

Challenging the paradigms of deep-sea ecology

Roberto Danovaro^{1,2*}, Paul V.R. Snelgrove^{3*}, and Paul Tyler^{4*}

¹ Stazione Zoologica Anton Dohrn, Villa Comunale Napoli, 80121, Italy

² Department of Life and Environmental Sciences (DiSVA), Polytechnic University of Marche, Via Brecce Bianche, 60131 Ancona, Italy

³ Ocean Sciences Centre and Biology Department, Memorial University of Newfoundland, St. John's, NL, A1C 5S7 Canada

⁴ Ocean and Earth Science, University of Southampton, NOC, Southampton SO14 3ZH, UK

Deep-sea ecosystems represent Earth's major ecological research frontier. Focusing on seafloor ecosystems, we demonstrate how new technologies underpin discoveries that challenge major ecological hypotheses and paradigms, illuminating new deep-sea geosphere–biosphere interactions. We now recognize greater habitat complexity, new ecological interactions and the importance of 'dark energy', and chemosynthetic production in fuelling biodiversity. We also acknowledge functional hotspots that contradict a food-poor, metabolically inactive, and minor component of global carbon cycles. Symbioses appear widespread, revealing novel adaptations. Populations show complex spatial structure and evolutionary histories. These new findings redefine deep-sea ecology and the role of Earth's largest biome in global biosphere functioning. Indeed, deep-sea exploration can open new perspectives in ecological research to help mitigate exploitation impacts.

Deep-sea investigations: from the past to the future

Compared to more familiar terrestrial or coastal environments, the deep sea, defined here as environments beyond continental shelf depths (≈ 200 m), encompasses many extremes on Earth, with an average depth of approximately 4.2 km, near total darkness, average temperatures $< 4^\circ\text{C}$, and average hydrostatic pressure of 400 atm. The lack of sunlight negates net photosynthetic primary production deeper than ≈ 200 m, further challenging the functioning of deep-sea systems. The deep sea also includes Earth's largest hypoxic (see [Glossary](#)) and anoxic environments (e.g., oxygen minimum zones, Black Sea). Researchers have documented life everywhere in the deep sea, with active metabolic life from -2°C to $> 150^\circ\text{C}$, even in sediments at 10 000 m depth and microbial life at 1000 m below the seafloor [1,2].

Although the 'heroic age' of deep-sea exploration established universal occurrence of a metazoan deep-sea fauna, high biodiversity was only recognized and quantified in the

1960s, first using semiquantitative anchor dredges and epibenthic sledges [3], and subsequently using box corers [4]. The application of submersibles to scientific and biological investigations enabled the discovery of hydrothermal vents [5] and seeps [6], the first manipulative experiments, the testing of ecological hypothesis in the deep sea [7], the use of videos and still imagery to document life in trenches, along with other advances aided by hybrid remotely operated vehicles (ROVs), bottom crawlers, and landers (Table 1).

Past exploration generated many paradigms, often drawing on information constrained by available measurements and technology [8,9], but the past decade has seen spectacular expansion in capability (see Figure 1A in Box 1).

Glossary

Abyssal: ocean floor depths from 3000 to 6000 m.

Bathyal: ocean floor depths of 200–3000 m, includes the continental slope.

Benthic: living in or on the aquatic seafloor. An operational classification based on sieve sizes used when sampling sediments subdivides benthos into megabenthos visible in bottom photographs or video (e.g., crabs, fish), macrobenthos $> 300\ \mu\text{m}$ (e.g., polychaete worms, small clams), and meiobenthos that pass through a 250–500- μm sieve but are retained on a 20–30- μm sieve (e.g., nematodes, copepods).

Beta diversity: rate of turnover of species across habitats, ecosystems, or an environmental gradient.

Bioirrigation: any form of enhanced solute transport that results from sediment reworking by organisms.

Bioturbators: organisms that enhance dispersal of particles by reworking sediment, typically by burrowing.

Chemoautotrophs: organisms capable of carbon fixation via chemical energy, typically via sulfide oxidation or methane oxidation.

Continental margin: ocean floor that separates the thin oceanic crust from the thick continental crust, and comprised of the continental shelf, continental slope, and continental rise.

Diagenesis: physical and chemical changes occurring during the conversion of sediment to sedimentary rock.

Ecosystem engineers: organisms or structures produced by organisms that alter substrate, flow regime, geochemical setting, food supply, or predation pressure for associated organisms.

Eurybathic: organisms able to occupy a wide range of depths.

Hadal: ocean depths 6000–11 000 m, the deepest areas of the ocean.

Hypoxic: low oxygen conditions (in the deep sea, oxygen concentrations of 22 mM, 0.5 ml/l, or $< 10\%$ saturation).

Lecithotrophic: non-feeding developmental mode (water column and/or benthic), relying on energy sources of maternal origin (e.g., a yolk sac).

Metagenomic: the study of nucleic acids from a given source, including environmental samples.

Planktotrophic: actively feeding and free-swimming developmental mode within the water column.

Remineralization: the process of degrading organic material.

Swath: multichannel echosounders giving a 3D image of the seabed.

Corresponding author: Danovaro, R. (r.danovaro@univpm.it).

Keywords: deep-sea ecology; ecological paradigms; biodiversity hot spots; ecosystem functioning.

*All authors contributed equally to this work.

0169-5347/

© 2014 Elsevier Ltd. All rights reserved. <http://dx.doi.org/10.1016/j.tree.2014.06.002>

Table 1. A history of discovery and development in the deep-sea benthos

Decade	Discovery and development	Refs
1960s	First quantitative data High deep-sea diversity	[71]
1970s	Hydrothermal vents Slow colonization of deep sea Discovery of depth diversity gradient	[5] [72] [73]
1980s	Understanding chemosynthesis, seeps Major flux events to seafloor (phytoplankton, whale falls) Seasonality Benthic storms	[6,74] [19] [75]
1990s	Rapid growth of deep-sea barnacles Global diversity estimates Discovery of latitudinal gradient of diversity Origin of deep-sea latitudinal gradient Identifying prokaryotic life in the deep subfloor biosphere Application of molecular techniques	[76] [4] [77] [78] [1] [79]
2000s	Recognition of Archaea as an important domain in the deep sea Relevance of the rare microbial biosphere Active microbial life in deep and subfloor sediments Recognition of viruses in deep-sea ecosystem functioning New insight in deep-sea biogeography and biodiversity Deep-sea metazoans living in permanently anoxic conditions Census of Marine Life (CoML) and Global Update of the Marine Species List and Development of GIS applications for habitat mapping Impact of climate change on deep-sea ecosystems	[80,81] [63] [33] [10] [62] [64] Completion of the CoML project [82–84]
2010 to present	Application metabolic energetic theory Extensive application of new molecular techniques and massive sequencing across biological domains New estimates of global marine biodiversity Digital revolution allowing mass observation in high definition Novel submersibles, hybrid ROVs, bottom crawlers, landers	[42] [57] [56,85]

Broader application of submersibles and the subsequent development of ROVs and autonomous underwater vehicles (AUVs), fiber optic communications, and novel imaging tools facilitated quantitative sampling of difficult-to-sample (e.g., canyons, seamounts, slumps, outcrops) and newly discovered habitats (pockmarks, brine pools, and domes). New molecular technologies fundamentally changed appreciation of biodiversity, particularly for microbes and cryptic species. New sensors and *in situ* technologies revealed new forms of life in every remote deep-sea habitat. Recent deep-sea studies contradict current ecological paradigms by illustrating new relationships between biodiversity and ecosystem functioning that point to the importance of diversity in sustaining the largest biome of the biosphere [10]. In short, deep-sea ecology has entered a new ‘golden age’ of discovery and raised new scientific questions. These recent discoveries challenge the prevailing view and current ecological paradigms for deep-sea ecosystems, which we revisit in order to propose new challenges and priorities for future deep-sea research.

Challenging deep-sea habitat paradigms: expanding the concept of topographic complexity

The British Royal Navy began to expand coastal exploration into deeper waters by the 19th century as they searched for the Northwest Passage; laying the first trans-Atlantic cable in 1857 required line soundings across the Atlantic that recognized a continental slope, abyssal plain, and the mid-ocean mountain chain (Mid-Atlantic Ridge). Subsequent cruises documented sills, seamounts (now estimated from 30 000 to >100 000 globally) and

trenches (see [Figure IB](#) in [Box 1](#)). The advent of echosounding in 1923 expedited depth data acquisition that accumulated rapidly after 1945, paving the way for the first global map of deep-ocean basin complexity. Geophysics in the 1970s predicted convective heat loss from the mid-ocean ridges, leading to the discovery of hydrothermal vents and their associated fauna along the Galapagos Rift in 1977 [5], followed by cold seeps in the 1980s on continental margins (see [Figure IB](#) in [Box 1](#)). That same decade saw swath bathymetry and submersibles and/or ROVs enable discovery of deep-water (cold-water) coral reefs previously known only from scattered coral specimens dredged from depth.

