Current Biology
Magazine

Primer

The deep-sea under global change

Roberto Danovaro[1,2,*],
Cinzia Corinaldesi[1], Antonio Dell'Anno[1],
and Paul V.R. Snelgrove[3]

The deep ocean encompasses 95% of the oceans' volume and is the largest and least explored biome of Earth's Biosphere. New life forms are continuously being discovered. The physiological mechanisms allowing organisms to adapt to extreme conditions of the deep ocean (high pressures, from very low to very high temperatures, food shortage, lack of solar light) are still largely unknown. Some deep-sea species have very long life-spans, whereas others can tolerate toxic compounds at high concentrations; these characteristics offer an opportunity to explore the specialized biochemical and physiological mechanisms associated with these responses. Widespread symbiotic relationships play fundamental roles in driving host functions, nutrition, health, and evolution. Deep-sea organisms communicate and interact through sound emissions, chemical signals and bioluminescence. Several giants of the oceans hunt exclusively at depth, and new studies reveal a tight connection between processes in the shallow water and some deep-sea species. Limited biological knowledge of the deep-sea limits our capacity to predict future response of deep-sea organisms subject to increasing human pressure and changing global environmental conditions. Molecular tools, sensor-tagged animals, *in situ* and laboratory experiments, and new technologies can enable unprecedented advancement of deep-sea biology, and facilitate the sustainable management of deep ocean use under global change.

Biology of extremes

Less than 0.0001% of the deep ocean's area (over 200 meters depth) has been investigated so far, making it the least explored biome of Earth. Indeed, we know the moon's surface better than the deep sea floor. Deep-sea ecosystems encompass a wide range of habitats and environmental conditions, unlike any others on Earth (Figure 1). The effective absence of light beyond 200–500 meters depth precludes photosynthesis and thus greatly limits food availability. Pressures range from 20 to >1100 atmospheres, and temperatures range from –1.8 to 2°C, though fluids emitted at hydrothermal vents may reach 450°C. Compounds toxic to most animals occur in high concentrations in hydrothermal vent fluids (see the Quick guide by William Brazelton in this issue). Some deep-sea habitats can be hypoxic or anoxic.

Despite sometimes very harsh conditions, living organisms occur throughout the water column and all seabed habitats to 11,000 meter depth. Even though microbes dominate deep-sea systems in abundance or biomass, complex multicellular life forms also are found at all depths. Some large shark species, for example, live permanently in the deep, exploring seafloor habitats at almost 4,000 meter depth. Some crustacean species flourish at depths of over 10,000 meters and large invertebrates such as cephalopods are present in the water column and sediments over wide bathymetric ranges (Figure 2). Deep-sea environments are difficult to explore, limiting knowledge on the biology of their inhabitants. Scientists continuously discover new life forms,

