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Review
The role of fish in the Antarctic marine food web: differences between inshore and offshore waters in the southern Scotia Arc and west Antarctic Peninsula

ESTEBAN BARRERA-ORO

Instituto Antártico Argentino, Cerrito 1248, A1010AAZ Buenos Aires, Argentina
Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", División Ictiología, Angel Gallardo 470, C1405DJR Buenos Aires, Argentina
eboro@muanbe.gov.ar and esteban@eboro.cyt.edu.ar

Abstract: The role of fish in the Antarctic food web in inshore and offshore waters is analysed, taking as an example the coastal marine communities of the southern Scotia Arc (South Orkney Islands and South Shetland Islands) and the west Antarctic Peninsula. Inshore, the ecological role of demersal fish is more important than that of krill. There, demersal fish are major consumers of benthos and also feed on zooplankton (mainly krill in summer). They are links between lower and upper levels of the food web and are common prey of other fish, birds and seals. Offshore, demersal fish depend less on benthos and feed more on zooplankton (mainly krill) and nekton, and are less accessible as prey of birds and seals. There, pelagic fish (especially lantern fish) are more abundant than inshore and play an important role in the energy flow from macrozooplankton to higher trophic levels (seabirds and seals). Through the higher fish predators, energy is transferred to land in the form of fish remains, pellets (birds), regurgitation and faeces (birds and seals). However, in the general context of the Antarctic marine ecosystem, krill (*Euphausia superba*) plays the central role in the food web because it is the main food source in terms of biomass for most of the high level predators from demersal fish up to whales. This has no obvious equivalent in other marine ecosystems. In Antarctic offshore coastal and oceanic waters the greatest proportion of energy from the ecosystem is transferred to land directly through krill consumers, such as flying birds, penguins, and seals. Beside krill, the populations of fish in the Antarctic Ocean are the second most important element for higher predators, in particular the energy-rich pelagic Myctophidae in open waters and the pelagic Antarctic silver fish (*Pleuragramma antarcticum*) in the high Antarctic zone. Although the occurrence of these pelagic fish inshore has been poorly documented, their abundance in neritic waters could be higher than previously believed.

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Key words: diet, ecosystem, krill, Notothenioidei, predators

Introduction

The Antarctic ichthyofauna is small in size and less diverse than might be expected, given the size and age of the Antarctic marine ecosystem (Eastman 1995). There are about 300 Antarctic marine fish species described in 49 families (Gon & Heemstra 1990, Eastman & Eakin 2000), which represent only *c.* 1.3% of the worldwide fish species estimated as at least 23 350 valid species in 480 families (Eschemeyer 1998). Marine fish diversity is greater in adjacent cold temperate regions. The last published data indicate 459 species in 150 families in Tasmanian waters (Last *et al.* 1983) and 1090 species in 208 families within 200 miles of New Zealand waters (Roberts & Paulin 1997); about 630 species in 143 families on the Argentine continental shelf and slope (Lloris & Rucabado 1991, Cousseau & Denegri 1995).

In contrast to boreal waters, pelagic fish are rare in the Southern Ocean. In oceanic waters the pelagic ichthyofauna is limited to deepwater bathypelagic and mesopelagic fish, dominated in terms of species and biomass by the family Myctophidae (lantern fish). The biomass of myctophids south of 40ºS has been estimated at 70–396 million tons (Sabourenkov 1991). However, pelagic fish and larvae are minor components of the Antarctic epiplankton (Morales-Nin *et al.* 1995, Hoddell *et al.* 2000). The Antarctic fish fauna is unique in being dominated in terms of diversity (35%) and biomass by an endemic coastal demersal group, the suborder Notothenioidei, which includes six families and can be found as deep as 1200–1500 m. There is a lower diversity of Antarctic fish species on the continental shelves (139 spp.) compared with other cold water seas (> 350 spp. in the North Atlantic). However, although the diversity of the notothenioids is limited compared with the large size of the ecosystem, there is no other fish group in the world with

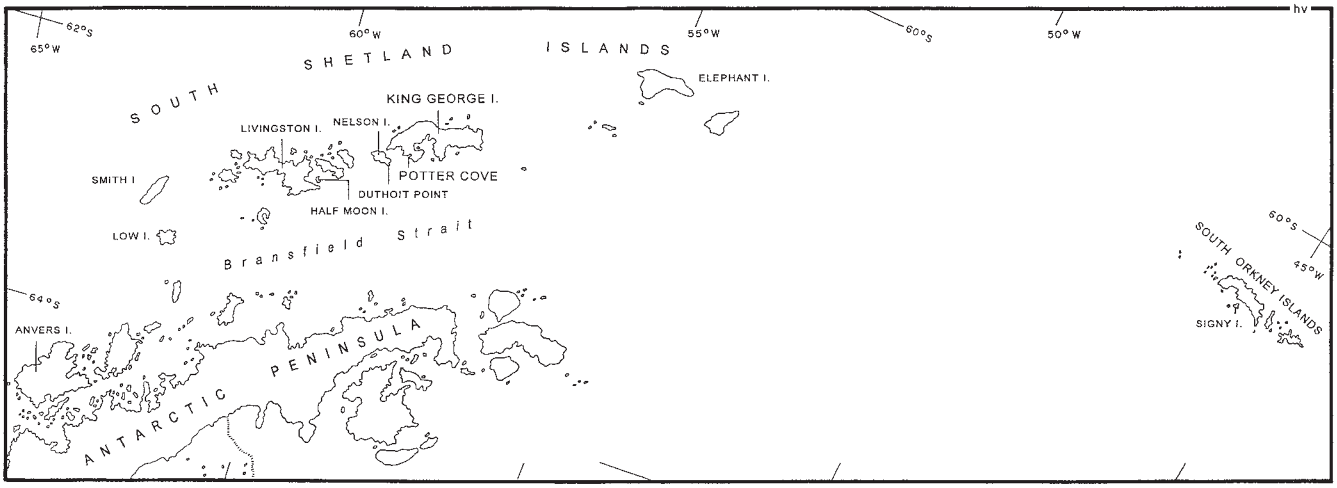

Fig. 1. The study area in the southern Scotia Arc (South Orkney Islands, South Shetland Islands) and west Antarctic Peninsula.

such a diversification and dominance in a continental shelf habitat (Eastman 1995).

Notothenioids lack a swim bladder. They have developed a wide range of feeding strategies, which allow them to utilize food resources in a variety of habitats (Gröhsler 1994). This diversification has been supported by a trend towards pelagization of demersal species (Nybelin 1947), which might be related to the abundance of available food in the water column, such as krill in parts of the Southern Ocean. Thus, fish are main predators of benthos, feeding on virtually all the organisms present from algae to fish, on zooplankton and nekton in the water column, and upon krill, copepods, hyperiid amphipods, squids and fish.

In the food web, krill (*Euphausia superba* Dana) is the most important link between primary production and top-level predators (seabirds, seals and whales). Early stages of krill are prey for carnivorous zooplankton, such as chaetognaths and amphipods (Marr 1962, Lomakina 1964, Miller & Hampton 1989, Marschoff 1996). Although salps may occasionally dominate the zooplankton community (Loeb *et al.* 1997), krill usually represent about 50% of the total zooplankton biomass (Holdgate 1970). After krill, fish is the main prey of most Antarctic vertebrates. Demersal fish predators are fish, some birds (Antarctic shag, gentoo penguin) and some seals (elephant, leopard, Weddell, fur). Pelagic fish (early stages, myctophids, *Pleuragramma antarcticum*) predators are fish, most of the flying seabirds, penguins and seals.

