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Impact of Climate Change on Fishes in Complex Antarctic Ecosystems

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Abstract

Antarctic marine ecosystems are increasingly threatened by climate change and are considered to be particularly sensitive because of the adaptation of most organisms to cold and stable environmental conditions. Fishes play a central role in the Antarctic marine food web and might be affected by climate change in different ways: (i) directly by increasing water temperatures, decreasing seawater salinity and/or increasing concentrations of CO_2; (ii) indirectly by alterations in the food web, in particular by changes in prey composition, and (iii) by alterations and loss of habitat due to sea ice retreat and increased ice scouring on the sea floor. Based on new data and data collected from the literature, we analyzed the vulnerability of the fish community to these threats.

The potential vulnerability and acting mechanisms differ among species, developmental stages and habitats. The icefishes (family Channichthyidae) are one group that are especially vulnerable to a changing South Polar Sea, as are the pelagic shoal fish species *Pleuragramma antarcticum*. Both will almost certainly be negatively affected by abiotic alterations and changes in food web structure associated with climate change, the latter additionally by habitat loss. The major bottleneck for the persistence of the majority of populations appears to be the survival of early developmental stages, which are apparently highly sensitive to many types of alterations. In the long term, if climate projections are realized, species loss seems inevitable: within the demersal fish community, the loss or decline of one species might be compensated by others, whereas the pelagic fish community in contrast is extremely poor in species and dominated by *P. antarcticum*. The loss of this key species could therefore have especially severe consequences for food web structure and the functioning of the entire ecosystem.

1. INTRODUCTION

Climate change in the Antarctic is not simply a future scenario but already a well-established fact (e.g. Curran et al., 2003; Gille, 2002; Jacob et al., 2011; Murphy et al., 2007, Rignot et al., 2008). Its impacts are most evident in the Antarctic Peninsula region (including the southern Bellingshausen and Amundsen seas), where average temperatures at the sea surface have increased by nearly 3 °C within just the past 50 years (~0.56 °C increase decade^{-1}; e.g. Domack et al., 2003; Turner et al., 2005), and winter temperatures have increased by 5–6 °C (Vaughan et al., 2003). This represents a dramatic increase in air temperature in this region far above the global mean and exceeds any other warming rate observed on Earth at comparable spatial scales; the causes, however, are still under discussion (Gille, 2008; Vaughan et al., 2003).

The corresponding warming of the seawater is less pronounced, though again highly significant: the upper water layers (down to about 50 m water depth) west off the Antarctic Peninsula have warmed by ~1 °C since 1955 (Meredith and King, 2005) and are predicted to rise by another 2 °C over the next century (Murphy and Mitchel, 1995). In Palmer Deep, West Antarctic Peninsula, bottom water temperature has been increasing at a rate of about 0.01 °C year^{-1} since the 1980s (Smith et al., 2012). Moreover, there is some indication of a warming trend emerging in the deep waters of the Ross and Weddell seas (Ozaki et al., 2009; Robertson et al., 2002).

Increasing temperatures significantly affect ice dynamics: the warming has already resulted in a significant reduction in extent and duration of sea ice in the Antarctic Peninsula region, the Amundsen and Bellingshausen seas (Jacobs and Comiso, 1997; Loeb et al., 1997; Stammerjohn et al., 2008a,b) and has also contributed to disintegration and collapses of large ice shelves, such as the northern part of the Larsen ice shelf in the northwestern Weddell Sea (Domack et al., 2005; Marshall et al., 2006). In some shelf regions at the Antarctic Peninsula and in the Ross Sea, melting ice shelves, increased glacial meltwater runoff and reduced sea ice production have led to reduced seawater salinity, particularly in surface water layers (Jacobs et al., 2002; Moline et al., 2004). In Potter Cove, King George Island (South Shetland Islands, west Antarctic Peninsula), a glacier retreat of hundreds of metres and significant freshening of the upper water column have been observed within the past 15 years alone (Schloss et al., 2008).

Ocean acidification is considered a major threat for marine ecosystems that is concomitant with warming and atmospheric change (IPCC, 2007). Anthropogenic CO_2 emissions have increased atmospheric CO_2 concentrations since the industrialization in the 1850s, and about one-third of anthropogenic CO_2 from the atmosphere is absorbed by the world's oceans (Sabine et al., 2004). CO_2 is physically dissolved in seawater and this leads to progressive ocean acidification: several models predict a drop of seawater pH by 0.3–0.5 units by the year 2100 (atmospheric pCO_2 of 1000 μatm) and up to 0.77 units until the year 2300 (atmospheric pCO_2 of 1900–2300 μatm; Caldeira and Wickett, 2003, 2005; Feely et al., 2004; IPCC, 2007). So far, information on CO_2 changes in the Antarctic marine ecosystem is scarce, but local measurements of atmospheric CO_2 concentrations recorded at the permanent Argentinian station 'Carlini[1]', at the shoreline of Potter Cove, revealed a trend of increasing concentrations over a

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[1] Formerly known as 'Jubany' (renamed in March 2012).

relatively short time (from 356 μatm in 1994 to 379 μatm in 2006; Ciattaglia et al., 2008).

Though all the mechanisms involved and their interactions are not yet fully understood, there is little doubt that many of these observed changes are beyond that associated with natural variability but caused at least in part by anthropogenic climate change. In the light of ongoing global climate change, it is most likely that those regions of the Antarctic where alterations are not yet evident will also be affected in the near future.

Extant Antarctic marine communities have already been significantly affected by these environmental changes. In Potter Cove, clear shifts in benthic community composition have been observed that appear to be related to increased sediment load in the water column and ice impact due to melting and disintegration of the glacier (Sahade et al., 2008). Changes in salinity alter seawater density and thus can affect stratification of the water column and the depth of the mixed layer: salinity and surface water stratification are two main factors determining phytoplankton composition (Arrigo et al., 1998; Moline et al., 2004). Off the west Antarctic Peninsula, Moline et al. (2004) observed a recurrent change in phytoplankton community structure, with a spatiotemporal shift from large diatoms towards small cryptophytes as salinity declined. Alterations in community structure are also evident in consumers higher in the food chain: since the 1970s, the abundance of krill (*Euphausia superba*) has declined in the southwestern Atlantic and salps have become more abundant (Atkinson et al., 2004). As life cycle and overwintering strategy of Antarctic krill are closely coupled to the sea ice, its accelerating retreat will suppress krill abundance (Atkinson et al., 2004; Loeb et al., 1997). Other factors contributing to krill decline might be water temperature itself, as krill prefers cooler water compared to salps (e.g. Pakhomov et al., 2002), and indirect (trophodynamic) effects, including predation of early krill stages by salps (Huntley et al., 1989) and the inability of krill to efficiently graze on small cryptophytes (see Moline et al., 2004 and references therein). Moreover, salps feed efficiently on a wide range of particles even when phytoplankton concentrations are low (Hopkins, 1985; Kremer and Madin, 1992; Madin, 1974) and are able to attain large population sizes and biomass rapidly (e.g. Mianzan et al., 2001). Under favourable environmental conditions, their efficient grazing and high ingestion rates (e.g. Perissinotto and Pakhomov, 1998a,b) could result in the competitive exclusion of other grazers, such as copepods.

Though there are no immediately obvious visible effects reported so far, Antarctic marine communities could be vulnerable to ocean acidification in the future. Recent experimental studies have shown that survival and development of early stages of calcifying invertebrates and Antarctic krill are significantly negatively affected by levels of predicted future CO_2 concentrations (Kawaguchi et al., 2011; Kurihara, 2008).

Increasing warming of the Southern Ocean will facilitate the invasion and/or introduction and colonization by species from adjacent oceans. Invasion by invertebrates via warming deep waters appears to be already underway. Lithodid crabs have been absent from Antarctic waters for millions of years (see e.g. Thatje et al., 2005), but reports of sightings in Antarctic waters have been accumulating in recent years (e.g. García Raso et al., 2005; Thatje et al., 2008). Recently, a large and reproductive population of king crabs (*Neolithodes yaldwyni*) was discovered in Palmer Deep, west of the Antarctic Peninsula (Smith et al., 2012). So far, the distribution of lithodids seems to be restricted to the deeper slope, but assuming a persistent warming of waters of the Antarctic Peninsula region, Smith et al. (2012) speculated that lithodids might migrate upwards and invade the shelf communities within the next 20 years. Invasion of such hitherto absent durophagous (i.e. shell- or skeleton-crushing) predators strongly affects benthic communities (Aronson et al., 2007). The presence of the king crabs in Palmer Deep has been associated with a decrease in diversity of the megabenthos, including an absence of echinoderms (Smith et al., 2012).

Another more direct impact of human activity is in the form of the increasing ship traffic by tourist cruise ships and research vessels, which further enhance the risk of introduction of exotic species to the South Polar Sea (Lee and Chown, 2007; Lewis et al., 2005, 2006). The North Atlantic spider crab *Hyas araneus*, for example, was found in benthic samples from the Antarctic Peninsula: a species usually only found in the North Atlantic and Arctic Ocean that was most likely introduced into the Southern Ocean via ships' sea chest or ballast water (Tavares and De Melo, 2004). Another passive, man-made pathway for invasion is the increasing amount of litter in the world's oceans. Non-indigenous species may be introduced into the Southern Ocean by transport on drifting plastic debris (Barnes, 2002; Lewis et al., 2005 and citations therein).

Invasion/introduction of alien species will most likely lead to strong alterations in food web structure owing to removal of prey for indigenous species, competition and predation (Woodward et al., 2010a). So far, only invasion by crustaceans has been detected, but if the warming trend continues, it is inevitable that further species, both benthic and pelagic, will invade the Antarctic marine ecosystem. As long as conditions in the South Polar Sea are appropriate for survival but still limit growth and in particular reproduction capacity of invasive species, the threat for indigenous species will remain low. However, once alien species become able to successfully reproduce and to build up populations (as it seems to be the case in the lithodids found in Palmer Deep; Smith et al., 2012), the threat for native Antarctic species significantly increases.

The direction and strength of ecosystem response to environmental change depend strongly upon responses of individual species and their interactions among each other. Fishes are an integral part of marine ecosystems and have been proposed to serve as useful bio-indicators of climate change (Dulvy et al., 2008; McFarlane et al., 2000). As organisms within an ecosystem are linked to each other directly or indirectly via trophodynamics, any kind of change affecting fishes will indirectly affect other members of the food web, with a huge range of potential indirect effects being triggered. For many decades, scientists retained a view that Antarctic food chains were relatively short and simple: essentially a connection from diatoms to krill to consumers. Krill, *E. superba*, in particular was regarded as an inexhaustible resource that underpinned the whole Antarctic food web, supporting fishes, penguins, seabirds, seals and whales (e.g. Murphy, 1962; Tranter, 1982). However, this paradigm has been challenged as being overly simplistic. Although krill does indeed seem to be a key species over large areas, many food chains are independent of it (e.g. Rodhouse and White, 1995), and high species numbers in the South Polar Sea (e.g. Gutt et al., 2004) suggest that the diatom–krill–consumer chain is only one component of a highly complex food web (Clarke, 1985; Jarre-Teichmann et al., 1995). Fishes take a central position in this ecological network: they occupy a variety of trophic niches, are the main consumers of benthos and plankton, and are an important food source for a multitude of species, including cephalopods, piscivorous fishes, penguins, flying birds, seals and whales (for review, see Barrera-Oro, 2002; Hureau, 1994; Kock, 1992; La Mesa et al., 2004). Fishes thus represent an important trophic link that connects small invertebrates and top predators of the Antarctic marine ecosystem, making their potential vulnerability to systemic shifts of particular interest.

In this chapter, we provide an overview of the potential effects of climate change on Antarctic fish species and communities. Based on our own data collected during several expeditions and data that were taken from the literature, we summarize the characteristics of the Antarctic marine ecosystem and the fish communities, and we evaluate the threats to fishes, the degree of endangerment of particular species and the potential consequences for overall ecosystem functioning.

2. THE ANTARCTIC MARINE ECOSYSTEM

2.1. Geographical and physical conditions

The ocean surrounding the Antarctic continent represents one of the most unique marine environments on Earth, an appreciation of which requires a brief review of the geological and climatological history and settings of the Antarctic and its adjacent waters and land masses (summarized in Clarke and Johnston, 1996; Eastman, 1991). In the Jurassic, Antarctica was still part of the supercontinent Gondwana, which subsequently broke up, leaving Antarctica connected to South America and Australia throughout the Cretaceous (about 65 Ma[2] ago), when the climate was temperate, with water temperatures above 10 °C. Between late Eocene and early Oligocene (about 38 Ma), separation of Antarctica from Australia was most likely completed, and seawater temperatures began to decrease sharply. The separation from South America and the formation of sea ice and the continental ice sheet began between 37 and 34 Ma (e.g. Ehrmann and Mackensen, 1992; Ivany et al., 2008; Pearson et al., 2009). The final separation from South America and the opening of the Drake Passage allowed for the development of the strongest current system in the world, the Antarctic Circumpolar Current (ACC), driven by strong westerly winds. The ACC encircles the whole continent and acts as a thermal barrier by effectively separating lower latitude warmer and higher latitude colder waters (see e.g. Orsi et al., 1995).

The Antarctic continent and shelf areas are now geographically isolated from other continents and shelves by great distances and the large abyssal basins of more than 4000 m water depths that surround it (Fig. 1): the only connection to other continents with water depths less than 2000 m is via the Scotia Ridge composed of numerous islands linking South America to the Antarctic Peninsula (Arntz et al., 2005; Tomczak and Godfrey, 1994). In addition, the continent and the surrounding ocean are thermally isolated by the ACC, which flows eastwards and connects the Atlantic, Indian

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[2] Millions of years before present (Ma).

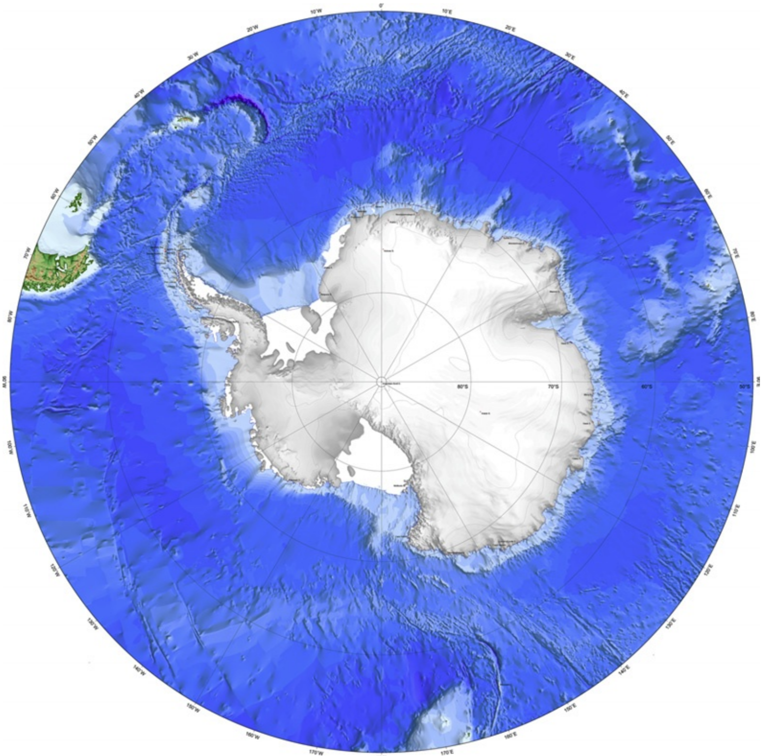


Figure 1 Map of Antarctica and the Southern Ocean *(Source: Centenary edition of the GEBCO Digital Atlas).*

and Pacific basins. This strong current system includes the Antarctic Polar Front, a region of downwelling and sharp temperature change of 3–4 °C (Knox, 1970). As a result, water temperatures in the South Polar Sea are consistently low (ranging from +1 to −1.86 °C close to the continent) with little seasonal variation (Deacon, 1984; Olbers et al., 1992). Close to the continent, the Antarctic Coastal Current (East Wind Drift) flows in the opposite direction and forms clockwise gyres in the Weddell Sea, Ross Sea and Bellingshausen Sea (Gordon and Goldberg, 1970). The region between both current systems is an area of wind- and density-driven upwelling of nutrient-rich circumpolar deep water (Antarctic Divergence), overlaid by Antarctic surface water in the upper layers (e.g. Eastman, 1993).

Beside the unique current system, the most important physical feature structuring the Antarctic marine ecosystem is the ice. The whole Antarctic shelf is narrow and depressed by the large continental ice sheet to depths of about 200 to >600 m. Shallow benthic habitats are thus extremely rare in the South Polar Sea and mostly restricted to the Islands of the Scotia Arc and along the Antarctic Peninsula. The continental ice sheet extends far beyond the coastline, forming large, floating ice shelves and a major source of calving icebergs (Nicol and Allison, 1997), which significantly affect vast areas of the shelf by grounding and seabed scouring (Gutt, 2001).

