The Deep Ocean: Which Climate Issues?

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The deep ocean (200m below the surface to 11,000m) represents over 98% of marine waters in volume. The image of a stable and homogeneous environment over vast areas, with low biological activity, does not actually reflect the diversity of deep-sea ecosystems nor their sensitivity to climate change. Even on the abyssal plains, variations in abundance of key species have been attributed to changes in the photosynthetic productivity at the surface of the ocean. Moreover, many biodiversity and productivity 'hot-spots' of the deep seafloor, and their foundation species such as deep-sea corals could be particularly vulnerable to the already observable changes at great depths, such as local or regional warming deep water, acidification and deoxygenation and modifications of the circulation of water masses. This vulnerability questions our ability to anticipate the consequences of climate change on poorly known ecosystems and the services they provide.

DYNAMIC DEEP-SEA ECOSYSTEMS IN A HETEROGENEOUS ENVIRONMENT

When it comes to climate, the deep ocean is first seen as a vast saltwater reservoir that allows heat distribution around the globe via thermohaline circulation. The sequestration of atmospheric CO_2 released by human activities, and of the excess heat that it generates, operates on secular to millennia scales during which ocean waters, after plunging to depths, flow over the seafloor across ocean basins before reemerging at the surface.

We can consider that the upper limit of the deep ocean lies about 200m below the surface, where there is no sunlight or seasonal temperature variations, and extends to the ocean floor down to a maximum depth of 11,000m. This environment represents over 98% of marine waters in volume. It is described as stable and uniform over large areas, isolated from continents and the atmosphere, with water chemical properties (like pH and oxygen, nitrate, CO_2 contents) changing very slowly as organic matter transported from the surface is being degraded by microorganisms.

This large scale view of the ocean circulation is mirrored in the perception of a deep ocean where biological activity is sparse, populated by species with slow metabolisms adapted to a cold and dark environment, low nutritional resources, and high pressures. Considered as uniform and quasi-desertic, these oceanic regions would be barely affected by ongoing climate change, or only in the very long term. However, this view is inconsistent with our current knowledge of the wide variety of deep-sea ecosystems. An increasing number of studies show that most of these deep-sea ecosystems interact with the climate system. Even the abyssal plains that are sustained by limited food supply, formed by planktonic remains and other organic debris, are subject to seasonal variations. In particular, changes in species abundance have been observed, revealing an unexpected ecological dynamics attributed to differences in surface ocean photosynthetic productivity from year to year.

Moreover, beside the vast abyssal sedimentary domain occupying 75% of the ocean floor, we can no longer overlook other types of deep-sea environments that are, at least, of equal ecological or societal importance. The topography of the ocean floor is indeed similar to the reliefs of continents (*i.e.* expanding over a depth range of 11,000m in the deepest trench, to be compared to the 8,500m of Mt. Everest). Interplaying with oceanic currents, this rugged seabed is home to a mosaic of ecosystems themselves composed of fragmented habitats (Ramires-Llodra *et al.* 2010). Today's satellite imaging techniques enable a detailed view of their distribution and diversity at global scale. This diverse environment creates major biomes equivalent to those linked to terrestrial climates (tundra, savanna, etc.) to which species have adapted. Like terrestrial or coastal environments, the deep ocean also hosts 'hot-spots' of biodiversity and productivity, special places of biodiversity and productivity, and their functioning and associated "services" could be particularly vulnerable to climate impacts and ocean acidification.

For example, seamounts that rise from hundreds to thousands of meters above the abyssal plains can promote vertical exchanges of chemical nutrients up to the surface layers of the ocean, boosting photosynthesis and the whole trophic food chain (Morato *et al.* 2010). Their flanks are home to a wide variety of deep water corals (also known as 'cold-water corals' due to their occurrence in shallower depths at high latitudes), and gorgonians that sometimes form large canopies or reefs. These internationally protected species function as refuge and nursery for many species of fish, crustaceans and invertebrates (Roberts *et al.* 2006). The 'services' identified for these ecosystems are largely related to artisanal or industrial fishery resources, but it is clear that these natural settings conceal treasures that are still largely unknown, including those of their biodiversity.

On continental margins, submarine canyons that cut into the shelf play a similar role as seamounts when they channel deep water upwelling (De Leo *et al.* 2010). These incised valleys can also, conversely accelerate transfers of material from the continental shelf or even from continents to the deep waters.

