

## Chapter 36F. Open Ocean Deep Sea

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### Introduction to the open ocean deep sea

The deep sea comprises the seafloor, water column and biota therein below a specified depth contour. There are differences in views among experts and agencies regarding the appropriate depth to delineate the “deep sea”. This chapter uses a 200 metre depth contour as a starting point, so that the “deep sea” represents 63 per cent of the Earth’s surface area and about 98.5 per cent of Earth’s habitat volume (96.5 per cent of which is pelagic). However, much of the information presented in this chapter focuses on biodiversity of waters substantially deeper than 200 m. Many of the other regional divisions of Chapter 36 include treatments of shelf and slope biodiversity in continental-shelf and slope areas deeper than 200 m. Moreover Chapters 42 and 45 on cold water corals and vents and seeps, respectively, and 51 on canyons, seamounts and other specialized morphological habitat types address aspects of areas in greater detail. The estimates of global biodiversity of the deep sea in this chapter do include all biodiversity in waters and the seafloor below 200 m. However, in the other sections of this chapter redundancy with the other regional chapters is avoided, so that biodiversity of shelf, slope, reef, vents, and specialized habitats is assessed in the respective regional or thematic chapters.

This truly vast deep-sea realm constitutes the largest source of species and ecosystem diversity on Earth, with great potential for mineral, energy, and living resources (e.g., Koslow, 2007). Despite major technological advances and increased deep-sea exploration in the past few decades (Danovaro et al., 2014), a remarkably small portion of the deep sea has been investigated in detail (Ramirez-Llodra et al., 2010), particularly in terms of time-series research (Glover et al., 2010). For the pelagic areas much less than 0.0001 per cent of the over 1.3 billion km<sup>3</sup> of deep water has been studied. The inevitable result is weaker characterization of deep-sea biodiversity compared to the shelf, slope and terrestrial realms. Correspondingly this also means that continued scientific and surveying efforts may potentially change our current understanding of deep-sea biodiversity. There is strong evidence that the richness and diversity of organisms in the deep sea exceeds all other known biomes from the metazoan to the microbial realms (Rex and Etter, 2010; Zinger et al., 2011) and supports the diverse ecosystem processes and functions necessary for the Earth’s natural systems to function (Thurber et al., 2014). Moreover, the extensive species, genetic, enzymatic, metabolic, and biogeochemical diversity

hosted by the deep ocean also holds the potential for new pharmaceutical and industrial applications. With up to millions of estimated deep-sea species (cf. Chapter 34; CoML, 2010; Grassle and Maciolek, 1992), although the true number of species may be less, (Appeltans et al., 2012, Costello et al., 2013; Mora et al., 2013a), it would take many generations to document deep-sea diversity in its entirety. In fact, this may not even be possible given the huge taxonomic effort required (Mora et al., 2013a) and the rate of species extinctions (Pimm et al., 1995). Nor is it necessary to have fully quantified deep-sea biodiversity to commence identification of risks and opportunities, and design of programmes for its conservation and sustainable use, even if new knowledge is later acquired that enables such programmes to be improved.

Over the years, deep-sea ecologists have posited several theories to explain high deep-sea biodiversity; many highlight aspects of habitat heterogeneity and the extended time scales at which the deep sea is thought to operate (e.g. Levin and Dayton, 2009; Rex and Etter, 2010; Snelgrove and Smith, 2002). Most experts agree that the presence of different habitats, along with temporal variation, critically support deep-sea diversity; for instance, geomorphological structures such as canyons, seamounts (Figure 36F.1; cf. Chapter 51), hydrothermal vents and methane seeps (cf. Chapter 45), as well as biotic structures, such as cold-water coral reefs (Figure 36F.1; Chapter 42), and whale falls sustain unique assemblages of organisms, diversifying the deep-sea species pool (Reed et al., 2013). At the same time, however, many deep-sea species are widely distributed (e.g., Havermans et al., 2013; Ingels et al., 2006; Pawlowski et al., 2007), although new genetic tools already suggest many species are less cosmopolitan than was previously thought. Small-scale heterogeneity further enhances diversity, through the provision of phytodetrital patches, biogenic structures such as sponges and xenophyophores, organic food falls, pits, and hillocks, (Buhl-Mortensen et al., 2010). Anthropogenic structures such as deep-water oil rigs and shipwrecks harbouring highly diverse faunal assemblages reflect deep-sea faunal responses to smaller-scale habitat heterogeneity (Church et al., 2009; Taylor et al., 2014; Friedlander et al., 2014).

Deep-sea ecosystems are crucial for global functioning; e.g., remineralization of organic matter in the deep sea regenerates nutrients that help fuel the oceanic primary production that accounts for about half of atmospheric oxygen production. Whilst coastal and shallow-water processes and functions produce services within tangible time scales and local and regional spatial scales, the deep-sea processes and ecosystem functions that occur on the scale of microns to meters and time scales up to years often translate to useful services only after centuries of integrated activity (Thurber et al., 2014). Evidence demonstrates, however, that interannual changes in climate can influence deep-sea systems over time scales not fundamentally different from terrestrial habitats. Climatically driven changes in sinking particulate organic matter can alter deep-sea abundance, community structure, diversity and functioning within days to months, depending in part on body size (Ruhl et al., 2008; Ruhl and Smith, 2004) along with temperature-driven interannual diversity changes (Danovaro et al., 2014).

Numerous human activities affect deep-sea ecosystems, goods, and services directly and indirectly now and will do so increasingly in the future (Glover and Smith, 2003;

Mengerink et al., 2014; Ramirez-Llodra et al., 2011). These are addressed in various chapters of Parts IV and V of this Assessment, with Chapters 11 (Capture Fisheries), 21 (Offshore Hydrocarbon Industries), 20 (Land-based Inputs), 23 (Other Mining Industries), 25 (Marine debris) and 27 (Tourism) of particular relevance.

## **Benthic realm**

### *2.1 Deep-sea margins*

The global continental margins extend for ~150,000 km (Jahnke, 2010) and encompass estuarine, open coast, shelf, canyon, slope, and enclosed-sea ecosystems (Levin and Sibuet, 2012). Deep-sea margins are those areas that lie beyond the shelf break, where the seafloor slopes down to the continental rise at abyssal depths, and encompasses bathyal depths. Numerous canyons and channels incise the continental slope (see Chapter 51), often featuring cold-water coral reefs (Chapter 42) or oxygen minimum zones (OMZs) as distinct habitats along the deep margin. Sediment covers much of the deep continental margin, but with exposed bedrock in areas where topography is too steep for sediment accumulation (e.g., steep canyon walls) or where sediment is washed away (e.g., parts of seamounts). Different faunas inhabit soft- and hard-bottom substrates.

Relative to their area, the margins account for a disproportionately large fraction of global primary production (10-15 per cent), nutrient recycling, carbon burial (>60 per cent of total settling organic carbon), and fisheries production (Muller-Karger et al., 2005). They are also exceptionally dynamic systems with ecosystem structures that can oscillate slowly or shift abruptly, but rarely remain static (Levin et al., 2014).

#### *1.1.1 Status of and trends for biodiversity*

In the well-studied North Atlantic, local macrofaunal (300 µm-3 cm) species diversity on the continental slope exceeds that of the adjacent continental shelf, and estimates of bathyal diversity in other parts of the world ocean are comparably high (Rex and Etter, 2010), but local environmental conditions drive regional differences: e.g., the Gulf of Mexico, the Norwegian and Mediterranean Seas (Narayanaswamy et al., 2013), the Eastern Pacific and the Arabian Sea (Levin et al., 2001). Most researchers agree that habitat heterogeneity on different spatial scales drives high diversity along the margins (Narayanaswamy et al., 2013) and that margins often exhibit upwelling and increased production that enhances biodiversity. Nonetheless, excess food availability can reduce diversity.

Depth-related species diversity gradients in macrofauna often peak unimodally at mid-bathyal depths of about 1500-2000 m (Rex and Etter, 2010), although shallower peaks in diversity have been observed in Arctic waters (Narayanaswamy et al., 2005; 2010; Svavarsson, 1997; Yasuhara et al., 2012b) for bivalves, polychaetes, gastropods and cumaceans (Rex, 1981), as well as for the entire macrofauna (Etter and Mullineaux, 2000; Levin et al., 2001) and some meiofauna (Yasuhara et al., 2012b) (32 µm-1000 µm). Even regions with very low diversity can host highly specialized species (e.g., OMZs) and contribute to overall margin diversity (Gooday et al., 2010).

Thus, throughout their depth gradient, continental margin slope areas exhibit the highest macrofaunal diversity and offer a potentially important refuge against future climate change, as mobile organisms could migrate upslope or downslope in search of suitable conditions (Rodriguez-Lazaro and Cronin, 1999; Yasuhara et al., 2008; 2009).

The diversity of meiofauna (32  $\mu\text{m}$ -1,000  $\mu\text{m}$ ) exceeds that of the macrofauna and their diversity generally increases with depth; however, groups such as foraminifera and ostracods exhibit unimodal peaks in diversity (Yasuhara et al., 2012b). Meiofaunal diversity may decline or increase with increasing bathyal depths (Narayanaswamy et al., 2013), generally driven by food availability and intensity and regularity of disturbance regimes, as well as by temperature and local environmental conditions (Corliss et al., 2009; Yasuhara et al., 2012a; 2009; 2012b; 2014).

Russian and Scandinavian deep-sea expeditions described peak benthic megafaunal (>3 cm) diversity at mid-bathyal depths as early as the 1950s and 1960s, despite observing much lower megafaunal than meio- and macrofaunal diversity (Vinogradova, 1959). Sponges, cnidarians, crustaceans (decapods and isopods) and echinoderms (echinoids, asteroids, crinoids, holothurians) all display this pattern; however later studies confirmed the pattern for some megafaunal invertebrates, but showed a decline or even increase in diversity with increasing depth for some taxa. Evidence to date suggests lower species richness in deep-sea bacterial communities than in coastal benthic environments, with the caveat that deep-sea environments remain underexplored (Zinger et al., 2011). However, the presence of extreme environments in the deep sea which have high phylogenetic diversity promises a rich source of bacterial diversity and genetic innovation (Sogin et al., 2006).

Several faunal groups also exhibit latitudinal gradients in species diversity (Narayanaswamy et al., 2010; Rex and Etter, 2010; Yasuhara et al., 2009): diversity of crustaceans, molluscs and foraminifera declines poleward (Gage et al., 2004; Rex et al., 2000), whilst others such as nematodes respond to phytodetrital input (Lambshhead et al., 2000). Latitudinal gradients have also been identified in bacteria (Fuhrman et al., 2008; Sul et al., 2013) but recent modelling indicates peak bacterial richness in temperate areas in winter (Ladau et al., 2013). The effect of seasons on macro-ecological patterns in the microbial ocean warrants continued investigation to test the mechanisms that underlie latitudinal patterns in different fauna.

Broad-scale depth and latitudinal patterns in benthic diversity are modified regionally by a variety of environmental factors operating at different scales. For example, OMZs strongly affect diversity where they impinge on the seafloor. OMZs typically occur between 200 m and 1000 m, often at major carbon burial sites along the continental margins where high productivity results in high carbon fluxes to the seafloor and low oxygen. The organic-rich sediments of these regions often support mats of large sulphide-oxidizing bacteria (*Thioploca*, *Beggiatoa*, *Thiomargarita*), and high-density, low-diversity metazoan assemblages. Protists are also well represented in OMZs such as the Cariaco Basin, where representatives of all major protistan clades occur (Edgcomb et al., 2011). Depressed diversity near OMZs centres favours taxa that can tolerate hypoxia, such as nematodes (Cook et al., 2000; Levin, 2003) and certain annelids and foraminifera (Levin, 2003). Other taxa that cannot tolerate

low-oxygen conditions may aggregate at the OMZs fringes where food is often abundant.

### 1.1.2 Major pressures

Multiple anthropogenic influences affect deep-sea habitats located close to land (e.g., canyons, fjords, upper slopes when continental shelves are very narrow), including organic matter loading (see Chapter 20), mine tailings disposal (Kvassnes and Iversen, 2013; Kvassnes et al., 2009), litter (Pham et al., 2014), bottom trawling (Pusceddu et al., 2014) and overfishing (Clark et al., 2007), enhanced or decreased terrestrial input, oil and gas exploitation (Ramirez-Llodra et al., 2011) and, potentially in future, deep-sea mining (see Chapter 23). Fishing on margins can also have indirect ecological effects at deeper depths (Bailey et al., 2009). These anthropogenic influences can modify deep-margin habitats through physical smothering and disturbance, sediment resuspension, organic loading, and toxic contamination and plume formation, with concomitant losses in biodiversity, declining energy flow back to higher trophic levels, and impacts on physiology from exposure to toxic compounds (e.g., hydrocarbons, polycyclic aromatic hydrocarbons (PAHs), heavy metals) (see Ramirez-Llodra et al., 2011 for review).

## 2.2 Abyss

### 2.2.1 Status and trends for biodiversity

The abyss (~3-6 km water depth) encompasses the largest area on Earth. Its vast areas of seafloor plains and rolling hills are generally covered in fine sediments with hard substrates associated with manganese nodules, rock outcrops and topographic highs (e.g. seamounts). The absence of *in situ* primary production in this comparatively stable habitat (apart from scant occurrence of chemosynthesis at hydrothermal vents and cold seeps; cf. Chapter 45) characterize an ecosystem adapted to a limiting and variable rain of particulate detrital material that sinks from euphotic zones. Nonetheless, the abyss supports higher levels of alpha and beta diversity of meiofauna, macrofauna and megafauna than was recognized only decades ago (Rex and Etter, 2010). The prevalence of environmental DNA preserved in the deep sea biases estimates of richness, at least in the microbial domain, adding a challenge to biodiversity study in the abyss using molecular methods (Pawlowski et al., 2011).

