

2014

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McBride, Margaret M.; Dalpadado, Padmini; Drinkwater, Kenneth F.; Godø, Olav Rune; Hobday, Alistair J.; Hollowed, Anne B.; Kristiansen, Trond; Murphy, Eugene J.; Ressler, Patrick H.; Subbey, Sam; Hofmann, Eileen E.; and Loeng, Harald, "Krill, Climate, and Contrasting Future Scenarios for Arctic and Antarctic Fisheries" (2014). *CCPO Publications*. 252.
https://digitalcommons.odu.edu/ccpo_pubs/252

Original Publication Citation

McBride, M. M., Dalpadado, P., Drinkwater, K. F., Godo, O. R., Hobday, A. J., Hollowed, A. B., . . . Loeng, H. (2014). Krill, climate, and contrasting future scenarios for Arctic and Antarctic fisheries. *ICES Journal of Marine Science*, 71(7), 1934-1955. doi:10.1093/icesjms/fsu002

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Contribution to the Themed Section: 'Marine Harvesting in the Arctic' Original Article

Krill, climate, and contrasting future scenarios for Arctic and Antarctic fisheries

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McBride, M. M., Dalpadado, P., Drinkwater, K. F., Godø, O. R., Hobday, A. J., Hollowed, A. B., Kristiansen, T., Murphy, E. J., Ressler, P. H., Subbey, S., Hofmann, E. E., and Loeng, H. Krill, climate, and contrasting future scenarios for Arctic and Antarctic fisheries. – ICES Journal of Marine Science, 71: 1934–1955.

Received 31 May 2013; accepted 1 January 2014; advance access publication 28 March 2014.

Arctic and Antarctic marine systems have in common high latitudes, large seasonal changes in light levels, cold air and sea temperatures, and sea ice. In other ways, however, they are strikingly different, including their: age, extent, geological structure, ice stability, and foodweb structure. Both regions contain very rapidly warming areas and climate impacts have been reported, as have dramatic future projections. However, the combined effects of a changing climate on oceanographic processes and foodweb dynamics are likely to influence their future fisheries in very different ways. Differences in the life-history strategies of the key zooplankton species (Antarctic krill in the Southern Ocean and *Calanus* copepods in the Arctic) will likely affect future productivity of fishery species and fisheries. To explore future scenarios for each region, this paper: (i) considers differing characteristics (including geographic, physical, and biological) that define polar marine ecosystems and reviews known and projected impacts of climate change on key zooplankton species that may impact fished species; (ii) summarizes existing fishery resources; (iii) synthesizes this information to generate future scenarios for fisheries; and (iv) considers the implications for future fisheries management. Published studies suggest that if an increase in open water during summer in Arctic and Subarctic seas results in increased primary and secondary production, biomass may increase for some important commercial fish stocks and new mixes of species may become targeted. In contrast, published studies suggest that in the Southern Ocean the potential for existing species to adapt is mixed and that the potential for the invasion of large and highly productive pelagic finfish species appears low. Thus, future Southern Ocean fisheries may largely be dependent on existing species. It is clear from this review that new management approaches will be needed that account for the changing dynamics in these regions under climate change.

Keywords: climate change, fish, fisheries, foodwebs, Polar Regions, zooplankton.

Introduction

Climate is already impacting the physics, chemistry, and biology of the oceans around the world (e.g. [Doney et al., 2012](#); [Poloczanska et al., 2013](#)). Projected future changes in physical features such as ocean temperature, ice conditions, stratification, and currents will

have further and considerable impacts on marine ecosystems ([Hays et al., 2005](#); [Doney et al., 2012](#)). Polar Regions are among the most sensitive areas to climate change ([Hagen et al., 2007](#)), which will affect the flow of energy from lower trophic levels such as phytoplankton and zooplankton to higher levels, such as fish,

seabirds, and marine mammals (Nicol *et al.*, 2008; Barbraud *et al.*, 2012) and ultimately to the humans that depend on these systems (Brander, 2013). Climate change is expected to affect fish stocks directly by causing major geographic shifts in distribution and abundance over the next 50–100 years (Barker and Knorr, 2007; Brander, 2007; Cheung *et al.*, 2009), and recent evidence shows that changes have already occurred in benthic community composition (Mecklenburg *et al.*, 2007; Kortsch *et al.*, 2012) and Arctic fish distribution (Wassmann *et al.*, 2011) have already occurred in association with warming waters. In Arctic and Antarctic foodwebs, copepods/krill/amphipods and Antarctic krill, respectively, contribute to a significant part of the total zooplankton production and form a major link between phytoplankton and predators at higher trophic levels. Spatial and temporal changes in phytoplankton and zooplankton distribution and abundance can have major consequences for the recruitment potential of commercially important fish (Friedland *et al.*, 2012; Kristiansen *et al.*, 2014). Together, these direct and indirect impacts on fished species can have major economic implications for the fisheries sector (Allison *et al.*, 2009; Brander, 2013), although considerable uncertainty still remains regarding the magnitude of impacts and the mechanisms that underlie them (Brander, 2007).

There are major differences in the number of publications available internationally on marine biology and ecology emanating from Arctic vs. Antarctic research. The mean number of Arctic publications on the subject is 51% of Antarctic publications over the period 1991–2008 (Wassmann *et al.*, 2011). In the Arctic, the lack of reliable baseline information, particularly with regard to the Arctic basin, is due to the relative scarcity of studies into the 1970s (Wassmann *et al.*, 2011). The reasons are multiple, but include that most research has been based on national efforts; international cooperation and access to the Arctic was difficult during the Cold War period—when most bases in the Arctic were military and international access to the Siberian shelf was banned. In contrast, substantial research activity has been focused on Antarctica and the Southern Ocean stimulated in connection with the Third International Polar Year in 1958. Subsequent signing of the Antarctic Treaty in 1961 also has provided substantial impetus for collaborative international research (Wassmann *et al.*, 2011).

In recent years, the response to the climate change of marine ecosystems in the Polar Regions has been the topic of considerable international research activity, and understanding has improved as a result. Further improving the ability to determine how climate change will affect the physical and biological conditions in Arctic and Antarctic marine systems, and the mechanisms that shape recruitment variability and production of important fishery species in these regions, is essential to develop sound marine resource management policies (e.g. Stram and Evans, 2009; Livingston *et al.*, 2011).

The salient question for this review is thus: how will the response to climate change of marine systems within these two regions affect their future fisheries? To address this question, we review the existing scientific literature to determine:

1. How and why do Arctic and Antarctic marine systems differ from each other; and how are these systems responding to climate forcing, particularly with regard to foodwebs and fishery productivity?
2. Which fishery resources are currently exploited in these regions?
3. What are the future prospects for fishery resource productivity in these regions?

4. What are important considerations for an ecosystem approach to management of future fisheries in these regions?

Other authors have investigated the potential future impacts of climate change on fish and fisheries on regional (e.g. Wassmann *et al.*, 2011; Hollowed *et al.*, 2013a, b; Kristiansen *et al.*, 2014) and global scales (e.g. Brander, 2007, 2010) and have included consideration of key factors determining the response of plankton/zooplankton to climate forcing.

Our review focuses on the effects of climate change on key zooplankton species which form the link between primary producers and upper-trophic levels (i.e. fish) in both the Arctic and Antarctic marine systems. Polar zooplankton species have larger lipid reserves than related species at lower latitudes, which serve as energy for species at higher trophic levels. If the abundance of zooplankton species in Polar marine systems should decline, the consequences for larger ocean animals would likely be severe (Clarke and Peck, 1991).

Basic differences between Arctic and Antarctic marine systems

Arctic and Antarctic marine systems have in common their high latitudes, seasonal light levels, cold air and sea temperatures, and sea ice. But, in other ways, they are strikingly different (Dayton *et al.*, 1994). The Intergovernmental Panel on Climate Change points out that “the Arctic is a frozen ocean surrounded by continental landmasses and open oceans, whereas Antarctica is a frozen continent surrounded solely by oceans” (IPCC, 2007; Figure 1).

Delineations of these systems may vary. This review adopts the Arctic Climate Impact Assessment’s delineation of the marine Arctic as comprising the Arctic Ocean, including the deep Eurasian and Canadian Basins and the surrounding continental shelf seas (Barents, White, Kara, Laptev, East Siberian, Chukchi, and Beaufort Seas), the Canadian Archipelago, and the transitional regions to the south through which exchanges between temperate and Arctic waters occur (Loeng *et al.*, 2005). The latter includes the Bering Sea in the Pacific Ocean and large parts of the northern North Atlantic Ocean, including the Nordic, Iceland, and Labrador Seas, and Baffin Bay. Also included are the Canadian inland seas of Foxe Basin, Hudson Bay, and Hudson Strait (Loeng *et al.*, 2005; Huntington and Weller, 2005). Historically, sea-ice coverage ranges from year-round cover in the central Arctic Ocean to seasonal cover in most of the remaining areas (Loeng *et al.*, 2005). The area of sea ice decreases from roughly 15 million km² in March to 7 million km² in September, as much of the first-year ice melts during summer (Cavalieri *et al.*, 1997). The area of multiyear sea ice, mostly over the Arctic Ocean basins, the East Siberian Sea, and the Canadian polar shelf, is ~5 million km² (Johannessen *et al.*, 1999). For Antarctica, we adopt the Aronson *et al.* (2007) delineation as the continent and southern ocean waters south of the Polar Front, a well-defined circum-Antarctic oceanographic feature that marks the northernmost extent of cold surface water. The total ocean is ~34.8 million km², of which up to 21 million km² are covered by ice at winter maximum and ~7 million km² are covered at summer minimum (Aronson *et al.*, 2007).

A number of other physical and biological characteristics differ between the Polar Regions (Table 1). The Arctic has broad shallow continental shelves with seasonally fluctuating physical conditions and a massive freshwater input in the north coastal zones. Historically, the Arctic has been characterized by the low seasonality of pack ice and little vertical mixing; this condition is changing,

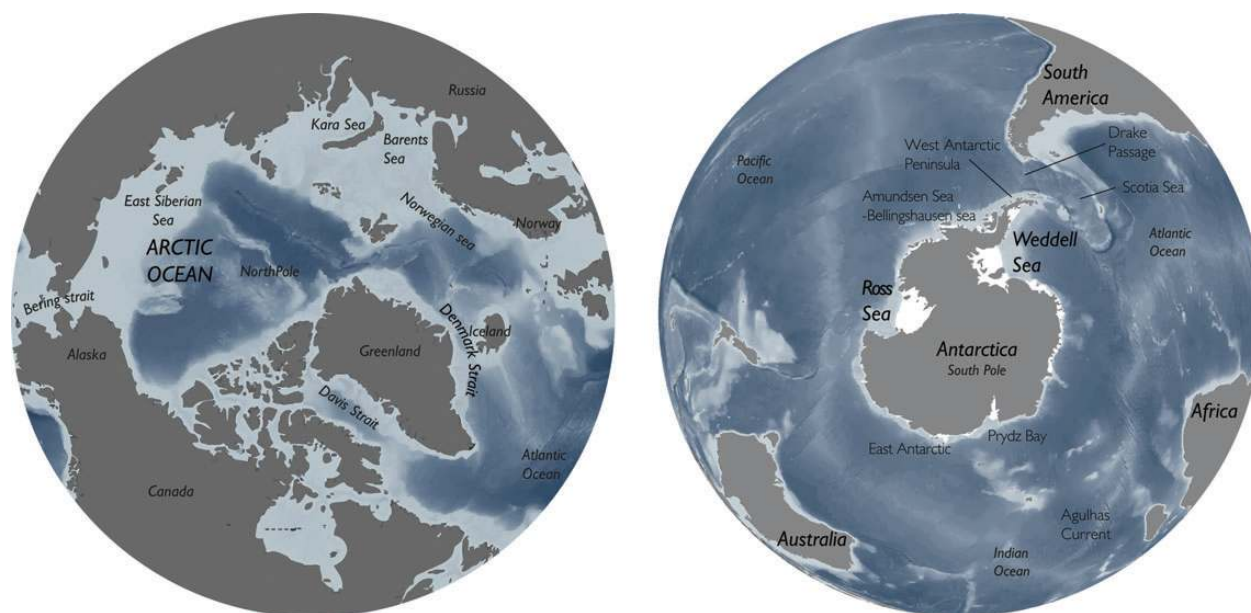


Figure 1. A fundamental difference between Arctic (left) and Antarctic (right) regions is that the Arctic is a frozen ocean surrounded by continents, while the Antarctic is a frozen continent surrounded by oceanic waters. (Original images courtesy of NOAA www.climate.gov).

