

**THE ROLE OF FISH AS PREDATORS OF KRILL (*EUPHAUSIA SUPERBA*)
AND OTHER PELAGIC RESOURCES IN THE SOUTHERN OCEAN**

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Abstract

Krill forms an important part of the diet of many Antarctic fish species. An understanding of the role of fish as krill predators in the Southern Ocean is critical to understanding how changes in fish abundance, such as through fishing or environmental change, are likely to impact on the food webs in the region. First attempts to estimate the krill and pelagic food consumption by Antarctic demersal fish in the low Antarctic were made in the late 1970s/early 1980s. Those estimates were constrained by a paucity of biomass estimates and the mostly qualitative nature of food studies. Food consumption estimates were extended to the mesopelagic realm and the high-Antarctic Zone in the late 1980s and early 1990s when these areas were exploited commercially for *Electrona carlsbergi*. Currently, the best estimates of annual krill consumption by fish are 23 000 000–29 000 000 tonnes of krill and other pelagic prey taken annually by demersal fish in the 1980s in the whole Southern Ocean, and 5 000 000–32 000 000 tonnes taken by mesopelagic fish in the Atlantic sector of the Southern Ocean.

It is clear from this review that fish are important predators of krill, in particular the larger myctophids and some channichthyids and nototheniids, and that the importance of krill in fish diets varies substantially both with time and location on various scales, as well as with the availability of alternate prey in the different regions in the Southern Ocean. Ecosystem models therefore need to account for their role. However, several key areas of uncertainty exist, which need to be considered in ecosystem and food-web models for the Southern Ocean. For instance, no robust estimates of food consumption by mesopelagic fish can be provided for the vast areas of the Indian and Pacific Ocean sectors, or for several of the most abundant myctophid species in the Atlantic sector, due to the paucity of relevant studies in these regions. Where biomass estimates do exist, such as in the Atlantic sector, there can be a lack of precision in trawl and hydroacoustic surveys. Studies that adequately capture the seasonal variation in consumption rates and changing importance of krill in the diet of fish are also rare. Furthermore, the effects of large changes in abundance and community structure of fishes brought about by industrial fishing need to be considered when evaluating patterns that have emerged in Southern Ocean ecosystems in the course of the 20th century.

As a first step towards a modelling approach to include fish in krill-based food-web models, it is suggested to incorporate data on *Champsocephalus gunnari* from the western Atlantic sector and *Dissostichus mawsoni* from the Ross Sea into modelling approaches within the CCAMLR Ecosystem Monitoring Program. Both species are important predators of krill (*C. gunnari*) and fish (*D. mawsoni*) in turn form key prey for top predators in each region.

Introduction

Antarctica is by no means a pristine environment. Human exploitation of the Southern Ocean started some 225 years ago and caused considerable disturbance to its upper trophic levels when seals, birds and whales were removed on a large scale (Kock, 2007). More recent exploitation has targeted medium trophic levels represented by demersal and mesopelagic fish and krill (*Euphausia superba*), the key organism to many food webs in the Southern Ocean (i.e. Kock et al., 2007a; Murphy et al., 2007a).

Whether the marine ecosystems of the Southern Ocean were stable before exploitation commenced, whether they oscillated within a range or whether they exhibited apparent trends is unknown. Many

predators either leave the Southern Ocean in winter or disperse over large areas (e.g. the Scotia Sea, the whole Southern Ocean or the whole southern hemisphere) (Murphy et al., 2007b) thus reducing the upper trophic level demand for energy during the low production period.

The Southern Ocean today, particularly its seasonal pack-ice zone, is considered as a network of dynamic systems centred around krill. There is considerable interannual variability superimposed upon apparent trends in both physical and biological parameters (e.g. Croxall, 1992; Guinet et al., 1994; Wilson et al., 2001; Boyd, 2002; Kock and Everson, 2003; Weimerskirch et al., 2003; Atkinson et al., 2004; Hirawake et al., 2005; Ballance et al., 2006; Trathan et al., 2006; Murphy et al., 2007a; Florindo et al., 2008).

70% of the total biomass of krill is concentrated between 0° and 90°W. 87% of krill occurs over deep water (>2 000 m) and occupies regions of moderate food abundance (0.5–1.0 mg chl a m⁻²). Advection models suggest some loss northwards from these regions into the low chlorophyll belt of the Antarctic Circumpolar Current (ACC). There is evidence for a southward migration, with an increasing proportion of krill found south of the ACC as the season progresses. The retention of krill in moderately productive oceanic habitats is a key factor in understanding their high total production (Atkinson et al., 2008). The last estimate of krill biomass in the Southern Ocean based on net catches yielded 379 000 000 tonnes (Atkinson et al., 2009). It should be noted, however, that this estimate integrates over the period from 1926 to 2004 during which krill abundance has fluctuated (SC-CAMLR, 2008a). The biomass estimate for the area covered by the CCAMLR 2000 Krill Synoptic Survey of Area 48 (CCAMLR-2000 Survey) (Hewitt et al., 2004) was 60 000 000 tonnes.

Krill has been found in waters deeper than 400 m in the Weddell Sea (Gutt and Siegel, 1994). Krill may be a food resource for skates and slope and deep-sea fishes such as grenadiers at certain times of the year suggesting that krill occurs even deeper: Pakhomov (1997) found that pelagic crustaceans constitute > 50% of the diet of *Macrourus holotrachys* close to the Antarctic continent which lives deeper than 500 m. Krill forms a substantial part of the diet of the skate *Amblyraja georgiana* at South Georgia indicating that krill occurs close to the bottom in some numbers (Main and Collins, 2011). Moreover, krill has recently been described in depths of 550 to 3 500 m west of the Antarctic Peninsula (Clarke and Tyler, 2008). However, Atkinson et al. (2008) estimated from various sources that only 2.7% of the krill lives below 200 m depth. This was confirmed by Taki et al. (2005) who found that although krill appears to occur deeper in winter, they primarily occur above 200 m depth.

It was during the days of early whaling at South Georgia that fish in the Southern Ocean were first commercially harvested (Matthews, 1978). As a by-product of whaling, fish served as local food at the whaling stations and were sold salted in some quantities to Buenos Aires a few years after whaling

had begun. However, it took another 60 years before large-scale commercial exploitation of these fish resources commenced.

Fisheries in the Southern Ocean quickly resulted in a dramatic depletion of certain fish stocks (Kock, 1992). Scientists collecting basic biological parameters of exploited fish species such as the marbled notothenia (*Nototothenia rossii*) and mackerel icefish (*Champscephalus gunnari*) soon recognised that a larger number of fish species, albeit demersal, depended on pelagic prey, primarily krill and also ice krill (*E. crystallophias*) in waters close to the continent (e.g. Permitin, 1970; Permitin and Tarverdiyeva 1972, 1978; Tarverdiyeva 1972, 1982; Linkowski and Rembiszewski, 1978; Shust and Pinskaya, 1978; Tarverdiyeva and Pinskaya, 1980; Kock, 1981; Gubsch, 1982; Sosinski, 1985a, 1985b; Tankevich, 1990; Pakhomov et al., 1991).

Fish occupy the intermediate trophic level in the food webs of the Southern Ocean being both predators and prey (e.g. Kock, 1992; La Mesa et al., 2004a; Ciaputa and Sicinski, 2006). In particular, mesopelagic fish are part of alternative energy pathways which regionally (such as in the Scotia Sea) may become as important as the krill–predator pathway (Murphy et al., 2007b). However, questions on how important fish are and/or were as predators of krill and prey to top-level predators and whether fish had benefited from past declines in fur seals (*Arctocephalus* spp.) in the 19th century and the large baleen whales in the first 80 years of the 20th century (the so called ‘krill surplus hypothesis’, Sladen, 1964; Laws, 1977) were not addressed until the late 1970s/mid-1980s (Ballance et al., 2006).

Everson (1977), Lubimova and Shust (1980), Lubimova (1984) and Kock (1985) provided early estimates of annual krill consumption by demersal fish and added those to krill consumption of other predators provided by Laws (1977). These estimates (some populations already being depleted at the time of the estimate) varied from 10 000 000 to 25 000 000 tonnes annually. These authors concluded that fish appeared to have played a less important role as predators of pelagic resources than have whales, seals and birds (Lubimova, 1984; Miller et al., 1985; Everson, 2000). Kock (1985) added that the amount of krill consumed by demersal fish must have declined substantially after commercial fishing from the late 1960s onwards had largely

removed those species which were known to feed on krill intensively. The lower importance of fish as krill consumers compared to other krill predators was, however, questioned by Pakhomov et al. (1996).

Mesopelagic fish, such as the myctophids, had long been omitted from these calculations. They are important in two respects: their high energy content make them as important a food resource as krill. They are known to form an important part of the diet of Antarctic top-level predators (Sabourenkov, 1990; Ainley et al., 1992). Mesopelagic fish create and facilitate a fast transport of energy to deeper layers of the ocean (Flores et al., 2008).

Fish have always played an important role in the diet of Antarctic fur seals (*Arctocephalus gazella*) at South Georgia (Reid and Arnould, 1996; McCafferty et al., 1998; Staniland and Boyd, 2003). Lactating Antarctic fur seals and incubating chinstrap penguins (*Pygoscelis antarctica*), for example, prefer energy-rich myctophids to krill even when krill is abundant close to their colonies (Ichii et al., 2007). Moreover, seabirds in the southern Scotia Sea chose myctophids over krill in winter (Ainley et al., 1992) or switch to fish when krill or ice krill becomes scarce (Ainley et al., 2006).

Myctophids, a predominant group among mesopelagic fish, form concentrations in the 50–300 m layer of the ACC between 55° and 62°S at night (Bogdanov and Lubimova, 1978; Hopkins and Torres, 1989). Some species, notably the larger ones of the genera *Electrona* and *Gymnoscopeus*, appear to consume krill in large quantities (e.g. Rowedder, 1979a; Lubimova, 1984; Kozlov and Tarverdiyeva, 1989; Gerasimova, 1990).

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) was negotiated in the aftermath of the demise of the great whales in the late 1970s and came into force in 1982 (Kock, 2007). Effective fisheries management under CCAMLR requires, among other responsibilities, the understanding of the life history characteristics of abundant and (potentially) exploitable species and factors controlling their dynamics (Kock et al., 2007a). Such considerations fuelled fish investigations within the remit of CCAMLR in the last three decades: results of fish

surveys and sophisticated stock assessment models became common tools of the Working Group on Fish Stock Assessment advising CCAMLR.

The CCAMLR Ecosystem Monitoring Program (CEMP) was launched in the second half of the 1980s in an attempt to link and analyse krill predator requirements and changes in prey abundance. CEMP considers the effect of an increase in krill harvesting on other components of the ecosystem with the ultimate goal of establishing catch limits for the krill fishery which does not negatively impact on predators. Discussions on this matter have been ongoing in CCAMLR since the mid-1990s (Butterworth and Thomson, 1995; Murphy, 1995; Mangel and Switzer, 1998; Thomson et al., 2000; Constable, 2001, 2002a, 2002b, 2006; Bredesen, 2003; Mori and Butterworth, 2004, 2006a, 2006b; Hill et al., 2006; Plagányi and Butterworth, 2006, 2007).

In the past, *C. gunnari* and *Dissostichus mawsoni* have been proposed to be included in CEMP. However, CEMP still does not include fish in its monitoring of krill predators, nor does it provide data on the effect of exploitation on fish as predators of krill. As a consequence, comprehensive and quantitative food studies of Antarctic fish both in summer and winter remain scarce.

As a group directly impacted by fishing in the past and the present, and important as an alternative food source for higher predators when krill vary in availability, fish are a critical component for representation in ecosystem and food-web models. As CCAMLR and the International Whaling Commission (IWC) invest more resources developing such models to assist with evaluating their management procedures, it was thus timely to re-evaluate the role of fish as krill predators and review the available data with respect to their relevance for modelling approaches. The analysis in this paper focused on:

- (i) fish population biomass and number estimates both for those mesopelagic and abundant demersal fish species which are known to utilise primarily pelagic resources
- (ii) foraging (diet in quantitative terms and its temporal and spatial variability, daily consumption rates, digestion time)
- (iii) refined estimates of krill consumption by fishes, where such estimates are possible.

Other aspects of the life history of fishes were dealt with to the extent that they are necessary for the understanding of the role of fish as predators and prey of krill and other pelagic resources in the Southern Ocean.

A brief introduction to the zoogeography of Antarctic fish

The Southern Ocean can roughly be divided into three major zoogeographical regions with respect to fish: the ice-free zone, the seasonal pack-ice zone and the high-Antarctic zone (Hempel, 1985; Kock, 1992). The ice-free zone occupies the area between the Antarctic Polar Frontal Zone (APFZ) and the northern limit of the pack-ice in winter/spring which is essentially the southern boundary of the ACC. The seasonal pack-ice zone extends between the limit of pack-ice in winter/spring and in summer/autumn (seasonal sea-ice zone, marginal ice zone, inner pack-ice zone) including the islands north of the pack-ice limit, such as South Georgia. The high-Antarctic zone encompasses the region close to the continent and is covered by ice (perennial sea-ice, coastal fast ice, including flaws, leads and polynyas) for most of the year (Kock, 1992).

The shelf and slope waters of the islands of the seasonal pack-ice zone can be further divided into an Atlantic province, including the Antarctic Peninsula, the islands of the Scotia Arc and Bouvetøya, and an Indian Ocean and a west Pacific province which comprises the islands and seamounts of the Indian sector and Macquarie Island (Kock, 1992). This scheme is similar to the one proposed by Eastman (1993) which is largely based on the zoogeographical units described by Andriashev (1987). Detailed descriptions of the zoogeography of Antarctic fishes are provided by Andriashev, 1987; Kock, 1992 and Eastman, 1993.

A high level of endemism (88% of species) is a distinct feature of the Antarctic coastal fish fauna while endemism is less pronounced in mesopelagic fish (Andriashev, 1987; Eastman, 2005). Each zoogeographic zone hosts a distinct fish fauna. These ichthyofaunas overlap to some extent in the deeper shelf/slope regions (mesopelagic fish/demersal fish) and in the seasonal pack-ice zone and the high-Antarctic zone (low-Antarctic and high-Antarctic ichthyofaunas). Descriptions of the evolution, taxonomy, life cycle and adaptations of Antarctic fish

can be found in Gon and Heemstra (1990), Kock (1992), Eastman (1993), Near (2004), Near et al. (2004), Kock (2005), Cheng and Detrich (2007), Pörtner et al. (2007) and Janko et al. (2007).

Groups of fishes important as predators of krill and other pelagic resources

Antarctic pelagic fish are descendants of several faunal groups of different origin: bathypelagic species, mesopelagic species and species that originated from coastal fish families and have secondarily adapted to temporary or permanent life in midwater. A number of fish species exhibit a tendency to spend part of their daily cycle in midwater. However, the only fish species which have become (secondarily) pelagic in the course of their evolution are the nototheniids *Pleuragramma antarcticum* and *D. mawsoni*. Being secondarily pelagic, they have been dealt with under demersal fish.

Epipelagic and vagrant species

Representatives of epipelagic families are uncommon in the Southern Ocean (Kock, 1992; Duhamel et al., 2005). The southern opah (*Lampris immaculatus*) has been caught as far south as the vicinity of the Antarctic Peninsula (Parin and Kukuyev, 1983; Gon, 1990). Five species of sharks have been recorded from inside the Southern Ocean: *Lamna nasus*, *Somniosus antarcticus*, *Squalus acanthias*, *Centroscyrmus coelolepis* and *Etmopterus c.f. granulosus* (Duhamel et al., 2005; SC-CAMLR, 2006a). The southern bluefin tuna (*Thunnus maccoyii*) (Nakamura, 1990b) is an occasional, or even permanent, invader of the peripheral waters of the Southern Ocean (South Georgia, Iles Crozet, Iles Kerguelen and Macquarie Island) (Williams, 1988; SC-CAMLR, 2006a). None of these species plays a significant role in terms of their krill consumption. They feed primarily on fish.

