



Editorial: Extreme Benthic Communities in the Age of Global Change

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Editorial on the Research Topic

Extreme Benthic Communities in the Age of Global Change

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The sea floor represents the largest solid ecosystem on our Planet. This heterogeneous realm consists of many different features shaped by millions of years of geological and chemical events, and biological and environmental evolution. "Extreme" benthic environments, defined as having abiotic conditions that demand organisms and resident communities be adapted in order to survive and thrive, are widespread and offer many opportunities for investigating the biological responses and adaptations of organisms to "abnormal" life conditions. At the same time, these adapted organisms may give insights into future ecosystem responses, as today's extreme ecosystems can be considered natural analogs of "normal" environments that may change under future climate change conditions. With continuing climate change and increased anthropogenic pressures, very few seafloor areas will remain untouched. Hence the future of the benthos will depend on how organisms, species, populations and communities will respond. Benthic communities are especially useful in long-term comparative investigations such as studying the effects of climate change and other pressures because most of their species are sessile or have low mobility, can be long-lived, and integrate the effects of environmental change over time. In addition, macro-, meio-, and microbenthos of hard and soft bottoms are found in almost any marine environment, including the most hostile or unusual, rendering them ideal to assess the impacts of environmental change and other pressures, as well as effects of multiple, simultaneous pressures. The continuous discovery of communities in extreme environments and the study of their variability, heterogeneity, and their relation to climate change and anthropogenic impacts, are slowly expanding as more evidence and long-term observations become increasingly available.

The present Special Issue of Frontiers in Marine Science aims at providing a significant contribution to understanding more of the above-mentioned topics. The issue contains 13 diverse scientific contributions from all over the world on many fundamental questions related to benthos in extreme environments, and how these environments and their biota respond to global change and human pressures.

Several papers have focused on chemosynthetic systems in shallow and deep water, covering hydrothermal vents and vent fields, illustrating the diversity of research conducted in these unique ecosystems. On one hand, some studies are demonstrating unique organism distributions, connectivity, and adaptations, while documenting undiscovered biodiversity with new species

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descriptions. On the other hand, other studies show that these systems are or will be subject to human pressures, including climate change, before we fully understand how they function and how their biodiversity is driven by the biotics and abiotics surrounding them. Åström et al. provide a thorough review of cold seeps benthic ecology in the Arctic, suggesting that chemosynthetic systems, operating on different spatial and temporal cycles than the surficial photosynthetic counterpart, may act as spatio-temporal bridges or refugia for benthic communities subject to climate change such as warming, and subsequent mismatches in phenologies and energy demands vs. surface supply (bentho-pelagic coupling). Along the Arctic Mid-Ocean Ridge, Ramirez-Llodra et al. examined benthic communities on inactive sulfide mounds (2,600 m depth), characterized by sponge and stalked crinoid fields, recognized as Vulnerable Marine Ecosystems. This has implications for marine management and conservation since these mounds may be targeted for deep-sea mining in the future. Spedicato et al. also draw attention to deep-sea mining by showing how meiofauna and nematodes are useful in describing the environmental heterogeneity, mainly in terms of substratum type and geochemistry, of hydrothermal vent fields along the Mid-Atlantic Ridge, which may be exploited for seafloor massive sulfide extraction. Food availability, geochemical settings, and biotic interactions were distinct drivers of the meiofauna communities. Cepeda et al. showed that, within meiofauna, kinorhynchs showed particular affinity with cold seep conditions (low oxygen, high sulfide, and methane) likely caused by reduced competition for space and resources by other organisms in these extreme environments. They also describe three new "mud dragon" species, indicating that much of the deepsea diversity remains undescribed. Moving into shallow-water chemosynthetic environments, Donnarumma et al. studied Secca delle Fumose, a hydrothermal vent system in the Mediterranean, showing that communities are adapted to the specific conditions of these vent systems, with resistant species and communities that are different from control sites outside the vent area. Further work on chemosynthetic species is presented by Eilertsen et al., who described a new species of Osedax from the Arctic Mid-Ocean Ridge. Few extreme ecosystems speak to the imagination as whale falls in the deep sea; the authors mimicked such food falls by deploying cow bones near a hydrothermal vent and observing dense aggregations of the newly described bone-eating worm, feasting on the lipids stored within. A prime example of how limited availability of energy in the oligotrophic deep-sea pushes evolution to exploit alternative chemosynthetic niches.