Sea ice is present year round but the overall coverage varies strongly with season, ranging from 4×10^6 km^2 in the austral summer to 20×10^6 km^2 in winter (Nicol and Allison, 1997; Zwally et al., 1983). Three major zones are distinguished based on prevailing sea ice conditions (Eicken, 1992): (i) the *high Antarctic zone* is almost permanently covered by ice and includes most areas close to the continent; (ii) the *seasonal sea ice zone* is characterized by open water in summer and ice coverage in winter; (iii) the *marginal ice zone* represents the transition from sea ice to the ice-free open ocean and is a region of enhanced ice drift, fragmentation and deformation. Sea ice dynamics significantly affect stratification of the underlying water column. During autumn, the depth of the mixed layer in the ice-free zone is mainly determined by the wind regime. During ice formation and growth, cold and highly saline (and thereby highly dense) seawater is ejected from the ice into the water below, resulting in thermohaline convection and a deepening of the mixed layer (and the pycnocline) to a depth of 50–200 m. In spring during sea ice melt, the entry of freshwater with low density lowers and stabilizes the pycnocline (Eicken, 1995; Gordon et al., 1984).

Light conditions in the Antarctic and in the upper layer of the South Polar Sea also undergo strong seasonal changes, ranging from 24 h of light in summer to complete darkness during the winter months.

Notwithstanding these strong seasonal fluctuations in ice coverage and light regime, the general physical conditions and cold climate in the South Polar Sea have been stable for more than 15 Ma (Dayton, 1990; Dayton et al., 1994).

2.2. Biological characteristics

The Antarctic marine biota are well adapted to the physical conditions in their environment, particularly in the high Antarctic where primary production, life cycles and strategies are closely coupled to seasonal sea ice dynamics. During winter, autotrophic primary production is low and mostly restricted to the sea ice (Arrigo et al., 1997; Lizotte, 2001). During spring and summer, when the sea ice is melting, the released ice algae fuel subsequent phytoplankton blooms in the shallow and stable mixed layer of the marginal ice edge (Lizotte, 2001; Smith and Nelson, 1986); these blooms are mainly formed by diatoms and *Phaeocystis* (Estrada and Delgado, 1990; Nöthig et al., 1991). In autumn, sea ice extends again and remaining algae are incorporated into newly formed ice (e.g. Melnikov, 1998). The large microphytoplankton (>20 μm) blooms account for most of the annual primary production (e.g. Scharek and Nöthig, 1995; Smith and Sakshaug, 1990) but their occurrence is limited in time and space. Pico- (0.2 to <2.0 μm) and nanoplankton (2.0 to <20 μm) are present in the water column throughout the whole year but these small size classes achieve much lower biomass and productivity compared with the bloom system (Detmer and Bathmann, 1997; Scharek and Nöthig, 1995).

Primary and secondary consumers in the water column are mainly represented by copepods, hyperiid amphipods, salps, fish larvae, chaetognaths and euphausiids; larger pelagic predators include squids and fishes (Hempel, 1985; Siegel et al., 1992). Antarctic krill, *E. superba*, is a dominate member of the community in the seasonal sea ice zone and the life history pattern of this species is closely linked to the seasonal sea ice cycle (Smetacek et al., 1990). In the high Antarctic zone, *E. superba* is replaced by a smaller congener *Euphausia crystallorophias*, the so-called ice krill (e.g. Hempel, 1985). Most zooplankton species are present and feeding in the upper water column or at the ice underside the whole year round (Bathmann et al., 1991; Marshall, 1988; Øresland, 1995; Smetacek et al., 1990).

Benthic shelf communities in the high Antarctic are characterized by extraordinarily high biomass and diversity (Brey and Gerdes, 1997; Dayton et al., 1994; Gutt et al., 2004) and are characterized by the dominance of suspension and deposit-feeding species such as sponges, ascidians and echinoderms (Dayton et al., 1974; Gutt and Starmans, 1998; Voss, 1988). In many regions, from shallow water coastal zones to deeper high Antarctic shelf areas, benthic community structure is shaped by physical disturbance, in particular by ice (Gutt, 2000, 2001; Sahade et al., 1998; Smale et al., 2008). In the eastern Weddell Sea, for example, the disturbance of the seafloor by grounding icebergs results in a patchy distribution of various successional stages, which increases between-habitat diversity (Gutt, 2000, 2001; Gutt and Piepenburg, 2003; Knust et al., 2003) which adds a spatiotemporal component to changes in the structure of the benthic food webs (Hagen et al., 2012).

In vast areas of the high Antarctic shelf, large sponges form a typical 3-dimensional habitat for a diverse invertebrate and fish community (Arntz et al., 1994; Gutt and Starmans, 1998). Sponges are often used by invertebrates and fishes as a refuge and/or nursery as well as an upper level substrate to benefit from enhanced access to the water column (Fig. 2A,B). In shallow, inshore areas (e.g. Potter Cove in King George Island), benthic macroalgae such as *Desmarestia* spp., *Himantothallus grandifolius* and *Palmaria decipiens* contribute significantly to primary production (Quartino and Boraso de Zaixso, 2008). As with the sponges on the deeper shelf, benthic macroalgae in shallow waters provide an analogously complex habitat and shelter for a multitude of species including fishes in coastal communities (e.g. Barrera-Oro and Casaux, 1990; Gambi et al., 1994; Moreno et al., 1982; Tada et al., 1996; Takeuchi and Watanabe, 2002) and are a major food source for secondary producers (Iken, 1996; Tatián et al., 2004). Below the depth zone of macroalgal presence, benthic consumers depend on pelagic production (e.g. Mincks et al., 2008). On the high Antarctic continental shelf, where benthic macroalgae are absent over vast areas, tight bentho-pelagic coupling plays an important role in the food web. The high benthic biomass found on the shelf indicates a highly efficient transfer of organic matter from surface waters towards the seafloor (Smith et al., 2006). The vertical export of energy is driven either passively, via sinking particulate organic matter (POM), or actively by migrating organisms.

POM flux on the shelves is dominated by faecal pellets and strings, and large diatoms (Bathmann et al., 1991; Bodungen et al., 1988; Fischer, 1989; Nöthig and Bodungen, 1989). Mass sedimentations of ice algae, *Phaeocystis*

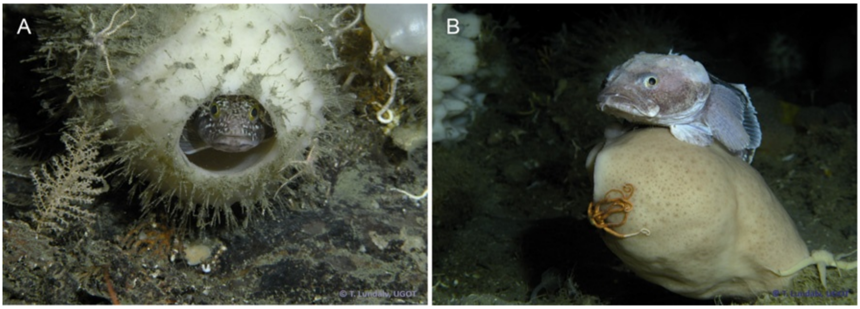


Figure 2 (A) *Trematomus* cf. *nicolai* hiding inside a sponge; (B) *Pogonophryne* sp. on top of a sponge (ANT XXVII-3 in 2011, western Weddell Sea). Photos: ©Tomas Lundälv, University of Gothenburg.

or diatoms after ice melt and termination of blooms are seasonally important export mechanisms (DiTullio et al., 2000; Riebesell et al., 1991; Scharek et al., 1999). Several zooplankton species including Antarctic krill, copepods and salps were observed to undertake extensive vertical migrations within the water column (Atkinson et al., 1992; Gili et al., 2006; Zhou and Dorland, 2004), thereby significantly contributing to the energy export from the euphotic zone towards the seafloor.

The marine living communities of the South Polar Sea are exploited by a multitude of endothermic animals. Whales and seabirds are seasonal visitors that forage in the seasonal sea ice zone and under the pack ice during summer (Boyd, 2002; Murase et al., 2002; Van Franeker et al., 1997). Penguins (mainly Emperor penguin, *Aptenodytes forsteri*, and Adélie penguin, *Pygoscelis adeliae*) and seals (Weddell seal, *Leptonychotes weddellii*; Ross seal, *Ommatophoca rossii*; Crabeater seal, *Lobodon carcinophagus*; Fur seal, *Arctocephalus gazella*; Elephant seal, *Mirounga leonina*) are permanent inhabitants of Antarctic coastal areas. Extensive cracks in the ice shelf covered by sea ice, such as the Drescher Inlet in the Riiser-Larsen Shelf ice (eastern Weddell Sea), represent particularly important breeding and foraging grounds for Weddell Seals and large Emperor Penguin colonies (Plötz et al., 1987).

3. ANTARCTIC FISH COMMUNITIES

3.1. Composition of the modern fauna

Despite the large area covered by the South Polar Sea (>20 million km^2), the modern fish fauna is composed of only about 320 species, belonging to 50 families (Eastman, 2005). This Antarctic ichthyofauna is unique for two reasons: (i) the modern fish fauna is highly endemic, with 88% of all species being confined to the South Polar Sea (Andriashev, 1987), and (ii) the communities are dominated by a single taxonomic group, the perciform suborder Notothenioidei, which accounts for about 35% of all Antarctic fish species (Eastman, 1993). In high Antarctic shelf areas, such as those of the eastern Weddell Sea, notothenioids form up to 98% of the total fish abundance and biomass (R. Knust and K. Mintenbeck, unpublished data). Groups typical of fish communities in temperate or boreal regions, such as clupeids, are absent. Non-notothenioid fish species inhabiting the South Polar Sea mostly belong to typical deep-sea groups such as zoarcids, liparids, macrourids and myctophids. The occurrence of these groups is largely restricted to the lower slope and the deep sea where notothenioid fishes, except for the two *Dissostichus* spp. (*Dissostichus eleginoides* and *Dissostichus mawsoni*), are absent (Boysen-Ennen and Piatkowski, 1988; Donnelly et al., 2004; Gon and Heemstra, 1990; Kock, 1992).

Close to 100 notothenioid fish species have been described from the South Polar Sea (Eastman and Eakin, 2000) but new species are still being discovered (see e.g. Eakin and Balushkin, 1998, 2000; Eakin and Eastman, 1998; Eakin et al., 2008). Most species belong to just five families: Nototheniidae (notothens), Channichthyidae (icefish), Artedidraconidae (plunderfish), Bathydraconidae (dragonfish) and Harpagiferidae (spiny plunderfish). Endemism within the suborder is extremely high, with 97% of notothenioid species being found only in the Antarctic (Andriashev, 1987).

The diversity of the demersal fish community differs regionally, with a latitudinal shift in species composition (Hureau, 1994; Kock, 1992; Mintenbeck et al., 2003, 2012; Permitin, 1977). In the ice-free zone, on the Sub-Antarctic island shelves, typical members of the demersal fish communities are the channichthyids *Chaenocephalus aceratus* and *Champsocephalus gunnari*, the nototheniids *Patagonotothen guntheri*, *Gobionotothen gibberifrons*, *Lepidonotothen* spp., *Notothenia* spp. and *D. eleginoides* (Patagonian toothfish).

At higher latitudes, in the seasonal sea ice zone, communities are dominated by *Lepidonotothen* spp., *Notothenia* spp., *Chionodraco rastrospinosus* (Channichthyidae) and some species of the genus *Trematomus* (see also Barrera-Oro, 2002). In inshore shallow waters, the harpagiferid *Harpagifer antarcticus* is also abundant (Barrera-Oro, 2002; Barrera-Oro and Casaux, 1998).

The demersal fish fauna in the high Antarctic zone is characterized by several *Trematomus* (Nototheniidae), artedidraconid and bathydraconid species, and the channichthyids *Chionodraco* spp. and *Cryodraco antarcticus* (Donnelly et al., 2004; Eastman and Hubold, 1999; Hubold, 1992; Schwarzbach, 1988). In high Antarctic shelf regions, such as the eastern Weddell Sea shelf, species diversity is much higher than on the Sub-Antarctic island shelves or west of the Antarctic Peninsula (Mintenbeck et al., 2012; Schröder et al., 2001). The major reasons for this high species diversity are the 3-dimensionality of the benthic habitat and the high between-habitat diversity shaped by grounding icebergs, both allowing for small-scale niche separation (horizontally and vertically) and thus for the coexistence of trophically similar species (Brenner et al., 2001; Gerdes et al., 2008; Knust et al., 2003).

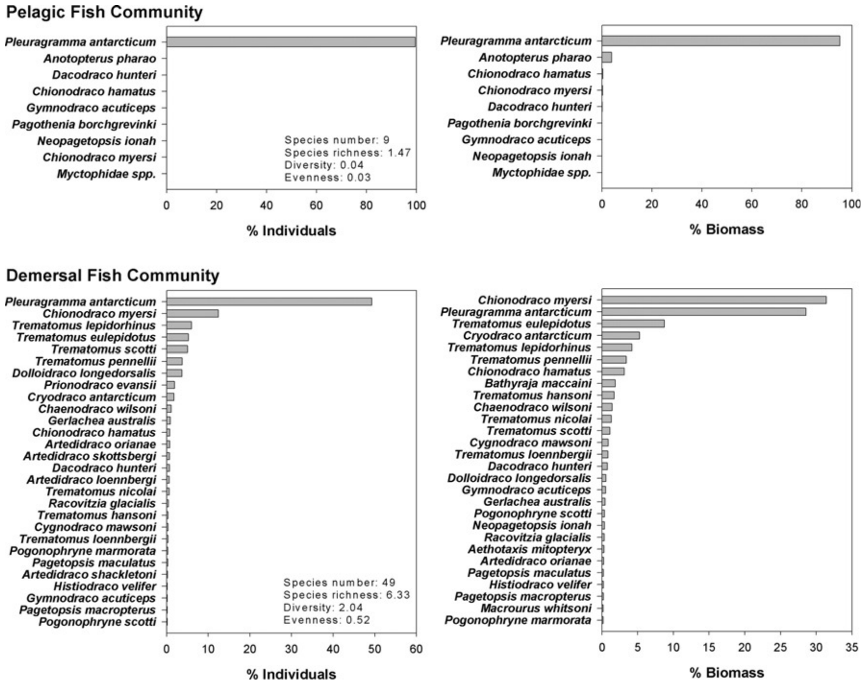


Figure 3 Composition of the pelagic and demersal fish communities on the eastern Weddell Sea shelf between 200 and 600 m water depth (samples from 26 otter trawl hauls and 10 hauls with a bentho-pelagic net taken between 1996 and 2004). Only the 28 out of 49 species contributing >0.15% to overall individuals and biomass are shown for the demersal community. Species number, species richness, diversity and evenness are given for the two communities using different scales.

The pelagic ichthyofauna of the South Polar Sea includes an oceanic and a neritic fish community. The oceanic pelagic communities off the shelves are mainly composed of several myctophid fish species (Barrera-Oro, 2002; Pusch et al., 2004). The neritic pelagic community differs significantly from the oceanic community and is extremely species poor compared with the demersal community on the shelf. In Fig. 3, this difference is exemplified by comparing the pelagic and the demersal fish communities on the eastern Weddell Sea shelf between 200 and 600 m water depth. The neritic pelagic fish community is composed of very few species, and most of them (e.g. the channichthyids *Chionodraco* spp., *Dacodraco hunteri*, *Neopagetopsis ionah* and the bathydraconid *Gymnodraco acuticeps*) are in fact demersal fishes that only occasionally move into the water column. The cryopelagic nototheniid *Pagothenia borchgrevinki* is closely associated with the underside of ice (e.g. Janssen et al., 1991) and is rarely found in open waters. Both the demersal and pelagic fish communities are distinctly dominated by a single nototheniid species, the Antarctic silverfish *P. antarcticum*. The only other species that attains higher biomass in the demersal community is the large icefish *Chionodraco myersi* (Fig. 3). *P. antarcticum* is an endemic species with circum-Antarctic distribution and is one of the few truly pelagic representatives of the entire suborder Notothenioidei. It is a shoaling species (Eastman, 1985a) and adults undertake diel vertical migrations from the sea floor towards the surface waters (Fuiman et al., 2002; K. Mintenbeck and R. Knust unpublished data; Plötz et al., 2001). This species dominates the pelagic fish biomass in coastal waters of the South Polar Sea by >90% (see also DeWitt, 1970; Donnelly et al., 2004; Hubold and Ekau, 1987). In the southern Weddell Sea, *P. antarcticum* accounts for most of the overall fish production, and stock density was estimated to amount at least 1 ton km^{-2} (Hubold, 1992). Though usually found in the free water column, its life cycle strategy, including its feeding dynamics, seems to be closely associated with the sea ice (Daniels, 1982; La Mesa and Eastman, 2012; Vacchi et al., 2004). Besides adult *P. antarcticum*, larvae and early juveniles of several notothenioid species dominate the neritic pelagic fish community numerically. The notothenioid ichthyoplankton community is also dominated by early life stages of *P. antarcticum*. Notothenioid larvae are mainly concentrated in the upper 50 m in well-stratified surface waters, while juveniles occur in slightly deeper waters (Granata et al., 2002; Hubold, 1984, 1985; Hubold and Ekau, 1987; Kellermann, 1986a, b; Morales-Nin et al., 1998). Due to their dominate role in Antarctic fish communities, this chapter largely focuses on notothenioids.