The composition of the inshore and offshore Antarctic fish fauna has been delimited by DeWitt (1971), based upon depth distribution and bottom topography. The ecological role that fish play in the Antarctic ecosystem has been well described by Kock (1992) and Hureau (1994), without distinction between the inshore and the offshore species. Some questions remain. Is the role of demersal fish in the Antarctic food web similar in inshore shallow waters and offshore waters? What is the role of fish in comparison to that of krill and other key organisms in these zones?

This review aims to provide some insight into these questions, taking as an example the coastal marine communities of the southern Scotia Arc (South Orkney Islands and South Shetland Islands) and the west Antarctic Peninsula (Fig. 1). These, according to the three ichthyofaunistic subregions defined by Kock (1992), are all shelf waters of the Seasonal Pack Ice Zone. This is the most productive ecological zone, with the highest concentrations of krill.

The bottom topography in the west and north of the Antarctic Peninsula might be described as a shelf surrounded by islands, communicating with the open sea by troughs of varying depths. To the east, the Scotia Sea is limited by the shelves of South Georgia, the volcanic South Sandwich Islands (very narrow)) and the South Orkney Islands. Typically, the shelves develop strong frontal zones. Around the South Orkney Islands the shelf is very narrow to the north and a broad plain to the south, breaking mainly below the 500 m isobath (sharp in the north, less in the south-east, Jones 2000). About 150 nautical miles to the west, the South Shetland Islands are located along 481 km of shelf in a NE–SW direction and separated from the Antarctic Peninsula by the Bransfield Strait (Acosta *et al.* 1989). The waters between the shelf areas of both archipelagos range from 2000–3000 m (Kock *et al.* 2000). Around the South Shetland Islands the shelf break lies at depths between 225 and 380 m in the north-east (Elephant Island) and between 250 and 450 m in the rest of the archipelago (250 m at the south-east of King George Island, Acosta *et al.* 1989).

The complex water circulation around the Antarctic Peninsula is dominated by an eastwards component originating from the Antarctic Circumpolar Current and waters from the Bellingshausen Sea. Along the coasts of the

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Table I. The most abundant (in number or biomass) fish species of the southern Scotia Arc and west Antarctic Peninsula (AP), their relative abundance in inshore and offshore waters and their geographical distribution.

Species	Geographical distribution	Relative abundance		
			Continental shelf	Open
		Inshore	Offshore	ocean
Bathydraconidae				
Parachaenichthys charcoti (Vaillant, 1906)	southern Scotia Arc and west AP	occasional	rare	
Channichthyidae				
Chaenocephalus aceratus (Lönnberg, 1906)	Scotia Arc and west AP, Bouvet Island	occasional	common	
Champsocephalus gunnari Lönnberg, 1905	Scotia Arc and west AP; Bouvet Island, Heard Island and Îles Kerguelen	rare	abundant	
Chionodraco rastrospinosus DeWitt & Hureau, 1979	southern Scotia Arc and west AP	rare	common	
Harpagiferidae				
Harpagifer antarcticus Nybelin, 1947	southern Scotia Arc and west AP; South Sandwich Islands	abundant	rare	
Nototheniidae				
Gobionotothen gibberifrons (Lönnberg, 1905)	Scotia Arc and west AP; Heard Island	common	abundant	
Lepidonotothen larseni Lönnberg, 1905	Scotia Arc and west AP; Bouvet Island; Crozet, Marion, Prince Edward Islands, Ob and Lena Banks; Balleny Island and Peter I Island	occasional	common	
Lepidonotothen nudifrons (Lönnberg, 1905)	Scotia Arc and west AP	abundant	occasional	
*Lepidonotothen squamifrons** (Günther, 1880)	Scotia Arc and west AP; Bouvet Island; sub-Antarctic islands of the Indian sector	rare	abundant	
Notothenia coriiceps Richardson, 1844	circum-Antarctic on shelves of the Antarctic continent and islands	abundant	common	
Notothenia rossii Richardson, 1844	Scotia Arc and west AP; circum-Antarctic on sub-Antarctic island shelves	occasional	occasional	
Pleuragramma antarcticum Boulenger, 1902	southern Scotia Arc; circum-Antarctic over pelagic waters of the Antarctic continental shelf	presumably occasional	abundant	rare
Trematomus bernacchii Boulenger, 1902	southern Scotia Arc; circum-Antarctic on the Antarctic continental shelf	common	occasional	
Trematomus eulepidotus Regan, 1914	southern Scotia Arc; circum-Antarctic on the Antarctic continental shelf	rare	common	
Trematomus newnesi Boulenger, 1902	southern Scotia Arc; circum-Antarctic on the Antarctic continental shelf	abundant	rare	
Myctophidae				
Electrona antarctica Günther, 1878	circum-Antarctic in open ocean, over continental shelf and slope	presumably occasional	common	abundant
Gymnoscopelus nicholsi Gilbert, 1911	circum-Antarctic in open ocean, over continental shelf and slope	presumably occasional	common	abundant

*In many studies identified as *L. kempi*; in this review, considered as a single species of the *L. squamifrons* group.
Scale of abundance: rare, occasional, common, abundant. Source: compiled from literature cited in the text.

Antarctic Peninsula the coastal currents generally flow to the west and south (Stein 1995). In the southern Scotia Sea, the Weddell/Scotia confluence follows approximately the Scotia Ridge (Deacon 1937, 1979). The circulation in the region is controlled by the Antarctic Circumpolar Current which balances the waters coming from the Antarctic Peninsula and the Weddell Sea, resulting in a highly variable pattern (Gordon 1988, Foster & Middleton 1984). The South Orkneys shelf receives a regular flow of Weddell Sea waters (Atkinson & Peck 1990).

The main fish species included in this work are the most abundant notothenioids distributed in the two contiguous portions of the continental shelf: inshore, shallow waters, at depths down to 110 m (littoral, coves, shallow fjords) to 200 m (deep fjords and bays) and offshore waters up to the shelf break, between 110 m and *c.* 450 m. The ecological role of the myctophids in the open ocean is also discussed. The nomenclature used is that of Gon & Heemstra (1990).

Fish fauna

General descriptions of the Antarctic ichthyofauna in terms of its bathymetric and geographical distribution are found in Regan (1914), Norman (1938), Nybelin (1947), Andriashev (1965), DeWitt (1971) and Kock (1992), amongst others. The notothenioids of the southern Scotia Arc and west Antarctic Peninsula shelves, listed in this review (Table I), inhabit other areas of the same ichthyofaunistic subregion in the Atlantic Ocean, but only a few occur in the Southern Indian Ocean (*Lepidonotothen larseni*, *L. squamifrons*, *Notothenia coriiceps*, *N. rossii*, *P. antarcticum*) and in the High Antarctic Zone (*N. coriiceps*, *P. antarcticum*, *Trematomus bernacchii*, *T. eulepidotus*, *T. newnesi*).

Inshore

Descriptions of the ichthyofauna inhabiting inshore waters

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Table II. Fish prey shown in feeding categories of coastal fish from the southern Scotia Arc and west Antarctic Peninsula.