Table 1. Comparison of physical and biological characteristics of the polar oceans (modified from [Eastman, 1997](#)).

Feature	Southern Ocean	Arctic Ocean
Geographic disposition	Surrounds Antarctica between 50 and 70°S	Enclosed by land between 70 and 80°N
Area	35–38 × 10 ⁶ km ²	14.6 × 10 ⁶ km ²
Extent of continental shelf	Narrow, few islands	Broad, extensive archipelagos
Depth of continental shelf	400–600 m	100–500 m
Shelf continuity with ocean	Open to oceans to the north	Open to the south at Fram and Bering Straits
Direction of currents	Circumpolar	Transpolar
Upwelling and vertical mixing	Extensive	Little
Nutrient availability	Continuously high	Seasonally depleted
Seasonality of solar illumination	Weak	Strong
Primary productivity	Moderate to high	Moderate
Fluvial input to ocean	None	Extensive
Salinity at 100–150 m	34.5–34.7‰	30–32‰
Seasonality of pack ice	High	Low
Physical disturbance of benthos by large predators	Low	Extensive
Physical disturbance of benthos by ice scour	High	Low

however, for large parts of the Arctic due to declining sea ice (e.g. [Hare et al., 2011](#)). In contrast, the Antarctic has over twice the oceanic surface area, deep narrow shelves, and except for ice cover, a relatively stable physical environment with very little terrestrial input. The Antarctic has great pack-ice seasonality and much vertical mixing ([Dayton et al., 1994](#)).

Geological and evolutionary histories

The geological and evolutionary histories of these regions differ greatly ([Dayton et al., 1994](#)). Antarctica is a very old system that tends to be thermally isolated from the rest of the planet. Biogeographers agree that most Antarctic biota are very old and unique ([Rogers et al., 2012](#)). During its geological history, it was first isolated for some 20–30 million years, and only then was it subject to intense cooling. This was followed by the opportunity to evolve in an isolated, relatively stable, and uniform system for

perhaps another 20 million years ([Dayton et al., 1994](#)), which has implications for evolution in response to current climate change.

In contrast, the biogeography of the Arctic is neither ancient nor well established and seems to be in a state of active colonization over the last 6000–14 000 years ([Dayton et al., 1994](#)). It is influenced strongly by seasonal atmospheric transport and river inflow from surrounding continents. The human imprint in these regions also differs. The Arctic has been populated for thousands of years. There is considerable economic activity, based on fishing and shipping. Recent decades have seen the establishment of urban areas and increased industrial activity related to petroleum, gas, and mining industries. In contrast, the Antarctic has limited resource use, apart from a history of industrial fishing for marine mammals and fish species, a fishery for krill (conducted since 1973), and a rapidly growing tourism industry ([Dayton et al., 1994](#); [Leaper and Miller, 2011](#); [Rintoul et al., 2012](#)).

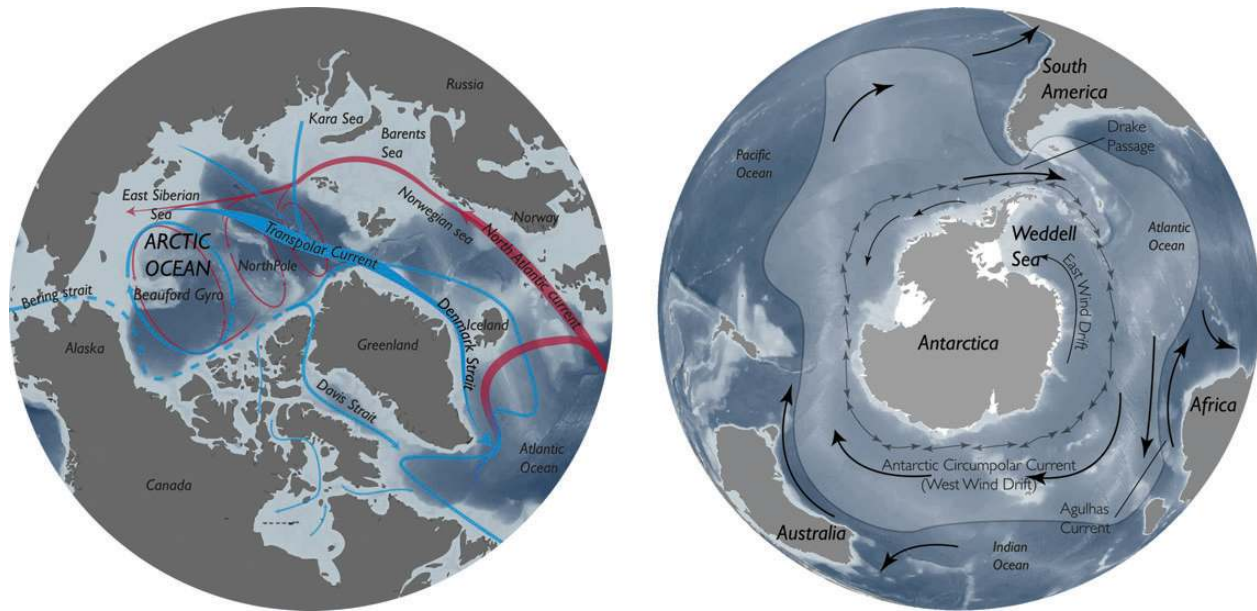


Figure 2. Patterns of circulation and inflow for Arctic (left) and Antarctic (right) marine systems. The Antarctic Circumpolar Current (also called the West Wind Drift) continuously flows around Antarctica in a clockwise direction (light blue). The Antarctic Coastal Current flows closer to the shore in a counter-clockwise direction. (Original images courtesy of NOAA www.climate.gov).

Ocean circulation

As a result of geological structure, patterns of circulation in these regions differ (Figure 2). Winds and currents play important roles in the advection of heat and salt, both into and out of the Arctic, and clockwise around Antarctica.

In the Arctic, dominant features of the surface circulation are the clockwise Beaufort Gyre that extends over the Canadian Basin, and the Transpolar Drift that flows from the Siberian coast out through the Fram Strait. Dominant river inflow comes from the Mackenzie River in Canada and the Ob, Yenisey, and Lena Rivers in Siberia. Warm Atlantic water flows in via the Barents Sea and through the Fram Strait, and relatively warm Pacific water flows across the Bering Sea and into the Arctic through the Bering Strait (Loeng *et al.*, 2005). In addition, three pathways of water flowing northward from the North Pacific Ocean through the Bering Strait and across the Chukchi Sea have been reported (Winsor and Chapman, 2004). The Southern Ocean circulation system interacts with deep-water systems in each of the Pacific, Atlantic, and Indian oceans. The Antarctic Circumpolar Current (ACC) is the strongest ocean current in the world and continuously circles the continent in a clockwise direction (Barker and Thomas, 2004). This current is driven by strong westerly winds that are unimpeded by land. Closer to the continent, easterly winds form a series of clockwise gyres, most notably in the Ross and Weddell seas, that form the west-flowing Antarctic Coastal Current. Most ACC water is transported by jets in the Subantarctic Front and the Polar Front. Water flows out of the Southern Ocean and enters the Pacific, Atlantic, and Indian Oceans. However, water flowing into the Southern Ocean from these same adjacent oceans is not well documented (Rintoul *et al.*, 2012). The Polar Front acts as a major barrier to the exchange of surface waters between Subantarctic waters to the north and Polar Waters to the south.

These systems also have different levels of connectivity or residence time of water masses: there is relatively rapid connectivity

in surface waters around the Antarctic on a scale of years (Thorpe *et al.*, 2007), whereas waters within the Arctic have a much longer residence time ranging from ~25 years in the mixed layer to 100 years in the halocline to 300 years in the bottom water (Becker and Björk, 1996; Anisimov *et al.*, 2007; Ghiglione *et al.*, 2012; CAFE, 2013). These differences in circulation, exchange, and transport have already influenced the movement, gene flow, and evolution of species inhabiting these systems and may also influence the movement of species into the Polar Regions in response to warming.

Primary and secondary production importance for foodwebs

The productivity of fisheries in Polar Regions is related to environmental conditions and the availability of prey. Thus, primary and secondary productivity can cause cascading effects through the marine foodweb which influence recruitment of fish stocks (Brander, 2007). In the Arctic Ocean, decreasing summer sea-ice coverage is expected to result in increased light penetration in the seawater, a longer production period, and higher primary production (Brown and Arrigo, 2012). Nutrient availability may be a limiting factor if water column stability increases (Frey *et al.*, 2012); however, currents from surrounding waters may carry nutrients and phytoplankton into the Arctic Ocean, resulting in higher production. Wegner *et al.* (2010) estimates that ice-algal activity currently accounts for ~50% of total primary productivity in the Arctic Ocean with diatoms and flagellates contributing significantly to the community of ice biota. Whereas, Wassmann *et al.* (2010) estimates that the European sector, stretching from the Fram Strait in the west to the northern Kara Sea in the east, accounts for far more than 50% of total primary production in the Arctic Ocean. In addition, protozoan and metazoan ice meiofauna, in particular turbellarians, nematodes, crustaceans, and rotifers, can be abundant in all ice types (Gradinger, 1995; Melnikov, 1997; Bluhm *et al.*, 2011). With earlier sea ice break-up, and earlier

plankton blooms, the match/mismatch in phytoplankton prey (under ice algae) with zooplankton predators will determine the effectiveness of foodweb energy transfer in the Arctic (Loeng *et al.*, 2005).

In the Antarctic, primary production is highest along the sea-ice edge (in areas the ice is thinning or has melted, thus allowing more light to penetrate) and in areas around the continent and islands. There is a distinctly seasonal pattern of phytoplankton blooms. As in the Arctic, diatoms are the major component of the phytoplankton assemblage, but there are regional differences in community structure and seasonal species succession. Nutrients for photosynthesis are supplied through oceanic upwelling and wind-driven upwelling along the continental shelf, particularly where topography forces upwelling onto the continental shelf along the western Antarctic Peninsula (Steinberg *et al.*, 2012). The dominant flow of energy is through production at the surface by phytoplankton, followed by sinking and breakdown in the benthic microbial loop. The availability of iron is limited, so phytoplankton blooms occur in areas of atmospheric dust deposition and in areas with natural sources of mineral iron, such as coastal continental regions or around islands through upwelling–sediment interaction processes. Advection by the ACC also plays a prominent role in primary production, with waters moving north and south as they flow around the continent and hence into different light regimes where they also influence nutrient dynamics (Hofmann and Murphy, 2004; Rintoul *et al.*, 2012).

In the Antarctic and the Arctic, krill and copepods/krill/amphipods, respectively, contribute largely to total zooplankton production and are the major grazers and modifiers of the primary production in the pelagic realm (Smetacek and Nicol, 2005). In the Barents Sea, *Calanus finmarchicus* dominates the mesozooplankton biomass across much of the coastal and deep North Atlantic Ocean. *Calanus marshallae* is one of the main copepods in the Bering Sea (Baier and Napp, 2003), while *C. glacialis* (particularly in the Chukchi Sea) and the larger *C. hyperboreus* are the biomass dominant copepods in the Arctic Ocean (Hopcroft *et al.*, 2005, 2008). Despite spatial variances within regions, krill generally appear less abundant in Arctic Ocean waters than in Antarctic waters, but they also can be important prey for higher trophic levels (Dalpadado *et al.*, 2001; Aydin and Mueter, 2007). They are common on the Atlantic side of the Arctic Ocean and in the Bering Sea where species include: *Meganyctiphanes norvegica*, *Thysanoessa inermis*, *T. raschii*, *T. longipes*, *T. longicaudata*, and *E. pacifica* (Vidal and Smith, 1986; Smith, 1991; Brinton *et al.*, 2000; Coyle and Pinchuk, 2002; Zhukova *et al.*, 2009; Dalpadado *et al.*, 2012; Ressler *et al.*, 2012). These species are not common in the central Arctic Ocean (Loeng *et al.*, 2005). Although not frequently captured in net sampling in the Western Arctic, euphausiids do occur locally in high abundance along the Chukotka Coast and near Barrow, Alaska, where they are important prey for the bowhead whale (e.g. Berline *et al.*, 2008; Ashjian *et al.*, 2010; Moore *et al.*, 2010).