3.2. Evolution and adaptive radiation

The uniqueness of the Antarctic fish fauna with its high degree of endemism and a single dominant group is the result of a long evolutionary history of adaptive radiation in isolation at sub-zero temperatures. Though fossil records are scarce, there is some evidence that the fish fauna in the Antarctic during the Eocene differed substantially from the modern fauna and that the community was composed of species from many, and more cosmopolitan, families (Eastman, 1993, 2005; Eastman and Grande, 1989). Following the complete separation of Antarctica and the progressive cooling of the region's waters, most components of the Eocene fish fauna vanished from shelf areas. Local extinctions likely occurred due to habitat loss associated with the massive expansion of the ice sheet and changes in trophic structure (Eastman, 2005). After this period of extinctions, a multitude of niches were available for other species. These niches were filled by species of the suborder Notothenioidei, which have undergone a remarkable diversification by adaptive radiation on the isolated shelf of the Antarctic continent. The lack of competition from other fish groups allowed increased morphological and ecological diversification of notothenioid fish and expansion into various niches (e.g. Eastman and McCune, 2000; Ekau, 1988; Ptacnik et al., 2010). Accordingly, notothenioid fish species now occupy benthic, bentho-pelagic, pelagic as well as cryopelagic habitats. However, due to the lack of a swimbladder in their common ancestor, the majority of recent notothenioid species are demersal (Clarke and Johnston, 1996). Adaptive radiation of notothenioids also included trophic diversification (Ekau, 1988; Schwarzbach, 1988), and notothenioid fishes now occupy a multitude of trophic niches. Kock (1992) distinguished five main feeding types according to their principal prey: benthos feeders, fish and benthos feeders, plankton and fish feeders, plankton and benthos feeders, and plankton feeders. As some species, such as the channichthyid *D. hunteri*, rely almost exclusively on piscivory (Eastman, 1999; Schwarzbach, 1988), a sixth group of pure ‘fish feeders’ also exists.

The point at which the characteristic modern fauna became established exactly is unknown (Clarke and Johnston, 1996; Eastman, 2005). The few existing fossil records indicate first appearance of this group in the early Tertiary (38 Ma; Balushkin, 1994), and according to a recent phylogenetic study, radiation of notothenioids began near the Oligocene–Miocene transition (~24 Ma), coinciding with the enhanced formation of sea ice (Matschiner et al., 2011).

3.3. Adaptations and characteristics of notothenioid fishes

3.3.1 Physiological and morphological adaptations

Notothenioid fishes are characterized by a multitude of physiological adaptations to life within cold waters, but the key innovation enabling species to survive and diversify was most likely the evolution of antifreeze glycoproteins (AFGPs; Matschiner et al., 2011). AFGPs provide a highly efficient protection from freezing of hypoosmotic (compared to seawater) body fluids by adhering to and blocking the growth of ice crystals (DeVries, 1971; Fletcher et al., 2001). Concentrations of AFGP differ between species and depend on ambient water temperature, depth distribution, life cycle, activity and phylogeny (Wöhrmann, 1996, 1997). AFGP synthesis is most likely regulated by ambient water temperature (Wöhrmann, 1997).

Beside the risk of freezing, another problem of life at sub-zero temperatures is the temperature dependence of viscosity of body fluids in ectotherms. Viscosity and temperature are strongly, negatively correlated, that is, body liquids become more viscous when cold, which affects membrane fluidity, blood circulation, enzyme kinetics and gas diffusion (e.g. Hochachka and Somero, 2002). Cell membrane fluidity is maintained in the cold by homeoviscous adaptation (see Sinensky, 1974), which involves an increased content of unsaturated fatty acids and specific membrane phospholipids (e.g. Eastman, 1993; Hazel, 1995). An increased blood viscosity is offset by reduced haematocrit and haemoglobin concentrations in notothenioid fishes (Egginton, 1996, 1997a,b; Kunzmann, 1991). The only known exceptions of fish with a relatively high haematocrit are *Notothenia coriiceps* and *N. rossii* from the Antarctic Peninsula (Beers and Sidell, 2011; Mark et al., 2012; Ralph and Everson, 1968). Owing to the low metabolic demands of notothenioids (e.g. Clarke, 1983; Clarke and Johnston, 1996) and the increased physical oxygen solubility in seawater, blood and cytosol at cold temperatures, the reduction in haematocrit and respiratory pigment is not detrimental to aerobic performance. In species of the family Channichthyidae, the so-called icefishes or white-blood fishes, functional red blood cells are completely absent: these fishes do not possess any oxygen-binding pigment (haemoglobin) in their blood and some species also lack intracellular myoglobin (Montgomery and Clements, 2000; Sidell and O'Brien, 2006).

The limited oxygen-carrying capacity of the blood is compensated by a multitude of secondary adaptive body modifications in icefishes, for example, a larger ventricle, increased blood volume and cardiac output, and increased skin vascularity (Kock, 2005a; O'Brien and Sidell, 2000; O'Brien et al., 2003; Sidell, 1991). Molecular adaptations also include the absence of heat-shock protein expression in some notothenioids (Carpenter and Hofmann, 2000) and a rearrangement of the mitochondrial genome that may have supported cold adaptation of mitochondrial properties (Mark et al., 2012; Mueller et al., 2011; Papetti et al., 2007; Zhuang and Cheng, 2010).

The increased viscosity of body fluids, together with cold temperatures, affect enzyme kinetics and cytosolic diffusion processes (Sidell, 1991). Both gas diffusion and enzyme kinetics are temperature dependent and decelerate rapidly at cold temperatures. Mitochondrial oxidative capacity of notothenioid fishes is low compared with warm water species

(Johnston et al., 1994), and reduced diffusion of gas and metabolites to and from mitochondria entails an additional reduction of available energy and oxygen. The negative effects of temperature and viscosity on enzymes and diffusion are counterbalanced in Antarctic fishes by two metabolic adaptations. First, these fishes have increased quantities and capacities of intracellular enzymes (Crockett and Sidell, 1990), which reduce diffusion distance and increase efficiency (Pörtner et al., 2000). Second, they display mitochondrial proliferation, an increase in mitochondrial abundance and ultra-structural density (Guderley and Johnston, 1996). Up to 60% of muscle fibre volume of the slow-swimming, pelagic notothenioid *P. antarcticum* is occupied by mitochondria (Clarke and Johnston, 1996). Additionally, many species have relatively high intracellular concentrations of lipids which may be used as energy stores (Crockett and Sidell, 1990; Eastman and DeVries, 1981) and aid gas diffusion (Kamler et al., 2001). These intracellular lipids also play a role in buoyancy (see below).

Notothenioid fishes are thus well adapted to cold waters. Nevertheless, these adaptations apparently involve an extreme stenothermy of physiological functions and seem to result in narrow thermal tolerance windows of this group (Johnston, 2003; Mueller et al., 2011; Pörtner and Peck, 2010; Somero and DeVries, 1967).

However, the success of notothenioid species in the South Polar Sea ecosystem is not only based on physiological adaptations, but also on morphological modifications related to buoyancy (Eastman, 2005; Eastman et al., 2011). Notothenioids lack a swim bladder and, without this organ, the exploitation of bentho-pelagic or pelagic food sources is extremely energy consuming. To compensate for the lack of a swim bladder, some notothenioid species developed modifications in body structure, which allow them to inhabit and to exploit the pelagic realm without an energetic disadvantage. In these species, mineralization of skeleton and scales is reduced, and the skeleton contains a high proportion of cartilage, which is less dense than bone (DeVries and Eastman, 1978; Eastman and DeVries, 1981, 1982; Eastman et al., 2011). *P. antarcticum* has a persistent notochord and large amounts of lipids (accounting for ~39% of muscle dry mass) are stored in subcutaneous and intramuscular lipid sacs which provide static lift (DeVries and Eastman, 1978). *D. mawsoni* possess extensive lipid deposits in adipose cells, which account for ~23% white muscle dry weight (Eastman and DeVries, 1981). The lipid deposits in these species mainly consist of triglycerols (Eastman and DeVries, 1981, 1982; Hubold and Hagen, 1997). However, neutral buoyancy is rare in notothenioids and limited to very few species, for example, *P. antarcticum*, *D. mawsoni* and *Aethotaxis mitopteryx* (Eastman, 2005).

3.3.2 Growth, reproduction and development

Most notothenioids are characterized by a rather sluggish mode of life and high longevity. High Antarctic fish species typically reach ages of 15–21 years (see Kock, 1992; La Mesa and Vacchi, 2001 for review). The pelagic *P. antarcticum* was estimated to live more than 30 years (Radtke et al., 1993). Growth performance of most species is similar to species from boreal or temperate regions (Kock and Everson, 1998; La Mesa and Vacchi, 2001) but there seems to be a trend towards lower growth performance in the high Antarctic notothenioids, relative to their congeners from the seasonal sea ice zone (Kock, 1992). However, in adult fish, growth performance is apparently related to lifestyle and tends to increase from pelagic towards benthic lifestyles (La Mesa and Vacchi, 2001). Pelagic fishes such as *P. antarcticum* are thus characterized by slow growth (e.g. Hubold and Tomo, 1989). Many notothenioids show a distinct seasonal growth pattern with high growth rates in summer and low growth rates in winter (Hureau, 1970; North et al., 1980; White, 1991). The interspecific latitudinal and intraspecific seasonal differences in growth rates of notothenioids most likely (primarily) stem from variations in food supply and/or prey composition, and feeding intensity (Kock, 1992). For example, *N. coriiceps* undergoes winter metabolic suppression and enters a dormant stage with periodic arousals lasting only a few hours, resulting in a net loss of growth rate during the winter months (Campbell et al., 2008). However, most notothenioids seem to feed year round (e.g. Casaux et al., 1990; Hubold, 1992).

Sexual maturity is delayed in most Antarctic fishes. With a few exceptions, species reach maturity at 50–80% of their maximum age and size (Kock and Everson, 1998; La Mesa and Vacchi, 2001). The spawning season is species- and location specific: in the seasonal sea ice zone, most species spawn in autumn/winter and in the high Antarctic zone, most species are summer and autumn spawners (Kock and Kellermann, 1991). Some species have demersal eggs, which are often laid on rocks or in the cavity of sponges. Nest-guarding and other parental care behaviours have been reported increasingly in notothenioids (e.g. Barrera-Oro and Lagger, 2010; Detrich et al., 2005; Kock et al., 2006; Moreno, 1980). Others species, for example, *P. antarcticum*, have pelagic eggs (Faleyeva and Gerasimchuk, 1990; Vacchi et al., 2004). The eggs are usually large and yolky, so relative fecundity is low in most species, particularly in high Antarctic nototheniods (Hubold, 1992; Kock, 1992; Kock and Kellermann, 1991). The incubation period of eggs is long and usually takes several months (Hubold, 1992; Kock and Kellermann, 1991; North and White, 1987). Larvae of many species apparently hatch in spring and summer (Efremenko, 1983) when food conditions are best; however, some species also hatch in winter (Ekau, 1989; North and White, 1987). Larvae are large at hatching (Kellermann, 1990; North and White, 1987) and the mouth is well-developed, so that even early yolk-sac larvae are able to feed (Kellermann, 1986b). Most, if not all, notothenioid larvae are pelagic.

3.4. Threats to the fish community

Antarctic fish communities are threatened by climate change in multiple ways. On the one hand, fishes might be affected at the physiological level directly by increasing water temperatures and pCO_2, and reduced water salinity. Due to the numerous adaptations to life in the South Polar Sea, fishes are likely to be affected on different organizational levels, from the cellular level up to the population level and beyond. In particular, an increase of water temperatures might pose a major threat to stenothermal species (see e.g. Somero, 2010), whereas increasing concentrations of CO_2 might have more general detrimental effects across many fish species (e.g. Ishimatsu et al., 2005). Whether and to what extent fitness and survival are affected by such changes depends on individual or species-specific physiological plasticity.

Climate change can additionally affect fishes indirectly by secondary effects, such as those due to changes in the abiotic environment that will entail alterations in the food web, as also reported for instance in many freshwaters (Meerhoff et al., 2012). Unfavourable abiotic conditions as well as invasion of Antarctic waters by non-indigenous species may result in changes in trophic structure and dynamics by alterations in composition and population density of prey and predator communities (Woodward et al., 2010a).

Changes in prey species composition will involve alterations in the type of prey available to fishes, particularly in size structure and energy content: a shift from diatoms to cryptophytes is accompanied by a strong shift in size structure of primary producers, and ultimately with a potential size shift in secondary producers; a shift from a krill dominated zooplankton community towards a community dominated by salps involves a drastic decrease in nutritional value of potential prey for higher trophic level consumers (but see also Gili et al., 2006). In the marine Antarctic, where life cycles are closely coupled to seasonal sea ice dynamics, changes in water temperature itself but also reduced sea ice extent and duration might entail phenological shifts and a trophic mismatch between prey and consumer species (Hagen et al., 2012). Secondary effects of climate change may also involve a reduction of habitat, which could lead to fragmentation of the food web (Hagen et al., 2012): sea ice reduction means a loss of habitat for ice-associated pelagic species, but demersal fish are threatened by habitat reduction as well, as warmer temperatures will most likely result in enhanced disintegration of glaciers and ice shelves. An increased iceberg calving and breakup will lead to a higher frequency of iceberg scouring events and thus to increased seafloor and habitat destruction.

From other ecosystems, it is well-known that many fish species are sensitive to these types of threats, via mechanisms operating directly at the ecophysiological level (e.g. McFarlane et al., 2000; Pörtner and Peck, 2010; Pörtner et al., 2008) but also indirectly at the trophic level (Beaugrand et al., 2003; Benson and Trites, 2002; Drinkwater et al., 2010), as well as by alterations in habitat structure and heterogeneity (Hughes et al., 2002; Yeager et al., 2011).

4. PHYSIOLOGICAL VULNERABILITY OF ANTARCTIC FISHES

4.1. Sensitivity to changes in temperature and salinity

Antarctic fishes have very narrow thermal windows due to cold adaptation (Clarke, 1991; Somero et al., 1968; Wohlschlag, 1963), resulting in high stenothermy in this group (Gonzalez-Cabrera et al., 1995; Podrabsky and Somero, 2006; Robinson et al., 2011; Somero and DeVries, 1967). Most species, for example, the bottom-dwelling *Trematomus bernacchii*, *Trematomus hansoni* and *Trematomus pennellii*, have an upper lethal temperature between just 4 and 6 °C (Robinson, 2008; Somero and DeVries, 1967). Fish performance is already affected well below the lethal limit. However, the paradigm that all notothenioid species are extremely stenothermal without exceptions has recently been revised.

Some species such as *H. antarcticus* and young *N. coriiceps* are frequently found in tide pools in King George Island (South Shetland Islands), where during sunny days individuals are exposed to warm temperatures for many hours (E.R. Barrera-Oro and E. Moreira, personal observation). Thus, these species can at least cope with acute, relatively short-term temperature increases. A few species are apparently also able to compensate for chronic exposure to higher temperatures, for example, the cryopelagic *P. borchgrevinki* shows some metabolic plasticity: long-term warm acclimation of *P. borchgrevinki* to 4 °C results in a shift of the thermal tolerance window towards warmer temperatures (Bilyk and DeVries, 2011; Franklin et al., 2007; Robinson and Davison, 2008) owing to metabolic compensation (Seebacher et al., 2005) which leads to a reduced performance at low temperatures (Franklin et al., 2007). Recent measurements of routine metabolic rate of *Notothenia rossii* and *Lepidonotothen squamifrons* from the Scotia Arc shelf revealed a partial compensation after long-term acclimation to elevated temperatures (A. Strobel and F.C. Mark, unpublished data). Similarly, long-term warm acclimation of the Antarctic eelpout *Pachycara brachycephalum* involves metabolic rearrangements (Lannig et al., 2005) and indicates an improvement of hepatic metabolism accompanied by a shift of energy sources from lipids to carbohydrates (Brodte et al., 2006, Windisch et al., 2011).