Despite poorly known biodiversity patterns at regional to global scales (especially regarding species ranges and connectivity), some regions, such as the abyssal Southern Ocean (Brandt et al., 2007; Griffiths, 2010) and the Pacific equatorial abyss, are likely to represent major reservoirs of biodiversity (Smith et al., 2008).

### 2.2.2 Major pressures

The food-limited nature of abyssal ecosystems, and reliance on particulate organic carbon (POC) flux from above, suggest that all groups, from microbes to megafauna, will be highly sensitive to changes in phytoplankton productivity and community structure, and especially to changes in the quantity and quality of the export flux (Billett et al., 2010; Ruhl et al., 2008; Ruhl and Smith, 2004; Smith et al., 2008; Smith

et al.,2013). Climate warming in some broad areas may increase ocean stratification, reduce primary production, and shift the dominant phytoplankton community structure from diatoms to picoplankton, and reduce export efficiency, driving biotic changes over major regions of the abyss, such as the equatorial Pacific (Smith et al., 2008). However the effects of climate change, including ocean warming, on biodiversity are likely to vary regionally and among species groups in ways that are poorly resolved with current models and knowledge of ecosystem dynamics in the deep sea. In the future, deep sea mining may also become a pressure on abyssal areas of the deep sea, and potential effects are addressed in Chapter 21.

## 2.3 *Hadal*

### 2.3.1 *The Hadal zone*

The Hadal zone, comprising ocean floor deeper than 6000 m, encompasses 3,437,930 km<sup>2</sup>, or less than 1 per cent of total ocean area (Harris et al., 2014) and represents 45 per cent of its depth and related gradients. Over 80 separate basins or depressions in the sea floor comprise the hadal zone, dominated by 7 great trenches (>6500 m) around the margins of the Pacific Ocean, five of which extend to over 10 km depth: the Japan-Kuril-Kamchatka, Kermadec, Tonga, Mariana, and Philippine trenches. The Arctic Ocean and Mediterranean Sea lack hadal depths. These trenches are often at the intersection of tectonic plates, exposing them as potential epicentres of severe earthquakes which can directly cause local and catastrophic disturbance to the trench fauna.

### 2.3.2 *Status and trends for biodiversity*

Although the hadal zone contains a wide range of macro- and megafaunal taxa (cnidarians, polychaetes, bivalves, gastropods, amphipods, decapods, echinurids, holothurians, asteroids, echinoids, sipunculids, ophiuroids and fishes (Beliaev, 1989; Wolff, 1970), all trenches occur below the Carbonate Compensation Depth (CCD), reducing the numbers of calcified protozoan and metazoan species found there (Jamieson, 2011). Chemosynthetic seep biota, including vesicomyid and thyasirid clams, occur in hadal depths in the Japan Trench; the deepest known methane seeps and associated communities are found at 7,434 m in this area (Fujikura et al., 1999; Watanabe et al., 2010). Cold seep communities also commonly occur in trench areas, such as the Aleutian and Kuril Trenches (Juniper and Sibuet, 1987; Ogawa et al., 1996; Suess et al., 1998). Benthic foraminifera are among the most widespread taxa at hadal depths and include calcareous, large agglutinated, and organic walled species (Beliaev, 1989; Gooday et al., 2008). Abundant metazoan meiofaunal taxa, such as nematodes, at hadal depths (Gambi et al., 2003; Itoh et al., 2011; Kitahashi et al., 2013; Tietjen, 1989; Vanhove et al., 2004) may exceed those found at bathyal depths by 10-fold (Danovaro et al., 2002); small numbers of ostracods, halacarids, cumaceans, kinorhynch, and meiofaunal-sized bivalves are also found there (Vanhove et al., 2004). Nematode and copepod communities in trenches differ greatly from those found at bathyal and abyssal depths (Gambi et al., 2003; Kitahashi et al., 2013), driven by opportunistic taxa and meiofaunal dwarfism in trench systems (Danovaro et al., 2002; Gambi et al., 2003).

Although not yet well quantified, and the mechanisms remain to be discerned, higher densities of fauna (Jamieson et al., 2009) and respiration have been found at trench axis points than would be expected from a purely vertical rain of POC flux (Glud et al., 2013). The exact number of species in trenches is not known, but the few quantitative studies made so far suggest that diversity is lower compared to diversity at abyssal depths (Grassle, 1989). Reasons for the lower diversity levels are not well understood but the high pressure, relatively high food supply and organic matter accumulation, relatively elevated temperature (due to adiabatic heating), or a combination thereof may attenuate trench diversity.

Sampling to date suggests that hadal basins are populated by a higher proportion of endemic species compared to much shallower waters, species that can survive the extreme hydrostatic pressure and, in some instances, remoteness from surface food supply (Wolff, 1970). Physiological and other evidence suggests that fishes cannot survive at depths greater than 8000 m (Yancey et al., 2014); the deepest hadal fish, the liparids (snail-fish), are unique to each trench system. Decapod crustaceans have been observed only to 8200 m (Gallo et al., in revision).

At depths over 8000 m, scavenging amphipod crustaceans dominate the mobile megafauna, along with potential predators, including penaeid shrimp, princaxelid amphipods and ulmarid jellyfish, as observed in the New Britain Trench and the Sirena Deep (Mariana Trench). Comparison of scavenging and epibenthic/demersal biota suggests that density, diversity, and incidence of demersal (near bottom) lifestyles all increase with greater food supply (Blankenship and Levin, 2007; Blankenship et al., 2006).

Wide separation between trenches in the northern and southern hemispheres and between the different oceans has likely facilitated speciation to result in distinct assemblages of fauna in each hadal basin (Fujii et al., 2013). Some 75 per cent of the species in Pacific Ocean trenches may be endemic to each trench. Despite their remoteness from the surface, many hadal trenches are close to land and receive organic inputs from terrestrial and coastal sources, yielding higher mega-, macro- and meio-faunal densities than expected for greater depths (Danovaro et al., 2003; Danovaro et al., 2002; Jamieson, 2011; Jumars and Hessler, 1976; Vanhove et al., 2004).

### *2.3.3 Major pressures*

The proximity of some trenches to land also increases their vulnerability to human activity in terms of dumping of materials and effluents, as well as from disaster debris, run off from land and pollution from ships. Some of these items, including anthropogenic litter, have been observed down to 7,200 m depth (George and Higgins, 1979). Evidence for the vulnerability of trench fauna is also provided by the levels of the radioisotope  $^{134}\text{Cs}$  detected in sediments in the Japan Trench, four months after the Fukushima Dai-ichi nuclear disaster (Oguri et al., 2013).

### *2.3.4 Knowledge gaps*

Trenches are arguably the most difficult deep-sea environments to access and current facilities are very limited worldwide, and consequently knowledge of their biodiversity is particularly incomplete.

In general, biodiversity patterns of non-nematode meiofauna and non-foraminiferal protists are especially poorly known in the deep sea.

Most information about biodiversity in the deep sea is for the predominant soft-substrate habitats. However, hard substrates abound in the deep sea in nearly all settings, and organisms that cannot be seen in a photograph or video image are hard to sample and study quantitatively. Thus knowledge of small-taxon biodiversity is best developed for deep-sea sediments.

Beyond cataloguing diversity, even in those systems we have characterized, almost nothing is known about the ranges of species, connectivity patterns or resilience of assemblages and their sensitivity to climate stressors or direct human disturbance. There is also currently a lack of appropriate tools to adequately evaluate human benefits that are derived from the deep sea (Jobstvogt et al., 2014a; 2014b; Thurber et al., 2014).

## **Pelagic realm**

### *3.1 Status and trends for biodiversity*

Between the deep-sea bottom and the sunlit surface waters are the open waters of the deep pelagic or “midwater” environment. This huge volume of water is the least explored environment on our planet (Webb et al., 2010). The deep pelagic realm is very diffuse, with generally low apparent abundances of inhabitants, although recent observations from submersibles indicate that some species may concentrate into narrow depth bands (Herring, 2002).

The major physical characteristics structuring the pelagic ecosystems are depth and pressure, temperature, and the penetration of sunlight. Below the surface zone (or epipelagic, down to about 200 m), the deep layer where sunlight penetrates with insufficient intensity to support primary production, is called the mesopelagic zone. In some geographic areas, microbial degradation of organic matter sinking from the surface zone results in low oxygen concentrations in the mesopelagic, called OMZs (Robinson et al., 2010). This mesopelagic zone is a particularly important habitat for fauna controlling the depth of CO<sub>2</sub> sequestration (Giering et al., 2014).

Below the depth to which sunlight can penetrate (about 1,000 m) is the largest layer of the deep pelagic realm and by far the largest ecosystem on our planet, the bathypelagic region. This comprises almost 75 per cent of the volume of the ocean and is mostly remote from the influence of the bottom and its communities. Temperatures there are usually just a few degrees Celsius above zero. The boundary layer where both physical and biological interactions with the bottom occur is called ‘benthopelagic’.

The transitions between the various vertical layers are gradients, not fixed surfaces; hence ecological distinctions among the zones are somewhat blurred across the transitions. Recent surveys have shown a great deal of connectivity between the major pelagic depth zones (Sutton, 2013). The abundance and biomass of organisms generally varies among these layers from a maximum near the surface, decreasing



through the mesopelagic, to very low levels in the bathypelagic, increasing somewhat in the benthopelagic (Angel, 1997; Haedrich, 1996). Although abundances are low, because such a huge volume of the ocean is bathypelagic, even species that are rarely encountered may have very large total population numbers (Herring, 2002).

The life cycles of deep-sea animals often involve shifts in vertical distribution among developmental stages. Even more spectacular are the daily vertical migrations of many mesopelagic species (Benoit-Bird and Au, 2006; Hays, 2003). This vertical migration may increase physical mixing of the ocean water and also contributes to a "biological pump" that drives the movement of carbon compounds and nutrients from the surface waters into the deep ocean (Robinson et al., 2010).

Sampling the deep pelagic biome shares the logistical difficulties of other deep-sea sampling, compounded by the extremely large volume and temporal variability of the environment and the widely dispersed populations of its inhabitants. New species continue to be discovered regularly. Whereas scientific information on the composition of mesopelagic assemblages is rapidly improving, very little is known of the structure of the deeper lower bathyal and abyssal pelagic zones.

Possibly because of high mobility and transport by ocean current, the overall diversity of species seems to be less than that found in other ecosystems (Angel, 1997). However, the number of distinct major evolutionary groups (i.e., phyla, classes, etc.) found in the deep pelagic is high.

Studies of microbes and their roles in the deep pelagic ecosystems are just beginning to reveal the great diversity of such organisms. The species richness of deep ocean bacteria surpasses that of the surface open ocean (Zinger et al., 2011).

As is true in other pelagic systems, crustaceans make up a large percentage of the deep zooplankton in both abundance and numbers of species. These crustaceans include numerous and diverse copepods, amphipods, ostracods and other major groups. Some groups, like arrow worms, are almost all pelagic and are important in deep waters. Large gelatinous animals, including comb jellies, jellyfishes, colonial siphonophores, salps and pyrosomes, are extremely important in deep pelagic ecosystems (Robison, 2004).

The strong swimmers of the deep pelagic, the "nekton", include many species of fishes and some sharks, crustaceans (shrimps, krill, and other shrimplike animals), and cephalopods (including squids, "dumbo" and other octopods, and "vampire squids") (Hoving et al., 2014). In terms of global fish abundance, deep pelagic fishes are by far the numerically dominant constituents; the genus *Cyclothone* alone outnumbers all coastal fishes combined and is likely to be the most abundant vertebrate on earth. Furthermore, at an estimated ~1,000 million tons, mesopelagic fishes dominate the world's total fish biomass and constitute a major component of the global carbon cycle. Acoustic surveys now suggest that an accurate figure of mesopelagic fish biomass may be an order of magnitude higher (10,000 - 15,000 million tons; Irigoien et al., 2014; Kaartvedt et al., 2012; Koslow, 2009). When bathypelagic fish biomass is included, deep pelagic fish biomass is likely to be the overwhelming majority of fish biomass on Earth (Sutton, 2013). The deep pelagic fauna is also important prey for mammals (toothed whales and elephant seals) and

even birds (emperor penguins) and reptiles (leatherback sea turtles). The amount of deep-sea squids consumed by sperm whales alone annually has been estimated to exceed the total landings of fisheries worldwide (Rodhouse and Nigmatullin, 1996).

Horizontal patterns exist in the global distribution of deep pelagic organisms. However, the faunal boundaries of deep pelagic assemblages are less distinct than those of near-surface or benthic assemblages (Pierrot-Bults and Angel, 2012). Generally, the low-latitude oligotrophic regimes that make up the majority of the global ocean house more species than higher-latitude regimes (Hopkins et al., 1996). Some major oceanic frontal boundaries, such as the polar and subpolar fronts, extend down into deep waters and appear to form biogeographic boundaries, although the distinctness of those boundaries may decrease with increasing depth.

The dark environment also means that production of light by bioluminescence is almost universal among deep pelagic organisms. Some animals produce the light independently, whereas others are symbiotic with luminescent bacteria.

### 3.2 *Major pressures*

A fundamental biological characteristic throughout the deep pelagic biome is that little or no primary production occurs and deep pelagic organisms are dependent on food produced elsewhere. Therefore, changes in surface productivity will be reflected in changes in the deep midwater. When midwater animals migrate into the surface waters at night, they are subjected to predation by near-surface species. Shifts in the abundance of those predators will affect the populations of the migrators and, indirectly, the deeper species that interact with the vertical migrators at their deeper daytime depths. Either or both of these effects may be caused by global climate change, fishing pressure and the impact of pollutants in surface waters (Robinson et al., 2010; Robison, 2009).

Climate change will likely increase stratification caused by warming of surface waters and expanded OMZs resulting from the interaction of shifts in productivity with increased stratification. If the so-called conveyor-belt of global circulation weakens, transport of oxygen by the production of deep water will affect the entire deep sea. The biomass of mesopelagic fishes in the California Current, for instance, has declined dramatically during recent decades of reduced midwater oxygen concentrations (Koslow et al., 2011). Furthermore, increases in carbon dioxide resulting in acidification may affect diverse deep pelagic animals, including pteropods (swimming snails) and crustaceans which use calcium carbonate to build their exoskeletons, fishes that need it for internal skeletons, and cephalopods for their balance organs. Acidification also changes how oxygen is transported in the blood of animals and those living in areas of low oxygen concentration may therefore be less capable of survival and reproduction (Rosa and Seibel, 2008).