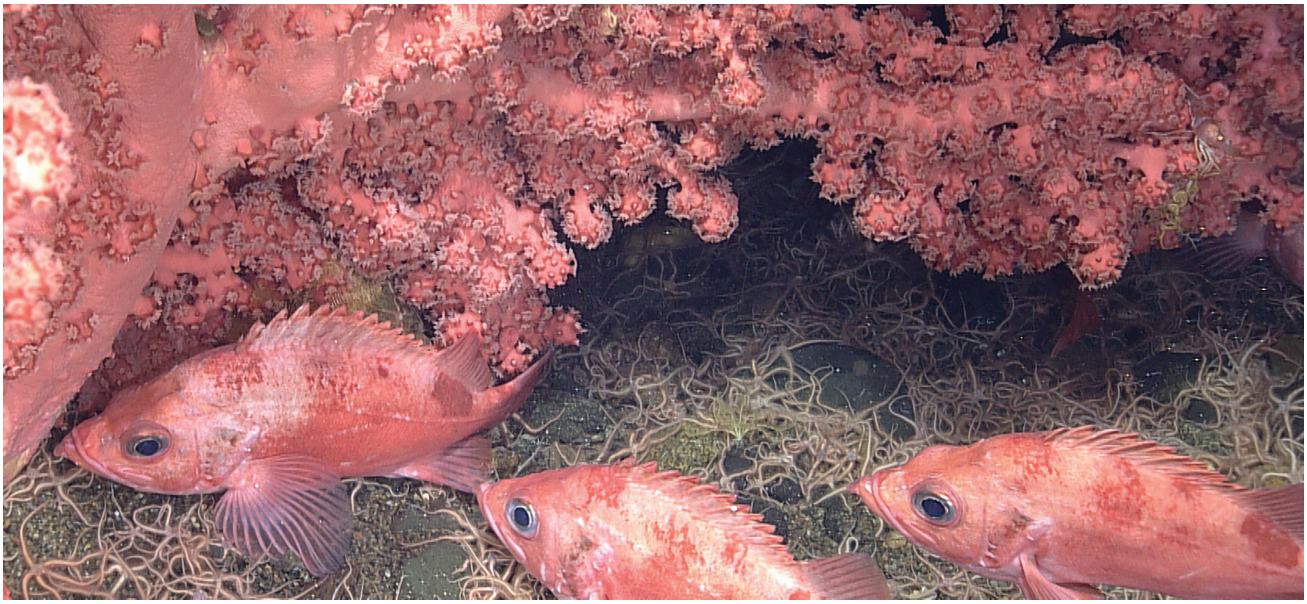

Figure 1. Deep-sea habitat.
Deep-sea habitats host a spectacular variety of seascapes and life forms, spanning from cold-seep habitats and abyssal soft sediments, to hard bottoms and hydrothermal vents. Often these show a complex topography, contributing to the heterogeneity of the deep seafloor. Illustrated is an example of hard bottom, off George's Bank, with gorgonian corals that create complex three-dimensional structures and offer refuge for several deep-sea species, such as redfish, and dense aggregations of brittle stars. (Photo: Peter Lawton, CSSF.)

Figure 2. Deep-sea life.
Most deep-sea organisms are ideal biological models to investigate adaptations to extreme conditions, tolerance to low and high temperatures, and biological processes that support long life spans. Cephalopods are also common in deep-sea ecosystems at abyssal depths and are present is some of the most extreme ecosystems on Earth, such as hydrothermal vents. The photo above illustrates the reaction of an octopus (*Graneledone verrucosa*) to the presence of a camera on the deep seafloor of the Atlantic canyon (Photo: NOC.)

many from novel habitats such as chemosynthetic systems, such as hydrothermal vents and cold-water hydrocarbon seeps, where uniquely adapted species thrive in conditions that would be toxic to most life forms. The deep ocean hosts representatives of almost all animal phyla, and a huge range of sizes, trophic guilds, life cycles, and reproduction strategies. Potentially, as many as 1.5 million species await discovery in the deep (for more on marine biodiversity, see the review by Mark Costello in this issue).

Adaptations, physiology and reproduction

The physiological mechanisms allowing deep-sea organisms to adapt to extreme physical and biological conditions of the deep ocean (high pressures, low to very high temperatures, limited food availability, absence of photosynthesis) remain largely unknown, in large part due to the difficulty in maintaining most deep-sea species in the laboratory. The environmental conditions of most deep-sea ecosystems are remarkably constant and typically change only over geological time scales. For this reason, in tandem with slow growth rates and late maturation, many deep-sea organisms are highly vulnerable to human impacts and to global change.

In contrast to terrestrial ecosystems, life in deep-sea ecosystems depends on external input of organic material produced by photosynthesis in distant surface waters of the oceans. Ephemeral chemosynthetic hotspots fueled by chemical energy offer important exceptions in an otherwise stable environment. Such organic material fuels the food web, dominated in the deep sea by microbial components, primarily bacteria and archaea. Viruses follow next in biomass and dominate in abundance. High microbial abundances in the deep-sea suggest greater relative importance for ecosystem processes than in most environments, and microbial and viral mediation of flux and transformation of chemical energy influences all levels of biological organization. Indeed, the predatory pressure exerted by viruses on deep-sea bacteria and archaea can reduce energy flow to higher trophic levels significantly. However, knowledge of the deep food web remains poor.