Fish species	Prey
Benthos feeders - benthic, epibenthic. Feed on infauna, epifauna and algae	
Harpagifer antarcticus	Benthic amphipods, polychaetes, gastropods, isopods, krill (occasional in summer)
Lepidonotothen nudifrons	Polychaetes, gammarideans, isopods, krill (occasional in summer)
Notothenia coriiceps	Algae, polychaetes, gastropods, limpets, clams, siphons, cephalopods, gammarideans, isopods, ascidians. In summer: krill, hyperiids, salps
Gobionotothen gibberifrons	As *N. coriiceps* plus oligochaetes, priapulids, & ophiuroids
Benthos and plankton feeders - benthic, benthopelagic	
Trematomus bernacchii &	algae, polychaetes, gastropods,
Trematomus newnesi	gammarideans, isopods, krill, hyperiids
Notothenia rossii (juvenile)	gammarideans, fish, krill, algae, polychaetes, gastropods, isopods, hyperiids, cephalopods, siphons
Lepidonotothen squamifrons	krill, salps, hyperiids, fish, polychaetes, ophiuroids, echinoids
Parachaenichthys charcoti & *N. rossii*	krill, fish
Chaenocephalus aceratus	fish, krill, cephalopods, mysids, ophiuroids
Plankton feeders - pelagic, benthopelagic	
Lepidonotothen larseni	krill, hyperiids, copepods, salps
Trematomus eulepidotus	as *L. larseni* plus young fish & polychaetes
Chaenocephalus aceratus (juvenile)	juvenile krill, mysids
Champsocephalus gunnari	krill, hyperiids, fish
Chionodraco rastrospinosus	krill, fish, hyperiids
Myctophidae sp.*	krill & other euphausiids, copepods, hyperiids, fish eggs & larvae
Pleuragramma antarcticum	as Myctophidae sp. plus salps

*Distributed mainly in the open ocean.
Source: Richardson 1975, Tarverdiyeva & Pinskaya 1980, Targett 1981, Daniels 1982, Linkowski *et al.* 1983, Barrera-Oro & Tomo 1987, Casaux *et al.* 1990, Gröhsler 1994, Takahashi & Iwami 1997, Casaux *et al.* 2000.

of the South Orkney Islands (Richardson 1975, Targett 1981), South Shetland Islands (Zukowski 1980, Skora 1993, Barrera-Oro & Casaux 1998) and west Antarctic Peninsula (Moreno *et al.* 1977, Daniels 1982, Casaux *et al.* 2000) agree on a similar composition of a few species (commonly < 6), whose number may increase with the presence of macroalgae beds (see Kock 1992). For the aim of this review, the most abundant (in biomass or numbers) fish species are listed for a single region comprising the southern Scotia Arc and west Antarctic Peninsula, instead of in separate areas (Table I).

The fish mostly found in this zone are coastal notothenioids, which spend all or part of their life cycles in inshore waters, although some species may also occur in the offshore fraction of the shelf (Table I). In these nearshore communities there are gradients in environmental heterogeneity, from rocky algal bottoms to soft bottoms of sand and mud barren of algae. On the shallow soft bottoms, mainly juveniles of some species are found in low density and there are fewer fishes than on the rocky bottoms (Moreno *et al.* 1982, Casaux *et al.* 1990). Macroalgal environments offer fish a diversity of prey and shelter from potential predators such as penguins and mammals.

The sampling gear used to catch inshore shallow-water fish has been small trawlers (less common), trammel/gill nets, hook and lines and traps (reviewed in Barrera-Oro & Casaux 1998). *Harpagifer antarcticus* (from tide-pools), *N. coriiceps* (from 5 m depth) and *N. rossii* (juveniles, from 10 m depth) are the more neritic species, *Gobionotothen gibberifrons*, *L. nudifrons* and *T. newnesi* occur more frequently from 30–45 m depth, whereas *T. bernacchii*, *Parachaenichthys charcoti* and *Chaenocephalus aceratus* are caught mainly from a depth range of 70–90 m downwards. *Harpagifer antarcticus*, *T. newnesi*, *L. nudifrons* and *P. charcoti* remain almost exclusively on the inner shelves throughout their entire ontogeny. *Notothenia rossii* occurs inshore in the juvenile stage exclusively (Linkowski *et al.* 1983, Casaux *et al.* 1990). *Gobionotothen gibberifrons* displays evident length stratification as a function of depth; mainly juvenile and part of the adult population coexist in inshore shallow waters (Moreno & Osorio 1977, Barrera-Oro 1989, Casaux *et al.* 1990, Kulesz 1994). *Notothenia coriiceps* is the dominant fish nearshore in the region, both in number and biomass (Everson 1970, Barrera-Oro *et al.* 2000, Casaux *et al.* 2000). Data on its depth distribution from Potter Cove, King George Island and data from South Georgia suggest that this species remains nearshore during its whole life cycle (Burchett *et al.* 1983, Casaux *et al.* 1990). However, other studies indicate that at least around Elephant Island, South Shetland Islands, *N. coriiceps* migrates to deeper waters to spawn (Everson 1970, Hureau 1970, Kock 1989).

The occurrence of pelagic fish (myctophids, *P. antarcticum*) inshore is rarely reported (Daniels 1982, Linkowski *et al.* 1983). Their presence in shallow water zones could be sporadic and has been related to temporal introduction of nekton from adjacent offshore areas (e.g. from the Bransfield Strait to Admiralty Bay, King George Island, Skora 1993). Recent observations of predator-prey interactions between flying birds and fish suggest that the

Table III. Feeding behaviour of coastal fish from the southern Scotia Arc and west Antarctic Peninsula.

Fish species	Ambush	Slurp on/near bottom	Grazing	Water column	Source
H. antarcticus	x				Duarte & Moreno 1981, Daniels & Lipps 1982, Casaux 1998a
L. larseni	x			x	Targett 1981, Barrera-Oro & Tomo 1987, Gröhsler 1994
L. nudifrons	x				Targett 1981, Daniels 1982, Gröhsler 1994
L. squamifrons	x			x	Tarverdiyeva & Pinskaya 1980, Gröhsler 1994
G. gibberifrons	x	x	x		Moreno & Osorio 1977, Tarverdiyeva & Pinskaya 1980, Targett 1981, Daniels 1982, Takahashi 1983, Casaux *et al.* 1990
N. coriiceps	x		x		Showers *et al.* 1977, Moreno & Zamorano 1980, Daniels 1982, Burchett *et al.* 1983, Barrera-Oro & Casaux 1990, Casaux *et al.* 1990
N. rossii	x		x	x	Moreno & Bahamonde 1975, Daniels 1982, Burchett 1983, Casaux *et al.* 1990, Gröhsler 1994
T. bernacchii	x		x	x	Moreno 1980, Daniels 1982, Ekau 1991, Kiest 1993, Vacchi *et al.* 1994
T. newnesi				x	Targett 1981, Daniels 1982, Casaux *et al.* 1990, Vacchi & La Mesa 1995
T. eulepidotus				x	Targett 1981, Takahashi 1983, Pakhomov & Tseytlin 1992
P. antarcticum				x	Linkowski *et al.* 1983, Gröhsler 1994, Takahashi & Iwami 1997
P. charcoti				x	Targett 1981, Gröhsler 1994, Takahashi & Iwami 1997
C. aceratus				x	Targett 1981, Takahashi 1983, Gröhsler 1994
C. gunnari				x	Tarverdiyeva & Pinskaya 1980, Targett 1981, Takahashi 1983, Gröhsler 1994
C. rastrospinosus				x	Takahashi 1983, Gröhsler 1994, Takahashi & Iwami 1997
Myctophidae sp.				x	Tarverdiyeva & Pinskaya 1980, Takahashi 1983, Takahashi & Iwami 1997

occurrence of pelagic fish in inshore areas might be higher than previously believed (discussed below).

Offshore

The ichthyofauna on the deeper, outer shelves of the South Orkney Islands (Targett 1981, Skora & Sosinski 1983, Kock 1986, Balguerías 1989, 1991, Jones *et al.* 2000), South Shetland Islands (Tarverdiyeva & Pinskaya 1980, Kock 1982, 1986, 1998, Skora & Sosinski 1983, Takahashi 1983, Skora 1988, Balguerías 1989, Tiedtke & Kock 1989, Gröhsler 1994, Takahashi & Iwami 1997, Jones *et al.* in press) and west Antarctic Peninsula (Tarverdiyeva & Pinskaya 1980, Daniels 1982, Skora & Sosinski 1983) is similar in species composition, with a higher species diversity than on the inner shelves. A complete list and new biological data of the fish species occurring in the shelves of the southern Scotia Arc, recorded in two recent extensive scientific surveys at the end of the nineties, is provided in Kock *et al.* (2000). For this review, a quantitative summary of only the dominant (> 95% by number or biomass) fish species in the whole southern Scotia Arc and the west Antarctic Peninsula is given (Table I).

