Chapter 36F Open Ocean Deep Sea

Contributors: Jeroen Ingels (Convenor), Malcolm R. Clark, Michael Vecchione, Jose Angel A. Perez, Lisa A. Levin, Imants G. Priede, Tracey Sutton, Ashley A. Rowden, Craig R. Smith, Moriaki Yasuhara, Andrew K. Sweetman, Thomas Soltwedel, Ricardo Santos, Bhavani E. Narayanaswamy, Henry A. Ruhl, Katsunori Fujikura, Linda Amaral Zettler, Daniel O. B. Jones, Andrew R. Gates, Paul Snelgrove, Patricio Bernal (Lead Member), Saskia Van Gaever (Co-Lead Member)

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. -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^3 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., 2013

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

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 µm–1,000 µm) 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 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 km2, 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-

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 value 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_2 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 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 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 high-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, tuna 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 bathyal species known from adjacent continental margins (See Chapter 5). The biomass of benthic faun4(ro) O5-(2d(n) din)6(e)-m4(e)-1masa(a)1(f3.9(imas)hin)6(e)-4(s)2(

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

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).es ar-2(n)-4(s)2-4(6o)-2

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 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 promi.22 Ty(lo-4(i)-1(

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-

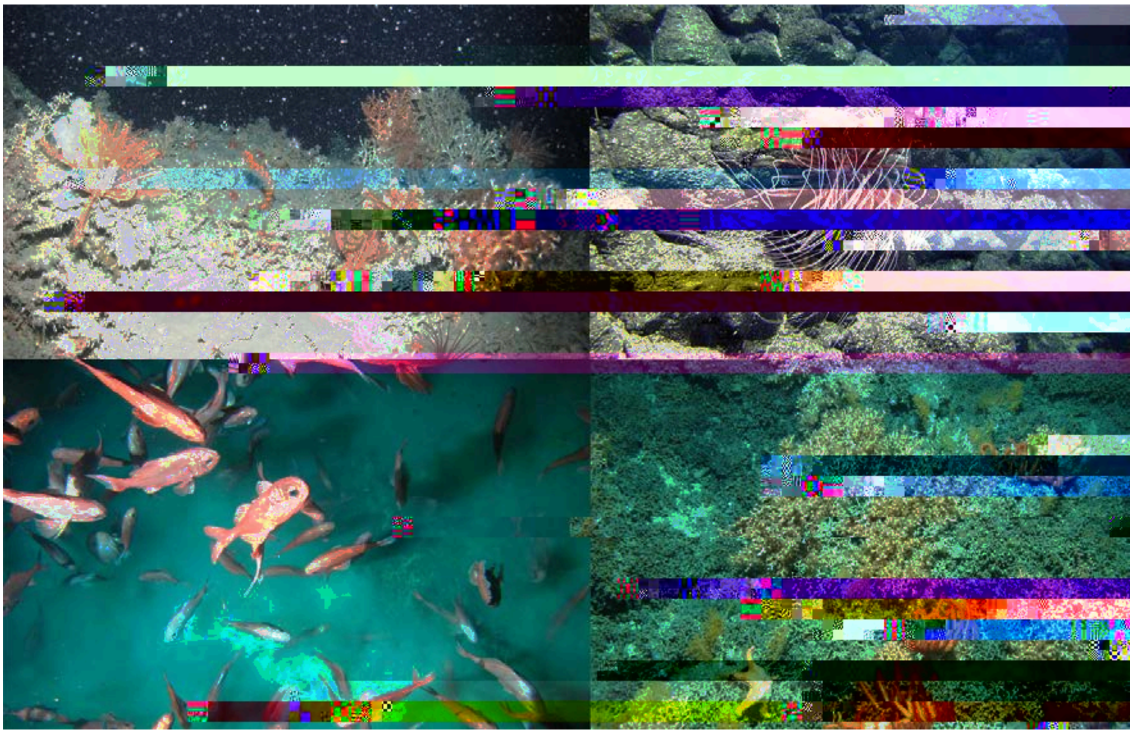

Figure 1. Deep-sea habitats. Top left: coral garden in the Whittard Canyon, NE Atlantic at approx 500 metres depth (2010; image courtesy of Jeroen Ingels); top right: A sea anemone, *Boloceroides daphneae*, on cobalt crust covering a seamount off Hawaii, 1000 metres depth (image courtesy of Chris Kelly, 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

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

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). Deep Water 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. -4(>BDC 0.001 T

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

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. (s.)1( )]

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 46.1((if)-45 twJf)-4pf.):420

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.R. (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.

T28</MCID 3 >>B3 Tw 0.23 0.

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 Calyptogena 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. Senkenbergiana Mar. 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-

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., 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 Monograph 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, [20d [(39(1)T1 078Tc 0 Tw 263j E2d1 2T6.)5

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. PLoS One 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.

g o e a eD Yamamoto, J., Hirose, M., Ohtani, T., Sugimoto, K., Hirase8): e13(,)1(H)4(iraa4(,)11e(e)-104( )

Yasuhara, M., Hunt, G., Cronin, T.M., Hokanishi, N., Kawahata, H., Tsujimoto, A., and Ishitake, M