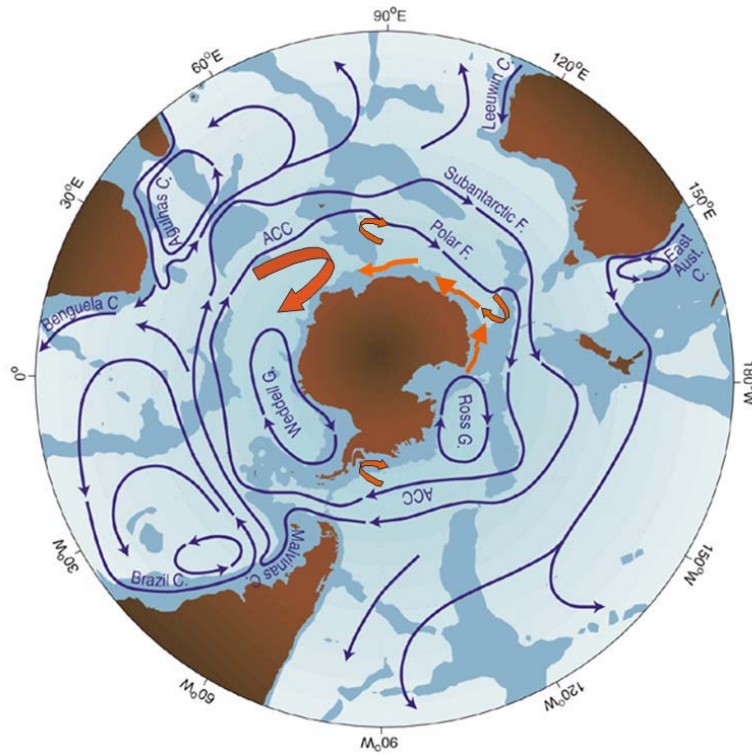# Chapter 36H. Southern Ocean

Contributors: Viviana Alder, Maurizio Azzaro, Rodrigo Hucke-Gaete, Renzo Mosetti, José Luis Orgeira, Liliana Quartino, Andrea Raya Rey, Laura Schejter, Michael Vecchione,
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The Southern Ocean is the common denomination given to the southern extrema of the Indian, Pacific and Atlantic Oceans, extending southwards to the Antarctic Continent. Its main oceanographic feature, the Antarctic Circumpolar Current (ACC), is the world's only global current, flowing eastwards around Antarctica in a closed circulation with its flow unimpeded by continents. The ACC is today the largest ocean current, and the major means of exchange of water between oceans; it is believed to be the cause of the development of Antarctic continental glaciation by reducing meridional heat transport across the Southern Ocean (e.g., Kennett, 1977; Barker et al., 2007). The formation of eddies in the Antarctic Circumpolar Current has a significant role in the distribution of plankton and in the warming observed in the Southern Ocean.
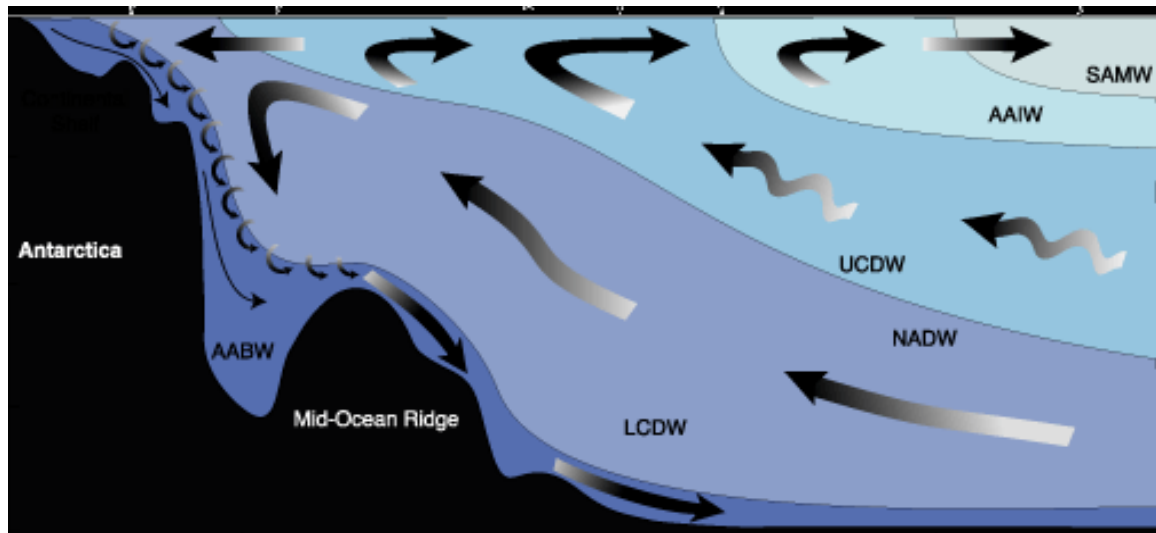
As with the ACC, the westward-flowing Antarctic Coastal Current, or East Wind Drift (EWD), is wind-driven. These two current systems are connected by a series of gyres and retroflections (e.g., gyres in the Prydz Bay region, in the Weddell Sea, in the Bellingshausen Sea) (Figure 1).

Figure 1. From Turner et al. (eds.), 2009. Schematic map of major currents south of 20ºS (F = Front; C = Current; G = Gyre) (Rintoul et al., 2001); showing (i) the Polar Front and Sub-Antarctic Front, which are the major fronts of the Antarctic Circumpolar Current; (ii) other regional currents; (iii) the Weddell and Ross Sea Gyres; and (iv) depths shallower than 3,500m shaded (all from Rintoul et al, 2001). In orange are shown (a) the cyclonic circulation west of the Kerguelen Plateau, (b) the Australian-Antarctic Gyre (south of Australia), (c) the slope current, and the (d) cyclonic circulation in the Bellingshausen Sea, as suggested by recent modelling studies (Wang and Meredith, 2008), and observations – e.g., the eastern Weddell Gyre - Prydz Bay Gyre (Smith et al., 1984), westward flow through Princess Elizabeth Trough (Heywood et al., 1999), and circulation east of Kerguelen Plateau (McCartney and Donohue, 2007).

The circumpolarity of the circulation is the principal factor determining the development of circumpolar frontal zones associated with this system of currents (Orsi et al., 1995). The biogeographical importance of these fronts was recognized practically from the beginning of Antarctic research (Tate Regan, 1914); their approximate positions are shown in Figure 2.

Figure 2. From Turner et al. (eds.), 2009. South (left) to north (right) section through the overturning circulation in the Southern Ocean. South-flowing products of deep convection in the North Atlantic are converted into upper-layer mode and intermediate waters and deeper bottom waters and returned northward. Marked are the positions of the main fronts (PF – Polar Front; SAF – Sub-Antarctic Front; and STF – Subtropical Front), and water masses (AABW – Antarctic Bottom Water; LCDW and UCDW, Lower and Upper Circumpolar Deep Waters; NADW – North Atlantic Deep Water; AAIW – Antarctic Intermediate Water and SAMW – Sub- Antarctic Mode Water) (from Speer et al., 2000, ©American Meteorological Society. Used with permission.). Note that as well as water moving north to south or *vice-versa*, it is also generally moving eastward (i.e., towards the observer in the case of this cross-section), except along the coast where coastal currents move water westward (away from the observer).