In the Southern Ocean, krill are the most important zooplankton forming the link between primary production and higher trophic levels (Schmidt *et al.*, 2011). Seven krill species, each with different latitudinal ranges, are known to occur: *Euphausia superba*, *E. crystallophias*, *E. frigida*, *E. longirostris*, *E. triacantha*, *E. valentini*, and *Thysanoessa macrura* (Kirkwood, 1984; Fischer and Hureau, 1985; Baker *et al.*, 1990; Brueggeman, 1998). Antarctic krill (*E. superba*) is dominant and very abundant (Rockliffe and Nicol, 2002) with an estimated 350–500 million tonnes of Antarctic krill in the

Southern Ocean (Nicol, 2006; Atkinson *et al.*, 2009). Copepods can dominate the zooplankton communities in areas where there are few krill and can also be the major consumers of primary production (Shreeve *et al.*, 2005). Copepods are also an important component of the diet of many species (including fish and seabirds) and crucial to maintain the overall structure of Southern Ocean foodwebs (Rockliffe and Nicol, 2002; Ducklow *et al.*, 2007; Murphy *et al.*, 2007a).

Arctic marine waters are home to species of marine and diadromous (mostly anadromous) fish species occurring in all three realms of the Arctic (pelagic, benthic, and sea ice), with the highest species richness occurring among benthic and demersal fish (87%; Mecklenburg and Mecklenburg, 2009). Most fish species found in the Arctic also live in northern boreal and even temperate regions (Loeng *et al.*, 2005). In the Arctic foodweb, two fish species (Arctic cod *Arctogadus glacialis* and polar cod *Boreogadus saida*) are closely associated with the sea ice and also serve as energy transmitters from the sea ice algae to higher trophic levels (Bluhm *et al.*, 2011). The diet of one abundant krill species (*M. norvegica*) in the North Atlantic consisted largely of copepods (*Calanus* species) and phytoplankton, suggesting that this species could be an important competitor for pelagic plankton-eating fish species (FAO, 1997). The diet of other krill species consists largely of phytoplankton, thus forming a short and efficient link between primary producers and higher trophic levels (OSPAR, 2000; Figure 3).

It should be noted that in both Arctic and Antarctic marine systems, krill and copepods also feed on microzooplankton (Wickham and Berninger, 2007) which act as trophic intermediates between the small bacteria, nanoplankton, and the larger mesozooplankton (Gifford, 1988; Gifford and Dagg, 1988, 1991; Gifford, 1991; Perissinotto *et al.*, 1997). Also of note in both systems, there is evidence that the occurrence of gelatinous zooplankton—jellyfish in the Arctic Ocean (Wassmann *et al.*, 2011) and salps in the Southern Ocean (Atkinson *et al.*, 2004)—appears to be increasing. These species are important components of marine foodwebs; they can be major consumers of production at lower trophic levels and compete with fish species for their food. The consequences of their trophic activities, and changes in them, are likely to have major effects on pelagic foodwebs in both regions, and through the sedimentation of particulate matter, on pelagic–benthic coupling (Raskoff *et al.*, 2005). In the Arctic, cnidarians, ctenophores, chaetognaths, and pelagic tunicates commonly occur in the water column (Raskoff *et al.*, 2005). In the Southern Ocean, species of tunicates (salps), siphonophores, and medusae commonly occur and feed efficiently on a wide size range of plankton (Foxton, 1956), but may not efficiently transmit that energy up the food chain.

The classical view of the Southern Ocean foodweb also has a small number of trophic levels and a large number of apex predators (Cleveland, 2009; Figure 4), but the importance of alternative and longer routes of energy flow has been increasingly recognized (Ducklow *et al.*, 2007; Murphy *et al.*, 2007a). The benthos is the richest element of the foodweb in terms of numbers of macrospecies, which are thought to be dominated by suspension-feeders. Although there is a larger number of individual species in the Antarctic compared with the Arctic, there are fewer families represented (Griffiths, 2010). Eastman (2005) characterizes Antarctic fish diversity as relatively low given the large size of the Southern Ocean. Some groups of fish and decapod crustaceans are completely absent in the Antarctic at present, despite having occurred there based on fossil records (Griffiths, 2010). As earlier noted, Antarctic krill form the major link between phytoplankton and

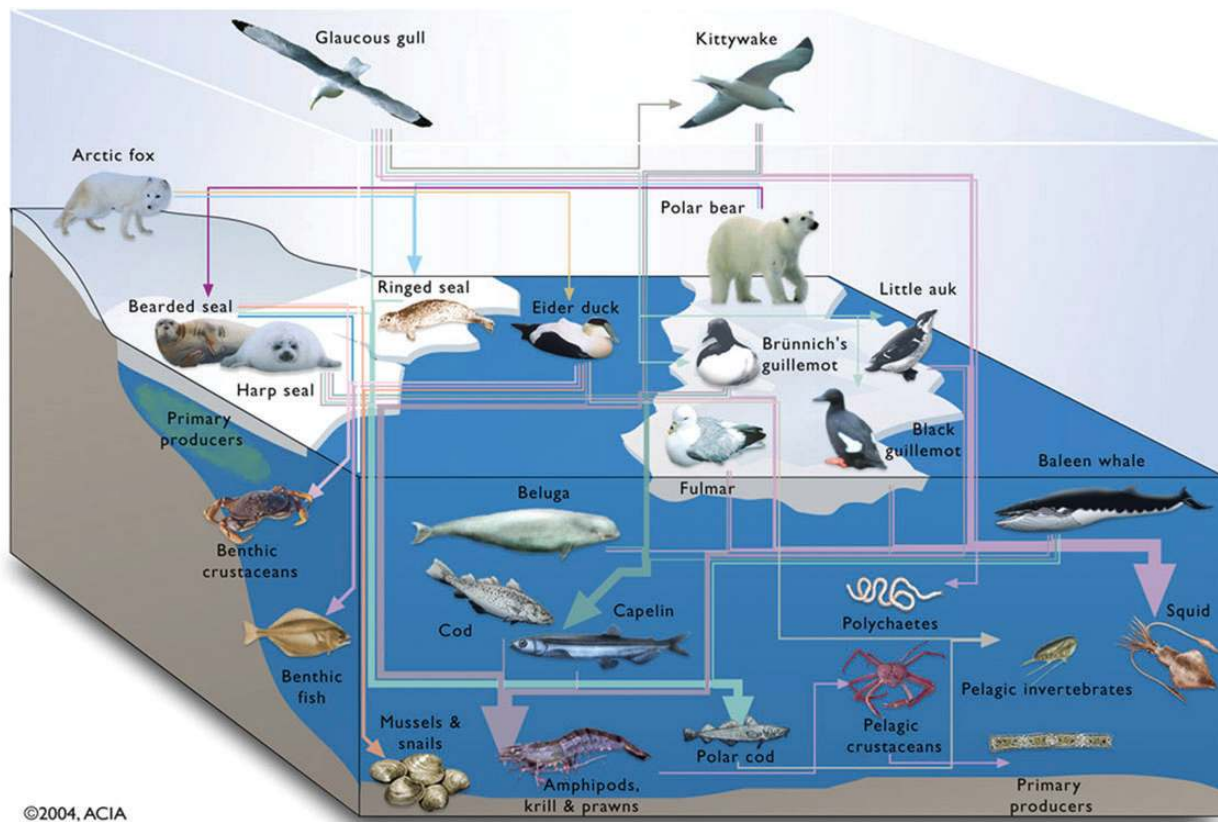


Figure 3. Arctic marine foodweb (Illustration courtesy of Arctic Climate Impact Assessment 2004).

higher trophic levels. Many higher trophic level marine species in the Southern Ocean feed on krill—including fish, whales, seals, penguins, albatrosses, petrels, and squid (Rintoul *et al.*, 2012; Rogers *et al.*, 2012). Although there are other ecological pathways in the Southern Ocean, the dependence of so many upper-level vertebrate predators on a single species results in a “wasp-waist ecosystem” where the intermediate trophic level is dominated by a single species (Bakun, 2006). Hence, any major perturbation in the krill population may have ramifications throughout the Southern Ocean system (Flores *et al.*, 2012).

In the Bering Sea, recent studies suggest that climate conditions and predator–prey interactions act in concert to create a complex relationship between the dominant pelagic fish species, walleye pollock (*Theragra chalcogramma*), and euphausiids (Ressler *et al.*, 2012). This relationship includes both bottom-up and top-down control of these interacting species.

Pelagic–benthic coupling

Pelagic–benthic coupling involves the supply of material from the euphotic zone to deeper waters and the seabed. This process is regulated by primary production (new production), the composition of primary producers (sinking ability), grazers (herbivores), remineralization rate (bacteria, microbial foodweb), physical processes (mixing, advection), active biological transport (vertical migration), and depth (sinking time from production to seabed; Wassmann, 2006; Renaud *et al.*, 2008; Wassmann and Reigstad, 2011). In both Arctic and Antarctic marine systems, zooplankton contributes in different ways to pelagic–benthic coupling, e.g. the

sinking faecal material from zooplankton grazing on phytoplankton and ice algae is a major contributor to vertical pellet flux enhancing energy flow to the deep layers (Tremblay *et al.*, 1989), and many species migrate vertically. In the Antarctic, observations of krill on the seabed at depths of >3000 m (Clarke and Tyler, 2008) have led to a reassessment of their distribution and has demonstrated that vertical migrations involving feeding interactions of krill in benthic ecosystems can be important (Schmidt *et al.*, 2011).

Production of pelagic larvae by benthic organisms also presents different pathways linking the two depth zones (Schnack-Schiel and Isla, 2005). Data from the high Arctic and Antarctic, indicate that a large percentage of surface-produced organic matter is consumed by both macro- and microzooplankton as well as recycled in the water column via the microbial loop (Grebmeier and Barry, 1991). Exceptions occur in the Arctic in the shallow shelf regions (<200 m), such as the Bering/Chukchi shelf system and certain regions of the Barents Sea, where a tight coupling between pelagic and benthic productivity occurs with higher food supply to the benthos influencing high benthic biomass (Campbell *et al.*, 2009; Sherr *et al.*, 2009). In both regions, however, this process is highly seasonal and influenced by seasonal ice zones. A major difference is that the nearshore deep Antarctic is characterized by relatively high benthic abundance and biomass despite low water column production, suggesting that stability, low disturbance levels, and cold temperatures enable benthic organisms to grow larger than in the Arctic. In contrast, levels of both oceanographic turbulence and biological variability are high in the marginal seas of the Arctic; this may directly influence benthic productivity (Grebmeier and

