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SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

▶ CHAPTER 7. BIOGEOGRAPHIC PATTERNS OF FISH.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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7. Biogeographic Patterns of Fish

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1. Introduction

1.1. History of descriptions of fish biodiversity

The isolation of the Southern Ocean after the opening of Drake Passage some 23–25 million years ago, the formation of the Antarctic Circumpolar Current, the subsequent cooling of the ocean and the formation of well-defined frontal systems has resulted in the evolution of a unique fish fauna with a high level of endemism.

The first descriptions of the marine ichthyofauna were published in the early 1840s when scientific expeditions were able for the first time to collect fish around sub-Antarctic islands. Descriptions of the Antarctic continental shelf and shelf margins around the Sub-Antarctic and Antarctic islands faunas started with the publication of the results of later expeditions (mainly British, French, German and Australian) around the turn of the 20th century. This work is on-going with investigation of the deep-sea fish fauna being sampled by research, exploratory and commercial toothfish fisheries (*Dissostichus* spp.). In recent years, fish biodiversity has been re-examined during a series of synoptic surveys such as the US ICEFISH 2004 cruise (Jones *et al.* 2008), and the surveys undertaken during the Census of Antarctic Marine Life (CAML) program such as CEAMARC (Collaborative East Antarctic Marine Census for the Census of Antarctic Marine Life) in East Antarctica (Koubbi *et al.* 2010, Causse *et al.* 2011) or the New Zealand International Polar Year IPY/CAML *Tangaroa* cruise in the Ross Sea (Clark *et al.* 2010, Hanchet *et al.* 2013).

The first descriptions of fishes from the Southern Ocean by Richardson (1844) included four species from R/V *Erebus* and *Terror* expedition (1839–1843). Thereafter the major contributors were:

- Günther (1877, 1880, 1887): descriptions of 28 species from the HMS *Challenger* expedition (1874–1883),
- Lönnberg (1905, 1906): descriptions of 17 species from the R/V *Antarctica* (1901–1904),
- Regan (1913, 1914): descriptions of 14 species from the *Terra Nova* Expedition (1910–1913),
- Norman (1935, 1937, 1938): descriptions of 14 species from the 14 expeditions of the HMS *Discovery* (1925–1951),
- Andriashev (2003): descriptions of 44 species (mainly liparids) sampled by expeditions from the former Soviet Union (USSR),
- Stein (2012): descriptions of 18 species of liparids from the Ross Sea.

New descriptions continued to be published (see Eastman 2005 and Fig. 1) for notothenioids and other highly diversified fish families such as Liparidae

and Zoarcidae, due to investigations conducted in poorly surveyed areas and the sea-ice zone, and with the use of new gear or remote underwater vehicles (ROVs). However, the asymptotic level in species richness has not yet been reached (Fig. 1). The introduction of molecular techniques as a tool for identifying cryptic species will also contribute to the extension of the progression. Several families (Rajidae, Muraenolepididae, Macrouridae, Harpagiferidae) still require taxonomic revision, and the geographical distribution of species still needs clarification because of the lack of detailed species diagnoses (molecular evidence but no taxonomic description) or because of misidentifications in the scientific record. Some rajids (genus *Bathyraja*) and grenadiers (genus *Macrourus*) continue to be described. Recent revisions (McMillan *et al.* 2012) and molecular analysis have greatly improved the systematics of these difficult families, and should allow for the identification of new cryptic species (Smith *et al.* 2008, 2011).

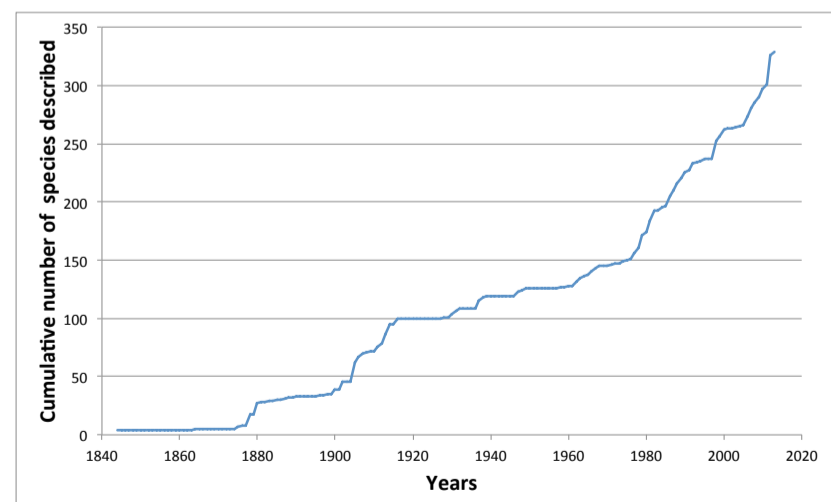


Figure 1 Time-line for descriptions of Southern Ocean fish species (adapted and updated from Eastman 2005).

For the purpose of this book, the Southern Ocean (s.l.) is considered as the area from the Sub-Tropical Front (STF) in the north to the Antarctic continent in the south. This differs from other definitions which use the Antarctic Polar Frontal Zone as the northern boundary of the Southern Ocean. Species only found in the Patagonian Shelf and Burdwood Bank, the Tasmanian Shelf

and South Tasman Ridge, the New Zealand Shelf and the Campbell Plateau have not been included.

Knowledge of circum-Antarctic neritic fish distributions has improved following recent surveys in the Weddell Sea (Schwarzbach 1988, Ekau 1990, Hubold 1992); the Bellingshausen Sea (Matallanas & Olaso 2007); East Antarctica (Koubbi *et al.* 2010, Causse *et al.* 2011, Dettai *et al.* 2011); the Ross Sea (Eastman & Hubold 1999, Donnelly *et al.* 2004, La Mesa *et al.* 2006, Clark *et al.* 2010, Hanchet *et al.* 2013); and the Antarctic Peninsula and Scotia Arc region (Jones *et al.* 2008). Some surveys which were undertaken by the Census of Antarctic Marine Life during the International Polar Year, have helped to delimit more precisely the biogeographic divisions which had been established by several authors (Regan 1914, Norman 1937, Andriashev 1965, Hureau 1973, Duhamel 1987, Kock 1992). The by-catch in commercial fisheries, both from deep-sea trawling and longlining (López-Abellán & González 1999, Piotrovskii 1999, Trunov 1999, Duhamel *et al.* 2005), has also played an important part in extending the knowledge of Antarctic fish biogeography.

The pelagic fish fauna has been extensively studied off South-Georgia and in the Scotia Sea (Piatkowski *et al.* 1994, Collins *et al.* 2008, 2012), the South Shetlands Islands (Pusch *et al.* 2004), on the Kerguelen Plateau (Duhamel 1998, 2000, Duhamel *et al.* 2005), Macquarie Island (Flynn & Williams 2012) and in East Antarctica (Hoddell *et al.* 2000, Van de Putte *et al.* 2010, Moteki *et al.* 2011, Koubbi *et al.* 2010, 2011).

More recent benthic investigations in the deep-sea, specially in abyssal depths of the Crozet Basin (Cousins & Priede 2012), have resulted in some unique new deep-sea records.

1.2. List of Southern Ocean fishes and their representation by family

Scientific references and biodiversity database records have facilitated the determination of the total number of fish species living in the Southern Ocean. In order to take the more recent systematic revisions into account we consider as valid all genera and species represented in the online Catalog of Fishes (Eschmeyer 2013): 47 families with 374 fish species (Table 1 and Appendix 5 at the end of volume); eight species (one in the genus *Trematomus* and seven in the genus *Channichthys*) need to be confirmed.

Additional species (63 species in the same families and 22 species in eight additional families) have occasionally been recorded south of the STF. They are mainly pelagic and their presence is either related to certain topographic features (i.e. the Drake Passage or the Kerguelen Plateau) which induce a frontal narrowing, or can be associated with local hydrographic events (such as eddies) associated with the northern frontal system that can transport subtropical and convergence species southwards.

Here, we update the synthesis provided in “*Fishes of the Southern Ocean*” (Gon & Heemstra 1990) by adding 117 new species (+7 to be confirmed) and 75 new records. This expands the partial checklists of Møller *et al.* (2005) and Eastman (2005) which had listed some 322 species. The latter author estimated that 30 to 60 species could still be described.

The list (Table 1) shows that few cartilaginous species (Chondrichthyes) are present in the Southern Ocean. Nearly three-quarters of the total number of species belong to a few families: Nototheniidae, Liparidae, Zoarcidae and Myctophidae. According to this study, the most dominant in terms of species is the largely endemic family Nototheniidae which account for 107 (with 8 still to be validated) mainly demersal species (see Appendix 5). Second (but first in terms of number of species by genus) are the Liparidae and Zoarcidae, with 85 and 40 species respectively; both families dominate the demersal fish fauna in the Southern and Arctic Oceans. Lanternfishes (family Myctophidae with 24 species) dominate the fish fauna of the meso- and bathypelagic zones. They are comparatively small-sized, and hardly grow larger than 18 cm SL. Large pelagic teleost families common in other oceans (such as Scombridae and Carangidae) are absent or only occasional migrants to the Southern Ocean.

With regard to marine species, about 2.06% of the world’s marine ichthyofauna (using FishBase, Froese & Pauly 2012) is represented by Southern Ocean fishes. However, the degree of endemism in the Southern Ocean is three times greater than that of other isolated marine regions (Eastman 2005).

