall LC, Sanchez-Vidal A, Canals M, Patterson GLJ, Coppock R, et al. 2014. The deep sea is a major sink for microplastic debris. *R. Soc. Open Sci.* 1:140317

110. Woodall LC, Robinson LF, Rogers AD, Narayanaswamy BE, Paterson GLJ. 2015. Deep-sea litter: a comparison of seamounts, banks and a ridge in the Atlantic and Indian oceans reveals both environmental and anthropogenic factors impact accumulation and composition. *Front. Mar. Sci.* 2:3

111. Caineng Z, Guangya Z, Shizhen T, Suyun H, Xiaodi L, Jianzhong L. 2010. Geological features, major discoveries, and unconventional petroleum geology in the global petroleum exploration. *Pet. Explor. Dev.* 37:129–45

112. Hein JR, Mizell K, Koschinsky A, Conrad TA. 2013. Deep-ocean mineral deposits as a source of critical metals for high- and green-technology applications: comparison with land-based resources. *Ore Geol. Rev.* 51:1–14

113. Nielsen SHH, McKenzie C, Miller A, Partington G, Payne C, et al. 2015. Chatham Rise nodular phosphate—modelling the prospectivity of a lag deposit (off-shore New Zealand): a critical tool for use in resource development and deep sea mining. *Ore Geol. Rev.* 71(Dec.):545–57. In press

114. Int. Seabed Auth. 2015. *Deep Seabed Minerals Contractors*. Kingston, Jam.: Int. Seabed Auth. **https://www.isa.org.jm/deep-seabed-minerals-contractors?page = 1&qt-contractors_tabs_alt = 0%20Accessed%207/05/2015**

115. United Nations General Assem. 2015. Advance and unedited outcome of the ad hoc open-ended informal working group to study issues relating to the conservation and sustainable use of marine biological diversity beyond national jurisdiction. Jan. 20–23, 2015. **http://www.un.org/depts/los/biodiversity workinggroup/documents/ahwg-9_report.pdf**

116. Rhein M, Rintoul SR, Aoki S, Campos E, Chambers D, et al. 2013. Observations: ocean. In *Climate Change 2013: The Physical Science Basis*. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, ed. Stocker TF, Qin D, Plattner G-K, Tignor MMB, Allen SK, et al., pp. 255–316. Cambridge, UK/New York: Cambridge Univ. Press

117. Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D et al. 2010. Global patterns and predictors of marine biodiversity across taxa. *Nature* 466:1098–101

118. Hoegh-Guldberg O, Bruno J. 2010. The impact of climate change on the world's marine ecosystems. *Science* 328:1523–28

119. Gregg WW, Conkright ME, Ginoux P, O'Reilly JE, Casey NW. 2003. Ocean primary production and climate: global decadal changes. *Geophys. Res. Lett.* 30:1809

120. Boyce DG, Lewis MR, Worm B. 2010. Global phytoplankton decline over the past century. *Nature* 466:591–96

121. Behrenfeld M, O'Malley R, Siegel D, McClain CR, Sarmiento JR, et al. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* 444:752–55

122. Chavez FP, Messié M, Pennington JP. 2011. Marine primary production in relation to climate variability and change. *Annu. Rev. Mar. Sci.* 3:227–60

123. Moore JK, Doney SC, Kleypas JA, Glover DM, Fung IY. 2002. An intermediate complexity marine ecosystem model for the global domain. *Deep-Sea Res. II* 49:403–62

124. Sarmiento JL, Slater R, Barber R, Bopp L, Doney SC, et al. 2004. Response of ocean ecosystems to climate warming. *Glob. Biogeochem. Cyles* 18:GB3003

125. Steinacher M, Joos F, Frölicher TL, Bopp L, Cadule P, et al. 2010. Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences* 7:979–1005

126. Jones DOB, Yool A, Wei C-L, Henson SA, Ruhl HA, et al. 2014. Global reductions in seafloor biomass in response to climate change. *Glob. Change Biol*. 20:1861–72

127. Riebesell U, Schulz KG, Bellerby RGJ, Botros M, Fritsche P, et al. 2007. Enhanced biological carbon consumption in a high CO_2 ocean. *Nature* 450:545–49

128. Wohlers J, Engel A, Zöllner E, Breithaupt P, Jürgens K, et al. 2009. Changes in biogenic carbon flow in response to sea surface warming. *PNAS* 106:7067–72

129. Taucher J, Schulz KG, Dittmar T, Sommer U, Oschlies A, Riebesell U. 2012. Enhanced carbon overconsumption in response to increasing temperatures during a mesocosm experiment. *Biogeosciences* 9:3531–45

130. Regaudie-de-Gioux A, Duarte CM 2012. Temperature dependence of planktonic metabolism in the ocean. *Glob. Biogeochem. Cyles* 26:GB1015