The ACC is usually considered to be the northern border of the Southern Ocean. As the ACC links the ocean basins of the Atlantic, Indian and Pacific Oceans, the waters carried in the ACC contain a mix of waters originating in different parts of the world. Water flows away from the ACC, to the north and to the south, where it becomes a primary source for the Antarctic Bottom Water. In the ACC the three oceans exchange heat, salinity and nutrients, playing an important role in the regulation of temperature and flow of the global conveyor belt. Along its course in the ACC, the water exchanges oxygen and carbon dioxide with the atmosphere while cooling; the resulting dense water sinks and transfers heat and gases into the deep ocean. These exchanges create water masses with different properties and distribution patterns which are responsible for water properties in all the world's oceans (Figure 3); see Turner et al. (eds.) (2009) for further information.
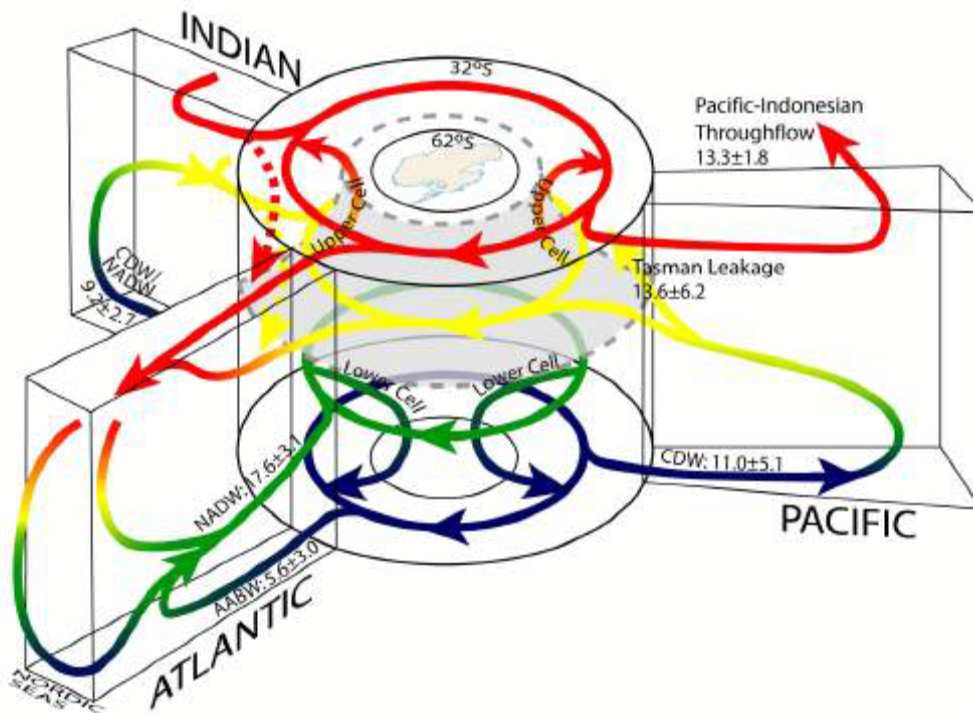
Figure 3. Model of the global ocean circulation, emphasizing the central role played by the Southern Ocean. NADW = North Atlantic Deep Water; CDW = Circumpolar Deep Water; AABW = Antarctic Bottom Water. Units are in Sverdrups (1 Sv = $10^6 \times m^3$ of water per second). The two primary overturning cells are the Upper Cell (red and yellow), and the Lower Cell (blue, green, yellow). The bottom water of the Lower Cell (blue) wells up and joins with the southward-flowing deep water (green or yellow), which connects with the upper cell (yellow and red). This demonstrates the global link between Southern Ocean convection and bottom water formation and convective processes in the Northern Hemisphere. From Lumpkin and Speer (2007; ©American Meteorological Society. Used with permission.) in Turner et al. (eds.), 2009.

About 50 per cent of the Southern Ocean is covered by ice in winter, decreasing to 10 per cent in summer. Ice cover has important effects both on climate and on the biota (e.g., Ainley et al., 2003). It is a defining structure in polar ecosystems. Antarctic sea ice is inhabited by prokaryotes, protists, algae, crustacea, worms (Schnack-Schiel et al., 1998), fish eggs and larvae (Vacchi et al., 2012), birds and seals (Ainley and DeMaster, 1990).

Overall, the Antarctic sea-ice cover has been increasing in the satellite records from 1978 to 2010 (Parkinson and Cavalieri, 2012; see Chapter 47), but modelling predicts a reduction of 33 per cent by the end of this century. This masks dramatic regional trends; declines in sea ice in the Bellingshausen Sea region have been matched by opposing increases in the Ross Sea (Maksym et al., 2012). Besides the seasonal sea ice, large portions of coastal waters are covered by permanent ice shelves. Ice shelves derive from land ice where glaciers or whole ice sheets flow towards the coastline and over the ocean surface (Trathan et al., 2013). Ice cover defines three biogeographic zones (Tréguer and Jacques, 1992): the northernmost part of the ACC, permanently ice free with high nutrient concentrations but low primary productivity

(see below); the region that is covered seasonally, where the movements of the ice margin significantly affect the cycle of primary production and zooplankton aggregations, and the sea below ice shelves where the fauna develop under unique oligotrophic conditions (Gutt et al., 2010). Of particular interest are the regions of contact between the sea-ice cover and the shelf ice, where regions of highly productive open-water areas develop (Comiso and Gordon, 1996; Smith and Comiso, 2008).

The present characteristics of the Antarctic were established at the time of the separation between Antarctica and South America, allowing the unimpeded flow of the ACC (Barker et al., 2007; Turner et al. (eds.), 2009) and the development of the Polar Front. Uncertainty exists with regard to the date of the opening, but it is widely accepted that it occurred about 34 million years ago in the Eocene/Oligocene limit (Barker et al., 2007).

From that time onwards, the oceans south of the Polar Front have been part of a single system comprising the basins of the Atlantic, Indian and Pacific Oceans and isolated from other shelf areas in the Southern Hemisphere. The Antarctic marine environment experienced a slow transition from warm water conditions to the present cold water system (from 15°C to 1.87°C) (Turner et al. (eds.), 2009). The result of evolution under these conditions is a highly specialized marine biota with high Antarctic endemism and little tolerance for warming (Bilyk and DeVries, 2011).

1. **Primary Production**

Research on Antarctic primary productivity started around 1840, the age of the pioneering expeditions to Antarctica. For some 100 years, most studies were of a qualitative nature and largely focused on net phytoplankton (>20 μm: diatoms, dinoflagellates, silicoflagellates, etc). The results of these investigations showed that phytoplankton distribution was linked to seasonality and latitude, with a fast and early growth in northern sectors and a southward shift of growth maxima as summer progresses.

A period of change started around 1950 with the development and application of new methods which involved a faster collection of quantitative data associated with the amount of biomass produced per unit of space and time. Such methods enabled estimating, for example, chlorophyll-a concentration as a proxy for actual phytoplankton biomass and primary productivity, and assimilation of dissolved inorganic carbon by phytoplankton as a proxy for the rate of photosynthetic production of organic matter in the euphotic zone. To date, these methods are the most widely used for estimating *in situ* primary productivity in Antarctic ecosystems at all scales, and at a global level as well.

More sophisticated techniques and equipment developed during the 1980s enabled quantifying fragile cells that are difficult to preserve. These improvements represented a substantial progress in the knowledge of newly identified taxa contributing to phytoplankton biomass, such as flagellates, and of some groups' capability of alternating their trophic strategies following the fluctuations of certain

environmental variables, such as nutrient and/or prey availability and light. Phytoplanktonic communities comprise at least three main size classes of algae: picoplankton (<2 μm), nanoplankton (2-20 μm) and microplankton (>20 μm). Blooms of microplanktonic and nanoplanktonic algae (e.g., diatoms, dinoflagellates, colonial and flagellated *Phaeocystis* cells) are mostly detected during the summer within the marginal ice zone (e.g., Buma et al., 1992; Olguín and Alder, 2011). However, little knowledge exists about the importance of mixotrophic groups, such as flagellates and dinoflagellates, as food for primary consumers (some of commercial importance) and their contribution to phytoplanktonic biomass (and chlorophyll-a levels) and primary productivity.

Finally, from 1990 on, many investigations on productivity have been largely based on data provided by satellites equipped with colour scanners. At present, ocean color remote sensing is our most effective tool for understanding ocean ecology and biogeochemistry at basin-to-global scales (Figure 4). Many of the algorithms used in satellite data processing and a number of predictive mathematical models employed at different ecological levels (fisheries, CO_2 dynamics, etc.) are based on *in situ* measurements which yield differing results depending on the methods used and are a cause of much current debate (Strutton et al., 2012).