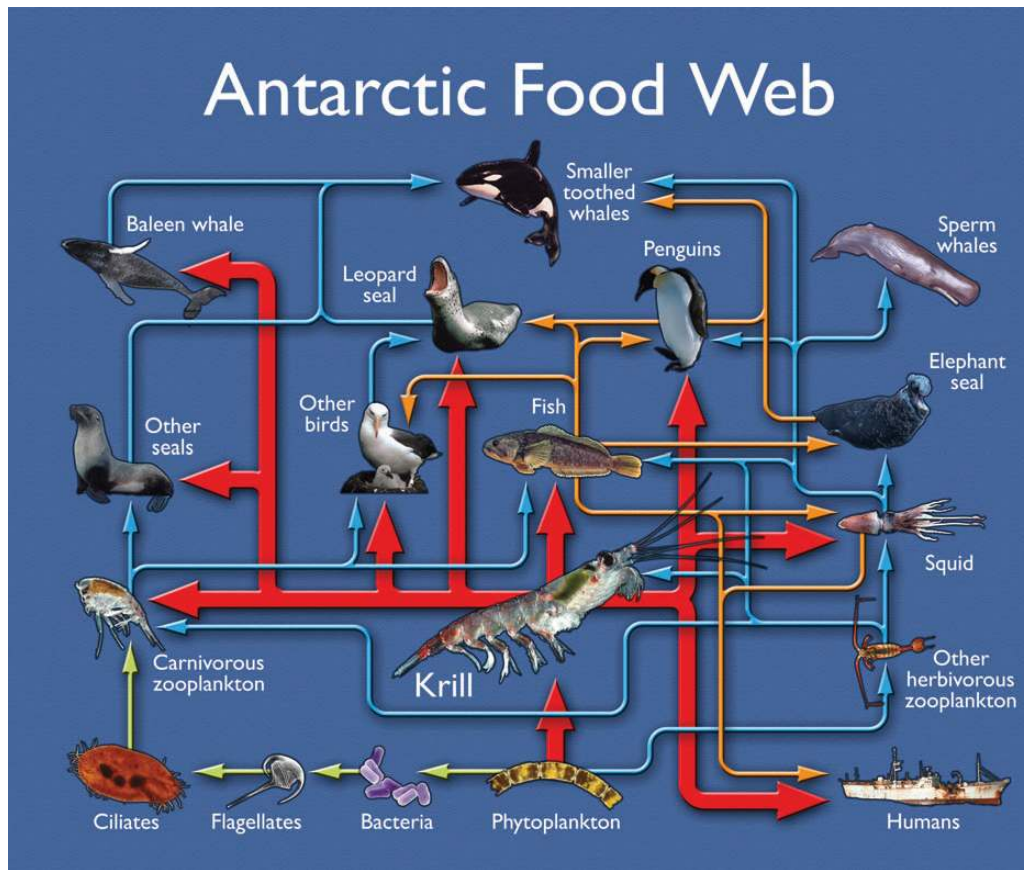


Figure 4. Antarctic Ocean (Southern Ocean) foodweb (Illustration courtesy of the British Antarctic Survey).

Barry, 1991). In Antarctic marine areas, where depths can reach 4000–5000 m, pelagic–benthic coupling may be less important compared with the Barents Sea and other shallow-shelf Arctic regions.

Fish fauna and biodiversity

Arctic and Antarctic fish fauna differ in age, endemism, taxonomic diversity, zoogeographic distinctiveness, and physiological plasticity. Species inhabiting these regions have evolved quite different life-history characteristics to cope with their hostile environments, which may limit their responses to climate change. Eastman (1997) presents a broad comparison of the polar fish faunas (Table 2). Although there are convergent organismal and organ system adaptations to certain habitats and physical and biological parameters, in many respects Arctic and Antarctic fauna are more dissimilar than similar (Eastman, 1997; Table 2).

Eastman (1997) estimated that Arctic fish fauna include 416 species in 96 families. In contrast, Southern Ocean fish fauna were estimated to include 274 species representing 49 families; this study delineates the Arctic Ocean as “enclosed by land between 70 and 80°N” and delineates the Southern Ocean as “surrounds Antarctica between 50 and 70°S”. Eastman (2005) revised the estimate of Southern Ocean fish fauna to consist of 322 species representing 50 families. In the Arctic, six dominant groups—zoarcoids, gadiforms, cottids, salmonids, pleuronectiforms, and chondrichthyans—comprise 58% of the fauna (Eastman, 1997). The Arctic has a relatively low rate of endemism: 20–25% in marine fish (Eastman, 1997). In the Arctic, mail-cheeked fish

(scorpaeniforms) come closest to dominance at ~24%. Arctic fauna has a wider taxonomic representation, especially among the bony or ray-finned fish, many of which are both euryhaline and eurythermal (Eastman, 1997). Currently, relatively few existing fish species are endemic to the Arctic (Bluhm *et al.*, 2011), and new Subarctic species are moving northward into the Arctic in response to climate forcing (Usher *et al.*, 2007; Mecklenburg *et al.*, 2011; Kotwicki and Lauth, 2013). It is likely that the relatively unpredictable conditions of this system would favour the establishment of new marine species that are r-selected, i.e. having early maturity, rapid growth, production of larger numbers of offspring at a given parental size, small body size, high rates of mortality, and shorter lifespan. For example, Arctic cod (*A. glacialis*), polar cod (*B. saida*), and capelin (*Mallotus villosus*) are all successful and abundant r-selected species which occur in the Arctic region (FAO, 1990, 2013).

In the Antarctic, five groups (notothenioids, myctophids, liparids, zoarcids, and gadiforms) account for ~74% of the fish species, with notothenioids alone comprising 35%. Only zoarcids and liparids are common to both polar systems and suitable freshwater habitats for fish do not exist in Antarctica (Eastman, 1997). The major feature of the Antarctic fish fauna are almost an entire absence of epipelagic fish species south of the Polar Front. An exception is the notothenioid shelf species *Peleuragramma antarcticum* (silverfish) which has a life cycle closely associated with the sea ice (Cullins *et al.*, 2011). In the Southern Ocean, endemic species predominate with an estimated 88% endemism (174 species) for benthic fauna

Table 2. Comparison of the polar fish faunas (modified from Eastman, 1997).

Feature	Antarctic region	Arctic region
Number of families	49	96
Number of species (freshwater/marine)	274 (0/274)	416 (58/358)
Species endemism for freshwater fish	–	Very low (2%)
Age of freshwater ecosystem (my)	–	0.01–0.1
Species endemism for marine fish	High (88%)	Low (20–25%)
Generic endemism for marine fish	High (76%)	0%
Familial endemism for marine fish	High (12%)	0%
Age of marine ecosystem (my)	13–22	0.7–2.0
Faunal boundaries	Distinct	Indistinct
Adaptive radiation of an old indigenous faunal element	Yes	No

my, million years.

of the shelf and upper slope. This high degree of species-level endemism is indication of a long period of evolution in isolation (Eastman, 1997). As such, any inability to cope or adapt to warming waters could result in reduced abundance of these species at both the regional level and from the global system (Hogg *et al.*, 2011). Antarctic fish tend to have a combination of life-history characteristics (often referred to as K-selection) which may increase their vulnerability to fishing pressure, and other ecosystem perturbations (King and McFarlane, 2003): including (i) delayed maturity, (ii) reduced growth rates, (iii) low mortality rates, (iv) large body size, and (v) longer lifespans. A number of fish species that were depleted through industrial fisheries conducted in the Southern Ocean during the 1970s had these characteristics of K-selected species including the Patagonian toothfish (*Dissostichus eleginoides*) and the marbled notothenia (*Notothenia rossii*; Ainley and Blight, 2008).

Existing fisheries in the Polar Regions

The broad spatial scope of the Arctic marine area includes a wide range of different ecosystems, fish stocks, and fisheries. Significant differences exist, for instance, between the Atlantic and Pacific sides of the Arctic. In the Arctic Climate Impact Assessment, Loeng *et al.* (2005) describe Arctic fisheries for selected species in the: Northeast Atlantic (Barents and Norwegian Seas), North Atlantic waters around Iceland and Greenland, waters off north-eastern Canada (Newfoundland/Labrador area), and waters in the North Pacific/Bering Sea area (Vilhjálmsón and Hoel, 2005). Most of these fisheries are conducted within ice free exclusive economic zone (EEZ) waters of respective countries in areas and seasons that are ice free. Vilhjálmsón and Hoel (2005) in the Arctic Climate Impact Assessment report that in the circumpolar Arctic, the main species targeted are: capelin (*M. villosus*), Greenland halibut (*Reinhardtius hippoglossoides*), northern shrimp (*Pandalus borealis*), and polar cod (*B. saida*). Other fisheries of commercial importance in specific regions (e.g., the Barents and southeast Bering Seas) include, but are not limited to: Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), walleye pollock (*Theragra chalcogramma*; originally described as *G. chalcogrammus*) (Byrkjedal *et al.*, 2008), Pacific cod (*G. macrocephalus*), snow crab (*Chionoecetes opilio*), Atlantic herring (*Clupea harengus*), Pacific herring (*C. pallasii*), salmon (*Salmo salar* and *Oncorhynchus* spp.), yellowfin sole (*Limanda aspera*), northern rock sole (*Lepidopsetta polyxystra*), snow crab (*C. opilio*), and red king crab (*Paralithodes camtschaticus*). Commercially harvested Arctic molluscs include clams (*Mya truncata*, *M. arenaria*), blue mussels (*Mytilus edulis*), and Iceland scallops

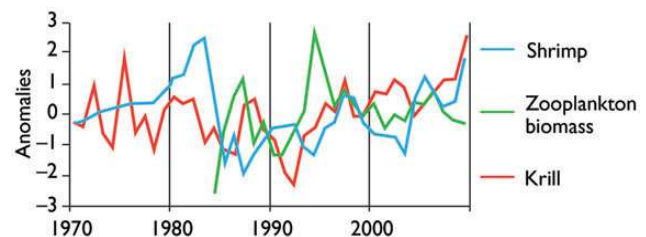


Figure 5. Temporal variation in the biomass of zooplankton, krill, and shrimp in the Barents Sea from 1970 through 2010. Data time-series for shrimp, krill, and zooplankton have been normalized (from Johannessen *et al.*, 2012).

(*Chlamys islandica*; Vilhjálmsón and Hoel, 2005). Fisheries for krill and copepods are also conducted in Subarctic waters, but are much smaller than in the Southern Ocean. On average 4000 t of *Euphausia pacifica* are removed each year from Japanese waters, whereas 50–300 t per year on average are removed from Canadian waters (Ichi, 2000). In addition, ~1000 t of the copepod, *C. finmarchicus*, are harvested each year from Norwegian waters (Grimaldo and Gjosund, 2012). In US Alaska federal waters, there is a minimum retention allowance on krill bycatch to deter directed fishing on krill (Livingston *et al.*, 2011). Off US West Coast States, directed fisheries on krill have been prohibited since 2009 (USDOC, 2009; PFMC, 2011).

Fishing is the major industry in Antarctic waters. Hundreds of thousands of tons are landed each year. Antarctic krill (*E. superba*) support the largest fishery (Figures 5 and 6). In the 1970s, development of the commercial krill fishery was facilitated by heavy fishing subsidies in the USSR, which became the most important krill-fishing nation during the 1970s and the 1980s (Nicol and Foster, 2003). Following the dissolution of the USSR at the end of 1991, krill catches decreased from ~400 000 to <100 000 t in the mid-1990s (Nicol and Endo, 1999; Nicol *et al.*, 2012). This was followed by a period when catch levels fluctuated between ~80 000 and 125 000 t (mean 114 707 t). The late 2010s had a period of high catches over 125 000 t, with the catches in 2009/10 reaching 211 984 t (Nicol *et al.*, 2012; Murphy and Hofmann, 2012). However, catches again decreased during the past 2 years (CCAMLR, 2013). This renewed interest in the krill fishery followed the introduction of new catching and processing technologies.