Although there are some differences in the abundance of the species between the offshore shelf areas, the low Antarctic species *G. gibberifrons*, *Champsocephalus gunnari*, *C. aceratus* and *L. squamifrons* (also identified as *L. kempi*, the taxonomic status of the group is still in question) are the predominant members of the ichthyofauna in the whole southern Scotia Arc region (Kock *et al.* 2000). High Antarctic species such as *Chionodraco rastrospinosus, Cryodraco antarcticus* and a number of *Trematomus* species also occur in the whole region (mainly around the South Orkney Islands), but with the exception of the first species, their abundance in terms of biomass and numbers is very low (Kock *et al.* (2000)). The occurrence of the former exploited species *N. rossii* remains low, and their stocks seem far from recovering two decades after the offshore commercial fishery in the area in the late 1970s.

Some fish species (e.g. *G. gibberifrons*, *C. aceratus*, *L. larseni*, *N. rossii*, *T. eulepidotus*) also occur in inshore waters but they are more abundant in the offshore part of the shelf, at depths down to *c.* 450 m (Table I). Other species (e.g. *C. gunnari*, *L. squamifrons*, *C. rastrospinosus*, *P. antarcticum*) are distributed almost exclusively on the outer shelf. *Pleuragramma antarcticum* is circum-Antarctic and abundant in coastal waters (DeWitt & Hopkins 1977, Hubold 1990), including the area off the Antarctic Peninsula (Kellermann 1987). Species of the family Myctophidae, mainly *Electrona antarctica* and *Gymnoscopelus nicholsi*, occur on the outer shelf, but the entire family reaches maximum abundance in terms of biomass and number of species in the open ocean pelagic ecosystem.

Fish prey

There are a considerable number of studies on the trophic ecology of fish communities of the southern Scotia Arc and west Antarctic Peninsula (summarized in Tables II & III). The feeding strategies of the fish species considered in this review are known from other coastal ecosystems and are not specific to the Antarctic; they are summarized to allow a comparison between the inshore and the offshore zones. The fish have been categorized into feeders on benthos, zooplankton or both (Table II). The feeding behaviour includes ambush feeding, bottom slurping, grazing and water column feeding (Daniels 1982) (Table III). The relevance of krill as fish prey in inshore and offshore waters

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Table IV. Chemical composition and energy content of muscle tissue in fish and of whole *E. superba* in summer (mean or range values). Composition expressed in g 100 g^{-1} wet weight; energy expressed in kJ 100 g^{-1}.

Species	Month	Water	Lipid	Protein	Carbohydrates	Energy
N. coriiceps	March	78.4[1]	1.9[1]	19.1[1]	-	395
	Jan–March	80.35[2]	0.94[2]	17.48[2]	0.80[2]	345
G. gibberifrons	March	79.8[1]	0.8[1]	18.5[1]	-	344
	Jan–March	79.55[3]	0.62[3]	18.53[3]	0.25[3]	341
	March	78[4]	0.7[4]	19.9[4]	-	364
C. aceratus	March	81.2[1]	0.9[1]	17.3[1]	-	327
C. gunnari	March	81.0[1]	1.5[1]	17.0[1]	-	345
	summer?	79.6–81.6[4]	0.4–1.5[4]	15.8–16[4]	-	283–327
E. carlsbergi	January	72.7[4]	7.7[4]	17.8[4]	-	587
G. nicholsi	March	67[4]	15.3[4]	16.3[4]	-	843
P. antarcticum	March	79.4[4]	7.7[4]	11.7[4]	-	484
	Jan–March	78.3[5]	10.2[5]	-	-	-
E. superba	March	75[6]	7.5[6]	12.72[6]	2.33[6]	531
	February	75.7[7]	6.9[7]	13.6[7]	-	486
Mollusca						237[8]
Polychaeta						271[8]
Amphipoda						327[8]
Echinodermata						217[8]

Source: 1 = Oehlenschläger 1991, 2 = Mazzotta *et al.* 1993, Casaux *et al.* 1995b, 3 = Márquez *et al.* 1996, 4 = VNIRO 2000, 5 = Friedrich & Hagen 1994, 6 = Márquez *et al.* 1978, 7 = Yanagimoto *et al.* 1979, 8 = Brey 2001, - = not provided.

is presented in a separate item, within this section.

Inshore

In this zone benthos feeders and benthophagous, non-generalist species, which also feed sporadically in the water column (benthos-plankton feeders) are predominant. Plankton feeders, which prey almost exclusively in the water column, are early juvenile stages of many notothenioids (e.g. *C. aceratus*) (Table II).

All the feeding behaviours are represented in this zone (Table III). Some species use these strategies alternatively or combine more than one strategy to feed on a wide range of organisms. Slurp feeding is represented by *G. gibberifrons* living on soft bottoms such as mud, clay or sand, and is associated with the intake of infaunal prey. Sediments are often found in the stomach of this species (Targett 1981, Casaux *et al.* 1990).

Grazing is an important feeding strategy in some Antarctic demersal shallow water fish species. Although it has been thought that the utilisation of macroalgae by fish in terms of energy is poor, fish can assimilate between 20% (Montgomery & Gerking 1980) and 90% (Horn 1989) of the algae ingested. It has been discussed whether fish deliberately eat algae, or if they are accidentally ingested with other prey (Showers *et al.* 1977, Moreno & Zamorano 1980, Daniels 1982, Burchett 1983). Recent studies indicate that algae are consumed deliberately (Barrera-Oro & Casaux 1990, Casaux *et al.* 1990) and moreover, actively selected by fish (Iken *et al.* 1997, 1998). Therefore, at least some Antarctic fish species (e.g. *N. coriiceps*, *G. gibberifrons*, *N. rossii*, *T. newnesi*) should be considered omnivorous.

Water column feeding is typical of the pelagic Antarctic silverfish *P. antarcticum* and the cryopelagic *Pagothenia borchgrevinki* and the semipelagic *T. newnesi* in the High Antarctic Zone (Andriashev 1970, Eastman & DeVries 1985, Gutt 2002). In inshore waters, water column feeding fish prey on krill when it is present and on other pelagic prey, but also feed on benthos when pelagic prey is not available (Tables II & III). The primary benthic taxa preyed on by fish are nudibranchs, gammaridean amphipods, isopods, chitons, bivalves, gastropods, ophiuroids, asteroids, echinoids and shrimps (decapods). The nutritive value of benthos is much lower than that of fish and krill (Grantham 1977, Coggan 1993, Brey 2001 and references therein). Furthermore, some of the benthic organisms preyed on throughout the year by generalist demersal fish species such as *G. gibberifrons*, *N. coriiceps* and juvenile *N. rossii* are of very low energetic value (e.g. algae, sponges, corals, asteroids, ophiuroids, ascidians). Only amphipods, which are the energy-richest taxa of the benthos, reach the lower energetic value of the range estimated for demersal fish (Table IV). It is likely that this apparent "energetic disadvantage" is balanced by seasonal variation in the demand for food (Coggan 1997, see below). Observations of seasonal variations in fish diets show that benthic amphipods are the main prey during most of the year, but during the summer months, fish take advantage of the occurrence of krill and other pelagic organisms (e.g. hyperiid amphipods) inshore, to feed on them intensively (Showers *et al.* 1977, Linkowski *et al.* 1983, Casaux *et al.* 1990).