At any scale, light and nutrients are the most crucial resources for phytoplankton growth. In addition, diverse physical, chemical and biological variables act as conditioning factors for phytoplankton development and biomass levels. For example, temperature, water column stability, advection, grazing, sinking, bottom topography, offshore distance, etc., usually lead to temporal and spatial variations in primary producers at different scales and also in primary productivity levels.
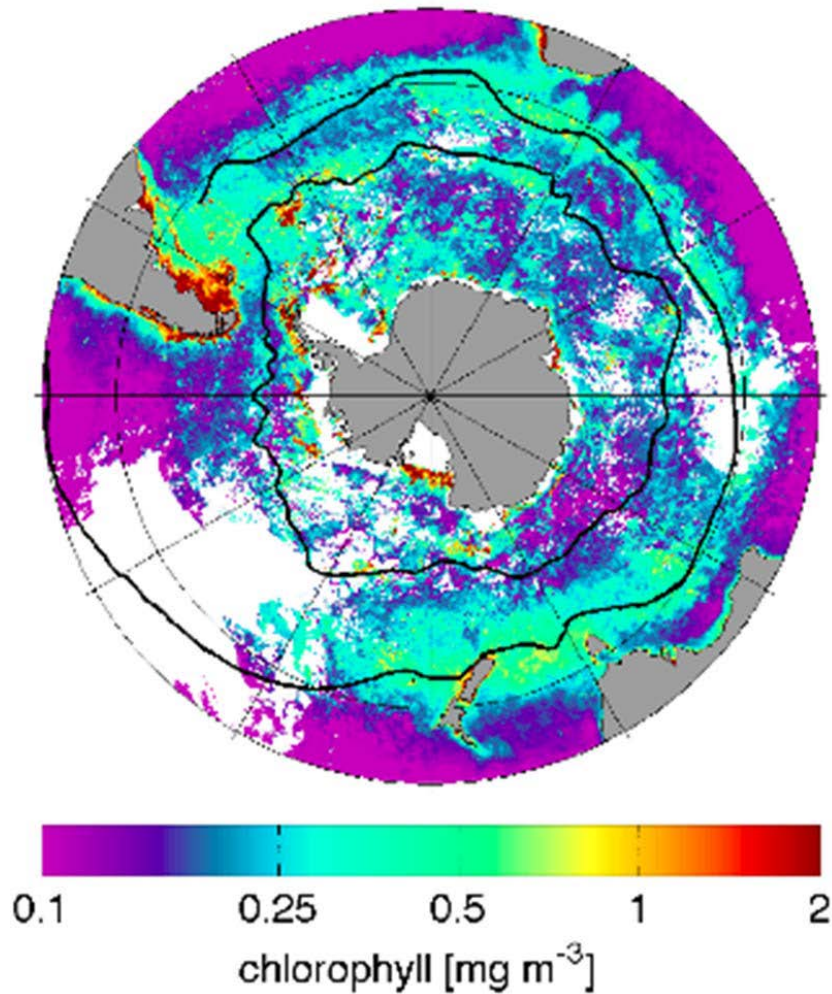
The overall distribution of phytoplankton biomass and primary production is associated with the position of frontal zones and water circulation resulting from the cyclonic circulation linked to the topography. This general scheme of distribution has been known since the first reports on Antarctic phytoplankton (Hardy and Gunther, 1935; Balech, 1968; El-Sayed, 1968a; 1968b; 1970). High local variability is superimposed on this general pattern as demonstrated by satellite information showing spots of very high chlorophyll concentration within areas of generally low concentration (El-Sayed and Hofmann, 1986).

Knox (2007) reviewed the levels reached by phytoplankton, chlorophyll and primary productivity in distinct Antarctic areas and showed the strong variability associated with different processes and sectors. In the case of Antarctic phytoplankton, variability is generally attributed to (a) extreme seasonal variability in solar radiation, (b) availability of iron (Fe), which is considered as a key limiting factor in the deep and open waters of the Southern Ocean, and (c) the extent, duration, and seasonality of sea ice and glacial discharge, which influence the life cycles of most Antarctic organisms (Ducklow et al., 2013). The annual retreat and melting of sea ice in spring causes the stratification of the upper ocean layer, thus activating the development of important phytoplankton blooms. The magnitude of these blooms is related to the winter extent of ice cover, which acts as a barrier to wind mixing (Ducklow et al., 2012; 2013).

Antarctic continental shelf regions have an annual productivity that ranges from 10 g C m^{-2} to 200 g C m^{-2}; the greatest rates occur in the Ross Sea and the western Antarctic Peninsula, but elevated productivity is found in nearly all coastal polynyas (Catalano et al., 2010; Smith et al., 2010).

Large variability in primary productivity was observed along a twelve-year time series (1995-2006; Palmer Long-Term Ecological Research). The average daily integrated primary productivity varied by an order of magnitude, from 250 C m^{-2}d^{-1} to 1100 mg C m^{-2}d^{-1}, with an average of 745 mg C m^{-2} d^{-1}. A marked onshore–offshore gradient from 1000 C m^{-2}d^{-1} to 100 mg C m^{-2}d^{-1} was found along the shelf with higher production rates inshore. Inter-annual regional variability ranged from 248 C m^{-2}d^{-1} to 1788 mg C m^{-2}d^{-1} (Vernet et al., 2008).

Satellite (SeaWiF) measurements of chlorophyll concentrations in the Southern Ocean from October 1997 through September 1998 reveal: (a) low-mean values (0.3 mg m^2- 0.4 mg m^2); (b) phytoplankton blooms and highest chlorophyll concentrations (>1.0 mg m^2) located in three areas: coastal waters above the continental shelf, the seasonally retreating sea ice, and the vicinity of the major fronts; (c) the SeaWiFS global chlorophyll algorithm works better than the Coastal Zone Color Scanner (CZCS); (d) based on the production model of Behrenfeld and Falkowski (1997), annual primary production south of 50°S was estimated in 2.9 Gt C yr-2 (Moore and Abbott, 2000).

Figure 4. From Strutton et al. (2012). Austral summer ocean pigment concentrations from the Coastal Zone Colour Scanner (CZCS). The data are available at 4 km and 9 km (this image) spatial resolution. The northern and southern solid lines represent the subtropical front and the polar front, respectively.

Marine food webs depend on primary productivity, which also contributes to the sequestration of carbon in the oceanic reservoir. In this region the models and observations for the global balance of CO_2 differ most in magnitude (Gruber et al., 2009). This disagreement highlights the importance of obtaining better estimates of all terms in the oceanic carbon budget, including primary productivity (Strutton et al., 2012).

In the seasonally ice-covered region, microalgae grow on sea ice. Their production is greatly exceeded by phytoplankton production in open waters, but their ecological role is significant. They constitute an important environment that provides refuge to cells and spores that will later seed blooms in open water (Lizotte, 2001) and provide food for ice-associated grazers, such as developmental stages of krill.

2. Zooplankton and Nekton

Multicellular animals in the water column are generally divided by size and swimming ability. This distinction is not always clear, however; some active swimmers may be quite small, whereas some large animals may be such poor swimmers that they are little more than drifters. Zooplankton species range from microscopic animals so small that the water is for them a very viscous environment, to large (sometimes very large) but slow-moving gelatinous animals from several evolutionary lineages. In addition to animals that are planktonic throughout their life cycles, zooplankton sometimes include eggs and larvae or, for some species, spawning stages of bottom-living (benthic) animals. The nekton include generally larger animals with swimming ability adequate to overcome movement by currents, e.g., primarily fish, shrimp, and cephalopods. The term nekton also encompasses diving air-breathers, including marine mammals, birds (e.g., penguins) and, in more temperate regions, reptiles; the first two groups are addressed in separate sections of this chapter.

Important for understanding zooplankton and especially for nekton is the distinction between the swimming animals that live on or closely associated with the bottom (i.e., demersal and benthopelagic) and those that spend their lives higher up in the water column and are not dependent on the bottom (pelagic). A further distinction in polar regions involves the species that are dependent, at least at some stage in their life, on sea ice (cryopelagic).

The overlap between the zooplankton and nekton that occurs in the smallest nekton (=micronekton) and large plankton (=megaplankton) is particularly important in the Southern Ocean. A unique characteristic of pelagic marine ecosystems is the alternating dominance as keystone grazers in the food webs by species from two very different evolutionary and ecological groups (Atkinson et al., 2004). These two groups are euphausiids, primarily the Antarctic Krill (*Euphausia superba*), and salps (especially *Salpa thompsoni*). The former are actively swimming shrimplike crustaceans, the adults of which dominate the micronekton community, whereas the latter form "blooms" and colonial chains of gelatinous megaplankton.

Good reviews of current knowledge about zooplankton and nekton in the Southern Ocean have recently been published. These include several chapters in Knox (2007), products of the Census of Antarctic Marine Life (Gutt et al., 2010; DeBroyer et al. (ed.), 2011; Schiaparelli and Hopcroft (eds.), 2011 and papers within that volume), and recent summaries of national research programmes, particularly around the Antarctic Peninsula (e.g., Ducklow et al., 2007; Steinberg et al., 2012) and in the Ross Sea (Faranda et al. (eds.), 2000).

Because of their swarming behaviour, krill form large patches of extremely high abundance and biomass, which are targeted by many Antarctic predators, including fish, squid, birds and mammals (Knox, 2007). The patches are also targeted for harvesting by humans (Nicol et al., 2012). The commercial potential of krill has, in turn, stimulated studies of zooplankton and micronekton assemblages and pelagic ecology more generally around Antarctica, especially near the Peninsula and in the Ross Sea.

Salps, which are megaplankton with jelly-like bodies, are chordates more closely related to vertebrates than to true jellyfish. They have complex life cycles, including both sexual and asexual (budding) reproduction and alternating generations of solitary individuals and chain-like colonial aggregates. Because they are capable of asexual reproduction, population abundance can respond rapidly to favourable conditions, resulting in a "bloom" (i.e., very high abundance).

Because a developmental stage of krill is dependent on ice algae and therefore on the amount of sea-ice habitat during that stage in the krill life cycle, alternation between high abundances of krill and salps is related to the amount of sea ice during the previous winter (Loeb et al., 1997). This alternation has very important implications for food webs in the Southern Ocean, especially pelagic food webs, but for benthic food webs as well. Krill are the preferred prey of many mid-level Antarctic predators (Knox, 2007). Although many of them can also feed on salps, the food quality obtained from salps compared with the energy expended in feeding is much less than for krill. Therefore, krill swarms are very important to maintain population levels for many species in the Southern Ocean.

