The Southern Ocean

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The southern part of the global ocean is furthest away from any industrial or human activity. Yet since several decades, many observers have reported significant changes within the ecosystems as well their indigenous species. In most cases, these disturbances have been connected to the consequences of human activities, whether indirect (increased temperature, changes in seasonal sea ice, consequences of the hole in the ozone layer, acidification) or direct (fisheries exploitation of living resources). The magnitude of these pressures varies across the different regions of the Southern Ocean. Although the image of an undiversified ocean is generally etched in the collective mind, the biogeographic atlas of the Southern Ocean (De Broyer *et al.*, 2014) in which over 9064 species have been identified, shows that this is certainly not the case. Disturbances that are now being observed are presumed to modify the functioning of these ecosystems and trophic webs. This also concerns the modification of habitats of pelagic and benthic species, from primary producers to top predators, from coastal to deep-water species, from the sub-Antarctic ice-free areas to sea ice-covered zones. A well-known example is the modification of the sea ice regime around the Antarctic Peninsula although changes have been observed at variable degrees of intensity all around the continent. This ice is nonetheless necessary for the completion of the life cycle of many species, such as Antarctic krill whose exceptional biomass is at the basis of the diet of many predators including birds or marine mammals. Icebergs or the recent dislocation of large ice shelves are also known to have a major impact on benthic communities. Finally, the sub-Antarctic areas, at the northern boundary of the Southern Ocean might be the most affected by climate change. In this context, it is important to estimate how the biodiversity of this ocean, which has been accustomed to extreme conditions for almost 34 million years, will be able to adapt to these new conditions.

INTRODUCTION

The Southern Ocean is the last ocean to have been explored. Located in the southern hemisphere, it is the only ocean which is not surrounded by continents (figure 1). The Antarctic continent at the South Pole is a land of science that is internationally managed by the Antarctic Treaty. This ocean therefore has an opposite configuration to the other Polar Ocean, the Arctic Ocean, which is surrounded by the American and Eurasian continents with the neighbouring countries exercising their sovereignty over it.

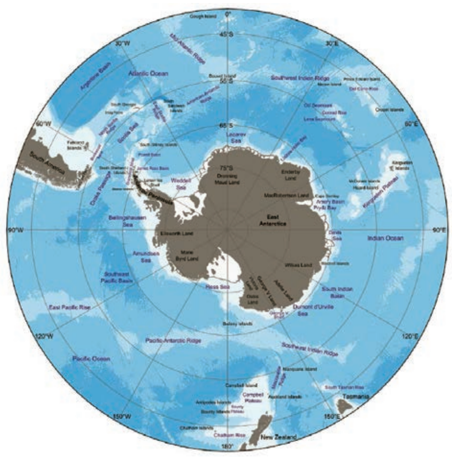

Fig.1 — The Southern Ocean (De Broyer *et al.*, 2014).

Antarctica and the Southern Ocean have not always been extreme environments. Antarctica used to be more temperate when it belonged to Gondwana, the great southern continent. Nearly 34 million years ago (Crame, 2014), it gradually detached from the other southern hemisphere continents which had allowed the opening of the Drake Passage. The Southern Ocean became hydrologically isolated with more than 4°C cooling of surface waters. This is when the formation of sea ice is supposed to have begun. Observations suggest several cooling events causing significant faunal changes with the extinction of a number of species (Crame, 2014).

The knowledge of this history is important to understand what the consequences of climate change could be on a biodiversity that has adapted to extreme conditions over such a long period. It is therefore necessary to assess the present state of the Southern Ocean marine biodiversity. All present knowledge on biodiversity has been compiled in the recent biogeographic atlas of the Southern Ocean (De Broyer *et al.*, 2014). Our knowledge began with the scientific expeditions conducted in 1772-1775 by Captain James Cook. It increased with numerous famous missions at sea (De Broyer *et al.*, 2014) until the recent International Polar Year (2007-2009) with the "Census of Antarctic Marine Life" program (2005-2010). During this program, 18 research vessels sailed the Southern Ocean to study all aspects of its biodiversity. The phylogeny of these species was also assessed. At a global level, species biogeography had to be ascertained by studying their potential habitats using statistical analysis and modelling tools, similarly to Cuzin *et al.* (2014) for euphausiids (krill), Duhamel *et al.* (2014) for fish or Eléaume *et al.* (2014) and Saucède *et al.* (2014) for echinoderms, for example. Obviously, temperature is one of the major factors controlling the biogeography of these species. Several studies have attempted to define ecoregions characterized by their abiotic hydrological and geographical features (Longhurst, 2007; Raymond, 2014) and by differences in prevailing species assemblages (Koubbi *et al.*, 2011; Hosie *et al.*, 2014). Despite these efforts, many unexplored regions still exist both along the Antarctica coastline as well as offshore. Moreover, deep waters generally still remain poorly understood in spite of many recent studies (Brandt *et al.*, 2014; Rogers and Linse, 2014).