1.3. Origin of recent ichthyofauna

According to Eastman (2005) “*A taxonomically restricted and endemic modern fauna succeeded a taxonomically diverse and cosmopolitan Eocene fauna*” in the Southern Ocean. Many Chondrichthyes and an unknown number of teleosts lived primarily in temperate seas. The Oligocene glaciation of Antarctica caused the extinction of this earlier fauna (Clarke & Johnston 1996). The onset of adaptative radiation in Antarctic notothenioids, which is characterized by the presence of Antifreeze Glycoproteins (AFGPs), commenced near the Oligocene-Miocene transition (mean 23.9 Ma) during a major period of global cooling and ice-sheet extension. Freezing avoidance would have allowed notothenioids to invade the newly developing, ice-associated niches, or to replace other clades which had become extinct, or which had to retreat from the Southern Ocean (Matschiner *et al.* 2011)

Notothenioids represent a ‘species flock’ (Rutschmann *et al.* 2011, Leconte *et al.* 2013) as defined by Eastman & McCune (2000) with the following criteria: monophyly, high species diversity and endemism, morphological and ecological diversity and biomass dominance. The phylogeny of notothenioids has been extensively revised using new molecular techniques (Matschiner *et al.* 2011, Rutschmann *et al.* 2011, Near *et al.* 2012, Dettai *et al.* 2012) and so up-

Table 1 Fish families and number of species recorded from the Southern Ocean (s.l.)

Family	Number of Southern Ocean (s.l.) species	Number of species occasionally recorded south of the STF
MYXINIDAE		1
PETROMYZONTIDAE	1	
LAMNIDAE	1	
SQUALIDAE	3	1
SOMNIOSIDAE	1	
RAJIDAE	9	1
HALOSAURIDAE	2	
NOTACANTHIDAE	2	
SYNAPHOBRANCHIDAE	2	1
NEMICHTHYIDAE		4
SERRIVOMERIDAE		1
MICROSTOMATIDAE	1	
BATHYLAGIDAE	5	
ALEPOCEPHALIDAE	4	
PLATYTROCTIDAE		2
GONOSTOMATIDAE	4	2
STERNOPTYCHIDAE		10
STOMIIDAE	5	2
SCOPELARCHIDAE	2	
NOTOSUDIDAE	2	
PARALEPIDIDAE	4	1
ANOPTERIDAE	1	
ALEPISAUROIDAE	1	
IPNOIDAE	1	
MYCTOPHIDAE	24	44
MURAENOLEPIDIDAE	8	
MACROURIDAE	10	1
MORIDAE	6	
MELANONIDAE	1	
GADIDAE		1
MERLUCCIIDAE		1
OPHIDIIDAE	4	
BYTHITIDAE	1	
CARAPIDAE	1	
CERATIIDAE	1	
ONEIRODIDAE	1	
MELANOCETIDAE	2	
GIGANTACTIDAE	1	
LAMPRIDAE	1	1
MELAMPHAIIDAE	3	
CETOMIMIDAE	3	
OREOSOMATIDAE	1	1
CONGIPODIDAE	1	
PSYCHROLUTIDAE	2	
LIPARIDAE	85	7
BATHYLUTICHTHYIDAE	1	
ZOARCIDAE	40	
BOVICTIDAE	1	
NOTOTHEIIDAE	115*	1
TRIPTEGYIIDAE	1	
CHIASMODONTIDAE	3	
GEMPYLIDAE	1	
SCOMBRIDAE		2
CENTROLOPHIDAE	1	
ACHIROPSETTIDAE	4	
total	374	85
	47 families	additional 8 families

setting the accepted classification. The notothenioids were followed by families of non-Antarctic origin (e.g. Liparidae, Zoarcidae, Rajidae, Macrouridae) that radiated in deeper zones in the Miocene (at least in the two former families).

1.4. Species and their habitat

The Southern Ocean ichthyofauna is divided here into three broad habitat categories (Appendix 5 at the end of volume):

- *Demersal neritic species*. They inhabit the continental, peri-insular shelves and oceanic seamounts, with 116 species and including 3 species occasionally recorded south of the STF and 7 doubtful *Channichthys* species from the Kerguelen Islands (Regan 1913, Shandikov 1995, 2008, 2011).
- *Deep-sea species*. They occur from the lower slopes (about 500 m in sub-Antarctic peri-insular shelves and down to 700m for the continental

Antarctic shelf) to the abyssal basins, with 207 species and including 13 already recorded in the neritic zone, 4 occasionally recorded south of the STF and 7 Liparidae distributed close to the northern boundary of the Southern Ocean.

- *Pelagic species* of the epipelagic (0–200 m), mesopelagic (200–1000 m) and bathypelagic zones (>1000 m). They comprise 89 species, with 13 already recorded as neritic/deep-sea; and additional 72 species occasionally recorded south of the STF.

Species can change habitat during their life cycle. Some have a long pelagic larval phase which allows for the geographical dispersion of individuals, whereas others inhabit coastal waters when young, but migrating to the deep-sea thereafter. There are many examples of such ontogenic migrations for notothenioids (Loeb *et al.* 1993, Koubbi *et al.* 2009).

Only one abundant nototheniid species, *Pleuragramma antarctica*, is fully pelagic. It seems to occupy a similar niche to the Clupeidae and Engraulidae in other parts of the World Ocean. A cryopelagic niche (occupied by the nototheniids *Pagothenia brachysoma*, *Trematomus borchgrevinki* and juveniles stages of *Trematomus newnesi*) occurs in a comparable niche comparable to that occupied by polar cod (*Boreogadus saida*) in the Arctic Ocean.

1.5. Recent biogeographical concepts

1.5.1. The demersal fish fauna

Two regions, with differing provinces and districts, are currently recognized for the neritic ichthyofauna (Anderson 1990). The most suitable grouping of provinces and districts follows Duhamel (1987), Arntz *et al.* (2005) and Roberts *et al.* (2011). The two regions are:

1. the Antarctic Region, consisting of:

- the circum-continental Antarctic Province (eastwards from the Weddell Sea to the Bellingshausen Sea) which is broader than the previously recognized 'East Antarctica' division
- the West-Antarctic Province including the South Shetland and the South Orkney Islands, the southern part of the South Sandwich Islands, and Bouvet Island.

2. the Sub-Antarctic Region, consisting of:

- the South Georgian Province:
 - South Georgia, and the northern part of the South Sandwich Islands
- the Kerguelenian Province divided into:
 - the West Indian District (Marion/Prince-Edward Islands, Del Cano Rise, Crozet Islands and various seamounts such as Ob and Lena)
 - the East Indian District (Kerguelen Plateau and surrounding seamounts)
 - the West-Pacific District (Macquarie Island).

1.5.2. The pelagic fish fauna

The distribution pattern of the pelagic ichthyofauna (epi-, meso- and bathypelagic) in the Southern Ocean follows the characteristics of water masses and annular frontal systems in the Southern Ocean. Hulley (1981), in his work on myctophids, summarizes the groupings. The patterns follow the rough sketches initially proposed by Backus *et al.* (1977), McGinnis (1974, 1982), for lanternfish and extended to other families (Krefft, 1974, 1978). They have been confirmed by Becker (1983), Duhamel *et al.* (2005), Koubbi *et al.* (2011c), Moteki *et al.* (2011), Collins *et al.* (2012) and Flynn & Williams (2012).

The mesopelagic and bathypelagic communities include two sub-groups in the 'cool-water group' as defined by Hulley (1981):

1. Temperate Sub-group with:

- *Bi-temperate Pattern*
- *South Temperate Pattern*
 - Sub-pattern Convergence
 - Sub-pattern Sub-Antarctic (with holo- and semi- sub-Antarctic)

2. Polar Sub-group with:

- *Broadly Antarctic Pattern*
- *Antarctic Pattern*

1.5.3. The deep-sea demersal and benthopelagic fauna

The biogeography of deep-sea benthic and benthopelagic fishes is still unclear. Two biogeographic provinces (West and East Antarctic) have been suggested to optimally describe the bathymetric distribution of the lower bathyal and abyssal demersal ichthyofaunas (Watling *et al.* 2013). The difficulty in understanding the distributional pattern of the deep-sea ichthyofauna is a consequence of localised and low intensity sampling efforts in the four major deep-sea basins of the Southern Ocean: Weddell (50°W to 30°E), Crozet (30°E to 80°E), South Indian (80°E to 150°E) and Southeast Pacific (150°E to 50°W) Basins.

The abyssal fish fauna does not seem to be Southern Ocean specific in terms of family and species composition. In that respect, it is very similar to other areas of the World Ocean (Cousins *et al.* 2012). Some speciation appears to occur in the bathyal depths of the Southern Ocean for the more diverse families such as Liparidae and Zoarcidae. In other families the stability of the physical environment (temperature, darkness, currents, etc.) in the deep-sea provides little scope for the diversification of the ichthyofauna.

1.6. Data sources for species distribution

Data on the distribution of Southern Ocean fishes were obtained from various national and international data sources (FishBase, CCAMLR, SCAR-MarBIN / OBIS, GBIF, etc.), from scientists involved in fish surveys, from Museum collections or Polar Institutes (Table 2) and directly from well-referenced published

Table 2 List of fish data sources.