Krill are high in omega-3 fatty acids, and krill-derived products (e.g. “Krill Oil”) are being marketed as human dietary supplements (Nicol *et al.*, 2012). New products also include raw materials for pharmaceutical and cosmetic industries. Although traditional fish-meal products still dominate the market in terms of weight, the

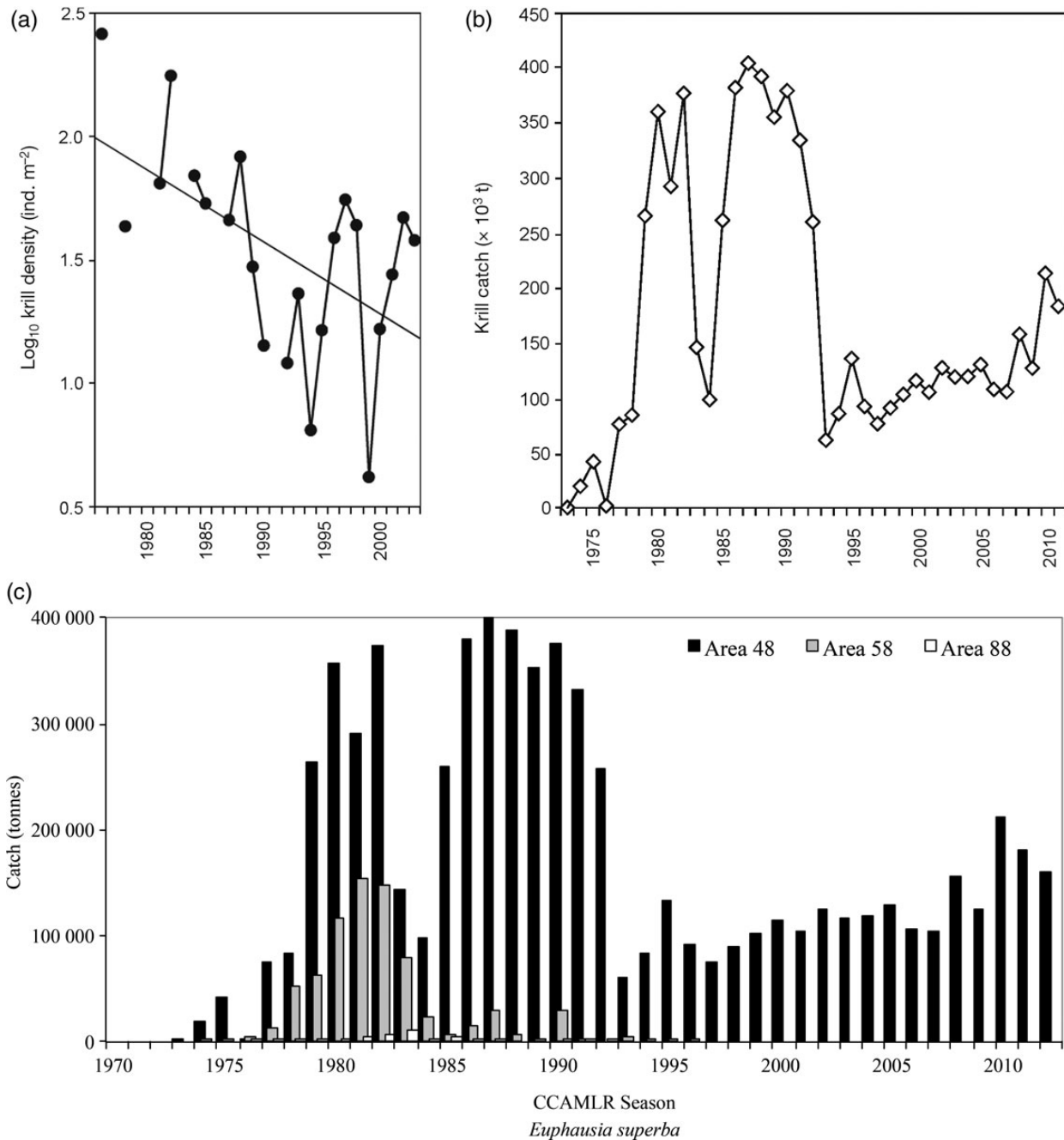


Figure 6. Antarctic krill *E. superba*. (a) Change in mean density of post-larval krill (ind. m⁻²) within the SW Atlantic sector (30–70°W) between 1976 and 2003. Based on the post-1976 dataset, there is a significant decline: $\log_{10}(\text{krill density}) = 60.07 - 0.0294(\text{year})$; $R^2 = 31\%$, $p = 0.007$, $n = 22$ years (Source: modified from Atkinson et al., 2008; © Inter-Research 2008). (b) Reported krill catches (in metric tonnes) in FAO Statistical Area 48, 1973 to 2011 (CCAMLR, 2010, 2011a) (source: Flores et al., 2012). (c) CCAMLR 2013 reported krill catches (source: <http://www.ccamlr.org/en/fisheries/krill-fisheries>).

economic viability of the fishery may depend on these new products (Nicol et al., 2012). Antarctic toothfish (*Dissostichus mawsoni*) have the highest economic value (Griffiths, 2010); in recent years, catches have been ~12–15 000 t. Fisheries also target Patagonian toothfish (*D. eleginoides*) and mackerel icefish (*Champscephalus gunnari*; CCAMLR, 2013).

Over the period from 1969 to the mid-1980s, several finfish stocks were on average reduced to <20% of their original size (Ainley and Blight, 2008). It has been hypothesized that during

the mid-1980s, a shift occurred in the ecological structure of significant portions of the Southern Ocean following the serial depletion of fish stocks by intensive industrial fishing, in combination with a reduction in the krill food base (Ainley and Blight, 2008). Subsequently, fisheries have been heavily regulated since establishment of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) in 1982. Despite CCAMLR's management actions (such as banning benthic trawling in several areas) few stocks have recovered, and in some regions, stocks such

as mackerel icefish may still be declining (Ainley and Blight, 2008; CCAMLR, 2011b; Shotton and Tandstad, 2011). Although commercial fishing in Antarctica is heavily regulated, illegal, unreported, and unregulated (IUU) fishing may have occurred (Fabra and Gascón, 2008). The Australian Heard Island mackerel icefish fishery was certified as a sustainable and well managed fishery by the Marine Stewardship Council (MSC) in 2006 and recertified in 2011. In March 2012, Australia's Heard Island toothfish fishery followed, and in May 2012, the Macquarie Island Toothfish Fishery was also certified, indicating that sustainable fishing is possible in these waters. International collaboration between fishing nations and companies is leading to improved practices and reductions in IUU fishing (<http://www.colto.org/>), and now over half of the world's toothfish catch is MSC-certified.

Future prospects for fishery resource productivity

The future productivity of exploited stocks in the Polar Regions will depend both on suitable environmental conditions and appropriate region-specific management regimes. We first review the changing environmental conditions, then consider foodweb response with focus on the critical zooplankton (copepods and krill) linking primary producers and target fishery species.

Changing environmental conditions

Sea ice

The states of Arctic and Antarctic climates are the result of complex interactions between external forcing, large-scale non-linear climate dynamics, and regional feedbacks. Recent and potential future changes in climate at both poles, while different, are consistent with known impacts from shifts in atmospheric circulation and from thermodynamic processes that are, in turn, a consequence of anthropogenic influences on the climate system (Overland *et al.*, 2008). Further reductions in summer sea ice are expected in both Polar Regions (Anisimov *et al.*, 2007; Drinkwater *et al.*, 2012).

In the Arctic, the ocean has warmed through increased advection of warm waters from the south, as well as air-sea heat fluxes. This warming has led to significant reductions in both the areal coverage of summer sea ice and in the amount of multiyear ice (Drinkwater *et al.*, 2012). With thinner ice and lower ice concentrations during summer, it has been easier for the winds to move the ice around, and currents have sped up in recent years (Drinkwater *et al.*, 2012). Given the recent dramatic loss of multiyear sea ice in the north and projections of continued global warming, it seems unlikely that summer Arctic sea ice will return to the climatological extent that existed before 1980 (Overland *et al.*, 2008).

In the Antarctic, analyses of satellite data show that sea ice around the continent has undergone a small, but significant, increase in circumpolar sea ice extent (SIE) of 0.97% per decade for the period from 1978 to 2007 (Turner and Overland, 2009). However, there are large regional variations with reductions in SIE around the West Antarctic Peninsula and across the Amundsen-Bellingshausen Sea and increases in the Ross Sea (IPCC, 2007; Comiso and Nishio, 2008). This spatial pattern of reduction and increase is associated with observed changes in atmospheric circulation (Turner *et al.*, 2009). Model studies have indicated that these changes may be the result of increased windspeeds around the continent associated with stratospheric ozone depletion. However, the observed sea ice increase was within the range of natural climate variability (Turner *et al.*, 2009). Modelling predictions for the 21st century show wide variability for changing sea ice in the Southern Ocean, with predicted decreases

ranging from 25 to 40% (Bracegirdle *et al.*, 2008; Turner *et al.*, 2009; Rintoul *et al.*, 2012). Recovery of stratospheric ozone concentrations may lead to reduced windspeeds, but temperatures and sea ice will potentially be affected by direct greenhouse gas impacts (Overland *et al.*, 2008; Turner *et al.*, 2009).

Ocean acidification

Loss of sea ice and high rates of primary production over the continental shelves, coupled with increased ocean-atmosphere gas exchange (CO_2), mean that both cold polar oceans, which more readily take up CO_2 , will be among the first to become undersaturated with respect to aragonite (McNeil and Matear, 2008; Fabry *et al.*, 2009; Feely *et al.*, 2009; Orr *et al.*, 2009; Weydmann *et al.*, 2012). This is likely to have biochemical and physiological effects on both krill and copepods, although the level of ocean acidification at which severe effects can be expected is unclear.

Results from experiments conducted by Kawaguchi *et al.* (2011) to assess the possible impact of elevated CO_2 levels on early development of krill demonstrated that krill embryos develop normally under a range of up to 1000 p CO_2 (partial pressure of atmospheric carbon dioxide). However, their development is almost totally inhibited at 2000 p CO_2 . Projections based on Intergovernmental Panel on Climate Change (IPCC, 2007) modelling scenarios suggest that Southern Ocean surface p CO_2 may rise to 1400 p CO_2 within this century, but are unlikely to reach 2000 p CO_2 . So the salient question is whether Southern Ocean p CO_2 will reach levels detrimental to krill or not (Kawaguchi *et al.*, 2010). Recent work showed that p CO_2 is much higher at the depth that krill eggs develop (700–1000 m); detrimental conditions will be encountered before the end of the century (Kawaguchi *et al.*, 2013). It is therefore important to continue sustained observations of population and condition parameters of krill at circumpolar scales throughout their life cycle to detect potential effects of ocean acidification in the future (Flores *et al.*, 2012).

A study of the Arctic copepod, *Calanus glacialis*, was conducted by Weydmann *et al.* (2012) to investigate how the reduction of sea surface pH—from present day levels (pH 8.2) to an extreme level (pH 6.9)—would affect egg production and hatching success under controlled laboratory conditions. A significant delay in the hatching of *C. glacialis* resulted when exposed to highly acidified (pH 6.9) conditions. This study showed no significant effect of seawater acidification on either egg production rates or the survival of adult females. Although inconclusive, these results suggest that copepod reproduction is only sensitive to extreme pH levels.

Foodweb responses in zooplankton

Richardson (2008) characterizes zooplankton as critical to the functioning of ocean foodwebs because of their sheer abundance and vital ecosystem roles. He explains that as poikilothermic organisms, zooplankton are beacons of climate change, because their physiological processes, e.g. ingestion, respiration, and reproductive development, are highly sensitive to temperature (Richardson, 2008; Arndt and Swadling, 2006). On this premise, we expect that the response of key zooplankton species—linking lower and higher trophic levels—to ecosystem and anthropogenic stresses associated with climate change will largely determine the character of future fisheries in the respective Polar Regions. But how well are key species of zooplankton in Arctic and Antarctic marine systems equipped to contend with their changing environments?

Can copepods cope?

There may be greater elasticity at the level of secondary productivity in the Arctic region where three copepod species—*C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*—typically dominate the zooplankton community in terms of biomass (Parent et al., 2012). The three are relatively similar morphologically, but show marked differences in life history, body size, and lipid content. They display a range of adaptations to highly seasonal Arctic/Subarctic environments, most notably: extensive energy reserves; and seasonal migrations into deep waters where the non-feeding season is spent in diapause (Søreide et al., 2008; Berge et al., 2012). The Arctic/Subarctic region also has a broad assemblage of non-copepod planktonic organisms which hold promise as potential new species of trophic importance, including larvaceans, chaetognaths, amphipods, ctenophores, cnidarians, etc. (Hopcroft, 2009).

