The deep ocean in a changing climate

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The largest inhabited space on the planet is located more than 200 m below the ocean surface, where darkness is almost total. These ocean depths play a major role in mitigating climate change through heat and anthropogenic CO_2 sequestration. In addition to undergoing gradual warming and acidification, deep waters are less well ventilated, which reduces oxygen availability. Changes in surface phytoplankton production also affect the quantity and quality of nutrient resources available in the deep ocean. What will be the consequences of these disturbances on this vast and largely unexplored environment? Models set the framework and predict 50 to 80-year trends, but struggle to provide answers about the near future. Since observations reveal faster changes than model predictions do, there is a pressing need to adapt human activities to address potential risks. Many ecosystem services are linked to exchanges between the seabed and ocean surface ecosystems. These ecosystems play a role in long-term CO_2 and CH_4 sequestration by trapping carbon in the form of carbonates or organic matter (living organisms, debris, particles, or compounds dissolved in water). Increasing temperature, and decreasing oxygen and pH affect species distribution and, more generally, the entire nutrient cycle on which sustainable economic activities, such as artisanal fisheries, are based. Without a better understanding of these phenomena in space and over time, anticipating the consequences of climate change on biodiversity and deep ecosystems remains very difficult, as does assessing the impacts of new industrial activities combining with climate change consequences. Implementing key climate change adaptation measures must be based on an unprecedented effort to acquire the new knowledge needed to establish a legislative framework and effective management tools.

A THERMAL BUFFER FOR THE CLIMATE

Covering nearly two thirds of the planet's surface and representing 98% of the ocean volume, the great depths still appear an inaccessible and marginal zone. Yet the ecological footprint of human activities is rapidly growing, and the deep ocean is now at the heart of major sustainable development challenges. The problems posed by extractive activities, including deep-sea fishing, increasingly deeper oil and gas exploration and exploitation, and deep seabed mining projects, which are by definition "unsustainable", are well known. What is less widely known is that submarine canyons, seamounts and other "animal forests" of sponges and deep-water corals are essential to the survival of some fish species. They also support local fisheries and are an integral part of their sustainability. So-called "ecosystem services" that some seek to quantify economically involve many other functions of these ecosystems. Globally, deep waters and the ocean floor play a predominant role in climate change mitigation, their volume acting as a thermal buffer against climate warming. Almost 30% of anthropogenic CO_2 emissions are stored in the ocean — half of which are sequestered at depths exceeding 400 m, and one quarter below 1,000 m (Gruber *et al.*, 2019). 90% of the heat trapped by greenhouse gases has been absorbed by the ocean — almost half of which is stored at depths exceeding 700 m (42% of the total heat, Abraham *et al.*, 2013).

WHAT CLIMATE MODELS SAY OR DO NOT SAY ABOUT CHANGES IN DEEP WATERS

Climate models describe with increasing precision deep-water warming and acidification, resulting of CO_2 and heat accumulation. They also simulate the transport of organic matter from the surface, where it is produced, to the great depths. In addition, models predict a general decline in organic matter and its progressive consumption by marine fauna and microorganisms during sedimentation (Bopp *et al.*, 2013). According to the atmospheric CO_2 emission scenarios, a decrease in pH, oxygen, and of the quantity of organic nutritive resources exported to deep waters is expected to occur in most deep ocean layers over the next few decades. The rate and magnitude of these changes vary greatly from one ocean region to another. Moreover, they combine with natural variations in seawater conditions with depth, amplifying the decrease in pH, oxygen and organic particulate concentration. Model predictions allow comparing changes among seabed ecosystems and better assess their vulnerability (Mora *et al.*, 2013; Sweetman *et al.*, 2017). These models are even being used to anticipate risks when establishing marine protection areas, such as done for Vulnerable Marine Ecosystems, where FAO limits fishing activities (FAO, 2019).

Factors likely to have a significant impact on biodiversity and the functions it provides depend on the ecosystem type. Scientists gave early warning of the vulnerability of ecosystems relying on deep-water coral colonies (Guinotte, 2006). In the absence of photosynthesis, deep waters are naturally richer in CO_2 and more acidic than surface waters. In many regions, the increase in CO_2 concentrations in the deep ocean, confirmed by long-term series of observation, creates corrosive conditions under which various deep-water coral species should grow their calcareous skeleton made of aragonite. Gehlen *et al.* (2015) predict that most seamount peaks in the North Atlantic Ocean will be affected by this phenomenon. In addition, nutrient-depleted abyssal plains are likely to lose a large share of their macrofauna as a result of increasingly scarce nutrient resources due to changing surface phytoplankton production.

Lastly, oxygen depletion is undoubtedly one of the most significant threats to deep ocean biodiversity and the functions it provides. The situation is particularly critical at intermediate depths (200-700 m), where oxygen concentration is already reduced due to oxygen consumption by microorganisms decomposing organic matter. Oxygen concentration sometimes reaches levels below which all animal life is excluded. These "dead zones", where only microorganisms proliferate, are expanding horizontally and thickening, thereby reducing the habitat of many fish or invertebrate species (Gilly *et al.*, 2013).