Few fisheries currently target deep pelagic species, but fisheries do affect the ecosystem. Whaling reduced worldwide populations of sperm whales and pilot whales to a small fraction of historical levels (Roman et al., 2014). Similarly, fisheries for surface predators such as sharks, tunas and billfishes, and on seamounts, reduce

predation pressure, particularly on vertical migrators like squids and lantern fishes (Zeidberg and Robison, 2007).

Increasing extraction of deep-sea hydrocarbon resources increases the likelihood of accidental deep release of oil and methane (Mengerink et al., 2014), as well as the deep use of dispersants to minimize apparent effects of such spills at the surface (See Chapter 21).

Deep sea mining and some forms of renewable energy production may also affect the pelagic realm of the deep ocean (Ramirez-Llodra et al., 2011), and potential effects are addressed in Chapters 23 and 22 respectively.

### 3.3 *Knowledge gaps*

Any summary of deep pelagic ecosystems emphasizes how little is known, especially relative to coastal systems. Sampling has been intensively conducted in only a few geographic areas, using selective methods, each of which illuminates only a fraction of the biodiversity. Sampling at lower bathyal or abyssal depths has been limited, and virtually nothing is known about pelagic fauna associated with deep trenches. There is also limited knowledge of the performance of conservation and management measures developed for coastal and shelf marine ecosystems when applied in deep ocean systems characterized by large spatial scales and variable but sometimes vertically and/or horizontally high-mobility organisms, and incomplete knowledge of ecosystem structure and processes.

## **Special areas typical for the open ocean deep sea**

### 4.1 *Ocean ridges*

The Mid-Ocean Ridge system is a continuous single feature on the earth's surface extending ca. 50,000 km around the planet; it defines the axis along which new oceanic crust is generated at tectonic plate boundaries (Heezen, 1969). The ridge sea floor is elevated above the surrounding abyssal plains, reaching the sea surface at mid-ocean islands, such as Iceland, the Azores and Ascension Island in the Atlantic Ocean, Easter Island and Galapagos in the Pacific Ocean. Typically there is a central axial rift valley bounded by ridges on both sides. A series of sediment-covered terraces slope down on the two sides of the ridge axis to the abyssal plains. The global ridge system, including associated island slopes, seamounts and knolls, represents a vast area of mid-ocean habitat at bathyal depths, accessible to fauna normally associated with narrow strips of suitable habitat on the continental slopes. The ocean ridges sub-divide the major ocean basins, but fracture zones at intervals permit movement of deep water and abyssal organisms between the two sides of the ridge.

Much attention has been directed to the importance of Mid-Ocean Ridges as sites of the hydrothermal vents and their unique fauna found close to the geothermally active ridge axis (German et al., 2011). However, the total area of hydrothermal vents is small and the dominant fauna on the mid-ocean ridges is made up of typical

bathyal species known from adjacent continental margins (See Chapter 45). The biomass of benthic fauna and demersal fishes on the ridges is generally similar to that found at corresponding depths on the nearest continental slopes (Priede et al., 2013). New species, potentially endemic to mid-ocean ridges, have been discovered (Priede et al., 2012). But these are likely to be found elsewhere as exploration of the deep sea progresses. The island slopes and summits of seamounts associated with ocean ridges are important areas for fisheries; evidence suggests that biodiversity, including large pelagic predators, is enhanced around such features (Morato et al., 2010; Morato et al., 2008). Chapter 51 considers the biodiversity of these mid-ocean ridges, and its threats, in greater detail.

#### 4.2 *Polar deep sea*

Polar marine ecosystems differ in many ways from other marine ecosystems on the planet (see Chapters 36G and 36H).

#### 4.3 *Arctic*

Arctic deep-sea areas have generally been poorly studied; although several studies over the past two decades have greatly advanced our knowledge of its marine diversity and deep-sea processes. They indicate that the Arctic deep sea is an oligotrophic area, featuring steep gradients in benthic biomass with increasing depth that are primarily driven by food availability (Bluhm et al., 2005, 2011).

The Arctic deep basins comprise ~50 per cent of the Arctic Ocean seafloor and differ from those of the North Atlantic, as the Arctic Sea is relatively young in age, semi-isolated from the world's oceans, and largely ice-covered. Moreover, the high Arctic experiences more pronounced seasonality in light, and hence in primary production, than lower latitudes.

The history and semi-isolation of the Arctic basin play a major role in its biodiversity patterns (Golikov and Scarlato, 1990). Originally an embayment of the North Pacific, the Arctic deep sea was influenced by Pacific fauna until ~80 million years ago, when the deep-water connection closed (Marincovich Jr. et al., 1990). Exchange with the deep Atlantic began ~40 Ma ago, coinciding with a strong cooling period (Savin et al., 1975). Although some Arctic shelf and deep-sea fauna were removed by Pleistocene glaciations, other shelf fauna in the Atlantic sector of the Arctic found refuge in the deep sea and are considered the ancestral fauna at least for some of the recent Arctic deep-sea fauna (Nesis, 1984). The bottom of the Arctic basin is filled with water originating from the North Atlantic (Rudels et al., 1994); the sediments are primarily silt and clay whilst the ridges and plateaus have a higher sand fraction (Stein et al., 1994). Exceptions include ice-rafted dropstones, enhancing diversity by providing isolated hard substrata and enhanced habitat heterogeneity for benthic fauna (Hasemann et al., 2013; Oschmann, 1990). Considerable inputs of refractory terrestrial organic matter from the large Russian and North American rivers characterize the organic component of sediments along the slopes, and in the basins (Stein and Macdonald, 2004). The only present-day deep-water connection to the Arctic is via the Fram Strait (~2,500m), providing immigrating species access via the

high water flux through this gateway. Submarine ridges within the Arctic form physical barriers, but current evidence suggests that these do not form biogeographic barriers (Deubel, 2000; Kosobokova et al., 2011; Vinogradova, 1997).

Bluhm et al. (2011) conservatively estimated the number of benthic invertebrate taxa in the Arctic deep sea to be ~1,125. As in other soft-sediment habitats, foraminiferans and nematodes generally dominate the meiofauna, whereas annelids, crustaceans and bivalves dominate the macrofauna, and echinoderms dominate the megafauna. The degree of endemism at the level of both genera and species is far lower than in the Antarctic, which has a similarly harsh environment. Just over 700 benthic species were catalogued from the central basin a decade ago (Sirenko, 2001). The latitudinal species-diversity gradient has been observed in the Arctic Ocean (Yasuhara et al., 2012b) and the peak of the unimodal species-diversity depth gradient occurs at much shallower depths compared to other oceans (Clarke, 2003; Svavarsson, 1997; Yasuhara et al., 2012b).

The Arctic, is populated by species that have experienced selection pressure for generalism and high vagility (Jansson and Dynesius, 2002), and should have inherent resilience in the face of climate change.

In a warmer future Arctic with less sea ice altered algal abundance and composition will affect zooplankton community structure (Caron and Hutchins, 2012) and subsequently the flux of particulate organic matter to the seafloor (Wohlers et al., 2009), where the changing quantity and quality of this matter will impact benthic communities (Jones et al., 2014; Kortsch et al., 2012).

#### 4.4 *Antarctic*

The Southern Ocean comprises three major deep ocean basins, i.e., the Pacific, Indian and Atlantic Basins, separated by submarine ridges and the Scotia Arc island chain. Oceanographically, the Southern Ocean is a major driver of global ocean circulation and plays a vital role in interacting with the deep water circulation in each of the major oceans.

Chapter 36H describes the general dynamics of the Southern Ocean, including seasonal changes. The winter sea-ice formation creates cold, dense, salty water that sinks to the seafloor and forms very dense Antarctic Bottom Water (Bullister et al., 2013). This in turn pushes the ocean's nutrient-rich, deep water closer to the surface, generating areas of high primary productivity in Antarctic waters, similar to areas of upwelling elsewhere in the world.

The remote Southern Ocean is home to a diverse and rich community of life that thrives in an environment dominated by glaciations and strong currents (Griffiths, 2010). However, although relatively little is known about the deep-sea fauna, or about the complex interactions between the highly seasonally variable physical environment and the species that inhabit the Southern Ocean, but our knowledge of Southern Ocean deep-sea fauna and biogeography is increasing rapidly (Griffiths, 2010; Kaiser et al., 2013). The range of ecosystems found in each of the marine realms can vary greatly within a small geographic area (e.g. Grange and Smith, 2013), or in other cases remain relatively constant across vast areas of the Southern Ocean.

The region also contains many completely un-sampled areas for which nothing is known (e.g., Amundsen Sea, Western Weddell Sea, Eastern Ross Sea). These areas include the majority of the intertidal zone, areas under the floating ice shelves, and the greater benthic part of the deep sea. However, several characteristic features of Southern Ocean ecosystems include circumpolar distributions and eurybathy of many species (Kaiser et al., 2013).

Both pelagic and benthic communities tend to show a high degree of patchiness in both diversity and abundance. The benthic populations show a decrease in biomass with increasing depth (Arntz et al., 1994), with notable differences in areas of disturbance due to anchor ice and icebergs in the shallows (Smale et al., 2008) and in highly productive deep fjord ecosystems (Grange and Smith, 2013). Hard and soft sediments from the region are known to be capable of supporting both extremes of diversity and biomass. In some cases, levels of biomass are far higher than those in equivalent habitats in temperate or tropical regions. A major international study led by Brandt revealed comparably high levels of biodiversity (higher than in the Arctic), thereby challenging suggestions that deep-sea diversity is depressed in the Southern Ocean (Brandt et al., 2007). Understanding of large-scale diversity distributions is improving (Brandt and Ebbe, 2009; Kaiser et al., 2013). For example, depth-diversity gradients of several taxa are known to be unimodal with a shallow peak comparable to those of the Arctic Ocean (Brandt et al., 2007; Brandt and Ebbe, 2009).

Longline fishing continues in the Southern Ocean, where the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has been implementing conservation measures for toothfish, icefish and krill fisheries, and has closed almost all of the regulatory area to bottom trawling since the 1980s (Reid et al., 2010; Hanchet et al., 2015). Climate change, is also a significant potential threat to the Antarctic marine communities (Griffiths, 2010; Smith et al., 2012), for reasons similar to those presented for the Arctic.

#### 4.5 *Seamounts*

Seamounts are important topographic features of the open ocean. Although they are small in area relative to the vast expanse of the abyssal plains, accounting for <5 per cent of the seafloor (Yesson et al., 2011), three important characteristics distinguish them from the surrounding deep-sea habitat (Figure 36F.1; see Chapter 34). First, they are “islands” of shallow sea floor, and provide a range of depths for different communities. Second, bare rock surfaces can be common, enabling sessile organisms to attach to the rock, in contrast to the majority of the ocean sea floor, which is covered with fine unconsolidated sediments. Third, the physical structure of some seamounts drives the formation of localised hydrographic features and current flows that can keep species and production processes concentrated over the seamount, even increasing the local deep pelagic biomass. They are a sufficiently important part of marine deep-sea biodiversity that seamounts are fully treated in Chapter 51 of this Assessment.

#### 4.6 *Organic falls*

The decay of large sources of organic matter (e.g., whales, wood, jellyfish) that ‘fall’ from surface or midwater provide a concentrated source of food on the deep sea floor directly, and indirectly through the decay of the organic matter, can yield hydrogen sulphide and methane. An array of scavenging species (hagfish, amphipods, ophiuroids, and crabs) is adapted to rapidly finding and consuming organic matter on the deep seabed. In addition, lipid-rich whale bones and wood support specialized taxa that have evolutionarily adapted to consume the substrate via symbionts (Smith and Baco, 2003; Smith et al., 2015). At least 30 species of polychaetes in the genus *Osedax* colonize and degrade whale bones, with the aid of heterotrophic symbionts in the group Oceanspirales (Goffredi et al., 2005; Rouse et al., 2009; Smith et al., 2015). *Osedax* and other taxa colonizing whale falls exhibit biogeographic separation, succession during the life of the whale fall (Smith and Baco, 2003; Braby et al., 2007; Glover et al., 2005; Smith et al., 2015), *Adipicola* and other deep-sea mussels also harbour chemoautotrophic endosymbionts and colonize sulphide-rich whale remains (Fujiwara et al., 2007; Thubaut et al., 2013). Similarly, members of the bivalve genus *Xylophaga* colonize and consume wood in the deep sea, with symbionts that aid cellulose degradation and nitrogen fixation. The activities of these ‘keystone’ species, in conjunction with microbial decay, transform the environment and facilitate colonization by a high diversity of other taxa, for example >100 species thus far found only on deep-sea whale falls (Smith et al., 2015). Human impacts have likely already affected these organic-fall ecosystems. For example, 20th century whaling drastically reduced the flux of whale carcasses to the deep seafloor (Roman et al., 2014; Smith, 2006; Smith et al., 2015).

Numerous areas throughout the world’s oceans have experienced large jellyfish population expansions. Although numerous studies have sought to identify the driving forces behind and the impacts of live jellyfish on marine ecosystems (Purcell, 2012; Purcell et al., 2007), very few have focused on the environmental consequences from the deposition of jellyfish carcasses (from natural die-off events). Recently it has become apparent that jellyfish carcasses have very high sinking speeds (1,500 m d<sup>-1</sup>, Lebrato et al., 2013a; 2013b). Thus, jellyfish blooms may affect seafloor habitats through the sedimentation of jellyfish carcasses (but also of macrozooplankton, see Smith et al. (2014)), the smothering of extensive areas of seafloor and reducing oxygen flux into seafloor sediments leading to hypoxic/anoxic conditions. Jelly falls may also be actively consumed by typical deep-sea scavengers, enhancing food-flux into deep-sea food webs (Sweetman et al., 2014). Jellyfish falls have so far been observed in the Atlantic, Indian and Pacific oceans (Billett et al., 2006; Lebrato and Jones, 2009; Yamamoto et al., 2008; Lebrato et al., 2013a; 2013b; Sweetman and Chapman, (2011), and are reviewed in Lebrato et al. (2012).