Data's providers				
Acronym	Name	Country	Vessels, (PROGRAMMES)	Date
AAD	Australian Antarctic Division, Kingston	Australia	<i>Aurora Australis</i> (AAMBER, ABDEX, BROKE, CEAMARC, FIBEX, FSHHOG, HIMS)	1968-2008
AMS	Australian Museum Sydney	Australia	<i>Courageous, Dimantina, Dmitry Mendeleev, Eitanin, Franklin, James Cook, Kapala, Kaiyo Maru, Petunia Endeavour, Solea, Sprightly, Wesermunde, Zeehaan</i>	1985-2011
AWI	Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven	Germany	<i>Polarstern</i>	1983-2012
BAS	British Antarctic Survey, Cambridge	UK	<i>James Clark Ross</i>	2006-2009
CCAMLR	Commission for the Conservation of Antarctic Marine Living resources		members exploratory and fishing cruises	1982- present
IEO	Instituto Español de Oceanografía	Spain	<i>IBSA Quinto</i> (Antartida 9711), <i>Galaecia</i> (RAI/AP/20-2004), <i>Cruper</i> (RAI/AP/7-2002), <i>Alcalde Uno</i> (RAI/AP/7-2002), <i>Viking Bay</i> (VB-2002, VB-2003, VB-2006 VB-2007, VB-2010)	1997 - 2010
ISH	Institute for Sea Fisheries Hamburg	Germany	<i>Polarstern, Walther Herwig, Meteor</i>	1966-2011
FMNH	Field Museum of Natural History	USA	<i>Anton Bruun</i>	1963-1984
LACM	Los Angeles County Museum of Natural History	USA	<i>Eitanin</i>	1962-1968
MCZ	Museum of Comparative Zoology Harvard University	USA	<i>Anton Bruun, Atlantis, Polar Duke, Prof. Siedlecki, Tazar</i>	1972-1998
MNHN & LOV	Muséum national d'histoire naturelle (Paris)- Laboratoire d'Océanographie de Villefranche-sur-Mer.	France	<i>Marion Dufresne</i> (MD 03, 04, 08, 25, 30, 42, SUZIL), <i>La Curieuse</i> (IPEKER, ICHTYOKER, KERAMS), <i>Skif</i> (SKALP), <i>Austral</i> (POKER 1 & 2), <i>Astrolabe</i> (ICOTA)	1974-2010
NIWA	National Institute of Water and Atmosphere research, Wellington	New Zealand	<i>Tangaroa</i> (TAN0802)	2008
NOAA	National Oceanic and Atmospheric Administration	USA	<i>Yuzhmorgeologiya, Palmer</i> (AMLR)	1998-2011
ROM	Royal Ontario Museum	Canada		1938-1981
RU	Rhodes University Zoology Department,	South Africa	<i>Iris</i>	2001
SAIAB	South African Institute for Aquatic Biodiversity, Grahamstown	South Africa	<i>Agulhas, Africana</i> (SIBEX)	1905-2010
SAM	Iziko-South Africa Museum, Cape Town	South Africa	<i>Africana, Mering Naude, Nansen</i>	1961-2002
SIO	Scripps Institution of Oceanography, La Jolla	USA	<i>Pesca, Piquero, Protea, Vulcan, Thomas Washington</i>	1953-2003
TUMSAT	Tokyo University of Marine Science and Technology	Japan	<i>Umitaka Maru</i> (CEAMARC)	2008
UFH	University of Fort Hare	South Africa	<i>Discovery, l'Atalante</i> (WOCE)	1993-1998
UWFC	University of Washington Fish Collection	USA	<i>N. B. Palmer</i>	1971-2001
ZMUC	Zoological Museum University of Copenhagen	Denmark	<i>Dana, Eitanin, Endeavour, Galathea, Jutlandia Seaways, Paamiut, Pacific, Tjalfe</i>	1832-2012
YPL	Yale Peabody Museum	USA	<i>Atlantis, Delaware, Discovery, Pawnee, Townsend Cromwell, Yuzhmorgeologiya</i>	1925-2009

lists of stations and catches (Iwami & Kubodera 1990, Piatkowski *et al.* 1994, Matallanas & Olaso 2007, Cousins & Friede 2012). The large dataset has been thoroughly scrutinized to exclude possible misidentifications, to update taxonomy and to eliminate errors in geographical position, fishing depth, etc.

2. Demersal fish

The data provided have arisen from national or international (i.e. BIOMASS FIBEX and SIBEX, IPY CEAMARC, etc.) scientific surveys using all sizes of fishing gear from small-sized traps to commercial-sized bottom trawls. They were either deployed from the shore (gill nets, trammel nets, fish traps, etc) or from various sizes of small boats to fully-fledged fishing trawlers and longliners (bottom trawls, pelagic trawls occasionally, used as benthopelagic trawls). For decades, the deployment of nets was restricted to 800–1000 m. It is only in the last 15 years that trawls have been deployed to 1500 m, and longlines to depths greater than 2000 m.

The locality point-data map (Map 1) reveals frequent and regular sampling of the continental and peri-insular shelves and seamounts, but large uninvestigated areas still exist in the deep-sea basins (more than 1,000 m) or hadal depths (down to 6000 m) in particular in the South Sandwich Trench. Thus far, very few abyssal stations have been occupied. The following section aggregates firstly the species belonging to the most endemic/diversified suborders/families Notothenioidei, Liparidae, and Zoarcidae, and secondly in terms of abundance (Chondrichthyes, Macrouridae). The remaining demersal families complete the section.

2.1. Notothenioidei

Until recently, the Notothenioidei suborder included 8 families. The Bovichtidae were the first to diverge, then the Pseudaphritidae and Eleginopsidae. Bovichtidae include one species from the Southern Ocean, the other species being temperate. The other two families are only distributed outside Southern Ocean (South America, Southern Australia/Tasmania and New-Zealand) and will not be presented in this section. The paraphyly of the Nototheniidae with its old composition (Nelson *et al.* 2006) is now well supported by molecular analysis. The rest of the families form a clade grouping all the antarctic and most sub-Antarctic species, where four of the previous families (Channichthyidae, Bathydraconidae, Harpagiferidae, Artedidraconidae) are nested within the Nototheniidae (Table 3) and considered here as subfamilies, with genus *Notothenia* as closest relative — sister group — (Rutschmann *et al.* 2011, Dettai *et al.* 2012, Near *et al.* 2012). Some genera are here erected as subfamilies (*Trematomus*, *Lepidonotothen*, *Patagonotothen* and *Indonotothenia* as Trematominae, *Notothenia* and *Paranotothenia* as Nototheniinae and *Gobionotothen* as Gobionototheninae). Family Bathydraconidae has been subdivided into Bathydraconinae, Gymnodraconinae, Cygnodraconinae. Other genera (*Aethotaxis*, *Dissostichus*, *Pleuragramma*) need to be correctly inserted within the new classification. *Pleuragramma* is highly divergent and closely associated with the other subfamilies; it is included in its own subfamily Pleuragramminae. It is still unclear whether *Dissostichus* and *Aethotaxis* should be grouped in a single subfamily or not. *Pagothenia borchgrevinki* belongs within *Trematomus* as *Trematomus borchgrevinki*. No molecular studies are yet available for other species of genera *Gvozdarus*, *Cryotheria* and *Pagothenia*. The proposed new classification (subfamilies) in Nototheniidae (Table 3) is based on part of cladogram of relationships among notothenioids.

2.1.2. Nototheniidae (Maps 2–20)

Nototheniidae are endemic and also form an important benthic component of the Southern Ocean and the Patagonian region. This family is the most ecologically and morphologically diverse among the notothenioids, with 36 genera and 115 described Southern Ocean species. Some genera (*Aethotaxis*, *Gvozdarus*, *Pleuragramma*) are pelagic and some species cryopelagic (*Cryotheria peninsulae*, *Pagothenia brachysoma*, *Trematomus amphitrete* and *T. borchgrevinki*) (see section 3.1).

Two groups of species can be distinguished in the previously established Nototheniidae (now split in five subfamilies, see Table 3) on the base of distribution patterns. Firstly, the high Antarctic group (South Polar Province) is composed of species of *Dissostichus mawsoni* (Map 2) and *Trematomus* spp. (Map 3) with a maximal northern range to the southern Scotia Arc and extending very occasionally to the southern slope of South Georgia. The second group is distributed in the northern part of the Southern Ocean (lower Antarctic-South Georgia and the Kerguelenian provinces). It includes *Dissostichus eleginoides* (Map 2), *Indonotothenia cyanobrancha* (Map 3), *Gobionotothen* spp. (Map 4), *Lepidonotothen* spp. (Map 5) but not *L. squamifrons* (Map 6) and *Nototheniinae* as *Notothenia microlepidota* and *Paranotothenia magellanica* (Map 7) or *N. rossii* (Map 8) but not *Notothenia coriiceps* (Map 9) and *Patagonotothen guntheri* (Map 9). *L. squamifrons* and *N. coriiceps* occur in the two regions. Some species occur as far south as the Scotia Sea and the tip of the Antarctic Peninsula. Other species live in temperate waters (New Zealand, Patagonian shelves).

Species occur from inshore (*Trematomus hansonii*, *T. newnesi* and *T. bernacchii*, *I. cyanobrancha*, *N. coriiceps*, *P. magellanica*) to deep slope waters (500 to 800 m) and sometimes down to 1200 m (*T. lepidorhinus* and *T. loenbergi*) (Causse *et al.* 2011) or even deeper than 2000 m as is the case in *Dissostichus* spp. (Duhamel *et al.* 2005). The deepest-living species occur along the continental slope and in the deep inner shelf depressions that were formed during the onset of the last Antarctic glaciation (Eocene-Oligocene boundary). The periods of alternating glaciations were responsible for the diversification into many species (particularly with respect to the notothenioids) on the Antarctic shelf. Ecological diversity is further enhanced by ontogenetic habitat shifts exhibited by some species during their transition from fingerlings through juveniles to adult stages (*N. rossii*, *Dissostichus* spp.) (Eastman 2005).

The subfamily Artedidraconinae (plunderfishes) contains 4 genera (*Artedidraco*, *Dolloidraco*, *Histiodraco* and *Pogonophryne*) and 32 species, all of which are benthic/epibenthic. *Artedidraco* ranges from the low-Antarctic to the high-Antarctic latitudes, *Dolloidraco* and *Histiodraco* are strictly high-Antarctic, *Pogonophryne* is high-Antarctic with an extension to the islands of the southern Scotia Arc (Eakin 1990). The mental barbel in *Pogonophryne*, which has been used to distinguish species appears to be highly variable in shape within the various species (Eakin *et al.* 2001) and makes species identification difficult.