Besides chemical energy, ambient temperature strongly influences deep-sea biota. Cold temperatures and little available energy create major metabolic constraints for deep-sea organisms. Below a critical threshold, organisms can maintain basic metabolic processes, but processes such as growth, reproduction, feeding and movement may be reduced. At the same time, deep-sea organisms can exhibit metabolic rates typical of shallow water organisms. Smaller organisms can tolerate temperature shifts better than larger organisms, potentially explaining greater persistence of small species through extinction events. The relative influence of thermal and chemical energy on deep-sea organisms varies considerably across levels of biological organization. Thermal energy apparently strongly influences biological assemblages at microscopic scales, whereas available chemical energy greatly affects processes at macroscopic scales. For instance, nematodes, the numerically dominant metazoans in all deep-seafloor ecosystems, can be particularly sensitive and vulnerable to temperature shifts. Temperature and food availability can greatly impact life span. Some deep-sea species can live to several hundreds of years. Clonal organisms such as the black coral *Leiopathes glaberrima* can live more than 1000 years, but even individual (non-colonial) animals such as the tube worm *Lamellibrachia luymesi* can live up to 600 years, and the Greenland shark up to 400 years. The estimated 11,300 year-old giant sponge collected at 1110 meters depth in the East China Sea is thought to be the oldest animal on Earth. Reproduction is metabolically expensive, and postponing sexual maturation offers one possible mechanism to reduce these metabolic costs; some deep-sea species require many years to reproduce. This delay might explain gigantism in some taxa, which in turn allows these organisms to produce many more gametes. Intriguingly, deep-sea biota also display extraordinarily unbalanced sex ratios. From nematodes to crustaceans to deep-sea sharks, females strongly dominate sex ratios, indicating evolutionary selection that favours investment in oocytes in order to maximize reproductive efforts. Knowledge about symbiotic relationships in the deep ocean is largely confined to associations between metazoans and microbes, in particular, chemosynthetic symbioses that occur ubiquitously at hydrothermal vents, whale falls, cold seeps and mud volcanoes. In such ecosystems, several different lineages of bacteria use a wide range of metabolic pathways to gain energy from the environment and establish symbioses. For example, bacterial utilization of hydrogen sulphide, manganese, iron, hydrogen and methane requires unique adaptations that support important energy pathways. Fungi and other parasites, including new species, have been isolated from deep-sea animals, suggesting a range of poorly known parasitic associations.

Communication and orientation in the deep sea

Deep-sea organisms communicate and interact through sound, chemical and light signals. Most ocean inhabitants live their lives in dim light or darkness. As visible light disappears below 1000 m, bioluminescence is an important survival strategy in darkness for some taxa. Bioluminescence is found in a broad range of organisms from bacteria and protists to fishes, and in numerous invertebrate phyla. In most of these cases, the organisms themselves rather than bacterial symbionts generate light, though some animals do harbor bioluminescent symbiotic bacteria within specialized structures. Bioluminescence generally appears more frequently in deep-sea pelagic organisms than in benthic species. Deep-sea organisms use bioluminescence to find food, attract mates and evade predators. Predator avoidance, perhaps the most common use, occurs in different ways. Some animals, including crustaceans, squid, jellyfish and fish, release light-emitting chemicals into the water, which creates clouds of light to distract or blind their predators. Other animals mark their predators with luminescent slime, making them easy targets for other predators.

Luminescence may also warn predators of un-palatability of prey or provide camouflage, whereby organisms utilize bioluminescence to match the intensity of downwelling light in an attempt to hide their silhouette from predators. This latter use of bioluminescence is common in fishes, crustaceans and squids that inhabit the twilight depths of the ocean, where many predators have upward-looking eyes adapted for locating silhouettes of prey. Improved technologies provide insights on the distribution of bioluminescent organisms in the deep ocean and its relationships with overall biomass and environmental conditions. Increased occurrence of bioluminescent organisms has been reported near carbonate and coral mounds, in eddies and near seamounts. Other studies report a significant increase in bioluminescence associated with the spring peak of primary production in the surface layers. Beyond use as a defense mechanism to disorient predators or to attract potential preys, bioluminescence may also play a role in finding and courting mates.