While it is necessary to consider the consequences of environmental change, this concern should be rapidly included in ecosystem management programs by the evaluation of areas to be protected. However, the limits of the Southern Ocean and the reasons why its biodiversity is so exceptional should first be defined.

WHAT ARE THE TYPICAL BOUNDARIES OF HABITATS IN THE SOUTHERN OCEAN?

The definition of oceanic regions begins with the analysis of oceanographic data (Post *et al.*, 2014). The Southern Ocean communicates in the North with the Atlantic, Indian and Pacific Oceans.

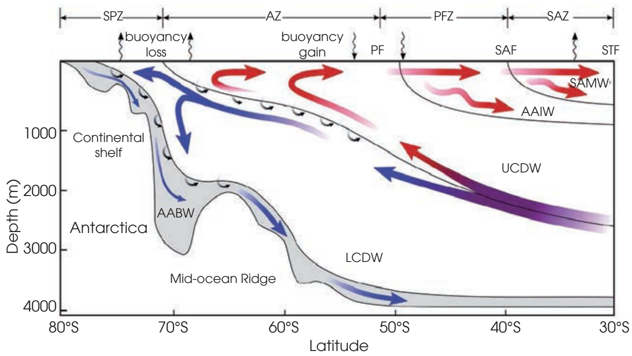

Fig.2 — Latitudinal section showing the water masses and fronts as a function of depth from the Antarctic continent to the Sub-Tropical Front (STF) (Post *et al.*, 2014.). The Antarctic Polar Front (APF) and the Sub-Antarctic Front (SAF) are shown. The fronts delimit different areas: the Sub-Antarctic zone (SAZ), the Polar Frontal Zone (PFZ), the Antarctic Zone (AZ) and Sub-Polar Zone (SPZ). The different water masses are illustrated: the Sub-Antarctic Modal Water (SAMW), the Antarctic Intermediate Water (AAIW), the Upper Circumpolar Deep Water (UCDW), the Lower Circumpolar Deep Water (LCDW) and the Antarctic Bottom Water (AABW). The arrows indicate the flow of water masses. Note that Antarctic Bottom Water is formed on the continental shelf and then circulates deeply.

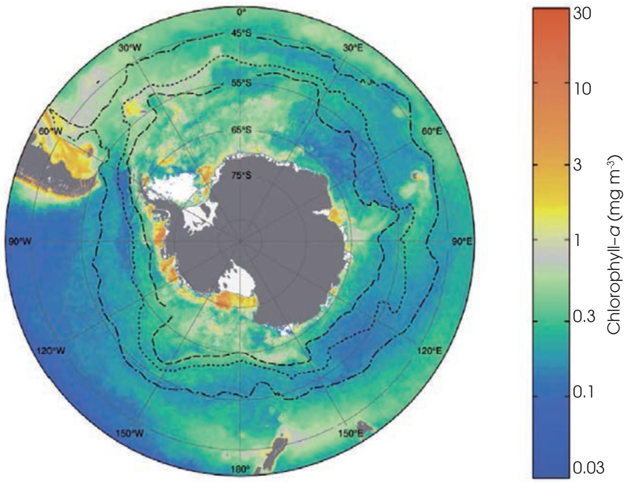

Fig.3 — Average summer chlorophyll a concentrations between 2002 and 2010 estimated by Aqua MODIS satellite data (Post *et al.*, 2014.). From South to North, the dotted lines mark the southern boundary of the Antarctic Circumpolar Current, the average position of the Antarctic Polar Front and Sub-Antarctic Front, respectively.