Except for *Artedidraco mirus* and *A. glareobarbatus*, which are endemic to South Georgia (Eakin 1990, 2006) and the Ross Sea respectively (Eastman & Eakin 1999, La Mesa & Vacchi 2005), all *Artedidraco* species are widely distributed on the Antarctic continental shelf and slope down to 900 m depth (Map 10). *Dolloidraco longedorsalis* has a circum-Antarctic distribution. It is found from sublittoral areas to the continental slope (down to more than 1100 m). *Histiodraco velifer* shows a similar pattern of distribution but is confined to shallower depths (down to about 600 m). The genus *Pogonophryne* appears

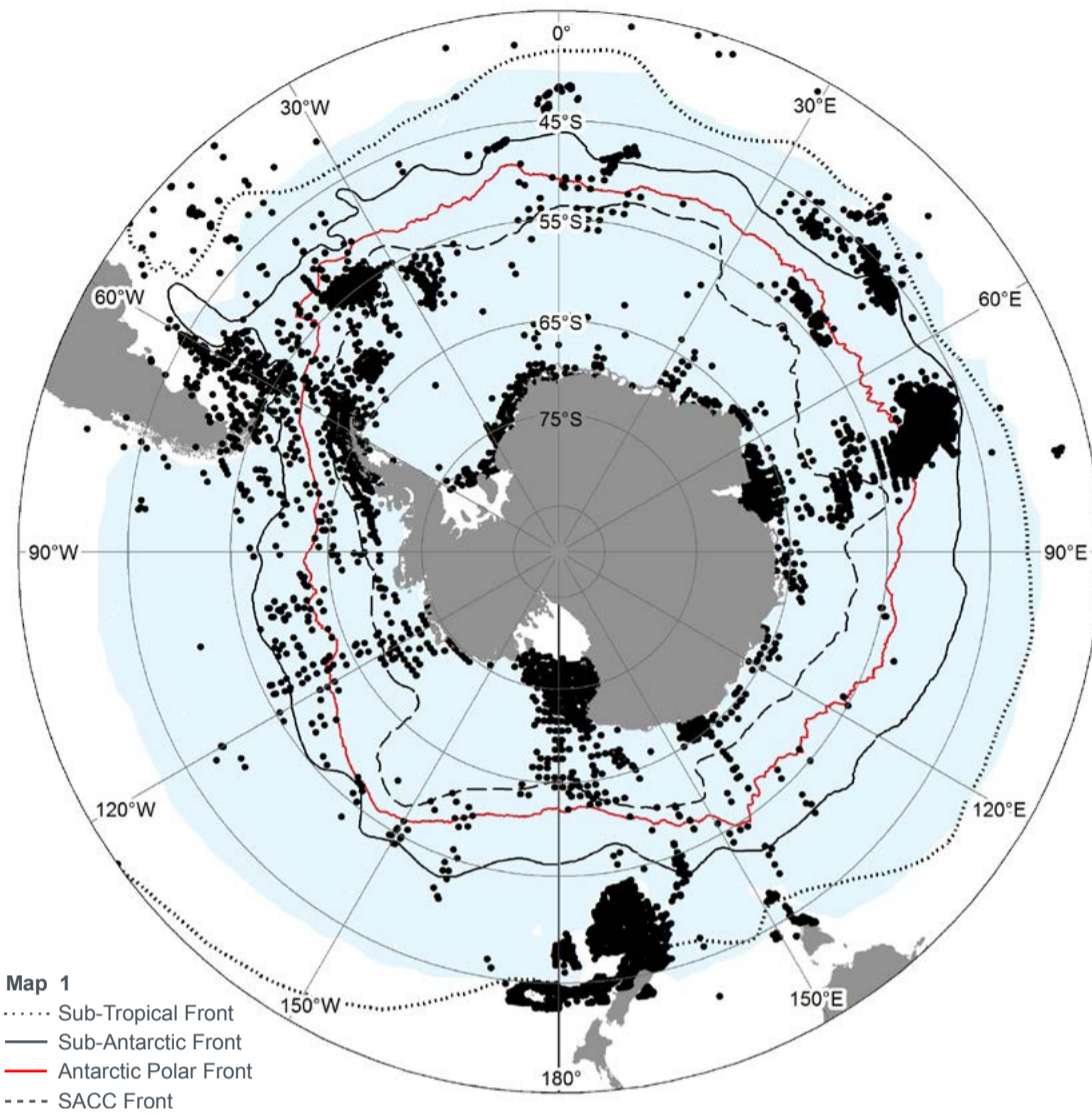
Table 3 Updated classification of Nototheniidae based on the more recent molecular studies and used in Appendix 4.

Former families that are inserted now in former Nototheniidae	Updated classification	New proposed sub-families
NOTOTHENIIDAE	genera <i>Dissostichus</i> + <i>Aethotaxis</i> + ?genus <i>Gvozdarus</i> ?	DISSOSTICHINAE
	genus <i>Gobionotothen</i>	GOBIONOTOTHENINAE
	genera <i>Notothenia</i> , <i>Paranotothenia</i>	NOTOTHENIINAE
	genus <i>Pleuragramma</i>	PLEURAGRAMMINAE
	genera <i>Cryotheria</i> , <i>Indonotothenia</i> , <i>Lepidonotothen</i> , <i>Pagothenia</i> , <i>Patagonotothen</i> , <i>Trematomus</i>	TREMATOMINAE
ARTEDIDRACONIDAE	ARTEDIDRACONINAE	ARTEDIDRACONINAE
HARPAGIFERIDAE	HARPAGIFERINAE	HARPAGIFERINAE
BATHYDRACONIDAE	genera <i>Gymnodraco</i> , <i>Acanthodraco</i> , <i>Psilodraco</i>	GYMNODRACONINAE
	genera <i>Bathydraco</i> , <i>Akarotaxis</i> , <i>Racovitzia</i> , <i>Prionodraco</i> , <i>Vomeridens</i>	BATHYDRACONINAE
	genera <i>Cygnodraco</i> , <i>Parachaenichthys</i> , <i>Gerlachea</i>	CYGNODRACONINAE
CHANNICHTHYIDAE	CHANNICHTHYINAE	CHANNICHTHYINAE

2.1.1. Bovichtidae

This mainly subtropical family has a late Cretaceous origin (Matschiner *et al.* 2011). It is considered to have first diverged outside Antarctic waters. The only Southern Ocean species, *Bovichtus elongatus*, occurs in the intertidal zone of the Antarctic Peninsula (Hureau & Tomo 1977) and is only known from few individuals.

to be the most speciose genus of plunderfishes with 24 presently recognized species, (Appendix 5) most of which are recently described (Eakin & Balushkin 2000, Eakin *et al.* 2008, Eakin *et al.* 2009, Balushkin *et al.* 2011, Balushkin & Spodareva 2013, Shandikov & Eakin, 2013, Shandikov *et al.* 2013). It exhibits little morphological and ecological diversification and may represent a recent radiation (Eastman 2005). Difficulties still exist in correctly identifying these species on board research vessels. The genus *Pogonophryne* has a circum-Antarctic distribution with some species extending as far north as the South Orkney Islands (Map 11), and in depths ranging from 100 m to more than 2500 m.



Map 1
 Sub-Tropical Front
 — Sub-Antarctic Front
 — Antarctic Polar Front
 - - - SACC Front

Fish Map 1 Point-data map of neritic and deep-sea fish samples in the Southern Ocean from oceanographic surveys (exact position) and fisheries surveys such as from CCAMLR (over 1° of latitude and 1° of longitude). The blue area represents the pelagic bioregions 1 to 17 from Raymond (this volume, chapter 10.1.1.)

Artedidraconinae, especially the *Pogonophryne* species, seem to be associated with complexly-structured invertebrate assemblages. These provide food and camouflage (Schwarzbach 1988, Ekau & Gutt 1991, Olaso *et al.* 2000). Local distributions do not appear to overlap for a majority of species. Trophic specialization among species is also observed and can be related to morphological diversifications (eye size, form and size of barbell, mouth width) which indicate trophic niche segregation and specialization (Lombarte *et al.* 2003).

The spiny plunderfishes (Harpagiferinae) have undergone primary phyletic diversification (Eastman 2005). One genus, *Harpagifer*, with 10 species has been described. Nine of the species are endemic to the Southern Ocean; one species occurs north of the Antarctic Polar frontal Zone (on the southern South American shelf and around the Falklands Islands). The distribution of eight species is restricted to the sub-Antarctic islands and islands of the southern Scotia Arc. One species, *Harpagifer antarcticus* is present along the western side of the Antarctic Peninsula. Littoral and sublittoral zones seem inhabited by different species (Neyelov & Prirodina 2006). *H. permitini* seems restricted to South Georgia; *H. crozetensis* and *H. spinosus* to the Crozet Islands; *H. kerguelensis* and *H. nybelini* to Kerguelen Islands and Heard Islands; *H. marionensis* to the Prince Edward Islands; *H. macquarensis* and *H. andriasevi* to Macquarie Island and *H. georgianus* in South Georgia, Prince Edward and Macquarie islands (Map 12).

They are small benthic/epibenthic species, their distribution are confined to coastal waters from 0 m (under rocks in pools at low tide) to 200 m depth. They are ecologically and morphologically similar species (Eastman, 2005). Further molecular studies could elucidate the validity of the 10 species currently described and identify the sympatric pairs (littoral and sub-littoral) in each area (Prirodina, 2004).