Current technologies facilitating deep-sea research

The refinement of multibeam acoustics and related technologies now facilitate habitat discovery by providing high resolution bottom topography that identifies not only seamounts, canyons, landslides, and other important topographic features of the seafloor but also small, highly heterogeneous, complex structures (that include some of the most extreme sub-ecosystems on Earth, [Box 2](#)), and even smaller structures, on a scale of meters or less (including furrows, pock marks, blocks) [11,12].

Habitats created by ecosystem engineers, such as sponge and xenophyophore fields, and deep-sea coral banks [13] further complement these structures. Seepage of different materials creates a huge variety and number of topographic features by altering sediment texture, seafloor 3D structure, and by influencing species composition (e.g., mud volcanoes, pinnacles, domes). Scientists increasingly recognize the deep sea as a highly complex and heterogeneous landscape of contrasting habitats that all add to a

rich and largely undocumented species pool [9,12,14]. By integrating different tools and habitat mapping, deep-sea ecologists now recognize a mosaic of heterogeneous ecosystems at multiple spatial scales.

Re-evaluating the spatial extent of deep-sea ecosystems

By simply analyzing bathymetric data in 200-m increments between 200 and 6000 m (GEBCO, BODC 2003) in a GIS Manifold System, we conservatively estimate a global deep seafloor area of 434 386 264 km². This estimate alone increases previous orthogonal projections by some 20% ($\approx 361\,254\,000$ km²), but specific smaller-scale topographic features require further upward re-evaluation of the actual extent of deep seafloor. Habitat mapping and improved knowledge of deep-sea topographic features at different spatial scales will facilitate a better understanding of the

relevance of these structures in driving deep-sea biodiversity and will provide new insights for defining high-sea protected areas [15] for the preservation of deep-sea biodiversity and ecosystem functioning.

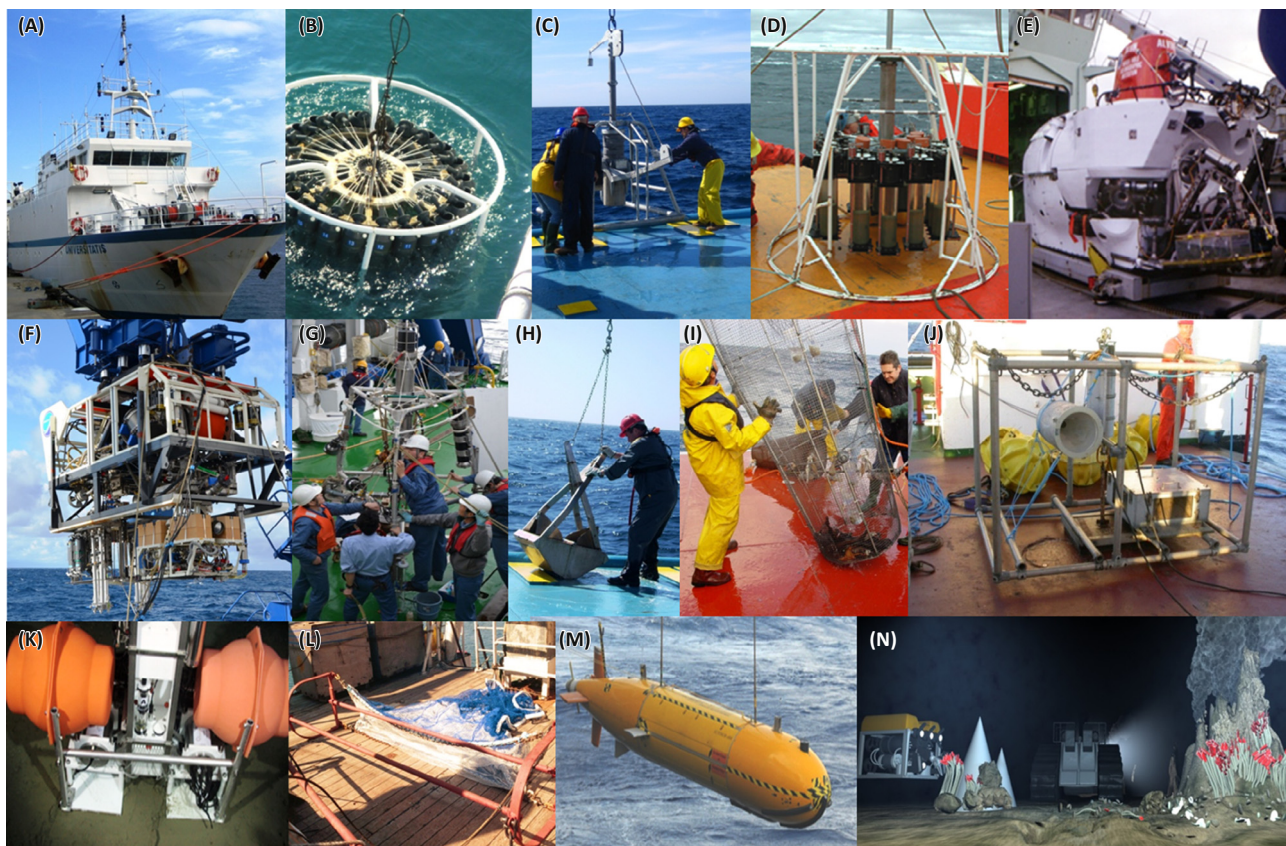
Challenging paradigms on deep-sea energetics: food poor or food rich?

Allochthonous and autochthonous sources contribute organic energy to the deep sea where heterotrophic life depends heavily on export of organic particles from the euphotic zone. Of ≈ 48.5 to 54 PgC/year marine surface primary production, only 0.2 to 0.79 PgC/year ($\approx 1\%$) is buried in marine sediments [16,17]. Heterotrophs recycle organic matter efficiently, recycling and/or consuming most primary production before it reaches the deep-sea floor. This observation supported the long-held paradigm

Box 1. An array of habitats, an array of tools

The past decade in particular has seen rapid expansion of tools (Figure I) to sample the deep ocean, leading to discoveries of new habitats [13]. The intricate and heterogeneous habitat distribution of

the deep ocean is now increasingly evident owing to the application of novel technologies [11,86,87]. Figure II illustrates the known distributions of some of these habitats.



TRENDS in Ecology & Evolution

Figure I. Technological developments enabling deep-sea investigations. Shown are: (A) a large research vessel necessary for open ocean research and handling of large instrumentation; (B) a rosette sampler with probes for measurements *in situ* and pumps for collecting water, inorganic particles, and plankton from any depth in the water column; (C) a large oceanic box corer with the ability to collect a large sediment surface to investigate the biodiversity of deep-sea macrofauna; (D) a large multiple corer for obtaining undisturbed sediment samples to investigate meiofauna and smaller benthic components; (E) the submersible Alvin used for observation and seabed experimentation; (F) a remotely operated vehicle (ROV) with high definition video, high precision telemetry, real-time control and sampling, which is becoming the main workhorse of *in situ* deep-sea biology programs; (G) a benthic lander deployed to investigate sediment community oxygen consumption (SCOC); (H) a large grab with video camera for sampling in the upper open slope; (I) a large baited cage deployed on the deep-sea floor to catch large epibenthic megafauna and predators (such as the Portuguese dogfish, in the bottom of the cage); (J) a lander amphipod trap, baited with dead fish to attract the mobile scavenging fauna; (K) a ROV-deployed SCOC measurement device placed on the seabed; (L) an Agassiz trawl used for decades and still in use today for large samples of megafauna and some epibenthic fish; (M) the autonomous underwater vehicle Autosub deployed independently of the mother ship and programmed to cover a specified area of seabed or water column; (N) future vision of exploited deep-sea habitat and of their possible restoration using ROVs.