There are several major fronts in the Southern Ocean (figure 2). First of all, the Subtropical Front (STF) is defined as the northern limit of this ocean. Heading southwards, the Sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF) are encountered. The Sub-Antarctic Zone extends between the STF and the SAF, the Polar Frontal Zone between the APF and SAF and the Antarctic area south of the APF. Further south, other fronts mark the southern boundary of the Antarctic Circumpolar Current. These fronts cannot be considered as fixed barriers, as they vary latitudinally according to seasonal climate forcing. Some of these fronts are the site of intense phytoplankton production that induces secondary plankton production (figure 3). This is the case in the vicinity of Sub-Antarctic Islands that enrich the environment with iron and other nutrients useful for phytoplankton growth. The area South of these islands, between the northern limit of the APF and the boundary of the seasonal ice zone, is under the influence of the Antarctic Circumpolar Current, with permanently open sea and no ice-cover. This is a particular area as it is characterized as a HNLC region with high nutrient concentrations but low chlorophyll or phytoplankton concentrations. This can be explained by the lack of certain essential elements, such as iron, that limit phytoplankton growth.

However, more than half of the Southern Ocean is characterized by a seasonal ice zone (figure 4) around the Antarctic continent. The highest concentrations in chlorophyll a, are observed during the summer (figure 3). Significant changes in the extent, in the duration of sea ice or in its thickness have been observed at the West Antarctic Peninsula, where the area of sea ice has been observed to decrease by 5 to 6% per decade. However, this trend does not apply all around the continent since, conversely, an increase of 4.5 to 5% has been observed in the Ross Sea, (Constable *et al.*, 2014). Sea ice extent is not the only factor to take into account. The duration of the presence of seasonal sea ice has also decreased in the Western region of the Antarctic Peninsula with an equivalent loss in number of days to what has been observed in the Arctic. Once again, these are regional observations, since opposite observations have been made in other sectors,

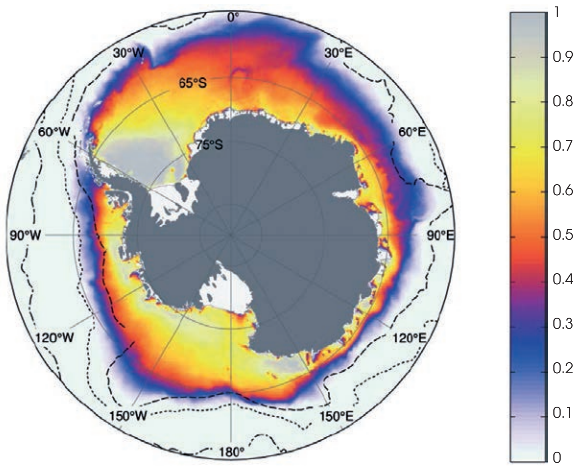

Fig.4 — Map of the proportion of 85% concentration of annual sea ice duration (Post et al, 2014.). Polynyas are visible along the continent (blue colours). Dashes indicate the position of the southern front of the Antarctic Circumpolar Current; the dots represent the average position of the Antarctic Polar Front and the dotted line with dashes in the North, the position of the Sub-Antarctic Front.

thus showing that the development of the sea ice involves different factors. Close to the continent, a number of areas are free of ice either all year round or periodically. These areas, called polynyas, are often located in the coastal zone where the topography and prevailing winds prevent sea ice from accumulating (figure 4). Polynyas have an important role for biological production, as during spring they allow light to penetrate into the water while the adjacent ice-covered areas remain in the dark. The onset of primary production comes with the first signs of spring and as the ice begins to break, thus feeding both the pelagic and benthic ecosystems.

Longhurst, in the "Ecological Geography of the Sea," identified four so-called "biogeochemical" provinces within the polar biome including the Southern Ocean. These provinces have been appointed respectively: South Subtropical Convergence province (SSTC), Sub-Antarctic water ring Province (SANT), Antarctic province (ANTA) and Polar Southern Province (APLR) (figure 5). Each of these provinces theoretically delimits the particular types of environmental or hydrological forcing that can be encountered. Longhurst spatially defined the distribution of these provinces using satellite observations combined with oceanographic and biological samples collected during cruises.