It is well-accepted that energy is limited in the deep sea, that, apart from the above-mentioned chemosynthetic habitats, appears to be mainly reliant on the scarce, intermittent cascading of organic matter and other compounds from surface waters. How are deep-sea communities adapted to this oligotrophy, that, other than darkness, low temperatures and high pressure, poses additional challenges to metabolism, physiology, and behavior? McClain et al. brings novel insight into this field, proposing an eco-evolutionary adaptive theory of the metabolic niche, whereby deep-sea species are adapted to specific energy regimes which scale with biodiversity patterns. They present 10

hypotheses centered around metabolic niches, energy demand, biodiversity, and biogeography, concluding that benthic deepsea invertebrates with high energy demands are located in areas with higher chemical availability being their distributions linked to geographic patterns of chemical energy availability. These findings suggest that species are likely adapted to specific energy regimes and imply a relation between adaptation and biogeographical distributions and patterns. An alternative view to geographic distributions and "energy" in the deep sea is provided by Castellan et al. on the distribution of the temperate coral *Dendrophyllia cornigera* across the Atlantic Ocean and whole Mediterranean. By analyzing temperature recordings at the collection sites they documented that this eurybathic coral lives between \sim 7 and 17°C, which may present an advantage for its survival in a warming ocean.

Much of the deep sea remains un- or under-explored. As deep-sea science progresses, so do the technologies used to study it. This is particularly important in light of global change and anthropogenic impacts; ecosystems are changing before we have a chance to study their communities in detail. Ríos et al. focused on rock sponge aggregations in the Cantabrian Sea, where they took physical samples and imagery to fine tune improved methodologies to calculate biomass and volume of sponge assemblages. Their image-based approach aimed at developing better techniques to avoid destructive sampling in studying these vulnerable habitats. An image-based approach was also used by Meyer et al., who documented megabenthic communities of the Sognefjord. A seaward sill in the fjord causes stratification, resulting in limited variability of abiotic factors in the deep basin, which provided a unique opportunity to study their effect on benthic community composition. Their study showed that highly-stratified fjords can hold stable communities (diversity, richness).

Submarine canyons, much like fjords, offer strong connections between land and sea. This is demonstrated in Liao et al., who studied the Gaoping Submarine Canyon off SW Taiwan. This canyon is fed by a mountain river with extremely high sediment loads. Transport of sediments through the canyon system results in a high-energy system that poses extreme challenges to the resident nematode communities that respond to the strong bottom currents, with reduced taxonomic, trophic and functional diversity and maturity. Their findings also suggest strong heterogeneity in the canyon system, with some degree of local extinction and dispersal limitation.

Apart from the phenomena associated with climate change, marine benthic ecosystems are exposed to human activities and disturbances, including several types of pollution with impacts on a global scale. Enough evidence has accumulated to demonstrate that the "remote" deep sea and the Antarctic have—in spite of their long-thought status as pristine environments—not remained unaffected. Using nematode and copepod communities, Stark et al. studied spatial variation and human impacts at Casey Station in East Antarctica. They found that these communities respond strongly to their immediate environment, and to large spatial scale contrasts. In addition, nematode and copepod communities markedly responded to metals concentrations (as proxy for historical anthropogenic

pollution), providing further evidence that they can be useful indicators of environmental changes in Antarctic ecosystems.

We are enhancing our understanding of our ocean and its ecosystems, but society also recognizes the impacts climate change and human activities are having; with newly emerging Blue Economies and increased reliance on ocean resources, sustainability is key in order to maintain healthy oceans for future generations. Useful in this process is having the ability to concretize the value of marine ecosystem services and the benefits they provide to humankind. This approach is used by the final study in this special issue, Barnes et al., who combined observations of benthic life around seamounts of the Ascension Islands with the calculation of Blue Carbon Natural Capital. Despite their young age, small size and isolation, these seamounts can provide meaningful ecosystem services and their conservation does generate a quantifiable economic return.

The studies in this special issue cover shallow and deep-water areas, ecosystems fed by chemosynthetic and photosynthetic energy, and species, populations, and communities across a large size spectra, from meiofauna to megafauna. They also enhance our understanding of ecosystems that challenge ocean life, while being subjected to pressures resulting from global change to anthropogenic activities. It is expected that under global change conditions, extreme ecosystems will be especially affected, because of the specific organism-tocommunity adaptations evolved in such systems. Global change is occurring on time scales much shorter than those required for the formation of extreme ecosystems and the bio-ecological evolutionary pathways that run alongside it. Future changes may modify population dynamics over time and space, and alter the phenology and the geographical distribution of benthic communities and species. These modifications can result in habitat loss and species extinctions, with consequences for biogeochemical fluxes, ecological interactions and cascades, ecosystem functioning, and biodiversity. Energy availability is likely to change in benthic ecosystems, posing additional challenges to well-adapted organisms. In addition to global change, anthropogenic activities are compounding the pressures on marine communities. As we enter the UN Decade of Ocean Science for Sustainable Development, the focus lies on developing the scientific research required to ensure the health and sustainable use of our oceans. The diversity of contributions in this special issue shows that we are only scratching the surface with regards to understanding biodiversity in extreme environments, and the complexities of biological and ecological interactions, as well as the nature of their change in the Anthropocene. However, it also shows their unique value to scientific comprehension of how ecosystems are changing, and the benefits to humankind that are at stake.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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