However, these metabolic acclimations apparently do not result in a full compensation and cannot be generalized across all species (c.f. the deepwater zoarcid *Lycodichthys dearborni*; Podrabsky and Somero, 2006), but seem rather dependent on the physical capacities of the circulatory system: studies of energy allocation in isolated cells of Antarctic notothenioids and *P. brachycephalum* suggest that within a thermal range of about −1 to 12 °C, thermal tolerance limits are defined at the whole organism level (Fig. 4), for

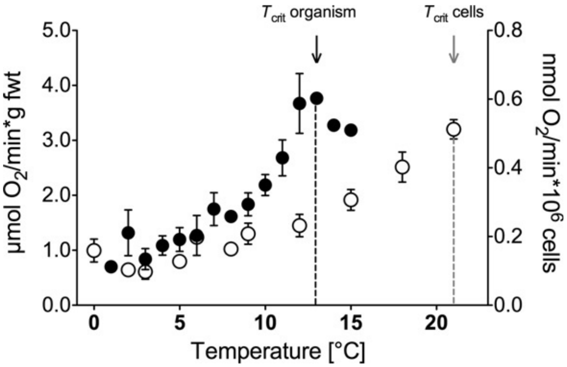


Figure 4 Temperature dependence of whole animal metabolic rate (filled symbols, left axis) and respiration rate of hepatocytes (open symbols, right axis) of the Antarctic eelpout *Pachycara brachycephalum*. Due to organismal complexity, acute whole animal critical temperatures (T_{crit}) that mark the onset of anaerobic metabolism are reached at lower temperatures (∼13 °C, black arrow) than in isolated cells (>21 °C, grey arrow; *redrawn from Mark et al., 2002, 2005; with permission from Springer).*

example, by capacity limitations of the circulatory system rather than by a general failure of cellular energy metabolism (Mark et al., 2002, 2005). Due to their lower level of organizational complexity, thermal tolerance windows of organelles generally span a wider temperature range than those of the whole organism (Mark et al., 2005). Thus, acclimatory capacities are mainly defined by the degree of changes in cellular energy metabolism and depend strongly on the mitochondrial oxidative capacities. The acute thermal tolerance of oxidative capacity varies between species and tissues (Mark et al., 2012; Urschel and O'Brien, 2009). However, these acclimatory capacities are always constrained within the frame of the thermal window set by the whole organism's physiological plasticity.

Fishes possess the flexibility to respond to chronically elevated temperatures via mitochondrial proliferation—modifications of the amount and volume of mitochondria to adjust aerobic capacity (Tyler and Sidell, 1984; Urschel and O'Brien, 2008). Mitochondrial oxygen demand rises with increasing temperature and aerobic capacities need to be adjusted accordingly. Only a few studies have demonstrated a full compensation of the increased oxygen demand at the mitochondrial level after warm acclimation, and these studies were exclusively performed on non-Antarctic organisms (e.g. Dahlhoff and Somero, 1993; Sloman et al., 2008). This indicates that there are limitations to mitochondrial acclimation, ultimately co-defining the rather narrow bandwidth of thermal acclimation, especially in Antarctic fishes (Mark et al., 2006). Increased mitochondrial oxygen demand in warmer conditions may be met by altering haemoglobin affinities (Tetens et al., 1984) and raising the haematocrit to optimize the oxygen-carrying capacity of the blood. Yet, haematocrit levels are correlated with haemoglobin expression (Beers and Sidell, 2011). Thus, species with low or no haemoglobin levels have less capacity to adjust haematocrit. This is further exacerbated by the fact that rising temperatures result in lower levels of physically dissolved oxygen in the blood. Therefore, icefishes that lack haemoglobin will be more vulnerable to warming than red-blooded species, because they cannot increase the oxygen-carrying capacity of the blood. According to Beers and Sidell (2011), Antarctic fishes with higher haematocrit levels thus possess higher temperature acclimatory capacities than species with lower haematocrit.

Studies on the impact of salinity changes on notothenioid fishes are extremely scarce. O'Grady and DeVries (1982) investigated the capacity for osmoregulation of adult *P. borchgrevinki* and *Trematomus* spp. at a wide range of salinities (25–200% of the salinity in their natural habitat, 35 psu) and found these species to be rather tolerant towards even large fluctuations from 50% to 175% normal salinity. Blood serum osmolarities in Antarctic fishes are among the highest in marine teleosts, which has been interpreted as an additional antifreezing protection (O'Grady and DeVries, 1982). After warm acclimation, serum osmolarities reduced to the levels found in temperate teleosts were measured in *T. bernacchii*, *T. newnesi* and *P. borchgrevinki* (Gonzalez-Cabrera et al., 1995; Hudson et al., 2008; Lowe and Davison, 2005), and also in *N. rossii* and *L. squamifrons* (A. Strobel and F.C. Mark, unpublished data). Thus, adult notothenioids are apparently capable of efficient osmoregulation and seem able to adapt blood osmolarity to ambient environmental conditions.

Almost all studies on physiological sensitivity of notothenioid fishes to changing abiotic parameters have been conducted on adults. Data from non-Antarctic fish species suggest an ontogenetic shift in temperature tolerance, with narrow thermal tolerance windows in eggs and larvae (e.g. Pörtner and Farrell, 2008; Pörtner and Peck, 2010). Most teleost fishes are able to osmoregulate at hatch, but the efficiency seems to be higher in more advanced developmental stages (Varsamos et al., 2005). To our knowledge, there are no experimental data for early developmental stages of notothenioid fishes, but indirect evidence from abundance and distribution of *P. antarcticum* larvae and juveniles indicate that these early stages likely have limited ability to tolerate changes in temperature and salinity. Larvae and juveniles of this species are mostly found within water masses of particular temperature and salinity (e.g. Granata et al., 2002; Guglielmo et al., 1998; Hubold, 1984; Kellermann, 1986a). West of the Antarctic Peninsula, *P. antarcticum* larvae and juveniles were clearly confined to cold and high salinity water masses originating from the Weddell Sea (Slósarczyk, 1986). Based on combined datasets of fish abundances in waters of Weddell Sea and Bellinghausen Sea origin, Slósarczyk (1986) calculated the range of approximate optimum conditions for larvae and juveniles in the Bransfield Strait: Abundances suggested optimal ranges in temperature and salinity of -0.50 to $+0.45$ °C and ~ 34.10–34.62 psu, respectively.

Though changes in salinity induced by climate change might be a locally restricted phenomenon, dense aggregations of larvae and juveniles that are concentrated close to the coast/shelf ice in the upper water layers might be significantly affected. Moline et al. (2004) found vast areas west of the Antarctic Peninsula covered by low salinity water (33.4–33.6 psu), and the meltwater plume extended to depths as great as 50 m (Dierssen et al., 2002). It still needs to be verified whether and to what degree temperatures and salinities outside the narrow ranges given by Slósarczyk (1986) limit physiological performance and survival of larvae and juveniles, but tolerance indeed seems to be low: *P. antarcticum* larvae acclimated to cold Weddell Sea water were observed to shrink and to die immediately at water temperatures >0 °C (Hubold, 1990). Whether or not this limited tolerance holds true for early stages of other species needs further investigation, but at least *P. antarcticum* larvae seem to be highly vulnerable to changes in the abiotic environment.

4.2. Sensitivity to increasing pCO_2

Ocean acidification, as an additional stressor in parallel to ongoing climate warming (Woodward et al., 2010a), may prove to be particularly threatening to polar ecosystems owing to enhanced CO_2 solubility in cold waters and body fluids. Thermal tolerance windows are narrow in most species and, thus, sensitivities to combined stressor effects are likely to be higher in cold-adapted polar compared to temperate species. Many notothenioids will eventually find themselves at the upper end of their thermal tolerance range, implying that they are energetically limited and their physiological performance is highly susceptible to further stressors, such as the increasing concentration of carbon dioxide (Pörtner and Peck, 2010).

Previous research on the effects of elevated CO_2 levels on marine fishes led to the general notion that fishes are not particularly vulnerable to the direct effects of ocean acidification alone, due to their powerful mechanisms of ion regulation (Fivelstad et al., 2003). Most adult fishes are able to compensate for acid–base disturbances (Larsen et al., 1997) and show only minimal effects of hypercapnia on physiological performance (Melzner et al., 2009) including an incomplete compensation of extracellular pH (Michaelidis et al., 2007).

However, several studies on different non-Antarctic fish species demonstrated chronic effects of environmental hypercapnia, with early developmental stages being particularly affected: exposure to elevated CO_2 concentrations impairs embryonic metabolism (Franke and Clemmesen, 2011), survival and growth of eggs and larvae (Baumann et al., 2012), and growth of juveniles (Moran and Støttrup, 2010), and causes severe to lethal tissue damage in many internal organs of larvae (Frommel et al., 2012). The sensitivity to ocean acidification may generally be enhanced by ocean warming, which has been confirmed in tropical fishes (Nilsson et al., 2009; Pörtner and Farrell, 2008). Still very little is known about how the physiology and distribution of Antarctic fishes and their various life stages may be altered by the additional effects of hypercapnia, but several current projects are dealing with this topic, and initial results indicate that chronic hypercapnia leads to significant reductions of mitochondrial capacities in *N. rossii* (A. Strobel and F.C. Mark, unpublished data), on top of the thermal sensitivity of its mitochondrial metabolism (see Section 4.1 above; Mark et al., 2012). Hypercapnia-induced regulatory shifts in intracellular metabolic pathways and capacities therefore may exacerbate the effects of increased temperature on cellular and whole animal metabolism.

We currently lack sufficient data on Antarctic fishes to be able to generalize as to whether all life stages respond similarly or whether early developmental stages represent potential bottlenecks for population survival. Another topic that needs to be addressed is how hypercapnia will modify interactions between species already affected by the warming trend. Recent findings in tropical coral reef fish demonstrated behavioural disturbances by moderate levels of ocean acidification (1050 ppm CO_2, pH 7.8, year 2100 scenario), presumably elicited by hypercapnia effects on the central nervous system (Munday et al., 2009). Hypercapnia therefore may also alter trophodynamic interactions in a particular ecosystem (cf. Ferrari et al., 2011), beyond those of the direct lethal effects on interacting organisms. These aspects have never been studied in Antarctic fishes and clearly need further research.

5. TROPHIC VULNERABILITY OF ANTARCTIC FISHES

5.1. Vulnerability to general changes in trophic structure and dynamics

The vulnerability of a particular species to changes in food web structure and dynamics depends on its ability to cope with both ‘bottom-up’ and ‘top-down’ effects (Jacob et al., 2011; Melian et al., 2011; O’Gorman and Emmerson, 2010). Trophic plasticity, that is, the capability to cope with fluctuations in resource availability, is positively related to prey diversity (specialist vs. generalist consumers; Johnson, 2000; Mihuc and Minshall, 1995). Predator-induced mortality is the principal ‘top-down’ effect, and suppression of a particular species strongly increases with increasing predator diversity (Snyder et al., 2006). Vulnerability to ‘top-down’ effects and resilience capability are thus related to the number of predator species. Accordingly, species vulnerability to food web-mediated alterations is expected to decrease with prey diversity and to increase with predator diversity. Whether and how the complete loss of one species will affect overall food web structure and ecosystem functioning depends on the community's capacity for functional compensation, that is, species trophic redundancy (Johnson, 2000; Naeem, 1998).

Here, the relative trophic vulnerability of the adult notothenioid fish community inhabiting the eastern Weddell Sea shelf (between 200 and 600 m water depth) to alterations in the food web was estimated. A simple, quantitative measure based on the number of feeding links to prey and predator species was used to assess vulnerability. Information on trophic linkages was extracted from the extensive trophic database published in Jacob et al. (2011) that includes information on feeding relations of 489 consumer and resource species from the Antarctic Weddell Sea (for detailed information and sources, see Jacob, 2005; Jacob et al., 2011). For seven more fish species, additional information on prey composition was collected from Foster et al. (1987), Gon and Heemstra (1990), La Mesa et al. (2004) and Schwarzbach (1988). All in all, information on prey composition and links to predators was available for 37 of the 42 notothenioid species inhabiting the shelf.

For each fish species i, the total number of prey species $\sum P_i$, the number of prey species belonging to the functional groups 'Benthos', 'Plankton' and 'Fish', $\sum P_{\mathrm{B},i}$, $\sum P_{\mathrm{P},i}$, $\sum P_{\mathrm{F},i}$, and the number of predators $\sum C_i$ were extracted from the database. Both $\sum P$ and $\sum C$ are common descriptors in theoretical food web ecology and usually referred to as 'generality' ($\sum P$) and 'vulnerability' ($\sum C$; see e.g. Memmot et al., 2000; Schoener, 1989). Here, both variables were combined to calculate consumers' relative trophic vulnerability, a comparative index with values located between 0 and 1. $\sum C$ was taken as a measure of vulnerability to top-down effects, and $\sum P$ as an (inverse) measure of vulnerability to bottom-up effects.

The relative trophic vulnerability VI_i of fish species i can thus be computed by

$$\mathrm{VI}_i = \frac{\sum\limits_{i=1}^{m} C_i}{\sum\limits_{i-1}^{n} P_i + \sum\limits_{i=1}^{m} C_i} \qquad [1]$$

where m is the total number of consumer species and n is the total number of prey species of fish species i. $\sum P_i + \sum C_i \geq 1$ and $0 \leq \mathrm{VI}_i \leq 1$; $\sum P_i = \sum P_{\mathrm{B},i} + \sum P_{\mathrm{P},i} + \sum P_{\mathrm{F},i}$. In this basic equation (Eq. 1), each C_i and P_i count 1.

However, there is a difference in relative top-down and bottom-up effects depending on (i) whether a particular consumer is a generalist feeder or specialized on fish species i and (ii) whether a particular prey species is exclusively consumed by fish species i or exploited by a multitude of predators. To account for these differences, each consumer of fish species i, C_i, was weighted by the number of its own prey species (P_j) and each prey species of fish species i, P_i, was weighted by the number of its own consumer species (C_k). These weighted consumer and prey values of fish species i are referred to as WC_i and WP_i, respectively. Accordingly, the calculation of the relative trophic vulnerability index VI_i of fish species i was adapted by

$$\mathrm{VI}_i = \frac{\sum_{i=1}^{m} \mathrm{WC}_i}{\sum_{i=1}^{n} \mathrm{WP}_i + \sum_{i=1}^{m} \mathrm{WC}_i} \qquad [2]$$

with

$$\mathrm{WP}_{i,k} = \left(\frac{1}{\sum_{k=1}^{m} C_k} \right) \text{and}\, \mathrm{WC}_{i,j} = \left(\frac{1}{\sum_{j=1}^{n} P_j} \right); \sum \mathrm{WP}_i + \sum \mathrm{WC}_i > 0$$

and $0 \leq \mathrm{VI}_i \leq 1$; $\sum \mathrm{WP}_i = \sum \mathrm{WP}_{\mathrm{B},i} + \sum \mathrm{WP}_{\mathrm{P},i} + \sum \mathrm{WP}_{\mathrm{F},i}$. Here, m is the total number of weighted consumer species and n is the total number of weighted prey species of fish species i. This index was used as an indicator of species' risk to be negatively affected by changes in the food web. Spearman's rank correlation was used to analyze relationships between all parameters with the aim to rank $\sum \mathrm{WC}$, $\sum \mathrm{WP}$, $\sum \mathrm{WP}_{\mathrm{B}}$, $\sum \mathrm{WP}_{\mathrm{P}}$ and $\sum \mathrm{WP}_{\mathrm{F}}$ according to their effect on VI.