Movement and orientation are far more difficult in the deep ocean than at shallow depths. The lack of light limits any visual orientation, and pressure differences can limit large migrations. In the deep sea, evolutionary convergence has resulted in generally elongated shapes for most fishes, and short movements and slow swim speed characterize movements at depth. *In situ* observations of the deep-sea squid *Grimalditeuthis bonplandi* reveal that tentacles also move slowly. The absence of jet-propulsion, a characteristic mode of locomotion typically employed by cephalopods, suggests that several behavioural aspects, from mating to predation, effectively occur in slow motion. Although little information exists on how deep-sea organisms utilize deep-water currents, several species clearly move to the upper ocean to exploit increased production associated with upwelling. Daily or seasonal vertical migrations on the order of >1–2 kilometers are well documented in crustaceans and deep-sea fishes, likely to exploit a broad range of bentho-pelagic food resources. Furthermore, tagging of deep-sea sharks demonstrates vertical ascension to shallower depths (from 600 to ~300 meters depth), but no large latitudinal migrations have been documented yet. Tagging studies of whales demonstrate that several species hunt exclusively in the deep, investing most of their search time either in the lower part of the deep scattering layer, where zooplankton accumulate, or near the deep seafloor. Echolocation can help some cetaceans orient in the deep, but perception distances of most species are likely limited to less than two meters. As a consequence, it may take days or weeks to find a mate, and considerably longer for sparsely distributed populations. Mechanisms that increase perception distances (e.g., olfaction) in deep-sea fishes should be particularly effective in enhancing mate location.

Deep-sea biogeography

Biogeographic patterns in deep-sea ecosystems vary strongly, with abundances and biomass of most phyla generally decreasing with increasing depth. Because most organisms in the lightless deep sea depend on sinking organic matter for energy, spatial variation of productivity at the surface strongly influences seafloor abundance and biomass. Circulation around topographic features such as canyons and seamounts often accumulates organic matter and thus creates biomass hotspots. Enhanced sensory structures enable mobile animals to quickly locate and utilize sporadic food sources, such as whale or fish carcasses. Chemoautotrophic habitats, including hydrothermal vents and cold seeps, support particularly high numbers of organisms. Sediments cover much of the seafloor, interspersed with exposed bedrock and other substrata that vary with topography and location. Specialized environments such as vents, seeps, seamounts and canyons support relatively unique faunas and adaptations, adding ‘islands’ of endemic biomes that contribute to a species mosaic in one of the most diverse species pools on Earth.

Size also matters in the deep sea, except that here the small dominate the large because small organisms can survive better on unpredictable and typically limited food. In sediments, meiofaunal and macrofaunal organisms feed on abundant microbes, simultaneously moving water and oxygen between sediment grains and thereby influencing ecosystem functions essential to life on Earth. Collectively, these organisms break down organic matter and regenerate the nutrients necessary to maintain