Former Bathydraconidae (dragonfishes), are

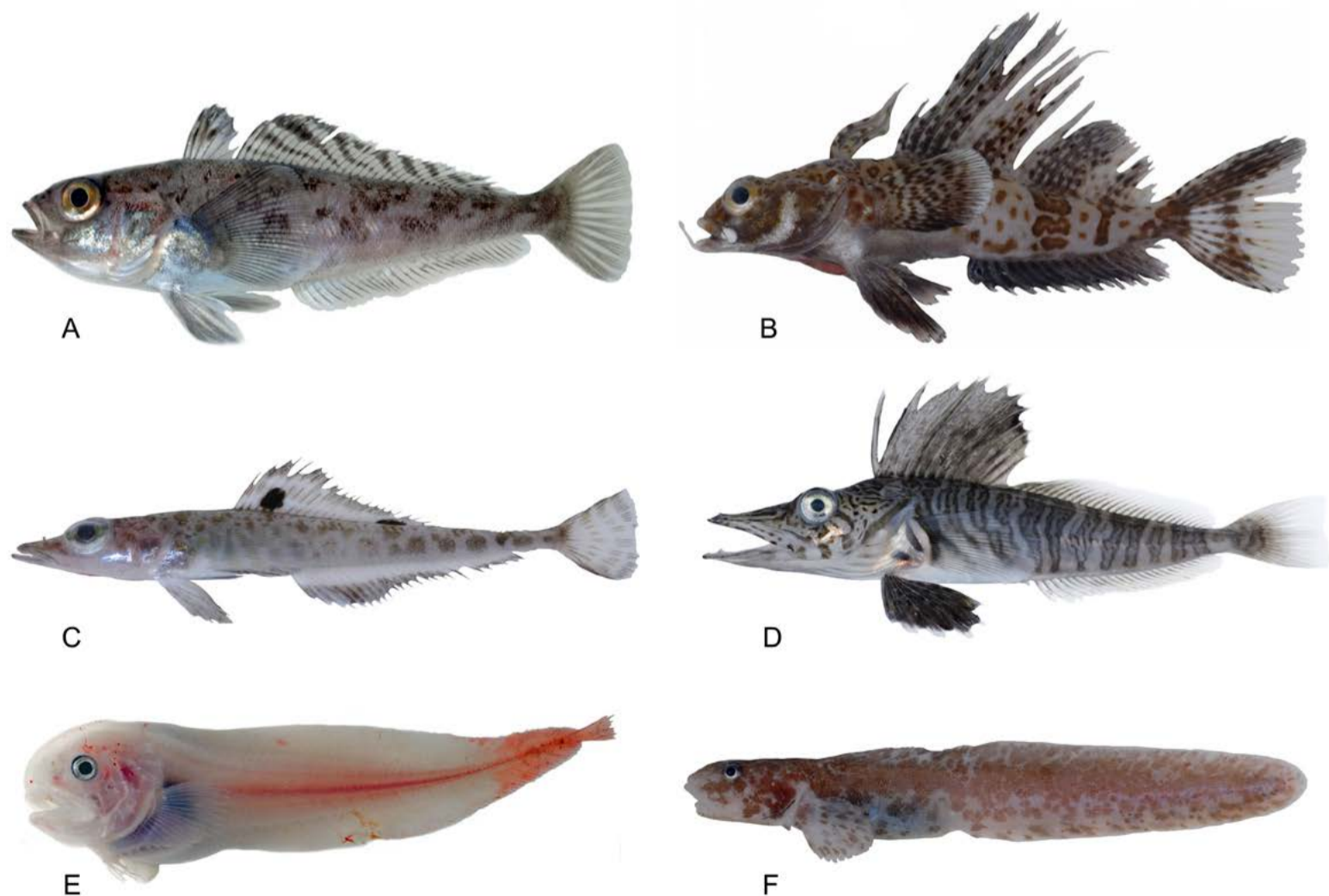
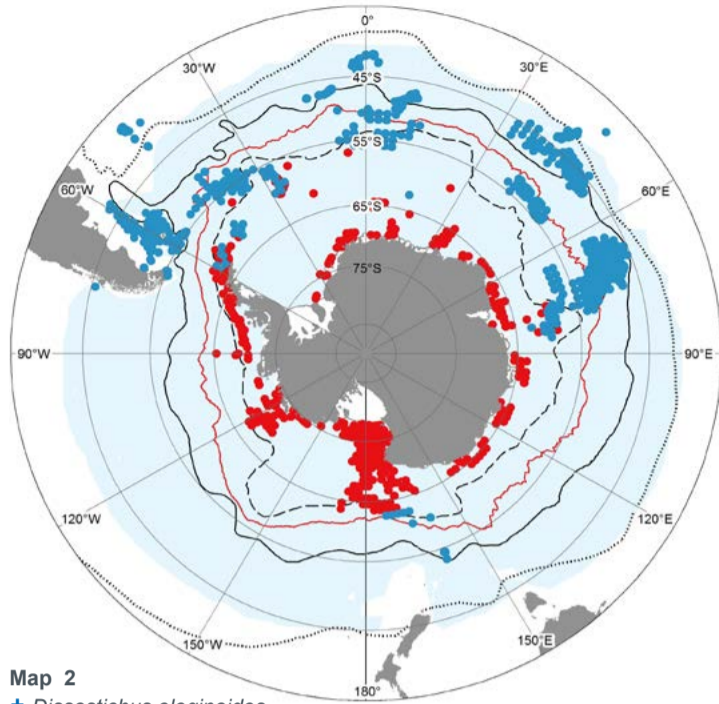
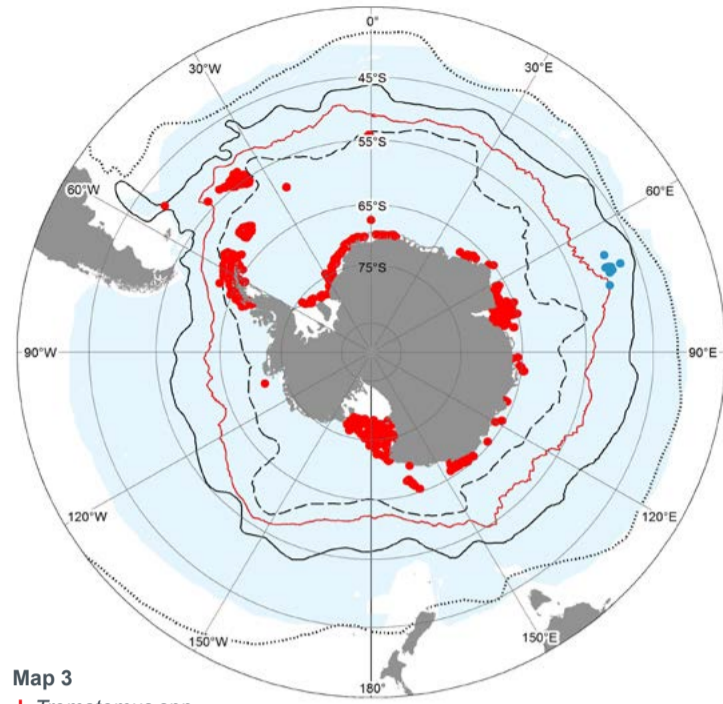


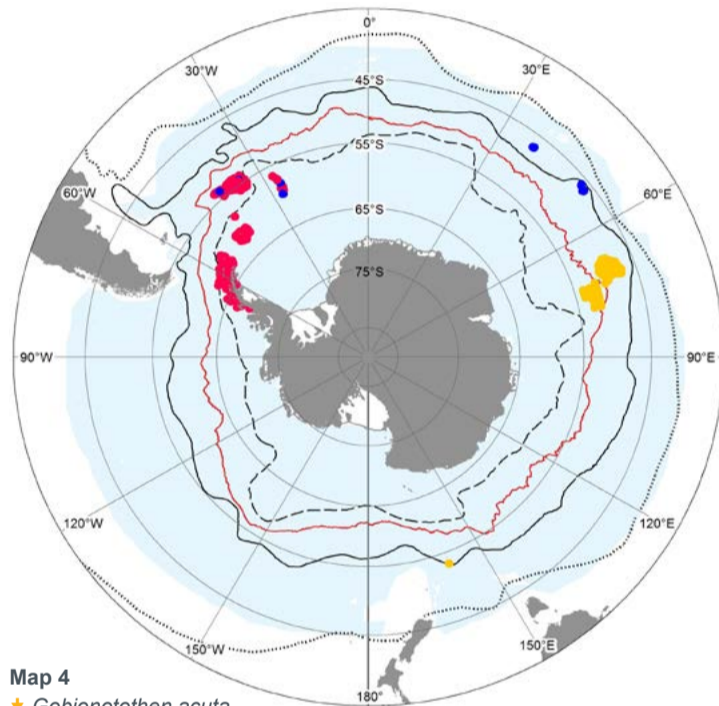
Photo 1 Demersal fish (A) *Trematomus eulepidotus* Regan, 1914. (B) *Artedidraco oriana* Regan, 1914. (C) *Prionodraco evansii* Regan, 1914. (D) *Pagetopsis macropterus* (Boulenger, 1907). (E) *Paraliparis antarcticus* Regan, 1914. (F) *Lycodichthys antarcticus* Pappenheim, 1911. Images © S. Iglesias, MNHN, CEAMARC programme.