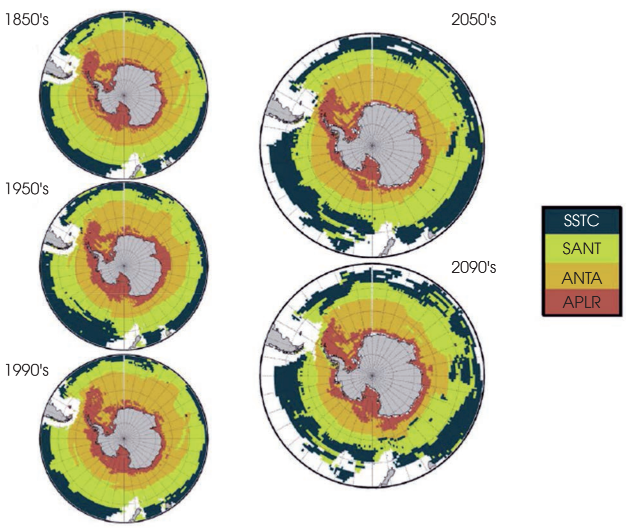

Fig.5 — Distribution of biogeochemical provinces of the Southern Ocean for the 1850, 1950 and 1990 decades as well as their projection for 2050 and 2100 (Reygondeau and Huettmann, 2014). The current provinces have been defined by Longhurst (2007).

Recently, Reygondeau and Huettmann (2014) have statistically characterized these biogeochemical provinces. The methodology they developed was used to assess the changes in the spatial distribution of these 4 provinces as a function of seasonal and interannual variations (Reygondeau *et al.*, 2013) or over a long-term. The results of the study presented in figure 5 point to a poleward shift of all southern provinces. However, the speed of change appears to be different between provinces (figure 6). In fact, the Sub-Antarctic provinces (SSTC and SANT) seem to be most strongly affected by variations in the environmental conditions induced by climate change. Their distribution centres are more rapidly displaced southwards than the polar provinces (ANTA and APLR). These changes result in a drastic reduction (approximately 15%) of the total area of the Sub-Antarctic zone while the northern Subtropical systems are expanding. Only the Southern zones maintain their initial characteristics (loss <5% of their areas).

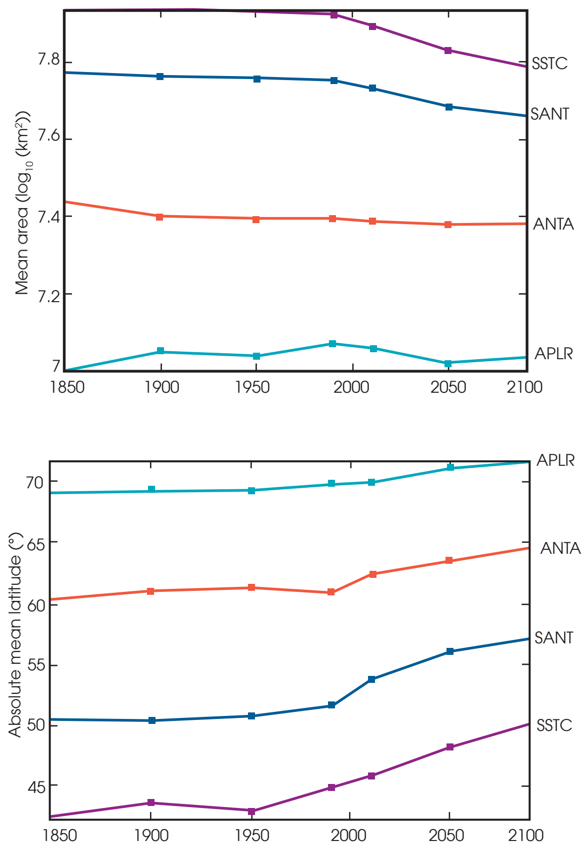

Fig.6 — Evolution of the mean absolute latitude and area of each biogeochemical province (Reygondeau and Huettmann, 2014).