Southern blue whiting

Southern blue whiting (*Micromesistius australis*) originating from the southwest Atlantic have been observed in large quantities during the summer months in surface waters south of the APFZ (Merrett, 1963; Mikheev, 1967) to feed on krill. It is unknown how big the proportion of the blue

whiting population was which crossed the APFZ to feed on krill (Subnikov et al., 1969; Shust and Silyanova, 1971). Given their large population size before the onset of commercial exploitation in the 1970s, it is likely that they have contributed significantly to the overall krill consumption by Antarctic fish. Russian sources speak of several hundred thousand tonnes of krill taken by blue whiting annually (Subnikov et al., 1969; Shust and Silyanova, 1971). With the onset of large-scale exploitation of blue whiting on the Patagonian shelf, the number of fish migrating into the Scotia Arc region diminished rapidly. No blue whiting had been caught south of the APFZ from the second half of the 1980s to the early 2000s. A few individuals have been caught again around South Georgia in 2004 (Collins, pers. comm.).

Mesopelagic species

Oceanic pelagic waters form the largest realm in the Southern Ocean. Myctophids are the most abundant group of mesopelagic fish roaming these waters (Rowedder, 1979a; Kozlov and Tarverdiyeva, 1989; Gerasimova, 1990; Hulley, 1990; Sabourenkov, 1990; Pakhomov et al., 1996). Lanternfish are short-lived fish which rarely grow older than five years (Linkowski, 1987; Greely et al., 1999). The larger-growing species of the genera *Electrona* and *Gymnoscopelus* primarily feed on krill. Other mesopelagic families taking krill and other euphausiids in various quantities are the Paralepididae (Post, 1990; Lipskaya et al., 1991), Gempylidae (Podrazhanskaya and Pinskaya, 1987; Nakamura, 1990a), Anotopteridae (Balanov and Radchenko, 1998), Bathylagidae (Gorelova and Kobylanskiy, 1985) and Notosudidae (Krefft, 1990). All other species of mesopelagic and bathypelagic fishes, to the extent their diet is known, appear to be of little (if any) importance with respect to their krill and larger zooplankton consumption.

Demersal fish

Two groups of bottom fish form the demersal and secondarily pelagic fish fauna: the deep-sea species that inhabit the lower continental slope, and the deep-sea basins and trenches, and the coastal species that occur on the continental shelves and the upper slopes. This division becomes somewhat blurred due to the submergence of the Antarctic shelf and the presence of deep innershelf

depressions which let a number of coastal species occur as deep as 1 500 m and more (Kock, 1992).

The Notothenioidei account for 45% of the species and about 95% of the fish biomass (Eastman, 2005). Six of their families are known to occur south of the APFZ. The two most abundant families are the Nototheniidae and the Channichthyidae representing 31 and 15 species respectively (Eastman and Eakin, 2000). Channichthyids are unique among vertebrates in that they lack the oxygen-binding haemoglobin.

A large number of species among the Nototheniidae, Channichthyidae and a third family, the Bathydraconidae, feed on krill and other zooplankton. The other notothenioid and non-notothenioid families, even if they are abundant in terms of species (Eastman, 2005) such as eelpouts (Zoarcidae) and snailfishes (Liparidae), are primarily benthos feeders, although it is important to note that rajids, as typical benthos and fish feeders, are able to take mostly krill when it is available close to the bottom.

Nototheniids and channichthyids have a life span of typically 10–20 years (Kock et al., 1985; La Mesa et al., 2000) with the exception of the two largest species: Patagonian (*D. eleginoides*) and Antarctic toothfish may grow 50 years and older (Horn, 2002).

Estimated consumption of krill and other pelagic prey

Lanternfish (Myctophidae) and other mesopelagic fish

Diversity is lowest in cold waters in the southern Scotia Sea, which is dominated by the myctophids *Electrona antarctica* and *Gymnoscopelus nicholsi* and *G. braueri* and the bathylagid *Bathylagus antarcticus*. Diversity increases further to the north with additional species such as *Krefftichthys anderssoni*, *Protomyctophum bolini* and *Electrona carlsbergi* occurring (Collins et al., 2012).

Most important predators of larger planktonic prey among mesopelagic fish are Myctophidae of the genera *Electrona* and *Gymnoscopelus* (Rowedder, 1979b; Linkowski, 1985, 1987; reviews of the Russian literature in Sabourenkov, 1990; Kozlov, 1995). Information on lanternfish originated primarily from the Atlantic sector where

the lanternfish *E. carlsbergi* had been fished commercially from the mid-1980s to the early 1990s. The abundance of myctophids decreases during autumn and winter with low-density concentrations scattered over large areas (Kozlov et al., 1990).

The centre of biomass of *E. carlsbergi* lies in the APFZ (Zemski and Zozulya, 1990). When dense aggregations of myctophids were fished just south of the APFZ, more than 90% of the catch consisted of *E. carlsbergi*. Loose aggregations often contained a larger proportion of other species, such as *G. nicholsi* (SC-CAMLR, 1992). The proportion of *E. carlsbergi* in myctophid associations decreased to 60–75% further south where the proportion of the truly Antarctic myctophids (sensu Hulley, 1981) *G. nicholsi*, *G. braueri* and *E. antarctica* increased in the catches (Filin et al., 1990). Truly Antarctic species occur in numbers as far south as the vicinity of the Antarctic continent.

Most of the biomass of myctophids north of 53°S consists of sexually mature 3–4-year-old *E. carlsbergi* while south of the APFZ 2–3-year-old immature fish are most abundant (SC-CAMLR, 1990). Dense concentrations of 1-year-old fish have been observed during winter in sub-Antarctic waters of the Indian sector (Ignatiev, 1990).

Biomass estimates

The density of myctophids estimated from hydroacoustic surveys in 1987–1989 was converted to biomass. However, information on target strength used to calculate abundance and the associated myctophid-discrimination algorithm were not provided. This made it impossible to validate these estimates, and indicates caution is advised when interpreting them.

The biomass of mesopelagic fish south of 40°S derived from hydroacoustic surveys and modelling studies was estimated at 337 million tonnes and 212–396 million tonnes respectively. Myctophids were estimated to form 70–200 million tonnes of this biomass (Lubimova, 1984). No biomass estimate exists for the waters of the APFZ and south only.

Biomass estimates derived from hydroacoustic surveys in the Atlantic sector in 1987–1989 varied considerably in time and space (Table 1a). The variability was mostly caused by the meandering of

the APFZ and gyres, eddies and upwelling forming in, and at, the margins of the APFZ (Maslennikov et al., 1991; Kozlov, 1995; Loots et al., 2007). Hydrographic conditions and food availability were identified as the major driving forces for *E. antarctica* to form concentrations (Loots et al., 2007; Flores et al., 2008).

A second source of biomass estimates were those derived from larger plankton net catches such as RMT8 and RMT25. The main biomass of myctophids and bathylagids in RMT25 catches occurred between 400 and 1 000 m during the day and between 0 and 400 m at night (Collins et al., 2008). Density from night hauls was 3.04 g 1000 m⁻³.

The biomass (wet weight per m⁻²) of myctophids estimated from RMT25 plankton catches in an area from the western side of South Georgia to the west of Shag Rocks in the depth range 0–1 000 m was 2.93 g m⁻² (Collins et al., 2008). This was lower than the myctophid biomass estimated from hydroacoustic surveys in the APFZ further to the north of South Georgia where biomasses of 5–15 g m⁻², 3.8–6.5 g m⁻² and 1.6–11.6 g m⁻² respectively were measured (Chindonova, 1987; Filin et al., 1990; Kozlov et al., 1990).

Further south (between the South Orkney Islands and Elephant Island and in the western Weddell Sea) the biomass of mesopelagic fish was estimated to be 3.3–4.4 g m⁻² in summer and thus similar to the biomass west of South Georgia (Lancraft et al., 1989; Collins et al., 2008). Two-thirds of the biomass (2.2–2.9 g m⁻²) was attributed to myctophids (Lancraft et al., 1989). Mesopelagic fish biomass appeared to be higher (6.93 g m⁻²) on the slope of King George Island (South Shetland Islands) than in offshore regions of the southern Scotia Sea.

Biomass of myctophids in the Scotia Sea estimated from night catches was 4 500 000 tonnes (Table 1b) (Collins et al., 2008, 2012). Biomass of mesopelagic fish declined in winter and was only 0.75 g m⁻² with little more than half (0.4 g m⁻²) contributed by myctophids (Lancraft et al., 1991).

Biomass estimates, in addition to the information presented in Table 1a, were provided in Perissinotto and McQuaid (1992), Pakhomov et al. (1996), Pakhomov and Froneman (1999) and Donnelly et al. (2004) for the Indian sector and the eastern Ross Sea. These were derived from samples

collected by RMT2 and Bongo nets. These types of nets are unlikely to catch myctophids quantitatively and have not been considered further here.

Prey composition and consumption rates

Myctophids prey on all abundant zooplankton over a certain minimum size (Williams, 1985; Russian publications before 1990 (summarised in Sabourenkov, 1990; Kozlov and Tarverdiyeva, 1989; Kozlov and Shust, 1990). The main components of their diet were copepods, hyperiids, particularly *Themisto gaudichaudii*, and euphausiids, mainly *E. superba*, *E. frigida*, *E. triacantha*, *E. vallentini* (around the Prince Edward Islands) and *Thysanoessa macrura* (Solyanik, 1967; Podrazhanskaya and Pinskaya, 1987; Hopkins, 1985; Perissinotto and McQuaid, 1992; Hopkins et al., 1993; Lancraft et al., 2004; Williams et al., in prep.). Krill (mostly furcilia, calyptopis and postlarvae) appear to be a predominant prey item in the Atlantic sector (Kozlov and Shust, 1990; Flores et al., 2008), while other euphausiids, such as *E. vallentini*, *E. similis*, *T. vicina* and *T. macrura* replace *E. superba* in the Indian sector (Perissinotto and McQuaid, 1992; Woehler and Green, 1992; Pakhomov, 1995; Guinet et al., 1996; Pakhomov and Froneman, 1999; Williams et al., in prep.).

The proportion of krill in the diet of *E. carlsbergi* in the north of the Atlantic sector was low (Podrazhanskaya and Tarverdiyeva, 1991). It appears unlikely that krill accounts for > 5% by weight in the diet of *E. carlsbergi* (Table 2a).

Krill (early life stages in the diet of *E. antarctica* and more juvenile krill and early adults in *Gymnoscopelus* species) usually accounted for > 50% by weight (Table 2b) or higher (Table 2a) in the diet of truly Antarctic myctophid species. Seasonal variation in the diet composition has not been observed (Lancraft et al., 1991; Hopkins et al., 1993). However, krill was found to be absent at times in the diet of *E. antarctica* in areas such as South Georgia and the Lazarev Sea (Pakhomov et al., 1996).

Williams et al. (in prep.) found that *K. anderssoni* in the Indian sector showed reverse diurnal migration, feeding heavily on copepods (e.g. *Rhinca lanus gigas*) near the surface during the day, and eating copepods and *E. vallentini* deeper in the water column at night. *Electrona antarctica* also had a different diet between day and night, related

to its migration into the epipelagic zone during the night, and the migrations of zooplankton prey. During the day, *E. antarctica* fed on copepods, *T. macrura*, euphausiid furcilia and to a lesser extent *T. gaudichaudii*, and pteropods. Close to the surface at night, copepods dominated the diet. *Gymnoscopelus braueri* also migrates to the surface at night, feeding on copepods and mysids (*Boreomysis rostrata*). They preyed on euphausiids (*T. macrura* and *Euphausia* spp.) in deeper waters during the day. Similar diet was recorded for these species in the French EEZ around Iles Kerguelen (Duhamel et al., 2005). Williams et al. (in prep.) estimated that copepods, and not euphausiids, received the highest predation pressure across a complete day–night cycle.

Mouth width in myctophids indicated that only larger individuals (>60–70 mm length) were able to feed on small krill. Their stomach contents consisted primarily of juvenile krill < 26 mm (Solyanik, 1967; Zasel'sliy et al., 1985) except in larger *G. nicholsi* which take adult krill of >40 mm (Podrazhanskaya and Pinskaya, 1987; Kozlov and Tarverdiyeva, 1989; Kozlov, 1995). Few krill occur around South Georgia that was < 26 mm (e.g. Reid et al., 1996; Brierley, 1999). This is corroborated by observations that, due to its size most krill at South Georgia is only available to larger myctophids such as *G. nicholsi* and *E. carlsbergi*. Smaller myctophids, such as *P. choriodon* and juvenile *E. antarctica*, prey on copepods and *T. gaudichaudii* (Shreeve et al., 2009; Stowasser et al., 2009).

Information on the proportion of krill in the diet by weight was much more sparse (Table 2b). Daily rations of *E. carlsbergi* varied from 1.4 to 5.6% of body wet weight (Table 3).

Gerasimova (1990) estimated an annual food intake of roughly 15 times the body weight. Rowedder (1979a) calculated an annual food intake of 18 to 24 times the body weight from information collected in summer. Given a lower food intake in winter (Geiger et al., 2000) values of annual food consumption appear to be in good agreement between the two authors.

The food consumption of *Gymnoscopelus* species is largely unknown. It remains unclear if data which suggest a comparatively low daily food intake are representative or are merely an expression of a low feeding intensity at the time of

investigation (Pusch et al., 2004). An annual food consumption of seven times the body weight was assumed for the purpose of this study. Estimates of annual consumption rates by myctophids are provided in Table 4.

Non-myctophid species

The only other species of mesopelagic fish for which limited diet information exists were the paralepidid *Notolepis coatsi*, the gempylid *Paradiplospinus gracilis*, the anotopterid *Anotopterus pharao*, and the bathylagid *B. antarcticus*, collected either over a wide area of the Southern Ocean or in a small area east of the tip of the Antarctic Peninsula (*B. antarcticus*).

Fatty acid analysis suggests that gelatinous prey (salps, chaetognaths) form an important part of the prey of *Nansenia antarctica* (Stowasser et al., 2009). *Notolepis coatsi* < 70 mm length preyed primarily on copepods and chaetognaths. Individuals > 70 mm took various stages of krill in the Atlantic and Pacific sectors and chaetognaths in the Indian sector (Lipskaya et al., 1991). A small sample of stomachs from Prydz Bay contained more than 95% krill by weight (Williams, 1985).

Main prey items of *P. gracilis* were myctophids and to a much lesser extent euphausiids (Podrazhanskaya and Pinskaya, 1987; Pusch et al., 2004). Krill was the sole food item of one individual caught in the Indian sector (Solyanik, 1964). The food of *A. pharao* is known from the north Pacific and north Atlantic where the species feeds entirely on fish and pieces of fish (Balanov and Radchenko, 1998). It was therefore assumed that fish also forms the predominant part of the diet of *A. pharao* in the Southern Ocean.

Soft-bodied plankton organisms were the most abundant prey of *B. antarcticus* east of the tip of the Antarctic Peninsula. No euphausiids were found in their stomachs (Geiger et al., 2000). The main diet of *B. antarcticus* in the Weddell Sea comprised copepods, euphausiids, their larvae and salps (Hopkins and Torres, 1989; Hopkins et al., 1993; Geiger et al., 2000). 46% of the diet by weight of *B. antarcticus* was composed of krill, other euphausiids and jelly fish in the Lazarev Sea (Gorelova and Kobylanskiy, 1985). Other potential krill feeders are the notosuidid *Scopelosaurus*

hamiltoni and the melamphaeid *Sio nordenskjoldi* (Parin and Svetlov, 1981) for which diet information is still lacking.