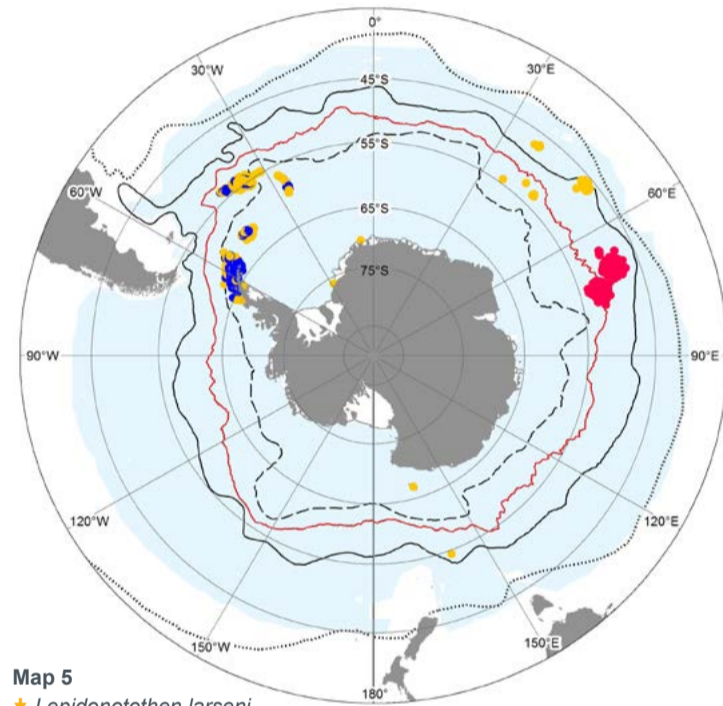
Map 2
 ◆ *Dissostichus eleginoides*
 ▼ *Dissostichus mawsoni*



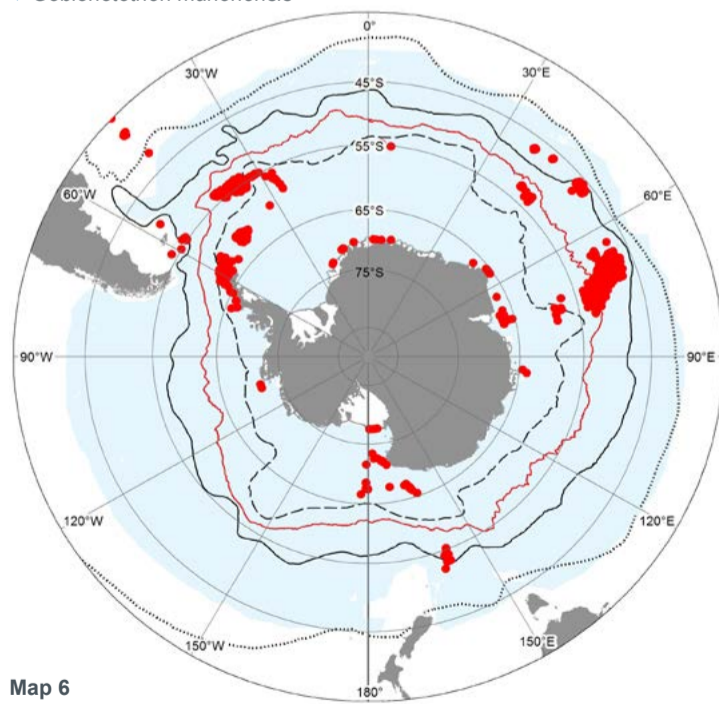
Map 3
 ▼ *Trematomus* spp.
 ◆ *Indonotothenia cyanobrancha*



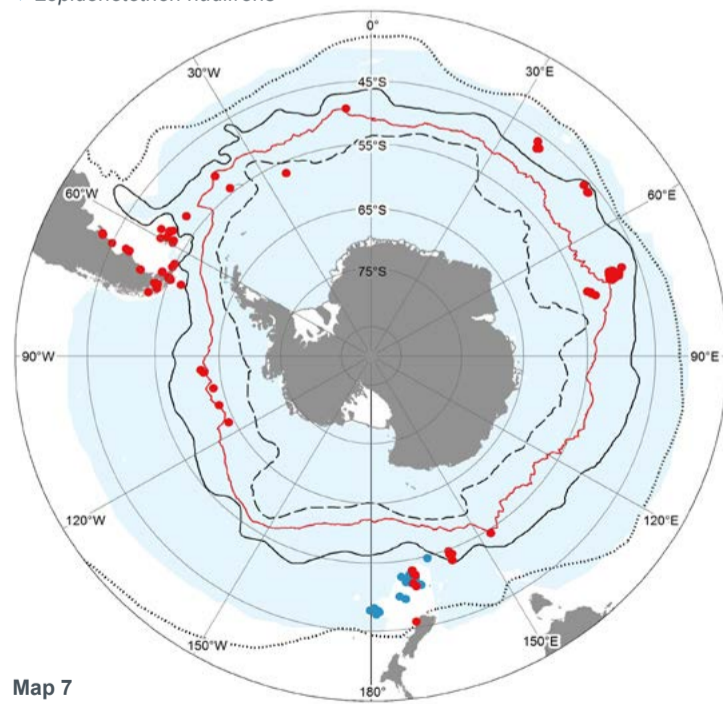
Map 4
 ◆ *Gobionotothen acuta*
 ▼ *Gobionotothen gibberirons*
 ◆ *Gobionotothen marionensis*



Map 5
 ◆ *Lepidonotothen larseni*
 ▼ *Lepidonotothen mizops*
 ◆ *Lepidonotothen nudifrons*

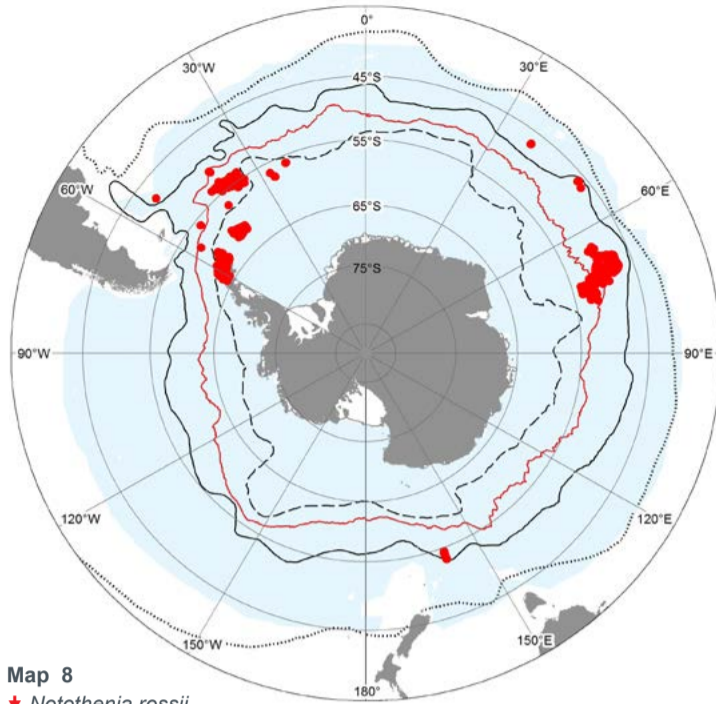


Map 6
 ▼ *Lepidonotothen squamifrons*

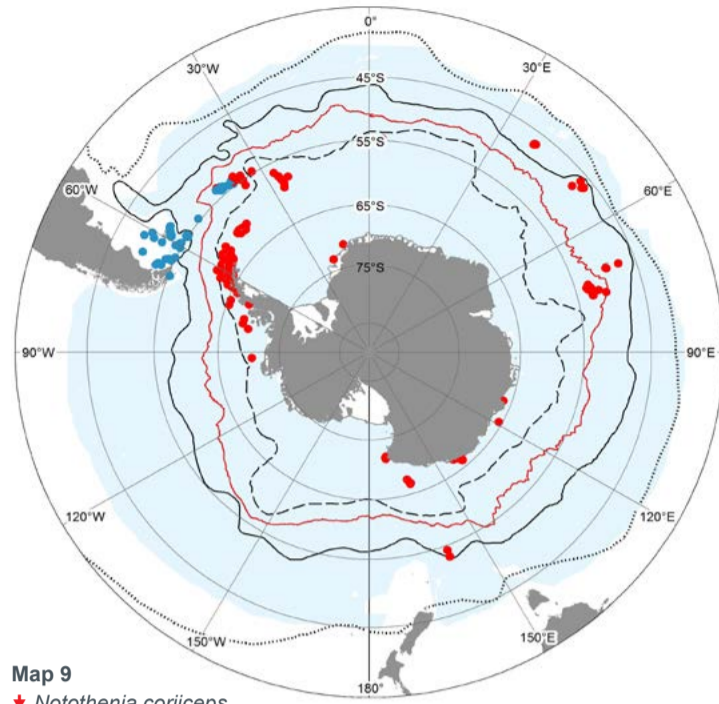


Map 7
 ◆ *Notothenia microlepidota*
 ▼ *Paranotothenia magellanica*

Fish Maps 2–7: Nototheniidae Map 2. Distribution of *Dissostichus eleginoides* Smitt, 1898 and *D. mawsoni* Norman, 1937. Map 3. Distribution of *Trematomus* spp. and *Indonotothenia cyanobrancha* Richardson, 1844. Map 4. Distribution of *Gobionotothen* spp. Map 5. Distribution of *Lepidonotothen* spp. (except *L. squamifrons*). Map 6. Distribution of *Lepidonotothen squamifrons* (Günther, 1880). Map 7. Distribution of *Notothenia microlepidota* Hutton, 1875 and *Paranotothenia magellanica* (Forster, 1801).