The number of prey items $\sum P$ ranged from 5 in some planktivorous fishes to >100 in benthos feeders. The number of predators $\sum C$ ranged from 12 to 47 (Table A1). The majority of notothenioid fish species are benthos feeders and mixed feeders, consuming varying proportions of benthos and plankton (Fig. 5). The number of pure plankton feeders and mixed feeders of plankton and fish is comparatively low and pure piscivorous species are extremely scarce. Relative vulnerability VI is related to

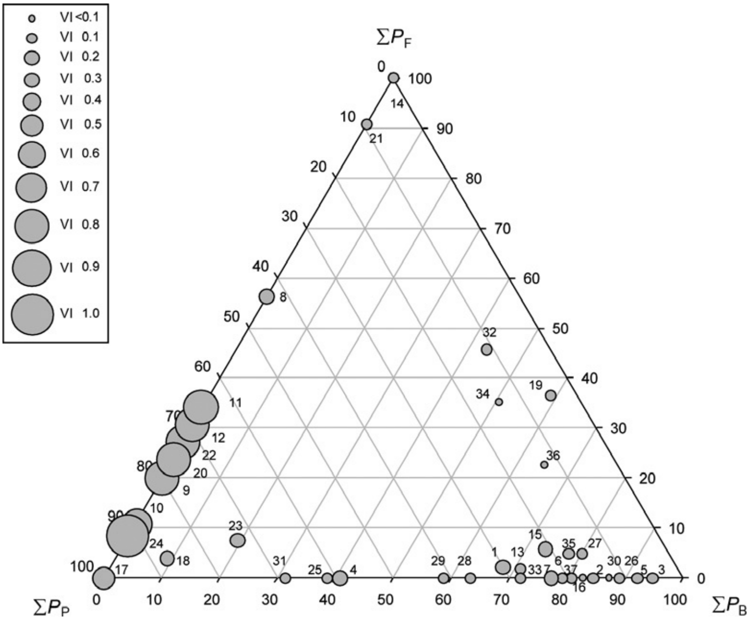


Figure 5 Relative proportions [%] of benthos ($\sum P_B$), plankton ($\sum P_P$) and fish ($\sum P_F$) in the diet of notothenioid fish species. Each circle represents one species; circle diameter indicates relative trophic vulnerability (VI). For species code numbers, see Table A1.

the distribution of prey species among the functional groups 'Benthos', 'Plankton' and 'Fish'. VI is lowest in benthos feeders (VI 0.02–0.11, mean ± SD 0.07 ± 0.03), fish feeders (VI 0.1, mean ± SD 0.1 ± 0) and benthos and fish feeders (VI 0.03–0.07, mean ± SD 0.05 ± 0.02), intermediate in mixed feeders of benthos and plankton (VI 0.02–0.28, mean ± SD 0.16 ± 0.07) and highest in species feeding almost exclusively on planktonic prey (VI 0.15–0.96, mean ± SD 0.56 ± 0.34) or on a mixture of plankton and fish (VI 0.28–0.77, mean ± SD 0.69 ± 0.20). The highest VI of 0.96 is found in the plankton-feeding *P. antarcticum,* followed by some channichthyid species such as *C. myersi* and *C. antarcticus* with VIs of 0.77 (see Table A1; Fig. 5). It appears that there is a certain accumulation of risk in the trophic group of plankton feeders. VI is correlated more strongly with $\sum$WP (Spearman's $r = -0.980$, $p < 0.0001$; Table 1) than to $\sum$WC ($r = 0.614$, $p < 0.0001$). In notothenioid fishes, differences in relative vulnerability VI between species are thus mainly determined by the number of prey items, that is, by the degree of generalism (see Table 1). The effect of predator diversity is of less significance, as most fish species share a similar number of potential predators that feed non-selectively.

Table 1 Spearman's rank correlations between relative trophic vulnerability index VI, weighted number of consumer species $\sum WC$ and weighted number of prey species $\sum WP$, with the functional prey groups benthos $\sum WP_B$, plankton $\sum WP_P$ and fish $\sum WP_F$

	VI	$\sum$**WC**	$\sum$**WP**	$\sum$**WP**$_B$	$\sum$**WP**$_P$
$\sum WC$	$r = 0.614$ $p < 0.0001$	–	–	–	–
$\sum WP$	$r = -0.980$ $p < 0.0001$	$r = -0.505$ $p = 0.0014$	–	–	–
$\sum WP_B$	$r = -0.861$ $p < 0.0001$	$r = -0.648$ $p < 0.0001$	$r = 0.817$ $p < 0.0001$	–	–
$\sum WP_P$	$r = -0.389$ $p = 0.0174$	$r = -0.469$ $p = 0.0034$	$r = 0.347$ $p = 0.0357$	$r = 0.490$ $p = 0.0021$	–
$\sum WP_F$	$r = 0.186$ ns	$r = 0.500$ $p = 0.0016$	$r = -0.101$ ns	$r = -0.436$ $p = 0.0070$	$r = -0.449$ $p = 0.0053$

For each parameter combination, correlation coefficient *r* and level of significance (*p* value) are given (ns, not significant, that is, $p > 0.05$). With respect to VI, *r* and *p* are interpreted as indicators of effect strength with signs indicating the direction of the effect.

Among functional prey groups, the number of benthic prey items $\sum WP_B$ exerts the strongest effect on VI ($r = -0.861$, $p < 0.0001$), followed by planktonic prey $\sum WP_P$ ($r = -0.389$, $p = 0.0174$). The number of fish species in the diet $\sum WP_F$ is not significantly related to VI ($p > 0.05$). The pattern of high benthic biomass and diversity on the high Antarctic shelf (see Section 2.2) is obviously reflected in notothenioid prey diversity and thus in trophic vulnerability: the number of benthic prey species $\sum WP_B$ exerts by far the strongest effect on VI; the higher the share of benthic species in the diet, the lower is VI (Table 1; Fig. 5).

The resilience of the entire system, that is, to what extent the extinction of particular consumer species from the system impacts overall food web stability and ecosystem functioning, strongly depends on the systems' ability to compensate for the loss by co-occurring species (Johnson, 2000; Naeem, 1998). As the majority of species include a certain proportion of benthic prey in their diet, functional redundancy seems to be high among benthos feeders (see Fig. 5). Feeding on the benthos is associated with a high degree of trophic generalism and functional redundancy, and hence with a certain capability to adapt food choice to prey availability and to dampen bottom-up effects. Plankton consumers tend to have higher vulnerability: specializing on a comparatively narrow prey spectrum makes them more sensitive to changes in prey availability. As there are fewer plankton-feeding species in the system, the potential for functional compensability is lower, too, making this part of the food web particularly sensitive to change.

Larvae and juveniles were not considered in this analysis because information on diet composition of early stages is not as complete as that of the adults for most species (except for *P. antarcticum*; see e.g. Granata et al., 2009; Kellermann, 1987; Vallet et al., 2011). However, as early stages of most notothenioids are pelagic, it is most likely that the relative trophic vulnerability is high compared with adult benthic stages. The number of potential predators ($\sum C$) is presumably size- (see Section 5.2) and/or density-dependent (e.g. Woodward et al., 2010b). Early stages of *P. antarcticum*, for example, occur in dense aggregations and are heavily preyed upon by other notothenioids (Eastman, 1985b; Hubold and Ekau, 1990; La Mesa et al., 2011). The degree of trophic generalism ($\sum P$) seems to differ strongly among families. Nototheniid larvae (including *P. antarcticum*) feed mainly on early copepod stages and eggs, whereas early juveniles feed on small copepod species. Compared with nototheniids, larvae and juveniles of the family Channichthyidae (e.g. *C. myersi*, *C. antarcticus*) are trophic specialists, with a narrow food spectrum that is exclusively composed of early developmental stages of krill and fish fry (Hubold and Ekau, 1990; Kellermann, 1986b, 1987, 1989). Accordingly, relative trophic vulnerability of larval and juvenile channichthyids is expected to be very high.

5.2. Vulnerability to changes in size structure and prey quality

5.2.1 Prey size

Body size is one of the major factors determining who eats whom in aquatic food webs (e.g. Brose et al., 2006; Castle et al., 2011; Woodward et al., 2005, 2010a,b). In particular for early developmental stages of fishes, the size of their prey seems to play an important role as the upper limit of consumable prey size is strongly limited by mouth width (Kellermann, 1986b, 1987). Accordingly, early stages always feed on a relatively narrow prey size range (Hubold and Ekau, 1990; Kellermann, 1986b). However, size of ingested prey is not only determined by morphological constraints but may also be the result of selective feeding behaviour. In postlarval and juvenile *P. antarcticum*, prey selection was found to be a function of prey density: at low food density conditions, larger prey species were selectively chosen, but when food density was high, size-selective feeding behaviour was distinctly less pronounced (Kellermann, 1986b, 1987).

There is also some evidence of size-selective feeding in adult *P. antarcticum*, with a negative selection of highly abundant small prey (K. Mintenbeck, unpublished data). However, whether this is the result of density-dependent selection (as observed in early stages) or due to other restrictions still needs to be verified.

In adult fish, mouth gape is less restrictive for prey handling than in larvae and juveniles, but sensory capabilities might be a limiting factor for efficient detection of small-sized prey. Depending on species' sensory capabilities, detection, capture success and feeding efficiency are likely to vary with prey size. To test for the impact of prey size on fish detection capability and feeding efficiency, feeding experiments with two nototheniid species were carried out during the expedition ANT/XXVII-3 with RV *Polarstern* in 2011.

N. coriiceps and *N. rossii* were caught by means of baited traps in February 2011 in Potter Cove. Both species belong to the family Nototheniidae and are common components of the inshore demersal fish fauna in waters of the northwestern Antarctic Península region (Barrera-Oro, 2003). Fishes were held unfed in large tanks at a water temperature of 0 °C for about 2 months prior to the experiments. Ten individuals were selected of each species (size ranges: *N. coriiceps* 24.2–33.6 cm standard length (SL), *N. rossii* 24.0–35.1 cm SL) and transferred into individual 85-l aquaria (0 °C water temperature, dim light conditions) 24 h before the feeding experiment started. Five different prey size classes were offered to each fish (prey size categories 1 (small) to 5 (large); see Table 2), starting with the smallest size category. Prey density was constant with 30 prey individuals per fish in all feeding trials. Times of first reaction, and each

Table 2 Food used in the feeding experiments to test for the impact of prey size on fish detection capability and feeding efficiency included five different prey size categories

Size category	Type	Size range [cm] (min–max)
1	Cyclopoid copepods	0.8–1.3
2	Daphnia	2.2–3.0
3	Mysids	9.2–14.5
4	Juvenile euphausiids	12.2–18.9
5	Adult euphausiids	27.9–33.5

Categories 1–4 were commercial frozen fish food (Erdmann Frostfutter, Germany) and category 5 was adult ice krill (*Euphausia crystallorophias*) caught during the RV *Polarstern* expedition. The food was defrosted prior to experiments.

Table 3 Number (*N*) of feeding individuals (*N. coriiceps* and *N. rossii*), and mean times (min:s; ± standard deviation) until first reaction to prey addition (movement of head towards prey), first detection of a prey item that was followed by an attack and first consumption are given for each prey size class (categories 1–5)

Prey category	*N* of feeding fish	First reaction	First prey detection	First consumption
Notothenia coriiceps				
1	0	–	–	–
2	0	–	–	–
3	6	2:12 ± 2:53	3:34 ± 3:50	3:36 ± 3:50
4	10	1:27 ± 3:21	1:47 ± 3:18	1:48 ± 3:17
5	10	0:10 ± 0:16	0:10 ± 0:16	0:12 ± 0:15
Notothenia rossii				
1	0	–	–	–
2	1	0:37	0:37	0:40
3	5	4:12 ± 6:04	4:12 ± 6:04	4:13 ± 6:04
4	9	1:18 ± 3:19	1:31 ± 3:16	1:34 ± 3:15
5	10	0:10 ± 0:08	0:10 ± 0:08	0:12 ± 0:07

particular prey detection and consumption were registered; overall experimental duration was 15 min. Depending on the amount of food consumed, the time lag between particular experiments was up to 3 days to avoid an effect of satiation on feeding behaviour. The offered food was not alive, but prey items were in motion in the tanks all the time owing to aeration and steady inflow of fresh seawater.

None of the fish fed on the smallest prey (category 1) and only one small *N. rossii* consumed a single prey item of category 2 (Table 3). Except for this single individual, no reaction to prey of categories 1 or 2 was observed. Both *N. coriiceps* and *N. rossii* started to react when prey of size category 3 was offered: a total of six *N. coriiceps* and five *N. rossi* detected and consumed prey of this category. All but one fish fed on size categories 4 and 5. Time until first reaction to prey addition (movement of the head towards prey), time of first prey detection that was followed by an attack and time of first consumption were all inversely related to prey size in both species (Table 3).

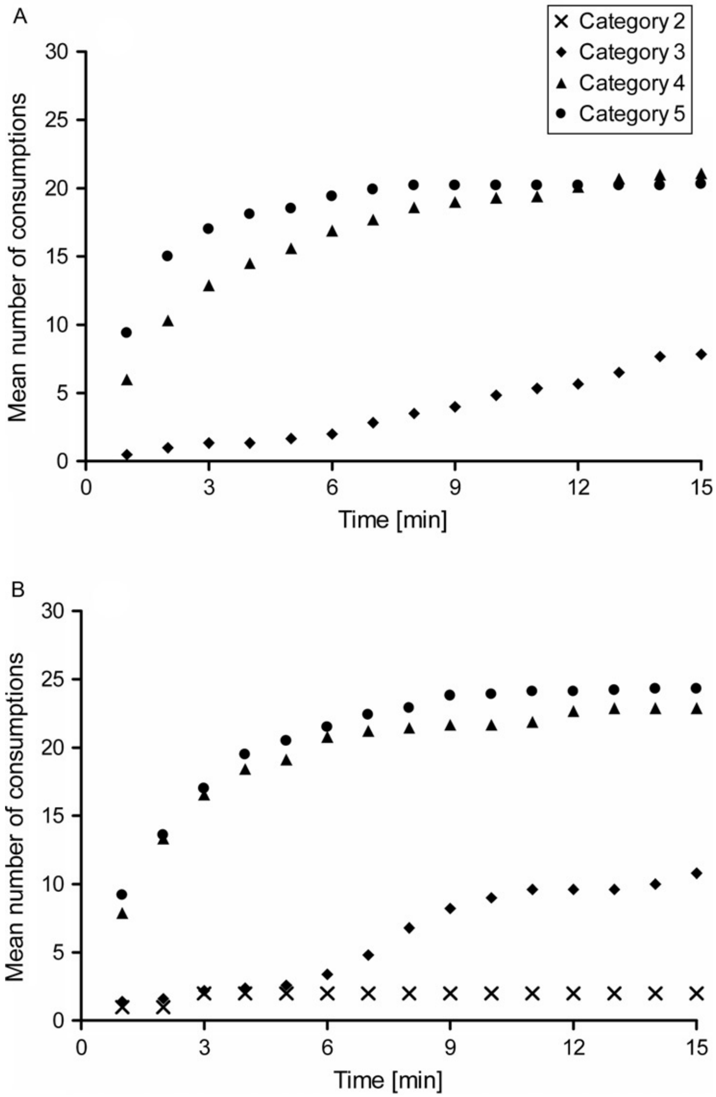


Figure 6 Mean consumption rate (number of consumptions × time^{-1}) in *N. coriiceps* (A) and *N. rossii* (B) depending on prey size category (2–5; 2: daphnia, 3: mysids, 4: juvenile euphausiids, 5: adult euphausiids). For the number (N) of feeding individuals, see Table 3.

The mean consumption rate (number of consumptions × time^{-1}) depended upon prey size category in both species (Fig. 6; Kruskal–Wallis ANOVA, *N. coriiceps*: $H = 29.45$, $p < 0.0001$; *N. rossii*: $H = 46.99$, $p < 0.0001$). The feeding rates were low when fish were offered size categories 2 and 3, and high for the two largest prey size categories. The feeding rates of fish offered the two small size categories (2 and 3) were significantly lower than the feeding rates of fish offered large prey (4 and 5; Dunn's post hoc test, $p < 0.01$), while no differences were found among the two small nor the two large categories (Dunn's post hoc test, $p > 0.05$). The mean time between detection and consumption was independent of prey size in both species (Kruskal–Wallis ANOVA, $p > 0.05$). Neither the total sum of consumed prey nor time until first reaction and mean time between detection and consumption were significantly correlated with fish size for any prey size category (Spearman's rank correlation, $p > 0.05$). However, the fish used in these experiments did not differ much in size, hence, further experiments using a broader range of fish sizes will be needed to verify the relationship between fish size and these parameters.

Nevertheless, these data clearly show that feeding rates depend strongly on prey size. Both species are obviously not capable (and/or willing) to attack small prey items and feeding efficiency is low below a certain prey size limit. This prey size-dependent detection and consumption rate are most likely not only found in these two species, but might be a limitation in many other Antarctic species (if not all).

5.2.2 Prey quality

The importance of prey quality for consumers is widely accepted, but only a few studies have dealt with this issue in fishes. Malzahn et al. (2007) found nutrient limitation of primary producers to propagate along the food chain, finally affecting condition of fish (larval herring *Clupea harengus*; condition assessed based on RNA/DNA ratios) feeding on herbivorous zooplankton. Based on the histology of the digestive organs, Koubbi et al. (2007) investigated the condition of larval *P. antarcticum* off Terre Adélie in relation to prey composition and found that larvae feeding on copepods were in better condition than those feeding on diatoms.

The energy contents of Antarctic and Sub-Antarctic species from various taxonomic groups are well studied (Ainley et al., 2003; Barrera-Oro, 2002; Clarke et al., 1992; Croxall and Prince, 1982; Donnelly et al., 1990, 1994; Eder and Lewis, 2005; Lea et al., 2002; Tierney et al., 2002; Torres et al., 1994) and are summarized in Fig. 7. Fishes and decapods have the highest energy contents; squid and crustaceans such as mysids, euphausiids and copepods have moderate energy contents. By far, the lowest energy content is found in gelatinous zooplankters such as salps, chaetognaths and cnidarians. Shifts in the zooplankton community with crustaceans being replaced by salps (see Section 1) thus involve a drastic decrease in energy density and nutritive value of prey for consumers such as fish.