#### 4.7 *Methane seeps*

Continental margins host a vast array of geomorphic environments associated with methane seepage and other types of seeps. Many support assemblages reliant on chemosynthesis fuelled by methane and sulphide oxidation (Levin and Sibuet, 2012;

Sibuet and Olu, 1998). Their specialized biodiversity features are assessed in Chapter 45.

### **Major ecosystem services being affected by the pressures**

Despite its apparent remoteness and inhospitability, the deep ocean and seafloor play a crucial role in human social and economic wellbeing through the ecosystem goods and services they provide (Armstrong et al., 2012; Thurber et al., 2014; van den Hove and Moreau, 2007) (Table 1). Whilst some services, such as deep-sea fisheries, oil and gas energy resources, potential CO<sub>2</sub> storage, and mineral resources directly benefit humans, other services support the processes that drive deep-sea and global ecosystem functioning. Despite its inaccessibility to most people, the deep sea nonetheless supports important cultural and existence values. The deep sea acts as a sink for anthropogenic CO<sub>2</sub>, provides habitat, regenerates nutrients, is a site of primary (including chemosynthetic) and secondary biomass production, as well as providing other biodiversity-related functions and services, including those the deep water and benthic assemblages provide (Irigoien et al., 2014).

Ocean warming and acidification associated with climate change already affect the deep sea, reaching abyssal depths in some areas (Østerhus and Gammelsrød, 1999). Ongoing global climatic changes driven by increasing anthropogenic emissions and subsequent biogeochemical changes portend further impacts for all ocean areas, including the deep-sea and open ocean (Mora et al., 2013b). Data from pre-anthropocene times indicates millennial-scale climate variability on deep-sea biodiversity (Cronin and Raymo, 1997; Cronin et al., 1999; Hunt et al., 2005; Wollenburg et al., 2007; Yasuhara and Cronin, 2008; Yasuhara et al., 2012a; 2009), as well as decadal-centennial climate events (Yasuhara et al., 2008; 2014). The potential impacts of climate change on the ocean are addressed in Part II of the Intergovernmental Panel on Climate Change (IPCC) 5<sup>th</sup> Assessment Report, Working Group II Chapters 6 and 30. Consistent with the mandate of this Assessment, they are only briefly summarized here.

Some impacts of climate change will be direct. For example, altered distributions and health of open-ocean and deep-sea fisheries are expected to result from warming-induced latitudinal or depth shifts (Brander, 2010); deoxygenation will induce habitat compression (Prince and Goodyear, 2006; Stramma et al., 2012; Koslow et al., 2011); and acidification will stress organismal function and thus organismal distribution. Climate change-related stressors are also likely to act in concert, and effects could be cumulative (Rosa and Seibel, 2008). Shifts in bottom-up, competitive, or top-down forcing will produce complex and indirect effects on the services described above. Acidification-slowed growth of carbonate skeletons, delayed development under hypoxic conditions, and increased respiratory demands with declining food availability illustrate how climate change could exacerbate anthropogenic impacts and compromise deep-sea ecosystem structure and function and ultimately benefits to human welfare.



The most important ecosystem service of the deep pelagic region is arguably the “biological pump”, in which biological processes, such as the daily vertical migration, package and accelerate the transport of carbon compounds, nutrients, and other materials out of surface waters and into the deep sea. However, the microbial diversity and processes of the deep-pelagic realm are not sufficiently known to predict confidently how the biological pump ecosystem service will respond to perturbations.

## **Deep-sea exploitation**

### *6.1 Deep-sea fisheries*

Deep-sea fishing has a long history, but it did not become an important activity until the mid-twentieth century, when technological advancement allowed the construction of large and powerful vessels, and the development of line and trawl gear that could be deployed to continental slope depths. FAO (2009) acknowledges that deep-sea fisheries often exploit species which have relatively slower growth rates, reach sexual maturity later and reproduce at lower rates than shelf and coastal species.

Deep-sea fish species were the basis of major commercial fisheries in the 1970s to early 2000s (Japp and Wilkinson, 2007) but started to decline as aggregations were fished out, and realisation grew about the low productivity, and hence low yields, of these species (Clark, 2001; Sissenwine and Mace, 2007) and impacts of some of these fisheries on seafloor structure and benthos (Clark and Dunn 2012). Globally the main commercial deep-sea fish species at present number about 20, comprising alfonsino, toothfish, redfish, slickheads, cardinalfish, scabbardfish, armourhead, orange roughy, oreos, roundnose and rough-headed grenadiers, blue ling and moras. The current commercial catch of these main deep-sea species is about 150,000 tons, and has been similar over the last five years, although the proportional species mix has changed. The ecosystem effects of these fisheries are discussed in Chapter 11 of this Assessment and in Chapter 51 relative to the seamounts which are centres for many of these fisheries.

### *6.2 Deep gas and oil reserves*

The oil and gas industry has been active in the open ocean since the 1970s. Over 10,000 hydrocarbon wells have been drilled globally; at least 1,000 are routinely drilled in water depths >200 m, and as deep as 2,896 m in the Gulf of Mexico. The scale of the exploration and development of hydrocarbon reserves and then ecosystem effects are discussed in Chapter 21.

### *6.3 Minerals*

Great interest exists in exploiting the deep sea for its various reserves of minerals, which include polymetallic nodules, seafloor massive sulphide (SMS) deposits,

mineral-rich sediments and cobalt-rich crusts. Currently no commercial mining projects have started, although several projects are in the exploratory or permitting phase. From those exploratory studies and related research some knowledge of potential ecosystem effects is accumulating.

Experimental studies to assess the potential impact of mining polymetallic nodules in the abyss have indicated that seafloor communities may take many decades before showing signs of recovery from disturbance (Bluhm, 2001; Miljutin et al., 2011), and may never recover if they rely directly on the nodules for habitat.

The recovery of communities at active hydrothermal vents where SMS deposits may be exploited may be relatively rapid, because vent sites undergo natural disturbances which have seen some communities appear to recover from catastrophic volcanic activity within a few years (Tunnicliffe et al., 1997). However, the rates of recovery of benthic communities are likely to vary among sites.

Other potential mining activities include exploiting mineral-rich sediments. For example in some deep marine sediments, phosphorite occurs as “nodules” (2 to >150 mm in diameter), in a mud or sand matrix, which can extend beneath the seafloor sediment surface to tens of centimetres depth.

No mining has yet been authorized for such deposits but could result in the removal of large volumes of both the phosphorite nodules and the surrounding soft sediments, together with associated faunal communities and generate large sediment plumes. In addition, cobalt-rich ferromanganese crusts are promising sources of cobalt and rare minerals required to sustain growing human population demands and emerging high and green technologies (Hein et al., 2013). Conditions favouring their formation are found in abrupt topography, especially on the flanks and summits of oceanic seamounts and ridges at depths of 800-2500 m, where the most Cobalt-rich deposits are known to concentrate, in habitats dominated by suspension-feeding sessile organisms (mostly cold-water corals and sponges) and comparatively rich biological communities (Clark, 2013; Clark et al., 2011; Fukushima, 2007; Schlacher et al. 2013). Interest in cobalt-rich crust resources is growing, although mining for cobalt-rich crusts has not yet started, and technological challenges mean it may develop later than for polymetallic nodule or SMS resources. Further information on these mining activities is found in Chapter 23, and the seamount and seep/vent habitats in Chapters 51 and 45, respectively.

## **Special conservation/management issues and sustainability for the future**

### *7.1 Special habitats (VMEs, EBSAs, MPAs) and conservation measures*

The United Nations General Assembly has adopted a number of resolutions that called for the identification and protection of vulnerable marine ecosystems (VMEs) from significant adverse impacts of bottom fishing (for example 61/105 of 2006), which has facilitated the development of the 2008 International Guidelines for the Management of Deep-Sea Fisheries in the High Seas (FAO, 2009). The concept and developments of VMEs and their protection is addressed in Chapter 11. Also in the

2000s, in response to the call in the World Summit on Sustainable Development (WSSD) for greater protection of the open ocean, the Conference of Parties to the Convention on Biological Diversity (CBD) developed and adopted criteria for the description of ecologically or biologically significant areas (EBSAs) in open-ocean waters and deep-sea habitats. The application of the EBSA criteria is a scientific and technical exercise, and areas that are described as meeting the criteria may receive protection through a variety of means, according to the choices of States and competent intergovernmental organizations (decision X/29 of the CBD COP10). Expert reviews have concluded that both approaches can be complementary in achieving effective sustainable management in the deep sea (Rice et al., 2014; Dunn et al., 2014).

## *7.2 Protection of the marine environment in the Area*

With regard to deep-sea mining the International Seabed Authority (ISA), established in 1994, is required to take the necessary measures ensure that the marine environment is protected from harmful effects from activities in the Area under its jurisdiction. Such measures may include assessing potential environmental impacts of deep-sea activities (exploration and possible mining) and setting standards for environmental data collection, establishment of environmental baselines, and monitoring programmes (ISA, 2000, 2007 2013).

## *7.3 Deep-ocean observatories-ocean networks*

Deep-sea observatories are becoming increasingly important in monitoring deep-sea ecosystems and the environmental changes that will affect them. The first long-term and real-time deep-sea observatory was deployed in 1993 at a methane seep site at 1,174 m depth in Sagami Bay, Japan (JAMSTEC, Japan), and is still operating. Several internationally organized projects have been initiated to achieve global integration of deep-sea observatories (e.g., Global Ocean Observing System (GOOS, NSF); FixO3 (Fixed Point Open Ocean Observatories, European Union Framework Programme 7), largely based on existing observing networks (e.g., Porcupine Abyssal Plain in the North Atlantic, (NOC, UK), Hausgarten Site in the transition between the North Atlantic and the Arctic (AWI, Germany), Ocean Network Canada with the Neptune Observatory on Canada's west coast) and aiming at achieving multidisciplinary integration, including physics, climate, biogeochemistry, biodiversity and ecosystems, geophysics with integration across sectors, and economics and sociology. Whilst moving towards a global strategy to obtain maximum efficiency, one of the major goals of deep-sea observatory initiatives is to better understand and predict the effects of climate change on the linked ocean-atmosphere system, and on marine ecosystems, biodiversity and community structure, In terms of biodiversity and ecosystems, several objectives need addressing: exploration and observation; prediction of future biological resources; understanding the functioning of deep-sea ecosystems; and understanding the roles of relationships between ecosystems and the services they provide.

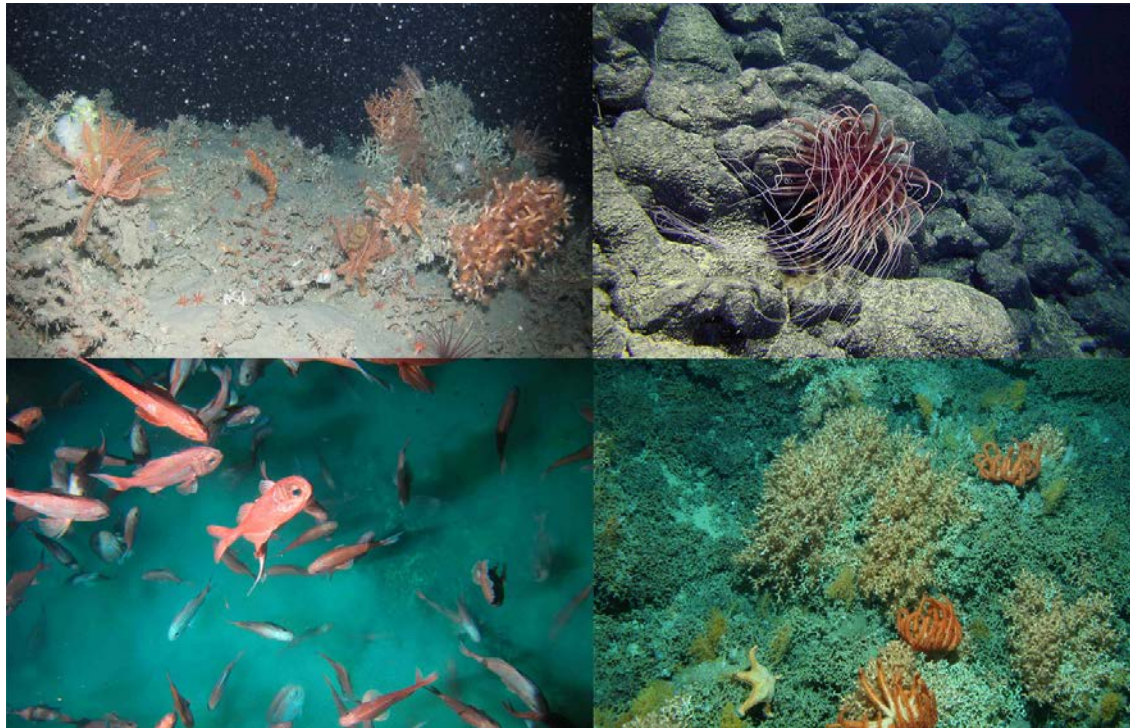


Figure 1. Deep-sea habitats. Top left: coral garden in the Whittard Canyon, NE Atlantic at approx. 500 metres depth (2010; image courtesy of Jeroen Ingels); top right: A sea anemone, *Boloceroides daphneae*, on cobalt crust covering a seamount off Hawaii, 1000 metres depth (image courtesy of Chris Kelly, HURL); bottom left: An orange roughy (*Hoplostethus atlanticus*) aggregation at 890 metres depth near the summit of a small seamount (termed "Morgue") off the east coast of New Zealand (image courtesy of Malcolm Clark); bottom right: A reef-like coverage by stony corals (*Solenosmilia variabilis*) together with prominent orange brisingid seastars on the summit of a small seamount (termed "Ghoul") feature at 950 metres off the east coast of New Zealand (image courtesy of Malcolm Clark).