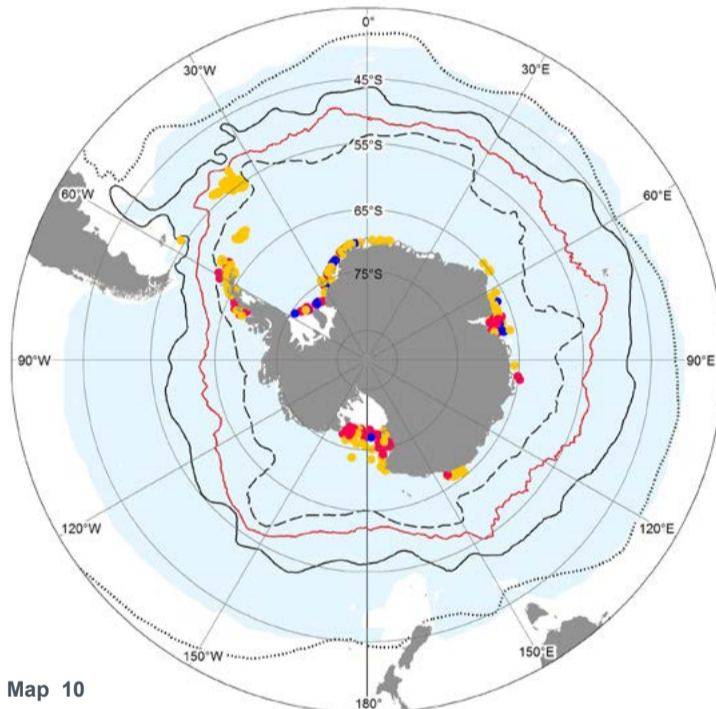


Map 8
 ▼ *Notothenia rossii*

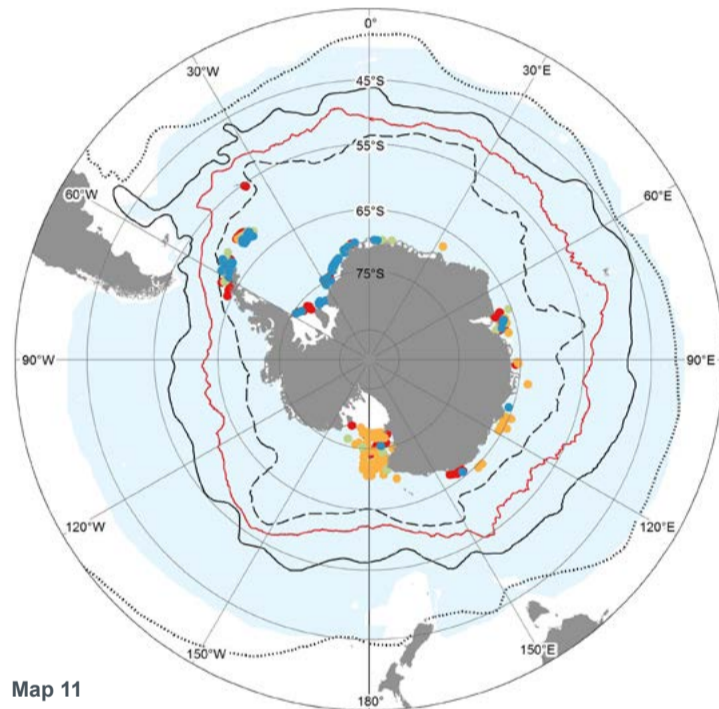


Map 9
 ▼ *Notothenia coriiceps*
 ▼ *Patagonotothen guntheri*

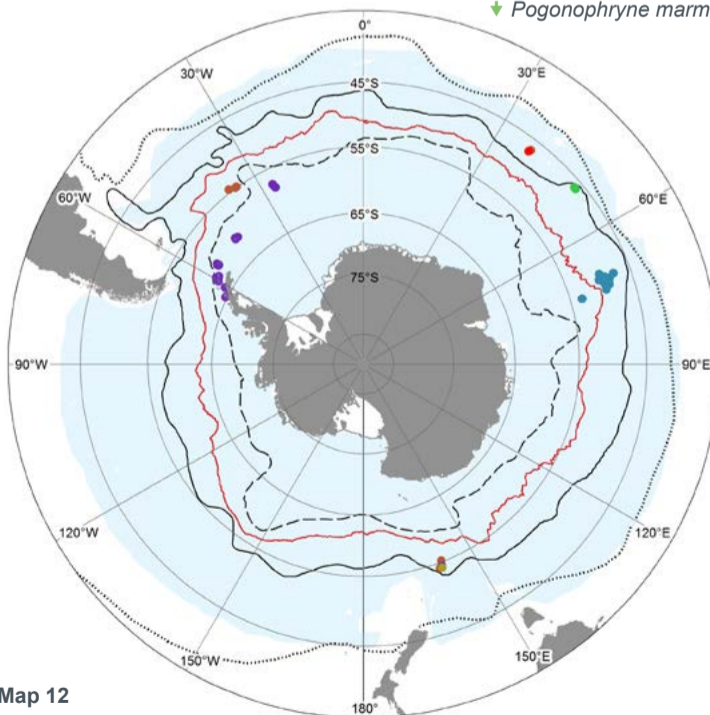
Fish Maps 8–9: Nototheniidae Map 8. Distribution of *Notothenia rossii* Richardson, 1844. Map 9. Distribution of *Notothenia coriiceps* Richardson, 1844 and *Patagonotothen guntheri* (Norman, 1937).



Map 10
 ▼ *Artedidraco* spp.
 ▼ *Dolloidraco longedorsalis*
 ▼ *Histiodraco velifer*



Map 11
 ▼ *Pogonophryne barsukovi*
 ▼ *Pogonophryne marmorata*
 ▼ *Pogonophryne permotini*
 ▼ *Pogonophryne scotti*



Map 12
 ▼ *Harpagifer marionensis*
 ▼ *Harpagifer antarcticus*
 ▼ *Harpagifer crozentensis*
 ▼ *Harpagifer georgianus*
 ▼ *Harpagifer kerguelensis*
 ▼ *Harpagifer macquariensis*

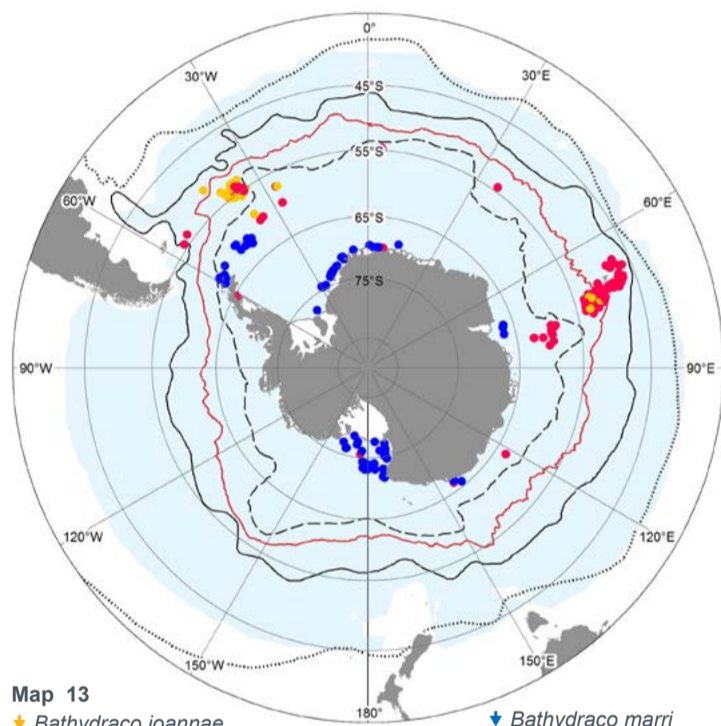
Fish Maps 10–12: Artedidraconinae and Harpagiferinae Map 10. Distribution of *Artedidraco* spp., *Dolloidraco longedorsalis* Roule, 1913 and *Histiodraco velifer* (Regan, 1914). Map 11. Distribution of *Pogonophryne* spp. Map 12. Distribution of *Harpagifer georgianus* Nybelin, 1947, *H. macquariensis* Prirodina, 2000, *H. antarcticus* Nybelin, 1947, *H. kerguelensis* Nybelin, 1947 and *H. crozentensis* Prirodina, 2004.

split here into three subfamilies: Bathydraconinae (genera *Akarotaxis*, *Bathydraco*, *Prionodraco*, *Psilodraco*, *Racovitzia*, *Vomeridens*), Cygnodraconinae (*Cygnodraco*, *Gerlachea*, *Parachaenichthys*) and Gymnodraconinae (*Gymnodraco* and *Acanthodraco*), and comprise 11 genera and 16 species. All have a slender body. They are endemic to the Southern Ocean and live mostly on the shelf and upper slope (Maps 13 to 16). The distribution of *Parachaenichthys charcoti* is confined to the western Antarctic Peninsula, the South Shetland and South Orkney Islands. The distribution of *Parachaenichthys georgianus* and of *Psilodraco breviceps* is restricted to South Georgia. *Bathydraco antarcticus* to Weddell Sea, South Sandwich and Kerguelen-Gaussberg Ridge, *B. joannae* to South Georgia and Kerguelen-Gaussberg Ridge. All other species have a circum-Antarctic distribution including the Antarctic Peninsula and sometimes reach the South Orkney and the South Sandwich Islands (Balushkin & Voskoboinikova 2011). *Acanthodraco dewitti*, originally described from Admiralty Bay in South Shetland Islands and known from Chile, also occurs in the Ross and Dumont d'Urville Seas. Bathydraconinae have been found as deep as 3 000m (*Bathydraco scotiae*). Dragonfishes are usually caught in small numbers in the various localities around the Antarctic continent, the only exceptions being *Gerlachea australis* and *Akarotaxis nudiceps* which form the major components of the demersal fish communities in the Dumont d'Urville Sea inner shelf depressions (Causse *et al.* 2011). Dragonfishes are less reliant on benthic food sources than are Artedidraconinae and Harpagiferinae (Eastman 2005).