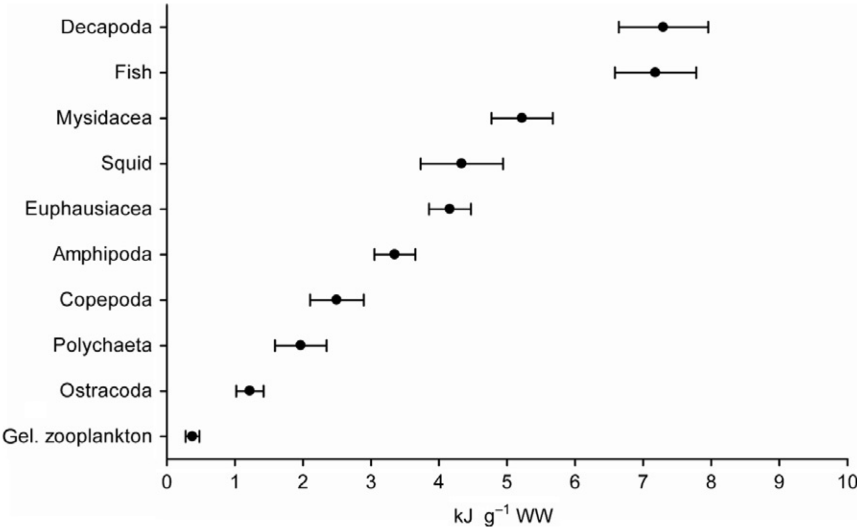


Figure 7 Energetic value (kJ g^{-1} wet weight; means ± SE) of Antarctic and Sub-Antarctic species belonging to several taxonomic groups (for details and data sources for each group, see Mintenbeck, 2008 and references therein).

Some species, such as *N. coriiceps*, feed on crustaceans (mainly krill and amphipods) and even on macroalgae (Iken, 1996; Iken et al., 1997). However, in feeding experiments, algae are only ingested in the absence of alternative animal prey (e.g. crustaceans; Fanta, 1999; K. Mintenbeck, unpublished data), providing evidence that macroalgae are not a favoured food source (see also Fanta et al., 2003). If krill is not available due to a shift in zooplankton composition, omnivorous fish species such as *N. coriiceps* might, however, be increasingly forced to feed on such low energy macroalgae.

Low energy food might affect survival, growth, body condition and reproductive output of consumers and ultimately might make fish species itself a low quality prey for its endothermic predators (see Österblom et al., 2006, 2008).

6. VULNERABILITY OF ANTARCTIC FISHES TO HABITAT DESTRUCTION

6.1. The impact of sea ice reduction

There is no doubt that a reduction in sea ice extent and duration of coverage due to climate-driven warming will affect the sympagic community living within the ice and invertebrates such as Antarctic krill, *E. superba*, whose life cycle is coupled to seasonal sea ice dynamics (see Moline et al., 2008 for review). However, there are also fish species whose life cycles and life styles are closely associated to the sea ice, namely *P. borchgrevinki* and *P. antarcticum*.

P. borchgrevinki is morphologically well adapted for a cryopelagic life (Eastman and DeVries, 1985) and is usually found closely associated with the underside of ice, where it frequently hides in crevices (e.g. Davis et al., 1999). Main prey items of this species include sympagic copepods (Hoshiai et al., 1989): sea ice thus provides the consumer with a habitat, refuge and feeding ground. Though *P. antarcticum* is usually found in the free water column, sea ice seems to be an important feeding ground for this species as well. Huge shoals of several thousand individuals have been observed feeding under the fast ice west off the Antarctic Peninsula (Daniels, 1982). The sea ice region is apparently also the spawning ground (La Mesa and Eastman, 2012) as the pelagic eggs were found floating under the sea ice (Vacchi et al., 2004). The reproductive cycle of *P. antarcticum* seems to be closely coupled to seasonal sea ice dynamics, and early stages depend on the temporal and spatial match with the seasonal zooplankton production (La Mesa and Eastman, 2012; La Mesa et al., 2010). The hatching period of *P. borchgrevinki* seems to be less strongly coupled to production peaks (Pankhurst, 1990), but both species are expected to be significantly affected by alterations in seasonal sea ice dynamics by loss of habitat/refuge and spawning ground and alterations at the base of the food web.

6.2. The impact of increased iceberg scouring

6.2.1 The role of habitat structure and disturbance events for species richness

For freshwater habitats (lakes and rivers) as well as for marine habitats, such as coral reefs and hard-substrate environments in the Mediterranean, a high diversity in habitat structures often promotes high species richness in the associated fish communities (Feld et al., 2011; Garcia and Ruzafa, 1998; Gratwicke and Speight, 2005; Guégan et al., 1998; Öhman and Rajasuriya, 1998). The benthic communities of the eastern Weddell Sea shelf in water depths between 200 and 450 m are characterized by a patchwork of structurally different successional stages; the two extremes are areas with a diverse epifauna forming the rich 3-dimensional habitat (Fig. 8A) on the one hand and desert-like areas with nearly no epibenthic fauna (Fig. 8B) on the other. This patchwork is the result of mechanical disturbance events by grounding icebergs, calving from the shelf ice and grounding at water depths between 200 and 500 m. This kind of

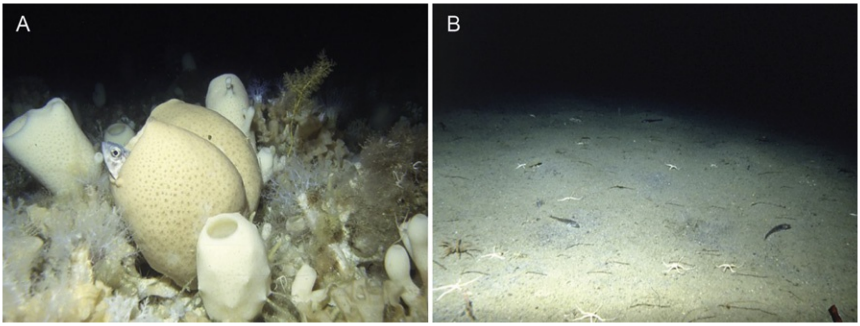
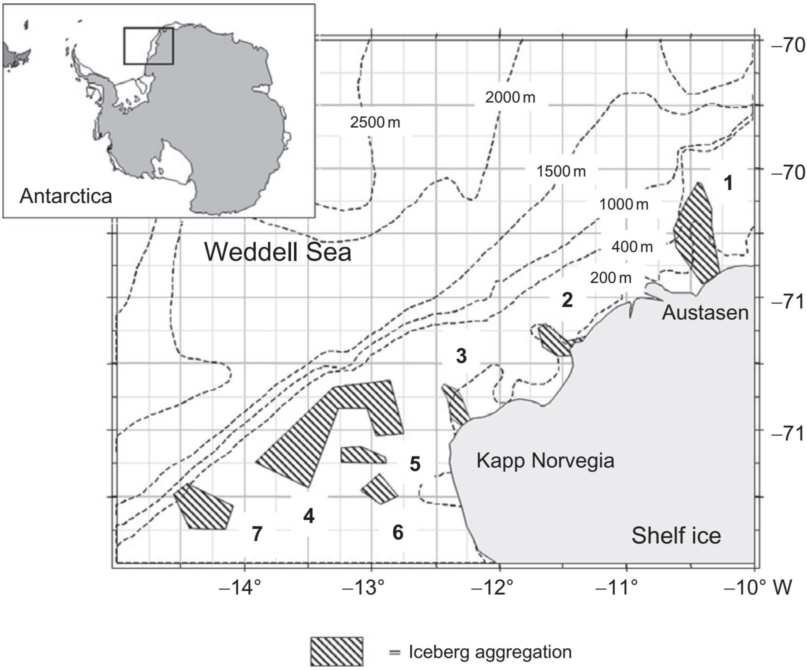


Figure 8 (A) Typical undisturbed site with a rich 3-dimensional habitat and *Trematomus* cf. *eulepidotus* hiding inside a large sponge; (B) Fresh iceberg scour habitat without any 3-dimensional megafauna species, only with a pycnogonid, some ophiuroids and *Prionodraco evansii*. Photos: ©Julian Gutt, AWI Bremerhaven.

disturbance by ice is a common phenomenon in polar regions and affects the sea floor up to a maximum water depth of 550 m (Conlan and Kvitek, 2005; Conlan et al., 1998; Gutt, 2001). Beside forest fires and hurricanes, iceberg scouring is one of the most significant natural physical perturbations imposed on ecosystems (Garwood et al., 1979; Gutt and Starmans, 2001; Peck et al., 1999) and is considered to be one of the strongest physical forces structuring the benthic environment in polar regions (Gutt and Piepenburg, 2003).

In the area of Austasen and Kapp Norvegia (eastern Weddell Sea), about 7% of the coastal zone (< 400 m) is covered by iceberg aggregations (Fig. 9; Knust et al., 2003). Gutt and Starmans (2001) analyzed video and photo material from this area and calculated that 42–70% of the sea bed is affected by iceberg scouring (Fig. 10). Depending on sea floor morphology, nearly 10–40% of the area showed young scour marks or early recolonization stages. On a smaller (local) scale, these iceberg disturbances completely destroy most of the in- and epifauna. However, on a regional scale, the sea floor destruction by icebergs creates new space for pioneer species that are specialized in recolonization (Gerdes et al., 2008; Teixidó et al., 2004), and the patchwork of structurally different successional stages increases the overall gamma diversity (Gray, 2000). Following the Intermediate Disturbance Hypothesis, which predicts a high diversity caused by intermediate levels of disturbance (Huston, 1979), Gutt and Piepenburg (2003) calculated an increased species diversity for the epibenthic megafauna on a regional scale (1–100 km) due to iceberg disturbances.

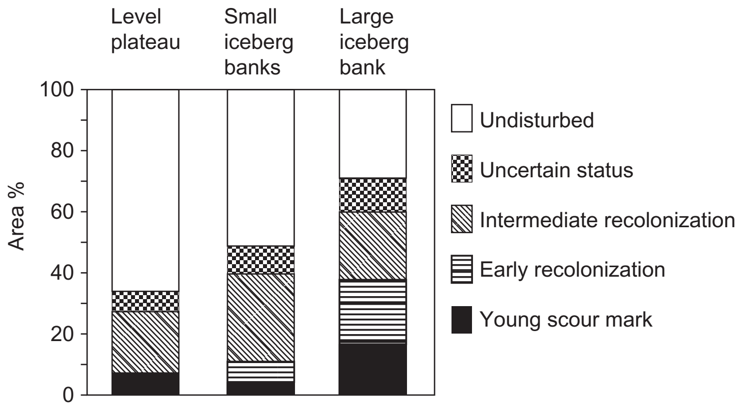
However, iceberg scouring not only affects benthic organisms, but also the demersal fish fauna, the composition of which differs significantly



1 : 29.0 × 11.5 km = 334 km²
2 : 10.4 × 4.6 km = 48 km²
3 : 12.3 × 3.9 km = 48 km²
4 : 41.8 × 14.4 km = 602 km²
5 : 12.5 × 4.2 km = 53 km²
6 : 7.2 × 5.9 km = 43 km²
7 : 16.0 × 10.1 km = 162 km²

Figure 9 Iceberg aggregations on the high Antarctic shelf off Austasen and Kapp Norvegia (eastern Weddell Sea) in March 2000 *(redrawn from Knust et al., 2003; with permission from Backhuys Publishers).*

between undisturbed and recently disturbed sites, with higher species richness and a higher diversity (Shannon's diversity) in undisturbed areas, and in species identity (Fig. 11; Knust et al., 2003). Some species, such as *Trematomus scotti*, *C. antarcticus*, *Pagetopsis maculatus* and *Artedidraco loennbergi*, are typical members of the fish community in undisturbed areas, while *T. pennellii*, *Trematomus nicolai* and *Prionodraco evansii* are specialized to live at disturbed sites. Iceberg disturbance events play a key role in small-scale niche separation of fishes, as the structurally different habitats allow for the coexistence of trophically similar species (Brenner et al., 2001; Hagen et al., 2012; Ptacnik et al., 2010).



			Areas analyzed
130	322	88	No.
12.3	21.2	16.5	Transect length (km)

Figure 10 Proportions of different recolonization stages at different morphological condition in the shelf area off Austasen and Kapp Norvegia (eastern Weddell Sea) *(redrawn from Knust et al., 2003, based on data from Gutt and Starmans, 2001; with permission from Backhuys).*

In view of climate change, the major questions are (i) whether the pattern of increased diversity at intermediate disturbance levels found for benthic megafauna (e.g. Gutt and Piepenburg, 2003; see above) does also hold true for the demersal fish community and (ii) how diversity and community structure will respond to increased disturbance events. To answer these questions, we analyzed the relationship between the level of disturbance events and the gamma diversity of the demersal fish fauna on the eastern Weddell Sea shelf using a simple simulation model.

6.2.2 The disturbance simulation model

The calculations of the model are based on abundance data from several bottom trawls (standard otter trawl, 20-mm mesh in codend) taken in undisturbed and disturbed areas off Austasen and Kapp Norvegia (eastern Weddell Sea) during four expeditions between 1996 and 2004. The position of iceberg scours was identified by side scan sonar, ROV underwater video and underwater photography. The composition of invertebrate by-catches of the otter trawls was used as an indicator for the degree of disturbance. In particular, the presence/absence of large, old hexactinellid sponges indicated the disturbance level of the sea floor (Gerdes et al.,

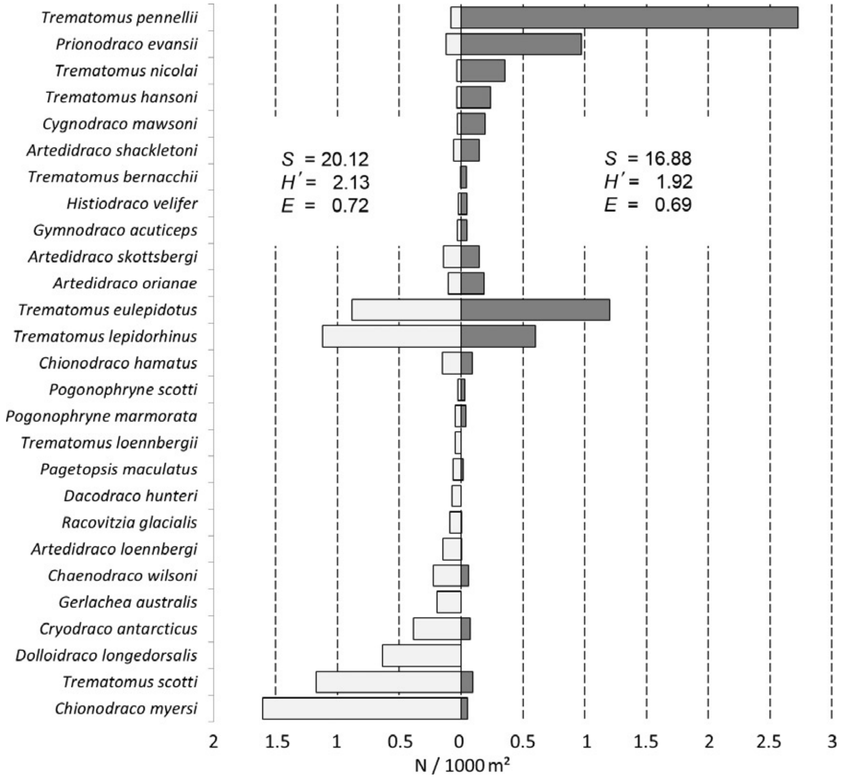


Figure 11 Mean abundance (N/1000 m^2) of the dominating fish species in undisturbed areas and on young iceberg scours (recalculated with data from Knust et al., 2003; R. Knust and K. Mintenbeck, unpublished data). For both communities, average number of species (*S*), average Shannon diversity (*H*′) and average evenness (*E*) are given.

2008; Knust et al., 2003). Overall 30 stations were sampled, 22 in undisturbed areas and 8 in disturbed areas. Fish abundance data were calculated based on 1000 m^2 swept area.

To simulate different disturbance levels, the abundance data of each catch from disturbed and undisturbed areas were randomly combined in a 200 station matrix by a Monte Carlo simulation. To simulate a completely undisturbed situation (disturbance level 0.0), data from exclusively undisturbed stations were randomly combined. The disturbance level 1.0 (the entire shelf is disturbed) was simulated by a random combination of catches from exclusively disturbed areas. For a disturbance level of 0.05 (5% of the shelf area is disturbed by iceberg scouring), 5% of the 200 stations in the matrix were filled with abundance data from disturbed stations and 95%

were filled with abundance data from undisturbed station. The stations were randomly selected. The disturbance level was increased in 0.05 steps. For each disturbance level, 100 iterations of random combination were computed.