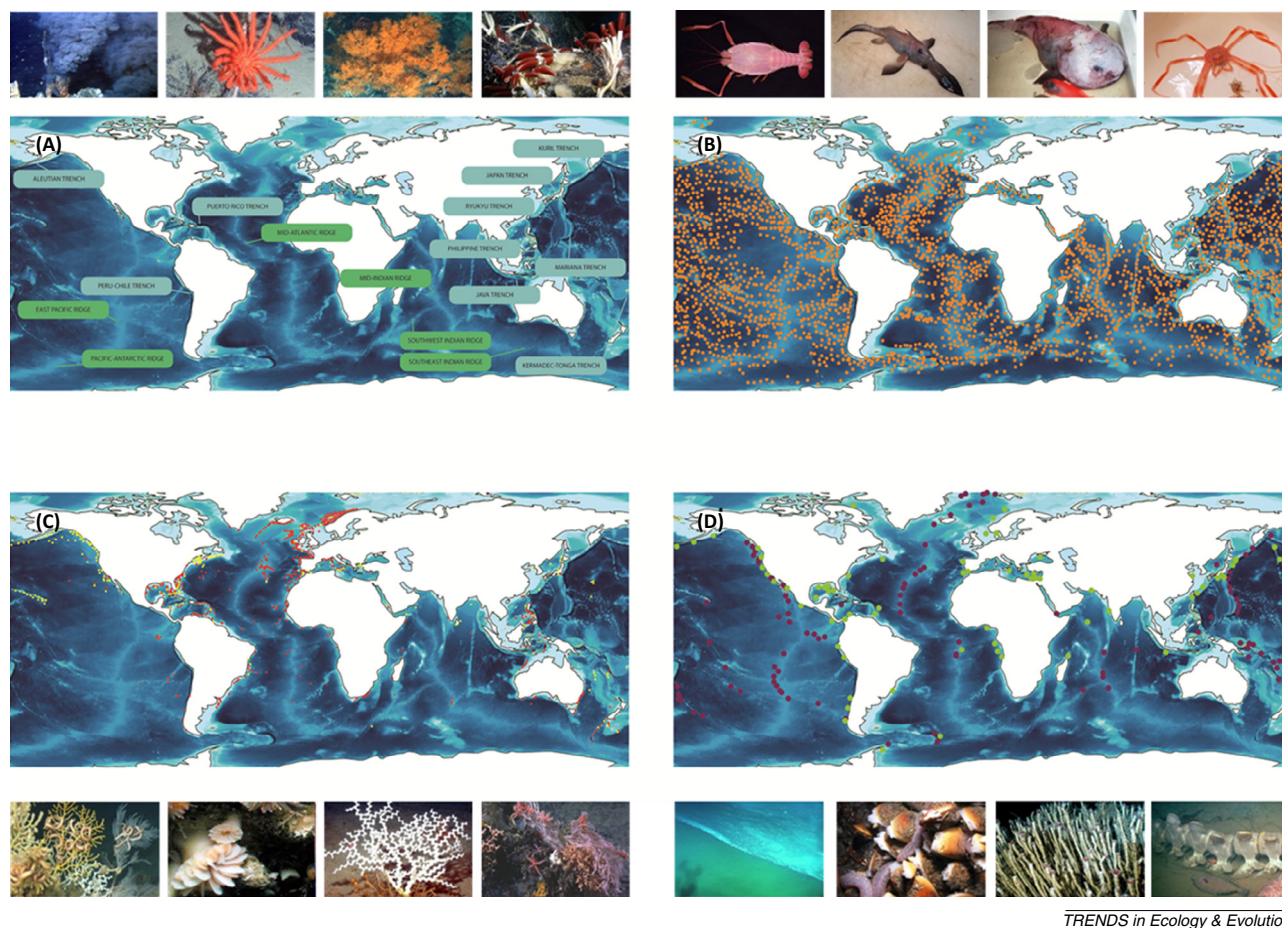


Figure 11. (A) The distribution of the main tectonic structures, the mid-ocean ridges (MORs), the abyssal plains, and the subduction zones (trenches). (B) Distribution of the many thousands (>30 000) of seamounts in the global ocean. (C) Distribution of canyons and cold-water corals on the continental margins of the global ocean. (D) Distribution of hydrothermal vents and cold seeps (including known mud volcanoes along both active and passive margins). Small images reported around each map provide examples of the habitat features and/or organisms characterizing the ecosystems illustrated.

of a food-poor environment [18]. However, although oligotrophy apparently characterizes most deep-sea sedimentary environments, time-lapse photography has demonstrated rapid and massive phytodetritus export from surface waters to the sedimentary deep-sea floor at 4000 m in 40 days [19]. These events deliver high quality, fresh organic material with important consequences for abundance, biomass, biodiversity, metabolism, and distribution of deep-sea species. Researchers have long debated whether these events are highly episodic and limited to short time scales, or occur more frequently. But what proportion of organic material delivered to the deep sea arrives through vertical versus lateral flux? Clear evidence shows that lateral advection delivers much of the organic flux on continental margins [20] with massive and frequent down-canyon transport [21]. These processes explain the absence of consistent trends in sediment organic matter with increasing depth in most systems (Figure 1), and organic matter depocenters at hadal depths [22]. Indeed, despite enormous hydrostatic pressure and cold temperatures these environments can support benthic abundances and biomasses that rival, or exceed, coastal systems [23,24]. In short, some deep-sea areas are eutrophic (i.e., rich in organic carbon and food for

consumers), fundamentally challenging our view of food- and energy-poor conditions in deep-sea ecosystems.

Vents and seeps represent hot spots of biomass, production, and adaptation (through symbioses with prokaryotes that convert hydrothermal fluid or hydrocarbons into organic matter) [25] (Box 3). These chemosynthetically-based ecosystems defy the general rule of food depletion that characterizes most of the dark ocean (e.g., bathyal and abyssal plains) and fundamentally change our view of biomass-poor deep-sea ecosystems [26,27].

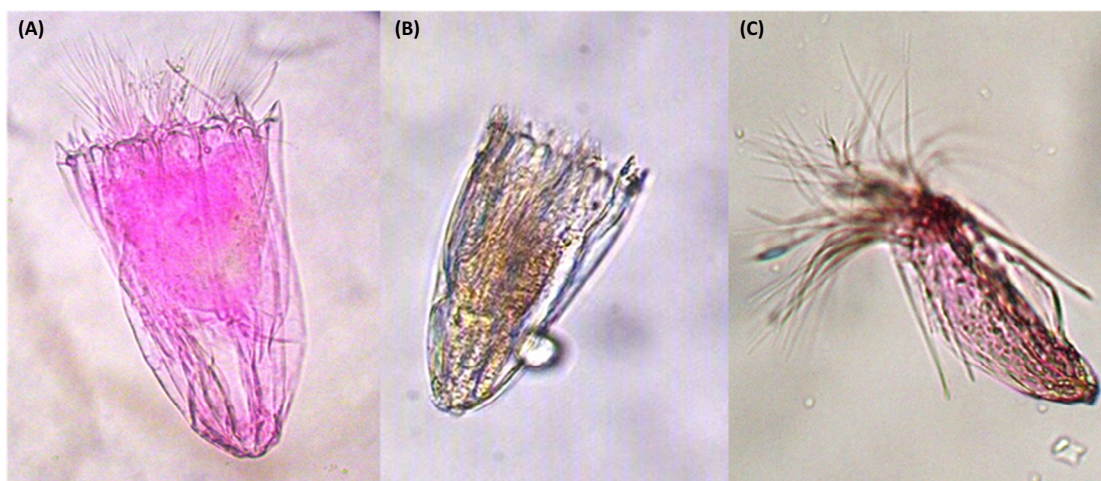
In the past, we quantified food availability to the benthos simply by measuring bulk organic matter, or characterizing its composition in detail but without considering the importance of food bioavailability to consumers [26,27]. In systems rich in organic matter, rapid transformation of organic molecules, and particularly biopolymers, leads to complexation processes that produce high molecular weight compounds (e.g., humic and fulvic acids) that consumers cannot digest easily. For detritus feeders, a potentially 20–50% digestible fraction in deep-sea sediments compares favorably with the 5–15% digestible fraction reported for most continental shelf sediments [26].

Therefore, the higher palatable deep-sea fraction might significantly offset the low overall quantity of

Box 2. Life in ultra-extreme systems

Along with the typical conditions of most deep-sea areas (high pressure, low temperatures, lack of solar light), some systems display a scarcity or complete lack of free oxygen, low pH, and extremely high salinity. Others display high H₂S and heavy metal concentrations. Oxygen minimum zones (between 200 and 1500 m depth) host prokaryotes, metabolically active protozoa, and a specialized fauna with the ability to cope with oxygen limitation [88]. Deep hypersaline anoxic basins (DHABs) of the Mediterranean Sea, Red Sea, and Gulf of Mexico combine high hydrostatic pressure, absence of light, anoxia, and sharp chemoclines with salt concentration near saturation (e.g., DHABs), placing these systems among the most extreme habitats on Earth [89]. Samples from 3200 to 3600 m depth in these extreme habitats of the Mediterranean revealed active prokaryotic life, dominated by bacteria in some basins and Archaea in others, together with a rich assemblage of viruses [89]. The isolation of microbes in anoxic basins with distinct geochemical conditions could have resulted in the evolution of specific microbial communities. In some basins, DNA sequencing suggests protozoan

presence [90]. Observations of metazoans in perfect condition in the anoxic deep Black Sea have generated ongoing debate whether these are highly adapted taxa or cadavers exported from oxygenated surface waters. The recent discovery of metazoans that live their entire life in anoxic conditions challenges the accepted view that all multicellular life forms require free oxygen. Three new species of the animal phylum Loricifera reported from the L'Atalante basin [64] (Figure 1) were metabolically active with specific adaptations to the extreme conditions in this basin, including replacement of mitochondria by hydrogenosome-like organelles and the presence of endosymbiotic prokaryotes. The presence of metazoans in anoxic conditions could have important consequences for rates and biogeochemical processes in these systems, given their ability to behave either as detritus consumers and/or microbial predators, thus potentially shaping their composition. Collectively, these examples illustrate the importance of even the most extreme habitat to some species and potential biological novelty in new adaptations from newly discovered habitats.