These observed changes in biogeochemical provinces of the Southern Ocean can be directly connected to the various effects caused by climate change. Analyses carried out under the NEREUS consortium (figure 7) used a set of environmental parameters that structure the marine environment (temperature, salinity, oxygen concentration, primary production, pH, % ice cover and U and V direction components of currents). Results confirm the spatial heterogeneity of the amplitude and driving forces of climate change in the Southern Ocean. Areas further North (sub-Antarctic areas) have been most severely affected by the different effects of climate change (figure 7a) and particularly by the increase in sea surface temperatures (figure 7b). The more southerly zones (ANTA and APLR) appear to remain best preserved from the severity of global change. However, certain parameters presenting a structural role in the development of marine species seem to have been altered in these latter areas (figure 7b). In fact, despite lesser variations compared to the sub-Antarctic areas, the changes in ice-cover, surface temperature and pH and primary production in the southern areas are significant. Even though the magnitude of these changes remains lower than that of the sub-Antarctic areas, like a sword of Damocles, their effects hang over the endemic organisms that are adapted to extreme conditions, thus menacing the biodiversity of these areas.

A UNIQUE BIODIVERSITY CONFRONTED TO MAJOR CHANGES

The different species in the Southern Ocean have adapted to extreme living conditions. Although the degree of impact of global warming varies according to the area in the Southern Ocean, it is particularly significant in the Antarctic Peninsula and around the sub-Antarctic islands (Constable *et al.*, 2014). Exposure to UV radiation has increased due to the presence of the Ozone Hole whose extent is at its maximum during the southern hemisphere spring season. Acidification has also become a new threat. Species habitats, ecosystems and food webs mechanisms are likely to suffer from these changes. Moreover, a number of anthropogenic impacts add to these threats, such as the exploitation of living resources.

Antarctic benthos

The Antarctic benthos is characterized by large biodiversity, a high endemism and, in some areas, the highest observed levels of biomass. In terms of composition, some groups are absent or poorly represented in the Southern Ocean (stomatopods, balanomorph barnacles, decapod "walkers", bivalves). Brachyuran crabs are totally absent from the Antarctic region while there is fossil evidence of their presence before

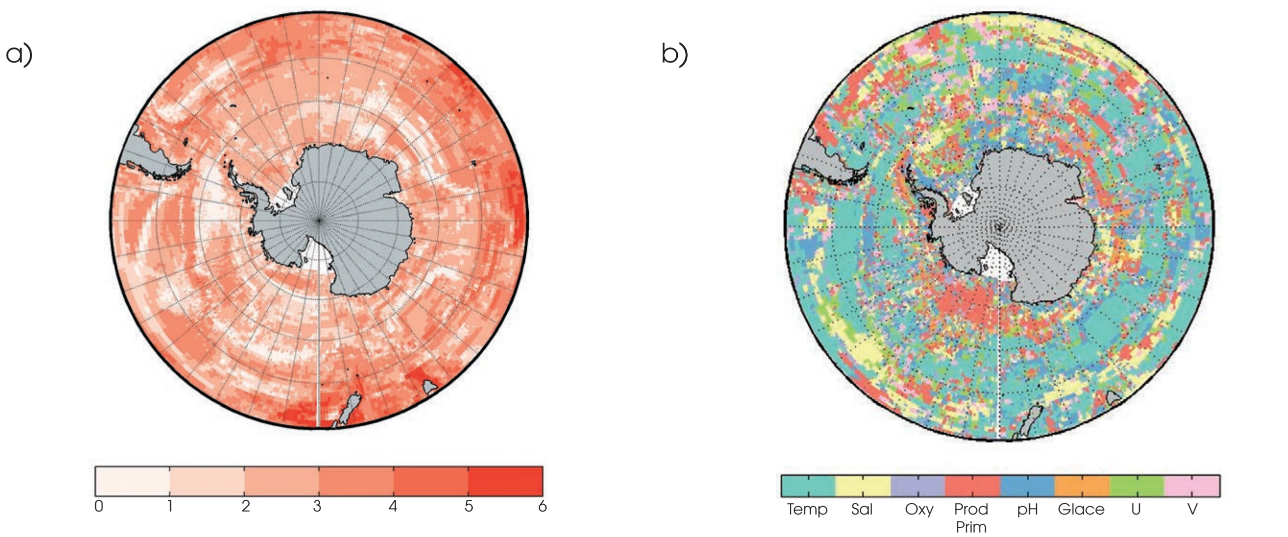

Fig.7 — (a): Status of environmental disturbances and (b) structuring parameter changes. Temperature (Temp), Salinity (Sal), oxygen concentration (0_2), Primary production (PP), pH; % ice cover; U and V, components of the current.