Other than salps and krill, the numerically dominant group of zooplankton is the copepod crustaceans. Copepods are also the most diverse group of zooplankton, with more than 70 species in the upper 100 m of the water column. Another important crustacean group is the amphipods, which may be free-swimming or associated as predators or commensals with gelatinous megaplankton.

Other important zooplankton groups, sometimes abundant although not diverse, include pteropod mollusks, pelagic polychaete worms, chaetognaths (arrow worms), larvaceans, and ostracods.

Because many Antarctic species develop directly in large eggs rather than as larvae hatching from many small eggs, benthic species that spend their early life history in the water column (meroplankton) make up a less important component of the zooplankton in the Southern Ocean than elsewhere, although larvae may be seasonally abundant in some coastal areas.

Among the nektonic fish, cephalopods, and shrimp, the fish are clearly dominant in diversity, abundance and biomass. Only about 300 fish species are found south of the South Polar Front; of these, sligthly over 100 species are considered to be endemic to the Southern Ocean (Knox, 2007). Most of these fish species are closely associated with the bottom (demersal). The common demersal fish are dominated by a unique evolutionary group, the suborder Notothenioidei, referred to as Antarctic blennies or southern cod-icefish.

The few species of shrimp (Caridea, <10 species) are primarily demersal. Three species have been reported locally in high abundances (Gorny et al., 1992). Southern Ocean cephalopods include both pelagic squid and demersal octopods. The former includes a few species each in at least nine families. Although rarely collected in large numbers, squid are important prey for many fish, birds and mammals, indicating that current sampling methods are not representative. Some attain large sizes, including *Mesonychoteuthis hamiltoni*, one of the largest known invertebrates.

The octopods include one finned (Cirrrata) species that can be locally very abundant (Vecchione et al., 1998) and a surprising diversity of incirrate species. Whereas the incirrate fauna were long thought to comprise a few variable species, careful examination of both morphology and DNA sequences has shown the species to number at least two dozen, including one very large species, *Megaleledone setebos* (the giant Antarctic octopus). One genus, *Pareledone*, is especially diverse and is an example of both circumpolar distributions and "ring evolution" of cryptic species around the Antarctic continent (Allcock et al., 2011). The incirrate octopods have also been shown to be both an evolutionary source of species for the world's deep oceans (Strugnell et al., 2008) and to have colonized the Southern Ocean from deep oceans elsewhere (Strugnell et al., 2011).

In general, both zooplankton and nekton include some nearshore species that are circumpolar and others for which distribution appears to be regionally limited. Some of the former, however, might include complexes of cryptic species with limited distributions. The regional patterns are strongest closest to shore. For both fully pelagic and demersal animals, a gradient exists from coastal through continental shelf and slope to fully oceanic assemblages. Also, species interactions occur across the Polar Front where some subpolar zooplankton and nekton species intrude into polar waters and the ranges of some Southern Ocean species extend into lower latitudes.

In spite of the extreme polar light regime, pelagic animals of the Southern Ocean undertake vertical migrations as are well known from other oceans. Daily variability in light intensity penetrates into the upper waters and diel vertical migrations by pelagic zooplankton and nekton follow this signal. Of course the seasonal variability in light is extreme, resulting from both the angle of solar incidence and seasonal expansion and contraction of sea ice. This seasonal variability results in extensive changes in the vertical distribution of many pelagic species, usually manifested by different life-history stages occupying different depths in the water (ontogenic vertical migration). In addition to the importance (e.g., role in the food web, development through life-history stages, etc.) of these vertical migrations to the individual species, they are also important in understanding the flow of biomass, nutrients, carbon, etc., between the surface and deeper waters and ultimately to the benthic environment.

Another important association for pelagic animals in the Southern Ocean is with ice, in the form of sea ice and icebergs. As mentioned above, some stages of some species, notably krill, are dependent on the protection of the physical ice structure and on the food that grows on sea ice (Thomas and Dieckmann, 2003). Furthermore, it has recently been demonstrated that drifting icebergs are "hotspots" of pelagic productivity and biomass (Smith et al., 2007; Vernet et al., 2012). As regards prokaryotic assemblages, a very high abundance has been reported for the bottom layer of sea ice (Archer et al., 1996; Delille and Rosiers, 1996) and the platelet ice (Guglielmo et al., 2000; Riaux-Gobin et al., 2000).

3. Microbes

The microbial community plays a pivotal role in the pelagic food web of the Southern Ocean; it controls many processes, including primary production, turnover of biogenic elements, degradation of organic matter and mineralization of xenobiotics and pollutants (Azam et al., 1991; Azzaro et al., 2006; Fuhrman and Azam, 1980; Karl, 1993; Manganelli et al., 2009; Smith et al., 2010; Yakimov et al., 2003). Prokaryotic abundance and activity shift significantly over the annual cycle as sea ice melts and phytoplankton blooms develop (Ducklow et al., 2001; Pearce et al., 2007). Microbial food chains develop even in regions where large euphausiids are abundant. These chains involve small metazoans and predominate in the northern open waters (Atkinson et al., 2012) with multiple trophic levels (copepods, chaetognaths, amphipods, myctophids, fish and birds) in contrast with the classical short chain of diatoms – krill – vertebrates. Marine microbes exhibit a diversity which also depends on the timing, location and sampling method (Pearce 2008; Murray et al., 1998); research devoted to this group is increasing, using genetic and molecular approaches in Antarctic surface (Murray and Grzymski, 2007) and deep waters (Moreira et al., 2004). Studies on diversity of bacterioplankton suggest that the diversity seems to rival that found in other ocean systems, although many polar phylotypes host a distinct biogeographic signal (Pommier et al., 2005). The Archaea (DeLong et al., 1994) have a distinct seasonal cycle in which Marine Group I. the Crenarchaeota, are abundant in late winter in surface Antarctic waters (Murray et al., 1998; Church et al., 2003; Murray and Grzymski, 2007). Southern Ocean environmental genomic studies focusing on identifying organisms and metabolic capabilities of the microbial community are limited (Béja et al., 2002; Grzymski et al., 2006). Grzymski et al. (2012) found that the most noteworthy change in the bacterioplanktonic community in nearshore surface waters of the Antarctic Peninsula was the presence of chemolithoautotrophic organisms in winter and their virtual absence in summer when incident solar irradiance is at a maximum and primary productivity is high. If chemolithoautotrophy is widespread in the Southern Ocean in winter, this process may be a previously unidentified carbon sink. Research trends point to microbial diversity in marine invertebrates (Webster et al., 2004; Webster and Bourne, 2007; Riesenfeld et al., 2008).

4. Benthos

Antarctic shelves are very deep, a process that developed from the glaciation that began with the isolation of the Southern Oceans because of the weight of the continent's massive ice sheet. Due to the isostatic depression of the Antarctic continent by the extant ice sheets, the features of Antarctic continental margins are distinct from those of the rest of the ocean and the continental shelf break occurs at a depth of ca. 1,000 m compared to about 200 m and less elsewhere in the world (Smith et al., 2010). Such evidence implies that (a) the continental margins tend to be narrow and often have deep canyons, (b) essentially no organic matter is derived from continental sources, and (c) the only significant effects of the continent are to

provide mineral material to the continental shelves via ice-rafted debris and glacial meltwater to restricted coastal environments. More than 95 per cent of the shelves are at depths outside the reach of photosynthetically active radiation (Turner et al. (eds.), 2009). Some 33 per cent of the continental shelves are covered by the floating ice shelves.

The shelf benthic fauna are dominated by sessile particle feeders with high biomass and low productivity. Many species are long-lived, have low metabolic rates, lack the pelagic larval phase and need longer development time. Benthic communities cover a full range from an extremely high biomass of several kg wet-weight m^{-2} to extremely low biomass, abundances and metabolic processes below ice shelves (Azam et al., 1979).

Knowledge of the benthic fauna has developed from historical surveys, individual national projects and cooperative projects, such as the European Polarstern Study (EPOS), Ecology of the Antarctic Sea Ice Zone (EASIZ), Evolution in the Antarctic (EVOLANTA), Census of Antarctic Marine Life (CAML), Latitudinal Gradient Project (LGP), Food for Benthos on the Antarctic Continental Shelf (FOODBANCS), Antarctic Benthos (BENTANTAR), and the Antarctic benthic DEEP-sea biodiversity: colonization history and recent community patterns (ANDEEP), but regionally many gaps in survey data remain (Griffiths et al., 2009). Some 4,000 species have been described (White, 1984; Arntz et al., 1997; Clarke and Johnston, 2003), of an estimated total macrofauna of more than 17,000 species (Gutt et al., 2004); the deep benthos remains largely unsampled (Brandt et al., 2004).

Close to the shoreline, benthic communities are strongly affected by ice scouring. This phenomenon provokes a continuous recolonization of benthos. Iceberg impacts are catastrophic events eliminating up to 96 per cent of the biomass of the community (Smale et al., 2008), interfering with community development in those areas where ice scouring becomes chronic (Dayton et al., 1974; McCook and Chapman, 1993; Barnes, 1995; Pugh and Davenport, 1997). In essence, long-lived species are selected against by this process which results in widely different community structures among areas with different scouring histories.