## References

- Angel, M.V. (1997). Pelagic Biodiversity. In: Ormond, R.F.G., Gage, J.D., and Angel, M.V., editors. *Marine biodiversity: patterns and processes*. Cambridge University Press, New York.
- Appeltans et al., The Magnitude of Global Marine Species Diversity, *Current Biology* (2012), <http://dx.doi.org/10.1016/j.cub.2012.09.036>
- Armstrong, C.W., Foley, N.S., Tinch, R., van den Hove, S. (2012). Services from the deep: Steps towards valuation of deep sea goods and services. *Ecosystem Services* 2, 2-13.
- Arntz, W.E., Brey, T., and Gallardo, V.A. (1994). Antarctic zoobenthos. *Oceanographic Marine Biology* 32: 241-304.

- Bailey, D.M., Collins, M.A., Gordon, J.D.M., Zuur, A.F., Priede, I.G. (2009). Long-term changes in deep-water fish populations in the northeast Atlantic: a deeper reaching effect of fisheries? *Proceedings of the Royal Society B: Biological Sciences*. DOI: 10.1098/rspb.2009.0098.
- Beliaev, G.M. (1989). *Deep-sea ocean trenches and their fauna*. Moscow: Nauka. 385 pp.
- Benoit-Bird, K.J., and Au, W.W.L. (2006). Extreme diel horizontal migrations by a tropical nearshore resident micronekton community. *Marine Ecology Progress Series* 319: 1–14.
- Billett, D.S.M., Bett, B., Jacobs, C., Rouse, I., Wigham, B. (2006). Mass deposition of jellyfish in the deep Arabian Sea. *Limnology and Oceanography* 51 (5), 2077-2083.
- Billett, D.S.M., Bett, B.J., Reid, W.D.K., Boorman, B., and Priede, I.G. (2010). Long-term change in the abyssal NE Atlantic: The ‘Amperima Event’ revisited. *Deep-Sea Research II* 57: 1406–1417.
- Blankenship, L., Yayanos, A., Cadien, D., and Levin, L. (2006). Vertical zonation patterns of scavenging amphipods from the hadal zone of the Tonga and Kermadec trenches. *Deep-Sea Research Part I: Oceanographic Research Papers* 53: 48-61.
- Blankenship, L.E., and Levin, L.A. (2007). Extreme food webs: foraging strategies and diets of scavenging amphipods from the ocean’s deepest 5 km. *Limnology and Oceanography* 52: 1685-1697.
- Bluhm, B.A., Ambrose, W.G., Bergmann, M., Clough, L.M., Gebruk, A.V., Hasemann, C., Iken, K., Klages, M., MacDonald, I.R., Renaud, P.E., Schewe, I., Soltwedel, T., and Wlodarska-Kowalczyk, M. (2011). Diversity of the Arctic deep-sea benthos. *Marine Biodiversity* 41: 87-107.
- Bluhm, B.A., MacDonald, I.R., Debenham, C., Iken, K. (2005). Macro- and megabenthic communities in the high Arctic Canada Basin: initial findings. *Polar Biology* 28: 218-231.
- Bluhm, H. (2001). Re-establishment of an abyssal megabenthic community after experimental physical disturbance of the seafloor. *Deep Sea Research Part II: Topical Studies in Oceanography* 48(17–18), 3841-3868.
- Braby, C.E., Rouse, G.W., Johnson, S.B., Jones, W.J., Vrijenhoek, R.C. (2007). Bathymetric and temporal variation among *Osedax* boneworms and associated megafauna on whale-falls in Monterey Bay, California. *Deep-Sea Research Part I: Oceanographic Research Papers* 54 (10), 1773-1791.
- Brander, K. (2010). Impacts of climate change on fisheries. *Journal of Marine Systems* 79: 389–402.
- Brandt, A., De Broyer, C., De Mesel, I., Ellingsen, K.E., Gooday, A.J., Hilbig, B., Linse, K., Thomson, M.R.A., Tyler, P.A. (2007). The biodiversity of the deep Southern Ocean benthos. *Philosophical Transactions of the Royal Society B-Biological Sciences* 362 (1477), 39-66.

- Brandt, A., Ebbe, B. (2009). Southern Ocean deep-sea biodiversity-From patterns to processes. *Deep-Sea Research Part II: Topical Studies in Oceanography* 56 (19-20), 1732-1738.
- Buhl-Mortensen, L., Vanreusel, A., Gooday, A.J., Levin, L.A., Priede, I.G., Buhl-Mortensen, P., Gheerardyn, H., King, N.J., Raes, M. (2010). Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Marine Ecology* 31, 21-50.
- Bullister, J.L., Rhein, M., and Mauritzen, C. (2013). Deepwater Formation. In: Siedler, G., Griffies, S.M., Gould, J., Church, J.A. (eds.) *Ocean Circulation and Climate - A 21 Century Perspective. International Geophysics* 103: 227-253.
- Caron, D.A., Hutchins, D.A. (2012). The effects of changing climate on microzooplankton grazing and community structure: drivers, predictions and knowledge gaps. *J. Plankton Res.*, 235-252, doi:10.1093/plankt/fbs091
- Church, R.A., Warren, D.J., Irion, J.B. (2009). Analysis of deepwater shipwrecks in the Gulf of Mexico: Artificial reef effect of Six World War II shipwrecks. *Oceanography* 22(2), 50-63.
- Clark, M. (2001). Are deepwater fisheries sustainable? - the example of orange roughy (*Hoplostethus atlanticus*) in New Zealand. *Fisheries Research* 51: 123–135.
- Clark, M.R. (2013). Biology associated with Cobalt-rich Ferromanganese crusts. In: Baker, E., Beaudoin, Y. (Eds.), Secretariat of the Pacific Community. *Deep Sea Minerals: Cobalt-rich Ferromanganese Crusts, a physical, biological, environmental, and technical review*. Vol. 1C, SPC.
- Clark, M.R., and Dunn, M.R. (2012). Spatial management of deep-sea seamount fisheries: balancing exploitation and habitat conservation. *Environmental Conservation* 39(2): 204-214. Doi:10.1017/S0376892912000021.
- Clark, M.R, Vinnichenko, V.I., Gordon, J.D.M., Beck-Bulat, G.Z., Kukharev, N.N., and Kakora, A.F. (2007). Large scale distant water trawl fisheries on seamounts. Chapter 17. In: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., and Santos, R.S., editors. *Seamounts: ecology, fisheries, and conservation*. Blackwell Fisheries and Aquatic Resources Series 12 Blackwell Publishing, Oxford. pp. 361–399.
- Clark, M.R., Kelley, C., Baco, A., and Rowden, A. (2011). Fauna of cobalt-rich ferromanganese crust seamounts. *International Seabed Authority Technical Study No. 8*. p. 83.
- Clarke, A. (2003). The polar deep seas. In: Tyler, P.A., ed. *Ecosystems of the World. Ecosystems of the Deep Oceans*. Vol. 28, Elsevier, Amsterdam, pp. 239–260.
- CoML, (2010). First Census of Marine Life 2010: Highlights of a Decade of Discovery. In: Ausubel, J.H., Crist, D.T., Waggoner, P.E. (Eds.), *Census of Marine Life International Secretariat*. Consortium for Ocean Leadership, Washington, p. 64.

- Cook, A.A., Lamshead, P.J.D., Hawkins, L.E., Mitchell, N., Levin, L.A. (2000). Nematode abundance at the oxygen minimum zone in the Arabian Sea. *Deep-Sea Research Part II: Topical Studies in Oceanography* 47 (1-2), 75-85.
- Corliss, B.H., Brown, C.W., Sun, X. and Showers, W.J. (2009). Deep-sea benthic diversity linked to seasonality of pelagic productivity. *Deep-Sea Research I* 56: 835–841.
- Costello, M.J., May, R.M., Stork, N.E. (2013). Can We Name Earth's Species Before They Go Extinct? *Science* 339(6118), 413-416.
- Cronin, T.M. and Raymo, M.E. (1997). Orbital forcing of deep-sea benthic species diversity. *Nature* 385(6617): 624–627.
- Cronin, T.M., DeMartino, D.M., Dwyer, G.S., and Rodriguez-Lazaro, J. (1999). Deep-sea ostracode species diversity: response to late Quaternary climate change. *Marine Micropaleontology* 37(3-4): 231–249.
- Danovaro, R., Gambi, C. and Della Croce, N. (2002). Meiofauna hotspot in the Atacama Trench, eastern South Pacific Ocean. *Deep-Sea Research, Part I: Oceanographic Research Papers* 49: 843–857.
- Danovaro, R., Della Croce, N., Dell'Anno, A., Pusceddu, A. (2003). A depocenter of organic matter at 7800 m depth in the SE Pacific Ocean. *Deep Sea Research Part I: Oceanographic Research Papers* 50 (12), 1411-1420.
- Danovaro, R., Snelgrove, P.V.R., Tyler, P. (2014). Challenging the paradigms of deep-sea ecology. *Trends in Ecology & Evolution* 29 (8), 465-475.
- Deubel, H. (2000). Structures and nutrition requirements of macrozoobenthic communities in the area of the Lomonosov Ridge in the Arctic Ocean (in German). *Reports on Polar Research* 370: 1-147.
- Dunn, D.C., Ardron, J., Bax, N., Bernal, P., Cleary, J., Cresswell, I., Donnelly, B., Dunstan, P., Gjerde, K., Johnson, D., Kaschner, K., Lascelles, B., Rice, J., von Nordheim, H., Wood, L., Halpin, P.N. (2014). The Convention on Biological Diversity's Ecologically or Biologically Significant Areas: Origins, development, and current status. *Marine Policy* 49, 137-145.
- Edgcomb, V., Orsi, W., Bunge, J., Jeon, S., Christen, R., Leslin, C., Holder, M., Taylor, G.T., Suarez, P., Varela, R., and Epstein, S. (2011). Protistan microbial observatory in the Cariaco Basin, Caribbean. I. Pyrosequencing vs Sanger insights into species richness. *The ISME Journal* 5(8): 1344-1356.
- Etter, R., Mullineaux, L. (2000). Deep-sea communities. In: Bertness, M.D., Gaines, S., Hay, M. (Eds.), *Marine Community Ecology*. Sinauer Associates, Inc., Sunderland, MA, USA, pp. 367-393.
- FAO (2009). *International Guidelines for the Management of Deep-sea Fisheries in the High Seas*. Rome, Italy: FAO: 73 pp. Available from: <http://www.fao.org/docrep/011/i0816t/i0816t00.htm>.
- Friedlander, A.M., Ballesteros, E., Fay, M., Sala, E. (2014). Marine Communities on Oil Platforms in Gabon, West Africa: High Biodiversity Oases in a Low Biodiversity Environment. *PLoS ONE* 9(8), e103709.

- Fuhrman, J.A., Steele, J.A., Hewson, I., Schwalback, M.S., Brown, M.V., Green, J.L., and Brown, J.H. (2008). A latitudinal diversity gradient in planktonic marine bacteria. *Proceedings of the National Academy of Science USA* 105(22): 7774–7778.
- Fujii, T., Kilgallen, N.M., Rowden, A.A., Jamieson, A.J. (2013). Deep-sea amphipod community structure across abyssal to hadal depths in the Peru-Chile and Kermadec trenches. *Marine Ecology Progress Series* 492, 125-138.
- Fujikura, K., Kojima, S., Tamaki, K., Maki, Y., Hunt, J., and Okutani, T. (1999). The deepest chemosynthesis-based community yet discovered from the hadal Zone, 7326 m deep, in the Japan Trench. *Marine Ecology Progress Series* 190: 17-26.
- Fujiwara, Y., Kawato, M., Yamamoto, T., Yamanaka, T., Sato-Okoshi, W., Noda, C., Tsuchida, S., Komai, T., Cubelio, S.S., Sasaki, T., Jacobsen, K., Kubokawa, K., Fujikura, K., Maruyama, T., Furushima, Y., Okoshi, K., Miyake, H., Miyazaki, M., Nogi, Y., Yatabe, A., Okutani, T. (2007). Three-year investigations into sperm whale-fall ecosystems in Japan. *Marine Ecology* 28 (1), 219-232.
- Fukushima, T. (2007). Amounts of megabenthic organisms in areas of manganese nodules, cobalt-rich crusts and polymetallic sulphides occurrences. Proceedings of the International Seabed Authority's (ISA) Workshop, September 2004: Polymetallic Sulphides and Cobalt-Rich Ferromanganese Crust Deposits: Establishment of Environmental Baselines and an Associated Monitoring Programme During Exploration (ed. by ISA), pp. 356–368. International Seabed Authority, Kingston, Jamaica. Available at: (<http://www.isa.org.jm/en/documents/publications>) (accessed 18 October 2013).
- Gage, J.D., Lambshead, P.J.D., Bishop, J.D.D., Stuart, C.T., Jones, N.S. (2004) Large-scale biodiversity pattern of Cumacea (Peracarida : Crustacea) in the deep Atlantic. *Marine Ecology-Progress Series* 277, 181-196.
- Gallo, N.D., Cameron, J., Hardy, K., Fryer, P., Bartlett, D., and Levin, L.A. Submersible and lander-observed community patterns in the Mariana and New Britain Trenches: Influence of productivity and depth on benthic community structure (in revision, *Deep-Sea Research Part I-Oceanographic Research Papers*).
- Gambi, C., Vanreusal, A., and Danovaro, R. (2003). Biodiversity of nematode assemblages from deep-sea sediments of the Atacama Slope and Trench. *Deep Sea Research I Part I: Oceanographic Research Papers* 50: 103-117.
- George, R.Y., and Higgins, R.P. (1979). Eutrophic Hadal Benthic Community in the Puerto Rico Trench. *Ambio Special Report, No. 6, The Deep Sea: Ecology and Exploitation*, pp. 51-58.
- German, C.R., Ramirez-Llodra, E., Baker, M.C., Tyler, P.A., and the ChEss Scientific Steering Committee (2011). Deep-Water Chemosynthetic Ecosystem Research during the Census of Marine Life Decade and Beyond: A Proposed Deep-Ocean Road Map. *PLoS ONE* 6(8): e23259. Doi:10.1371/journal.pone.0023259.