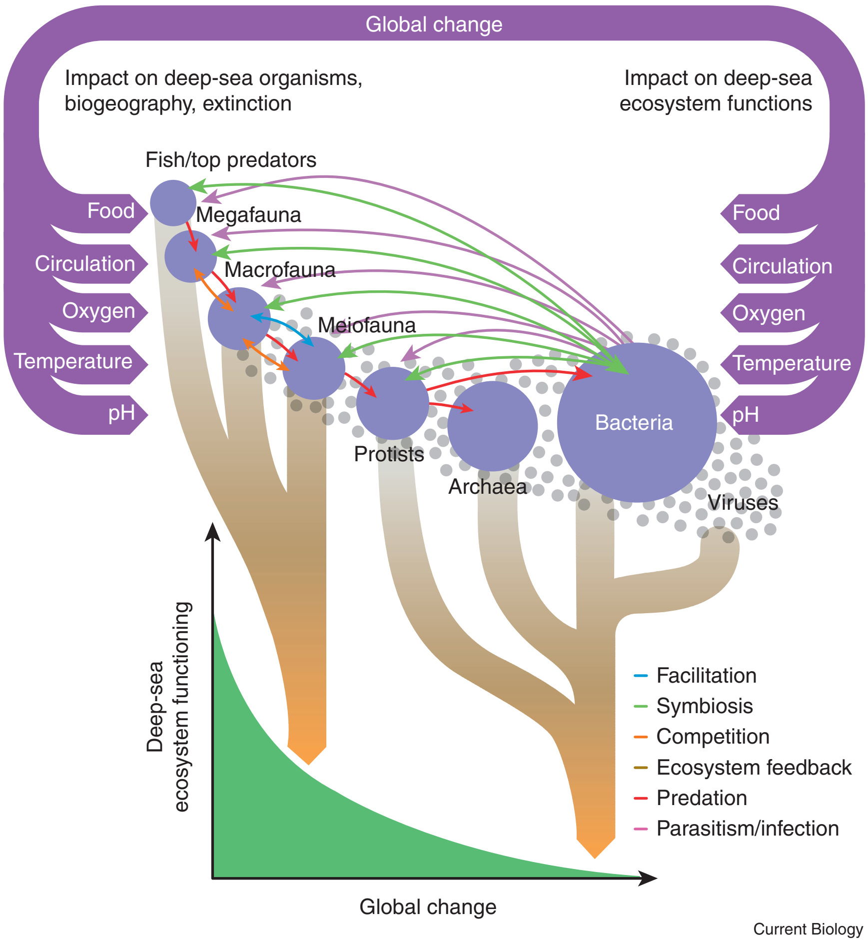

Figure 3. Complex biological interactions in the deep sea, under global change.
The result of the impacts of global change on the biology of single organisms will alter biogeography, demography and extinction rates (among others), whereas the impact on their inter-specific interactions and on microbial components will primarily affect deep-sea ecosystem functions. The size of the different components illustrated provides an idea of their relative importance in terms of biomass (though not to scale).

ocean productivity. The largest organisms, the megafauna, include fixed organisms such as cold water corals and sponges that provide habitat for fishes and smaller invertebrates.

Dispersal varies greatly among taxa, with greater potential for speciation and genetic variation in species with low dispersal capability, as they have a higher probability of remaining genetically isolated. Apart from fishes, most species living on or near the seafloor in the deep are relatively immobile; others disperse mainly through larval stages. Within a seemingly open environment without barriers to dispersal, the low dispersal capacity in taxa such as nematodes that lack a pelagic stage contrasts with the pelagic larvae seen in many polychaetes, molluscs and fishes that may disperse distances of hundreds of kilometers.

The high biodiversity of deep-sea fauna and the lack of obvious isolating barriers raise intriguing questions about how and where new species evolve in this vast, remote and complex ecosystem. Recent population genetic and phylogenetic analyses of deep-water taxa (e.g., gastropods, amphipods, echinoderms, bentho-pelagic fish) document a narrow bathymetric distribution that can potentially limit gene flow, thus leading to divergence population and ultimately speciation at different depths. Low abundances and fecundity of deep-sea organisms result in fewer propagules than in shallow water, potentially reducing realized dispersal and increasing isolation. Rare species further complicate dispersal and reproduction in the deep sea; rare species typically dominate samples from many deep habitats, so that only a single individual may occur in multiple samples (or indeed all samples ever collected). How do such species find mates and persist at such low numbers, do they occur in high abundances elsewhere, and what ecological role do they play? Unfortunately, our understanding of deep-sea dispersal remains limited.