polar waters cooled down during the Cenozoic. Other groups, however, have radiated intensely in these waters. It is the case of the highly diverse pycnogonids, amphipods and isopods, probably partly due - for the latter two groups – to the occupation of niches left vacant by the disappearance of the decapods.

Nowadays, species diversity of the Antarctic benthos appears to have been largely underestimated. Firstly, the molecular approach has highlighted many cryptic species (Held, 2014; Eléaume *et al.* 2014; Havermans, 2014.) Secondly, large areas of the Southern Ocean still remain to be documented, in particular the deep waters where the first systematic surveys have yielded the existence of many unknown species (Brandt *et al.*, 2014).

The molecular approach has also challenged the paradigm of a circumpolar distribution of benthic species: many species, initially considered as circumpolar or even cosmopolitan, have proved to rather represent species complexes with a restricted and often allopatric distribution. Nonetheless, the same molecular approach also confirmed the broad circumpolar distribution of other species.

The macrobenthic populations of the continental shelf can be remarkably abundant: in some parts they even erect massive biological structures, essentially composed of suspension feeders such as sponges, bryozoans, hydrocorals, ascidians or crinoids. These represent a three-dimensional substrate, a food resource as well as symbiotic opportunities for many other organisms. Nevertheless, the spatial distribution of these populations, as well as their composition, abundance and biomass, or their eco-functional role can all vary greatly according to the depth or geography (Gutt *et al.*, 2014).

The potential impacts of climate change (temperature, pH, ice cover, iceberg scouring, quantity and quality of food resources) on benthic communities are still difficult to determine. There remains a lack of sufficient knowledge on the life cycles and eco-functional role of benthic species, on their different degrees of sensitivity to environmental factors involved, on their multiple interactions, as well as on the different spatial and temporal scale factors governing the great diversity of benthic populations (see Ingels *et al.*, 2012).

Recent experimental approaches on the potential vulnerability of selected benthic organisms (sea urchins, foraminifera...) towards the impacts of physical changes in the environment (especially temperature increase and fall in pH) have clearly evidenced the lethal physiological and functional limits of these endemic species (Peck *et al.*, 2010). However, these results cannot yet be generalised to the entire benthic biodiversity (Kaiser *et al.*, 2013).

The scouring of the seabed by icebergs is a physical process that most strongly affects the benthic communities of the Antarctic continental shelf down to 300 m depth or more. Increasingly warmer waters now tend to undermine the base of the ice shelves surrounding the continent, leading to an increase in the calving of icebergs with a subsequently greater impact on the pericontinental benthos.

Demersal Antarctic Fish

The case of Antarctic demersal fish is also unique. Their evolutionary history has been studied and one of its groups, the Notothenioidei are nearly 86% endemic to the Southern Ocean (Duhamel *et al.*, 2014). Originally derived from temperate waters, they adapted to the Southern Ocean during its cooling period. The most polar species have thus developed antifreeze glycoproteins that prevent their blood and tissues from crystallizing in freezing sea water temperatures. During the cooling period, these fish colonized all available ecological niches that were left following the extinction of other species that were incapable of adapting to this change. Certain Notothenioidei species are endemic to their region or to their island, while others are circumpolar, surviving both in stable environments (such as in sponges) or in disturbed environments (e.g. icebergs). Some species of fish, like the cryopelagic fish *Pagothenia borchgrevincki* can even survive in the sea ice. A few species are commercially exploited such as the Antarctic toothfish or the Patagonian toothfish. Some of these fish, have been living in waters with low thermal variations and have lost their physiological ability to adapt to the warming environment. At present, the ecological and economic consequences of global warming still remain difficult to conceive.