For each disturbance level, the averages of total number of species (S), gamma diversity (Shannon's diversity, H') and evenness (Pielou, E) were calculated:

$$H' = \sum_{i=1}^{S} p_i \cdot \ln(p_i) \qquad [3]$$

where $p_i = n_i/N$, with n_i is the abundance of species i and N the sum of all individuals;

$$E = \frac{H'}{H'_{\max}} \qquad [4]$$

where $H'_{\max} = \log_2(S)$. To avoid an oversized effect of very rare species on the total number of species, only species with an abundance of >0.001 individuals per $1000\ \mathrm{m}^2$ were taken into account for each combination.

The results of the Monte Carlo simulation are shown in Fig. 12. The results of the different catch combinations were fitted to a univariate, second-order polynomial (solid line), the dots represent the particular results of each combination. All three parameters increased with increasing disturbance level up to a maximum between disturbance values of 0.25–0.40, representing 25–40% of the shelf area disturbed by icebergs. Average species richness was highest (57.9 species) at a disturbance level of 0.25, average gamma diversity was highest ($H' = 2.80$) at a level of 0.34 and average evenness (0.69) was highest at a disturbance level of 0.40.

The comparison of these results with the estimated disturbance level on the shelf of the eastern Weddell Sea (Gutt and Starmans, 2001; see above) shows that the fish fauna on the eastern Weddell Sea shelf is obviously well adapted to this kind of mechanical disturbances and to the average level of disturbance occurrence there. The gamma diversity (and evenness) of the fish fauna is highest at the disturbance level we find nowadays, but rapidly decreases at higher levels according to the model predictions. Future climate scenarios suggest an increasing rate of iceberg calving in the shelf ice areas of Antarctica, with an enhanced risk of iceberg groundings and an increasing disturbance level in the benthic communities.

Such a reduction in habitat structure and heterogeneity means on the one hand a reduction of habitat and refuge for demersal fishes (e.g. Moreno et al.,

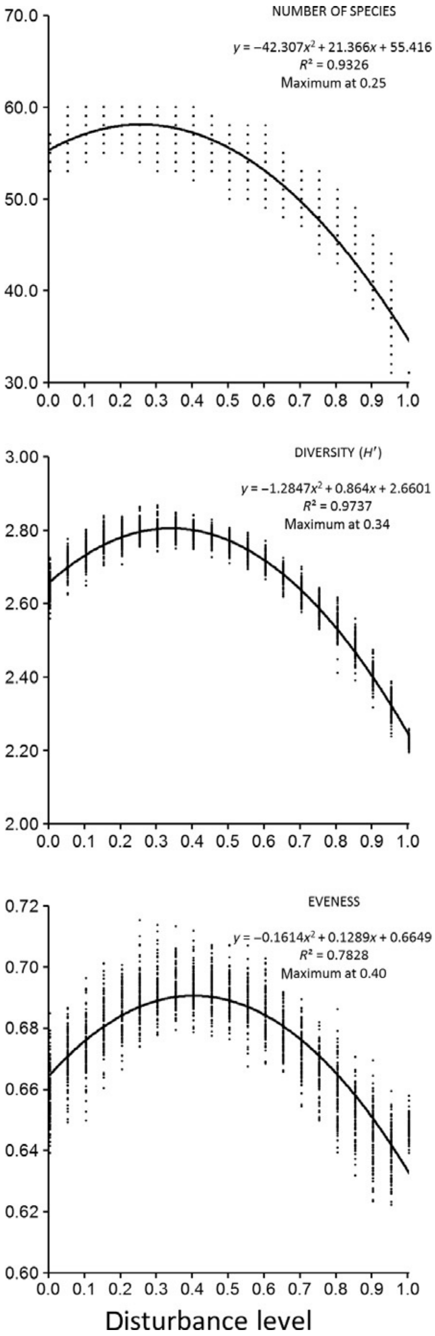


Figure 12 Results of the Monte Carlo simulation: total number of species, gamma diversity (*H′*) and evenness (*E*) of the demersal fish community depending on disturbance rates. The calculations are based on fish abundance data from disturbed and undisturbed areas on the eastern Weddell Sea shelf (R. Knust and K. Mintenbeck unpublished data).

1982), with an increased predation risk for all developmental stages. On the other hand, a reduction in habitat diversity will result in an increased competition among species with overlapping trophic niches, which at the present disturbance level perfectly avoid competition by small-scale niche separation (Brenner et al., 2001). If the disturbance level increases in the future, a loss in species diversity seems to be inevitable.

7. DISCUSSION

7.1. The impact of climate change on Antarctic fish species

Notothenioid fishes are well adapted to their habitat, and alterations in the abiotic environment directly affect physiological functions. Increasing water temperatures, particularly in combination with ocean acidification, pose a major thread to the persistence of notothenioid fishes. Some species such as *P. borchgrevinki* and *Notothenia* spp. show some physiological plasticity and are able to compensate for increasing oxygen demand, for example, by mitochondrial proliferation and/or increased haematocrit. However, these compensatory mechanisms are limited and most notothenioid species are in fact stenothermal and are not capable to adjust metabolic functioning. Channichthyids are highly vulnerable to changes in the abiotic environment as they lack any capacity to adjust blood parameters to an increasing oxygen demand. Early developmental stages as well seem to be highly vulnerable to all kinds of abiotic alterations, including salinity.

General vulnerability to changes in food web structure and dynamics was analyzed using a conceptual approach, with a quantitative measure (VI) that served as an indicator of the risk of consumer species to be negatively affected by such changes. Relative trophic vulnerability was found to be low in all fish species that include a certain proportion of benthic organisms in their diet. Obviously, feeding on benthos goes along with a high degree of trophic generalism and, hence, with a certain capability to adapt food choice to prey availability and to dampen bottom-up effects. Plankton consumers displayed a distinctly higher vulnerability, as these species tend to specialize on a comparatively narrow prey spectrum, which makes them more sensitive to changes in prey availability. Thus, there exists an accumulation of risk in the trophic group of plankton feeders, making this part of the food web particularly sensitive to change. Highest trophic vulnerability was found in channichthyids, such as *C. myersi*, *C. antarcticus* and *P. maculatus*, which are all specialized on very few prey items, and in the nototheniid *P. antarcticum*, which not only has a narrow food spectrum but is additionally exploited by a multitude of predators. Relative trophic vulnerability of plankton-feeding larvae and early juveniles is expected to be very high, as well.

Trophic vulnerability to shifts in prey size was investigated in two fish species, *N. coriiceps* and *N. rossii*. In the two species studied, feeding efficiency and prey detection capability were found to strongly depend upon prey size, with a complete detection failure (or ignorance) of smallest prey. However, the general susceptibility to prey size shifts might differ among species and age/size classes. As large fish species/individuals usually have a larger size range of available prey than small species/specimens, large fish are expected to be less susceptible to shifts in prey size compared with small fish. Trophic vulnerability to shifts in energy content is likely similar for most fish species. Nutritive value varies strongly among taxonomic groups, with lowest energy contents found in gelatinous zooplankton. Salps with their guts filled with fresh phytoplankton are a valuable food source for some Antarctic benthic suspension feeders, which usually depend on more or less degraded POM (Gili et al., 2006). Nevertheless, in comparison with other zooplankton species such as decapods, euphausiaceans and copepods, their nutritive value for fishes is extremely low. Prey of inappropriate size and/or quality affects the nutritional status and condition of fishes (see also Beaugrand et al., 2003; Koubbi et al., 2007; Malzahn et al., 2007), and in the worst case even survival.

The loss of habitat poses a threat to the majority of Antarctic fish species. There is no doubt that a reduction in sea ice extent and duration due to climate-driven warming will particular affect the life stages of those fish species that are strongly associated with sea ice, namely *P. borchgrevinki* and *P. antarcticum*. Habitat structure and heterogeneity are of particular importance for the demersal fish community because their loss would imply a loss of refuge and shelter for juveniles, adults and eggs (see Barrera-Oro and Casaux, 1990; Moreno, 1980; Moreno et al., 1982), with the consequent increase in competition among trophically similar species (e.g. Brenner et al., 2001). Model simulations based on abundance data indicated that an increase in ice scouring will lead to a steep decrease in diversity and evenness, and to the loss of species.

7.2. Effects of climate change in other marine systems

In general, the changes detected so far in the South Polar Sea resemble many of those observed on a worldwide scale. The world's oceans are warming, atmospherical pCO_2 is rising, leading to potential ocean acidification

(IPCC, 2007), and seawater salinity is decreasing in the vicinity of melting ice and glaciers (e.g. Curry and Mauritzen, 2005). Fishes, for example, in temperate regions, have been shown to be significantly affected at the physiological level, in particular by increasing water temperatures, resulting in reduced growth performance, recruitment and abundance (e.g. Pörtner and Knust, 2007; Pörtner et al., 2008; Sirabella et al., 2001). In response to such environmental alterations, several fish species have already shifted their distributional ranges and have migrated into waters with more favourable conditions (Dulvy et al., 2008; Perry et al., 2005).

The risk of habitat loss and alteration of habitat structure and heterogeneity due to sea ice retreat (Stroeve et al., 2007) and increasing occurrence of iceberg scouring events (Conlan et al., 1998; Gutt et al., 1996) is comparable in the Arctic Ocean. Invasion by lithodids as observed west of the Antarctic Peninsula is also found in the northern hemisphere. The most popular example is the red king crab (*Paralithodes camtschaticus*), which was introduced into the Barents Sea and subsequently invaded Norwegian waters. In the presence of these invaders, benthic biomass and diversity is drastically reduced; these crabs thus remove potential prey for benthos feeding fish species and even prey upon fish eggs (reviewed in Falk-Petersen et al., 2011).

Alterations in plankton community composition due to climate forcing are common in many ecosystems and often include a shift from larger to smaller phytoplankton (Yvon-Durocher et al., 2011) and zooplankton species, in particular in copepods (e.g. in the North Sea, Beaugrand et al., 2003; Helaouët and Beaugrand, 2007; and in the Humboldt Current ecosystem reviewed in Alheit and Niquen, 2004). Substantial increases in gelatinous zooplankton have been observed in different marine systems in recent years (e.g. Attril et al., 2007; Brodeur et al., 1999; Purcell, 2005). High abundances of gelatinous zooplankton are often related to water temperature and salinity, suggesting that population density of gelatinous zooplankton will further increase under future climate change scenarios (reviewed in Purcell, 2005). In the central North Sea, the occurrence of jellyfish was also negatively correlated with seawater pH, thus, future levels of CO_2 may synergistically promote the presence of gelatinous zooplankton (Attril et al., 2007). Gelatinous zooplankton prey upon fish eggs and larvae (Doyle et al., 2008; Purcell, 1985) and also represent strong competitors for plankton-feeding fish by efficiently removing potential prey, such as copepods (Purcell and Decker, 2005) or euphausiids (Suchman et al., 2008). Some gelatinous zooplankton such as salps or ctenophores are occasionally consumed by fishes (including notothenioids), but appear to be a form of 'survival food' when preferred zooplankton prey are not abundant (Kashkina, 1986; Mianzan et al., 2001).

Taking a closer look at the effects of climatic shifts in the world's oceans, an intriguing pattern seems to emerge: the most severe (or most rapid) effects of climate forcing on marine biota appear to be found within pelagic communities (Alheit, 2009; Alheit and Niquen, 2004; Alheit et al., 2005; Arntz, 1986; Beaugrand et al., 2003; Benson and Trites, 2002). These observed changes in the pelagic realm are not restricted to one or two trophic levels, or to specific species, but usually involve strong alterations in food web structure and ecosystem functioning and dynamics. In the central Baltic and the North Sea (Alheit et al., 2005; Beaugrand et al., 2003), in the Bering Sea and the North Pacific (Benson and Trites, 2002) as well as in the Humboldt Current ecosystem (Alheit and Niquen, 2004; Arntz, 1986; Arntz and Fahrbach, 1991), all trophic levels in the pelagial, from primary producers to apex predators, were affected by direct and/or indirect climate forcing. In particular, pelagic fishes with short plankton-based food chains, such as clupeids, may undergo strong fluctuations in stock density (Alheit and Niquen, 2004), with severe consequences for their endothermic consumers (e.g. Alheit, 2009; Arntz, 1986; Cury et al., 2000).

To our knowledge, there are no reports on such extensive severe effects of climatic shifts on benthic biota, suggesting that they are less affected, but whether this is really a common pattern or just due to a greater focus on the pelagic realm still needs to be verified.

Overall, the general effects of climate forcing and the potential direct and indirect impact on marine living communities thus appear to be similar in the South Polar Sea compared with marine systems worldwide. Nevertheless, there are some significant differences: (i) fishes inhabiting temperate and tropical regions often have the opportunity to emigrate into waters with more favourable abiotic and biotic (prey) conditions (see Arntz, 1986; Dulvy et al., 2008; Perry et al., 2005). For notothenioid fishes, particularly for high Antarctic species, emigration is strongly limited by stenothermy and the lack of alternative habitats, as they are already living at the highest latitudes. (ii) Fish species such as clupeids in upwelling systems are evolutionarily adapted to strong environmental fluctuations by possessing traits associated with fast growth (Cubillos et al., 2002) and high fecundity (Alheit and Alegre, 1986), both facilitating population recovery after stock decline. In tropical reef fish, a rapid transgenerational acclimation to increasing water temperatures has also been observed (Donelsen et al., 2012). In contrast, notothenioid fish species are characterized by slow development rates and low fecundity, and their recovery potential is thus strongly limited. Due to the low recovery capacity, even a modest increase in the amplitude of interannual climate fluctuations could affect long-term population dynamics of notothenioid fish, with ramifications that would ripple through the wider food web. Given the rate of alterations due to climate change observed off the Antarctic Peninsula and fish species' life history characteristics, an evolutionary adaptation of notothenioid fishes that keeps pace with the rate of change in conditions is unlikely, if not impossible (see Somero, 2010).

7.3. Antarctic fish community persistence—Winners and losers

Given the current state of knowledge, it is unlikely that there will be any true 'winners' of climate change among notothenioid fish species. There will be only 'survivors' and many 'losers'. *P. borchgrevinki*, for example, might be among the survivors in a changing South Polar Sea as this species is characterized by relatively high metabolic plasticity and a wide thermal tolerance window (Robinson and Davison, 2008), and low trophic vulnerability. But still, *P. borchgrevinki* is threatened by habitat reduction owing to retreat of sea ice and so far it is unknown whether this species can cope with loss of its ice habitat. Demersal fish species (except for plankton-feeding channichthyids) show low relative trophic vulnerability, but will be significantly affected by the loss of habitat structure and diversity. Which species will ultimately survive and which will not in the long run depends on a combination of species-specific physiological and trophical plasticity, and population dynamics, in addition to higher-level food web effects. Trophic plasticity is apparently high in benthos feeders, but acclimation capacity seems to differ strongly among species: some, such as *N. rossii*, possess partially compensatory mechanisms (A. Strobel and F.C. Mark, unpublished data), whereas the potential for acclimation is apparently low for many others (e.g. high Antarctic Trematomus spp.; Robinson, 2008). However, which demersal species exactly will be lost due to habitat loss on the high Antarctic shelf remains unknown for now. Population dynamic parameters such as relative fecundity and growth rate are rather similar among most demersal high Antarctic notothenioids (e.g. Kock and Kellermann, 1991; La Mesa and Vacchi, 2001), but much more work is needed on the effects that changes in the abiotic environment exert on population dynamics.

Icefishes, however, are one group that will almost certainly be on the losing side in a warming South Polar Sea with increasing levels of CO_2, as the oxygen-carrying capacity of their blood is limited, and there is no potential for physiological acclimation to satisfy the increasing tissue oxygen demand. Moreover, many channichtyids, such as *C. myersi*, are specialist consumers with a high relative trophic vulnerability, making this group additionally susceptible to changes in food web structure and dynamics. Another potential 'loser' which is affected by direct and indirect effects of climate change is the currently dominant pelagic species, *P. antarcticum*, which will be most likely affected by sea ice reduction. It also seems to be highly vulnerable to alterations in the food web, and indirect evidence suggests that at least larvae and juveniles are highly vulnerable to abiotic changes. Theoretically, all fish species are threatened by a shift in prey size structure and a decrease in prey nutritive value. However, the pelagic realm in the South Polar Sea (and elsewhere) will likely be among the first to react to climate fluctuations, and the shifts in question have thus so far only been observed in the plankton community. Plankton consumers are, therefore, especially vulnerable. Shifts in size distribution from large to small phytoplankton organisms in the marine Antarctic (as observed west off the Antarctic Peninsula; Moline et al., 2004) will thus most likely favour the prevalence of small zooplankton species, such as cyclopoid copepods (as observed in other marine systems). Given the size dependency of prey detection and feeding efficiency in notothenioid fish, it is questionable whether plankton consumers such as *P. antarcticum* but also icefish can cope with such a prey size shift. Feeding on low quality 'survival food' such as salps is not a suitable alternative to energy-rich crustaceous zooplankton in the long run. In particular, at the edge of their thermal tolerance window, fish species will be highly sensitive to such additional stressors.