131. Taucher J, Oschlies A. 2011. Can we predict the direction of marine primary production change under global warming? *Geophys. Res. Lett*. 38:L02603

132. Nehring S. 1998. Establishment of thermophilic phytoplankton species in the North Sea: biological indicators of climate change? *ICES J. Mar. Sci*. 55:818–23

133. Johnson CR, Banks SC, Barrett NS, Cazassus F, Dunstan PK, et al. 2011. Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *J. Exp. Mar. Biol. Ecol*. 400:17–32

134. Polovina JJ, Woodworth PA. 2012. Declines in phytoplankton cell size in the subtropical oceans estimated from satellite remotely-sensed temperature and chlorophyll, 1998–2007. *Deep-Sea Res. II* 77–80:82–88

135. Cheung W, Lam VWY, Sarmiento J, Kearney K, Watson R, et al. 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish*. 10:235–51

136. Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, et al. 2013. Global imprint of climate change on marine life. *Nat. Clim. Change* 3:919–25

137. Yasuhara M, Danovaro R. 2014. Temperature impacts on deep-sea biodiversity. *Biol. Rev*. doi: 10.1111/brv.12169.

138. McClain CR, Allen AP, Tittensor DP, Rex MA. 2012. Energetics of life on the deep seafloor. *PNAS* 109:15366–71

139. Doney SC, Fabry VJ, Feely RA, Kleypas JA. 2009. Ocean acidification: the other CO_2 problem. *Annu. Rev. Mar. Sci*. 1:169–92

140. Cao L, Caldeira K. 2008. Atmospheric CO_2 stabilization and ocean acidification. *Geophys. Res. Lett*. 35:L19609

141. Eur. Sci. Found. 2009. *Impacts of ocean acidification*. Sci. Policy Brief. 37, Eur. Sci. Found., Brussels, Belg., **http://www.esf.org/fileadmin/Public_documents/Publications/SPB37_OceanAcidification.pdf**

142. Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, et al. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681–86

143. Caldeira K. 2007. What corals are dying to tell us about CO_2 and ocean acidification. *Oceanography* 20:188–95

144. Ridgwell A, Schmidt DN, Turley C, Brownlee C, Maldonado MT, et al. 2009. From laboratory manipulations to Earth system models: scaling calcification impacts of ocean acidification. *Biogeosciences* 6:2611–23

145. Iglesias-Rodriguez MD, Halloran PR, Rickaby REM, Hall IR, Colmenero-Hidalgo E, et al. 2008. Phytoplankton calcification in a high-CO_2 world. *Science* 320:336–40

146. Spero HJ, Bijma J, Lea DW, Bemis BE. 1997. Effect of seawater carbonate concentration on foraminiferal carbon and oxygen isotopes. *Nature* 390:497–500

147. Bijma J, Spero HJ, Lea DW. 1999. Reassessing foraminiferal stable isotope geochemistry: impact of the oceanic carbonate system (experimental results). In *Use of Proxies in Paleoceanography: Examples from the South Atlantic*, ed. G Fischer, G Wefer, pp. 489–512. Berlin: Springer-Verlag

148. Comeau S, Gorsky G, Jeffree R, Teyssié J-L, Gattuso J-P. 2009. Impact of ocean acidification on a key Arctic pelagic mollusc (*Limacina helicina*). *Biogeosciences* 6:1877–82

149. Comeau S, Alliouane S, Gattuso J-P. 2012. Effects of ocean acidification on overwintering juvenile Arctic pteropods *Limacina helicina*. *Mar. Ecol. Prog. Ser*. 456:279–84

150. Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, et al. 2004. Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science* 305:362–66

151. Bednaršek N, Tarling GA, Bakker DCE, Fielding S, Jones EM, et al. 2012. Extensive dissolution of live pteropods in the Southern Ocean. *Nat. Geosci.* 5:881–85

152. Shi D, Xu Y, Hopkinson BM, Morel FMM. 2010. Effect of ocean acidification on iron availability to marine phytoplankton. *Science* 327:676–79

153. Sunda WG. 2010. Iron and the carbon pump. *Science* 327:654–55

154. Flynn KJ, Blackford JC, Baird ME, Raven JA, Clark DR, et al. 2012. Changes in pH at the exterior surface of plankton with ocean acidification. *Nat. Clim. Change* 2:510–13

155. Milligan AJ. 2012. Plankton in an acidified ocean. *Nat. Clim. Change* 2:489–90

156. Hutchins DA, Mulholland MR, Fu F. 2009. Nutrient cycles and marine microbes in a CO_2-enriched ocean. *Oceanography* 22:128–45

157. Beman JM, Chow C-E, King AL, Feng Y, Fuhrman JA, et al. 2011. Global declines in oceanic nitrification rates as a consequence of ocean acidification. *PNAS* 108:208–13