The annual food consumption by mesopelagic fish

Estimating the proportion of krill in the diet of myctophids other than *E. carlsbergi* was problematic. Russian investigations in the late 1980s, as well as those of Rowedder (1979a), were mostly conducted in areas where dense krill aggregations were located and a substantial krill fishery had taken place. *Electrona antarctica* taken in areas of the Atlantic sector only thinly populated by krill, consumed very little krill (Pakhomov et al., 1996; Flores et al., 2008). To what extent *Gymnoscopelus* species (which are approximately twice the size of *Electrona*) prey on krill in these areas remains still unknown. Hotspots of high krill and high myctophid abundance, and a resulting large proportion of krill in the diet of abundant myctophid species, may be misleading and overestimate the true proportion of krill in the diet of *E. antarctica*. Consequently, the proportion of krill in the diet of *E. antarctica* was conservatively estimated at 20%.

Estimates were limited to myctophids in the area of the western part of the Atlantic sector between 8° and 50°W for which some abundance estimates and daily and annual consumption estimates exist (Table 3). The area was divided into two zones: the area from 50° (approximate position of the APFZ) to 56°S where *E. carlsbergi* accounted for most of the myctophid biomass (Podrazhanskaya and Tarverdiyeva, 1991), and the area south of 56°S where *E. antarctica* and *Gymnoscopelus* species predominated (Lancraft et al., 1989; Pusch et al., 2004). The estimate (Table 4) is based on the following assumptions:

- (i) the mesopelagic community feeding on krill is made up of 30% *E. antarctica* and 70% *Gymnoscopelus* species (Lancraft et al., 1989; Pusch et al., 2004)
- (ii) the biomass of myctophids other than *E. carlsbergi* is 2.5 g m⁻² in summer and 0.4 g m⁻² in winter (Lancraft et al., 1989, 1991)
- (iii) their small mouth opening does not allow myctophids to start feeding on krill (except

krill larvae) before they reach 60–70 mm (SL) (Rowedder, 1979a), and that 50% of the population of *E. antarctica* was > 60 mm

- (iv) the proportion of krill by weight accounted for 5% in the diet of *E. carlsbergi*, for 20% in *E. antarctica* and 55% in *Gymnoscopelus* species (Tables 2(b) and 4)
- (v) the annual food consumption of *E. carlsbergi* of 15 times the body weight equals the annual food consumption of *E. antarctica* (Gerasimova, 1990)
- (vi) the annual food consumption of *Gymnoscopelus* species is seven times the body weight (Lancraft et al., 1991).

Annual krill consumption by mesopelagic fish in the Atlantic sector was estimated to be 5 300 000–32 000 000 tonnes. The database is still insufficient to provide annual krill consumption by myctophids for the Indian and Pacific sectors.

Demersal fish

Abundance of Antarctic demersal fish is highest in the depth range 100–400 m around sub-Antarctic and peri-Antarctic islands. It is assumed for management purposes that each shelf region of islands or island groups is inhabited by a separate population of a particular species, although this has been validated only in a few species (Siegel, 1980; Kock, 1981; Sosinski, 1985a; Sosinski and Janusz, 2000; Duhamel, 1991; Williams et al., 1994; Duhamel et al., 1995; Kock et al., 2000). Fish stock biomass has been commonly estimated by the standard ‘swept area method’ (Saville, 1977) with Aitchison’s delta distribution as the underlying statistical model (Pennington, 1983; de la Mare, 1994).

Information on pre-exploitation sizes of Antarctic fish stocks is sparse (Kock, 1991). Most biomass estimates have been obtained from surveys conducted well after the start of commercial exploitation at a time when stock sizes of some important krill predators had already been largely reduced.

With the exception of a biomass estimate for *N. coriiceps* in inshore waters of the South Orkney Islands (Everson, 1970) and *Lepidotothen larseni* and *Gobionotothen marionensis* (Bushula et al., 2005), no biomass estimates exist for inshore

waters of the Southern Ocean. Some of the fish species occurring inshore in some numbers, such as *N. coriiceps*, juvenile *N. rossii*, or *Trematomus* spp. are known to take krill in some quantities when available inshore (Iken et al., 1998; Barrera-Oro, 2002; Casaux et al., 2003). Krill appears to be much more abundant inshore in summer than in winter (Stepnik, 1982; Ross et al., 1998). The data to produce precise estimates of the quantity of predation on krill by inshore fishes were not available for this review. However, given estimates of fish production in inshore waters and the availability of large quantities of fish to birds foraging inshore such as blue-eyed shags (*Phalacrocorax atriceps*) indicate that a substantial biomass of fish may be consuming krill at least in summer (Everson, 1977; Barrera-Oro, 2002 and references therein).

Post-larval and juvenile icefish and, to a smaller extent, nototheniids, prey heavily on krill. Their abundance in slope and oceanic waters is often closely associated with the abundance of krill (Rembiszewski et al., 1978; Slosarczyk and Rembiszewski, 1982; Williams, 1985; Slosarczyk, 1986; Skora, 1988; Pakhomov and Pankratov, 1991). Given their small size, their contribution to overall krill consumption by fishes is probably small.

Southern Scotia Arc (Subareas 48.1 (part) and 48.2)

Low-Antarctic species dominate the fish fauna in terms of biomass (Andriashev, 1965, 1987; Jones et al., 2000; Kock and Stransky, 2000). High-Antarctic species contribute less to the abundance of the ichthyofauna (Kock, 1992). Time series of surveys were in general too short and the coefficients of variation (CVs) of the abundance estimates often too wide to detect trends in abundance. Thus, minimum and maximum biomass estimates were selected to estimate annual food consumption.

Pre-exploitation fish biomass

The main krill predators before the onset of commercial exploitation in the southern Scotia Arc in 1977/78 have been *C. gunnari*, other icefish species, southern blue whiting (until the mid-1970s) and several nototheniids, including *N. rossii*. Large concentrations of *C. gunnari* were found both in the South Orkney Islands in 1977/78 and along the South Shetland Islands from Elephant Island in the

north to Livingston Island in the south in 1978/79 (Kock, 1992). Biomass of *N. rossii* was concentrated in an area north and northwest of Elephant Island (Kock et al., 2004) where its main prey, krill, occurs in large quantities (Reiss et al., 2008).

Pre-exploitation biomass estimates of fish stocks were available for the split-years (1 July to 30 June) 1975/76 and 1977/78 (Table 5). Biomass estimates of *C. gunnari* were in the order of the large commercial catches taken in the South Orkney Islands in 1977/78 and the South Shetland Islands in 1978/79 and for *N. rossii* taken west and northwest of Elephant Island in 1979/80 (Kock, 1991).

Everson (1970, 1977) provided a biomass estimate of 194 kg hectare⁻¹ (= 19.4 tonnes km⁻²) of *N. coriiceps* from trammel net catches in inshore waters off Signy Island (South Orkney Islands) before any exploitation of the fish stocks around the islands started. Biomass estimates obtained from trawl surveys were only available from waters deeper than 100 m further offshore after exploitation had started, making it difficult to combine data to estimate an overall abundance estimate for *N. coriiceps* on the shelf.

Biomass after exploitation

The catch record of the commercial fishery is incomplete. It is assumed that fishing removed in excess of 220 000 tonnes of finfish from 1977/78 to 1989/90. Most catch was taken in the initial phase of the fishery. The species mostly affected were the krill-feeding *C. gunnari*, and *N. rossii* as target species, and *C. aceratus* and *G. gibberifrons* as by-catch species (Tables 6 and 7) (Kock, 1992). It is known for *C. gunnari* and *N. rossii* that their stock sizes have declined substantially due to fishing. Biomass estimates of *N. rossii*, *N. coriiceps*, *G. gibberifrons*, *L. squamifrons*, *L. larseni*, *C. gunnari*, *C. aceratus*, *C. rastrispinosus* and *P. georgianus* estimated from bottom trawl surveys over the past 25 years (Kock, 1986; Jones et al., 1998, 2000, 2001, 2003; Jones and Kock, 2006, 2009; Kock, 1986; Kock et al., 2002, 2007a) suggested that stocks of by-catch species have largely recovered from the impact of fishing. *Champscephalus gunnari* remained at low stock sizes until the first decade of the 2000s (SC-CAMLR, 2007a; SC-CAMLR, 2012).

Proportion of krill and other zooplankton in diet and consumption rates

A large proportion of the diet of the nine most abundant fish species consists of krill (Table 8). Even species known to feed primarily on benthos organisms, such as *G. gibberifrons*, take krill in some quantities when it becomes available close to the bottom (Table 8). Other species occurring mostly inshore not accessible by trawl surveys and feeding on krill are *T. newnesi* (Linkowski et al., 1983; Casaux et al., 1990) and *Parachaenichthys charcoti* (Gröhsler, 1992; Kompowski, 1992).

Feeding rates

In order to estimate krill consumption, the following information on daily feeding rates has been used, obtained from:

- (i) *N. rossii*, *N. coriiceps*, *L. squamifrons*, *L. larseni*, *G. gibberifrons*, *C. gunnari*, *C. aceratus*, *P. georgianus*, *C. rastrispinosus* and *C. wilsoni* at South Georgia, in the southern Scotia Arc and west of the Antarctic Peninsula (Kock, 1992)
- (ii) *L. larseni* at the Prince Edward Islands (Bushula et al., 2005)
- (iii) *L. squamifrons* on Ob and Lena Banks (Pakhomov, 1993) (Table 9)
- (iv) mean and lower and upper confidence intervals of the biomass estimates (Tables 6 and 7).

Annual krill consumption by demersal fish

Estimates of daily food intake for both summer and winter were used to estimate annual krill consumption. The majority of this information was taken from summer data (Table 9). Winter data with respect to krill feeding species were available only for *N. coriiceps*, juvenile *N. rossii*, *G. gibberifrons* and *T. newnesi* from Admiralty Bay and Potter Cove (King George Island, South Shetland Islands) (Linkowski et al., 1983; Casaux et al., 1990), from a quantitative food study of a range of species around Elephant Island collected in May–June 1986 (Gröhsler, 1992), and a year-round qualitative food study of near-shore fish assemblages west of the Antarctic Peninsula in 1975 (Daniels, 1982).

South Georgia and Shag Rocks (Subarea 48.3)

The species inventory of South Georgia is provided in Andriashev (1965, 1987), Jones and Kock (2006) and CCAMLR working papers from various UK bottom trawl surveys from the late 1980s to 2006 (Collins et al., 2006).

Biomass in the first years of exploitation

No pre-exploitation biomass estimates existed for *N. rossii*. Given the large catches of *N. rossii* in the order of 500 000 tonnes in 1969/70 and 1970/71, it is likely that the pre-exploitation biomass of *N. rossii* exceeded 500 000 tonnes. The target species of the fishery from the mid-1970s was *C. gunnari* with the exception of 1977/78 when the abundance of *C. gunnari* was low. *Chaenocephalus aceratus*, *P. georgianus* and *G. gibberifrons* were then targeted. Biomass estimates of *C. gunnari* existed for 1975/76, one year before large-scale exploitation of the species started. The substantial decline in estimated biomass from 141 000 tonnes in 1975/76 to 34 000 tonnes in 1977/78 clearly reflected the toll which exploitation had taken when catches in the order of 100 000 tonnes were taken in 1976/77. It is likely that pre-exploitation biomass was in the order of the 141 000 tonnes estimated for 1975/76 by Kock (1981).

Biomass under exploitation

Biomass estimates of the most abundant demersal species around South Georgia and Shag Rocks were available from trawl surveys conducted from 1987 to 2006 (Table 10). They were largely restricted to depths < 400 m. The targeted fishery on *N. rossii* was already closed by CCAMLR when the series of bottom trawl surveys started in 1987. The only species allowed to be taken was *C. gunnari* with a limited by-catch of *C. aceratus*, *P. georgianus* and *G. gibberifrons*.

Qualitative and quantitative composition of the diet

The composition of the diet of most of the abundant fish species is well documented (see Table 11 and references therein), including a number of recent detailed studies of the diet of the channichthyids at South Georgia (Reid et al., 2007;

Clarke et al., 2008; Main et al., 2009). However, the vast majority of data has been obtained during the austral summer period.

Consequently, little information is available on seasonal variability in diet composition.

In contrast to diet composition, few data are available on which to calculate daily consumption rates of krill and other zooplankton. Estimates of daily food intake were in the order of 0.3–2.2% of body weight (Table 11). Uncertainty remains as to whether feeding rates remain constant throughout the year or whether there is a considerable reduction during gonadal development and/or the winter period.

Mackerel icefish (*Champsocephalus gunnari*) biomass

Mackerel icefish is currently the most abundant demersal fish species (in terms of biomass) in bottom trawl surveys at South Georgia (Table 10). Biomass estimates obtained by bottom trawl surveys have wide confidence intervals reflecting the patchy distribution of fish, and considerable inter-annual variability in standing stock biomass. The lowest trawl survey estimate was 9 000 tonnes in 2005 and the highest 37 000 tonnes in 1990, and in both years the trawl survey estimate was more than a factor of 10 different from the value in adjacent years (Table 10). The reasons for this extreme variability are not fully understood, but imply years in which there are mass mortality events (if emigration is ruled out, see Kock and Everson, 2003) probably linked to krill availability and icefish condition (Everson et al., 1997; Agnew et al., 1998).

Diet

The qualitative and quantitative composition of the diet of mackerel icefish in the Shag Rocks–South Georgia region has been studied extensively (Permitin and Tarverdiyeva, 1972; Kock, 1981; Sosinski, 1985a; Kock et al., 1994; Barrera-Oro et al., 1998; Everson et al., 1999; Kock and Everson, 2003; Main et al., 2009) (Table 11). The majority of studies have provided qualitative information on the composition of the diet. Diet composition and stomach fullness has been observed to vary significantly between years and age classes but there appeared to be little regional differences in the diet. In general, the diet is dominated by krill and the

hyperiid amphipod *Parathemisto gaudichaudii*. Smaller individuals tend to prey on a higher proportion of *P. gaudichaudii* and smaller euphausiids such as *Thysanoessa* sp. and took smaller quantities of *E. superba* (Main et al., 2009). In years of krill scarcity around South Georgia, the proportion of krill in the diet, the stomach fullness and fish condition were significantly less than in seasons of 'normal' krill abundance (Everson and Kock, 2001; Main et al., 2009).

Limited information exists on the intra-annual (seasonal) variation in the diet composition as few studies have been conducted outside the summer months. The diet of *C. gunnari* is dominated by pelagic macro-zooplankton and to a small extent fish (Table 11). In most studies, krill have been shown to be the most important dietary item but this is not the case for all size classes or years (Kock, 1981; Kock et al., 1994; Barrera-Oro et al., 1998; Main et al., 2009).

Krill consumption by mackerel icefish

Updated estimates of the annual consumption of krill by mackerel icefish are provided in Main et al. (2009). In this study, a consumption rate of 3% wet body weight per day was assumed (see Kock, 1992), multiplied by the proportion of krill in the diet (Table 11) and the mackerel icefish biomass in the study area. This provided estimates of krill consumed by icefish as 260 000 tonnes in 2003/04, 71 000 tonnes in 2004/05 and 818 000 tonnes in 2005/06. However, it was noted earlier that biomass is likely to be underestimated as the surveys were conducted with a bottom trawl (headline height approx. 6 m) and an unknown portion of the icefish population is benthopelagic at the time of day when the survey is conducted (Frolkina, 2002). Using the biomass estimates presented in Table 10 and the range of values for consumption rates obtained from the literature, estimated krill consumption by icefish ranged from 5 000 to 213 000 tonnes (in 2005 and 1990 respectively) using the lower parameter values for consumption rate and ratio of krill in the diet.

Consumption by other demersal fish species

Estimated total annual consumption of krill by demersal fish species other than *C. gunnari* ranged

from 154 000 to 839 000 tonnes. These species accounted for 35–75% of the total consumption of krill by demersal fish around South Georgia. Estimates of annual krill consumption by all demersal fish species around Shag Rocks/South Georgia ranged from 253 000 tonnes to 2 760 000 tonnes. Since 1990 when exceptionally large catches of icefish were taken during the groundfish survey, estimates of annual krill consumption have not exceeded 1 240 000 tonnes.