TRENDS in Ecology & Evolution

Figure 1. An example of different species of deep-sea Loricifera living in permanently anoxic conditions in a deep, hypersaline anoxic basin of the Mediterranean Sea. These multicellular organisms spend their entire life cycle in the absence of free oxygen. Reported are: (A) *Spineloricus cinziae* (novel species) stained with rose bengal; (B) the same species unstained; (C) *Pliciloricus* sp. (novel species not yet described).

organic carbon observed in many deep-sea sediments, reducing differences from their shallow counterparts [27]. Indeed, optimal foraging theory suggests that selective deep-sea consumers could find quality food sources more easily than their shallow water counterparts (Box 4). In addition, symbionts of the bivalve *Xylophaga* and of amphipod guts, which allow digestion of cellulose in sunken wood, as well as those of bone-boring *Osedax* that allow digestion of refractory compounds, make possible the exploitation of food sources that would otherwise be unavailable.

Current information (see Figure 1 in Box 4) indicates that several types of deep-sea ecosystems (including hydrothermal vents and cold seeps) and a potentially important portion of the deep-sea biome are less food limited than previously thought, requiring significant revision of the past ecological paradigm of a 'deep-sea on a perpetual diet' [18].

Challenging and re-evaluating the role of the deep sea in global carbon cycling

The ocean interior and surface sediments of the deep-sea floor can be enormous bioreactors of organic matter cycling

[22,28]. In oxygenated regions, rapid diagenesis of organic material regenerates inorganic nutrients needed for primary production. Microbes and macroorganisms both add significantly to these molecular-scale processes. Bioturbation and bioirrigation by benthic organisms largely control remineralization of sedimentary organic matter and recycling of many elements [16]. The importance of microbial life forms relative to other seafloor components increases at greater depths to more than 80–90% of total benthic biomass (Figure 1B) so that microbes inhabiting deep-sea sediments control the global cycling of carbon, nitrogen, silica, and iron. However, the largely unknown contribution of the ocean interior to global biogeochemical processes limits our understanding of the global carbon and other cycles. Moreover, our conceptual view of the relative importance of organic carbon sources in the deep sea continues to evolve. Export from the photic zone of photosynthetic biomass and large and small animal carcasses (e.g., salps) represent important sources of organic matter for the deep-sea floor, but fisheries removal of most large vertebrates, from fishes to mammals, has reduced delivery of these food parcels to the deep-sea floor. In addition,

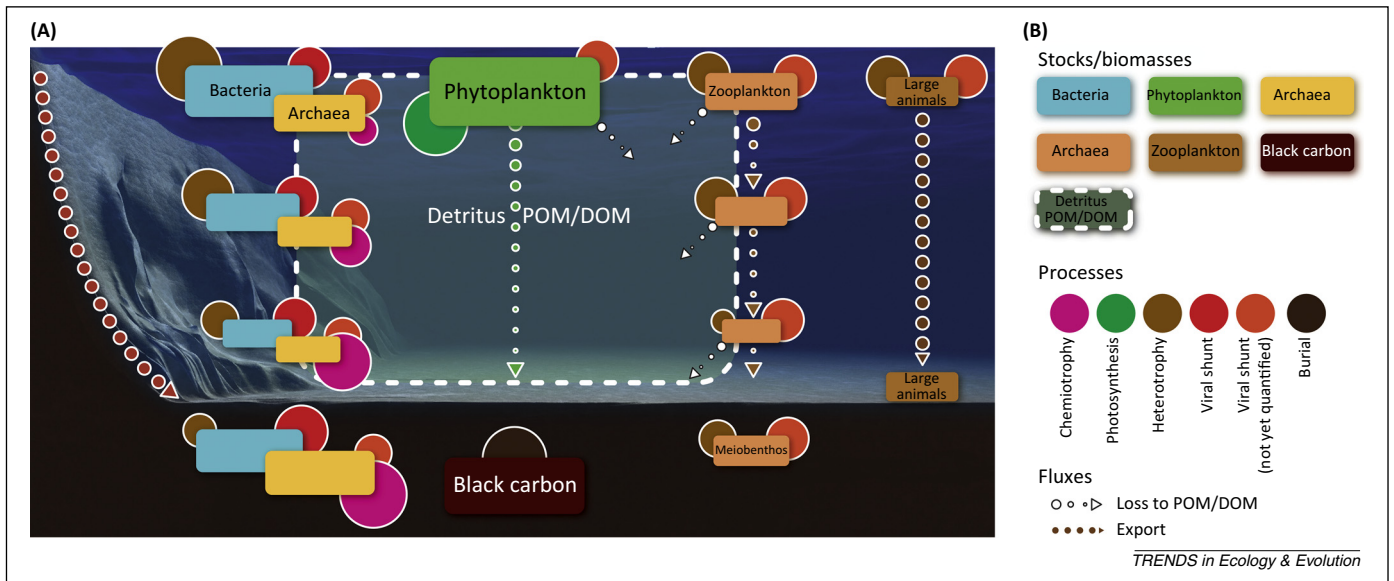


Figure 1. Components of life, biomass, and mass fluxes in the deep ocean interior. Reported are: **(A)** interconnections and magnitude of biomass, carbon supply, and transfer from surface water layers to the deep ocean, and among different biotic components. The schematic also identifies potential sources of carbon production and the relative importance of the standing stock associated with different living and detrital components inhabiting the deep-sea floor. Box dimensions indicate the relative importance (not to scale) of biomass or carbon storage, circles indicate associated processes (heterotrophic, phototrophic, chemoautotrophic production, infections), whereas arrows denote fluxes across different components and compartments. **(B)** Relative importance of different benthic components in terms of biomass and potential production in the deep sea. The illustration summarizes the increasing relevance of prokaryotic biomass versus a progressing decrease in importance for larger biotic components (particularly megafauna and meiofauna) moving from shallow to deeper depths.

climate change can alter primary production and export to the ocean interior, thus modifying particle flux to the deep-sea interior [29]. A full understanding of these processes will require manipulative experiments [30].

Box 3. Are symbioses increasingly important in the dark ocean?

Symbiotic interactions offer another mechanism to cope with limiting or unpredictable food supply, enabling deep-sea species to increase their efficiency in using specific resources or elements. The quantitative importance of these interactions, although still unresolved, might be far more widespread than previously thought. Symbioses in the deep sea could play a key role in supporting metazoan life and facilitating adaptation to extreme physical and chemical conditions. For example, oxygen limitation or fluid emissions offer opportunities for symbiosis. In the Santa Barbara hypoxic basin, many different phyla display symbiotic associations with endosymbiotic and epibiotic microbes [90,91]. These interactions extend to oxygen minimum zones (OMZs), where metazoans exhibit biochemical and morphological adaptation to limited oxygen concentration and the presence of sulfide-oxidizing symbionts [92]. Hydrothermal vents and cold seeps display numerous symbiotic associations, including siboglinid tubeworms, crustaceans, and bivalves [93]. Remarkably, these associations increase with decreasing distance from the fluid emissions, but persist far from the source and in some systems without fluid emissions. For instance, symbiotic bacteria within *Osedax* worms that colonize whale bones exploit organic sources contained therein [94]. The guts of holothurians and nematodes in deep-sea sediments support rich bacterial taxa [95] that are absent in surrounding sediments. The bacterium *Vibrio fischeri*, a bioluminescent symbiont within the squid *Euprymna scolopes*, uses a cytotoxin-like molecule with the ability to induce host development [96]. Deep-water corals support more than 100 species of associated invertebrates and illustrate symbioses not dependent upon geochemical fluid exploitation, also showing that >50% of obligate deep-water coral symbionts were endoparasites [97,98]. These findings suggest important and widespread symbioses between microbes and macro-organisms on bathyal slopes, abyssal plains, and beyond.

The importance of 'dark energy' in fuelling deep-sea ecosystems

Our estimate of deep-sea sediment surface area elevates the global biomass of organisms inhabiting the top 10 cm of the seafloor to somewhere on the order of 0.34 PgC with overall carbon production of 0.6 to 1.5 PgC/year (assuming carbon conversion efficiency between 20% and 50%). Although we do not know exactly what proportion of carbon export from the photic zone that deep-sea heterotrophs utilize, new evidence suggests even greater importance for 'dark energy' (methane, hydrogen sulfide, and inorganic elements) in sustaining deep-sea [31,32] and sub-seafloor functioning [33]. Organic matter recycling releases ammonium, and under anoxic conditions new studies at hydrothermal vents and cold seeps show that chemoautotrophs use other reduced metabolites to fix inorganic carbon and fuel highly productive invertebrate communities on the seafloor [34].