Benthic communities are marked by the absence of crabs and sharks and by a limited diversity of skates and finfish; skeleton-breaking predation is limited. Slow-moving invertebrates are present at high trophic levels. These characteristics, together with dense ophiuroid and crinoid populations, resemble the worldwide Palaeozoic faunal assemblages (Aronson and Blake, 2001). Detritivores, feeding on deposited organic material, include the infauna (mainly mollusks) and vagrant deposit feeders such as holothurians (Gutt, 2007).

At regional and local levels, patchiness is high, due to differences in environmental conditions, food supply and disturbances; but at very coarse spatial resolution, benthic assemblages are typical of the Antarctic with circumpolar distributions (Turner et al. (eds.), 2009).

Below the depth scoured by drifting ice, the invertebrate benthic fauna typically comprise a dense community of sessile species (e.g., sponges, ascidians, gorgonians, anemones, corals, bryozoans, crinoids) in a three-dimensional pattern (Arntz et al., 1994, 1997; Gutt, 2000) with an associated mobile fauna (echinoids, pycnogonids,

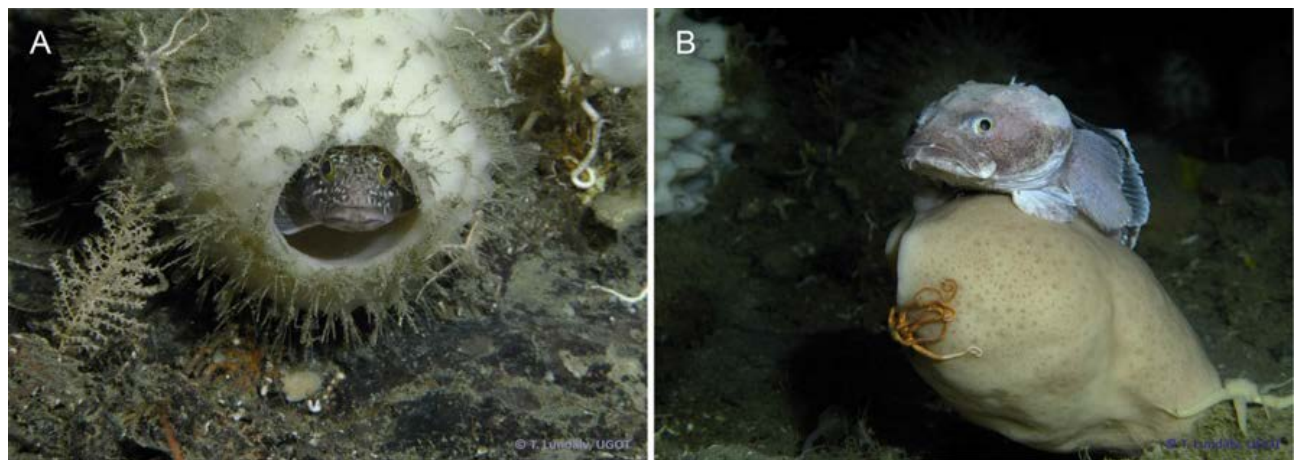isopods, amphipods, polychaetes, etc.) developing complex relations among different species (Figure 5).

Figure 5. From Mintenbeck et al. 2012. (A) *Trematomus cf. nicolai* hiding inside a sponge; (B) *Pogonophryne sp.* on top of a sponge (ANT XXVII-3 in 2011, western Weddell Sea). Photos: ©Tomas Lundälv, University of Gothenburg.

The highly seasonal primary production in the Antarctic results in a seasonal flux of organic material deposited in the sediment. This provides an abundant persistent food supply for detritivores which might be resuspended as a result of water mixing or ice scouring. This was identified as a "food bank" by Mincks et al. (2005) and Mincks and Smith (2007).

Macroalgae are common elements of nearshore hard-substratum communities in Antarctic and Sub Antarctic regions (Wulff et al., 2011). The areas with hard substrata (e.g., rocks and boulders) are particularly suitable for macroalgal colonization (Quartino et al., 2013). Macroalgae occur in a distinct vertical zonation, mainly between the intertidal and the subtidal zone, down to 30 m depth. The lower distribution is related to their capacity to survive under low light conditions. The South Atlantic Ocean is a nutrient-replete system where nutrients rarely become limiting for macroalgae (Zacher et al., 2009).

Macroalgal communities play a key role in the coastal ecosystem. They are important primary producers, constituting food supply for benthic organisms, such as amphipods, gastropods, annelids and fish (Barrera-Oro, 2002), and represent a significant contribution to the particulate and dissolved organic matter for the coastal food web (Iken et al., 2011). Furthermore, macroalgae provide habitat and structural refuges (Barrera-Oro, 2002; Huang et al., 2007). Macroalgal coastal carbon production seems to be an important food source for the benthic Antarctic communities. If not grazed, macroalgae die and decompose, returning particulate organic matter and mineral nutrients to the system (Quartino and Boraso, 2008).

The sublittoral rocky shores are colonized by macroalgae; the deeper macroalgal assemblages are dominated by canopies of large brown algae from the Order Desmarestiales (*Desmarestia anceps*, *D. menziessi* and *Himantothallus grandifolius*), which replace ecologically the role of the Order Laminariales (i.e., the kelp *Macrocystis pyrifera*) in temperate waters (Wulff et al., 2011).

The strong isolation of the benthic seaweed flora of the South Atlantic Ocean has resulted in a high degree of endemism in Antarctica. Thirty-five per cent of all seaweed species are endemic to the Antarctic region. Within the Heterokontophyta (brown and golden algae) 44 per cent of the species are endemic, within the Rhodophyta (red algae) 36 per cent and within the Chlorophyta (green algae) 18 per cent; and the number of endemic species is continuously increasing (Wiencke and Amsler, 2012). The northern distribution of endemic Antarctic species is often limited by the temperature demands for growth. The southern-most location of open water where macroalgae occur is the Ross Sea, Antarctica (Wiencke and Clayton 2002).

5. Fish

The Antarctic ichthyofauna is small in size and less diverse than might be expected, given the size and age of the Antarctic marine ecosystem (Eastman, 1995). The knowledge of Antarctic fish began in the nineteenth century through zoogeographic and taxonomic descriptions. Fish fauna in the Antarctic is dominated by the Suborder Notothenioidei; approximately 66 per cent of the Antarctic species and 95 per cent in numbers belong to this Suborder. They live from tide pools (genus *Harpagifer*) to great depths (genus *Bathydraco*). Conversely, Antarctic habitats dominate within the Suborder: from about 100 species of notothenioids, 92 are Antarctic, 12 are found in Patagonia, 4 in New Zealand, 2 in Tasmania and 1 from Saint Paul and Amsterdam Islands. In Antarctica, the Notothenioidei are represented by six families: Bovichtidae, Nototheniidae, Harpagiferidae, Artedidraconidae, Bathydraconidae and Channichthyidae (Kock, 1992). The family Chaennichthydae (ice-fish) is exceptional because it has a colorless blood due to lack of haemoglobin (Kock, 2005); only one species lives outside the Antarctic (*Champsocephalus esox*, Calvo et al., 1999).

Notothenioids lack a swim bladder and have antifreeze glycoproteins in their blood (Matschiner et al., 2011). They have developed a wide range of feeding strategies, which allow them to utilize food resources in a variety of habitats (Gröhsler, 1994). This diversification has been supported by a trend towards pelagization of demersal species (Nybelin, 1947), which might be related to the abundance of available food in the water column, such as krill, in zones of the Southern Ocean. Thus, fish are main predators of benthos, zooplankton and nekton in the water column, including krill, copepods, hyperiid amphipods, squid and fish.

Besides the Notothenioids, demersal fish of the families Zoarcidae, Liparidae, Muraenolepidae, Macrouridae, Moridae, Achiropsettidae, etc. are represented with significant numbers of species endemic to the Southern Ocean. Chondrichthyes

(sharks and rays) are also found with bottom dwelling (e.g. *Somniosus antarcticus, Amblyraja spp.* and *Bathyraja spp.)* and mesopelagic species (e.g. *Lamna nasus).*

The Southern Ocean lacks the epipelagic fish typically found in surface waters of other oceans. The few species of mesopelagic fish, living in the open ocean down to depths of about 1000 m, are members of cosmopolitan families. Typically antarctic is the nothotheniid *Pleurogramma antarctica.* Closely related with ice are the species *Trematomus borchgrevinki,*

T. amphitreta, and *Pagothenia brachysoma.* A recent revision of Southern Ocean fish, their diversity and biogeography can be found in Duhamel et al. 2014.