South Sandwich Islands (Subarea 48.4) and Bouvetøya (Subarea 48.6)

Both islands have not been fished commercially except for longlining on *Dissostichus* spp. Trawling around the islands has been restricted to scientific hauls (Gubsch and Hoffmann, 1981; Targett, 1981, Jones et al., 2004; Kock, unpublished). The species inventories are likely to be incomplete for two reasons: species determination of less abundant species was a low priority (Gubsch and Hoffmann, 1981) or a trawl with too small a mouth opening to collect fish quantitatively was used (Targett, 1981; Jones et al., 2004).

The only three hauls with a commercially sized trawl conducted in April revealed a similar catch composition as around South Georgia with *C. gunnari*, *C. aceratus*, *G. gibberifrons*, *N. rossii* and *L. larseni* as the most abundant species. Catches yielded up to 131 kg 30 min⁻¹ in the 40–200 m depth range.

Main species in commercially sized trawls around Bouvetøya in 1980 were *C. gunnari*, *C. aceratus* and *L. squamifrons*. Catches taken deeper than 350 m always yielded less than 100 kg 60 min⁻¹ (Gubsch and Hoffmann, 1981). No stomach content analysis has been conducted on fish from Bouvetøya. The limited number of quantitative stomach content analyses (Targett, 1981) does not allow an estimate of fish biomass and annual food consumption for the two island groups.

Prince Edward Islands (Subarea 58.7)

The Prince Edward Islands host an impoverished Antarctic fish fauna with 33 species of which only 10 are notothenioids (Gon and Klages, 1988). Very little is known about their abundance. Based on calculations of the excess supply of crustaceans, it was estimated that it could sustain a fish

biomass of 23 000 tonnes. Most of the existing biomass is made up of mesopelagic myctophids with *K. anderssoni* as the dominant species. They feed on copepods and ostracods (Perissinotto and McQuaid, 1992).

The prey composition of demersal fish in the Prince Edward Islands has been studied in five species (two offshore: *L. larseni* and *G. marionensis*, and three inshore: *N. macrocephala*, *N. coriiceps* and *Harpagifer georgianus*) (Blankley, 1982; Perissinotto and McQuaid, 1992; Bushula et al., 2005). All three inshore species preyed almost entirely on benthic prey (Blankley, 1982). *Gobionotothen marionensis* fed on benthic organisms (Bushula et al., 2005). *Lepidonotothen larseni* appear to feed mostly on chaetognaths and copepods. It was only the size class 50–59 mm SL that took euphausiids (mostly *E. vallentini*) in small numbers (Bushula et al., 2005). A small sample of *L. larseni* obtained in the winter of 1989 contained larger numbers of euphausiids (Perissinotto and McQuaid, 1992). The limited information suggests that it is unlikely that fish have a significant impact on pelagic prey resources around the Prince Edward Islands (Miller and Hampton, 1989).

Daily mean food consumption was 4.5 and 5.2% of the mass dry weight of *L. larseni* and *G. marionensis* respectively (Bushula et al., 2005). No conversion factor from dry weight to wet weight was available.

Iles Kerguelen and Heard and McDonald Islands (Divisions 58.5.1 and 58.5.2)

Inventories of the coastal fish fauna have been provided in Andriashev (1965, 1987), Duhamel (1987), Duhamel et al. (2005), Williams and de la Mare (1995), Williams (2006), Nowara and Lamb (2007) and Duhamel and Hauteceur (2009). The coastal fish fauna at Heard and McDonald Islands almost completely overlaps with that described for the French EEZ around Iles Kerguelen, and shows broad similarities with the fish faunas of other sub-Antarctic islands in the southern Indian Ocean, and also with Macquarie Island and the islands of the South Atlantic (e.g. Gon and Heemstra, 1990; Kock, 1992; Duhamel et al., 2005; Williams, 2006). The pelagic environment over the deeper plateau is dominated by myctophids, with at least

19 species of lanternfish in six genera (Duhamel, 1998; Duhamel et al., 2000; Duhamel et al., 2005; Williams et al., in prep.).

Biomass estimates

As in other areas of the Southern Ocean, bottom trawl surveys formed the basis for biomass estimates of demersal and benthopelagic fish in the region (Williams and de la Mare, 1995; Nowara and Lamb 2007; Duhamel and Hauteceur, 2009). The stratification and sampling was designed around the distribution of Patagonian toothfish and icefish (Welsford et al., 2006). Biomass estimates for other species have not been derived routinely. For example, *L. squamifrons* is known to have high densities of adult fish within a small area south of Shell Bank, which is only occasionally sampled if stations are randomly allocated to this deep southeast stratum (Nowara and Lamb, 2007). Similarly, in the recent POKER demersal trawl survey in the French EEZ between 100 and 1 000 m, biomass of *L. squamifrons* was considered underestimated as the area of historically high abundance was not sampled (Duhamel and Hauteceur, 2009).

Diet and feeding rates

In the absence of *E. superba*, which does not occur around these islands, zooplanktivorous fishes prey on a broader range of euphausiids, mysids, hyperiid amphipods, copepods, ostracods and gelatinous zooplankton.

Demersal nearshore fishes

The most abundant nearshore fish species at Heard and McDonald Islands, and at Iles Kerguelen prior to exploitation, were the unicorn icefish (*Channichthys rhinoceratus*) and mackerel icefish. *Channichthys rhinoceratus* is an active zooplankton predator (especially *E. vallentini* and *T. gaudichaudii*) when young and of fish (*C. gunnari*, *L. mizops*, *L. squamifrons* and *G. acuta*) when adult (Duhamel and Hureau, 1985; Duhamel et al., 2005; Williams et al., in prep.). Daily feeding rates are unknown. However it is common to sample fish with empty stomachs, suggesting that feeding rates are highly variable and may depend on encounters with transient concentrations of prey (Duhamel and Hureau, 1985; Duhamel, 1998).

C. gunnari is likely to be the most important predator of euphausiids in the region. While in the Atlantic sector *C. gunnari* feeds heavily on *E. superba*, this species is absent from the zooplankton on the Kerguelen Plateau. On the Kerguelen Plateau it feeds primarily on other euphausiids (71.4–75.0% occurrence of *E. similis* in gut sampled near Iles Kerguelen, or *E. vallentini*, *E. triacantha* and *T. macrura* near Heard Island), hyperiid amphipods (e.g. *T. gaudichaudii*) and mysids, as well as other fish, including myctophids and juvenile conspecifics (Chechun, 1984; Duhamel and Hureau, 1985; Duhamel 1998; Williams et al., in prep). Daily feeding rations are unknown.

Larger juvenile and adult *D. eleginoides* prey primarily on *L. squamifrons*, *C. gunnari*, mesopelagic fish and squid. Small juveniles (<30 cm) have been recorded preying on zooplankton, including *T. gaudichaudii* and *E. vallentini*, as well as myctophids and planktonic juveniles of *C. gunnari* on the plateau near Iles Kerguelen (Duhamel and Hureau, 1985; Duhamel et al., 2005).

Abundant in the recent POKER survey (Duhamel and Hautecoeur, 2009), *Z. spinifer* exclusively consumes benthic invertebrates. *Notothenia rossii* consumes a broad range of prey, including gelatinous zooplankton (salps, cnidarians and ctenophores), euphausiids, isopods (*Exosphaeroma gigas* and *Serolis* spp.), hyperiid amphipods including *T. gaudichaudii*, and small fish, including *C. gunnari* (Duhamel and Hureau 1985; Duhamel et al., 2005). *Lepidonotothen squamifrons* has a similar generalist diet on the Kerguelen Plateau, eating a mix of planktonic and benthic groups, including gelatinous zooplankton, hyperiid, gammarid and caprellid amphipods, mysids, euphausiids, isopods, decapods, echinoderms, annelids and molluscs, as well as fish eggs and larvae (Duhamel and Hureau 1985; Duhamel et al., 2005).

Impact of predation on euphausiids

Recent sampling indicates that the biomass of *D. eleginoides* < 30 cm, and hence their contribution to zooplankton predation, is insignificant relative to that by other groups due to their low overall biomass. Although approximately 125 000 tonnes (c. 75 million individuals) of toothfish were estimated to be present from 100 to 1 000 m depth in the French EEZ (Duhamel and Hautecoeur, 2009), small fish made up less than 10% of estimated

number, and as the average weight of a < 30 cm fish is < 0.2 kg, < 2 000 tonnes of juvenile toothfish are likely to be present on the Kerguelen Plateau. Abundance of juveniles prior to exploitation was unknown.

Biomass and population structure of *C. gunnari* varies widely from year to year, as reflected in the wide interannual range of yield estimates for the fishery in the Australian EEZ around Heard and McDonald Islands, e.g. 292 tonnes in 2003/04 increasing to 1 864 tonnes in the following year (SC-CAMLR, 2007a). Hence their impact on the zooplankton community is likely to vary substantially from year to year. Table 12 shows estimates of biomass for *C. gunnari* from French surveys in 1987/88 and 2006, and Australian surveys over the last three years and prior to fishing in the early 1990s (Williams and de la Mare 1995; Constable et al., 2005; Welsford, 2006; Welsford et al., 2006; Duhamel and Hautecoeur, 2009; Duhamel et al., 2011).

Mean biomass estimates provided in Table 12, the proportion of euphausiids in the diet of fish from near Iles Kerguelen (Duhamel and Hureau, 1985) and estimates of annual consumption by body weight from the South Atlantic (7.3 times the body weight per year, this paper), these data indicate that the expected euphausiid predation could range from around 11 000 tonnes in years of low abundance, such as in 2007, to up to 162 000 tonnes in years of high abundance, such as 1993. If these rates of consumption were valid when during unregulated fishing upwards of 70 000 tonnes were removed in a single season in 1978, these fish could have predated upwards of 357 000 tonnes of euphausiids in one year.

The high-Antarctic zone

The waters of the northern Antarctic Peninsula host elements of the low- and high-Antarctic ichthyofaunas (Kock and Stransky, 2000; Jones and Kock, 2006): low-Antarctic species, such as *C. gunnari* or *C. aceratus* have disappeared while others, such as *G. gibberifrons* and *L. nudifrons*, appear to be more resilient to lower temperatures and are still abundant. The abundance of high-Antarctic species such as *C. wilsoni* or *T. newnesi*, increases substantially compared to the South Shetland Islands. The air temperature and the sea-surface temperature of the northern Antarctic Peninsula have increased by

almost 3°C and more than 2°C respectively in the past 50 years (King and Comiso, 2003; Turner et al., 2005, 2008; Ducklow et al., 2007). It may be debatable from a zoogeographical point of view if, or to what extent, the northern Antarctic Peninsula still forms part of the high-Antarctic zone or is now better included in the southern Scotia Arc (as CCAMLR does for statistical reasons). For the time being, the Antarctic Peninsula is still considered as part of the high-Antarctic region.

Biomass estimates

Abundance estimates obtained from fishing trials in the second half of the 1970s and early 1980s resulted in a mean fish biomass of 4.6–5.1 tonnes km⁻² extrapolated over the whole area (Lubimova and Shust, 1980).

Antarctic Peninsula (Subareas 48.1 (part) and 88.3)

It is likely that fish biomass, at least of *C. wilsoni*, was much larger than normal in those years when concentrations of the species were targeted by the fishery. Soviet investigations measured biomasses of 25 000 and 75 000 tonnes for two concentrations of *C. wilsoni* in the 1980s (Shust, 1998). However, these estimates need to be considered with considerable caution. No information on the method used to obtain these estimates was provided.

The only research survey west of the Antarctic Peninsula was conducted from Trinity Island to the area northeast of Joinville Island in February–March 2006. Biomass estimates obtained from the survey were provided in Table 13. The two most abundant species were *G. gibberifrons* and *C. ras-trospinus* (Table 13).

Cosmonauts and Cooperation Seas and Prydz Bay (Divisions 58.4.1 and 58.4.2)

Using hydroacoustic and standard trawl survey methods, Pakhomov et al. (1991) estimated a demersal fish biomass of 255 715 tonnes in the Cooperation Sea from 30° to 80°E. The total fish biomass in the Cosmonauts and Cooperation Seas from 100–500 m depth was estimated at 552 000 tonnes (Pakhomov, 1997). 46.4% of the biomass was composed of *C. wilsoni*, while 43.3% was formed by *P. antarcticum*. Australian

exploratory fishing conducted in Division 58.4.2 (between 40 and 50°E) in 1999/2000 and 2000/01 confirmed the predominance of *C. wilsoni* in the region (Delegation of Australia, 2001).

Exploratory fisheries were conducted on *Dis-sostichus* spp. on the deep slopes in these divisions. However, no estimates of stock size exist.

Ross Sea (Subareas 88.1 and 88.2)

New Zealand conducted only bottom trawl surveys in the Ross Sea in February–March 2008. Biomass estimates of the most abundant eight species are set out in Table 14(a). By far the most abundant species was *P. antarcticum* on the shelf and *M. whitsoni* on the slope (Table 14a).

Stock size of *D. mawsoni* in the Ross Sea was estimated by CCAMLR to be 71 200 tonnes (59 720–87 900) in 2007 (SC-CAMLR, 2007b). Stock size for *D. mawsoni* in part of Subarea 88.2 (SSRU 882E) was estimated to be 9 530 tonnes (5 340–25 210) in 2006 (SC-CAMLR, 2006b). Information on the abundance of other species has been provided by Eastman and Hubold (1999) and Vacchi et al. (1999). However, their collections have been taken by either small trawls (e.g. Eastman and Hubold, 1999) or various static gear (e.g. Vacchi et al., 1994) and are not readily comparable to biomass estimates obtained from commercially sized trawls and longlines (Hanchet et al., 2008a, 2008b). A comparison of the biomass estimates provided in Table 14(a) with those from other areas of the high-Antarctic is still pending.

Abundance of the slope-dwelling *M. whitsoni* was provided in Table 14(b). No biomass estimates exist for other slope species of the high-Antarctic region. The use of the constant density estimate was the most conservative of the three estimates.

Prey composition

The food composition of small pelagic *D. mawsoni* (<15 cm) consisted of krill and other euphausiids (Rembiszewski et al., 1978 (misidentifying the fish as *D. eleginoides*); Pakhomov and Pankratov, 1991) while larger bottom-dwelling juveniles (17–50 cm long) preyed on fish, mysids and amphipod, and only to a small proportion on pelagic

crustaceans, such as krill (Yukhov, 1982; Eastman, 1985; Gröhsler, 1992; Pakhomov and Tseitlin, 1992; Jones et al., 2003; Kock, unpublished).

Larger (>50 cm) *D. mawsoni* taken in longline fisheries in the Ross Sea fed almost exclusively on bottom-dwelling fish, squid/octopods and larger crustaceans (Fenaughty et al., 2003; Stevens, 2004, 2006; Petrov, 2006; Kokorin, 2008).

The prey composition of *Trematomus* species, *P. antarcticum* and other notothenioids is diverse. Krill and mesopelagic fish as potential prey are absent from the shelf waters of the Ross Sea (La Mesa, 2004a). Most benthic nototheniids are opportunistic feeders: their prey is composed of seasonally and locally abundant zooplankton. Arctedidraconids are benthic sit-and-wait predators. Large bathydraconids prey mostly on fish, while smaller species take mostly benthic crustaceans. Icefish are less dependent on benthic prey. Some combine benthic and pelagic life styles while others feed predominantly on euphausiids (La Mesa et al., 2004a).

Prey composition of most inshore living *Trematomus* spp., such as those taken in the vicinity of scientific stations on the continent, is dominated by benthic organisms (Hureau, 1970; Kiest, 1993; Montgomery et al., 1993; La Mesa et al., 1997, 2000, 2004b; Vacchi et al., 1994). Notable exceptions are *T. newnesi* and *T. eulepidotus* which feed primarily on euphausiids. *Trematomus* species caught in the Cosmonauts and Cooperation Seas feed largely on euphausiids (*E. superba* when taken offshore and more often *E. crystallorophias* when taken closer to the continent) (Roshchin, 1991; Pakhomov, 1997). *Pleuragramma* spp. and several icefish species in the western Ross Sea feed on either fish or *E. crystallorophias* and *T. gaudichaudii* (Takahashi and Nemoto, 1984; La Mesa et al., 1997, 2000, 2004a).