The importance of chemoautotrophic primary production in the deep

Recent estimates of global oceanic carbon fixation rates by chemoautotrophs (0.77 PgC/year) indicate a primary role for the deep water column (with 0.11 PgC/year, or 15% of total chemoautotrophic carbon fixation [31]). The estimated benthic chemoautotrophy production is 0.37 PgC/year, and although this value can be significantly lower in deep-sea sediments (0.004 PgC/year [31]) chemoautotrophic production could represent an important source of organic carbon for deep-sea benthic consumers [32]. This production occurs everywhere in deep-sea sediments, and recent findings indicate that chemosynthetic primary production by benthic Archaea can account for up to 20% or more of total heterotrophic biomass production and does not show depth-related patterns [32]. Benthic

Box 4. A matter of size: major food falls versus tiny rain

Size selectivity, patch selection, and differences in species mobility all critically reduce competition for available food in the deep [99], which arrives either as concentrated food falls (whale and fish carcasses, salp blooms, sunken wood, kelp) or as a rain of small particles settling through the water column [100]. The two contrasting inputs produce strikingly different responses. Large predators (deep-sea sharks) and fishes quickly arrive and exploit whale carcasses, consuming large chunks of flesh within hours of carcass arrival [70]. Experimental simulations of phytoplankton deposition at slope depths indicate rapid macrofaunal response to organic input within weeks [101,102]. Similarly, *in situ* pulsing of phytoplankton at approximately 5000 m depth showed immediate doubling of sediment community oxygen consumption (SCOC) and macrofaunal response in days [103], but a

delayed response of weeks for bacteria and foraminifera. However, by contrast, steady rain of micron-sized organic particles distributed over the seafloor and vertically mixed by bioturbators can favor rapid response and growth of small organisms such as meiofauna, protozoa, and heterotrophic prokaryotes over larger animals. Future manipulative experiments offer an opportunity to partition how different major size groupings (megafauna, macrofauna, meiofauna) and species utilize food falls within different habitats over short (annual, inter-annual) and long-term (decadal) time scales. Despite many unanswered questions regarding food quality and supply, sophisticated instruments can now characterize organic matter composition and structure, and thereby trace the origin of organic inputs and link ocean surface processes to deep-sea biological responses (Figure I).

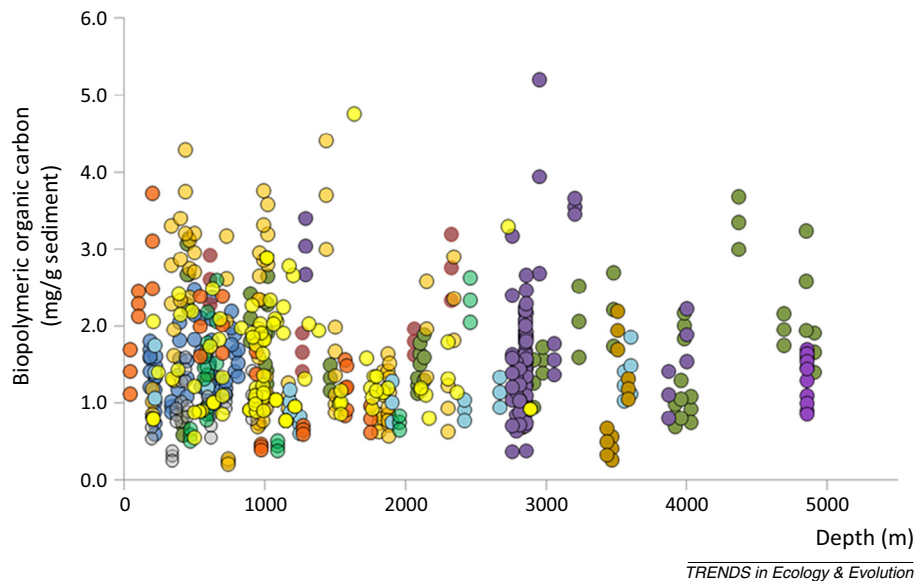


Figure I. Patterns of sediment organic matter distribution with increasing water depth. In order to provide information on the more readily digestible fraction of the sediment organic matter, instead of the bulk of organic carbon, here we report the concentrations of biopolymeric organic carbon (expressed as the sum of protein, carbohydrate, and lipid content of the sediment converted into carbon equivalents; data are expressed in mgC/g of sediment dry weight). The biopolymeric fraction of organic matter can be used as a proxy of the food potentially available to benthic consumers as protein, lipid, and carbohydrate fractions are potentially more promptly utilized for nutrition by benthos. The data summarize 604 sampling sites from all oceans (including the Pacific, Atlantic, Indian, and Southern Oceans and the Mediterranean Sea). The lack of any significant relationship with sampling depth and a slope of approximately 0.00002 illustrate the absence of the bathymetric pattern. Prokaryotes exhibit this same bathymetric pattern in terms of abundance and biomass, suggesting that microbes, more so than metazoans (which decline with depth), exploit available organic matter more effectively at all depths. Data from different areas of the Atlantic Ocean (yellow, blue, light blue, green) and the Mediterranean Sea (violet, orange, light green).

archaeal assemblages are thus mixotrophs and contribute a large fraction of heterotrophic carbon consumption. Other sources of reduced chemical inorganic compounds such as sulfide, hydrogen, and reduced iron from hydrothermal vents and water–rock interactions further support chemosynthetic food webs [34,35]. However, dissolved inorganic carbon fixation rates in hydrothermal vents have been estimated at 0.002 PgC/year [30], whereas use of iron, sulfide, and hydrogen in basaltic ocean crust appears even lower (0.001 PgC/year). Collectively, these findings suggest a potentially important role for chemoautotrophic carbon production in supplementing organic sources supporting deep-sea food webs and global carbon cycling [31]. The overall contribution of chemosynthetic primary production in deep-sea ecosystems might be much higher than previously thought, punctuating the need to account for chemoautotrophic production in future analyses of deep-sea metabolism and trophodynamics.

Challenging deep-sea metabolism paradigms: starving or active?

Low temperatures and the assumption of generalized food scarcity supported the long-held paradigm of slow growth and metabolism in deep-sea organisms, but testing the paradigm has proved challenging. Measuring metabolism of single organisms in the deep sea requires highly sensitive instruments and the ability to isolate organisms without altering their metabolism. For this reason, most such measurements come from captive animals in controlled conditions. Some evidence indicates that metabolism of deep-sea organisms could depend more on their biomass than on temperature [36]. The metabolism of abyssal echinoderms determined *in situ* did not change with depth, confirming the suitability of mass-dependent metabolic rates in ecosystem models [37]. In this respect, limited abundance of organisms and miniaturization of some deep-sea species (dwarfism) should decrease oxygen consumption per square meter. Whereas reduced average body size at depth was reported

for deep-sea nematodes [23] and gastropods [38], other organisms such as isopods, amphipods, pycnogonids, ostracods, and anemones showed gigantism [39] and a large portion of the fauna at hydrothermal vents and cold seeps greatly exceeds their shallow water counterparts in size (e.g., Mytilidae [7]). Whereas metabolic rates decline strongly with depth in several abundant animal groups, metabolisms in other abyssal species proceed as fast as in ecologically similar shallow-water species at equivalent temperatures [40]. At the same time, recent measurements proved that food inputs can control benthic metabolism down to almost 11 000-m depth in the Mariana Trench, where biological consumption of oxygen at least doubled that at 6000 m. Thus, despite extreme pressures in this environment, elevated deposition of organic matter stimulated impressive microbial activity [41]. A recent meta-analysis of available data framed within the metabolic theory of ecology suggests that individual metabolic rates, growth, and turnover of deep-sea fauna proceed as quickly as temperature-influenced biochemical kinetics allow, but that chemical energy set up higher-order community structure and function [42]. Thus, although deep-sea organisms operate under extreme conditions, they follow the same energetic rules as other systems. These findings once again contradict previous paradigms.

Challenging the origin of deep-sea faunas: whence deep-sea biodiversity?