The environmental factors related to fish distribution can only be described in general terms. On the deep Antarctic shelves (500 m deep on average in the Antarctic, against some 200 m deep worldwide) lying in the area of seasonal ice and the islands in the Scotia arc, the fish fauna are dominated by the families Notothenidae and Channichthydae. In the high Antarctic, although the biomass and numbers are smaller, the diversity and endemism are the highest (Kock, 1992) (e.g., genera *Trematomus, Pleuragramma, Aethotaxis* and *Pagothenia*).

Pelagic fish include occasional species like *Lampris spp., Lamna nasus* and *Thunnus maccoyii,* and, in general, species also found in waters north of the Polar Front. About 85 per cent of the shelf fish fauna are endemic to the Antarctic against only 25 per cent of the deep sea fish. The vertical distribution of mesopelagic fish is related to the Antarctic surface water (Lubimova et al., 1983).

High energetic costs are associated with pelagic feeding, which may hamper the development of shark species in the southern basins. On the other hand, the benthos is a seasonally stable resource, but most of the benthic epifauna are not very suitable for utilization by fish (Kock, 1992).

The mesopelagic fish fauna are mainly composed of Myctophidae (the dominant group) and Gonostomatidae (Kozlov, 1995); the distribution is mainly circumpolar and always related to the Antarctic surface water (Lubimova et al., 1983). This water mass drifts northwards and sinks at the Polar Front. *Gymnoscopelus nicholsi*, found in surface waters down to 700 m near the subtropical convergence, reaches more than 2000 m depth; they are prey of other fish, squid, fur seals and penguins (Sabourenkov, 1991). *Pleuragramma antarcticum* is the nototheniid present in the mesopelagic over the shelves.

Inshore, the ecological role of demersal fish is more important than that of krill. There, demersal fish are major consumers of benthos and also feed on zooplankton (mainly krill in summer). They are links between lower and upper levels of the food web and are common prey of other fish, birds and seals. Offshore, pelagic fish (e.g., myctophids, *Pleuragramma antarcticum*) play an important role in the energy flow from macrozooplankton to higher trophic levels (Barrera-Oro, 2002). As krill predators, fish play an important role in the Southern Ocean ecosystems (Kock et al., 2012). Nototheniids and Channichthyids are relevant predators of krill and myctophids (Kock et al., 2012); the latter also prey on all development stages of krill.

6. Higher-order predators

Many sub-Antarctic species of birds, pinnipeds and cetaceans occur in northern ice-free waters of the Southern Ocean, and move south in the summer as the pack ice recedes (see chapter 36B). Oceanic fronts present sharp discontinuities in the properties of surface water and food availability; it is well known that predators associate with fronts where they find favourable feeding conditions and are critical for the distribution of seabirds and marine mammals (Bost et al., 2009).

Numerous species of seabirds have been recorded in the Southern Ocean; most are vagrant with only 16 of them nesting in the Antarctic continent (Clements, 2000; Woehler et al., 2001; Harris et al., 2011; Coria et al., 2011; Santora and Veit, 2013; Joiris and Dochy, 2013; Ropert-Coudert et al., 2014). Vagrant species forage within the productive Southern Ocean waters during summer and come mainly from sub-Antarctic islands, although some, such as the Arctic tern *Sterna paradisaea*, fly thousands of kilometres from very distant places (Egevang et al., 2010). A community of seabirds with very stable composition is found in the pack ice; it is probably the most unvarying of any seabird assemblage in the Southern Hemisphere (Ribic and Ainley, 1988). Penguins (Adélie and Emperor) are the typical species, together with snow and Antarctic petrels and, in summer, the South Polar skua and Wilson and storm petrels.

Penguins are the dominant component of the seabird communities in the Southern Ocean in terms both of biomass and prey consumption (Croxall and Lishman, 1987). Nine out of the 18 penguin species inhabit the Southern Ocean; their distributions are reflected in their diets and adaptations to the particular environmental conditions found in their respective ranges, as summarized by Ratcliffe and Trathan (2011):

- Emperor penguins (*Aptenodytes forsteri*) are inhabitants of the high Antarctic; this is the only species that breeds on the land-fast ice along the Antarctic coast during winter. When foraging during winter, emperor penguins have to travel to the edge of the fast ice to feed (Wienecke and Robertson 1997; Zimmer et al., 2008).

- King penguins (*Aptenodytes patagonicus*) feed close to the Polar Front in summer, predominantly on myctophids (*Krefftichthys anderssoni* and *Electrona carlsbergi).* In winter the birds move closer to the ice edge.

- Adélie penguins (*Pygoscelis adeliae*) breed on the Antarctic continent and nearby islands, but their breeding season is in summer, roughly from October to March, and their foraging activity is heavily dependent on sea-ice conditions (Ainley, 2002). Their diet is dominated by euphausiid crustaceans and fish (e.g., Coria et al., 1995; Libertelli et al., 2003). Foraging is mainly confined to pack ice, and seasonal variations in the distribution of this ice cause marked seasonal and spatial variations in foraging ranges, migration routes and wintering areas.

- Chinstrap penguins (*Pygoscelis antarctica*) have a diet comprised almost entirely of *Euphausia superba*; diet and reproductive success are dependent on ice conditions (Rombolá et al., 2003; 2006). Chinstrap penguins tend to forage in open water and avoid areas of pack ice (Ainley et al., 1992).

- Gentoo penguins (*Pygoscelis papua*) have a diet comprised of a wide range of crustacean and fish taxa, with crustaceans typically less important than for other *Pygoscelis* or *Eudyptes* spp. breeding at the same sites.

- Royal penguins (*Eudyptes schlegeli*) are found only on Macquarie Island and macaroni penguins (*Eudyptes chrysolophus*) are found at all other localities. Their diet comprises mostly euphausiid crustaceans and myctophid fish throughout their biogeographic range, with small contributions by amphipods and squid.

Among flying seabirds, the families that are best represented in the Antarctic marine avifauna are Procellariiformes, including albatrosses (Diomedeidae), petrels, prions and shearwaters (Procellariidae), storm petrels (Hydrobatidae) and diving petrels (Pelecanoididae). The order Suliformes is represented by cormorants (Phalacrocoracidae) and the order Charadriiformes by skuas (Stercorariidae) and, to a lesser extent, the gulls and terns (Laridae). Most of the Procellariiformes travel hundreds or thousands of kilometres from the colony during the breeding season to feed on patchily distributed resources and they migrate even further during the non-breeding period (Phillips et al., 2008).

Antarctic marine mammals can be defined as those species whose populations rely on the Southern Ocean as a critical habitat for a part or all of their life history, either through the provision of habitat for breeding and/or through the provision of a major food source (Boyd, 2009). The Southern Ocean accounts for about 10 per cent of the world's oceans, but is estimated to support 80 per cent of the world's pinniped biomass (Laws, 1977) and is a critical feeding ground for several cetaceans, particularly the highly migratory baleen whales (Mackintosh, 1965). Many subfamilies and genera are missing in the Southern Ocean. In spite of the species richness of the family Otariidae (sea lions and fur seals) in the South Atlantic, Indian and Pacific Oceans, only Antarctic fur seals (*Arctocephalus gazella*) are found south of the Polar Front in island rookeries and open waters; sometimes they reach the boundary of the pack ice during the austral summer, and some 50 per cent of the population migrates north during winter. This species feeds mainly on krill, with fish and squid found in their diet in proportions that vary with area and season.

True seals (family Phocidae) are represented by five species. The elephant seal (*Mirounga leonina)*, also found north of the Polar Front in open waters, is seldom found in the pack-ice area and also migrates to the north in winter. The remaining seal species are more or less associated with the pack ice: the leopard seal (*Hydrurga leptonix)* preys on krill (about half of its diet), seabirds (mainly penguins), other seals and fish. The Weddell seal's (*Leptonychotes weddellii)* diet is practically all fish and a small proportion of krill. The crabeater seal is the most abundant marine mammal in the world (*Lobodon carcinophaga)* and is a pack-ice inhabitant feeding mostly on krill. Finally, the Ross seal (*Ommatophoca rossii)* is very scarce and little is known of its diet.

A main ecological distinction exists between seals: those breeding in shore colonies (fur and elephant seals) and those breeding on the pack ice (leopard, Weddell, crabeater and Ross seals). The difference is a key element in our ability to estimate population sizes: ice-breeding seals can only be studied through large-scale surveys and it is very difficult to sample the same population year after year; shore colonies

offer easier conditions (Southwell et al., 2012). Crabeater seal numbers were estimated from the Antarctic Pack Ice Seals (APIS) International Programme at 10 million individuals, albeit with large confidence intervals and this is likely to be an overestimate (Southwell et al., 2012). Populations of the other three species are much smaller.