- Giering, S., Sanders, R., Lampitt, R., Anderson, T., Tamburini, C., Boutrif, M., Zubkov, M., Marsay, C., Henson, S., Saw, K., Cook, K., and Mayor, D. (2014). Reconciliation of the carbon budget in the ocean's twilight zone. *Nature* 507: 480-483.
- Glover, A.G., and Smith, C.R. (2003). The deep-sea floor ecosystem: current status and prospects of anthropogenic change by the year 2025. *Environmental Conservation* 30: 219–41.
- Glover, A.G., Gooday, A.J., Bailey, D.M., Billett, D.S.M., Chevaldonné, P., Colaço, A., Copley, J., Cuvelier, D., Desbruyères, D., Kalogeropoulou, V., Klages, M., Lampadariou, N., Lejeusne, C., Mestre, N.C., Paterson, G.L.J., Perez, T., Ruhl, H., Sarrazin, J., Soltwedel, T., Soto, E.H., Thatje, S., Tselepides, A., Van Gaever, S., and Vanreusel, A. (2010). Temporal change in deep-sea benthic ecosystems: a review of the evidence from recent time-series studies. *Advances in Marine Biology* 58: 1-95.
- Glover, A.G., Källström, B., Smith, C.R., Dahlgren, T.G. (2005). World-wide whale worms? A new species of *Osedax* from the shallow north Atlantic. *Proceedings of the Royal Society B: Biological Sciences* 272 (1581), 2587-2592.
- Glud, R.N., Wenzhofer, F., Middelboe, M., Oguri, K., Turnewitsch, R., Canfield, D.E., Kitazato, H. (2013). High rates of microbial carbon turnover in sediments in the deepest oceanic trench on Earth. *Nature Geoscience* 6 (4), 284-288.
- Goffredi, S.K., Orphan, V.J., Rouse, G.W., Jahnke, L., Embaye, T., Turk, K., Lee, R., Vrijenhoek, R.C. (2005). Evolutionary innovation: a bone-eating marine symbiosis. *Environmental Microbiology* 7 (9), 1369-1378.
- Golikov, A.N., and Scarlato, O.A. (1990). History of the development of the Arctic marine ecosystem and their functional peculiarities. In: Kotlyakov, V.M., and Sokolov, V.E., eds., *Arctic Research: Advances and prospects, Proceedings of the Conference of Arctic and Nordic countries on coordination of research in the Arctic*, Leningrad, December 1988, Moscow, pp. 196-206.
- Gooday, A.J., Todo, Y., Uematsu, K., and Kitazato, H. (2008). New organic-walled Foraminifera (Protista) from the ocean's deepest point, the Challenger Deep (western Pacific Ocean). *Zoological Journal of the Linnean Society* 153: 399–423.
- Gooday, A.J., Bett, B.J., Escobar, E., Ingole, B., Levin, L.A., Neira, C., Raman, A.V., Sellanes, J. (2010). Habitat heterogeneity and its influence on benthic biodiversity in oxygen minimum zones. *Marine Ecology* 31, 125-147.
- Grange, L. J. and Smith, C.R. (2013). Megafaunal Communities in Rapidly Warming Fjords Along the West Antarctic Peninsula: Hotspots of Abundance and Beta Diversity. *PLoS ONE*, 8(11): e77917. doi:10.1371/journal.pone.0077917
- Grassle, J.F. (1989). Species diversity in deep-sea communities. *Trends in Ecology and Evolution* 4 (1), 12-15.
- Grassle, J.F., Maciolek, N.J. (1992). Deep-sea species richness: Regional and local diversity estimates from quantitative bottom samples. *American Naturalist* 139 (2), 313-341.

- Griffiths, H.J. (2010). Antarctic Marine Biodiversity – What Do We Know About the Distribution of Life in the Southern Ocean? *PLoS ONE* 5(8): e11683.
- Haedrich, R.L. (1996). Deep-water fishes: evolution and adaptation in Earth's largest living spaces. *Journal of Fish Biology* 49(Suppl. A): 40–53.
- Hanchet, S., Sainsbury, K., Butterworth, D., Darby, C., Bizikov, V., Rune Godø, O., Ichii, T., Kock, K.-H., López Abellán, L., Vacchi, M. (2015). CCAMLR's precautionary approach to management focusing on Ross Sea toothfish fishery. *Antarctic Science FirstView*, 1-8.
- Harris, P.T., Macmillan-Lawler, M., Rupp, J., and Baker, E.K. (2014). Geomorphology of the oceans. *Marine Geology* 352: 4–24. Doi:10.1016/j.margeo.2014.01.011.
- Hasemann, C., Bergmann, M., Kanzog, C., Lochthofen, N., Sauter, E., Schewe, I., and Soltwedel, T. (2013). Effects of dropstone-induced habitat heterogeneity on Arctic deep-sea benthos with special reference to nematode communities. *Marine Biological Research* 9(3): 276-292.
- Havermans, C., Sonet, G., d'Udekem d'Acoz, C., Nagy, Z.T., Martin P., Briz, S., Riehl, T., Agrawal, S., and Held, C. (2013). Genetic and Morphological Divergences in the Cosmopolitan Deep-Sea Amphipod *Eurythenes gryllus* Reveal a Diverse Abyss and a Bipolar Species. *PLoS ONE* 8(9): e74218. Doi:10.1371/journal.pone.0074218.
- Hays, G.C. (2003). A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503: 163–170.
- Heezen, B.C. (1969). The world rift system: an introduction to the symposium. *Technophysics* 8: 269–279.
- Hein, J.R., Mizell, K., Koschinsky, A., and Conrad, T.A. (2013). Deep-ocean mineral deposits as a source for critical metals for high- and green technology applications: comparison with land-based resources. *Ore Geology Reviews* 51: 1-14.
- Herring, P. (2002). *The biology of the deep ocean*. Oxford University Press, Oxford, UK, 314 pp.
- Hopkins, T.L., Sutton, T.T., and Lancraft, T.M. (1996). Trophic structure and predation impact of a low latitude midwater fish community. *Progress in Oceanography* 38: 205-239.
- Hoving, H.T., Perez, J.A.A., Bolstad, K.S.R., Braid, H.E., Evans, A.B., Fuchs, D., Judkins, H., Kelly, J.T., Marian, J.E.A.R., Nakajima, R., Piatkowski, U., Reid, A., Vecchione, M., and Xavier, J.C.C. (2014). The Study of Deep-Sea Cephalopods. In: Vidal, E.A.G., editor. *Advances in Marine Biology, Vol. 67*. Oxford, UK.: 235-359.
- Hunt, G., Cronin, T.M., and Roy, K. (2005). Species–energy relationship in the deep sea: a test using the Quaternary fossil record. *Ecology Letters* 8: 739–747.
- Ingels, J., Vanhove, S., De Mesel, I., and Vanreusel, A. (2006). The biodiversity and biogeography of the free-living nematode genera *Desmodora* and

- Desmodorella (family Desmodoridae) at both sides of the Scotia Arc. *Polar Biology* 29(11): 936-949.
- Irigoien, X., Klevjer, T.A., Rostad, A., Martinez, U., Boyra, G., Acuña, J.L., Bode, A., Echevarria, F., Gonzales-Gordillo, J.I., Hernandez-León, S., Agusti, S., Aksnes, D.L., Duarte, C.M., Kaardvedt, S. (2014). Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nature Communications* 5:3271.
- ISA (2013). *Recommendations for the guidance of contractors for the assessment of the possible environmental impacts arising from exploration for marine minerals in the Area*. ISBA/19/LTC/8.
- ISA (2000). *Decision of the Assembly relating to the regulations on prospecting and exploration for polymetallic nodules in the Area*. ISBA/6/A/18.
- ISA (2007). *Polymetallic Sulphides and Cobalt-Rich Ferromanganese crusts deposits: Establishment of environmental baselines and an associated monitoring programme during exploration*. Proceedings of the International Seabed Authority Workshop held in Kingston, Jamaica, 6-10 September 2004, 491 pp.
- Itoh, M., Kawamura, K., Kitahashi, T., Kojima, S., Katagiri, H., and Shimanaga, M. (2011). Bathymetric patterns of meiofaunal abundance and biomass associated with the Kuril and Ryukyu trenches, western North Pacific Ocean. *Deep-Sea Research I* 58: 86–97.
- Jahnke, R.A. (2010). Global Synthesis. In: Liu, K.-K., Atkinson, L., Quinones, R., Talaue-McManus, L. (Eds.) *Carbon and Nutrient Fluxes in Continental Margins*. Springer, pp. 597-615.
- Jamieson, A.J. (2011). Ecology of Deep Oceans: Hadal Trenches. In: *Encyclopedia of Life Sciences (ELS)*. John Wiley & Sons, Ltd, Chichester. Doi: 10.1002/9780470015902.a0023606. Jamieson, A.J., Fujii, T., Mayor, D.J., Solan, M., Priede, I.G. (2009). Hadal trenches: the ecology of the deepest places on Earth. *Trends in Ecology and Evolution* 25 (3), 190-197.
- Jansson, R., and Dynesius, M. (2002). The fate of clades in a world of recurrent climate change: Milankovitch oscillations and evolution. *Annual Review of Ecological Systematics* 33: 741-777.
- Japp, D.W., and Wilkinson, S. (2007). Deep-sea resources and fisheries. Report and documentation of the expert consultation on deep-sea fisheries in the High Seas. *FAO Fisheries Report 838*: pp. 39–59. Rome, Italy: FAO. Available from: <ftp://ftp.fao.org/docrep/fao/010/a1341e/a1341e00.pdf>.
- Jobstovgt, N., Hanley, N., Hynes, S., Kenter, J., Witte, U. (2014a). Twenty thousand sterling under the sea: Estimating the value of protecting deep-sea biodiversity. *Ecological Economics* 97, 10-19.
- Jobstovgt, N., Townsend, M., Witte, U., Hanley, N. (2014b). How Can We Identify and Communicate the Ecological Value of Deep-Sea Ecosystem Services? *PLoS ONE* 9 (7), e100646.

- Jones, D.O.B., Yool, A., Wei, C.L., Henson, S.A., Ruhl, H.A., Watson, R.A., and Gehlen, M. (2014). Global reductions in seafloor biomass in response to climate change. *Global Change Biology* 20: 1861–1872, Doi: 10.1111/gcb.12480.
- Jumars, P.A., and Hessler, R.H. (1976). Hadal community structure: implications from the Aleutian Trench. *Journal of Marine Research* 34: 547–560.
- Juniper, S.K., and Sibuet, M. (1987). Cold seep benthic communities in Japan subduction zones: spatial organization, trophic strategies and evidence for temporal evolution. *Marine Ecology Progress Series* 40: 115-126.
- Kaartvedt, S., Staby, A., and Aksnes, D. (2012). Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. *Marine Ecology Progress Series* 456: 1–6.
- Kaiser, S., Brandao, S.N., Brix, S., Barnes, D.K.A., Bowden, D.A., Ingels, J., Leese, F., Schiaparelli, S., Arango, C.P., Badhe, R., Bax, N., Blazewicz-Paszkwycz, M., Brandt, A., Brenke, N., Catarino, A.I., David, B., De Ridder, C., Dubois, P., Ellingsen, K.E., Glover, A.G., Griffiths, H.J., Gutt, J., Halanych, K.M., Havermans, C., Held, C., Janussen, D., Lorz, A.N., Pearce, D.A., Pierrat, B., Riehl, T., Rose, A., Sands, C.J., Soler-Membrives, A., Schuller, M., Strugnell, J.M., Vanreusel, A., Veit-Kohler, G., Wilson, N.G., Yasuhara, M. (2013). Patterns, processes and vulnerability of Southern Ocean benthos: a decadal leap in knowledge and understanding. *Marine Biology* 160 (9), 2295-2317.
- Kitahashi, T., Kawamura, K., Kojima, S., and Shimanaga, M. (2013). Assemblages gradually change from bathyal to hadal depth: A case study on harpacticoid copepods around the Kuril Trench (north-west Pacific Ocean). *Deep Sea Research I* 74: 39–47.
- Kortsch, S., Primicerio, R., Beuchel, F., Renaud, P.E., Rodrigez, J., Lønne, O.J., Gulliksen, B. (2012). Climate-driven regime shifts in Arctic marine benthos. *Proc. Natl. Acad. Sci. USA* 109(35), 14,052-14,057.
- Koslow, J.A. (2009). The role of acoustics in ecosystem-based fishery management. *ICES Journal of Marine Science* 66: 966–973.
- Koslow, J.A. (2007). The biological environment of cobalt-rich ferromanganese crusts deposits, the potential impact of exploration and mining on this environment, and data required to establish environmental baselines. In: *Polymetallic Sulphides and Cobalt-Rich Ferromanganese crusts deposits: Establishment of environmental baselines and a monitoring program during exploration*. Proceedings of the International Seabed Authority's Workshop held in Kingston, Jamaica, 6-10 September 2004, p: 274-294.
- Koslow, J.A., Goericke, R., Lara-Lopez, A., Watson, W. (2011). Impact of declining intermediate-water oxygen on deepwater fishes in the California Current. *Marine Ecology Progress Series* 436, 207-218.
- Kosobokova, K.N., Hirche, H.J., and Hopcroft, R.R. (2011). Patterns of zooplankton diversity through the depths of the Arctic's central basin. *Marine Biodiversity* 41: 29-50.