Table V. Comparison of seasonal krill consumption between inshore and offshore demersal fish in waters around the South Orkney Islands, South Shetland Islands and west Antarctic Peninsula. Diet as frequency of occurrence (F%) and percentage by weight (W%) of krill in the stomach.

	Offshore krill				Inshore krill			
	Summer		Winter		Summer		Winter	
Fish species	F%	W%	F%	W%	F%	W%	F%	W%
Notothenia rossii (adults)	90–100[1]	47–95[2]		45[10]	6–45[11]	1.3[12]	1–11[17]	0.6[12]
Champsocephalus gunnari	90–100[1]	95–99[3]		75[10]				
Lepidonotothen larseni	21–95[4]	38–92[5]		24[10]				
Gobionotothen gibberifrons		4–50[6]		17[10]	3–6[13]		0[16]	
Notothenia coriiceps		24[7]		11[10]	12–27[14]	1.8–49[15]	0–14[17]	< 1[18]
Chaenocephalus aceratus (adults)		<10[8]		0[10]				
Chionodraco rastrospinosus		70–95[9]		18[10]				
Trematomus eulepidotus		85[7]						
Trematomus newnesi		59[7]			8[16]			
Lepidonotothen nudifrons		4.6[7]	3[10]		8[12]	< 1[12]		

Sources: 1 = Freytag 1977, Permitin & Tarverdiyeva 1978, Tarverdiyeva & Pinskaya 1980, Kock *et al.* 1980, Kock 1982, 2 = Tarverdiyeva 1982, Takahashi & Iwami 1997, 3 = Tarverdiyeva 1982, Takahashi 1983, Takahashi & Iwami 1997, 4 = Permitin & Tarverdiyeva 1978, Tarverdiyeva & Pinskaya 1980, Daniels 1982, Takahashi 1983, Barrera Oro & Tomo 1987, Takahashi & Iwami 1997, 5 = Targett 1981, Takahashi 1983, Rowedder 1984, Takahashi & Iwami 1997, 6 = Rowedder 1984, Takahashi & Iwami 1997, 7 = Takahashi & Iwami 1997, 8 = Kock 1985a, Takahashi & Iwami 1997, 9 = Takahashi 1983, Takahashi & Iwami 1997, 10 = Gröhsler 1994, 11 = Moreno & Bahamonde 1975, Linkowski *et al.* 1983, Casaux *et al.* 1990*, 12 = Linkowski *et al.* 1983, 13 = Moreno & Osorio 1977, Daniels 1982, Casaux *et al.* 1990*, 14 = Moreno & Bahamonde 1975, Moreno & Zamorano 1980, Linkowski *et al.* 1983, Barrera-Oro & Casaux 1990*, 15 = Showers *et al.* 1977, Barrera-Oro & Casaux 1990*, Iken *et al.* 1997*, 16 = Casaux *et al.* 1990, 17 = Linkowski *et al.* 1983, Casaux *et al.* 1990, 18 = Showers *et al.* 1977, Linkowski *et al.* 1983. *Sampling included late spring and/or early autumn.

Offshore

The feeding types and feeding behaviours described for fish inshore are also represented in offshore waters, but fish depend less on benthic organisms and feed more intensively on krill and other pelagic forms such as salps, hyperiid amphipods (mostly *Themisto gaudichaudii*) and pelagic fish (i.e. myctophids, *P. antarcticum*, juvenile stages). Water column feeding is a common feeding behaviour of fish in the offshore zone. For example, *N. rossii* occurs inshore in the juvenile stage, where they are mainly benthos feeders but also feed on epibenthos, plankton and nekton (Burchett 1982, 1983, Linkowski *et al.* 1983, Casaux *et al.* 1990) (Table II). After the juvenile phase, this species migrates offshore to join the adult population, that feed mainly on krill and fish (Burchett 1982, Kock 1992, Gröhsler 1994). The benthos feeder *G. gibberifrons* in offshore waters north of the South Shetland Islands showed a main diet of krill, supplemented with benthic organisms (Takahashi 1983). Similarly in the same area (offshore north of King George Island), *G. gibberifrons* and other demersal notothenioids were caught from the water column with the stomachs containing mainly krill and hyperiid amphipods (Rembiszewski *et al.* 1978). *Lepidonotothen larseni* and *T. eulepidotus*, which occur inshore but have a wider offshore distribution, feed mainly on krill and secondarily on gammarideans, isopods and polychaetes (Permitin 1970, Takahashi 1983, Barrera-Oro & Tomo 1987, Gröhsler 1994, Takahashi & Iwami 1997). *Trematomus eulepidotus* at 300–350 m depth in the Cosmonaut Sea (East Antarctica) preys mainly on krill and to a lesser degree on myctophids and *P. antarcticum* (Pakhomov & Tseytlin 1992).

Pelagic feeding species occurring offshore are more abundant than inshore species, presumably due to a greater abundance or more continuous availability of pelagic prey, mainly krill (Kock 1992). Commercially exploited species, such as *N. rossii* and the mackerel ice fish *C. gunnari* amongst others, may constitute examples for this observation.

Krill as fish prey in inshore and offshore waters

The importance of krill in the diet of Antarctic fish has been widely recognized (Permitin 1970, Targett 1981, Kock 1985a, Williams 1985, Nast *et al.* 1988, Takahashi & Iwami 1997). Based on a number of qualitative studies in different seasons (mainly summer) and years, Kock (1985a) estimated the proportion of krill in the diet of several demersal notothenioids from offshore waters in the Atlantic sector. This and information from later studies both in offshore and inshore areas in summer and winter at the South Orkney Islands, South Shetland Islands and west Antarctic Peninsula areas is summarized in Table V. Except for *N. coriiceps* in summer, a higher krill consumption by fish offshore than inshore is evident for both pelagic and benthic feeders in all seasons. The apparent higher feeding on krill by *N. coriiceps* inshore in summer is probably an artefact, since the observed value of 49% by weight of krill in the stomachs was atypical (Iken *et al.* 1997), whereas the observed lower value of 24% obtained offshore comes from the analysis of a limited number of fish (58) which were caught within a short interval of time (nine days) in few hauls (Takahashi & Iwami 1997).

Information on seasonal abundance of krill in the region

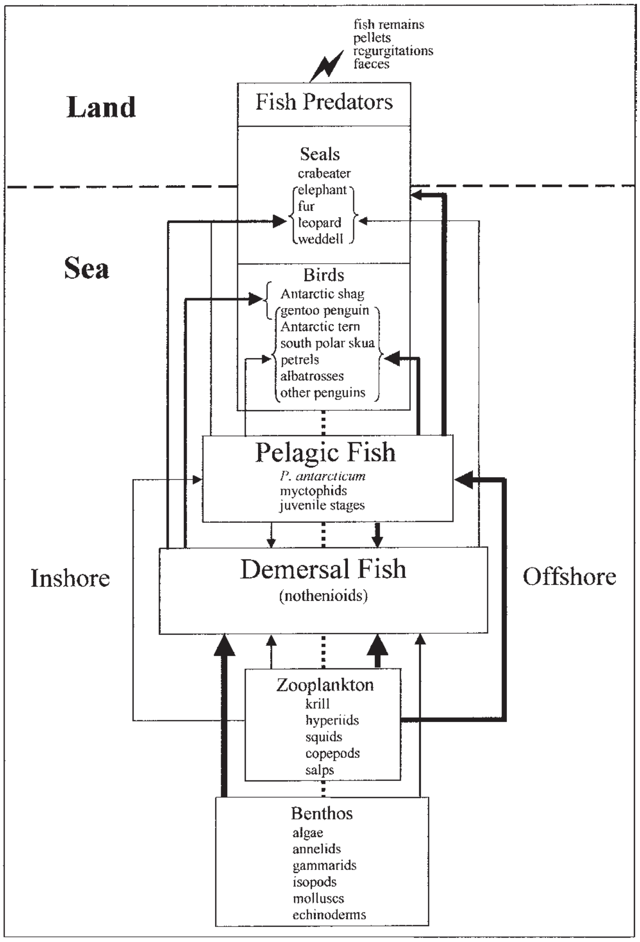

Fig. 2. Diagram indicating the position of fish in the food web of the inshore-shallow water and the offshore communities.