Pelagic organisms

The spatio-temporal patterns that influence pelagic organisms, whether they are plankton, pelagic fish or cephalopods, are closely related to the structures of water masses, to the currents, and to the characteristics of the frontal zones and seasonal dynamics of the ice. To date, knowledge on pelagic species is mostly restricted to the epipelagic zone where the penetration of sunlight supports phytoplankton photosynthesis. Yet little is known of the deeper areas such as the mesopelagic zone where many predators prey on the very abundant mesopelagic fish.

Studies in recent decades have shown that the SAF is a major biogeographical front for several sectors of the Southern Ocean. This has been observed by Hosie *et al.* (2014) for plankton or Koubbi (1993) and Duhamel *et al.* (2014) for mesopelagic fish. The STF and APF have already been considered as such for a long time. The latitudinal distributions of many pelagic species (Atkinson *et al.*, 2012 ; Hunt and Hosie, 2005, 2006a, b) that are essential for the good functioning of the food web can be explained by the position of the three northern fronts of the Southern Ocean (STF, SAF and APF), the extent of seasonal ice and the Antarctic continental shelf. These species comprise copepods (Hosie *et al.*, 2014), euphausiids which include Antarctic krill and ice krill (Cuzin *et al.*, 2014), or mesopelagic fish (Koubbi *et al.*, 2011 and Duhamel *et al.*, 2014). In addition, there are regional peculiarities around the sub-Antarctic islands. For example, endemic species such as the planktonic copepods *Drepanopus pectinatus* can be found in the vicinity of the Crozet, Kerguelen and Heard Islands. These endemic species are not necessarily locally rare as this type of copepod dominates more than 90% of the whole zooplankton pool of the Bay of Morbihan in the Kerguelen Islands (Razouls and Razouls, 1990). Nonetheless, how they will adapt to the rise in temperatures is still uncertain. From the sub-Antarctic Zone to the continent, the distribution of pelagic species is expected to shift southwards concurrently with the southward displacement of the frontal zones (Constable *et al.*, 2014). Neritic species (associated with islands or continental shelves), however, do not migrate, which implies that the pelagic environment of many sub-Antarctic islands might undergo profound modifications.

On the Antarctic continental shelf, ice krill is dominant, while Antarctic krill takes over at the slope. This symbolic species of the Southern Ocean is greatly abundant, especially in the Atlantic sector of the Southern Ocean in the Scotia Sea and Antarctic Peninsula. Antarctic krill strongly depend on winter ice conditions that are important for their reproduction, their survival and the development of the young stages. Krill densities have fallen by almost 30% since the 1980s (Atkinson *et al.*, 2004). Reasons for explaining this decrease could primarily be the reduction in the duration and northward extension of the icecap. However, other hypotheses have been proposed, such as modifications in the abundance of predators and the increase in whale populations (Murphy *et al.*, 2012). Current preoccupations attempt to understand how the Antarctic krill-based pelagic food web might, under the effect of global warming, convert into a food web based on other species like copepods and lantern fish for example, as observed in the Polar Frontal Zone. In addition, the proliferation of gelatinous organisms such as salps might dominate the ecosystem during "warmer" episodes. This would result in years when krill abundances would be lower, while salps would unfortunately not be interesting targets for predators.

In this sea ice zone , several species spend all or part of their life cycle under the ice or in its fractures (Swadling *et al.*, 2014). Some of these species are able to adjust the duration of their various development stages to the dynamics of sea ice. For example, for the copepod *Paralabidocera antarctica*, the duration of its copepodite stages varies in conjunction with the duration of the presence of sea ice from one region of East Antarctica to another (Loots *et al.*, 2009, Swadling *et al.*, 2014). This plasticity, however, does not exist for all species.

Seabirds
With new satellite telemetry technology and marine observations, the distribution of birds and marine mammals at sea and throughout all seasons can be monitored. There are as many answers as there are species. Current and future changes are expected to alter either the habitats of these species or their tolerance and adaptation to abiotic conditions (Constable *et al.*, 2014). In the Antarctic Peninsula, declining Adelie penguin populations seem to be related to the decrease in the extent of sea ice. This differs from observations in the Ross Sea and parts of East Antarctica where ice conditions are different (Constable *et al.*, 2014). These current signs suggest that the major change should concern food webs. The trophic habitats of certain species are pelagic and depend on oceanographic structures such as fronts. For example, the Crozet Island King penguins feed south of the archipelago, in the APF area, where the mesopelagic fish that they catch are more abundant and accessible. Should the forecasted variations occur, the southward shifting of the APF will double the travelling distance for these penguins to their fishing grounds (Peron *et al.*, 2012).