Daily and annual food consumption

Rates of daily food consumption exist for various species in parts of the Indian sector of the high-Antarctic (Table 15). Daily food consumption varied considerably between different studies, for example in *C. wilsoni* from 0.6 to 3.6% of body weight and in *T. eulepidotus* from 1.5 to 4.9% of body weight (Table 15).

The annual feeding rate in proportion of the body weight varied from 2.6 times the body weight in *Cygnodraco mawsoni* to 9.1 times the body weight in *G. acuticeps* (Table 16).

Miller et al. (1985) estimated an annual krill consumption of 1 300 000 tonnes by fish in the Lazarev Sea. Annual krill consumption by fish in the Cosmonauts Sea is provided in Tables 17 and 18. Pakhomov (1997), in summarising previous studies (Pakhomov et al., 1991), estimated that fish occurring in the commercial fishery in the Indian sector of the high-Antarctic took 444 663 tonnes of krill from December to April. Assuming an additional 30% of the summer consumption was taken in winter, the estimated overall krill consumption amounted to 578 062 tonnes annually. It was estimated that shelf species consume 2 320 000 to 3 880 000 tonnes of krill and other pelagic crustaceans in the Indian sector of the high-Antarctic.

Slope-dwelling grenadiers in the Lazarev, Cooperation and Cosmonauts Seas such as *M. holotrachys* and *M. whitsoni*, which live from 400–1 700 m depth, feed on krill when it becomes available. Krill proportion in the diet ranged from 14.5 to 50.0% (Trunov, 1984; Pakhomov, 1997) and declined with increasing depth. To what extent slope-dwelling fish contribute to overall krill consumption by fish is unknown.

Discussion

Euphausiids are by far the most abundant food organisms for mesopelagic and demersal fish in the Southern Ocean. While *E. superba* is a predominant prey item in the Atlantic province, other euphausiids such as *E. vallentini*, *E. similis*, *T. vicina* and *T. macrura* replace *E. superba* in the Prince Edward Islands (Perissinotto and McQuaid, 1992; Pakhomov and Froneman, 1999), around Iles Kerguelen (Pakhomov, 1995) and Heard and McDonald Islands (Williams et al., in prep.). Krill is largely taken by fish occurring on the shelf but is also found regularly in the diet of fish in inshore waters in the South Shetland Islands (Barrera-Oro, 2002), less frequently at South Georgia (Burchett, 1983) and probably also in the South Orkney Islands. In addition, recent investigations revealed that krill is a much more important food item for some abundant slope species than hitherto thought.

Ice krill replaced krill in coastal areas of the high-Antarctic such the Cosmonauts, Commonwealth and Ross Seas.

In order to estimate annual consumption of krill and other pelagic resources by mesopelagic and demersal fish, the following information is required:

- (i) biomass estimates of the fish predators of krill
- (ii) quantitative diet composition
- (iii) meal size, digestion and gastric evacuation rate.

Such estimates will be affected by uncertainties or biases introduced by the methods whereby the information has been collected, as well as temporal and spatial variation.

Uncertainties in biomass (abundance) estimates

Mesopelagic fish

Estimates of the overall food consumption by myctophids bear significant uncertainties.

Uncertainties are:

- (i) the lack of target strength verification of any myctophid species to bound hydroacoustic biomass estimates (note that the interspecific variability in swim bladder size will require species (and possibly size) specific values for target strength)
- (ii) the lack of information on the variability of myctophid aggregations over space and time, except in some generic terms.

Some myctophids have either a residual swim bladder (e.g. *Gymnoscopelus*) or a small one (*E. antarctica*). These are likely to be difficult to discriminate from macro-zooplankton even with multi-frequency echosounders. Others (*E. carlsbergi*, *Protomyctophum* sp.) have large well-developed swim bladders that give a strong signal easily distinguishable from macro-zooplankton with high target strength.

Considerable advances have been made in the design and analysis of hydroacoustic surveys in the past 30 years. Measurements changed from

analogous single-frequency measurements to multi-frequency measurements and new methods of estimating target strength were designed (Reiss et al., 2008). This led to several recalculations of the krill biomass estimated from the First International BIOMASS Experiment (FIBEX) survey in 1980/81 (Trathan et al., 1995) and the CCAMLR-2000 Survey (Hewitt et al., 2004; SC-CAMLR, 2010). Biomass from the CCAMLR-2000 Survey is currently estimated at 60 million tonnes in the western Atlantic sector. This value is likely to change in the future as new methodology is being developed.

These advances have not been applied to abundance estimates of myctophid fish. Given the lack of target strength estimation being provided for myctophids, it seems questionable that estimates of myctophid abundance from hydroacoustic surveys in the late 1980s are valid. Given the considerable progress being made in acoustic estimates of mesopelagic fish in recent years, it is likely that new hydroacoustic surveys in the Southern Ocean could be conducted to provide valid estimates of the biomass of mesopelagic fish.

The design of surveys to estimate demersal fish biomass

Bottom trawl surveys in CCAMLR waters are designed to estimate biomass of a range of species of potential commercial interest with similar precision. They were conducted (with very few exceptions when semi-pelagic trawls were used, e.g. Balguerías, 1989) using commercially sized two-panel or four-panel bottom trawls. Net width (horizontal opening) was in the range of 16–20 m. Net height (vertical opening) ranged from 3 to 8 m with the vertical opening of two-panel trawls at the lower end of the range (see Jones et al., 2000; Kock and Jones, 2005 for discussion).

However, precision of simultaneous abundance estimates of a range of species may be compromised because survey design does not capture the abundance patterns of all species adequately. *Nottothenia rossii*, for example, forms large aggregations in very limited areas while large areas are only thinly populated (Kock et al., 2004; Duhamel and Hautecoeur, 2009). Missing these concentrations during a survey would lead to gross underestimates of the biomass of *N. rossii*. The comparatively low number of hauls per survey stratum and a large variability in catches could lead to comparatively

large confidence intervals of the biomass estimates and consequently a low precision of the survey estimate(s).

Moreover, it is assumed that all species are equally vulnerable to the trawl and that all fish in the path of the trawl are being caught, i.e. catchability c is assumed to be 100% (or $c = 1$). This is unlikely to be the case: species such as larger *C. aceratus* appear to stay on the bottom during the day (and catchability may be as high as 0.9 or even 1). Young *C. gunnari* to age 2–3 lead a benthopelagic mode of life. Echosounder recordings demonstrate that they occur regularly 5–20 m above the bottom, i.e. often outside the reach of a bottom trawl (Frolkina, 2002). As a consequence, surveys with a benthopelagic trawl catch young *C. gunnari* much more quantitatively than do bottom trawls (Balguerías, 1989). Acoustic data showed that older *C. gunnari* stay close to, or at, the bottom during the day (when most surveys are being conducted). Their vertical migration appears to be closely tied to the diel light signal (van Wijk et al., 2001).

Abundance estimates originating from trawl surveys have so far been considered in absolute terms. Given the problems caused by the compromise to try and estimate several species with different catchability simultaneously, it is suggested that estimates from CCAMLR trawl surveys provide relative abundance rather than estimates of absolute abundance.

Diet composition

Mesopelagic fish

It is generally accepted that mesopelagic fish feed on krill and other euphausiids only if their mouth width exceeds a certain threshold (Sabourenkov, 1990; Lipskaya et al., 1991). This limits the number of mesopelagic species capable of feeding on Antarctic euphausiids to a few species of the genera *Electrona* and *Gymnoscopelus* and some representatives of the families Paralepididae, Gempylidae, Anotopteridae, Notosudidae and Bathylagidae. The small size (<50–60 mm) of the majority of myctophids in the Southern Ocean, such as *Protomyctophum* species and the closely related *K. anderssoni* (Hulley, 1990), does not allow them to include juvenile and adult krill and other larger prey in their diet.

The limited number of quantitative food studies conducted thus far suggests that the true Antarctic myctophids of the genera *Electrona* and *Gymnoscopelus* are the main consumers of krill and other larger zooplankton south of the APFZ. The most abundant myctophid in the northern part of the Southern Ocean, *E. carlsbergi* (Filin et al., 1990), consumes krill only in small numbers (5–6% by weight).

Most studies on the food composition and daily food intake of *E. antarctica* and *Gymnoscopelus* species originate from areas of comparatively high krill concentrations in the Scotia Sea and adjacent waters (e.g. Rowedder, 1979b; Lancraft et al., 1989, 1991; Pusch et al., 2004). There is evidence from *E. antarctica* caught in areas of low krill density that they feed primarily on copepods and zooplankton other than krill (Pakhomov et al., 1996). Fatty acid profiles suggest that the diet of *G. opisthopterus* and *G. nicholsi*, previously thought to be mainly krill feeders, includes copepods and other zooplankton to a much larger extent than previously thought (Phleger et al., 1999). Therefore, stomach contents collected from mesopelagic fish taken in, or in the vicinity of, krill aggregations may lead to overestimation of the true proportion of krill in the diet of mesopelagic myctophids due to the unknown extent of opportunistic feeding on krill aggregations.

Investigations on the food and feeding of mesopelagic fish other than myctophids were often confined to small sample sizes spread over a large area of the Southern Ocean. Findings from these studies may not be representative of the diet of these species in the Southern Ocean. The paucity of quantitative food studies in these species prevented any assessment of the extent to which non-myctophid species contribute to the krill and other euphausiid consumption in the Southern Ocean.

Demersal fish

Icefish feed primarily on krill and fish while a number of nototheniid species prey largely on benthic species (Kock, 1992). Many fish species are opportunistic feeders which expand/shift their food niche when krill becomes available. Food studies show that in typical benthos feeders, such as *G. gibberifrons*, krill forms 30–40% of their diet (e.g. Gröhsler, 1992).

Another question to be resolved is if, and to what extent, food intake is reduced or stopped in the final stage of gonad development. Studies to date have been too short term to estimate how often benthos feeders switch to pelagic prey and if estimates of pelagic prey consumption are robust enough to be used as estimates of krill consumption over a longer period of time such as months or season.

A further question that awaits resolution is to what extent food composition remains the same seasonally and between seasons. A change in food composition is apparent in some species in winter, such as juvenile *N. rossii* (Burchett, 1983; Casaux et al., 1990), *N. coriiceps* and *Harpagifer antarcticus* in the Antarctic Peninsula region (Daniels, 1982), and *T. eulepidotus* and *C. myersi* (Wöhrmann, 1988) and juvenile *P. antarcticum* in the Weddell Sea (Hubold, 1991). Concomitant with an increase in gonad weight, the proportion of fish with empty stomachs increases (Kock, 1981; Duhamel and Hureau, 1985; Duhamel, 1987; Gorelova and Shandikov, 1988; Wöhrmann, 1988). In *C. gunnari* at South Georgia, for example, more than 90% of the spawners were found to have empty stomachs when starting the final stage of the spawning migration towards inshore waters (Kock, 1981).

Food composition in quantitative terms is much better understood in demersal fish than in mesopelagic fish. Much of the seasonal difference in feeding between summer and winter is due to temperature and photoperiodicity effects (Targett, 1990).

Stomach content wet weight, meal size, their seasonal variation and gastric evacuation rates

Mesopelagic fish

Information on daily feeding rations of mesopelagic fish is limited. The 1.16–5.6% of body wet weight estimated for *E. carlsbergi* and *E. antarctica* (Rowedder, 1979a; Naumov et al., 1981; Gerasimova, 1990; Podrazhanskaya and Tarverdiyeva, 1991; Pusch et al., 2004) may indicate the range of daily food consumption in periods of various prey availability over the whole summer period. They are similar to feeding rations of demersal fish (see below). It is unknown if, or to what extent, myctophids and other mesopelagic fish reduce their food intake in winter.

Demersal fish

Most of the estimates of daily food intake of demersal fish ranged from 0.5–2.5% body weight. These values may be exceeded in summer locally and temporarily when krill is abundant and fish feed intensely on krill (Kock, 1992).

Johnston (1993) suggested that the limited aerobic scope of Antarctic fish may necessitate marked seasonal changes in energy allocation. Limited field experiments (Coggan, 1997) and laboratory experiments under stable feeding conditions indicate a decline in food intake in winter (Johnston and Battram, 1993; Boyce et al., 2000). Studies on energy requirements of notothenioid fish suggest that the food demands of adult *N. rossii* and *G. gibberifrons* at South Georgia are reduced by a factor of 2–3 in winter compared to summer (Chekunova and Naumov, 1982a, 1982b). The condition factor of juvenile *N. rossii* at South Georgia exhibited a strong seasonal signal usually being lowest in winter (Burchett, 1983) corroborating these results. Similar results were obtained for *T. newnesi* and *N. coriiceps* (Linkowski et al., 1983). *Notothenia coriiceps* spent most time in summer foraging and had a positive growth rate, and in winter was mostly sedentary, showing a decline in growth (Campbell et al., 2008). Feeding ratios in *Harpagifer* spp. fed mysid shrimps ad libitum also declined by a factor of 2 (1.3 vs. 2.5%) from summer to winter. *Harpagifer* spp. fed only at maintenance level during winter conditions despite abundant food being available (Boyce et al., 2000).

Other investigations, however, showed no decline in feeding intensity during winter (Tarverdiyeva, 1972; Hubold, 1991). The lower energy content of some prey organisms in winter and a resulting lower energy intake at the same level of feeding may partly resolve this contradiction (Burchett, 1983).

Crucial parameters to estimate food consumption are average stomach content weight (in terms of mass or meal size in captive fish), seasonal variation, gut evacuation rate (as a proxy to digestion time) in relation to meal size and relative gut evacuation time (as a proxy to daily feeding rate) (Kock, 1992; Boyce et al., 2000). The question whether fish empty their stomachs completely before starting to feed again or not still awaits resolution. Planktivorous species, such as *L. larseni*, appear not to empty their stomachs

completely before they commence feeding again (Gorelova and Shandikov, 1988). Other species, such as piscivorous adult *C. aceratus*, *Cryodraco antarcticus* or *Chionobathyscus dewitti* (Kock, 1981; Kock and Jones, 2002) are commonly found to have their guts empty. It is still unknown if this represents a low feeding intensity, if gut contents are regurgitated while being caught (Kock, 1981) or if it is a combination of the two.

Experiments under controlled environmental and feeding conditions appear to be an ideal way of making progress in estimating food consumption. However, such experiments are only feasible in a few small-sized relatively sluggish Antarctic species living in shallow water such as *H. antarcticus*. *Harpagifer antarcticus* is small enough to be kept under semi-natural conditions in large tanks (Boyce et al., 2000). However, it is unknown to what extent food consumption rates estimated from laboratory studies are representative for conditions in the wild and/or for other Antarctic fish, in particular when occupying different ecological niches.

A number of studies on fish and invertebrates in the Southern Ocean indicate that physiological processes, such as digestion, take considerably longer than in temperate- or tropical-water species (Johnston et al., 1991; Boyce and Clarke, 1997). The limited information on digestion time obtained so far (Crawford, 1978; Montgomery et al., 1989) fall within the range of values which could be expected from extrapolating from temperate-water fish (Montgomery et al., 1989) and corroborates assumptions that gastric evacuation rates might not be cold-adapted (Crawford, 1978). However, Härtling (1991) found evidence in *P. antarcticum* that the digestion enzyme pepsine may be cold-adapted while trypsin is not.

Digestion times have been determined either by:

- (i) collecting faeces in aquarium experiments at regular time intervals after fish had been fed (Boyce et al., 2000)
- (ii) killing fed fish at certain time intervals, or
- (iii) catching fish in the wild at certain time intervals in order to follow the break-down of the stomach content under the assumption that fish in localised areas share a common feeding history.

(Everson, 1970; Tarverdiyeva, 1972, 1982; Crawford, 1978; Gorelova and Gerasimchuk, 1981; Kock, 1981; Naumov et al., 1983; Montgomery et al., 1989; Kock et al., 1994, 2007a; Flores et al., 2004).