indicates highest levels in summer and lowest levels in winter (Stepnik 1982, Siegel 1988, Ross *et al.* 1998, Lascara *et al.* 1999). It has been suggested there is an active migration of adult krill during summer into offshore waters and a return to coastal waters in autumn (Siegel 1988). Nevertheless, independent of habitat and feeding style, krill is the main prey for most of the offshore demersal notothenioids. Moreover, it has been indicated that mesopelagic fish, such as myctophids, might have a greater impact on krill than coastal species (summarized in Sabourenkov 1991, Hureau 1994).

The information on krill intake by fish (Table V) is incomplete, in part due to a paucity of studies in which appropriate analytical methods were used, but also because there are few studies outside the summer season. Consequently it is impossible to give a general quantitative estimate of the utilisation of krill by offshore and inshore demersal fish species. However, it seems evident that the role of krill in inshore waters is less important for fish and the benthic community than in the offshore portion of the shelf. One explanation is that the occurrence of krill in inshore waters is restricted mainly to the summer season. On the other hand, there is evidence for inshore demersal fish of seasonal variation in the demand for food (Coggan 1997). Laboratory experiments on *N. coriiceps* and *H. antarcticus* showed a lower feeding rate in winter than in summer, under stable conditions of food supply (Targett 1990, Johnston & Battram 1993, Coggan 1997).

The accessibility of krill to demersal fish has been historically explained in two ways:

1) the vertical distribution of krill reaches the bottom (Everson 1977, Kock 1985a, Barrera-Oro & Casaux 1990, Gröhsler 1994, Takahashi & Iwami 1997, among others),

2) demersal fish migrate up in the water column to feed (Everson 1977, Freytag 1980, Daniels 1982, Duhamel & Hureau 1985, Kock 1985a, Barrera-Oro & Casaux 1990, Foster & Montgomery 1993).

In recent years, these phenomena have been demonstrated in the wild by the use of video cameras (Gutt & Siegel 1994, North 1996a) and echo sounders. In shallow waters, the krill become available to the fish through a combination of both mechanisms.

Fish and krill predators

Inshore

In their turn, the demersal fish are common prey of birds and seals (Fig. 2). Pelagic fish species, like myctophids and *P. antarcticum*, occur in oceanic and coastal waters and it has been believed that they only occasionally approach inshore, neritic waters. Recent observations of flying birds feeding nearshore close to the sea surface add new information on the matter that needs to be clarified (discussed below).

In Antarctica, the only flying bird that feeds chiefly on demersal coastal fish is the Antarctic shag *Phalacrocorax bransfieldensis* (formerly the blue-eyed shag *P. atriceps*; at South Georgia and South Orkney Islands = *P. georgianus*) (Fig. 2). Shag predation on inshore fish has been studied by analysis of pellets and stomach contents in the South Shetland Islands (Casaux & Barrera-Oro 1993, Coria *et al.* 1995, Barrera-Oro & Casaux 1996, Favero *et al.* 1998), the South Orkney Islands (Shaw 1984, Casaux *et al.* 1997a) and in the west Antarctic Peninsula (Schlatter & Moreno 1976, Casaux *et al.* 2002). Jobling & Breiby (1986), among others, discussed in detail the errors arising when using otoliths in diet investigations. Such errors were substantiated by trials with captive cormorants (Johnstone *et al.* 1990, Zijlstra & Van Eerden 1995) including the Antarctic shag (Casaux *et al.* 1995a) After correction for potential errors caused by digestive processes, demersal fish were estimated to represent about 90% by weight in the diet of *P. bransfieldensis* (Casaux *et al.* 1995a, Casaux *et al.* 1998a). The fish species represented in pellets agreed

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qualitatively and in relative numbers with those regularly sampled by means of hook and lines, and by trammel/gill nets in the same area (e.g. *N. coriiceps, N. rossii, T. newnesi, L. nudifrons, G. gibberifrons*) (Casaux & Barrera-Oro 1993, Barrera-Oro & Casaux 1996). This is not surprising, since the depth distribution of all inshore fish is within the maximum foraging depth of the Antarctic shag, of 125 m (Croxall *et al.* 1991, Wanless *et al.* 1992, Casaux *et al.* 2001). Hence, the potential use of *P. bransfieldensis* to monitor changes in coastal fish populations was suggested (Casaux & Barrera-Oro 1993, 1995) and then implemented in 1997 for a test period of five years (CCAMLR 2001).

The fish taken by Antarctic penguins are mostly pelagic, only the gentoo (*Pygoscelis papua*) feeds inshore on pelagic and demersal species (Brown *et al.* 1990, Bost *et al.* 1994, Casaux 1998b, Coria *et al.* 2000).

Within the area of study at Laurie Island, South Orkney Islands, fish, mainly demersal species, constituted the main prey of the gentoo penguin in two consecutive years (Coria *et al.* 2000). Fish was the most important prey by mass in 1995 (81.1%) and 1996 (60.5%) and occurred in 98% and 93% of the samples, respectively. The dominant species in the diet were demersal nototheniids, particularly *G. gibberifrons*, *L. nudifrons*, *N. nybelini* and *T. newnesi*, whereas the occurrence of channichthyids and myctophids was negligible (Coria *et al.* 2000). For other Antarctic areas it has been reported that demersal notothenioids, the nototheniid *L. larseni* and the channichthyid *C. gunnari*, were the main fish prey at South Georgia (Croxall & Prince 1980, Croxall *et al.* 1988, Williams 1991), whereas at Heard Island the myctophid *Krefftichthys anderssoni* (Green & Wong 1992) and at Macquarie Island the demersal nototheniid and myctophid species *Paranotothenia magellanica* and *Gymnoscopelus* sp. (Hindell 1989, Robinson & Hindell 1996) were the dominant prey.

The fish eaten by Antarctic pinnipeds are also mostly pelagic (mainly myctophids) but the southern elephant seal (*Mirounga leonina*), the leopard seal (*Hydrurga leptonyx*), the Weddell seal (*Leptonychotes weddellii)* and the Antarctic fur seal (*Arctocephalus gazella*) prey on demersal fish at least partially (Everson 1970, Green & Williams 1986, Plötz *et al.* 1991, Casaux *et al.* 1997b, Burns *et al.* 1998, Casaux *et al.* 1998b, Daneri & Carlini 2002) (Fig. 2).