PROTECT AND MONITOR ECOSYSTEMS

The major changes that have been observed for nearly 30 years are therefore essentially related to the increase in temperature, resulting in a southward shift of the frontal zones and areas described above. These changes are not uniform across the whole Southern Ocean but can reach various degrees of importance depending on the region (Constable *et al.*, 2014). Among these changes, the increase in atmospheric carbon dioxide and its absorption by the Southern Ocean causes seawater acidification (Midorikawa *et al.*, 2012). As the solubility of CO2 is higher in cold water, polar waters attack organisms with calcium carbonate shells more easily, including pteropod molluscs. These planktonic organisms are covered by a thin shell and they have an essential role as herbivores (Roberts *et al.*, 2014). Benthic invertebrates with calcified shells are also affected.

Assumptions can be made about the coming changes that the Southern Ocean will undergo. It is necessary to protect marine areas that are most outstanding for their biodiversity and also the most vulnerable. Reference scientific zones should also be established, where human impact would be reduced, so as to monitor the variations in ecosystems due to climate change. The CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) aims at assessing the marine resources of the Southern Ocean each year using an Ecosystem Approach. As part of the Antarctic Treaty system, the CCAMLR has set up monitoring programs to detect changes in the marine ecosystem (www.ccamlr.org). More recently, the CCAMLR has undertaken to define a representative system of Marine Protected Areas (MPAs). Although various MPAs have been declared around the Sub-Antarctic Islands by their sovereign states, the offshore waters outside national jurisdiction can only be protected by the consensus of the 25 members at the head of the CCAMLR. Consequently, in 2009, CCAMLR defined a first MPA of 94,000 km² surrounding the South Orkney Islands. Other candidate areas are being proposed, such as East Antarctica, the Ross Sea and soon the Weddell Sea and the Antarctic Peninsula. On each of these sectors, the objective is to maintain the biodiversity that is representative of these regions and to propose scientific reference zones. However, the outcome of these negotiations is difficult and might even last a very long time. It is crucial to justly take into account the impacts of climate change for conservation.

In the meantime, it is necessary to carry out long term monitoring of the marine ecosystem. Several international programs have been developed under the auspices of the SCAR (Scientific Committee on Antarctic Research). The SOOS program (Southern Ocean Observing System), for example, encourages the monitoring of physical, chemical and biological parameters. Another SCAR program is the SO-CPR (Southern Ocean Continuous

Plankton Recorder). The Continuous Plankton Recorder (CPR) has been used since the 1930s in the North Atlantic and has highlighted major changes in plankton communities in the Atlantic Ocean. The SO-CPR program began in 1991. Monitoring is mainly carried out on research vessels from different countries, including the "R/V Marion Dufresne" since 2013, around the French Southern and Antarctic Territories. Nearly 200 planktonic taxa have been identified in this program, which allowed the study of the spatial distribution of zooplankton as well as its seasonal and inter-annual variability. Latitudinal variations of monthly assemblages of zooplankton have been revealed by Hosie *et al.* (2014). In France, this program is part of the CNRS "Zone Atelier Antarctique" http://za-antarctique.univ-rennes1.fr. Its objectives involve the development and maintenance of a long-term observation network of polar biodiversity using the principle of LTER (Long Term Ecological Research). Research laboratories involved in the program benefit from the logistical support of the French Polar Institute: IPEV (Institut Paul Emile Victor, www.ipev.fr).

These national and international initiatives and the few examples mentioned above are essential to understand the effects of climate change, not only at the scale of the Southern Ocean but also at a regional level. Indeed, important distinctions can be made between the sub-Antarctic islands, the Antarctic Peninsula, East Antarctica and other areas of this ocean. While we are just starting to sense the consequences of these changes on the surface waters, it remains crucial to study the deep benthic and pelagic environments.

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