Results obtained by methods 2 and 3 suggest digestion times of 48–96 hours, depending on the nature of the prey, meal size and environmental temperature. It is possible that experiments using method 2 have been negatively influenced by handling-stress. Digestion times derived from intervals between periods of intensive feeding (method 3) were lower, ranging from 24–72 hours. However, digestion times well in excess of 24 hours make it extremely difficult to detect feeding cycles because cycles detected may not necessarily reflect periods between one stomach filling and the other.

An exponential decay model fitted to the decline in stomach content of *Pagothenia borchgrevinki* in the Ross Sea resulted in half-life times varying by a factor of 3–4 from soft-bodied smaller prey to crustaceans with a hard exoskeleton (Montgomery et al., 1989). Decay times of fish prey have not been considered yet. They are likely to be much longer than for crustaceans.

The significance of krill as prey for Antarctic fish

Krill is the dominant food item of the most abundant mesopelagic and demersal fish species in the seasonal pack-ice zone of the Atlantic sector and most of the high-Antarctic zone in the Atlantic and Indian sectors. Krill is replaced by ice krill in some areas close to the Antarctic continent such as the inner Ross Sea, and by other euphausiids around sub-Antarctic islands of the Indian sector.

The distribution and abundance of krill and other zooplankton is a function of the timing and pattern of sea-ice extent and retreat in spring–summer, affecting local phytoplankton production and krill emergence from the marginal ice zone (Murphy et al., 2007b). Changes in the krill biomass have occurred in the Atlantic sector. While the origin of this change probably reflects changes in the physical environment and a potential competition with salps, the proximate effects of these changes are almost certainly mediated through changes in food-web processes (Kock and Everson, 2003).

Information on the reproduction of krill is mostly available from the Atlantic sector as data from the Indian and Pacific sectors is scarce (e.g. Fraser, 1936; Kawaguchi et al., 2010). Krill reproduction in the Atlantic sector occurs in a broad belt from west of the Antarctic Peninsula to at least the South Orkney Islands, but not at South Georgia. The abundance of krill (and other zooplankton) around the island is strongly influenced by advection from different regions such as the Southern Antarctic Circumpolar Current Front and the Weddell Gyre, in proportions varying on a monthly and annual scale (Fedoulov et al., 1996; Murphy et al., 2004; Siegel et al., 2004). Years of krill scarcity seem to have occurred more frequently at South Georgia since 1990 (Reid and Croxall, 2001).

These pulses of krill at South Georgia are clearly reflected in large variations of the proportion of krill in the diet of fish over space and time (Kock et al., 1991, 1994). In 1977/78, 1990/91, 1993/94 or 2003/04 (Reid et al., 1999; Reid and Croxall, 2001) when krill was scarce around the island, most predators experienced low breeding success.

The balance between krill supply and predator demand may have changed. Some krill predators, such as Antarctic fur seals, have the capacity to adapt to changes in the availability of their diet to the extent that they can forage as far out as the shelf edge or the slope (e.g. Boyd et al., 1994). Others such as gentoo penguins (*P. papua*) who mostly feed inshore, and certain fish species which live on the upper part of the shelf (<300 m), such as mackerel icefish, cannot. Mackerel icefish, as the most abundant among the krill-feeding fish species is unable to replace krill with food items of similar energetic content. As a consequence, condition indices of mackerel icefish declined in seasons when krill is scarce (Everson et al., 1997; Everson and Kock, 2001). A large proportion of fish which had spawned this season were dying in the following months (Main et al., 2009) because most fish were unable to replenish their energy stores after spawning. In addition, the proportion of fish not spawning that season increased substantially (Kock, 1989; Everson et al., 1997; Kock and Everson, 2003).

Notothernia rossii and *C. gunnari* were primarily krill feeders in the Atlantic sector and fed on other euphausiid species in the Indian sector. The commercial fishery depleted those species. Consequently, the krill consumption by fish was reduced

substantially during the period of intensive fishing (Kock, 1992). Krill consumption around Elephant Island in the second half of the 1980s, for example, was only 10–20% of the krill consumption before the onset of commercial exploitation in the mid-1970s (Kock, 1985; Gröhsler, 1992).

Little is known on the fishery in the high-Antarctic Zone from the second half of the 1970s to the second half of the 1980s, other than the catches reported to CCAMLR. It was again one of the main krill predators, the spiny icefish *C. wilsoni*, which was targeted. It is unknown to what extent stocks of *C. wilsoni* and some *Trematomus* species, such as *T. eulepidotus*, which feed on krill, have been affected by the fishery. However, it is likely that krill consumption has declined in the wake of these fisheries in the high-Antarctic zone as well.

Most fisheries in the Southern Ocean had been closed by the end of the 1989/90 season, including those in the southern Scotia Arc and around the Antarctic continent. To what extent krill consumption by demersal fish had increased following the closure is unknown. Mackerel icefish as an important krill predator does not seem to have increased in biomass substantially since then (Jones et al., 2000, 2001, 2003; Jones and Kock, 2009; Kock et al., 2002, 2007a). Occasional large catches during surveys in the late 1990s and the 2000s (e.g. Kock et al., 2007a) and increased catches of juveniles in inshore waters (Barrera-Oro and Marschoff, 2007) suggest that *N. rossii* have recovered to some extent from depletion in 1979/80. However, surveys targeting *N. rossii* have not been conducted to demonstrate such increase (Kock et al., 2004).

It was more than 30 years ago that first attempts were made to quantify food consumption and generate estimates of overall krill consumption by Antarctic fish (Everson, 1977; Lubimova and Shust, 1980; Kock, 1985, 1992). These estimates were extrapolations from the few biomass estimates of fish available at that time and the proportion of krill in the diet of fish mostly derived from qualitative studies. Both Lubimova and Shust (1980) and Kock (1985) reported similar estimates of krill consumption in the seasonal pack-ice zone at the onset of commercial harvesting of finfish in 1969/70: 5 400 000–6 600 000 and 5 000 000 tonnes respectively. However, the assumptions underlying their calculations were also similar. The mean estimate in this paper of the annual krill consumption of the

nine most abundant species in the Southern Scotia Arc was 34 200 tonnes (Table 18). This is likely to be an underestimate of the true krill consumption given that coastal fish species, such as *N. coriiceps*, juvenile *N. rossii* or *T. newnesi* which also take krill in some numbers, were addressed either partially or not at all by trawl surveys.

Pakhomov (1997) estimated the annual consumption of krill and other pelagic crustaceans by demersal fish at 2 320 000 to 3 880 000 tonnes in the Cosmonauts, Cooperation Seas and in Prydz Bay. Lubimova and Shust (1980) calculated the annual consumption of euphausiids (primarily *E. superba* and *E. crystallorophias*) in the high-Antarctic zone at 18 000 000 to 20 000 000 tonnes. Extrapolating this figure would imply that demersal fish consume 26 000 000 to 29 000 000 tonnes year⁻¹ of euphausiids in the Southern Ocean (Pakhomov, 1997). This estimate is remarkably similar to a previous estimate of 23 400 000 to 26 600 000 tonnes of euphausiids taken by demersal fish in the Southern Ocean (Lubimova and Shust, 1980) (Table 19). However, the closeness of the two estimates should not be considered as indicating any degree of precision.

A few new estimates of krill consumption have become available regionally since the 1980s (e.g. Pakhomov and Pankratov, 1991; Pakhomov et al., 1991; Pakhomov and Tseitlin, 1992; Gröhsler, 1992). However, the many gaps still existing in Table 19 clearly indicate how little we have advanced since the 1980s and how far we still are from providing more precise estimates of krill consumption by Antarctic fish. The imprecise nature of abundance estimators, coupled with a wide range of estimates for daily food consumption in summer and a scarcity of such data in winter, are daunting problems to overcome if we are to successfully construct ecosystem and food-web models in the Southern Ocean in the near future. It is considered to be premature to add new estimates of krill consumption on an ocean-wide or Southern Ocean-wide scale to those which already exist.

Ainley and Blight (2008) hypothesised that a major mid-1980s shift in the ecological structure of significant portions of the Southern Ocean was partially due to the serial depletion of fish by intensive industrial fishing from the late 1960s to the early 1980s, rather than solely an effect of climate factors as previously hypothesised. Over a brief

period of time (1969–1973), the two largest finfish populations in the Southern Ocean, with one of them, *N. rossii* at South Georgia, a large krill predator, were depleted (Kock, 1991). Another abundant species, *C. gunnari*, a prime krill feeder in the Atlantic sector, was depleted at Iles Kerguelen, Heard and McDonald Islands, South Georgia, the South Orkney Islands and South Shetland Islands, from 1975 to 1985 (Kock, 1981).

At the same time, a climate index, the Southern Annular Mode, once oscillating between two states, has remained in its ‘positive mode’ since the time of the fish extraction. Correlations between predator populations and fish biomass within predator foraging areas appear to indicate that some predators of fish such as southern elephant seals (*Mirounga leonina*), macaroni penguins (*Eudyptes chrysolophus*) and imperial shags (*P. atriceps*) declined in some areas of the Southern Ocean over the past decades. Ainley and Blight (2008) concluded that the major extraction of fish which were an important part of the food web of the Southern Ocean’s northern continental and insular shelves, compounded the ecosystem effects of the historical extraction of whales.

Some inconsistencies rested with the analysis: Antarctic fur seals feed predominantly on krill at South Georgia (Reid, 1995; Reid and Arnould, 1996) and krill and myctophids in the southern Scotia Arc (Daneri and Coria, 1992, 1993; Osman et al., 2004) while they take myctophids in parts of the Indian Ocean (Duhamel, 1991; Green et al., 1989, 1991; Williams et al., 2001). At South Georgia, for example, Antarctic fur seals are able to switch their prey to fish at times when krill is sparse (Everson et al., 1991; 1999; Main et al., 2009) such as at South Georgia in certain years (Reid and Croxall, 2001). Macaroni penguins eat small krill and copepods at South Georgia (Reid and Croxall, 2001) and mostly myctophids around sub-Antarctic islands of the Indian Ocean (Cooper et al., 1990; Deagle et al., 2007).

Champtocephalus gunnari stock around South Georgia increased in size only after *N. rossii* had been depleted (Frolkina et al., 1998). The Prince Edward Islands and Iles Crozet Islands have been exploited only by longlining targeting *D. eleginoides* (SC-CAMLR, 2008b and 2008c) whereas other species remained unaffected by fishing (Blankley, 1982; Bushula et al., 2005).

Elephant seals, considered to be another important fish predator, feed mostly over the slope and in pelagic waters with squid as their primary prey. They appear to take shelf fish species only to a limited extent (e.g. Jonker and Bester, 1998; Brown et al., 1999; Guinet et al., 1999; Daneri et al., 2000; Bradshaw et al., 2003; Green and Burton, 2006; Reid and Nevitt, 2006). The decline of elephant seals and other predators in parts of the Southern Ocean is only partly (if at all) consistent with the decline of potential fish prey as suggested by Ainley and Blight (2008). Instead, in elephant seals, for example, a conglomerate of factors including local predation by killer whales and intraspecific resource competition is currently considered as a cause for regional difference in declining trends in various southern elephant seal populations (McMahon et al., 2003). Similar conglomerates of several factors are likely to explain declines in other species.

Conclusion

This review demonstrates that substantial progress has been made in assessing the importance of fish in Southern Ocean food webs since the first concerted attempts had been made to elucidate their role in the late 1970s/early 1980s. Despite the progress being made, it is still impossible to quantify consumption of krill and other pelagic organisms except in broad terms and with wide confidence limits. This difficulty was highlighted when Hill et al. (2007) attempted to estimate predator demands for krill within proposed small-scale management units (SSMUs) by combining data from generic notothenioids and generic myctophids.

Similarly, estimates of consumption of krill by demersal fish are substantially affected by the high variability in densities of these fish. This may be a result of high variability in suitable fish habitat in the region. It is recommended that improvements in understanding the linkages between demersal fish and krill will require a better understanding of the distribution of fish habitats and the relationships of different demersal species with those habitats.

In addition to demersal fish which had been the focus of research in the last four decades, a substantial step forward to improve our understanding of the role of fish in various Antarctic ecosystems would be to focus research on mesopelagic fish and their role as predators of krill and other pelagic resources. In doing so, it is necessary to:

- (i) obtain reliable estimates of current biomass of mesopelagic fish with narrower confidence limits
- (ii) if possible, reanalyse data from past hydro-acoustic surveys to estimate a time series of abundance of mesopelagic fish
- (iii) obtain estimates of the quantitative composition and daily food intake of the most abundant myctophid species over a wide range of ocean, including krill-rich and krill-poor areas
- (iv) identify the spatial distribution of benthic fish habitats and the distribution and abundance of demersal fish relative to those habitats.

Lastly, it is considered important to incorporate *C. gunnari* in the western Atlantic sector into CEMP in order to satisfactorily account for the requirements and dynamics of this species in consideration of ecosystem-based fisheries management of Antarctic krill fisheries.

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Table 1(a): Biomass (103 tonnes) and density (g m^{-2}) of myctophids in the Atlantic sector estimated from hydroacoustic surveys in the summer seasons 1987 to 1989 (Filin et al., 1990; Kozlov et al., 1990; Shust and Kozlov, 1990; Collins et al., 2012).

| Area | Biomass (10 ³ tonnes) | Density (g m^{-2}) | Proportion of main species | Other species |
|--------------------------------------|----------------------------------|-------------------------------|---|--|
| 48°–54°S 40–48°W | 1.200 | 3.22 | <i>Electrona carlsbergi</i> 91–97% north of 53°S, 75–60% south of 53°S | <i>Gymnoscopelus nicholsi</i> , <i>G. braueri</i> , <i>G. fraseri</i> , <i>E. antarctica</i> |
| Shag/Black Rocks (South Georgia) | 160 | 22.0 | <i>E. carlsbergi</i> 90% | <i>G. nicholsi</i> , <i>Krefflichthys anderssoni</i> , <i>Paradiplospinus gracilis</i> |
| NE South Georgia APF 48–51°S 36–41°W | 1 200 300 | 15.0 2.49 | <i>E. carlsbergi</i> > 90% <i>E. carlsbergi</i> 90% | <i>G. nicholsi</i> , <i>G. piabilis</i> , <i>Protomyctophum choriodon</i> , <i>K. anderssoni</i> |
| 51°30'–56°S 20°30'–26°30'W | 855 | 4.33 | <i>E. carlsbergi</i> 98–100% | |
| 51°30'S–55°S 8°–18°30'W | 829 | 3.06 | <i>E. carlsbergi</i> 98–100% | |
| 49°–54°S 25°–40°W | 743–2 944 | 1.3–5.11 | <i>E. carlsbergi</i> 100% | |
| 56–70°S 50–8°W summer | 12 302 | 2.5 | <i>E. antarctica</i> , <i>Gymnoscopelus</i> spp. | |
| 56–70°S 50–8°W winter | 2 428 | 0.4 | <i>E. antarctica</i> , <i>Gymnoscopelus</i> spp. (proportions not provided) | |

Table 1(b): Biomass and density (g m^{-2}) of myctophids from night hauls in the Atlantic sector estimated from RMT25 catches (Piatkowski, 1985; Collins et al., 2012).

| Area | Biomass (10 ⁶ tonnes) | Density (g m^{-2}) | Main species |
|------------|----------------------------------|-------------------------------|---|
| Scotia Sea | 4.5 | 3.04 | <i>Electrona carlsbergi</i> , <i>E. antarctica</i> , <i>Gymnoscopelus</i> sp. |

Table 2(a): Frequency of occurrence (%) of krill (*Euphausia superba*) in the diet of various myctophid species in various areas of the Southern Ocean in austral summer (the true proportion of *E. superba* was likely to be higher given the high proportion of unidentified euphausiids in the stomachs) (compiled from Rowedder, 1979a; Naumov et al., 1981; Lubimova et al., 1983; Kozlov and Tarverdiyeva, 1989; Oven et al., 1990; Sabourenkov, 1990; Flores et al., 2008).