Variable patterns in diversity with depth across taxa and habitats suggest multiple forces driving distributions and evolution of deep-sea biodiversity, and created two camps, one proposing a deep-sea invasion from shallow water during the Paleogene–Neogene and the other proposing species evolution exclusively in the deep sea. High deep-sea isopod diversity supports a shallow water origin, especially in the Southern Ocean [43], but a contrasting view suggests that isopods evolved in the deep sea and that the time scale proposed previously was insufficient for the observed species evolution [44]. Molecular methods showed that asellote isopods belonged to a single ancient clade with shallow water origins [45]. However, data collected so far suggest no single pathway to high deep-sea species diversity. Extensive taxonomic study of protobranch bivalves indicated the main radiation also took place within the deep sea, while acknowledging possible downslope migration and speciation [46]. Other authors argued that a variety of echinoderm species invaded the deep Northeast Atlantic from shallow waters because they would otherwise have lost their seasonal processes during periods of climate change during the Paleogene–Neogene [44]. Experiments on shallow- and deep-water echinoid larvae demonstrated larval tolerance for very high pressures, but sensitivity to temperature [47]. Cultured embryos and larvae of a bathyal species tolerated pressure increases more than their shallow water conspecifics, whereas embryos and larvae of a deep bathyal species were truly barophilic and did not develop at lower pressures [48]. Two characteristics tie potentially recent invaders of the deep sea: the seasonal production of planktotrophic larvae and a depth-related distribution of congeneric species down the slope [49]. Gage

and Tyler [50] demonstrated potential post-larval dispersal of *Ophiocten gracilis* (distribution ≈ 1000 m depth) to 2900 m although juveniles survived to maturity only at ambient depths, suggesting a selective pressure for depth over many generations will support deep-sea invasion and allopatric speciation by depth separation. Depth separation can significantly affect protobranch bivalve speciation [51], especially at upper bathyal depths where genetic and morphological divergence couple with strong biotic and abiotic heterogeneity. Another study revisited the suggestion of isopod radiation in the deep sea in flabellerid isopods, a taxon that invaded the South Atlantic deep sea from shallow water and radiated therein [52]. Octopod (Class Cephalopoda) evolution could have radiated from populations around the Southern Ocean and spread throughout the deep sea coincident with the formation of deep thermohaline circulation [53]. Echinoid fossil records suggested a major off-shelf migration between 75 and 55 Myr ago following major oceanic anoxic events in the Cretaceous [54]. This off-shelf migration coincided with significant increases in organic matter flux to the ocean basins and marked seasonality, mirroring processes observed since the last ice age. However, a considerably older deep-sea fauna (based on echinoderms) than assumed and that might extend back to the early Cretaceous, re-established the hypothesis of a deep-sea biodiversity refuge during major climatic change events at the surface and anoxic events in deeper water [55]. Untangling the conflicting and sometime contradictory evidence for faunal origins remains one of the grand challenges in deep-sea biology.

The importance of molecular tools in deep-sea ecology

New molecular technologies can increasingly distinguish morphologically similar taxa and assess connectivity, cosmopolitanism, phylogeny, and cryptic biodiversity [56]. Ultrasequencing platforms for metagenetic identification that use homologous gene regions are replacing DNA barcoding of deep-sea organisms, based on the analysis of a segment of the genome. Recent increases in sequencing throughput could significantly advance our ability to investigate deep-sea ecosystem complexity. These molecular tools were developed on shallow-water organisms and although promising, their application to deep-sea organisms remains problematic [57]. Molecular tools can also help reconcile possible contradictions with fossil methods [58] by amplifying fossil DNA preserved in sediments [59]. In fact, sequences of DNA can be extracted and sequenced from subsurface sediments, allowing detailed reconstruction of the biodiversity of past assemblages without fossilized or identifiable organisms [60,61].

Challenging deep-sea connectivity: open or structured populations?

Sexual reproduction and the dispersal of reproductive propagules maintain all deep-sea animal populations. With few exceptions, deep-sea invertebrates lack special reproductive adaptations, suggesting that phylogeny constrains sexual reproduction. Planktotrophic and lecithotrophic dispersal both occur in deep-sea invertebrates, but the prevalence of the latter could limit dispersal potential. However, lecithotrophic Antarctic echinoids and sea stars

exhibit wide dispersal, and lecithotrophic eggs can explain many apparently cosmopolitan distributions. Some 95% of deep-sea bivalve propagules from 270 sites across the Atlantic Ocean can disperse ≈ 750 km from their natal site. Moreover, analyses of Southern Ocean deep-sea fauna revealed high levels of biodiversity and strong links between Antarctic abyssal faunas and Atlantic diversity for taxa that can disperse well (such as Foraminifera [62]). However, poorly dispersing species (isopods and ostracods) exhibited distributions apparently restricted to the Southern Ocean region [62]. Recent metagenomic analyses of microbes in the deep sea suggested huge numbers of rare species along with rapid spatial turnover in species [63]. Metagenetic analyses of deep-sea and coastal meiofaunal assemblages revealed few cosmopolitan deep-sea species (9–11%), and even fewer eurybathic species (1.4–1.5% [64]). Analysis of beta diversity patterns at multiple fine and large scales confirmed these results, demonstrating significant differences among assemblages across and within bathymetric zones [65]. Therefore, even though some deep-sea taxa, including some hydrothermal vent metazoans, might disperse over large deep-sea areas many others, including several species endemic to deep seamounts, exhibit highly restricted distributions. Evidence of speciation starting in the deep and spreading to shallow waters and vice versa, and the recent hypothesis of enhanced speciation at bathyal depths spreading to shallow and abyssal depths, suggests that different marine environments can act as hotspots of speciation, irrespective of their bathymetric depth. Again, metagenomic analyses could shed new light on the prevalence of specific environments in promoting new biodiversity.

Challenging the state of the discipline: time for a new era?

Despite recent major advances in ecological research, we still lack the knowledge to manage human use of deep-sea ecosystems effectively. The advent of new technologies offers unprecedented opportunities. Below we propose priority research areas for developing knowledge needed for more effective management of deep-sea ecosystems.

Large-scale, long-term investigations and habitat mapping for extending macroecological approaches in deep-sea ecosystems

Better, smarter sampling tools now allow high-resolution, large-scale, and long-term data collection. AUVs fitted with high definition cameras and water samples can map extensive seafloor habitats and define species distributions in great detail. The rapid advances in temporal observation potential with cabled observatories could fundamentally change our view of deep-sea dynamics. Large-scale observations nonetheless must be coupled with physical samples of organisms to ensure accurate identification, discovery of new species, and defining distributions. In addition, novel tagging of deep-sea organisms can decipher their interactions and dispersal. Deep-sea observatories with the ability to sample biological components represent the future for long-term monitoring needed to evaluate the impact of climate change on deep-sea ecosystems.

Molecular tools to investigate unknown biodiversity and functions

In situ molecular tools offer great promise for high-resolution observation from microbes to larger invertebrates, including cryptic species [57,66]. Currently available molecular tools and new chips allow sequencing DNA *in situ*, offering new opportunities to investigate biodiversity, symbiotic interactions, connectivity, and functions of deep-sea species.

New generation of deep-sea ecological experiments and habitat restoration

In situ deep-sea experiments, now made possible by the availability of sophisticated technologies, will allow increasingly complex ecological manipulations, launching a new era of better understanding of deep-sea ecosystem functioning and restoration strategies for deep-sea habitats degraded by mining, oil spills, or bottom trawling [67,68]. Pressure vessels can transport organisms from the seafloor to the surface for manipulative experiments, or to evaluate larval dispersal potential and other ecological characteristics [69] at a time when molecular tools offer novel insights into connectivity questions. ROVs and programmed landers can now deploy respiration chambers, release isotopically labeled food resources onto the seafloor at preprogrammed intervals [70], and inject carbon dioxide into deep-sea ecosystems at different concentrations to study faunal response to acidification. A similar strategy might be used to deploy other substances (e.g., antibiotics) to evaluate microbial–macrobial interactions.

Restoration of degraded deep-sea habitats must be a priority. Deep-water corals survive and grow in laboratory conditions and experimental reintroduction to the seafloor has proved successful [69]; plans are underway to initiate experiments for restoration of hydrothermal vents, cold seeps (with mineral crusts), and manganese nodules after mining [69]. Efforts are also ongoing to develop swarms of autonomous undersea vehicles to transplant and monitor deep-sea restoration over relatively broad areas [69].

Concluding remarks

New results demonstrate that most widely accepted ecological hypotheses and paradigms proposed in past decades for deep-sea ecosystems require major revision. Moreover, the new findings from the deep are challenging hypotheses developed in other ecosystems (e.g., the importance of positive species interactions and the possibility of metazoan life without oxygen). We now face a new golden age for deep-sea research, more challenging than ever, rich with new tools and technologies, offering unprecedented opportunities for new discoveries that could enable the development of novel ecological theories. We close with a final challenge to terrestrial and freshwater scientists to consider whether dark carbon, chemosynthesis, and historical perspectives on carbon cycling may require re-evaluation in those domains, and whether similar adaptations (e.g., living in anoxia) may exist if we ‘dig’ deeper.

Acknowledgments

This work has been produced within the framework of the international network LICO (Life in a Changing Ocean) and INDEEP (International

Network for Scientific Investigation of Deep-sea Ecosystems). R.D. was financially supported by the Flagship project Ricerca Italiana per il Mare (RITMARE) (Consiglio Nazionale delle Ricerche (CNR), Ministero dell'Istruzione, dell'Università e della Ricerca (MIUR)) and Managing impacts of deep sea resource exploitation (MIDAS) (EU funded programme Seventh Framework Programme (FPVII)). P.S. was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) Canadian Healthy Oceans Network and an NSERC Discovery Grant.