The future of deep-sea biology and conservation

Molecular methods (including DNA barcoding and metagenomics) have revolutionized deep-sea biology, revealing a spectacular diversity of deep-sea animals and microbes (for more, see the review by Patrick Keeling in this issue). Molecular tools have been crucial in the discovery of cryptic deep-sea species and taxonomic synonymies resulting from the phenotypic plasticity of a wide range of taxa. Indeed, genetic analyses of seemingly cosmopolitan species of crustaceans, molluscs, and polychaetes demonstrate multiple cryptic species with much more limited distributional ranges than previously thought, suggesting that we currently overestimate the proportion of cosmopolitan species and underestimate deep-sea species richness. However, despite the significant advances provided by molecular tools, current technological constraints (such as non-appropriate genetic markers, limited coverage of databases, lack of situ molecular analyses) limit the knowledge of deep-sea biogeography, biodiversity and functioning. Expanding our knowledge of deep-sea biology, and identifying optimal or comprehensive strategies for its conservation given alterations resulting from human induced pressures, will require further technological and methodological developments. The availability of sophisticated technologies enables novel *in situ* deep-sea experiments and increasingly complex ecological manipulations, accelerating understanding of deep-sea biological response to global change and multiple stressors. Pressure vessels can transport organisms from the seafloor to the surface for manipulative experiments, at a time when molecular tools offer novel insights into connectivity questions. Extreme environmental conditions (pressure, salt, low (or high) temperatures, lack of light) combined with remote location create a need for novel sampling platforms spanning from autonomous underwater vehicles (AUVs) to fixed cables to ocean gliders to moving animals equipped with novel environmental or physiological sensors ('biologgers'). Remotely operated vehicles and landers can deploy experimental chambers to investigate faunal response to ongoing changes in physical and biological variables. Collectively these new approaches can support breakthroughs in understanding the most widespread and pristine ecosystem on Earth, with wider application of those tools for science and society.

Human impacts and global change in the deep-sea

The long-lived, late reproducing, and low fecundity life histories of many deep-sea organisms increase vulnerability to multiple human pressures and global climate change. Low rates of replacement result in extreme sensitivity to fishing pressure, and weak currents and the absence of wave action result in sometimes fragile organisms that are easily damaged by bottom-contact fishing gear, which now penetrates to thousands of meters depth. The Deepwater Horizon blowout in the Gulf of Mexico clearly demonstrated not only the increasing range of environments in which extraction occurs, but also the ecological ramifications of major blowouts for deep-sea fauna. Deep-sea mining, while still in its infancy, necessarily destroys habitat, whether it concerns extracting polymetallic sulphides at hydrothermal vent chimneys, cobalt rich crusts from seamounts, or manganese nodules from abyssal sediments. But the global footprint of climate change represents the single greatest concern regarding human impacts on ocean environments, largely through indirect effects.

Available projections suggest that by 2100, temperatures at abyssal depths (3000–6000 m) could increase by 1°C and contribute to reductions in water-column oxygen concentrations. Values of pH will show the most significant reduction at bathyal depths (from 0.29 to 0.37 pH units) and O_2 concentrations will decline for up to 3.7% or more, together with reduced flux of organic matter to the seafloor. Because most deep-sea environments depend largely on surface production, climate change effects on surface processes will alter deep-sea ecosystems globally with evidence of change already happening (Figure 3). Such changes can significantly affect the growth rates, survival and recruitment of deep-sea organisms with severe consequences for potential recovery of deep-sea assemblages compounded by other effects of human activities listed above. These consequences can compromise the success of restoration actions in deep-sea ecosystems affected by different anthropogenic pressures. At the same time, the projected increase in temperature and decrease in oxygen and pH in the deep ocean under present climate change scenarios could have additional detrimental impacts on the metabolism of deep-sea organisms, which appear more sensitive than shallow-water counterparts to any change in environmental conditions. Of course, the response of deep-sea life to global changes will depend on the ability of these organisms to adapt (rapidly) to altered conditions and to maintain their biological interactions with other living components. This is the reason why we should make a special effort to expand the knowledge of their biology, from their physiology and symbiotic interactions, to the factors controlling food webs and the dispersal of deep-sea organisms. The additive effects of human pressures and global climate change are still almost completely unknown and can be addressed only by increasing knowledge on basic and system biology of deep-sea ecosystems, and through better understanding of the complex biological interactions that enable their efficient functioning. Given the extreme features of the deep ocean, deep-sea biology is thus a discipline increasingly oriented to the investigation of some of the most challenging, complex and intriguing aspects of ocean life.