To this must be added the ecosystems that exploit the energy stored in the heart of the ocean floor as magmatic heat or hydrocarbons. Hydrothermal vent ecosystems or those associated to methane seeps have in common the local production of organic matter by chemosynthetic microorganisms from CO_2 or methane. Limited to exchange zones between the lithosphere and hydrosphere, they are home to communities as opulent as those of the most productive photosynthetic marine ecosystems. Their influence in the major ocean processes, particularly those driving the carbon cycle, remains to be quantified. This is especially the case concerning methane, a powerful greenhouse gas, which is partly sequestered under the form of carbonates at the seafloor. Although their vulnerability is not well evaluated, their patrimonial value in terms of foundamental knowledge (e.g. evolution of life) as well as for genetic innovations (e.g. bio-inspiration) is already largely recognized.

HOW CHANGES IN DEEP WATER PROPERTIES MAY DIRECTLY IMPACT ECOSYSTEMS

The temperature of the water masses that supply certain deep-sea basins has increased significantly in recent decades. For example, on the Hausgarten observatory site at the junction of the Arctic and Atlantic Oceans, an average increase of 0.1°C was observed between 2000 and 2008 at 2,500m depth (Soltwedel *et al.*, 2005). The temperature of the Eastern Mediterranean, as well, increased by 0.2°C between 1995 and 1999. Insufficient knowledge of natural fluctuations, however, limits the assessment of possible impacts. In this case, the observed warming followed a decrease of 0.4°C in the previous 4 years. Nevertheless, these observations reveal the possibility of a gradual warming of the deep water that could impact the species more severely when they are close to their tolerance; particularly in the polar regions where species have adapted to temperatures as low as -1°C at 1,000m or, to the opposite, in the Mediterranean sea where the temperature of deep waters does not drop below 12°C.

Ocean acidification, the other CO_2 problem, is even more critical as the pH of deep waters is already low due to CO_2 production from the breakdown of organic matter. Corrosive conditions for aragonite are anticipated in large regions of the deep ocean (Guinotte *et al.* 2006). These conditions would be unfavorable for the formation of skeletons by deep-sea corals, even if recent *ex situ* experiments show that their response to this constraint is complex. Similar to tropical coral reefs, the ecosystems they support could suffer major damage and will be difficult to predict, especially because they are largely out of our sight.

INDIRECT IMPACTS COMBINED WITH CARBON CYCLING AND SYNERGY EFFECTS

The biological pump that allows carbon transfer to the depths is also the main source of nutrition for abyssal communities. Changes in surface photosynthetic productivity and in the diversity of phytoplankton may affect the transfer. The relative decrease in diatoms, where larger cell size and mass favour sedimentation via a so-called ballast effect could notably reduce food inputs to the depths. A decrease in large fauna density (e.g. sea cucumber, echinoderms…) at the Hausgarten Arctic site, or the long-term trends at the PAP site on the Atlantic Porcupine abyssal plain, suggest that these phenomena are already occuring (Glover *et al.* 2010). In the Arctic and Antarctic regions, this phenomenon is amplified by ice melting and could significantly influence deep-sea ecosystems (Boetius *et al.* 2012).

Other indirect effects may result from the reduction of oxygen content related not only to an increase in surface photosynthetic productivity resulting in higher microbial degradation rates consuming oxygen but also to a decrease of deep water mass ventilation. For example, the deep Caribbean basin is ventilated by the transfer of cold oxygenated Atlantic waters via a sill at 1850m depth. The flow rate of these cold waters appears to have declined since the 1970s. Similarly the waters off Greenland tend to become less oxygenated, and at the same time they are warmer and saltier, reflecting a less effective ventilation (Soltwedel *et al.* 2005). The effects of a limited but persistent oxygen reduction on ocean biodiversity are poorly known. In certain cases, very poorly oxygenated waters are formed, leading to a major reduction in the depth range of the habitat for pelagic fish species like marlin and tuna (Stramma *et al.* 2010). Certain continental margins and semi-enclosed seas, such as the Black Sea, are considered as dead zones with oxygen-depleted deep waters that exclude aerobic marine organisms and especially all animal life.

CONSEQUENCES OF INTERMITTENT EVENTS UNDER ATMOSPHERIC INFLUENCE

The influence of climate on deep-sea ecosystems also occurs through intermittent phenomena that affect the circulation of water masses at local and regional scales. One of the best documented phenomenon is called 'cascading'. This phenomenon occurs irregularly and lasts several weeks. It has been described especially in the Arctic where it is linked to the formation of sea ice, and in the Mediterranean where cold, dense waters are formed in winter under the influence of winds. 'Cascades' are formed when surface waters cool down and get enriched in salt, becoming denser than deeper water. When 'flowing' into the depths, these water masses transport sediment from the shelf. These are intense events that can significantly affect ecosystems by transferring large amounts of particulate matter to the deep basins (Canals *et al.* 2006).