Cetaceans in the Southern Ocean are represented by six species of baleen whale: blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*), humpback (*Megaptera novaeangliae*), Antarctic minke (*Balaenoptera bonaerensis*) and southern right whales (*Eubalaena australis*). Among these, the Antarctic blue whale was depleted close to extinction by the whaling industry (from 239,000 (95 per cent confidence interval; 202,000-311,000) to a low of 360 (150-840) in 1973) (Branch et al., 2004). Current estimates suggest that some populations are recovering, but that others are not (e.g., those seldom sighted in the Antarctic Peninsula region); others, such as the southern right whale and especially the humpback whale, are both increasing in numbers (Branch, 2011).

At least nine species of odontocetes are found: sperm whale (*Physeter macrocephalus*), southern bottlenose (*Hyperoodon planifrons*), Arnoux's (*Berardius arnuxii*), Cuvier's (*Ziphius cavirostris*) and strap-toothed (*Mesoplodon layardii*) beaked whales, long-finned pilot whale (*Globicephala melas*), orca (*Orcinus orca*), hourglass dolphin (*Lagenorhynchus cruciger*) and the spectacled porpoise (*Phocoena dioptrica*)) (Brownell, 1974; Laws, 1977; Jefferson et al., 2008). Female sperm whales do not reach the Southern Ocean, and only large adult males reach the pack ice.

All in all, cetaceans in the Southern Ocean represent a little less than one-fifth of the world's cetacean species in spite of the large diversity of this family (86 species). Those species that sustain a large biomass are related to the direct plankton food chain (diatoms-krill-vertebrates) which has on average one trophic level less and is more efficient in terms of the transfer of energy and mass than those that include squid or fish as intermediate steps (Boyd, 2009).

7. Pressures and Trends

By-catch, habitat loss, introduced species, human disturbance, pollution and climate change pose severe, albeit of different intensity, threats for seabirds at sea and in colonies in the Southern Ocean and along the Antarctic continent (Micol and Jouventin, 2001; Croxall et al., 2002; Weimerskirch et al., 2003; Jenouvrier et al., 2005). Population trends are variable between species and colonies within a species (Woehler et al., 2001). Significant decreases in populations are evident for those species known to be caught on longline fisheries (albatrosses, Southern giant petrel and *Procellaria* spp.: Woehler et al., 2001; Tuck et al., 2003). Penguin population trends vary in terms of degree and direction among species and geographical areas (Forcada et al., 2006; Lynch et al., 2010; Trivelpiece et al., 2011; Coria et al., 2011). Burrowing petrel species are poorly known, in particular their abundance and trends (Woehler et al., 2001).

8. Harvesting of living resources

Early exploration of the Southern Ocean was driven by the potential of harvesting its nekton – first mammals, then finfish, and finally krill. The discovery of islands lying south of the Antarctic Polar Front rapidly led to the initiation of massive sealing expeditions from various nations during the early 1800s. The outcome of these intensive sealing activities was the near-extermination of fur seals in Antarctic and Sub-Antarctic Islands by the mid-19th century. Combined with the hunting of fur seals, a rather less relentless pursuit of elephant seals (*Mirounga leonina*) followed for the production of an oil equivalent to whale oil (Bonner, 1984). In 1812, a new method to process seal skins was introduced in London factories, increasing the value of southern pelts. Despite efforts to regulate the catches, Patagonian seals were depleted below commercial levels by 1825, and the Antarctic exploration and harvesting finally resulted in severe depletion and loss of commercial value of seal colonies by 1840. Around 1870, technological improvements led to the growth of pelagic whaling with the development of faster, steam-powered catching vessels, and whaling in the Southern Ocean entered a new era in the early years of the 20th century, which saw the industrialization of whale exploitation. In 1904, the first shore station was built at Grytviken. In 1912, about 11,000 whales were killed annually to be processed at six Antarctic shore stations, a level deemed to be unsustainable (Suarez, 1927). Over the following decades (1904-1960s), more than 2 million large whales were caught, reducing their populations to less than 35 per cent of their initial numbers and 16 per cent of their original biomass (Laws, 1977; Clapham et al.,1999).

The ensuing extraction of other resources followed the same pattern as in other parts of the world; from the highest trophic levels down the trophic web (Kock, 2007; Ainley and Pauly, 2014). The impacts of the reduction to less than 20 per cent of their original size of several fish stocks by 1980, stocks which are not experiencing significant recovery despite management actions by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Ainley and Blight, 2008; Marschoff et al., 2012) are still felt in spite of significant harvest reductions (including fisheries closures in large areas). Species' relationships might be altered by harvesting: for example, evidence exists that the decrease in demersal fish in the fishing area was followed by a long-term increase in populations of benthic octopods (Vecchione et al., 2009).

Although the targets and intensity of harvesting have shifted over the years, the ecosystem effects continue. Removal of large predators, such as seals and especially whales, reduces predation pressure on species in the mid-level of the food web, including fish and squid. Some of the large predators (e.g., baleen whales, fur and crabeater seals) feed directly on krill, whereas others (e.g., toothed whales) feed on krill predators. Therefore, the ecosystem effects of sealing, whaling and fishing are potentially complex and were initially related to the "whale reduction" or "krill surplus" hypothesis (Sladen, 1964), in which the outcome from the dramatic exploitation of whale stocks was a presumed excess of food (krill) which was being redistributed throughout the system. Although sealing has ceased and historical levels of whaling have been reduced (a reduced harvest of baleen whales continues),

impacts from the reduced levels of these top-level species arguably still reverberate through the pelagic ecosystem.

The reduction of whaling brought about increased harvesting of fish. Rapid reduction of the target fish stocks was a major reason for the adoption of the CCAMLR, which implemented international fisheries and ecosystem research and resulted in a moratorium on bottom fishing for notothenioids. Kock and Jones (2007) reviewed the fisheries data for the primary fishing area around the Antarctic Peninsula. They found that populations of several fish species declined as a result of the fishery primarily targeting mackerel icefish, *Champsocephalus gunnari,* and marbled notothenia, *Notothenia rossii*. Since the CCAMLR moratorium was implemented in 1989-90 for the South Shetland area, populations of several fish species have recovered, but not of the two main target species. The observed recovery in *Notothenia rossii* in the South Shetland Islands shelf is taking longer than the objective set by CCAMLR of two or three decades and *Gobionotothen gibberifrons* remains at low levels (Barrera-Oro and Marschoff, 2007).

Finfish fishing was conducted by bottom trawling until 1985, when regulation of by-catch of depleted finfish species moved the *Champsocephalus gunnari* fishery to introduce midwater trawls. Since 2008, fisheries where the fishing gear interacts with the bottom (e.g., longlining and demersal trawling) are subject to mitigation measures to protect Vulnerable Marine Ecosystems, for example the positions where substantial amounts of VME indicator species are encountered are closed to fishing (see CCAMLR – Conservation Measures at www.ccamlr.org). Further, marine reserves have been established by France and Australia (Welsford et al. 2011; Falguier and Marteau 2011) and in South Orkney Islands where fishing is restricted.

Antarctic fur seals may have recovered (and may even have become overpopulated on South Orkneys during the late 1990s (Hodgson et al., 1998)) after being severely depleted, but some breeding rookeries have reached carrying capacity well below historical records (Hucke-Gaete et al., 2004). Trends in the ice-breeding seals are difficult to establish (Southwell et al., 2012). In other circumstances it might become impossible to determine the causes behind the observed population trends. For example, it is difficult (if not impossible) to disentangle the effects of climate change, recovery of seals, and variations in krill availability on the population trends observed for pack-ice seals   (Trathan et al., 2012). However, recent evidence suggests that climate change might actually be responsible for the declining trend in Antarctic fur seals, where food stress provoked by climate variation has significantly reduced female longevity, juvenile and adult survival, fecundity and pup birth weight, among other symptoms, since 2003, after a three-decade monitoring programme of biometric, life history and genetic aspects (Forcada and Hoffman, 2014).

A decrease in density of krill (Euphausia superba) and a correlated increase in salp abundance has been suggested from the analysis of net samples (Atkinson et al., 2004). Krill decrease has also been inferred by stable isotope studies in krill predators (e.g., Huang et al., 2011).

The regulation of Antarctic fisheries under CCAMLR operates in the framework of the Antarctic Treaty System. Since its inception (1980), CCAMLR requires the application

of the ecosystem approach, aiming to limit the changes induced by the fisheries to those reversible in two to three decades. Catch limits and *inter alia,* fishing methods and data collection requirements are established by a Comission, based on the assessments and advice provided by the Scientific Committee. To date, no methods of catch allocation among members are in place. Several of the 25 Commission Members and 11 acceding do not participate in harvesting. However, the management developed along 30 years has proved to be effective in the sense that this organization is highly regarded in terms of the achievement of conservation objectives (Cullis-Suzuki and Pauly, 2010).