FURTHER READING

Breusing, C., Biastoch, A., Drews, A., Metaxas, A., Jollivet, D., Vrijenhoek, R.C., Bayer, T., Melzer, F., Sayavedra, L., Petersen, J.M. *et al*. (2016). Biophysical and population genetic models predict the presence of "phantom" stepping stones connecting Mid-Atlantic Ridge vent ecosystems. Curr. Biol. *26*, 2257–2267.

Brown, A., and Thatje, S. (2014). Explaining bathymetric diversity patterns in marine benthic invertebrates and demersal fishes: physiological contributions to adaptation of life at depth. Biol. Rev. 89, 406–426.

Danovaro, R., Gambi, C., Dell'Anno, A., Corinaldesi, C., Pusceddu, A., Neves, R.C., and Kristensen, R.M. (2016). The challenge of proving the existence of metazoan life in permanently anoxic deep-sea sediments. BMC Biol. 14, 4.

Danovaro, R., Snelgrove, P.V.R., and Tyler, P. (2014). Challenging the paradigms of deep-sea ecology Trends Ecol. Evol. 29, 465–475.

Danovaro, R., Dell'Anno, A., Corinaldesi, C., Rastelli, E., Cavicchioli, R., Krupovic, M., Noble, R.T., Nunoura, T., and Prangishvili, D. (2016). Virus-mediated archaeal hecatomb in the deep seafloor. Science Adv. 2, e1600492.

Danovaro, R., Canals, M., Tangherlini, M., Dell'Anno, A., Gambi C., Lastras G, Amblas, D., Sanchez-Vidal, A., Frigola, J., Calafat, A.M., *et al*., (2017). A submarine volcanic eruption leads to a novel microbial habitat. Nat. Ecol. Evol. *1*, 0144, http://dx.doi.org/10.1038/s41559-017-0144.

Drazen, J.C., and Sutton, T.T. (2017). Dining in the deep: the feeding ecology of deep-sea fishes. Annu. Rev. Mar. Sci. *9*, 337–366.

Easton, E.E., and Thistle, D. (2016). Do some deep-sea, sediment-dwelling species of harpacticoid copepods have 1000-km-scale range sizes? Mol. Ecol. *25*, 4301-4318.

McClain C.R., and Hardy S.M. (2010). The dynamics of biogeographic ranges in the deep sea. Proc. R. Soc. B. 277, 3533–3546.

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., *et al*. (2010) Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. Biogeosciences 7, 2851–2899.

Smith K., and Thatje, S. (2012). The secret to successful deep-sea invasion: does low temperature hold the key? PLoS One 7, e51219.

Sweetman, A.K., Thurber, A.R., Smith, C.R., Levin, L.A., Mora, C., Wei, C-L., Gooday, A.J., Jones, D.O.B., Rex, M., Yasuhara, M. *et al*. (2017). Major impacts of climate change on deep-sea benthic ecosystems. Elem. Sci. Anth. *5*, 4. http://dx.doi.org/10.1525/elementa.203.

Van Dover, C.L., German, C.R., Speer, K.G., Parson, L.M., and Vrijenhoek, R.C. (2002). Evolution and biogeography of deep-sea vent and seep invertebrates. Science *295*, 1253–1257.

Wentrup, C., Wendeberg, A., Schimak, M., Borowski, C., and Dubilier, N. (2014). Forever competent: deep-sea bivalves are colonized by their chemosynthetic symbionts throughout their lifetime. Env. Microbiol. *16*, 3699–3713.

Woolley, S.N., Tittensor, D.P., Dunstan, P.K., Guillera-Arroita, G., Lahoz-Monfort, J.J., Wintle, B.A., Worm, B., and O'Hara, T.D. (2016). Deep-sea diversity patterns are shaped by energy availability. Nature *533*, 393–396.

[1]Department of Life and Environmental Sciences, Polytechnic University of Marche, Italy. [2]Stazione Zoologica Anton Dohrn Naples, Italy. [3]Departments of Ocean Sciences and Biology, Memorial University of Newfoundland. St, John's NL AIC 5S7, Canada.
*E-mail: r.danovaro@univpm.it