Overall, information on species identity and the proportion of demersal fish in seal diets is very scarce, especially in the South Shetland Islands archipelago and west of the Antarctic Peninsula. Around King George Island, the frequency of occurrence of demersal fish in the diet of the elephant seal was only 3.4%, while that of pelagic fish (mostly myctophids) was 11.6% (Daneri & Carlini 2002). However, elephant seals may travel long distances to and from feeding areas and so otolith digestion may lead to a large underestimate of fish in the diet (Green & Williams 1986, Croxall 1993, Daneri & Carlini 2002). More recent methods (Iverson *et al.* 1997) have showed that the fatty acid signature composition of milk and seal blubber can provide useful information for studying the foraging ecology of seals. For example, using this methodology on southern elephant seals sampled at South Georgia, it was concluded that fish was a very important food item (Brown *et al.* 1999). However, up to now, in most pinniped diet studies conventional methods have been used. Around Nelson Island, fish were the most frequent (96%) and numerous (46%) prey of the Weddell seal, but the frequency of demersal species was only 30% of the total prey (Casaux *et al.* 1997b). In the same locality, atypically in February 1996, two demersal fish species (*Cryodraco antarcticus* and *G. gibberifrons,* 66% by mass) were more important than myctophids (34% by mass) in the diet of the Antarctic fur seal (Casaux *et al.* 1998b). Interestingly in the South Georgia area, some demersal fish species (mainly *C. gunnari* and secondarily *G. gibberifrons* and *L. larseni*) were regularly a higher resource as food of the fur seal than pelagic fish (North *et al.* 1983, Reid 1995, North 1996b, Reid & Arnould 1996).

It has been said that inshore fish feed opportunistically on krill when swarms get carried inshore. Some higher predators may conduct a similar feeding behaviour in this zone, for example, the humpback whale *Megaptera novaeangliae* (personal observation), the crabeater seal *Lobodon carcinophagus* and the fur and leopard seals (see Costa & Crocker 1996).

Offshore

Predation on demersal fish by birds and seals in the offshore fraction of the continental shelf is conditioned by their diving ability (Fig. 2). For example, around South Georgia, the intensity of predation of the fur seal on *C. gunnari* is limited by the main depth distribution range (150–250 m) of the fish (Everson *et al.* 1999). Although this seal can dive deeper than 100 m, 95% of dives are less than 50 m (Boyd & Croxall 1992, Boyd *et al.* 1997, quoted in Everson *et al.* 1999). Among the higher predators that also feed in nearshore waters, only Weddell (Kooyman 1981, Testa 1994, Burns *et al.* 1997) elephant (Boyd & Arnbom 1991, Hindell *et al.* 1991, Jonker & Bester 1994) and presumably leopard seals (due to their large mass, see Costa 1991) have the diving capacity to feed on demersal fish offshore, close to the seabed at depths deeper than 200 m. The Weddell seal is the most piscivorous one. The comparison of bottom trawl catches on the eastern shelf of the Weddell Sea with stomachs contents of Weddell seals collected within the same region (Drescher Inlet, 72°52'S, 19°25'W) in the same season, gave evidence that this seal during the spring of 1986 generally foraged on demersal fish (e.g. *Chionodraco myersi*, *T. eulepidotus*) in the deep water layers, below 400 m (Plötz *et al.* 1991). However, deep dives on the bottom would not be the usual diving mode of Weddell seals, but continuous foraging on available midwater species (mainly *P. antarcticum*), with occasional shifts to benthic feeding (see Testa 1994, Plötz *et al.* 2001). Elephant seals are exceptional in their deep diving ability (down to 1400 m, Jonker & Bester 1994, Slip *et al.* 1994) and can prey on large demersal fish species such as *Dissostichus eleginoides* (Slip 1995), presumably on the deeper shelf and slope. However, the fish prey of the elephant seal are mostly pelagic and, as it was suggested for pinnipeds and penguins in general, deep diving is only economical when the predator is foraging on large prey which compensate energetically the effort of each dive (Costa 1991).

In offshore waters, predation by birds and seals on pelagic fish, instead, is more important quantitatively. The lanternfish, especially *E. antarctica*, is a key component of the oceanic pelagic ecosystem in terms of fish biomass and as a dominant krill predator (Rowedder 1979, Kock 1985b, Williams 1985, Lancraft *et al.* 1989). Myctophids are the primary prey of king and macaroni penguins in the southern Indian Ocean (Adams & Brown 1989, Adams *et al.* 1993, Raclot *et al.* 1998) and may be more important than krill as food of flying birds feeding in open water near the ice edge (Hopkins *et al.* 1993). In the Atlantic sector of the Southern Ocean, seabirds and seals consume about 250 000 tonnes of myctophids (mainly *E. carlsbergi* and *K. anderssoni*) annually (CCAMLR 1991). In the southern Scotia Arc, myctophids (mainly *E. antarctica*) constitute an important item in the diet of flying birds such as cape petrels *Daption capense* (Casaux *et al.* 1998c, Soave *et al.* 2000), blackbellied stormpetrel *Fregetta tropica* (Hahn 1998), snow petrels *Pagodroma nivea* (Ferretti *et al.* 2001) and south polar skuas *Catharacta maccormicki* (Montalti *et al.* 1996). Around the South Orkney Islands (Daneri & Coria 1993), the South Shetland Islands (Daneri 1996, Casaux *et al.* 1998b, Daneri & Carlini 1999) and Heard Island (Green *et al.* 1989, 1991) Antarctic fur seals feed mainly on myctophids, while krill is their main prey at South Georgia (Reid & Arnould 1996, Iverson *et al.* 1997).

The other circum-Antarctic pelagic fish, *P. antarcticum,* is also an important prey of seabirds and seals; it plays a key role in the marine food web in the high Antarctic zone (Kellermann & North 1994, Williams & Duhamel 1994). *Pleuragramma antarcticum* was an important item in the diet of cape petrels at the Windmill Islands, in the southern Pacific Ocean (van Franeker *et al.* 1992) and at King George Island (Creet *et al.* 1994) in the South Shetland Islands. In this last archipelago, at Half Moon Island, *P. antarcticum* was the second fish prey (after *E. antarctica*) of south polar skuas (Montalti *et al.* 1996). The same fish species was the main food item for Weddell seals in the Weddell Sea (Plötz 1986) and in McMurdo Sound in the Ross Sea (Davis *et al.* 1982, Testa *et al.* 1985, Burns *et al.* 1998). After krill, *P. antarcticum* was second prey of leopard and crabeater seals in winter in the area west of the Antarctic Peninsula (Lowry *et al.* 1988) and in the vicinity of Davis station (Green & Williams 1986). In years of availability, *P. antarcticum* may constitute an important prey of the southern elephant seal, at the west coast of the Antarctic Peninsula (Bornemann *et al.* 2000).

In the outer shelf and the open ocean ecosystem krill is the main prey for most of vertebrates. The accessibility of krill to fish could be explained in terms of occasional availability due to the highly aggregated distribution of krill (Miller & Hampton 1989). However, to higher predators the accessibility to krill depends also on its foraging behaviour, allowing them to search for krill over larger areas.

Estimates of global krill abundance based on recent acoustic methods range from 61 to 155 million tonnes, and are probably more realistic than earlier figures of 500 million tonnes (Nicol *et al.* 2000). Similarly, recent results of the multinational CCAMLR 2000 acoustic survey gave a krill biomass estimate of 44 million tonnes for the western part of the Atlantic sector of the Southern Ocean (CCAMLR 2000a).

The quantification of Antarctic krill consumption by marine and land-based predators is difficult and has produced a wide range of estimates. Although these calculations have not been refined lately, annual krill intake is about 30–50 Mt (million tonnes) by squids (Miller & Hampton 1989); 40–50 Mt by fish (Hureau 1994); 115 Mt by birds (Croxall *et al.* 1984); 130 Mt by seals (Laws 1985); 43 Mt by whales (Laws 1985) and 36–140 Mt (Armstrong & Siegfried 1991, Ichii & Kato 1991) by minke whales. Recent estimates suggest that higher predators (Adélie, gentoo and chinstrap penguins and fur seals) in the South Shetland Islands eat about 830 000 tonnes of krill per year (Croll & Tershy 1998). On the other hand, annual fish consumption by birds and mammals has been estimated to be up to 15 Mt (Everson 1977, Laws 1985), which is lower than consumption of krill. The annual predator consumption of cephalopods (mostly *Martialia hyadesi*) is also comparatively low, estimated at 330 000 tonnes in the Scotia Sea (Rodhouse *et al.* 1993).