The krill fishery is the largest in the Southern Ocean. Recent annual catch has exceeded 200,000 tons. The fishery developed on a relatively small scale in the 1970s, but rapidly increased during the 1980s to a peak of >500,000 tons/year (Nicol et al., 2012). This is actually much less than the precautionary catch limit set by CCAMLR at a total of over 8.6 million tons. Therefore, krill are considered to be "underexploited", but the fishery is expanding and management methods to take into account ecosystem considerations are under development (e.g., CCAMLR, 2013, paragraph 5.5; SC-CAMLR, 2013, paragraphs 3.11 to 3.27). A trigger level (a level that cannot be exceeded until more advanced management procedures are in place) of 620,000 tons throughout the main fishing ground is being applied by CCAMLR. However, ecosystem effects of the removal of large numbers of krill remain to be determined, especially when considered in light of climate change.

9. Climate change

In addition to harvesting, the other major pressure on Antarctic biota is the changing climate. The Scientific Committee on Antarctic Research (SCAR) produced a comprehensive Antarctic Climate Impact Assessment (Turner et al. (eds.), 2009). The following discussion is largely based on this report.

For the past 50 years the Antarctic marine ecosystem has been affected by climate change, especially on the western side of the Peninsula, with its warming water and declining sea ice. Westerly winds around the continent have increased by 20 per cent since the 1970s and surface air temperature has increased over the Antarctic Peninsula. Information from ice cores suggest that warming started around 1800. The Antarctic Circumpolar Current temperature increased by approximately 0.5°C between 300 m to 1000 m. Böning et al. (2008) analyzed historical and recent data from drifting buoys, finding that the wind-driven Antarctic Circumpolar Current has not augmented its transport, but reported warming and freshening of the current on a hemispherical scale extending below 1000 m, meaning that transport and meridional overturning are insensitive to changes in wind stress. Although the response of the Antarctic Circumpolar Current and the carbon sink to wind-stress changes is under debate, it has been suggested (Hallberg and Gnanadesikan, 2006; Meredith and Hogg, 2006) that the Antarctic Circumpolar Current's response to an increase in wind is a change in eddy activity rather than a change in transport. Given the importance of the Antarctic Circumpolar Current and its system of eddies in

structuring the pelagic ecosystem, the consequences of these changes cannot be foreseen.

Ship observations suggest that the extent of sea ice was greater in the first half of the twentieth century, but satellite measurements from 1979 to 2006show a positive trend of around 1 per cent per decade. The greatest increase, at around 4.5 per cent per decade, occurred in the Ross Sea; the reduction in sea-ice cover affected the Bellingshausen sea.

The pelagic ecosystem was affected by the consequences of the regional sea-ice reduction. Krill population has not increased after the near-extinction of some whale stocks. Although predation by seals and birds increased, the total bird and seal biomass remains only a fraction of that of the former whale population (Flores et al., 2012). The krill stock, of which 150 million tons were being eaten by whales, would have been an estimated three times larger in the pre-whaling time. Commensurate primary production would be around that estimated for the North Sea, not leaving much for other grazers and copepods. This means that phytoplankton also decreased, but the details of the phenomenon are still unclear.

Sea bird monitoring in the Scotia Sea has shown a significant decline in the abundance of krill predators, such as the cape petrel, *Daption capense*, the southern fulmar, *Fulmarus glacialoides,* and Wilson's storm petrel, *Oceanites oceanicus*; other species with generalist diets have increased their number: the Antarctic Prion, *Pachyptila desolata,* and the Black-browed Albatross, *Thalassarche melanophris* (Orgeira and Montalti, 1998). Other non-Antarctic species, such as the white-chinned petrel, *Procellaria aequinoctialis,* have extended their pelagic ranges further south, (Montalti et al., 1999).

At least a conceptual model of the structure and functioning of the ecosystem is necessary to understand these phenomena. *In-situ* iron fertilization experiments demonstrated that iron, as a micronutrient, may limit phytoplankton growth even in presence of large concentrations of nitrate and phosphate. In the whale feeding grounds, krill stocks were close to, if not at, the carrying capacity of the ecosystem prior to whaling; this is consistent with the frequent observations in the 1930s of krill swarms at the surface, an observation now seldom made from tourist or scientific vessels.

Estimates of krill abundance derived from the analysis of net samples indicate a decline of up to 81 per cent in the krill stock (Atkinson et al., 2004) and an increase in salp populations, suggesting the replacement of krill by salps and of the typical short food chain of diatoms-krill-higher predators by the longer food chain implied in the microbial food webs to which salps are better adapted. The actual dimension of these changes is currently under debate, because of the large difficulties associated with the analysis of the simultaneous effects of whale depletion, sea-ice retreat at one of the most important recruitment sites of krill (the western Antarctic Peninsula), iron-limited phytoplankton growth, and more complex ecological phenomena (Ainley et al., 2007; Nicol et al., 2007). The lower rate of recycling of iron in the microbial planktonic food web when compared to the short diatom-krill-predators "chain of the giants" may also contribute to the reduction in iron. Large

predators also contribute to iron recycling while accumulating blubber and excreting nutrients in surface waters; a significant proportion of plankton biomass is degraded below the euphotic zone. Thus the productive "chain of the giants" may have maintained itself via recycling the nutrients at a rate compatible with the growth of phytoplankton.

With the decline in sea ice, more phytoplankon blooms should be supplying food to benthic organisms on the shelf. A resulting increase in phytodetritus on the shelf may cause a decline in suspension feeders adapted to limited food supplies, and to their associated fauna. The positive correlation between the extent and duration of sea-ice cover over krill reproduction and survival (Loeb et al., 1997), the negative trends of sea-ice extent (Stammerjohn et al., 2008) and the overall decrease in krill biomass over the last decades (Siegel and Loeb 1995; Atkinson et al., 2004) would be expected to have profound implications for the Southern Ocean food web and is the most relevant issue affecting krill-dependent fauna particularly. When ice shelves collapse, the changes from a unique ice-shelf-covered ecosystem to a typical Antarctic shelf ecosystem, with high primary production during a short summer, are likely to be among the largest ecosystem changes on the planet, a process that seems to develop faster than was previously thought (Gutt et al., 2013).

Another expected impact of climate change is the change in pH levels, with seawater becoming more acid. It seems likely that the skeletons of planktonic pteropoda and of cold water corals will become thinner. Hatching rates of krill eggs are also demonstrated to be negatively affected by the level of ocean acidification projected for the end of the century and beyond (Kawaguchi et al., 2013). The Southern Ocean is at higher risk from this than other oceans, because it has low saturation levels of $CaCO_3$.

10. Invasive species

The slow rates of growth and endemism of Antarctic species may lead to the establishment of non-indigenous species, probably restricted by their own physiological limits. The incomplete taxonomic knowledge of the Antarctic biota will make it difficult to recognize whether a particular specimen is the result of a natural southern distribution limit or an invasive species. Examples include: the occasional findings of anomuran and brachyuran larvae in the South Shetland Islands (Thatje and Fuentes, 2003); *Euphausia superba* in Chilean fjords; Antarctic diatoms in Tasmania, etc. (Clarke et al., 2005).

There is concern that several factors associated with ocean warming and increased vessel activity (scientific expeditions, tourism, fisheries, etc.) in the Antarctic increase the risk of the introduction of alien species and even pathogens (Kerry and Riddle, 2009). In the crab-eater population of the Antarctic Peninsula, one-third of the population carries antibodies to the canine distemper (Bengtson et al., 1991), attributed to contagion from sled dogs, which were removed from the Antarctic Treaty Area. The introduction of non-native living organisms is banned, except in accordance with a permit.

11. Contamination

At the local level, contaminants from coastal stations are introduced through waste water, dump sites and particulates from the activity of stations and ships. Persistent organic pollutants (POPs) have been found in water, sediments and organisms in the vicinity of several stations (e.g., UNEP, 2002; Bargagli, 2005). Since 1991, the Protocol on Environmental Protection to the Antarctic Treaty[1] has imposed severe restrictions and regulations on disposal and treatment of wastes and emissions from stations and tourism vessels. Thus, locally originated contamination is not expected to become a significant problem.

Global contamination reaches Antarctica through the global circulation of the oceans. Persistent pollutants are transported and biomagnified, these include DDT (dichlorodiphenyltrichloroethane) and other organophospates. While DDT has been little used since the 1970s a possible source of DDT maintaining high levels in penguin populations is glacier ablation (Geisz et al., 2008). Anthropogenic radionuclides stemming from above-ground nuclear bomb testing are also present throughout Antarctica, including evidence of the Chernobyl nuclear accident (Dibb et al., 1990), and have even been used to provide dating controls within long-lived biological systems (Clarke, 2008). Snow samples enabled the reconstruction of lead pollution of Antarctica that started as early as the 1880s, related to non-ferrous metal production activities in South America, South Africa and Australia and coal-powered ships that crossed Cape Horn en route between the Atlantic and Pacific Oceans. Lead pollution declined in the 1920s, correlated with the opening of the Panama Canal in 1914, and decreased from the mid-1980s because of lead-free modern cars. Antarctica is significantly contaminated with other metals, such as Cr, Cu, Zn, Ag, Bi and U, as a consequence of long-distance transport from the surrounding continents.

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