However, the major bottleneck for the persistence of most (if not all) species' populations is most likely the survival of early developmental stages. Eggs and larvae appear particularly sensitive to alterations in the abiotic environment, some might be affected by sea ice reduction (e.g. early stages of *P. antarcticum*), and larvae and juveniles are apparently vulnerable to indirect food-web-mediated effects of climate change. For non-Antarctic pelagic larval fish, three key parameters were identified: prey abundance, prey type and seasonal timing (Beaugrand et al., 2003). Shifts in any of these three parameters might significantly compromise larval condition and survival. Most notothenioid larvae depend on seasonal timing as well (Efremenko, 1983; La Mesa and Eastman, 2012; La Mesa et al., 2010), and the capacity to avoid a mismatch depends on species' plasticity in their reproductive cycle. In some species, a certain plasticity to adapt the reproductive cycle might exist, as indicated by differences in spawning time among populations in different locations (see Kock and Kellermann, 1991), but it is unknown whether all species are able to adapt their reproductive cycle and by which factors the timing is triggered. Without offspring sustaining the stocks, populations will progressively age and density will inexorably decline.

So far, our knowledge on species-specific vulnerability, potential plasticity, and acclimation and/or adaptation potential is still limited. However, based on what we already know from the Antarctic and from what we can observe in other systems, we can at least identify some potential bottlenecks. Nevertheless, there is an urgent need for more experimental studies on a broad range of species to gain a cause-and-effect understanding of the consequences of the potentially complex interactions between abiotic and biotic mechanisms (Woodward et al., 2010a).

7.4. Consequences of fish species loss for the marine Antarctic ecosystem

Fishes of the South Polar Sea will be affected by climate change in multiple ways, with the potential vulnerability and mechanisms differing among species, developmental stages and habitats. What we know about the effects of climate change and the vulnerability of Antarctic fish species leaves little doubt that the population density of many species will decline and some species will go extinct in the long run. The resilience of the entire system, that is, to what extent the decline or extinction of particular notothenioid fish species from the system impacts overall food web stability and ecosystem functioning, depends strongly on the species' functional role and the systems' ability to absorb for the loss by compensatory mechanisms among co-occurring species (Johnson, 2000; Naeem, 1998).

In the South Polar Sea, demersal fish communities are characterized by relatively high species richness in comparison with the very limited diversity of the pelagic ichthyofauna. The majority of demersal fish species are opportunistic generalist consumers with high trophic niche overlap, indicating a high functional redundancy. It is therefore likely that within the demersal community, the decline or loss of some species can be compensated for by others. However, the model on the impact of disturbance events on demersal fish communities indicated not only a future decrease in species number but also in evenness. Thus, one or a few species might become extremely dominant, and the impact of such an alteration in community composition on overall ecosystem functioning ultimately depends on a species' identity, its specific traits and its potential to serve as valuable prey for top predators. As the role of demersal fish as a food source for endothermic predators is more important in inshore compared to offshore areas (Barrera-Oro, 2002), the effects of alterations in the demersal community on fish consumers might be stronger in shallow coastal zones. In inshore waters of the South Shetland Islands, for example, *N. coriiceps* proliferated and became the dominant demersal fish species after the stocks of the demersal *N. rossii* and *G. gibberifrons* were drastically diminished in the early 1980s due to anthropogenic actions (Barrera-Oro et al., 2000; see Section 7.5 below). Simultaneously, the breeding populations of one of their most important consumers in this area, the Antarctic shag *Phalacrocorax bransfieldensis*, now mainly preying upon *N. coriiceps*, steadily declined. Thus, though *N. coriiceps* is similar to *N. rossii* and *G. gibberifrons* in terms of ecology and body size, it could apparently not fully compensate for the reduction of the two fish species within the food web (Casaux and Barrera-Oro, 2006).

The extent to which the loss of channichthyids such as *C. myersi* or *C. antarcticus* can be compensated by other fish species is not clear. Channichthyids feed almost exclusively on krill and fish (reviewed in Hureau, 1994; Kock, 2005a; La Mesa et al., 2004). While a multitude of other fish species also feed on krill, true piscivores are rare among other notothenioids (e.g. Hureau, 1994). Some species occasionally feed on fish (see Fig. 5; La Mesa et al., 2004) but to a much lesser extent compared to channichthyids. Hence, the loss of channichthyids from the system might release some fish populations from top-down control. Though icefish are an abundant component in Antarctic fish communities, they seem to be of minor importance in the diet of endothermic predators, but their importance increases regionally when other prey, such as krill, is scarce (Kock, 2005a,b and references therein). Compared with most other notothenioids, adult channichthyid fishes are large and show only weak escape responses (authors' personal observation from ROV videos), making them an easy-to-catch prey for large consumers. At our current state of knowledge, we can only speculate, but it is likely that the loss of channichthyids will have detrimental effects on many components of the Antarctic marine food web.

The pelagic fish community is composed of very few species only, and the whole community is dominated by a single fish species, *P. antarcticum* (see above), which on the high Antarctic shelf seems to occupy a similar ecological key role in the food web as Antarctic krill in the seasonal sea ice zone

(Hubold, 1992; Hureau, 1994; La Mesa et al., 2004; Takahashi and Nemoto, 1984). It is one of the principal consumers of zooplankton, and all developmental stages are among the most important food sources for a multitude of predators, in particular for endotherms inhabiting Antarctic shelf areas (e.g. Daneri and Carlini, 2002; Hureau, 1994; La Mesa et al., 2004; Plötz, 1986). This pelagic fish species occurs in loose shoals (Eastman, 1985a; Fuiman et al., 2002) and undertakes nocturnal migrations into upper water layers (K. Mintenbeck and R. Knust, unpublished data; Plötz et al., 2001), where it provides a rich and easily accessible food source. It is thus of critical importance in the Antarctic marine food web. No other species, neither other pelagic notothenioids nor invertebrates (e.g. squid or krill), may be able to provide full functional compensation in the case of its extinction or reduction of the stock, in particular because none combines a pelagic shoaling life style and vertical migration with a comparable size spectrum and energy content (see e.g. Ainley et al., 2003). In its appearance (Fig. 13) and life style, as well as in its central role in a relatively simply structured and highly productive pelagic system, *P. antarcticum* strongly resembles shoaling clupeid fishes in upwelling systems (see Section 7.2 above).

Figure 13 Catch of *Pleuragramma antarcticum* in the eastern Weddell Sea (Photo by J. Plötz, AWI Bremerhaven).

In the eastern South Pacific, for example, El Niño events involve strong reductions in stocks of anchovy and sardine (owing to direct and indirect climate forcing in combination with fisheries effects), causing starvation and mortality in the very top predators, birds and seals (e.g. Arntz, 1986). But life history traits of clupeids and the nototheniid *P. antarcticum* (see Table 4) and recovery potential differ significantly: population doubling time was estimated to be often less than 15 months in clupeid fish species and 5–14 years in *P. antarcticum* (Froese et al., 2002), making populations of the latter extremely vulnerable to any kind of disturbance or systemic shifts.

Nevertheless, seals and penguins do not depend exclusively on pelagic prey but also prey upon demersal fishes (e.g. Casaux et al., 2006; Coria et al., 2000; Plötz et al., 1991). In many high Antarctic shelf areas, exploitation of this resource requires deep diving. Though Weddell seal and Emperor penguin are both excellent divers (Burns and Kooyman, 2001; Wienecke et al., 2007), exploitation of fishes at great depth is energetically disadvantageous for these air-breathing endothermic predators as it involves an increased swimming effort, shorter times at feeding depth, and/or longer dives followed by longer recovery phases (Kooyman, 1989; Kooyman and Kooyman, 1995; Wilson and Quintana, 2004). Moreover, foraging efficiency is higher in shallow dives (Croxall et al., 1985), while encounter rates are probably lower in light-depleted deep waters, as indicated by a lower number of feeding events at depth (see Liebsch et al., 2007; Plötz et al., 2005). Hence, declining stocks or complete loss of *P. antarcticum* will in either case severely affect the top predators in the Antarctic marine ecosystem.

Table 4 Life history traits of clupeid fishes (sardines and anchovies) and the nototheniid *P. antarcticum*

	Clupeids	***Pleuragramma antarcticum***
Von Bertalanffy growth constant *K*	0.5–0.8[3]	0.05–0.07[5]
Age at first spawning (years)	1–1.5[2,8]	7–9[7]
Relative fecundity (eggs g^{-1} wet weight)	550–600[1]	70–160[4]
Duration of larval phase (days)	~37–74[6]	180–365[5]

Data sources are indicated by superscripts: [1]Alheit and Alegre (1986), [2]Cubillos and Claramunt (2009), [3]Cubillos et al. (2002), [4]Gerasimchuk (1988), [5]Hubold and Tomo (1989), [6]Houde and Zastrow (1993), [7]Kock and Kellermann (1991) and [8]Whitehead (1985).

What are the future perspectives for Antarctic fish communities? There is no doubt that fishes still will be an important and abundant component of the Antarctic marine ecosystem in the future, but the composition of communities will change significantly in the long run. It is likely that, with an ongoing warming trend, Sub-Antarctic demersal fish species such as *Notothenia* spp. (but also non-notothenioids) will move southwards into high Antarctic shelf areas, taking over the role of extinct or declining species in the present-day food web. Possible future scenarios for the pelagic community are the occupation of the 'small pelagic zooplankton feeder' niche by myctophid fishes or by clupeids such as the Falkland sprat, *Sprattus fuegensis*. Whether myctophids or clupeids can effectively replace *P. antarcticum* in its functional role in the food web, however, remains to be seen.

7.5. Final thoughts—Is climate change exclusively to blame?

Though our knowledge is steadily improving, we are in fact just starting to comprehend the structure, dynamics and functioning of the Antarctic marine ecosystem, while the system apparently has already started to respond to climate change. This, however, is not the only threat to marine living communities in the South Polar Sea, and human activities have already caused significant alterations in the past and still affect Antarctic communities today. Commercial fisheries in the Antarctic started in the late 1960s/early 1970s (see Kock et al., 2007 for review), and the destructive impact of bottom trawling on benthic communities is comparable to the impact of iceberg scouring (discussed in Barnes and Conlan, 2007). Commercial sealing and whaling activities in the South Polar Sea in the nineteenth and twentieth centuries (see Kock, 2007; Laws, 1977) resulted in large-scale and long-term alterations of food web structure and population dynamics of prey and competitors (Ainley et al., 2007, 2010; Laws, 1985). Industrial exploitation of Antarctic fish species (and krill) between the 1970s and 1990s resulted in dramatic stock decreases and rapid overexploitation of some species (reviewed in Ainley and Blight, 2008; Kock, 1992, 2007). Since 1982, the fisheries are regulated by CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources), and many were closed between 1985 and 1990 due to overexploitation (Ainley and Blight, 2008; Kock et al., 2007). Nevertheless (to provide some examples only), regular monitoring of the stocks of many commercially exploited fish species, such as *N. rossii* and *G. gibberifrons*, around the South Shetland Islands, indicates a lack of recovery more than three decades after the end of fisheries (Barrera-Oro and Marschoff, 2007; Barrera-Oro et al., 2000). Similarly, stocks of the channichthyid *C. gunnari* in the Indian Ocean did not recover to pre-exploitation levels after the fishery had ceased for many years (Kock, 2005b). One reason for the slow stock recovery may be the low fecundity and slow development (see Section 3.3.2 above) of many species. However, two additional factors that may adversely affect stock recovery of *C. gunnari* were proposed (Kock, 2005b and references therein): (i) an increase in top-down pressure, that is, increased predation by seals owing to fluctuations in alternative prey (krill) and (ii) possible direct effects of climate change, in particular increasing water temperature. Owing to strict regulation, the numbers of some whale species seem to be increasing again in the South Polar Sea (Branch, 2006, 2007), which is on the one hand desirable, but on the other hand might entail an additional increased top-down pressure on zooplankton and fish communities.

These examples emphasize the complexity of relationships among human activities (historic and current), abiotic climate forcing and altered trophic structure, and how these factors can interact to control fish populations in the South Polar Sea. Thus, multiple drivers act synergistically to affect a particularly sensitive ecosystem, and projecting the future trajectories of fish stocks is particularly challenging, but we are better placed than ever before to start to anticipate and respond to likely scenarios of future change.

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APPENDIX

Table A1 Species names, family and code no. (see Fig. 5) of the species used for the analysis and comparison of the trophic vulnerability to general changes in food web structure and dynamics

No.	Species name	Family	ΣP	ΣC	VI	TG
1	*Aethotaxis mitopteryx*	Nototheniidae	53	14	0.20	BP
2	*Akarotaxis nudiceps*	Bathydraconidae	79	13	0.09	B
3	*Artedidraco loennbergi*	Artedidraconidae	108	14	0.06	B
4	*Artedidraco orianae*	Artedidraconidae	27	14	0.21	BP
5	*Artedidraco shackletoni*	Artedidraconidae	110	14	0.07	B
6	*Artedidraco skottsbergi*	Artedidraconidae	86	13	0.09	BP
7	*Bathydraco marri*	Bathydraconidae	47	13	0.17	BP
8	*Chaenodraco wilsoni*	Channichthyidae	16	15	0.28	PF
9	*Chionobathyscus dewitti*	Channichthyidae	5	14	0.77	PF
10	*Chionodraco hamatus*	Channichthyidae	10	15	0.67	P
11	*Chionodraco myersi*	Channichthyidae	5	15	0.77	PF
12	*Cryodraco antarcticus*	Channichthyidae	5	15	0.77	PF
13	*Cygnodraco mawsoni*	Bathydraconidae	55	14	0.14	BP
14	*Dacodraco hunteri*	Channichthyidae	37	15	0.10	F
15	*Dissostichus mawsoni*	Nototheniidae	52	21	0.28	BP
16	*Dolloidraco longedorsalis*	Artedidraconidae	142	14	0.04	B
17	*Gerlachea australis*	Bathydraconidae	14	14	0.46	P
18	*Gymnodraco acuticeps*	Bathydraconidae	33	14	0.15	P
19	*Histiodraco velifer*	Artedidraconidae	85	13	0.07	BF
20	*Neopagetopsis ionah*	Channichthyidae	5	14	0.77	PF
21	*Pagetopsis macropterus*	Channichthyidae	43	15	0.10	F
22	*Pagetopsis maculatus*	Channichthyidae	5	15	0.77	PF
23	*Pagothenia borchgrevinki*	Nototheniidae	17	12	0.27	BP
24	*Pleuragramma antarcticum*	Nototheniidae	12	47	0.96	P
25	*Pogonophryne marmorata*	Artedidraconidae	45	14	0.13	BP

Table A1 Species names, family and code no. (see Fig. 5) of the species used for the analysis and comparison of the trophic vulnerability to general changes in food web structure and dynamics—cont'd

No.	Species name	Family	ΣP	ΣC	VI	TG
26	*Pogonophryne permitini*	Artedidraconidae	79	14	0.10	B
27	*Pogonophryne scotti*	Artedidraconidae	78	14	0.11	B
28	*Prionodraco evansii*	Bathydraconidae	88	14	0.08	BP
29	*Racovitzia glacialis*	Bathydraconidae	89	14	0.08	BP
30	*Trematomus bernacchii*	Nototheniidae	93	14	0.02	B
31	*Trematomus eulepidotus*	Nototheniidae	45	14	0.12	BP
32	*Trematomus hansoni*	Nototheniidae	81	14	0.06	BF
33	*Trematomus lepidorhinus*	Nototheniidae	71	14	0.10	BP
34	*Trematomus loennbergii*	Nototheniidae	105	14	0.05	BF
35	*Trematomus nicolai*	Nototheniidae	88	14	0.09	B
36	*Trematomus pennellii*	Nototheniidae	164	14	0.03	BF
37	*Trematomus scotti*	Nototheniidae	121	14	0.06	B

All species are members of the fish community on the eastern Weddell Sea shelf. Species are listed in alphabetical order; for authorities, please consult Gon and Heemstra (1990). For each notothenioid species, the number of prey ($\sum P$) and consumer species ($\sum C$), the relative trophic vulnerability (VI) and trophic group (TG) are given. The index of relative vulnerability VI was calculated from the weighted number of prey species ($\sum$WP) and weighted number of consumer species ($\sum$WC) (see Eq. 2). Data on trophic links are part of the database published in Jacob et al. (2011). Trophic groups were assigned according to main food components as shown in Fig. 5, with B, benthos; P, plankton; F, fish.

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