The Arctic species, *C. glacialis*, and Subarctic/North Atlantic, *C. finmarchicus*, have different periods for reproduction and growth. When sympatric, it is generally considered that *C. glacialis* and *C. finmarchicus* reproduce and grow during different periods and under different temperature regimes (Carstensen et al., 2012; Parent et al., 2012). They also have different strategies of energy (lipid) storage and utilization—involving the timing of egg production relative to the spring phytoplankton bloom, and reproduction before the bloom using lipids stored the previous feeding season (Melle and Skjoldal, 1998). Such differences may improve their chances of survival during changing seasonal cycles and food availability. However, distribution of these two species overlaps in transitional zones between Subarctic (North Atlantic) and Arctic water masses. Recent research results clearly indicate that these two species are also able to hybridize and that these hybrids are fertile and reproductive (Parent et al., 2012). This evolutionary development may improve their chances of survival with positive effects at upper trophic levels of Arctic marine foodwebs.

Direct advection of zooplankton into the Arctic also occurs. During summer, the Chukchi Sea zooplankton community is dominated by Bering Sea fauna, which has been advected through the Bering Strait (Hopcroft et al., 2010; Hopcroft and Kosobokova, 2010; Matsuno et al., 2011; Drinkwater et al., 2012; Hunt et al., 2013). It should be noted that *C. glacialis* is associated with shelf waters as well as ice-associated areas. It is not clear, however, whether this species can thrive and establish itself in the deeper parts of the Arctic Ocean. Temperature increase and the reduction in sea ice may lead to shifts in optimal conditions for the *Calanus* species with different life strategies (Søreide et al., 2010).

Also of note in the Arctic, a unique marine habitat containing abundant algal species in “melt holes” has been observed in perennial sea ice in the central Arctic Ocean (Lee et al., 2011, 2012; Frey et al., 2012). These open-pond habitats have high nutrient concentrations and contain abundant algal species known to be important for zooplankton consumption (Frey et al., 2012). Lee et al. (2011) suggest that continued warming and decreases in SIE and thickness may result in a northward extension of these open pond areas (potentially enhancing overall primary production in these habitats). This may provide an important food supplement for zooplankton and higher trophic levels. During recent decades with increasing temperatures, an increase in the overall biomass of the zooplankton community is apparent in Atlantic-influenced Arctic waters despite strong interannual fluctuations (Figure 5 from Johannesen et al., 2012).

What's ill with krill?

There appears less elasticity at the level of secondary production in the Southern Ocean foodweb. Antarctic krill have adapted to low temperatures conditions which have remained stable during the last 20–30 million years. As stenotherm crustaceans, Antarctic krill are unlikely to tolerate large oscillations in temperature outside the main range of their habitat (Flores et al., 2012; Mackey et al., 2012). Changes $\sim 1\text{--}2^\circ\text{C}$ are likely to have a significant impact on the physiological performance, distribution, and behaviour of krill (Whitehouse et al., 2008). Adults are more flexible than larval or juvenile krill and can exist in different aggregation states, use a wide variety of food sources, and can express various overwintering strategies (Quetin et al., 2003; Meyer et al., 2009; Flores et al., 2012). They may also be able to buffer their physiological sensitivity, e.g. to small temperature increases or pH changes. They are not restricted to surface waters and have been found on the seabed down to 3500 m (Takahashi et al., 2003; Clarke and Tyler, 2008; Kawaguchi et al., 2011; Schmidt et al., 2011). The dependence of larval and juvenile krill on sea ice, combined with their limited physiological flexibility, may be the likely driver determining winter survival and recruitment levels in a warming and acidifying ocean (Arndt and Swadling, 2006; Flores et al., 2012).

Within the Atlantic sector of the Southern Ocean where 50% of the circumpolar krill population occurs, observations suggest that their abundance, recruitment success, and population structure already are changing with an overall decreasing trend since the 1970s, although there is also marked interannual variability (Murphy et al., 2007b; Atkinson et al., 2008). The current increase in krill harvesting is occurring after a period of declining krill populations in the SW Atlantic sector (Figure 6a and b from Flores et al., 2012 and c from CCAMLR, 2013, <http://www.ccamlr.org/en/fisheries/krill-fisheries>). Harvesting of Antarctic krill has increased in recent years, potentially increasing stress on the Antarctic foodweb. Concern has been raised about the future sustainability of krill harvesting (Flores et al., 2012), although current catches are far below the allocated quota. The combined impact of increasing temperatures with associated declines in sea ice, ocean acidification, and changes in circulation is predicted to increase considerably during the present century. These environmental changes will likely act in concert to have negative impacts on the abundance, distribution, and life cycle of krill (Flores et al., 2012). CCAMLR has therefore decided to adapt fishing strategies and management regulations, including precautionary catch limitations and spatial management, as new knowledge becomes available (CCAMLR, 2013).

Around the West Antarctic Peninsula, salps can become a dominant component of the plankton in years when krill abundance is low (Loeb et al., 1997, 2009). These changes reflect shifts in ocean circulation that result in zooplankton communities occurring in warmer waters close to the continental shelf (Loeb et al., 2009; Steinberg et al., 2012). There also are suggestions that salps may be increasing more generally around the Southern Ocean, penetrating further south as surface waters have warmed during the last half-century (Pakhomov et al., 2002; Atkinson et al., 2004; Loeb and Santora, 2012). Salps may have an important role in biogeochemical cycles of the Southern Ocean (Pakhomov et al., 2002), but they are not considered to be a major link to higher trophic levels, i.e. pelagic fish, seabirds, whales, etc. (Steinberg et al., 2012). Any increase in salp abundance associated with reduced krill abundance is,

therefore, likely to reduce food availability to fish species and higher predators. As a consequence, tertiary and fishery production would be expected to decrease. However, indirect effects may be important as the role of salps in mesopelagic foodwebs of the Southern Ocean is poorly understood.

Krill in the Antarctic represent a huge circumpolar biomass of several hundred million tonnes. A regional acoustic estimate in 2000 for the Scotia Sea indicated a biomass of 60 million tonnes (CCAMLR approved estimate; CCAMLR 2010). Further, most abundance estimates consider Antarctic krill as an epipelagic organism, while more recent studies indicate an additional stock component of up to 20% distributed in deep waters and along bottom, representing unaccounted biomass in the stock assessments (Gutt and Siegel, 1994; Schmidt *et al.*, 2011). Estimates of the circumpolar biomass vary (Atkinson *et al.*, 2008, 2009), thus the present commercial harvest level, and even the permitted quota, may represent a very small part of the stock. Notwithstanding the estimated huge circumpolar abundance of Antarctic krill concerns persist about the potential to maintain its key role in support the Southern Ocean foodwebs in a changing environment (Nicol, 2006). CCAMLR aspires to maintain a management system for the krill fishery that does not have adverse impacts upon the marine predators that feed upon krill, particularly around seal and seabird breeding islands. In 2012, an interim catch limit of 620 000 t was in place for the southwest Atlantic sector. This limit is equivalent to ~1% of the estimated krill biomass in the southwest Atlantic sector where most commercial harvesting takes place. More local reduction or depletion of krill biomass close to land-based predators is also of concern within CCAMLR (Alonzo *et al.*, 2003; Grant *et al.*, 2013). It is clear that the wide and regionally dense distribution of Antarctic krill and its harvest potential exceeds that of the much lower and scattered distribution of krill species in the Arctic/Subarctic region.

In the northern hemisphere, krill has largely been considered a Subarctic species which rarely venture into high Arctic waters. Research results indicate that the total abundance of euphausiids in the Barents Sea has been relatively stable with respect to environmental changes, since euphausiid species with different zoogeographical characteristics tend to replace each other due to the prevailing climate conditions in the sea (Zhukova *et al.*, 2009). The composition of species, however, appears to be altering; the more boreal krill, *Nematoscelis megalops*, occurs more frequently in the Norwegian Sea and the Barents Sea. Similarly, the Atlantic species, *M. norvegica*, occurs more frequently in the Barents Sea (Zhukova *et al.*, 2009). A different pattern has been observed in the Bering Sea, where warmer than average temperatures have been associated with low krill abundance (Coyle *et al.*, 2011; Hunt *et al.*, 2011) and recent cold years with increases in krill abundance and the southward movement of boreal amphipod species (Pinchuk *et al.*, 2013). In the long term, warming is expected in the Bering Sea, which could have negative consequences for the biomass of krill and for fish recruitment (Hunt *et al.*, 2011).

Responses by fished species—movement towards the poles

Concurrent with key zooplankton species moving northward in response to warming temperatures, key fishery species may be moving towards the poles, as predicted by the IPCC (2007). Investigating the underlying mechanisms that account for changes in population distribution is a topic of high research priority, particularly because

plankton production and trophic interactions may be significantly altered by changes in climate.

In the Arctic, it has been reported that this “polar shift” is an ongoing process. Wassmann *et al.* (2011) reviewed the published literature (51 reports) to determine the footprints of climate change in the Arctic marine ecosystem. Reported footprints for fish species with warming as the climate driver included: northward spread and increased spawning-stock biomass and recruitment of Atlantic cod (*G. morhua*) in the North Atlantic region; northward range shift for snake pipefish (*Entelurus aequoreus*) in West Svalbard; increased recruitment and length of cod in the Barents Sea; increased spawning biomass for Greenland turbot in the Bering Sea (driven by warming and ice changes); and increased biomass for walleye Pollock in the Bering Sea. Footprints with warming as driver for benthic organisms included: increased biomass for clams (*Macoma calcareea*) in the Chukchi Sea region. The reports also provide evidence of an increased phytoplankton biomass and primary production in the open Arctic Ocean, particularly the Pacific sector. The abundance of larger zooplankton and amphipod species associated with sea ice was reported to have declined, whereas jellyfish abundance was reported to have increased (Wassmann *et al.*, 2011). Although Wassmann *et al.* (2011) also include a northward range shift for walleye pollock (*Theragra chalcogramma*) in the Chukchi and Bering Seas region as a footprint driven by a warming climate, more recent reports on this topic indicate such evidence (for walleye pollock and other species in the Bering Sea) is not very strong (Mueter and Litzow, 2008; Kotwicki and Lauth, 2013).

In a different study, Hollowed *et al.* (2013b) using a panel of experts conducted a qualitative assessment of the potential for 17 fish or shellfish stocks to move from Subarctic areas into the Arctic or to expand within the Arctic. They considered: (i) the exposure of these species to climate change; (ii) their sensitivity to these changes; and (iii) the adaptive capacity of each stock. Using this method, six stocks were determined to have a high potential to expand or move into the Arctic Ocean, six stocks had some potential to expand or move into the Arctic Ocean, and five stocks or stock groups had low potential to expand in, or move into the Arctic Ocean. They also suggest that the production of oceanic phytoplankton in the Arctic is expected to increase in response to declines in summer sea ice but this increase in production may be off-set by declines in the spatial extent of ice algal blooms, and changes in oceanic species composition to a smaller size. Secondary production is likely to increase with a greater fraction of the annual production being grazed by zooplankton. Warmer ocean conditions and shifts in advection may change the species composition of zooplankton the Arctic. The size and lipid content of dominant copepods may also change and may increase the production of smaller zooplankton (Hollowed *et al.*, 2013b).

In the Southern Ocean, poleward shifts in distribution of zooplankton species may be modified by foodweb processes and have wider consequences for foodwebs and fished species (Murphy *et al.*, 2013). For example, shifts towards higher latitudes of suitable krill habitat may result in reduced overall production and abundance of krill and concentration of the demand by predators for food into a reduced area nearer the continent. Competition for krill between predators and fisheries could become more intense under such a scenario. It has been suggested that in some areas certain previously exploited fish populations are being maintained at low levels because of an increased abundance of fish-consuming predators. At South Georgia, in the Atlantic sector, fur seal

populations have increased over the last 50 years to levels that may be greater than before exploitation began, resulting in enhanced mortality of fish and suppressed population sizes (Hanson *et al.*, 2009).