Changes in the intensity and frequency of these events may affect the functioning and stability of deep-sea ecosystems more rapidly than long-term changes in ocean circulation. The cycles of disturbance-recolonization due to these cascading events or other extreme events such as storms are just beginning to be described (Puscheddu *et al.* 2013, Sanchez-Vidal 2012).

DEEP SEDIMENTS: RESERVOIRS OR SOURCE OF GREENHOUSE GASES?

Continental margins are the most important ocean carbon reservoirs. Land-ocean interfaces are among the most productive marine ecosystems, and most of the carbon formed there is quickly buried in sediments. Seafloor ecosystems play a major role in this sequestration (Levin and Sibuet 2012).

The fate of fossil carbon buried in the form of hydrocarbons and, particularly, methane (as hydrates and gas) remains one of the main unknowns. The dissociation of hydrates under the effect of warming could greatly increase the concentration of GHGs in the atmosphere if methane gas is emitted massively. Conversely, methane dissolved in seawater is efficiently consumed by microorganisms in the water column and sediment. The dissociation of hydrates additionnally affect seafloor ecosystems, through physical disturbance of the sediment (volcanic mud eruption), limiting the effectiveness of this biological filter.

A MORE DETAILED GLOBAL VIEW, BUT FEW LONG-TERM OBSERVATIONS

Given the difficulty of accessing this vast and fragmented environment where instruments are exposed to extreme physical constraints, observation data at scales relevant to climate are still sparse. However, current technologies are rapidly evolving and series of multi-annual data documenting the physical properties of water masses are becoming available through deep-sea observatories. Observations on scales representative of climatic impacts (10-50 years) are are still lacking, however.

Moreover, observation from satellites now allow more precise and detailed mapping of deep-sea 'hot-spots' and fleets of drifting buoys have brought better views of regional ocean circulation dynamics. The role of the seafloor heterogeneity and its role in carbon exchange and recycling of essential plankton nutrients (nitrogen, phosphorus, iron in particular) is being identified as essential on local scales, although the importance of this relief effect in the overall global balance has yet to be established.

Knowledge of ecological variability in the deep ocean, is still based on a limited number of data sets obtained during oceanographic expeditions. The technological advances of recent decades (ROV, AUV and HD imaging) have made these environments more accessible, and promote their exploration. A few dozen of deep sites, at most, have been the subject of multi-annual monitoring and allows a first analysis of the causes of variability (Glover *et al.* 2010).

A NEED FOR INTEGRATED EXPERIMENTAL STUDIES

To assess the impact of climate-driven disturbances, it is essential to set up observation sites and long-term experiments to investigate the synergistic effects of different phenomena on deep-sea habitats and their biological and functional diversity (Mora *et al.* 2013). On this basis it would be possible to consider mechanistic models, but this requires taking into account multiple influences on organisms and the response of whole communities to change. The latter is undoubtedly the most difficult to grasp.

The sensitivity of deep ecosystems to climate change largely depends on the plasticity of species, and particularly of the so-called foundation species or engineers of the ecosystem. The deep-sea corals for example play a major role in building reef-like structures that form the habitat for many other species. The sensitivity of these species to environmental changes is complex and in situ studies are just beginning. The acclimatation and adaptation capacities may vary from one region to another (as for example in the Red Sea where metabolic adaptations allow their development at 20° C, while elsewhere their temperature upper range is estimated to be around 13° C; Roder *et al.* 2013).

The capacity of larvae to dispersed between deep-sea hotspots, isolated in space but connected to each other by ocean water circulation, remains an enigma for most of their endemic species. Again climate change appears likely to play a role. Even if we are unable to describe the consequences of combined climate change effects, studies dedicated to the most iconic hydrothermal species are providing first insights to this issue. Sporadic events in the circulation of deep water masses induced by atmospheric events such as cyclones, for example, were only recently identified among the potential factors that play a role in larval migration at depth. Under the influence of El Nino and La Nina oscillations, it was recently shown that episodic hurricanes off Mexico generate eddies that extend from the surface to 2500m deep, promoting larval transport over distances of several hundred kilometers between usually isolated ecosystems (Adams *et al.*, 2011).

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