These estimates are still very uncertain for many deep-sea regions where measurements are too scarce to calibrate models. Nevertheless, observations confirm that the amount of oxygen in the ocean has decreased by almost 2% per decade since 1960, and low ventilation of deep waters accounts for a large part of the continued decrease in the mean oxygen concentration observed at depths below 1,000 m (Schmidtko *et al.*, 2017). More importantly, oxygen minimum zone expansion exceeds model predictions, and oxygen depletion can reach -4% per decade on the periphery of some of these zones, where critical thresholds are then exceeded (Schmidtko et al., 2017).

As a result, many species' habitats are reduced. For instance, some zooplankton species that migrate from the surface to deep ocean layers during the day and large pelagic fish with high oxygen requirements that dive several hundred meters to feed, are impacted (Stramma *et al.*, 2010, Gilly *et al.*, 2013). Others, such as the Humboldt squid which hunts at the boundary of hypoxic waters (hypoxic zone), benefit from these conditions.

In fact, the physical, chemical, or biological changes occurring at the surface can spread to deeper waters faster than the circulation of large seawater masses on which climate models are based would suggest. Deep ocean ecosystems are closely linked to what is happening at the surface. Particle sedimentation (marine snow), massive deposits of large organisms (salps), daily or seasonal migrations of nekton (free-swimming fish, crustaceans and invertebrates), gyres or downwellings (sinking of surface waters down to the depths under the influence of wind) are all episodic phenomena that directly propagate the disturbances affecting surface ecosystems in the deep ocean.

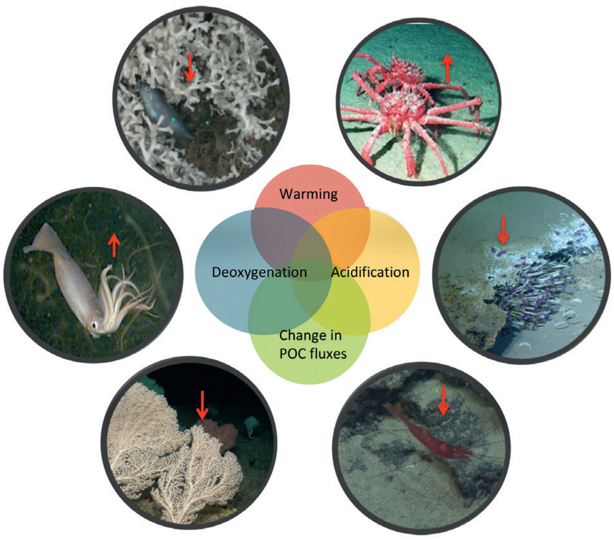

Fig.1 — Deep species exposed to various climate stress factors that are likely to cause major ecological changes. Clockwise: The red king crab is invading the Antarctic Peninsula margin as a result of Atlantic water warming. Fauna living in carbonate crusts in the vicinity of methane seeps, influenced by warming and acidification. Deep-sea shrimps on seamount flanks of the Mediterranean Sea affected by the reduction of organic particle fluxes at depth, gorgonian on the mid-Atlantic ridge exposed to change in organic resource supply and deoxygenation, The Humboldt squid is taking advantage of the decrease in oxygen levels in eastern Pacific mid-depth waters. Cold-water coral is subject to ocean acidification and deoxygenation and is particularly sensitive to water warming in the Mediterranean Sea.

Photo credits: K. Heirman and C. Smith, NSF LARISSA and Ghent University HOLANT projects. C. Pierre & J. Sarazin Ifremer-CNRS, MEDECO cruise 2008, M. Carreiro-Silva & T. Morato, IMAR - University of the Azores, Ocean Azul Fondation). N. Le Bris Ifremer-SU-CNRS CYLICE-ECO cruise 2018. NOAA/MBARI 2006. N. Le Bris, UPMC, Fondation Total, CNRS.

Seabed relief also plays a role in this propagation by locally enhancing vertical mixing of water masses, favoring the upwelling of nutrient-rich deep water, acceleration of currents, and sediment transport to the abyssal zone. The typical kilometer scale of such seafloor features is however lower than the resolution of climate models and they are not accounted. Seamounts, canyons, valleys and faults in oceanic ridges create a mosaic of rocky and sedimentary habitats, in which seafloor biological communities depend on those thriving along the water column. In addition to seabed relief, multiple hydrological structures promote exchanges across various depth ranges, such as fronts, gyres, upwellings, deep convections, and downwellings. All these dynamic interactions are influenced by many climate-related factors, making scientific studies particularly complex when it comes to understanding local interactions and consequences.

So far, detailed bathymetric mapping (*i.e.*, a fine relief description, representative of deep habitats, with a resolution of less than 100 m) has only been conducted on less than 10% of the ocean floor.

WHY WORRY ABOUT DEEP OCEAN CHANGES IN A CONTEXT OF SUSTAINABLE DEVELOPMENT?