Circumpolar contrasting future scenarios

The structure and function of ecosystems within both Arctic and Antarctic regions also vary spatially, which affects circumpolar contrasts in response to climate forcing. Such differing responses will play a critical role in determining future productivity in different areas within these regions. Wassmann (2006) acknowledged that scientific exploration of the Arctic Ocean was still inadequate to determine circumpolar features, local/regional disparities, and the complexities of the ecosystem. Although instances of such contrasts within Arctic and Antarctic circumpolar regions may be many, only a few studies actually provide examples.

Hunt *et al.* (2013) compare and contrast ecosystems of the Barents and Chukchi Seas; both high latitude, seasonally ice-covered, Arctic shelf seas. Although primary production on average is similar in these two seas, fish biomass density is an order of magnitude greater in the Barents than the Chukchi Sea. The Barents Sea supports immense fisheries, whereas the Chukchi Sea does not. They hypothesized that the difference in fish production in the two seas can be explained mostly by differences in temperature, advected plankton and the amount of primary production consumed in the upper water column. They also project different responses in these two seas under climate change. In the Barents Sea, increasing the open water area via reducing ice cover will increase productivity at most trophic levels, and “warm water” boreal fish species will likely invade, and in some cases become established. In the Chukchi Sea, warming should also reduce summer sea ice cover, permitting a longer production season. However, the shallow northern Bering and Chukchi Seas are expected to continue to be ice covered in winter, so water there will continue to be cold in winter and spring, and a barrier to the movement of temperate fish species into the Chukchi Sea (Stabeno *et al.*, 2012; Hunt *et al.*, 2013).

In the Southern Ocean, there has been little integration of quantitative information on foodwebs for most areas. Murphy *et al.* (2012, 2013), however, began a process of comparative analyses of ecosystems around the Southern Ocean and Murphy *et al.* (2013) compare the regions of the western Antarctic Peninsula and South Georgia, in the Atlantic sector. These two areas edge the south Atlantic region of the Southern Ocean; one in the west and south; the other one in the east and north. Both areas are strongly influenced by flows of the ACC which also act to connect them; and, both are areas of enhanced production probably due to natural iron fertilization. Although the structures of these two systems are relatively similar, there are significant differences in the species occurring within them. The major factor driving these differences is the winter sea ice, which is extensive around the Antarctic Peninsula and less prominent around South Georgia which is to the north of the seasonal ice zone. Krill are a key component of foodwebs in both areas, but other components linking zooplankton to predators at higher trophic levels are different. For example, around the southern Peninsula, the main penguin species are the ice obligate Adelie penguins; while Macaroni penguins dominate in northern areas around South Georgia, which is ice free during summer. In the more ice-covered areas, the Antarctic silverfish is also a key prey species for upper-trophic level predators, whereas in the north semi-demersal species and myctophids are more important.

The strong physical connectivity of the Southern Ocean is a major feature of the foodwebs. Murphy *et al.* (2013) propose that the Scotia Sea region between the West Antarctic Peninsula and South Georgia is a continuum, from more ice-covered areas in the south to the open water regions in the north. Within this continuum, major structural drivers are ice, iron, and connectivity, all of which are also associated with the changing temperatures, general nutrient regimes, and major current systems (Murphy *et al.*, 2012, 2013). This concept of a connected continuum may also be a useful basis for considering the general transition from the high latitude regions of the Ross Sea, where the ice obligate species dominate, through to the polar frontal regions in the southern Indian Ocean, where Antarctic krill are absent and fish are the main prey items (Murphy *et al.*, 2012, 2013). However, the changes across different ecosystems have yet to be fully examined and so far there has been little quantitative basis for comparative analyses. There are major regions around the Antarctic (including large areas of the East Antarctic) where chlorophyll concentrations are low and macronutrients are high [high nutrient-low chlorophyll (HNLC) regions]. Productivity in these HNLC regions is generally low and iron-limited and communities of autotrophs tend to be dominated by smaller species and groups. In turn, these tend to be areas where the main grazers are smaller zooplankton and there are few larger organisms supported.

Projections of change in the Southern Ocean vary regionally and are highly uncertain. A general warming and reduction of sea ice is expected, but the system is currently affected by the ozone hole which is thought to have modified patterns of atmospheric circulation (Turner *et al.*, 2009). Warming is expected to continue on the Antarctic Peninsula region and this is likely to further reduce sea ice. Warming and reduced ice is projected to lead to a reduced dispersal of krill into more northern regions of the Scotia Sea and reduced growth rates (Murphy *et al.*, 2007a; Wiedenmann *et al.*, 2008; Flores *et al.*, 2012). A general shift southward has been projected for the cold water zooplankton species including Antarctic krill across the Scotia Sea (Mackey *et al.*, 2012). For a krill-dominated foodweb, such a shift southward would lead to a reduction in the abundance of large krill-dependent predators in more northern regions. This could also lead to major shifts in foodweb structure from a krill- to a more copepod-dominated ecosystem (Murphy *et al.*, 2007a; Hill *et al.*, 2012). Contraction southwards of ice-obligate and ice-influenced Southern Ocean foodwebs would be an expected consequence of further warming and ice retreat. However, the specific outcomes will be modified by other processes that may be determined spatially, such as areas of natural ice fertilization and exposure of shelf areas. High latitude regions of the Weddell and Ross Sea regions are likely to continue to be strongly ice influenced, and ice-obligate species are likely to remain the dominant components of these ecosystems. The effects of ocean acidification on calcifying and non-calcifying species are also likely to be important; these effects are likely to be observed earlier in areas north of the Southern Boundary of the ACC. Moreover, these effects will likely have further impacts on particular species that will lead to changes in foodweb structure and balance. The effects of such changes, however, are unknown.

Modelling future scenarios

A central question is to what extent existing models are able to incorporate emergent properties to predict how foodwebs will respond to future climate change. Current climate models predict a decrease of 2–20% in net primary productivity globally by 2100, with average

decreases of 7–53 g C m⁻² year⁻¹ over the North Atlantic (Steinacher *et al.*, 2010). In Arctic marine ecosystems, however, some project that fish productivity may increase (Vilhjálmsón and Hoel, 2005; Anisimov *et al.*, 2007; Cheung *et al.*, 2013). Others conclude that fish production will be the outcome of a complex suite of responses, but do not expect that the Arctic Ocean will become a biodiversity hotspot (Hollowed *et al.*, 2013a; Hunt *et al.*, 2013).

A recent study using a high-resolution ecosystem model (20 × 20 km) in the Barents Sea found that decreased SIE and thickness may open up new areas to increased phytoplankton and zooplankton production (Slagstad *et al.*, 2011). The Arctic zooplankton species *C. glacialis* may move farther north into the Arctic Ocean, whereas the abundance of *C. finmarchicus* could increase in the Barents Sea (Slagstad *et al.*, 2011).

Ji *et al.* (2012) used a different approach and arrived at different results. They coupled a three-dimensional individual-based model for copepods occurring in the Arctic Ocean to a realistic physical ocean model to explore the response under different climate-change scenarios—increasing the length of the growth season or increasing water temperature by 2°C—for endemic Arctic Ocean species (*C. glacialis* and *C. hyperboreus*) and expatriate Arctic Ocean species (*C. finmarchicus* and *C. marshallae*). These modelled conditions increased development rates and greatly increased the area of the central Arctic Ocean in which the Arctic endemics could reach diapauses, but had little effect on the regions where successful diapause for the expatriate species could occur. Results of this study suggest that for endemic Arctic species a prolonged growth season contributes to their population sustainability in the Arctic Ocean. Results also suggest that under existing environmental conditions in the central Arctic the population of *C. hyperboreus*, the population occurring there may be advected from the surrounding shelf regions (Ji *et al.*, 2012).

Other studies have linked the output from climate models such as the Earth System Model (ESM) with fisheries recruitment models (Hare *et al.*, 2010; Kristiansen *et al.*, 2014). Such studies allow new insights into how changes in the physical environment may impact lower trophic levels and propagate through the foodweb shaping growth, survival, and recruitment patterns at higher trophic levels such as fish. Still, the current resolution of the ESMs are quite coarse with typical resolution of 1° by 1° longitude–latitude, which does not resolve mesoscale features of the oceans such as eddies and meanders. Current ESM estimates of primary and secondary production use information on mixed-layer depth, ocean temperature, light, and nutrients and can adequately describe the large-scale trends in marine biological productivity. However, to gain information at the local and regional level, it is necessary to resolve mesoscale activities in the oceans.

In the Southern Ocean, the central role played by krill has influenced model development. Most models have been developed under the auspices of CCAMLR to assess the impact of Antarctic krill harvesting on krill predator populations. These models can therefore be classified as simple “krill-centric” predator–prey type models. Vilhjálmsón and Hoel (2005) explain that challenges to modelling these systems include difficulties to simulate and project long-term changes based on our present understanding, using data that have been measured and monitored over a relatively short period. Also, scenarios require information on ocean temperatures, water mass mixing, upwelling, and other relevant ocean variables such as primary and secondary production, on a regional basis. As fisheries often depend on many such variables, any predictions

concerning fisheries in a changing climate can only be of a very tentative nature with limited use as management tools.

Bioenvelope models based on current characteristics of fish and invertebrate habitats (e.g. temperature and depth range) indicate that there will be significant changes in fish and invertebrate production in polar regions over the coming century (Cheung *et al.*, 2009, 2010). These studies suggest that in the Antarctic, catch potential would decrease as a result of a shift in species distribution over much of the Southern Ocean (Cheung *et al.*, 2010). However, in many areas where catch potential is expected to decrease, there are no current fisheries. The projected outcomes may, therefore, reflect the lack of detailed knowledge of the biology of the main polar species and highlight the difficulty of applying such simplified models without consideration of ecological constraints that may be crucial. It also emphasizes the importance of understanding foodweb interactions that may modify the response of individual species to projected habitat changes (Murphy *et al.*, 2012, 2013). In contrast to the Antarctic, Cheung *et al.* (2010) predicted that catch potential in the Arctic may rise significantly. However, the above-discussed caveats also apply to this projection.

Most current suggestions of poleward shifts in species distribution are largely based on very simple linear responses to changing temperatures or sea ice loss in Polar systems. Such direct impacts of climate change may be modified by changes in seasonality and the timing of productivity (Burrows *et al.*, 2011). This may result in significant mismatches between critical phases in life cycles of zooplankton species and the timing of ice formation and retreat, or seasonal patterns of temperature and productivity. This highlights the need for more detailed understanding and models of the life cycles of species to understand impacts of climate driven change in polar ecosystems.

Future management considerations

Arctic and Antarctic marine systems present unique and very different sets of issues, problems, and concerns to consider regarding an ecosystem approach to management. Systems within both regions are being impacted by a rapidly changing climate confounded with other anthropogenic ecosystem pressures. These should be considered stressed systems and managed as such. The differing vulnerabilities relative to life strategies of fishery species being exploited should be incorporated into setting appropriate management strategies.

In the Arctic, the loss of permanent sea ice during recent summers has left open as much as 40% of international waters, opening up the potential for new commercial fisheries (Anisimov *et al.*, 2007). Arctic ecosystems, such as the Bering and Barents Seas, represent areas that may potentially increase markedly in commercial fisheries exploitation. Concern has been raised that the international community needs to create a precautionary management system for central Arctic Ocean fisheries conducted beyond the EEZ of respective countries and that fishing activity should be postponed until the biology and ecology of the region are understood sufficiently well to allow setting scientifically sound catch levels (Zeller *et al.*, 2011). In response, the North Pacific Fisheries Management Council voted to ban industrial fishing and limit bottom trawling in newly ice free US waters north of the Bering Strait, including the Chukchi and Beaufort seas (Stram and Evans, 2009). The existing prohibitions on commercial activity within the US Arctic provide an opportunity to design a management strategy for future fisheries that is rooted in an ecosystem approach

to fisheries management (Hopcroft *et al.*, 2008; Hollowed and Sigler, 2012).