| Area | <i>Electrona carlsbergi</i> | <i>E. antarctica</i> | <i>Gymnoscopelus nicholsi</i> | <i>G. braueri</i> | <i>G. opisthopterus</i> |
|------------------------|-----------------------------|----------------------|-------------------------------|-------------------|-------------------------|
| Bellingshausen Sea | 5.0–6.0 | | | | |
| D'Urville Sea | 2.3–3.3 | | | | |
| Cosmonauts Sea | 0 | 31.3 | 60.2 | 40.0 | |
| Lazarev Sea | | 45.7 | | 72.7–73.0 | 100 |
| | | 27.8** | | | |
| South Georgia | 1–10.4 | 41.1–72* | 21–90 | | |
| South Orkney Islands | | 90* | 100 | | |
| South Shetland Islands | | 85* | 92–96 | | |
| | | 53.1 | 58.3 | | |
| Peter 1st Island | | 100 | | | |
| South Sandwich Islands | | 47* | | | |

* *E. superba* and *Thysanoessa macrura*

** euphausiids

Table 2(b): Quantitative proportion of krill (in %) in the diet of two myctophids by weight.

| Locality | <i>Electrona antarctica</i> | <i>Gymnoscopelus nicholsi</i> | Source |
|------------------------|-----------------------------|-------------------------------|--------------------|
| South Georgia | 54.4 | | Rowedder, 1979a |
| Elephant Island | 57.7 | | Rowedder, 1979a |
| South Shetland Islands | 53.3 | 58.1 | Pusch et al., 2004 |
| South Sandwich Islands | 56.2 | | Rowedder, 1979a |

Table 3: Daily food rations (in % of the body wet weight) of myctophids in the Southern Ocean.

| Region/Area | <i>Electrona carlsbergi</i> | <i>E. antarctica</i> | <i>Gymnoscopelus nicholsi</i> | <i>G. braueri</i> | Source |
|--------------------|-----------------------------|----------------------|-------------------------------|-------------------|---------------------------------------|
| Scotia Sea | | appr. 5% | | | Rowedder, 1979a |
| Atlantic sector | 3.3 | | | | Naumov et al., 1981 |
| Atlantic sector | 3.7–5.6 | | | | Gerasimova, 1990 |
| APF and south | 1.4 | | | | Podrazhanskaya and Tarverdiyeva, 1991 |
| King George Island | | 1.16–2.54 | 0.65–1.57 | 0.5–1.19 | Pusch et al., 2004 |

Table 4: Biomass of myctophids in the western Atlantic Ocean sector and their estimated annual consumption of krill.

| Species | <i>Electrona carlsbergi</i> | <i>E. antarctica</i> | <i>Gymnoscopelus</i> spp. |
|---|-----------------------------|---|---|
| Area | APF–56°S 8°–50°W | 56°S–close to Antarctic continent 8°–50°W | 56°S–close to Antarctic continent 8°–50°W |
| Biomass (10 ³ tonnes) | 500–2 900 | 389–2 429 | 907–5 667 |
| % weight of krill in diet | 5 | 55 | 55 |
| Annual food consumption × body weight | 15 | 15 | 7 |
| Annual krill consumption (in 10 ⁶ tonnes) | 0.375–2.175 | 1.167–8.016 | 3.491–21.818 |

Table 5: Pre-exploitation biomass estimates of seven species of finfish in the southern Scotia Arc and their standard deviations (sd) (Kock, 1985).

| Species | Split year | South Orkney Islands | | Elephant Island | | South Shetland Islands | |
|--------------------------------------|---------------|-------------------------|-------|--------------------|-------|---------------------------|------|
| | | (tonnes) | (sd) | (tonnes) | (sd) | (tonnes) | (sd) |
| <i>Notothenia rossii</i> | 1975/76 | 133 | 100.5 | 9 378 | 74.0 | 1 626 | 88.7 |
| | 1977/78 | 284 | 43.6 | 15 663 | 76.7 | - | - |
| <i>Gobionotothen gibberifrons</i> | 1975/76 | 68 430 | 80.4 | 16 421 | 92.0 | 53 680 | 43.9 |
| | 1977/78 | 29 187 | 77.6 | 17 824 | 145.6 | - | - |
| <i>Lepidonotothen larseni</i> | 1975/76 | 562 | 57.9 | 100 | - | 4 065 | 81.9 |
| | 1977/78 | 505 | 62.5 | 90 | 113.7 | - | - |
| <i>Champocephalus gunnari</i> | 1975/76 | 140 000 | - | 20 000 | - | 22 162 | 82.6 |
| | 1977/78 | 40 000 | - | 20 000 | - | - | - |
| <i>Chaenocephalus aceratus</i> | 1975/76 | - | - | - | - | 25 084 | 35.6 |
| | 1977/78 | 9 854 | 52.4 | 1 249 | 57.9 | - | - |
| <i>Pseudochaenichthys georgianus</i> | 1975/76 | - | - | - | - | 2 282 | 52.9 |
| | 1977/78 | 8 270 | 139.3 | - | - | - | - |
| <i>Chionodraco rastrospinosus</i> | 1975/76 | 8 759 | 64.0 | - | - | 22 144 | 44.9 |
| | 1977/78 | - | - | 1 015 | 59.6 | - | - |

Table 6: Biomass estimates (metric tonnes) and the confidence intervals (in parentheses) for the most abundant demersal fish species (stratum 50–500 m) in the South Orkney Islands region (Kock, 1986; Balguerías, 1989; Jones and Kock, 2009; Jones et al., 2000).

| Species | Year of survey | | | | |
|--------------------------------------|----------------|--------|--------|--------|-----------------|
| | 1985 | 1991 | 1999 | 2009 | |
| <i>Notothenia rossii</i> | 163 | 412 | 3 278 | 714 | (383–1 254) |
| <i>Gobionotothen gibberifrons</i> | 18 965 | 53 483 | 38 900 | 28 861 | (21 058–50 565) |
| <i>Lepidonotothen squamifrons</i> | 6 073 | 14 156 | 50 934 | 5 831 | (2 920–15 124) |
| <i>L. larseni</i> | 446 | 455 | 288 | 441 | (298–747) |
| <i>Champscephalus gunnari</i> | 4 824 | 23 621 | 3 016 | 6 312 | (4 104–12 728) |
| <i>Chaenocephalus aceratus</i> | 5 175 | 16 031 | 10 431 | 14 696 | (8 814–36 586) |
| <i>Chionodraco rastrispinosus</i> | 4 983 | 15 410 | 13 434 | 10 680 | (6 072–22 893) |
| <i>Pseudochaenichthys georgianus</i> | 4 739 | 18 847 | 8 728 | 10 704 | (5 856–27 723) |

Table 7: Biomass estimates (tonnes) for the most abundant demersal fish (stratum 50–500 m) around Elephant Island and the South Shetland Islands region (Jones et al., 1998, 2001, 2003; Kock et al., 2002, 2007).

| Species | Year of survey | | | | |
|-----------------------------------|------------------|----------------|----------------|----------------|------------------------------|
| | 1998 | 2001 | 2002 | 2003 | 2007 |
| <i>Champscephalus gunnari</i> | 8 166 | 5 121 | 3 019 | 8 034 | 1 452 |
| | (4 036–24 586) | (3 402–9 587) | (1 509–16 787) | (4 765–21 153) | (597–16 267) |
| <i>Chaenocephalus aceratus</i> | 4 440 | 4 581 | 2 209 | 4 362 | 2 536 |
| | (2 782–615 956) | (2 856–8 861) | (1 444–3 987) | (2 618–9 143) | (834–14 655) |
| <i>Chionodraco rastrispinosus</i> | 3 011 | 4 122 | 3 420 | 4 866 | 1 166 |
| | (1 785–6 323) | (2 694–7 375) | (1 864–8 545) | (2 949–9 857) | (516–3 911) |
| <i>Gobionotothen gibberifrons</i> | 38 709 | 14 022 | 3 883 | 9 898 | 7 258 |
| | (17 882–119 902) | (7 689–32 927) | (1 819–3 014) | (5 383–28 239) | (3 191–39 664) |
| <i>Lepidonotothen larseni</i> | 237 | 265 | 3 595 | 629 | 356 |
| | (157–406) | (170–473) | (1 170–19 983) | (382–1 237) | (101–3 370) |
| <i>L. squamifrons</i> | 3 068 | 1 007 | 1 411 | 2 235 | 315 |
| | (1 289–11 579) | (491–2 885) | (412–11 808) | (1 286–7 717) | (124–1 401) |
| <i>Notothenia coriiceps</i> | 3 232 | 7 548 | 4 485 | 5 012 | 25 129 |
| | (1 719–9 186) | (3 510–27 519) | (1 886–21 634) | (3 011–12 427) | (2 716–1.3*10 ⁷) |
| <i>N. rossii</i> | 344 | 873 | 1 793 | 772 | 37 634 |
| | (211–602) | (500–2 089) | (817–6 861) | (344–3 400) | (2 941–2.7*10 ⁷) |

Table 8: Comparison of seasonal krill consumption by demersal fish in waters of the southern Scotia Arc (references until 1984 in Kock, 1985; Gröhsler, 1992; Takahashi and Iwami, 1997; Barrera-Oro, 2002; Jones et al., 2003; Flores et al., 2004).

| Species | Proportion by weight (%) of krill in the diet | | | |
|------------------------------------|---|--------|--|------------|
| | Summer | Winter | Mean proportion used for estimating annual krill consumption | |
| | | | Kock (1985) | This study |
| <i>Champocephalus gunnari</i> | 95–99 | 75 | 50 (South Georgia) | 85 |
| <i>Chaenocephalus aceratus</i> | <10 juv–50 adults | 0 | 30 | 30 |
| <i>Chiono draco rastrospinosus</i> | 68–95 | 18 | 60 | 60 |
| <i>Parachaenichthys georgianus</i> | 61–75 | 7 | 60 | 60 |
| <i>Gobionotothen gibberifrons</i> | 4–50 | 17 | 10 | 25 |
| <i>Lepidonotothen larseni</i> | 38–92 | 24 | 50 | 50 |
| <i>L. squamifrons</i> | 20 | - | - | 10 |
| <i>L. nudifrons</i> | 4.6 | 3 | - | 4 |
| <i>Notothenia coriiceps</i> | 24–51 | 11 | - | 10 |
| <i>N. rossii</i> (mostly adults) | 47–95 | 45 | 50 (South Georgia) | 70 |
| <i>Trematomus eulepidotus</i> | 85 | | | 85 |
| <i>T. newnesi</i> | 59 | | | 59 |

Table 9: Daily feeding rates expressed as proportions of the body weight (%) of coastal demersal fish in waters of the southern Scotia Arc (literature until 1991 in Kock, 1992; Gröhsler, 1992; Pakhomov, 1993; Flores et al., 2004).

| Species | Daily ration | | | Feeding rates for estimation of annual krill consumption | | |
|------------------------------------|--|---|-----------------------|--|---------------|--------------------|
| | Summer–autumn | Winter–spring | Annual | Used in Kock, 1985 | | Used in this study |
| | | | | Summer–autumn | Winter–spring | |
| <i>Champocephalus gunnari</i> | 10.1 1–1.5 0.99 | 0.14–1.09 | | 5 | 1 | 2 |
| <i>Chaenocephalus aceratus</i> | 0.72–1.75 | 0.59–0.80 | | 3 | 1 | 1.5 |
| <i>Chionodraco rastrospinosus</i> | 0.24–0.6 | 0.5 | < 2 | 2 | 1 | 1.5 |
| <i>Gobionotothen gibberifrons</i> | 1.51–2.76 | 0.91–1.39 0.85 | | 2 | 1 | 1.5 |
| <i>Lepidonotothen larseni</i> | 0.9 1.2–2 Juv 4.5 | | 2 | 2 | 1 | 1.5 |
| <i>L. squamifrons</i> | | 0.9–1.30 | 3.4–3.85* | | | 2.5 |
| <i>Notothenia coriiceps</i> | 2 | < 1.5 | 0.46–1.21 1.4–2.22 | | | 1 |
| <i>N. rossii</i> | Adult 0.94–1.26 (krill) Juv 2.8–3.6 Adult 7.4–8.9 | 0.23–1.09 Juv 1.8–2.4 Adult 1.1–1.3 | | 5 | 1 | 3 |
| <i>Parachaenichthys georgianus</i> | 2.86 | 3.8–4.8 | | | | 3.5 |
| <i>Chaenodraco wilsoni</i> | 3.4 | 1.6 | | | | 2.5 |

* Annual food consumption 11–14 × body weight (Pakhomov, 1993)

Table 10: Biomass estimates of key demersal fish species that are known to consume krill. Biomass estimates are mean swept area estimates (Collins et al., 2006).

| Year | <i>Champscephalus gunnari</i> | <i>Dissostichus eleginoides</i> (juveniles) | <i>Chaenocephalus aceratus</i> | Lower 95% CI | Upper 95% CI | <i>Parachaenichthys georgianus</i> | Lower 95% CI | Upper 95% CI | <i>Notothenia rossii</i> | <i>Lepidonotothen squamifrons</i> | <i>Trematomus hansonii</i> | <i>L. larseni</i> | <i>Patagonotothen guntheri</i> | <i>Gobionotothen gibberifrons</i> |
|------|-------------------------------|---|--------------------------------|--------------|--------------|------------------------------------|--------------|--------------|--------------------------|-----------------------------------|----------------------------|-------------------|--------------------------------|-----------------------------------|
| 1987 | 56 884 | 1 980 | 13 561 | 9 248 | 23 709 | 5 322 | 3 556 | 9 207 | 4 110 | 28 030 | 514 | 1 984 | 264 | 13 499 |
| 1988 | 17 709 | 1 202 | 8 158 | 6 030 | 12 200 | 12 652 | 8 329 | 37 992 | 1 296 | 498 | 738 | 1 408 | * | 9 444 |
| 1989 | 31 686 | 606 | 9 759 | 6 850 | 6 869 | 16 529 | 7 227 | 521 815 | 2 800 | 286 | 245 | 1 428 | * | 13 676 |
| 1990 | 374 372 | 9 966 | 28 740 | 9 781 | 192 246 | 8 836 | 3 771 | 36 913 | 1 482 | 1 360 | 103 | 641 | 1 700 | 12 684 |
| 1991 | 25 958 | 19 872 | 14 690 | 10 600 | 23 100 | 14 945 | 10 286 | 25 673 | 4 284 | 1 980 | 114 | 1 375 | 529 | 28 111 |
| 1992 | 40 230 | 5 811 | 17 990 | 11 299 | 47 624 | 16 036 | 10 825 | 46 010 | 7 306 | 1 236 | 357 | 1 126 | 10 694 | 29 563 |
| 1994 | 19 748 | 3 994 | 12 821 | 7 542 | 29 650 | 8 964 | 5 117 | 22 251 | 6 658 | 1 736 | 112 | 824 | 8 505 | 23 563 |
| 1997 | 72 206 | 4 098 | 14 554 | 4 639 | 173 459 | 8 615 | 3 915 | 32 717 | 12 918 | 1 154 | 583 | 87 | 4 302 | 2 510 |
| 2000 | 24 757 | 1 495 | 4 717 | 2 869 | 11 807 | 4 728 | 3 092 | 8 806 | 4 872 | 44 725 | 44 | 240 | 1 388 | 6 453 |
| 2002 | 56 485 | 2 717 | 9 000 | 5 923 | 17 153 | 9 352 | 5 918 | 20 387 | 58 780 | 325 | 217 | 192 | 1 746 | 10 117 |
| 2004 | 98 403 | 1 343 | 8 030 | 5 289 | 27 560 | 9 964 | 5 464 | 27 169 | 7 969 | 547 | 1 503 | 474 | 4 382 | 13 773 |
| 2005 | 9 061 | 3 142 | 4 462 | 2 360 | 44 139 | 2 948 | 1 546 | 21 253 | 7 916 | 12 356 | 241 | 785 | 666 | 10 299 |
| 2006 | 117 260 | 4 286 | 10 807 | 6 780 | 23 168 | 9 222 | 4 898 | 30 128 | 14 131 | 20 856 | 1 020 | 529 | 10 038 | 14 840 |