158. Bignami S, Sponaugle S, Cowen RK. 2013. Response to ocean acidification in larvae of a large tropical marine fish, *Rachycentron canadum*. *Glob. Change Biol.* 19:996–1006

159. Kawaguchi S, Ishida A, King R, Raymond B, Waller N, et al. 2013. Risk maps for Antarctic krill under projected Southern Ocean acidification. *Nat. Clim. Change* 3:843–47

160. Atkinson A, Siegel V, Pakhomov E, Rothery P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–3

161. Quetin LB, Ross RM. 2009. Life under Antarctic pack ice: a krill perspective. In *Smithsonian at the Poles: Contributions to International Polar Year Science*, ed. I Krupnik, MA Lang, SE Miller, pp. 285–98. Washington, DC: Smithson. Inst. Sch. Press

162. Hofmann M, Schellnhuber H-J. 2009. Oceanic acidification affects marine carbon pump and triggers extended marine oxygen holes. *PNAS* 106:3017–22

163. Rogers AD, Baco A, Griffiths H, Hart T, Hall-Spencer JM. 2007. Corals on seamounts. In *Seamounts: Ecology, Fisheries and Conservation*, ed. TJ Pitcher, T Morato, PJB Hart, MR Clark, N Haggan, RS Santos, pp. 141–69. Oxford, UK: Blackwell

164. Tittensor DP, Baco AR, Brewin PE, Clark MR, Consalvey M, et al. 2009. Predicting global habitat suitability for stony corals on seamounts. *J. Biogeogr.* 36:1111–28

165. Yesson C, Taylor M, Tittensor DP, Davies A, Guinotte J, et al. 2012. Global distribution and habitat preferences of deep-sea octocorals. *J. Biogeogr.* 39:1278–92

166. Tittensor DP, Baco AR, Hall-Spencer JM, Orr JC, Rogers AD. 2010. Seamounts as refugia from ocean acidification for cold-water stony corals. *Mar. Ecol.* 31(Suppl. 1):212–25

167. Munday PL, Dixson DL, Donelson JM, Jones GP, Pratchett MS, et al. 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *PNAS* 106:1848–52

168. Keeling RF, Körtzinger A, Gruber N. 2010. Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci.* 2:199–229

169. Karstensen J, Stramma L, Visbeck M. 2008. Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans. *Prog. Oceanogr.* 77:331–50

170. Levin LA. 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanogr. Mar. Biol. Annu. Rev.* 41:1–45

171. Thierry V, Gilbert D, Kobayashi T, Schmid C. 2013. Processing Argo oxygen data at the DAC level, Version 1.3. Inst. Fr. Rech. l'Exploit. Mer, Brest, Fr. **http://www.argodatamgt.org/content/download/16300/106561/file/argo_oxygen_proposition_v1p3.pdf**

172. Gilly WF, Beman JM, Litvin SY, Robison BH. 2013. Oceanographic and biological effects of shoaling of the oxygen minimum zone. *Annu. Rev. Mar. Sci.* 5:393–420

173. Vaquer-Sunyer R, Duarte CM. 2008. Thresholds of hypoxia for marine biodiversity. *PNAS* 105:15452–57

174. Stramma L, Schmidtko S, Levin LA, Johnson GC. 2010. Ocean oxygen minima expansions and their biological impacts. *Deep-Sea Res. I* 57:587–95

175. Canfield DE, Glazer AN, Falkowski PG. 2010. The evolution and future of Earth's nitrogen cycle. *Science* 330:192–96

176. Seibel BA. 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *J. Exp. Biol.* 214:326–36

177. Brill RW. 1994. A review of temperature and oxygen tolerance studies of tunas, pertinent to fisheries oceanography, movement models and stock assessments. *Fish. Oceanogr*. 3:204–16

178. Rosa R, Seibel BA. 2008. Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. *PNAS* 105:20776–80

179. Song H, Wignall PB, Chu D, Tong J, Sun Y, et al. 2014. Anoxia/high temperature double whammy during the Permian-Triassic marine crisis and its aftermath. *Sci. Rep*. 4:4132

180. Stramma L, Prince ED, Schmidtko S, Luo J, Hoolihan JP, et al. 2011. Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nat. Clim. Change* 2:33–37

181. Bijma J, Pörtner H-O, Yesson C, Rogers AD. 2013. Climate change and the oceans—What does the future hold? *Mar. Pollut. Bull*. 74:495–505

182. Brown A, Thatje S. 2015. The effects of changing climate on faunal depth distributions determines winners and losers. *Glob. Change Biol*. 21:173–80

183. Armstrong CW, Foley NS, Tinch R, Van Den Hive S. 2012. Services from the deep: steps towards valuation of deep-sea goods and services. *Ecosyst. Serv*. 2:2–13