Indeed, there are important lessons to be learned from the history of fishing in the Southern Ocean. CCAMLR was established by international convention in 1982 with the objective to conserve Antarctic marine life. As it happens, CCAMLR was established in response to IUU fishing conducted since the late 1960s. By the time of its establishment, decades of heavy exploitation had already occurred (Ainley and Blight, 2008). Despite CCAMLR regulatory actions, stocks of K-selected fish species that were dramatically reduced during the late 1960s–early 1970s have not recovered, and some are still declining (Ainley and Blight, 2008). However, the overall success of CCAMLR in developing ecosystem-based management procedures centred on the krill fishery before over-exploitation has occurred, and through a consensus approach, suggests that it provides a valuable framework in discussions to develop international governance of fisheries (Österblom and Folke, 2013), including for the Arctic. For the Arctic, this underscores the importance of establishing, before commercial fishing activity starts, an international body to research and manage central Arctic basin fisheries that also has enforcement authority. CCAMLR has also begun to discuss the development of “feedback management procedures” that can account for the multiple processes that contribute to change (e.g. natural variability and climate or fishery-driven change; Grant *et al.*, 2013), and such an approach is also likely to be required in the Arctic.

Recognizing the vulnerability of each species to fishing pressure, species interactions, and other ecosystem-induced pressures relative to its life strategy has implications for effective management (Adams, 1980). Basic life-history information essential for stock assessment is currently lacking for both systems. To address these information gaps, knowledge of life-history parameters could provide a starting point for management frameworks. Characterizing commercially exploited species into life-history groupings can help establish an understanding of the probable nature of that species population dynamics, in relation to both environment and fisheries impacts. Such conceptual management scenarios based on life-history traits may be particularly useful for newly exploited species (King and McFarlane, 2003; Doyle and Mier, 2012).

This last point concurs with the ecological theory that sustainable ecosystem services depend on a diverse biota. A management system that conserves biodiversity will help to accrue more “ecosystem capital” for multiple human uses and will maintain a hedge against unanticipated ecosystem changes from natural and anthropogenic causes (Palumbi *et al.*, 2009). In this sense, biodiversity might also serve as a proxy measurement of ecosystem resilience. Indeed, developing perspectives that take account of the wider ecosystem services that polar ecosystems provide is likely to be valuable (Grant *et al.*, 2013).

The combination of changes in physics and biology determine how growth and survival of larval fish will be affected by climate change. In fact, the underlying complexity of these ecosystems suggests that no single variable determines the survival of larval fish. Several mechanisms may operate at the same time, all having a cumulative effect (Kristiansen *et al.*, 2011). In all probability, the community structure, life strategies, and adaptive responses of zooplankton species to climate forcing will be a key factor determining future fisheries scenarios in both regions.

The continued development and application of ecosystem models that are firmly rooted in ecology and physiology is essential for improving confidence in projections of climate change impacts

on living marine resources (Stock *et al.*, 2011). Therefore, scenarios, predictions, and analyses that increase understanding of how climate change may shape biological production and species distributions in the oceans are critical to integrate climate change impacts on fisheries into wider marine spatial planning exercises. Marine spatial planning can organize optimal placement for fisheries to conduct their activities and many Subarctic and Arctic regions are currently evaluating or developing marine spatial plans for their waters (Hoel *et al.*, 2009; Kenny *et al.*, 2009; Hoel, 2010; White *et al.*, 2012; see also Grant *et al.*, 2013 for the Antarctic). With realistic climate and ecological predictions, managers and policy-makers can incorporate predicted changes in fisheries dynamics into long-term management processes.

Discussion

Prospects for future expanded fishery production in these regions differ and are tentative. In the Barents Sea, Loeng and Drinkwater (2007) projected that changing conditions would lead to a general increase in fish productivity and a northern shift in geographical distribution of fish. Such an increase in fishery production will largely depend on continual reductions in the extent of sea ice, sufficient nutrient availability, and favourable temporal match–mismatch between plankton blooms and secondary producers which would facilitate the continued northward expansion of desirable fishery species. Potentially, this increase in primary production could be off-set by declines in the spatial extent of ice algal blooms, and changes in oceanic algal species composition to a smaller size (Li *et al.*, 2009). Secondary production is likely to increase, however, if a greater fraction of the annual primary production could be grazed by zooplankton. Warmer ocean conditions and shifts in advection may change the species composition of zooplankton in the Arctic/Subarctic region. The size and lipid content of dominant copepods may also change and may increase the production of smaller zooplankton (Hunt *et al.*, 2011).

The northward expansion of warmer waters from the Subarctic into the Arctic may alter the distribution of suitable habitat for many temperature-limited fish species of commercial value. Findings of Wassmann *et al.* (2011) and Hollowed *et al.* (2013a, b) indicate that such a “polar shift” is ongoing with a warming climate as the driver. Wassmann *et al.* (2011) detail reports of a northward spread or range shift for Atlantic cod (*G. morhua*) and walleye pollock (*T. chalcogramma*). Hollowed *et al.* (2013b) determined that species with a high potential to establish viable resident populations in the Arctic exhibited life-history characteristics that would allow them to survive the challenging environmental conditions that will continue to prevail in the north, including a large proportion of shallow continental shelves, extreme seasonal weather variations, low temperature, extensive permanent and seasonal ice cover, and a large supply of freshwater from rivers and melting ice (Hollowed *et al.*, 2013b).

In the Southern Ocean, there are limited shelf areas, so a reduction in winter sea ice and ice-shelves may open up new areas of potential primary production (Peck *et al.*, 2010). This would potentially enhance demersal and semi-demersal fish production. However, these high-latitude habitats will remain highly seasonal and ice covered in winter so large increases in fish production in these regions are unlikely. Further north, around islands where natural iron fertilisation occurs, productivity is already high compared with much of the rest of the Southern Ocean (Murphy *et al.*, 2007a). These regions also maintain large numbers of higher predators and, historically, have been some of the main regions of

concentrated fishing effort. Reductions in predator numbers associated with reductions in krill populations in such areas may release some fish populations from intense top-down pressure, reducing mortality, allowing populations to increase. However, the presence of such a wide range of predators, with significantly different diet compositions, would suggest that such an outcome is unlikely. The Southern Ocean Polar Front forms a significant circulatory and thermal barrier to the poleward movement of pelagic fish species; this results in a lack of connectivity between ocean currents at high and low latitudes and may inhibit pelagic fish species from completing their life cycles within the different habitats found north and south of the Front. Other factors may make it difficult for pelagic species found north of the Polar Front to successfully colonize the Southern Ocean, where ecosystems are highly seasonal, temperatures are low, habitats are heterogeneous and variable, and there is relatively little highly productive shelf area. Some combination of these factors has acted as a barrier to the colonization of the Southern Ocean by truly pelagic fish species and has constrained the evolution of endemic species.

Highly mobile species, such as the southern bluefin tuna (*Thunnus maccoyii*), occur in areas to the north of the Polar Front and the Subantarctic Front. However, they do not have the energetic flexibility to survive in the low temperature systems to the south of the Polar Front. Some species of squid and finfish are distributed across the Polar Front, and these may increase in abundance as the habitat warms, but the life cycles of many of these species are poorly understood and potential impacts of future changes are unclear.

Analyses of surface temperature variability of the Southern Ocean suggest that there has been a southward shift in the position of frontal zones in some regions, such as around the Kerguelan Plateau, and in the South Atlantic around South Georgia (Sokolov and Rintoul, 2009a, b). Such changes would potentially allow more southward movement of Subantarctic species, but current projections of changes in ocean circulation do not suggest major changes in the ACC or a large reduction in the thermal gradient of the Polar Front. The potential for invasion into the Southern Ocean of large and highly productive pelagic finfish therefore appears low.

In the Southern Ocean the potential to fish for other species and groups such as crabs and skate has been explored, but such fisheries have not been developed commercially. Invasion of polar deep-sea or benthic habitats in shelf areas by invertebrate species from outside the Southern Ocean may be occurring (Aronson *et al.*, 2007; Fox, 2012; Griffiths *et al.*, 2013), but the productivity potential of these species would appear relatively low. Developing projections of the potential for invasion of polar habitats by subpolar species will require a more detailed understanding of their life cycles and life-history constraints, coupled with improved sampling (Griffiths *et al.*, 2013).

Direct fisheries on mesopelagic fish and squid species are also possible in the Southern Ocean (Collins and Rodhouse, 2006; Donnelly and Torres, 2008). Although these species are abundant, they are not targeted at this time due to their relatively deep and dispersed distributions. Such fisheries may become more attractive as access to other species becomes more limited, and technological solutions allowing detection of fishable concentrations are found. The life strategies, and thus the ecological and biogeochemical consequences, of exploiting mesopelagic species are not fully understood, but they are clearly important in maintaining pelagic ecosystems and higher predators.

Conclusion

This comparative review of the scientific literature on the response to climate forcing in marine systems in Arctic and Antarctic regions illustrates how and why the polar marine systems differ from each other with regard to: geological and evolutionary history, circulation, primary and secondary productivity, foodwebs, fish fauna and biodiversity, and existing fisheries. These differences influence responses to a climate forcing with regard to foodwebs, fishery productivity, and future fisheries both between and within regions. Different characteristics and life strategies of key zooplankton species linking primary producers and higher trophic levels in these systems, and how they cope with their harsh environments, may influence their ability to maintain their key role in foodwebs for respective Polar Regions under the effects of a changing climate.

Although the spatio-temporal and trophic resolution of existing biophysical models is insufficient for some questions, they have helped to advance our general understanding of how marine foodwebs in the Polar Regions may respond to future climate change, and a number of changes anticipated from model results have now been documented *in situ*. Although substantial uncertainties remain, this type of validation together with development of integrated monitoring networks and manipulation experiments, improved collection and collation of long-term datasets, increased use of local knowledge, and further development of appropriate models will increase our confidence in projecting future changes in the Polar Regions.

Climate change in the Polar Regions is projected to continue over the course of this century given the current global warming commitment (Meehl *et al.*, 2012) and have many direct and indirect regional impacts on marine organisms in these systems. We suggest that the community structure, life strategies, and adaptive responses of zooplankton species to climate forcing will be a key factor determining future fisheries scenarios in both regions. As the sea-ice edge moves northward in the Atlantic-influenced Arctic region, so will the distribution of zooplankton (copepods, krill, and amphipods) and their fish predators. An increase in open water, and subsequent increases in primary and secondary production south of the ice edge, will likely benefit many important commercial fish stocks in Arctic and Subarctic seas. Thus, fisheries in these regions may see new mixes of species and enhanced biomass for the present target species. Significant changes in air temperatures, sea ice, and ocean temperatures in key regions of the Southern Ocean in recent decades are believed to have already impacted krill abundance in some regions. Future reductions in sea ice may therefore lead to further changes in distribution and abundance across the whole area, with consequent impacts on foodwebs where krill are currently key prey items for many predator species and where krill fishing occurs. There is uncertainty in projection of impacts, but increases in temperatures and reductions in winter sea ice will likely affect the reproduction, growth, and development of krill and fish, leading to further changes in population sizes and distributions. Published studies suggest that the potential for existing species to adapt is mixed and that the potential for invasion into the Southern Ocean of large and highly productive pelagic finfish species appears low. Thus, fisheries in the Southern Ocean may largely be dependent on the species which currently exist.

Acknowledgements

Many thanks to the Ecosystem Studies of Sub-Arctic Seas (ESSAS) project for having funded travel and work hours needed to complete this review. We sincerely thank the authors of papers (and their

publishers), and sponsoring organizations of websites used in our review, for allowing us to include their figures, tables, and diagrams to illustrate points and support discussions, i.e. NOAA (US National Oceanic and Atmospheric Administration) www.climate.gov, the Arctic Council/Arctic Climate Impact Assessment/Cambridge University Press, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR/David Ramm), the British Antarctic Survey, Joseph Eastman, Hauke Flores, and Edda Johannesen. Technical assistance from Aleksander Sandvik (IMR) to the enhance quality of all figures before publication is greatly appreciated. Thanks also to Drs Michael Fogarty, Jeff Napp, and Elizabeth Logerwell (NOAA Fisheries, USA) for having conducted early reviews of the manuscript.

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Handling editor: Rubao Ji