Relative importance of krill and fish consumption by predators

The reliance of offshore fish, and most of the higher predators in general, on krill as a food supply is probably because of the general availability of krill offshore throughout much of the year in most years. The high energy content of krill in comparison with other organisms may also constitute a significant benefit for its predators. This last fact may be important also for the myctophids in oceanic waters (elsewhere in the Antarctic Polar Frontal Zone) and for *P. antarcticum* in the high Antarctic zone, explaining its high consumption by higher predators.

To calculate the energy value of prey the following energy equivalents for 1 g of food were used: carbohydrate 16 kJ, fat 37 kJ, protein 17 kJ (FAO/WHO/UNU 1985). The proximate composition of whole *E. superba* and muscle for two myctophids, *P. antarcticum* and four demersal fish species, for the summer (January–March), were used to calculate their energy content (Table IV). The energy content of krill was estimated at 486–531 kJ 100 g^{-1} wet weight, which is similar to that for *P. antarcticum* but is higher (ratio 3.3:5) than those estimated for the demersal nototheniids (*N. coriiceps* and *G. gibberifrons*) and channichthyids (*C. aceratus* and *C. gunnari*), which ranged between 327 and 395 and averaged 351 kJ 100 g^{-1}. The difference is even higher, if the calculations for fish are for the whole animal. The energetic content of the two myctophids, *E. carlsbergi* and *G. nicholsi*, was the highest and was even higher than that of krill (Table IV).

This difference in nutritive value is explained by the high fat (lipid) content of krill and pelagic fish such as Myctophidae and *P. antarcticum* in comparison to demersal fish, since the calories provided by the proteins and the carbohydrates are lower. The lipid contents of the fish are in agreement with their mode of life, since lipids have an important buoyancy function in the pelagic species (Eastman & DeVries 1982, Friedrich & Hagen 1994, Phleger *et al.* 1997).

Some examples may highlight the importance of krill for fish and higher predators. The Antarctic fish *N. rossii* and *C. gunnari* when feeding on krill grow as fast as the cod *Gadus morhua* in Greenland (Fischer & Hureau 1985). The reproductive success of the mackerel icefish *C. gunnari* off South Georgia is related to the availability of krill, its main food source (Kock *et al.* 1994, Everson *et al.* 1999). This suggestion is based on the generalized oocyte resorption process found in a high proportion of individuals caught in years of krill scarcity (Everson *et al.* 1996, Barrera-Oro *et al.* 1998). Kozlov (1980) also found that final maturation in *N. rossii* and *G. gibberifrons* occurs when these species can feed intensively on the energy-rich krill.

The breeding success of many seabirds and seals relies heavily on krill availability. At South Georgia a tenfold decrease in krill abundance between 1986–94 resulted in the markedly reduced breeding success of most higher predators, except macaroni penguin which switched from eating krill feeding on pelagic amphipods (CCAMLR 1998).

Minke whales (*Balaenoptera acutorostrata*) are large consumers of krill in the southern Indian Ocean and Ross Sea and the seasonal increase in the girth of these whales was lowest in years of low krill abundance (CCAMLR 1997).

Likewise, the availability of the energy-rich myctophids seems to be related to the increase in the populations of king penguins and south polar skuas, which are two of its main predators. Adult king penguins prey on myctophid fish not only to feed their chicks but also for their own nutrition (Raclot *et al.* 1998). In the Antarctic Peninsula during the 1970s and 1980s, there were no myctophids in the diet of *C. maccormicki*, and *P. antarcticum* was the dominant prey species. In this period there were years when south polar skuas failed to produce any chicks and *P. antarcticum* was absent from the diet. During the 1990s myctophids increased in the diet and this has been associated with increased breeding success and no years of complete breeding failure (CCAMLR 2000b).

Discussion

Shore based icthyological studies in the southern Scotia Arc and west Antarctic Peninsula deal almost exclusively with demersal notothenioid fish. The occurrence of pelagic fish (myctophids, *P. antarcticum*) inshore is rarely documented (Daniels 1982, Linkowski *et al.* 1983) and could be attributed to temporal introduction of nekton from adjacent offshore areas (e.g. from the Bransfield Strait to Admiralty Bay, King George Island, Skora 1993). However, regular samplings of pelagic fish by means of adequate gears have not been reported and therefore the occurrence of these fish in inshore waters could have been underestimated. Field observations throughout the breeding season of flying birds feeding nearshore on the sea surface, followed by identification of fish found around the nests and of predigested fish (by otolith exam.) found in regurgitations collected at the arrival of these bird foraging trips indicate that the occurrence of myctophids in inshore waters might be more important than previously believed. Examples of this predator-prey interaction are the Antarctic tern, *Sterna vitatta*, on *E. antarctica* at Harmony Cove, Nelson Island, during January–March 2002 (R. Casaux, personal communication 2002) and the Wilson's petrel, *Oceanites oceanicus*, also on *E. antarctica* at Uruguay Cove, Laurie Island, during January–February 1997/2000 (N. Coria, personal communication 2002). A similar feeding behaviour could be also expected for the piscivorous south polar skua and the black-bellied storm petrel.

The main pathway of energy flow through fish in the food web in the study area is shown in Fig. 2. Inshore, the ecological role of demersal fish is more important than that of krill. There, demersal fish are major consumers of benthos and also feed on zooplankton (mainly krill in summer), and are links between lower and upper levels of the food web; they are common prey of other fish, birds and seals. Besides the fact that pelagic fish species are less abundant inshore, the role of these and other pelagic stages of fish (larvae, postlarvae, early juvenile) is not comparable to that of demersal fish, since the former feed in the water column exclusively on zooplankton, and there is little or no energy transfer (e.g. faeces, dead animals) between them and the benthos community (see Hoddell *et al.* 2000).

Offshore, demersal fish depend less on benthos, and feed more on zooplankton (mainly krill) and nekton, and are less accessible as prey of birds and seals. Pelagic fish (especially lanternfish) are more abundant than inshore and play an important role in the energy flow from macrozooplankton to higher trophic levels (seabirds and seals) (Greely *et al.* 1999). Through the higher fish predators, energy is transferred to land in the form of fish remains, pellets (birds), regurgitations and faeces (birds and seals).

Information from Antarctic research over the last fifteen years indicates that many predators feed on species other than krill. However, in the general context of the Antarctic marine ecosystem, krill (*E. superba*) plays the central role in the food web because it is the main food source in terms of biomass for most of the high level predators from demersal fish up to whales.

In recent years, a non krill-dependent trophic system in the open Southern Ocean has been reported (Rodhouse & White 1995). In the Antarctic Polar Frontal Zone of the Scotia Sea a copepod, fish (myctophids) and squid (mainly *M. hyadesi*) may provide the food chain links between primary producers and higher predators. However, the predator consumption of cephalopods is low in comparison to that of krill. In offshore coastal and oceanic waters the greatest proportion of energy from the ecosystem is transferred to land directly through krill consumers, such as flying birds, penguins, and seals.

In conclusion, the Antarctic ecosystem is unique because its higher vertebrate predators largely depend on one component of the food web, namely krill. This has no obvious equivalent in other marine ecosystems. Beside krill, the populations of fish in the Antarctic Ocean are the second most important element for higher predators (Fischer & Hureau 1985), in particular the energy-rich pelagic Myctophidae in open waters and the Antarctic silver fish *P. antarcticum* in the high Antarctic zone. However, inshore the role of krill is less significant, and there many predators (fish, gentoo penguins, shags, seals) rely on demersal fish.

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