Table 11: Summary table of diet information obtained from literature for the major demersal fish species found at South Georgia and Shag Rocks.

| Species | % (mass) krill in diet (range from literature) | % (mass) other zooplankton (non- <i>Euphausia superba</i>) | R, daily food consumption (% of body mass) | References |
|--|--|--|--|--|
| <i>Champscephalus gunnari</i> | 52–85 | 12–29 | 0.3–2.2 | Permitin and Tarverdiyeva (1972); Kompowski (1980); McKenna (1991); Kock et al. (1994); Main et al. (2009) |
| <i>Dissostichus eleginoides</i> (juveniles) | 2–8 | 0.3–2 | 1.7–5.1 | Tarverdiyeva (1972); Barrera-Oro (2002); Collins et al. (2008) |
| <i>Chaenocephalus aceratus</i> | 0.78–7.9 | 0.5–1.6 | | McKenna (1991); Reid et al. (2007) |
| <i>Pseudochaenichthys georgianus</i> | 35.5–68 (100% in Juveniles) | 0.5–1 | | Kompowski (1980); McKenna (1991); Clarke et al. (2008) |
| <i>Notothenia rossii</i> | 38.6–56 | 10 | 0.24–5.7 | Tarverdiyeva (1972); Chekunova and Naumov (1982a); McKenna (1991) |
| <i>Lepidonotothen squamifrons</i> | 1.5 | 67 | | McKenna (1991) |
| <i>Patagonotothen guntheri</i> | 50 | 39 | 5.27 | Naumov et al. (1983); McKenna (1991); Collins et al. (2008) |
| <i>Lepidonotothen larseni</i> | 31.9–75 | 33–70 | 1.2–2 | Crawford (1978); Targett (1981); McKenna (1991) |
| <i>Trematomus hansonii</i> | 71.2 | | 3.7–5.2* | McKenna (1991); Pakhomov and Tseitlin (1992); Kosmonavtov Sea* |
| <i>Gobionotothen gibberifrons</i> | 1.4–50 | 10–20 | 0.24–2.76 | Targett (1981); McKenna (1991); Kock (1992) |

* Signifies that parameters were obtained from other regions of the Southern Ocean

Table 12: Biomass estimates for *Champocephalus gunnari* on the Kerguelen Plateau, derived from trawl surveys. Estimates for Heard Island and McDonald Islands (HIMI) are derived from Williams and de la Mare (1995); Constable et al. (2005); Welsford (2006). Estimates for Iles Kerguelen derive from Duhamel and Hauteceur (2008).

| Area | Year | Mean biomass (tonnes) | 95% confidence intervals |
|----------------------------|---------|-----------------------|--------------------------|
| Heard and McDonald Islands | 1990 | 4 584 | 2 606–113 019 |
| | 1992 | 3 112 | 945–427 728 |
| | 1993 | 31 701 | 4 113–14 712 200 |
| | 2005 | 8 762 | 3 899–14 896 |
| | 2006 | 2 396 | 1 120–4 013 |
| | 2007 | 2 121 | 1 477–2 840 |
| Iles Kerguelen | 1987/88 | - | 15 024–429 052 |
| | 2006 | 4 090 | - |

Table 13: Biomass estimates (tonnes) and confidence intervals (CIs) (95%) of the most abundant fish stocks west of the Antarctic Peninsula (Jones and Kock, 2006).

| Species | Biomass estimate | 95% CI |
|-----------------------------------|------------------|------------|
| <i>Chaenodraco wilsoni</i> | 1031 | 648–2593 |
| <i>Chionodraco rastrospinosus</i> | 3999 | 2969–6201 |
| <i>Cryodraco antarcticus</i> | 1154 | 623–3240 |
| <i>Gobionotothen gibberifrons</i> | 5987 | 4210–13349 |
| <i>Lepidonotothen larseni</i> | 142 | 92–245 |
| <i>L. squamifrons</i> | 687 | 266–3208 |
| <i>Notothenia coriiceps</i> | 2178 | 2079–3877 |
| <i>Trematomus eulepidotus</i> | 2027 | 1408–5048 |

Table 14(a): Biomass estimates of demersal finfish in the Ross Sea (Hanchet et al., 2008a) estimated by two methods. sd – standard deviation.

| Species | Shelf: biomass (sd) method 1 ¹ | | Slope: biomass (sd) | | Shelf: biomass (sd) method 2 ² | | Slope: biomass (sd) | |
|---------------------------------|---|------|---------------------|-------|---|------|---------------------|-------|
| <i>Pleuragramma antarcticum</i> | 22 473 | (39) | 21 | (100) | 25 626 | (52) | 22 | (100) |
| <i>Chionobath dewitti</i> | 0 | | 365 | (100) | 0 | | 367 | (100) |
| <i>Chionodraco myersi</i> | 3 573 | (29) | 18 | (63) | 3 643 | (41) | 18 | (66) |
| <i>Neopagetopsis ionah</i> | 2 423 | (62) | 100 | (30) | 2 952 | (66) | 179 | (48) |
| <i>Trematomus eulepidotus</i> | 1 918 | (58) | 0 | | 2 778 | (67) | 0 | |
| <i>Chionodraco hamatus</i> | 1 771 | (68) | 0 | | 2 273 | (69) | 0 | |
| <i>Trematomus lepidorhinus</i> | 1 293 | (43) | 197 | (30) | 1 072 | (48) | 242 | (32) |
| <i>Macrourus whitsoni</i> | 0 | | 4 332 | (40) | 0 | | 4 463 | (46) |
| All fish combined | 55 745 | (19) | 6 390 | (31) | | | | |

¹ Method 1: New Zealand Trawl Survey Analysis Program

² Method 2: CCAMLR Trawl C1 Program

Table 14(b): Abundance of macrourids on the slope of the Ross Sea (Hanchet et al., 2008b) using three methods of extrapolation.

| Estimated biomass (tonnes) | Methods of extrapolation | | |
|-------------------------------|--|--|---|
| | Constant density (standard deviation) | CPUE (all vessels) (standard deviation) | CPUE (all NZ vessels) (standard deviation) |
| 7 092 | 26 892 (29) | 41 823 (28) | 36 542 (30) |

Table 15: Proportion of pelagic crustaceans in the diet and estimated daily food consumption by high-Antarctic notothenioids, *Macrourus whitsoni*, and two species of rajids (Gorelova and Gerasimchuk, 1981; Pakhomov and Shumatova, 1988, 1992; Pakhomov et al., 1991; Pakhomov and Tseitlin, 1992; Pakhomov, 1997; Olaso et al., 2004; Kock et al., 2008).

| Species | Area | Daily ration in % body weight | Proportion of pelagic crustaceans in the diet |
|---------------------------------|---|---|--|
| <i>Chaenodraco wilsoni</i> | Division 58.4.2 | 2.4–3.1 2.5–3.0 2.5, 2.61, 3.64 0.6–0.9 | 75.0–100 64 |
| <i>Neopagetopsis ionah</i> | Cooperation Sea | 3.3 | 8.0–95.5 40 |
| <i>Chionodraco hamatus</i> | Cooperation/ Cosmonauts Seas | 2.4 1.6–2.4 | 2.6–49.5 48 |
| <i>Chionodraco myersi</i> | Cooperation Sea | 2.4 | 10 |
| <i>Cryodraco antarcticus</i> | Cooperation/ Cosmonauts Seas | 3.3 2.25–4.2 | 0–1.7 0.2 |
| <i>Trematomus eulepidotus</i> | Cooperation/ Cosmonauts Seas | 1.5–2.8 3.0, 4.97 1.9–2.8 3.7–5.2 | 34.1–85.1 53 |
| <i>Trematomus lepidorhinus</i> | Cooperation/ Cosmonauts Seas | 3.75 | 25.1–78.8 |
| <i>Trematomus hansonii</i> | Davis, Cooperation, Cosmonauts Seas | 3.0–5.2 5.25 | 0.7–90.0 12 |
| <i>Trematomus pennellii</i> | Davis, Cooperation, Cosmonauts Seas | 1.3–3.4, 3.0 2.0–3.4 | 5.1–48.8 8.5 |
| <i>Trematomus scotti</i> | Cooperation Sea | 3.75 | 53.0 |
| <i>Trematomus nicolai</i> | Cooperation Sea | 3.75 | 1.1–15.7 |
| <i>Pleuragramma antarcticum</i> | Cooperation Sea | 1.5 0.5–1.2 0.48–1.10 | 92.9 90 |
| <i>Notothenia coriiceps</i> | Cooperation Sea | 5.25 | 0.2 0.0 |
| <i>Dissostichus mawsoni</i> | Cooperation/ Cosmonauts Seas | 3.1–5.4 5.25 | 2.7 3.0 |
| <i>Gymnodraco acuticeps</i> | Cosmonauts Sea | 3.9–5.4 3.7–5.7 3.75 4.4–5.7 | 2.3 |
| <i>Cygnodraco mawsoni</i> | Cooperation/ Cosmonauts Seas | 0.6–1.7 1.5 1.0–1.7 | 5.2–18.4 18 |
| <i>Histiodraco velifer</i> | Cooperation/ Cosmonauts Seas | | 17.9 |
| <i>Pogonophryne scotti</i> | Cooperation Sea | 3.0 | 8.3 5 |
| <i>Pogonophryne macropogon</i> | Cosmonauts Sea | | 0.5 5 |
| <i>Pogonophryne permitini</i> | Cosmonauts Sea | | 2.4 5 |
| <i>Macrourus whitsoni</i> | Cooperation/ Cosmonauts Seas | 3.75 | 14.5–57.5 |
| <i>Bathyraja eatonii</i> | Cosmonauts Sea | 1.5 | 30.0 20 |
| <i>Bathyraja maccaini</i> | Cosmonauts Sea | | 14.8 20 |

Table 16: Seasonal and annual feeding rates (in proportion of the body weight) in seven notothenioid species (from Pakhomov and Tseitlin, 1992).

| Species | Summer | Winter | Annual |
|-------------------------------|--------|--------|--------|
| <i>Chaenodraco wilsoni</i> | 4.3 | 1.3 | 5.6 |
| <i>Trematomus eulepidotus</i> | 3.6 | 1.1 | 4.7 |
| <i>Trematomus pennellii</i> | 3.6 | 1.1 | 4.7 |
| <i>Trematomus hansonii</i> | 6.0 | 1.8 | 7.8 |
| <i>Dissostichus mawsoni</i> | 5.5 | 1.7 | 6.2 |
| <i>Cygnodraco mawsoni</i> | 2.0 | 0.6 | 2.6 |
| <i>Gymnodraco acuticeps</i> | 7.0 | 2.1 | 9.1 |

Table 17: Consumption of krill by coastal fish species in the Cosmonauts Sea (30°–50°E) from December to April (stratum 100–500 m).

| Species | Stock size (tonnes) | Diet weight in % body weight | % of krill by weight in the diet | Annual krill consumption (tonnes) |
|-----------------------------------|---------------------|------------------------------|----------------------------------|-----------------------------------|
| <i>Chaenodraco wilsoni</i> | 137 090 | 2.61 | 90 | 322 024 |
| <i>Chionodraco hamatus</i> | 3 200 | 2.4 | 3 | 230 |
| <i>Cryodraco antarcticus</i> | 1 143 | 3.3 | 1 | 1 |
| <i>Trematomus eulepidotus</i> | 1 028 | 3.0 | 50 | 1 543 |
| <i>Trematomus hansonii</i> | 7 593 | 5.25 | 12 | 4 784 |
| <i>Trematomus pennellii</i> | 522 | 3.0 | 20 | 313 |
| <i>Pleuragramma antarcticum</i> | 128 046 | 1.5 | 90 | 172 862 |
| <i>Dissostichus mawsoni</i> | 711 | 5.25 | 5 | 75 |
| <i>Lepidonotothen squamifrons</i> | 9 987 | 5.25 | 20 | 10 486 |
| <i>Cygnodraco mawsoni</i> | 700 | 1.5 | 5 | 53 |
| <i>Gymnodraco acuticeps</i> | 277 | 6.0 | 3.5 | 58 |
| Others | 5 279 | 3.75 | 1–50, mean 15 | 2 969 |
| Total | 295 577 | | | 515 398 |

Table 18: Input data and calculations of annual krill consumption of the main krill predators among demersal fish species in the southern Scotia Arc.

| Species | W% of krill in the diet | Annual food consumption × body weight | South Orkney Islands | | | South Shetland Islands | | | Southern Scotia Arc | | |
|-------------------------------------|-------------------------|---------------------------------------|-------------------------------|--------------------------|-------------|-------------------------------|--------------------------|-------------|--------------------------|-------------|--|
| | | | Biomass estimates Survey 1999 | Annual krill consumption | Limits mean | Biomass estimates Survey 2003 | Annual krill consumption | Limits mean | Annual krill consumption | Limits mean | |
| <i>Champsocephalus gunnari</i> | 85 | 7.3 | 3 016 (2 027–6 073) | 12 577–37 683 | 18 714 | 8 034 (4 765–21 153) | 29 567–131 254 | 49 851 | 42 144–168 937 | 68 565 | |
| <i>Chaenocephalus aceratus</i> | 30 | 5.5 | 10 431 (6 628–22 220) | 10 936–36 663 | 17 211 | 4 362 (2 618–9 143) | 4 320–15 086 | 7 197 | 15 256–51 749 | 24 408 | |
| <i>Chionodraco rastrospinosus</i> | 60 | 5.5 | 13 434 (7 921–28 796) | 26 139–95 026 | 44 332 | 4 866 (2 949–9 857) | 9 732–32 528 | 16 058 | 35 871–127 554 | 60 390 | |
| <i>Gobionotothen gibberifrons</i> | 25 | 5.5 | 38 900 (26 091–82 780) | 35 875–113 822 | 53 487 | 9 898 (5 383–28 239) | 7 402–38 829 | 13 610 | 43 277–152 651 | 67 097 | |
| <i>Lepidionotothen larseni</i> | 50 | 5.5 | 288 (205–718) | 564–1 974 | 792 | 629 (382–1 237) | 1 050–3 402 | 1 730 | 1 614–5 376 | 2 522 | |
| <i>L. squamifrons</i> | 10 | 9.1 | 50 934 (15 129–373 309) | 13 767–339 711 | 46 350 | 2 235 (1 286–7 717) | 1 170–7 022 | 2 034 | 14 937–346 733 | 48 384 | |
| <i>Notothenia coriiceps</i> | 10 | 3.6 | - | - | - | 5 012 (3 011–12 427) | 1 084–4 474 | 1 804 | 1 084–4 474 | 1 804 | |
| <i>N. rossii</i> | 70 | 10.9 | 3 278 (790–60 672) | 6 028–462 927 | 25 011 | 772 (344–3 400) | 2 625–25 942 | 5 890 | 8 653–488 869 | 30 901 | |
| <i>Parachannaichthys georgianus</i> | 60 | 7.3 | 8 728 (4 138–36 461) | 18 124–159 699 | 38 229 | - | - | - | 18 124–159 699 | 38 229 | |
| Total | | | | 124 010–1 247 505 | 244 126 | | 56 950–258 537 | 98 174 | 180 960–1 506 042 | 342 300 | |

Table 19: Euphausiid consumption by Antarctic mesopelagic and demersal fish species (in 10^6 tonnes).

| Area | Author: | Lubimova and Shust, 1980 | Kock, 1985 | Pakhomov, 1997 | Kock et al., this paper |
|------------------------------------|---------|--------------------------------|------------|-------------------|----------------------------|
| Atlantic Ocean sector pelagic | | | | | 7–44 |
| Atlantic Ocean sector demersal | | 5.4–6.6 | 5 | | |
| High-Antarctic Indian Ocean sector | | | | 2.32–3.88 | |
| High-Antarctic overall | | 18–20 | | | |
| Southern Ocean | | 23.4–26.6 | | 26–29 | |