The ocean floor and deep waters are already impacted by human activities to varying degrees, from the continental slope to the deepest trenches, due to the accumulation of persistent pollutants and debris, landscape alteration and massive habitat destruction by trawlers, ocean mining disposal and toxic waste dumping. However, these environments are often ignored in discussions on climate change impacts, biodiversity protection, or sustainable development issues. Beyond the regulations imposed on resource exploitation, does the deep ocean deserve special attention? Should its alteration be considered minor because it does not directly deprive humans of habitat or food?

In 1840, researchers declared that life disappeared at depth exceeding 550 m, based on the assumption that marine species cannot survive in the absence of food freshly produced by planktonic micro-algae. This statement was wrong. Since the major expeditions of the late 19th century, deep ocean exploration has revealed a wide variety of dark habitats, which keep growing in number with the advent of robotic exploration and mapping. The ocean floor and deep waters are home to exceptional biodiversity as diverse as the available food sources are, from energy-poor marine snow to chemosynthetic bacteria capable of exploiting chemical compounds issued from the sub-seafloor to grow, whale carcasses or wood falls on the abyssal plains. The inventory of services associated with these ecosystems is just beginning, but the variety of metabolic innovations in deep-sea lineages facing extreme environmental conditions (temperature, acidity, toxicity, corrosive or oxidative stress) constitutes an outstanding heritage (Armstrong *et al.*, 2012; Thurber *et al.*, 2014).

Among the ecosystem services sustained by the deep ocean, carbon dioxide (CO_2) and methane (CH_4) sequestration, nutrient recycling, and the availability of shelter and food for the juveniles of many species are the most cited. The deep ocean is the largest carbon reservoir on Earth. Seabed ecosystems contribute to sequester carbon in several ways, by converting methane and carbon dioxide into carbonate rocks or through deep-sea biomass (Marlow *et al.*, 2014; Trueman *et al.*, 2014; James *et al.*, 2016). This long-ignored deep "blue carbon" now appears to be a significant component of anthropogenic CO_2 sequestration (Boyd *et al.*, 2019).

WHAT KNOWLEDGE IS NEEDED TO ASSESS THREATS AND IDENTIFY EFFECTIVE PROTECTIVE MEASURES?

Research on the vulnerability of terrestrial and marine ecosystems to climate stressors has highlighted the complexity of physiological responses and acclimatization and adaptation capabilities, depending on species' life cycles, potential population migrations and geographical areas. The combination of ocean warming and other stress factors is a crucial element for marine species. The physiological tolerance thresholds of species to hypoxia depend, among other parameters, on temperature and CO_2 concentration (Pörtner, 2010). Adaptation to acidification, as demonstrated for several deep-water coral species, is, however, being undermined by rising temperature (Lunden *et al.*, 2014; Gori *et al.*, 2016).

Climate stress factors, temperature, acidity, oxygen, and nutrient resources must be assessed across the habitats currently occupied by these species and those likely to shelter them in the future, and their natural variability taken into account.

The spatial distribution of deep species is strongly influenced by abrupt transitions between oxygen-depleted waters and those more oxygenated at the surface or in the abyssal zone, along the continental slope, on seamount sides and canyon walls. Even minor changes in deep water temperature and oxygen gradients can cause dominant species turnover and change the entire ecosystem structure. Scientists have suggested that this occurred in the Antarctic Peninsula, where a two-tenths of a degree warming over 30 years allowed alien red king crabs to invade the ecosystem. This predator's distribution area on the continental margin has thus spread to the detriment of many species (Smith *et al.*, 2014).

There are many unknowns in establishing environmental management measures for industrial activities, supporting the development of sustainable economic activities, or implementing deep habitat conservation policies in national and international waters. The current state of knowledge is too fragmented to accurately anticipate the impacts of climate change and requires the expansion of deep-water observation programs on relevant spatial and temporal scales. Given the tools used, their very high cost, and the need for specialized technical expertise shared by too few countries, mapping the risk is out of reach at present. Biodiversity and productivity "hotspots" on the ocean floor are mostly composed of assemblages, with links ranging from a few tens of meters to a few kilometers. Furthermore, most deep ecosystems are subject to seasonal and episodic phenomena driving their proper functioning, such as food intake or deep-water ventilation (Danovaro *et al.*, 2004; Smith *et al.*, 2012; Soltwedel *et al.*, 2016).

Knowledge is currently largely lacking to better understand how these intermittent events influence species' interactions with each other and with their environment. In particular, there is a lack of multidecadal ecological studies for the most vulnerable ecosystems facing cumulative pressures of exploitation and climate change (Smith *et al.*, 2013).

Building realistic vulnerability scenarios and incorporating them into marine public policies is a challenge that will have to be taken up in order to address sustainable development issues and effectively assess the impacts of large-scale human activities on deep marine areas. New international regulations (*e.g.* regarding mining) and treaties (*e.g.*, on marine biodiversity beyond national jurisdiction), as well as environmental management and spatial planning will need to include the deep ocean's role in the global climate and its processes.

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