- Kvassnes, A.J.S., Iversen, E. (2013). Waste sites from mines in Norwegian Fjords. *Mineralproduksjon 3*, A27-A38.
- Kvassnes, A.J.S., Sweetman, A.K., Iversen, E., Skei, J. (2009). Sustainable use and future of submarine tailings placements in the Norwegian extractive Industry. *Securing the Future (Mining, metals and the environments in a sustainable society) and 8th ICARD (International Conference on Acid Rock Drainage)*. <http://www.proceedings-stfandicard-2009.com/>, Skelleftea, Sweden.
- Ladau, J., Sharpton, T.J., Finucane, M.M., Jospin, G., Kembel, S.W., O'Dwyer, J., Koepfel, A.F., Green, J.L. and Pollard, K.S. (2013). Global marine bacterial diversity peaks at high latitudes in winter. *The ISME journal* 7(9): 1669-1677.
- Lamshead, P.J.D., Tietjen, J., Ferrero, T., Jensen, P. (2000). Latitudinal diversity gradients in the deep sea with special reference to North Atlantic nematodes. *Marine Ecology-Progress Series* 194, 159-167.
- Lebrato, M., Jones, D.O.B. (2009). Mass deposition event of *Pyrosoma atlanticum* carcasses off Ivory Coast (West Africa). *Limnology and Oceanography* 54(4), 1197-1209.
- Lebrato, M., Pitt, K., Sweetman, A., Jones, D.B., Cartes, J., Oschlies, A., Condon, R., Molinero, J., Adler, L., Gaillard, C., Lloris, D., Billett, D.M. (2012). Jelly-falls historic and recent observations: a review to drive future research directions. *Hydrobiologia* 690(1), 227-245.
- Lebrato, M., Mendes, P., Steinberg, D.K., Cartes, J.E., Jones, B., Birsa, L.M., Benavides, R., Oschlies, A. (2013a). Jelly biomass sinking speed reveals a fast carbon export mechanism. *Limnology and Oceanography* 58 (3), 1113-1122.
- Lebrato, M., Molinero, J.-C., Cartes, J.E., Lloris, D., Mélin, F., Beni-Casadella, L. (2013b). Sinking Jelly-Carbon Unveils Potential Environmental Variability along a Continental Margin. *PLoS ONE* 8 (12), e82070.
- Levin, L.A. (2003). Oxygen minimum zone benthos: Adaptation and community response to hypoxia. *Oceanography and Marine Biology*, 41, 1-45.
- Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., and Pawson, D. (2001). Environmental influences on regional deep-sea species diversity. *Annual Review of Ecological Systematics* 32: 51-93.
- Levin, L.A., Liu, K.-K., Emeis, K.-C., Breitburg, D.L., Cloern, J., Deutsch, C., Giani, M., Goffart, A., Hofmann, E.E., Lachkar, Z. (2014). Comparative biogeochemistry–ecosystem–human interactions on dynamic continental margins. *Journal of Marine Systems*.
- Levin, L.A., Sibuet, M. (2012). Understanding Continental Margin Biodiversity: A New Imperative. *Annual Review of Marine Science* 4 (1), 79-112.
- Levin, L.A. and Dayton, P.K. (2009). Ecological theory and continental margins: where shallow meets deep. *Trends in Ecology and Evolution* 24: 606-617.
- Marincovich, L. Jr., Brouwers, E.M., Hopkins, D.M., and McKenna, M.C. (1990). Late Mesozoic and Cenozoic paleogeographic and paleoclimatic history of the Arctic Ocean Basin, based upon shallow-water marine faunas and terrestrial

- vertebrates. In: Gantz, A., Johnson, L., Sweeny, J.F., editors. *The Arctic Ocean Region. The Geology of North America, vol. L*. Geological Society of America, Boulder, Colorado. pp. 403-426.
- Mengerink, K.J., Van Dover, C.L., Ardron, J., Baker, M., Escobar-Briones, E., Gjerde, K., Koslow, J.A., Ramirez-Llodra, E., Lara-Lopez, A., Squires, D., Sutton, T.T., Sweetman, A.K., and Levin, L.A. (2014). A Call for Deep-Ocean Stewardship. *Science* 344: 696-698.
- Miljutin, D.M., Miljutina, M.A., Arbizu, P.M., and Galéron, J. (2011). Deep-sea nematode assemblage has not recovered 26 years after experimental mining of polymetallic nodules (Clarion-Clipperton Fracture Zone, Tropical Eastern Pacific). *Deep-Sea Research*. 58(8): 885-897.
- Mora, C., Rollo, A., Tittensor, D.P. (2013a). Comment on Can We Name Earth's Species Before They Go Extinct?. *Science*, 341(6143), p. 237. DOI: 10.1126/science.1237254.
- Mora, C., Wei, C.-L., Rollo, A., Amaro, T., Baco, A.R., Billett, D., Bopp, L., Chen, Q., Collier, M., Danovaro, R., Gooday, A.J., Grupe, B.M., Halloran, P.R., Ingels, J., Jones, D.O.B., Levin, L.A., Nakano, H., Norling, K., Ramirez-Llodra, E., Rex, M., Ruhl, H.A., Smith, C.R., Sweetman, A.K., Thurber, A.R., Tjiputra, J.F., Usseglio, P., Watling, L., Wu, T., Yasuhara, M. (2013b). Biotic and Human Vulnerability to Projected Changes in Ocean Biogeochemistry over the 21st Century. *PLoS Biol* 11 (10), e1001682.
- Morato, T., Hoyle, S.D., Allain, V., and Nicol, S.J. (2010). Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proceedings of the National Academy of Science USA* 107: 9707–9711.
- Morato, T., Varkey, D.A., Dâmaso, C., Machete, M., Santos, M., Prieto, R., Santos, R.S., and Pitcher, T.J. (2008). Evidence of a seamount effect on aggregating visitors. *Marine Ecology Progress Series* 357: 23-32. Doi:10.3354/meps07269.
- Muller-Karger, F.E., Varela, R., Thunell, R., Luerksen, R., Hu, C., Walsh, J.J. (2005). The importance of continental margins in the global carbon cycle. *Geophysical research letters* 32 (1), L01602.
- Narayanaswamy, B.E., Bett, B.J., and Gage, J.D. (2005). Ecology of bathyal polychaete fauna at an Arctic-Atlantic boundary (Faroe-Shetland Channel, North-east Atlantic). *Marine Biology Research* 1: 20-32.
- Narayanaswamy, B.E., Renaud, P., Duineveld, G., Berge, J., Lavaleye, M.S.S., Reiss, H. and Brattegard, T. (2010). Biodiversity trends along the western European Margin. *PLoS ONE* 5(12): e14295.
- Narayanaswamy, B.E., Coll, M., Danovaro, R., Davidson, K., Ojaveer, H., and Renaud, P.E. (2013). Synthesis of knowledge on marine biodiversity in European Seas: from Census to sustainable management. *PLoS ONE* 8(3): e58909. Doi:10.1371/journal.pone.0058909.

- Nesis, K.N. (1984). A hypothesis on the origin of western and eastern Arctic distribution of areas of marine bottom animals. *Soviet Journal of Marine Biology* 9: 235-243.
- Ogawa, Y., Fujioka, K., Fujikura, K. and Iwabuchi, Y. (1996). En echelon patterns of Calyptogenina colonies in the Japan Trench. *Geology* 24: 807-810.
- Oguri, K., Kawamura, K., Sakaguchi, A., Toyofuku, T., Kasaya, T., Murayama, M., Fujikura, K., Glud, R.N., and Kitazato, H. (2013). Hadal disturbance in the Japan Trench induced by the 2011 Tohoku–Oki Earthquake. *Scientific Reports* 3: 1915. Doi: 10.1038/srep01915.
- Oschmann, W. (1990). Dropstones - rocky mini-islands in high-latitude pelagic soft substrate environments. *Senckenbergiana Marit* 21: 55-75.
- Østerhus, S., and Gammelsrod, T. (1999). The abyss of the Nordic Seas is warming. *Journal of Climate* 12: 3297–3304.
- Pawlowski, J., Christen, R., Lecroq, B., Bachar, D., Shahbazkia, H.R., Amaral-Zettler, L., and Guillou, L. (2011). Eukaryotic richness in the abyss: insights from pyrotag sequencing. *PLoS One* 6(4): e18169.
- Pawlowski, J., Fahrni, J., Lecroq, B., Longet, D., Cornelius, N., Excoffier, L., Cedhagen, T., and Gooday, A.J. (2007). Bipolar gene flow in deep-sea benthic foraminifera. *Molecular Ecology* 16(19): 4089-4096.
- Pham, C.K., Ramirez-Llodra, E., Alt, C.H.S., Amaro, T., Bergmann, M., Canals, M., Company, J.B., Davies, J., Duineveld, G., Galgani, F., Howell, K.L., Huvenne, V.A.I., Isidro, E., Jones, D.O.B., Lastras, G., Morato, T., Gomes-Pereira, J.N., Purser, A., Stewart, H., Tojeira, I., Tubau, X., Van Rooij, D., Tyler, P.A. (2014). Marine Litter Distribution and Density in European Seas, from the Shelves to Deep Basins. *PLoS ONE* 9 (4), e95839.
- Pierrot-Bults, A., and Angel, M. (2012). Pelagic Biodiversity and Biogeography of the Oceans. *Biology International* 51: 9-35.
- Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M. (1995). The future of biodiversity. *Science* 269(5222), 347-349.
- Priede, I.G., Bergstad, O.A., Miller, P.I., Vecchione, M., Gebruk, A., Falkenhaus, T., Billett, D.S.M., Craig, J., Dale, A.C., Shields, M.A., Tilstone, G.H., Sutton, T.T., Gooday, A.J., Inall, M.E., Jones, D.O.B., Martinze-Vicente, V., Menezes, G.M., Niedzielski, T., Sigurosson, P., Rothe, N. Rogacheva, A., Alt, C.H.S., Brand, T., Abell, R., Brierley, A.S., Cousins, N.J., Crockard, D., Hoelzel, A.R., Hoines, A., Letessier, T.B., Read, J.F., Shimmield, T. Cox, M.J., Galbraith, J.K, Gordon, J.D.M., Horton, T., Neat, F., and Lorange, P. (2013). Does Presence of a Mid-Ocean Ridge Enhance Biomass and Biodiversity? *PLoS ONE* 8(5): e61550. Doi:10.1371/journal.pone.0061550.
- Priede, I.G., Osborn, K.J., Gebruk, A.V., Jones, D., Shale, D., Rogacheva, A., and Holland N.D. (2012). Observations on torquaratorid acorn worms (Hemichordata, Enteropneusta) from the North Atlantic with descriptions of a new genus and three new species. *Invertebrate Biology* 131: 244-257. Doi:10.1111/j.1744-7410.2012.00266.x.

- Prince, E.D., Goodyear, C.P., (2006). Hypoxia-based habitat compression of tropical pelagic fishes. *Fisheries Oceanography* 15 (6), 451-464.
- Purcell, J.E. (2012). Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annual Review of Marine Science* 4, 209-235.
- Purcell, J.E., Uye, S.-i., Lo, W.-T. (2007). Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology - Progress Series* 350, 153.
- Pusceddu, A., Bianchelli, S., Martín, J., Puig, P., Palanques, A., Masqué, P., Danovaro, R. (2014). Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. *Proceedings of the National Academy of Sciences*, 111 (24) 8861-8866. Doi: 10.1073/pnas.1405454111.
- Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C.R., Levin, L.A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy, B.E., Smith, C.R., Tittensor, D.P., Tyler, P.A., Vanreusel, A., Vecchione, M. (2010). Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. *Biogeosciences* 7 (9), 2851-2899.
- Ramirez-Llodra, E., Tyler, P.A., Baker, M.C., Bergstad, O.A., Clark, M.R., Escobar, E., Levin, L.A., Menot, L., Rowden, A.A., Smith, C.R., Van Dover, C.L. (2011). Man and the Last Great Wilderness: Human Impact on the Deep Sea. *PLoS ONE* 6 (8), e22588.
- Reed, J.K., Messing, C., Walker, B., Brooke, S., Correa, T., Brouwer, M., and Udouj, T. (2013). Habitat characterization, distribution, and areal extent of deep-sea coral ecosystem habitat off Florida, southeastern United States. *Journal of Caribbean Science* 47: 13-30.
- Reid, E., Sullivan, B., Clark, J. (2010). Mitigation of seabird captures during hauling in CCAMLR longline fisheries. *CCAMLR Science* 17, 155-162.
- Rex, M.A. (1981). Community structure in the deep-sea benthos. *Annual Review of Ecology and Systematics* 12, 331-353.
- Rex, M.A., and Etter, R.H. (2010). *Deep-Sea Biodiversity: Pattern and Scale*. Harvard University Press, Boston, United States, 354 pp.
- Rex, M.A., Stuart, C.T., Coyne, G. (2000). Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. *Proceedings of the National Academy of Sciences* 97 (8), 4082-4085.
- Rice, J., Lee, J., Tandstad, M., 2014. Parallel initiatives. Governance of Marine Fisheries and Biodiversity Conservation. John Wiley & Sons, Ltd., pp. 195-208.
- Robinson, C., Steinberg, D.K., Anderson, T.R., Arístegui, J., Carlson, C.A., Frost, J.R., Ghiglione, J.F., Hernández-León, S., Jackson, G.A., Koppelman, R., Quéguiner, B., Ragueneau, O., Rassoulzadegan, F., Robison, B.H., Tamburini, C., Tanaka, T., Wishner, K.F., and Zhang, J. (2010). Mesopelagic zone ecology and biogeochemistry – a synthesis. *Deep-Sea Research Part II* 57: 1504-1518.