References

- Parkes, R.J. *et al.* (1994) Deep bacterial biosphere in Pacific Ocean sediments. *Nature* 371, 410–413
- Todo, Y. *et al.* (2005) Simple foraminifera flourish at the ocean's deepest point. *Science* 307, 689
- Sanders, H.L. and Hessler, R.R. (1969) Ecology of the deep-sea benthos. *Science* 163, 1419–1424
- Grassle, J.F. and Maciolek, N.J. (1992) Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *Am. Nat.* 139, 313–341
- Corliss, J.B. *et al.* (1979) Submarine thermal springs on the Galapagos Rift. *Science* 203, 1073–1083
- Paull, C.K. *et al.* (1985) Stable isotope evidence for chemosynthesis in an abyssal seep community. *Nature* 317, 709–711
- Micheli, F. *et al.* (2002) Predation structures communities at deep-sea hydrothermal vents. *Ecol. Monogr.* 72, 365–382
- Snelgrove, P.V.R. and Smith, C.R. (2002) A riot of species in an environmental calm: the paradox of the species-rich deep-sea floor. *Oceanogr. Mar. Biol. Ann. Rev.* 40, 211–242
- Levin, L.A. and Dayton, P.K. (2009) Ecological theory and continental margins: where shallow meets deep. *Trends Ecol. Evol.* 24, 606–617
- Danovaro, R. *et al.* (2008) Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. *Curr. Biol.* 18, 1–8
- Huvenne, V.A.I. *et al.* (2012) Habitat heterogeneity in the Nazaré deep-sea canyon offshore Portugal. In *Seafloor Geomorphology as Benthic Habitat: GeoHAB Atlas of Seafloor Geomorphic Features and Benthic Habitats* Harris (P.T. and Baker, E.K., eds), pp. 691–701, Elsevier
- Zeppilli, D. *et al.* (2012) Pockmarks enhance deep-sea benthic biodiversity: a case study in the western Mediterranean Sea. *Divers. Distrib.* 18, 832–846
- Ramirez-Llodra, E. *et al.* (2010) Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. *Biogeosciences* 7, 2851–2899
- McClain, C.R. and Barry, J.P. (2010) Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. *Ecology* 91, 964–976
- Game, E.T. *et al.* (2009) Pelagic protected areas: the missing dimension in ocean conservation. *Trends Ecol. Evol.* 24, 360–369
- Meysman, F.J.R. *et al.* (2006) Bioturbation: a fresh look at Darwin's last idea. *Trends Ecol. Evol.* 21, 688–695
- Dunne, J.P. *et al.* (2007) A synthesis of global particle export from the surface ocean and cycling through the ocean interior and on the seafloor. *Global Biogeochem. Cycles* 21, GB4006
- Druffel, E.R.M. and Robison, B.H. (1999) Is the deep sea on a diet? *Science* 284, 1139–1140
- Billett, D.S.M. *et al.* (1983) Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* 302, 520–522
- Jahnke, R.A. *et al.* (1990) Intensification of recycling of organic matter at the sea floor near ocean margins. *Nature* 348, 50–54
- Canals, M. *et al.* (2006) Flushing submarine canyons. *Nature* 444, 354–357
- Danovaro, R. *et al.* (2003) A depocenter of organic matter cycling at 7800-m depth in the South Pacific Ocean. *Deep Sea Res. I* 50, 1411–1420
- Danovaro, R. (2002) Meiofauna hotspot in the Atacama Trench, eastern South Pacific Ocean. *Deep Sea Res. I* 49, 843–857
- Olu, K. *et al.* (1997) Cold seep communities as indicators of fluid expulsion patterns through mud volcanoes seaward of the Barbados accretionary prism. *Deep Sea Res. I* 44, 811–841
- Tunnicliffe, V. *et al.* (2003) Reducing environments of the deep-sea floor. In *Ecosystems of the World: Ecosystems of the Deep Sea* (Vol. 28) (Tyler, P., ed.), In pp. 81–110, Elsevier
- Pusceddu, A. *et al.* (2009) Quantity and bioavailability of sediment organic matter as signatures of benthic trophic status. *Mar. Ecol. Prog. Ser.* 375, 41–52
- Danovaro, R. *et al.* (2001) Bioavailability of organic matter in the sediments of the Porcupine Abyssal Plain, Northeast Atlantic. *Mar. Ecol. Prog. Ser.* 220, 25–32
- Luna, G.M. *et al.* (2012) The dark portion of the Mediterranean Sea is a bioreactor of organic matter cycling. *Global Biogeochem. Cycles* 26, GB2017
- Mora, C. *et al.* (2013) Biotic and human vulnerability to projected changes in ocean biogeochemistry over the 21st century. *PLoS Biol.* 11, e1001682
- Nomaki, H. *et al.* (2005) Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: in situ tracer experiments. *Limnol. Oceanogr.* 50, 134–146
- Middelburg, J.J. (2011) Chemoautotrophy in the ocean. *Geophys. Res. Lett.* 38, L24604
- Molari, M. *et al.* (2013) Dark inorganic carbon fixation sustains the functioning of benthic deep-sea ecosystems. *Global Biogeochem. Cycles* 27, 212–221
- Schippers, A. *et al.* (2005) Prokaryotic cells of the deep sub-seafloor biosphere identified as living bacteria. *Nature* 433, 861–864
- German, C.R. *et al.* (2011) Deep-water chemosynthetic ecosystem research during the census of marine life decade and beyond: a proposed deep-ocean road map. *PLoS ONE* 6, e23259
- Marsh, A.G. *et al.* (2001) Larval dispersal potential of the tubeworm *Riftia pachyptila* at deep-sea hydrothermal vents. *Nature* 411, 77–80
- Baguley, J.G. *et al.* (2008) Metazoan meiofauna biomass, grazing, and weight-dependent respiration in the Northern Gulf of Mexico deep sea. *Deep Sea Res. II* 55, 2607–2616
- Hughes, S.J.M. *et al.* (2011) Deep-sea echinoderm oxygen consumption rates and an interclass comparison of metabolic rates in Asteroidea, Crinoidea, Echinoidea, Holothuroidea and Ophiuroidea. *J. Exp. Biol.* 214, 2512–2521
- McClain, C.R. *et al.* (2005) Deconstructing bathymetric patterns of body size in deep-sea gastropods. *Mar. Ecol. Prog. Ser.* 297, 181–187
- Timofeev, S.F. (2001) Bergmann's principle and deep-water gigantism in marine crustaceans. *Biol. Bull.* 28, 646–650
- Seibel, B.A. and Drazen, J.C. (2007) The rate of metabolism in marine animals: environmental constraints, ecological demands and energetic opportunities. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 362, 2061–2078
- Glud, R.N. *et al.* (2013) High rates of microbial carbon turnover in sediments in the deepest oceanic trench on Earth. *Nat. Geosci.* 6, 284–288
- McClain, C.R. *et al.* (2012) Energetics of life on the deep seafloor. *Proc. Natl. Acad. Sci. U.S.A.* 109, 15366–15371
- Menzies, R.J. *et al.* (1973) *Abyssal Environment and Ecology of the World Oceans*, John Wiley
- Hessler, R.R. *et al.* (1979) The deep-sea isopods: a biogeographic and phylogenetic overview. *Sarsia* 64, 67–75
- Raupach, M.J. *et al.* (2009) Multiple origins of deep-sea Asellota (Crustacea: Isopoda) from shallow waters revealed by molecular data. *Proc. R. Soc. B* 276, 799–808
- Allen, J.A. and Sanders, H.L. (1996) The zoogeography, diversity and origin of the deep-sea protobranch bivalves of the Atlantic: the epilogue. *Prog. Oceanogr.* 38, 95–153
- Tyler, P.A. and Young, C.M. (1998) Temperature and pressure tolerances in dispersal stages of the genus *Echinus* (Echinodermata: Echinoidea): prerequisites for deep-sea invasion and speciation. *Deep Sea Res. II* 45, 253–277
- Young, C.M. and Tyler, P.A. (1993) Embryos of the deep-sea echinoid *Echinus affinis* require high pressure for development. *Limnol. Oceanogr.* 38, 178–181
- Bronsdon, S.K. *et al.* (1993) Reproductive biology of two epizoaic anemones from bathyal and abyssal depths in the NE Atlantic Ocean. *J. Mar. Biol. Ass. UK* 73, 531–541
- Gage, J. and Tyler, P.A. (1991) *Deep-sea Biology: A Natural History of Organisms at the Deep-sea Floor*, Cambridge University Press
- Etter, R.J. *et al.* (2005) Population differentiation decreases with depth in deep-sea bivalves. *Evolution* 59, 1479–1491
- Wilson, G.D.F. (1998) Historical influences on deep-sea isopod diversity in the Atlantic Ocean. *Deep Sea Res. II* 45, 279–301