- Robison, B.H. (2004). Deep pelagic biology. *Journal of Experimental Marine Biology and Ecology* 300: 253-272.
- Robison, B.H. (2009). Conservation of deep pelagic biodiversity. *Conservation Biology* 23(4): 847-858.
- Rodhouse, P.G., and Nigmatullin, C.M. (1996). Role as consumers. *Philosophical Transactions of the Royal Society of London B* 351 (1343), 1003-1022.
- Rodriguez-Lazaro, J., Cronin, T.M. (1999). Quaternary glacial and deglacial Ostracoda in the thermocline of the Little Bahama Bank (NW Atlantic): palaeoceanographic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 152 (3–4), 339-364.
- Rogers, A.D. (2007). Evolution and biodiversity of Antarctic organisms: a molecular perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362 (1488), 2191-2214.
- Roman, J., Estes, J., Morissette, L., Smith, C.R., Costa, D., McCarthy, J., Nation, J.B., Nicol, S., Pershing, A., Smetacek, V. (2014). Whales as ecosystem engineers. *Frontiers in Ecology and the Environment*, doi:10.1890/130220.
- Rosa, R., and Seibel, B.A. (2008). Synergistic effects of climate –related variables suggest future physiological impairment in a top oceanic predator. *Proceedings of the National Academy of Science USA* 105(52): 20776–20780.
- Rouse, G.W., Wilson, N.G., Goffredi, S.K., Johnson, S.B., Smart, T., Widmer, C., Young, C.M., Vrijenhoek, R.C. (2009). Spawning and development in Osedax boneworms (Siboglinidae, Annelida). *Marine Biology* 156 (3), 395-405.
- Rudels, B., Jones, E.P., Anderson, L.G., and Kattner, G. (1994). On the intermediate depth waters of the Arctic Ocean. *Geophysical Monogram* 85: 33-46.
- Ruhl, H.A., and Smith, K.L. Jr. (2004). Shifts in deep-sea community structure linked to climate and food supply. *Science* 305: 513-515.
- Ruhl, H.A., Ellena, J.A., and Smith, K.L. Jr. (2008). Connections between climate, food limitation, and carbon cycling in abyssal sediment communities: a long time-series perspective. *Proceedings of the National Academy of Science USA* 105: 17006–17011.
- Savin, S.M., Douglas, R.C., and Stehli, F.G. (1975). Tertiary marine paleotemperatures. *Geological Society of American Bulletin* 86: 1499-1510.
- Schlacher, T.A., Baco, A.R., Rowden, A.A., O’Hara, T.D., Clark, M.R., Kelley, C., and Dower, J.F. (2013). Seamount benthos in a cobalt-rich crust region of the central Pacific: conservation challenges for future seabed mining. *Diversity and Distributions* 1-12.
- Sibuet, M., Olu, K. (1998). Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep-Sea Research Part II* 45 (1-3), 517-567.
- Sirenko, B.I. (2001). List of species of free-living invertebrates of Eurasian Arctic seas and adjacent deep waters. *Explorations of the Fauna of the Seas* 51: 1-129.

- Sissenwine, M.P., and Mace, P.M. (2007). Can deep water fisheries be managed sustainably? In: *Report and documentation of the Expert Consultation on Deep-Sea fisheries in the High Seas*. FAO Fisheries Report 838. Rome, Italy: FAO. pp. 61–111.
- Smale, D.A., Barnes, D.K.A., Fraser, K.P.P., and Peck, L.S. (2008). Benthic community response to iceberg scouring at an intensely disturbed shallow water site at Adelaide Island Antarctica. *Marine Ecology Progress Series* 355: 85-94.
- Smith, C.R. (2006). *Bigger is better: The role of whales as detritus in marine ecosystems*. In: Whales, Whaling and Ocean Ecosystems, Estes, J.A., DeMaster, D.P., Brownell Jr., R.L., Doak, D.F., and Williams, T.M. (eds.). University of California Press, Berkeley, CA, USA, pp. 286 – 301.
- Smith, C.R., De Leo, F.C., Bernardino, A.F., Sweetman, A.K., Arbizu, P.M. (2008). Abyssal food limitation, ecosystem structure and climate change. *Trends in Ecology and Evolution* 23 (9), 518-528.
- Smith, C.R., Grange, L., Honig, D.L., Naudts, L., Huber, B., Guidi, L. and Domack, E. (2012). A large population of king crabs in Palmer Deep on the West Antarctic Peninsula and potential invasive impacts. *Proceedings of the Royal Society B*, 279: 1017-1026. doi: 10.1098/rspb.2011.1496
- Smith, C.R. and Baco, A.R. (2003). The ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology Annual Review*, 41: 311-354.
- Smith, C.R., Glover, A.G., Treude, T., Higgs, N.D. and Amon, D.J. (2015). Whale-fall ecosystems: recent insights into ecology, paleoecology and evolution. *Annual Review of Marine Science*, 96. doi: 10.1146/annurev-marine-010213-135144.
- Smith, K.L., Ruhl, H.A., Kahru, M., Huffard, C.L., Sherman, A.D. (2013). Deep ocean communities impacted by changing climate over 24 y in the abyssal northeast Pacific Ocean. *Proceedings of the National Academy of Sciences*. Doi: 10.1073/pnas.1315447110.
- Smith, K. L., Sherman, A.D., Huffard, C.L., McGill, P.R., Henthorn, R., Von Thun, S., Ruhl, H.A., Kahru, M., Ohman, M.D. (2014). Large salp bloom export from the upper ocean and benthic community response in the abyssal northeast Pacific: Day to week resolution. *Limnology and Oceanography* 59 (3), 745-757.
- Snelgrove, P.V.R., Smith, C.R. (2002). A riot of species in an environmental calm: The paradox of the species-rich deep-sea floor. In: Gibson, R.N., Barnes, M., Atkinson, R.J.A. (Eds.), *Oceanography and Marine Biology*, Vol. 40. Taylor & Francis Ltd, London, pp. 311-342.
- Sogin, M.L., Morrison, H.G., Huber, J.A., Welch, D.M., Huse, S.M., Neal, P.R., Arrieta, J.M., Herndl, G.J. (2006). Microbial diversity in the deep sea and the underexplored “rare biosphere”. *Proceedings of the National Academy of Sciences USA* 103 (32), 12115-12120.
- Stein, R., Grobe, H., and Wahsner, M. (1994). Organic carbon, carbonate, and clay mineral distribution in eastern central Arctic surface sediments. *Marine Geology* 119: 269-285.

- Stein, R., MacDonald, R.W., eds (2004). *The organic carbon cycle in the Arctic Ocean*. Springer, Berlin, 363 pp.
- Stramma, L., Prince, E.D., Schmidtko, S., Luo, J., Hoolihan, J.P., Visbeck, M., Wallace, D.W., Brandt, P., Körtzinger, A. (2012). Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nature Climate Change* 2 (1), 33-37.
- Suess, E., Bohrnann, G., von Huene, R., Linke, P., Waiimann, K.W., Larnmers, S., and Sahling, H. (1998). Fluid venting in the eastern Aleutian subduction zone. *Journal of Geophysical Research* 103: 2597-2614.
- Sul, W.J., Oliver, T.A., Ducklow, H.W., Amaral-Zettler, L.A, and Sogin, M.L. (2013). Marine bacteria exhibit a bipolar distribution. *Proceedings of the National Academy of Science USA*. Doi:10.1073/pnas.1212424110.
- Sutton, T.T. (2013). Vertical ecology of the pelagic ocean: classical patterns and new perspectives. *Journal of Fish Biology* 83: 1508-1527.
- Svavarsson, J. (1997). Diversity of isopods (Crustacea): new data from the Arctic and Atlantic Oceans. *Biodiversity and Conservation* 6: 1571-1579.
- Sweetman, A.K., Chapman, A. (2011). First observations of jelly-falls at the seafloor in a deep-sea fjord. *Deep Sea Research Part I: Oceanographic Research Papers* 58 (12), 1206-1211.
- Sweetman, A.K, Smith, C.R., Dale, T. and Jones, D.O.B. (2014). Rapid scavenging of jellyfish carcasses reveals the importance of gelatinous material to deep-sea food webs. *Proceedings of the Royal Society B*: 281: 20142210
- Taylor, J.R., DeVogelaere, A.P., Burton, E.J., Frey, O., Lundsten, L., Kuhnz, L.A., Whaling, P.J., Lovera, C., Buck, K.R., Barry, J.P., 2014. Deep-sea faunal communities associated with a lost intermodal shipping container in the Monterey Bay National Marine Sanctuary, CA. *Marine Pollution Bulletin* 83(1), 92-106.
- Thubaut, J., Puillandre, N., Faure, B., Cruaud, C., Samadi, S. (2013). The contrasted evolutionary fates of deep sea chemosynthetic mussels (*Bivalvia*, *Bathymodiolinae*). *Ecology and Evolution* 3:4748–66
- Thurber, A.R., Sweetman, A.K., Narayanaswamy, B.E., Jones, D.O.B., Ingels, J., Hansman, R.L., (2014). Ecosystem function and services provided by the deep sea. *Biogeosciences* 11 (14), 3941-3963.
- Tietjen, J.H. (1989). Ecology of deep-sea nematodes from the Puerto Rico Trench area and Hatteras Plain. *Deep-Sea Research* 36: 1579–1594.
- Tunnicliffe, V., Embley, R.W., Holden, J.F., Butterfield, D.A., Massoth, G.J., Juniper, S.K. (1997). Biological colonization of new hydrothermal vents following an eruption on Juan de Fuca Ridge. *Deep Sea Research Part I: Oceanographic Research Papers* 44 (9), 1627-1644.
- Van den Hove, S., Moreau, V. (2007). *Deep-Sea Biodiversity and Ecosystems: A scoping report on their socio-economy, management and governance*, UNEP-WCMC Biodiversity Series 28. 88pp.

- Vanhove, S., Vermeeren, H., and Vanreusel, A. (2004). Meiofauna towards the South Sandwich Trench (750–6300m), focus on nematodes. *Deep-Sea Research II* 51: 1665–1687.
- Vinogradova, N. (1959). The zoogeographical distribution of the deep-water bottom fauna in the abyssal zone of the ocean. *Deep Sea Research* (1953) 5 (2), 205-208. Doi: 10.1016/0146-6313(58)90012-1.
- Vinogradova, N.G. (1997). Zoogeography of the abyssal and hadal zones. *Advanced Marine Biology* 32: 326-387.
- Watanabe, H., Fujikura, K., Kojima, S., Miyazaki, J.I., and Fujiwara, Y. (2010). Ch. 12 Japan: Vents and seeps in close proximity. In: Kiel, S., editor. *The Vent and Seep Biota: Aspects from Microbes to Ecosystems*. Springer, Dordrecht, Netherlands, pp. 379-402
- Webb, T., Vanden Berghe, E., and 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. *PLoSOne* 5(8): e10223.
- Wohlers, J., Engel, A., Zöllner, E., Breithaupt, P., Jürgens, K., Hoppe, H.-G., Sommer, U., Riebesell, U. (2009). Changes in biogenic carbon flow in response to sea surface warming. *Proceedings of the National Academy of Sciences of the United States of America* 106, 7067-7072.
- Wolff, T. (1970). The concept of hadal or ultra abyssal fauna. *Deep-Sea Research* 17: 983-1003.
- Wollenburg, J.E., Mackensen, A., and Kuhnt, W. (2007). Benthic foraminiferal biodiversity response to a changing Arctic palaeoclimate in the last 24,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology* 255: 195–222.
- Yamamoto, J., Hirose, M., Ohtani, T., Sugimoto, K., Hirase, K., Shimamoto, N., Shimura, T., Honda, N., Fujimori, Y., and Mukai, T. (2008) Transportation of organic matter to the sea floor by carrion falls of the giant jellyfish *Nemopilema nomurai* in the Sea of Japan. *Marine Biology* 153: 311-317.
- Yancey, P.H., Gerringera, M.E., Drazen, J.C., Rowdenc, A.A., and Jamieson, A. (2014). Marine fish may be biochemically constrained from inhabiting the deepest ocean depths. *Proceedings of the National Academy of Sciences of the United States of America* 111: 4461–4465.
- Yasuhara, M., and Cronin, T.M. (2008). Climatic influences on deep-sea ostracode (Crustacea) diversity for the last three million years. *Ecology* 89(11): S52–S65.
- Yasuhara, M., Cronin, T.M., deMenocal, P.B., Okahashi, H., and Linsley, B.K. (2008). Abrupt climate change and collapse of deep-sea ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 105(5): 1556–1560.
- Yasuhara, M., Hunt, G., Cronin, T.M., and Okahashi, H. (2009). Temporal latitudinal-gradient dynamics and tropical instability of deep-sea species diversity. *Proceedings of the National Academy of Sciences of the United States of America* 106(51): 21717–21720.

- Yasuhara, M., Hunt, G., Cronin, T.M., Hokanishi, N., Kawahata, H., Tsujimoto, A., and Ishitake, M., (2012a). Climatic forcing of Quaternary deep-sea benthic communities in the North Pacific Ocean. *Paleobiology* 38: 162–179.
- Yasuhara, M., Hunt, G., van Dijken, G., Arrigo, K.R., Cronin, T.M., and Wollenburg, J.E. (2012b). Patterns and controlling factors of species diversity in the Arctic Ocean. *Journal of Biogeography* 39: 2081–2088.
- Yasuhara, M., Okahashi, H., Cronin, T.M., Rasmussen, T.L., and Hunt, G. (2014). Deep-sea biodiversity response to deglacial and Holocene abrupt climate changes in the North Atlantic Ocean. *Global Ecology and Biogeography*. Doi:10.1111/geb.12178.
- Yesson, C., Clark, M.R., Taylor, M., and Rogers, A.D. (2011). The global distribution of seamounts based on 30-second bathymetry data. *Deep Sea Research I*. 58: 442–453. Doi: 10.1016/j.dsr.2011.02.004.
- Zeidberg, L.D., and Robison, B.H. (2007). Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *Proceedings of the National Academy of Sciences of the United States of America* 104, 12948–12950.
- Zinger, L., Amaral-Zettler, L.A., Fuhrman, J.A., Horner-Devine, M.C., Huse, S.M., Welch, D.B.M, Martiny, J.B.H., Sogin, M., Boetius, A., and Ramette, A. (2011). Global patterns of bacterial beta-diversity in seafloor and seawater ecosystems. *PLoS ONE* 6(9): e24570.