- 53 Strugnell, J. *et al.* (2008) The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. *Cladistics* 24, 1–8
- 54 Smith, A.B. and Stockley, B. (2005) The geological history of deep-sea colonization by echinoids: roles of surface productivity and deep-water ventilation. *Proc. Biol. Sci.* 272, 865–869
- 55 Thuy, B. *et al.* (2013) New ophiacanthid brittle stars (Echinodermata: Ophiuroidea) from the Upper Triassic of Japan: first insights into the origin and evolution of an extant deep-sea group. *J. Syst. Palaeontol.* 11, 5
- 56 Appeltans, W. *et al.* (2012) The magnitude of global marine species diversity. *Curr. Biol.* 22, 2189–2202
- 57 Bik, H.M. *et al.* (2012) Sequencing our way towards understanding global eukaryotic biodiversity. *Trends Ecol. Evol.* 27, 233–243
- 58 Little, C.T.S. and Vrijenhoek, R.C. (2003) Are hydrothermal vent animals living fossils? *Trends Ecol. Evol.* 18, 582–588
- 59 Corinaldesi, C. *et al.* (2011) Preservation, origin and genetic imprint of extracellular DNA in permanently anoxic deep-sea sediments. *Mol. Ecol.* 20, 642–654
- 60 Corinaldesi, C. *et al.* (2008) Damage and degradation rates of extracellular DNA in marine sediments: implications for the preservation of gene sequences. *Mol. Ecol.* 17, 3939–3951
- 61 Corinaldesi, C. *et al.* (2014) Extracellular DNA can preserve the genetic signatures of present and past viral infection events in deep hypersaline anoxic basins. *Proc. R. Soc. B* 281, 20133299
- 62 Brandt, A. *et al.* (2007) First insights into the biodiversity and biogeography of the Southern Ocean deep sea. *Nature* 447, 307–311
- 63 Sogin, M.L. *et al.* (2006) Microbial diversity in the deep sea and the underexplored “rare biosphere”. *Proc. Natl. Acad. Sci. U.S.A.* 103, 12115–12120
- 64 Danovaro, R. *et al.* (2010) The first metazoa living in permanently anoxic conditions. *BMC Biol.* 8, 30
- 65 Gambi, C. *et al.* (2014) Species richness, species turnover, and functional diversity in nematodes of the deep Mediterranean Sea: searching for drivers at different spatial scales. *Global Ecol. Biogeogr.* 23, 24–39
- 66 Scholin, C. *et al.* (2009) Remote detection of marine microbes, small invertebrates, harmful algae, and biotoxins using the environmental sample processor (ESP). *Oceanography* 22, 158–167
- 67 Pusceddu, A. *et al.* (2014) Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. *Proc. Natl. Acad. Sci. U.S.A.* <http://dx.doi.org/10.1073/pnas.1405454111>
- 68 Pradillon, F. *et al.* (2004) Pressure vessels for in vivo studies of deep-sea fauna. *High Pressure Res.* 24, 237–246
- 69 Barbier, E.B. *et al.* (2014) Protect the deep sea. *Nature* 505, 475–477
- 70 Smith, C.R. and Baco, A.R. (2003) Ecology of whale falls at the deep sea floor. *Oceanogr. Mar. Biol. Annu. Rev.* 41, 311–354
- 71 Hessler, R.R. and Sanders, H. (1967) Faunal diversity in the deep-sea. *Deep-sea Res.* 14, 65–78
- 72 Grassle, J.F. (1977) Slow recolonisation of deep-sea sediment. *Nature* 265, 618–619
- 73 Rex, M.A. (1973) Deep-sea species diversity: decreased gastropod diversity at abyssal depths. *Science* 181, 1051–1052
- 74 Cavanaugh, C.M. *et al.* (1981) Prokaryotic cells in hydrothermal vent tube worm *Riftia pachyptila* Jones: possible chemoautotrophic symbionts. *Science* 213, 340–342
- 75 Hollister, C.D. and McCave, I.N. (1984) Sedimentation under deep-sea storms. *Nature* 309, 220–225
- 76 Lampitt, R.S. (1990) Directly measured rapid growth of a deep-sea barnacle. *Nature* 345, 805–807
- 77 Rex, M.A. *et al.* (1993) Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* 365, 636–639
- 78 Thomas, E. and Gooday, A.J. (1996) Cenozoic deep-sea benthic foraminifers: tracers for changes in oceanic productivity? *Geology* 24, 355–358
- 79 Kato, C. *et al.* (1996) Isolating and characterizing deep-sea marine microorganisms. *Trends Biotechnol.* 14, 6–12
- 80 Karner, M.B. *et al.* (2001) Archaeal dominance in the mesopelagic zone of the Pacific Ocean. *Nature* 409, 507–510
- 81 Lipp, J.S. *et al.* (2008) Significant contribution of Archaea to extant biomass in marine subsurface sediments. *Nature* 454, 991–994
- 82 Danovaro, R. *et al.* (2001) Deep-sea ecosystem response to climate changes: the eastern Mediterranean case study. *Trends Ecol. Evol.* 16, 505–510
- 83 Ruhl, H.A. *et al.* (2008) Connections between climate, food limitation, and carbon cycling in abyssal sediment communities. *Proc. Natl. Acad. Sci. U.S.A.* 105, 17006–17011
- 84 Yasuhara, M. *et al.* (2008) Abrupt climate change and collapse of deep-sea ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* 105, 1556–1560
- 85 Mora, C. *et al.* (2011) How many species are there on Earth and in the ocean? *PLoS Biol.* 9, e1001127
- 86 Buhl-Mortensen, L. *et al.* (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Mar. Ecol.* 31, 21–50
- 87 Harris, P.T. *et al.* (2014) Geomorphology of the oceans. *Mar. Geol.* 352, 4–24
- 88 Vaquer-Sunyer, R. and Duarte, C.M. (2008) Thresholds of hypoxia for marine biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* 105, 15452–15457
- 89 Danovaro, R. *et al.* (2005) Viruses, prokaryotes and DNA in the sediments of a deep-hypersaline anoxic basin (DHAB) of the Mediterranean Sea. *Environ. Microbiol.* 7, 586–592
- 90 Edgcomb, V. *et al.* (2011) Accessing marine protists from the anoxic Cariaco Basin. *ISME J.* 5, 1237–1241
- 91 Bernhard, J.M. *et al.* (2000) The Santa Barbara Basin is a symbiosis oasis. *Nature* 403, 77–80
- 92 Levin, L.A. *et al.* (2003) Bioturbation by symbiont-bearing annelids in near-anoxic sediments: implications for biofacies models and paleo-oxygen assessments. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 199, 129–140
- 93 Boutet, I. *et al.* (2011) Conjugating effects of symbionts and environmental factors on gene expression in deep-sea hydrothermal vent mussels. *BMC Genomics* 12, 530
- 94 Rouse, G.W. *et al.* (2004) Osedax: bone-eating marine worms with dwarf males. *Science* 305, 668–671
- 95 Amaro, T. *et al.* (2012) High prokaryotic biodiversity associated with gut contents of the holothurian *Molpadia musculus* from the Nazaré Canyon (NE Atlantic). *Deep Sea Res I* 63, 82–90
- 96 Visick, K.L. and Ruby, E.G. (2006) *Vibrio fischeri* and its host: it takes two to tango. *Curr. Opin. Microbiol.* 9, 632–638
- 97 Buhl-Mortensen, L. and Mortensen, P.B. (2004) Symbiosis in deep-water corals. *Symbiosis* 37, 33–61
- 98 Ward, M.E. *et al.* (2004) Parasitism in species of Bathymodiolus (Bivalvia: Mytilidae) mussels from deep-sea seep and hydrothermal vents. *Dis. Aquat. Organ.* 62, 1–16
- 99 Miller, R.J. *et al.* (2000) Feeding selectivity and rapid particle processing by deep-sea megafaunal deposit feeders: A ²³⁴Th tracer approach. *J. Mar. Res.* 58, 653–673
- 100 Smith, C.R. *et al.* (2008) Abyssal food limitation, ecosystem structure and climate change. *Trends Ecol. Evol.* 23, 518–528
- 101 Snelgrove, P.V.R. *et al.* (1992) The role of food patches in maintaining high deep-sea diversity: field experiments with hydrodynamically unbiased colonization trays. *Limnol. Oceanogr.* 37, 1543–1550
- 102 Snelgrove, P.V.R. *et al.* (1996) Experimental evidence for aging food patches as a factor contributing to high deep-sea macrofaunal diversity. *Limnol. Oceanogr.* 41, 605–614
- 103 Witte, U. *et al.* (2003) In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. *Nature* 424, 763–766