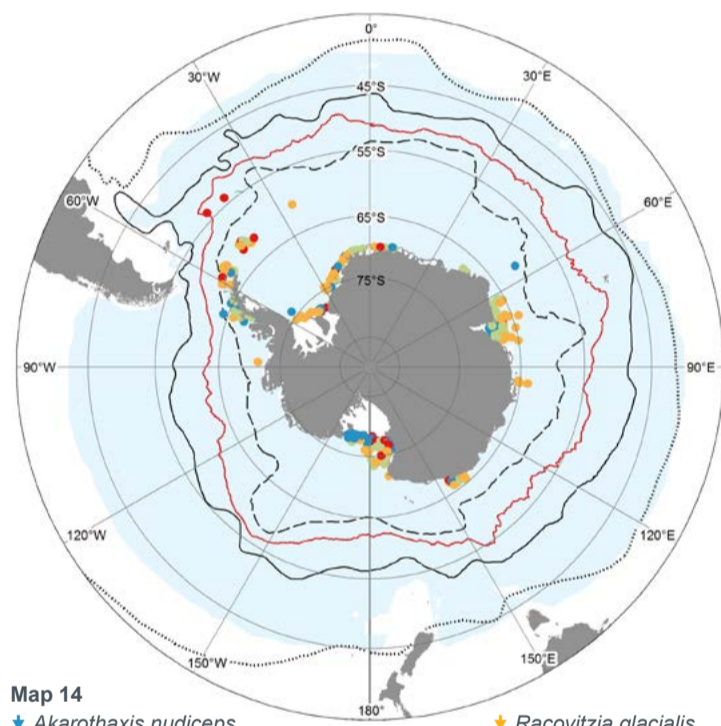
Channichthyinae are unique among vertebrates in lacking haemoglobin. The icefish subfamily contains 11 genera, and includes 24 species. Revision of the genus *Channichthys* is needed to validate the 7 doubtful species (*C. aelitae*, *C. bospori*, *C. irinae*, *C. mithridatis*, *C. panticapaei*, *C. richardsoni*, *C. rugosus*) described for the Kerguelen Plateau (Regan 1913, Shandikov 1995a, 1995b, 2008, 2011). The distribution of the subfamily is confined to the Southern Ocean with the exception of one species, *Champscephalus*

esox, which occurs from the southern Patagonian and Falkland shelves to the Strait of Magellan and rarely at South Georgia (Iwami & Kock 1990). The three species *Champscephalus gunnari* (Map 17), *Chaenocephalus aceratus* (Map 18) and *Pseudochaenichthys georgianus* (Map 19) are distributed in the northern part of the Southern Ocean, close to the Polar Front (South Georgia Province and West-Antarctic, East Indian districts). *C. gunnari* lives usually over shallow banks and islands shelves from the Scotia Arc (South Georgia to the South Shetland Islands, and with single individuals occurring as close to the continent as the western side of the Antarctic Peninsula) to Bouvet and the Kerguelen Plateau (Map 17). *C. aceratus* does not extend into the Indian sector. *P. georgianus* is limited to the western Atlantic Ocean sector. In the Indian Ocean sector the genus *Channichthys* is limited to the Kerguelen Plateau (Map 18). Other Channichthyidae species have a high-Antarctic type of distribution (circum-continental Antarctic district), limited to the continental shelf and the slope. Four species, *Chaenodraco wilsoni* (Map 19), *Pagetopsis macropterus* (Map 19), *Chionodraco rastrospinosus* (Map 20) and *Cryodraco antarcticus* (Map 20), are distributed around the Antarctic continental shelf but also occur in small numbers as far north as the southern Scotia Arc, (Kock 1992, Kock *et al.* 2002).

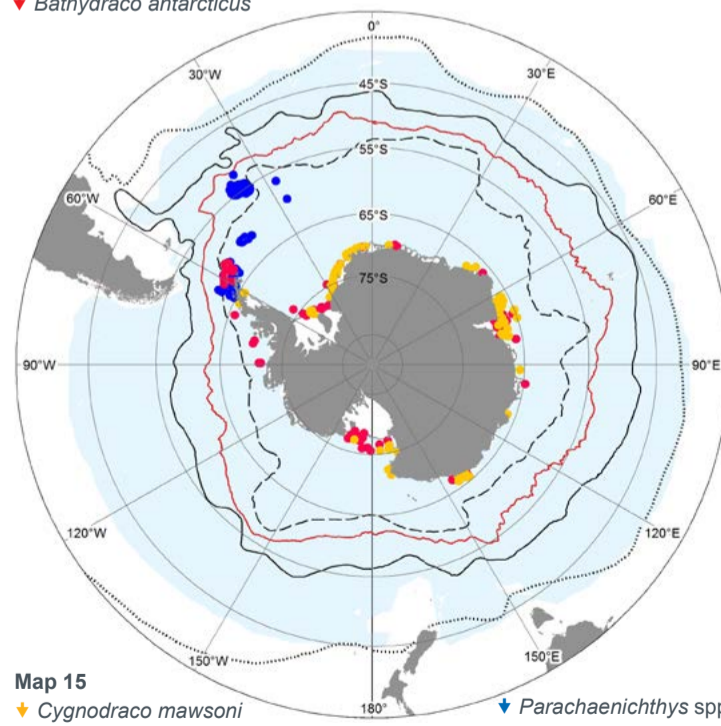
The bathymetric distribution differs according to age and species. Larvae, postlarvae and juveniles are mostly present in the upper 100 m of the water column (Loeb *et al.* 1993, Kellermann 1996). After 2–3 years, most species (e.g. *C. aceratus*, *C. antarcticus*) become bottom-dwelling, and ambush-feed on prey close to the bottom. Others (*C. gunnari*, *P. georgianus*, *Neopagetopsis ionah*) perform regular diel vertical migrations to feed in the water column (Kock 1992, 2005) or may probably permanently inhabit the water column (*Dacodraco hunteri*) (Eastman 1999). Low-Antarctic species are mostly distributed down to 450 m, with a few individuals occurring in depths of 500–770 m. High-Antarctic species occur down to 700–900 m in the Weddell Sea, Ross



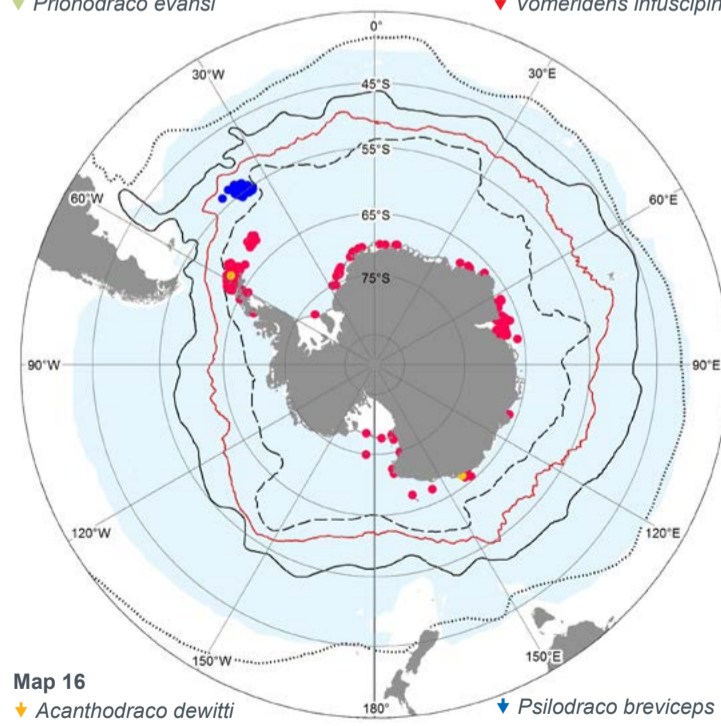
Map 13
 ▲ *Bathydraco joannae*
 ▼ *Bathydraco antarcticus*
 ▲ *Bathydraco marri*



Map 14
 ▲ *Akarotaxis nudiceps*
 ▼ *Prionodraco evansi*
 ▲ *Racovitzia glacialis*
 ▼ *Vomeridens infuscipinnis*

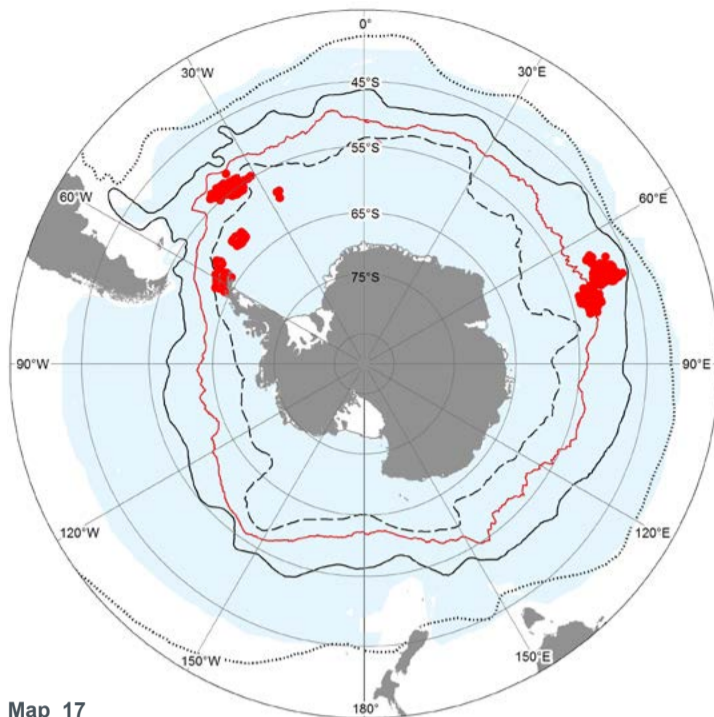


Map 15
 ▲ *Cygnodraco mawsoni*
 ▼ *Gerlachea australis*
 ▲ *Parachaenichthys* spp.

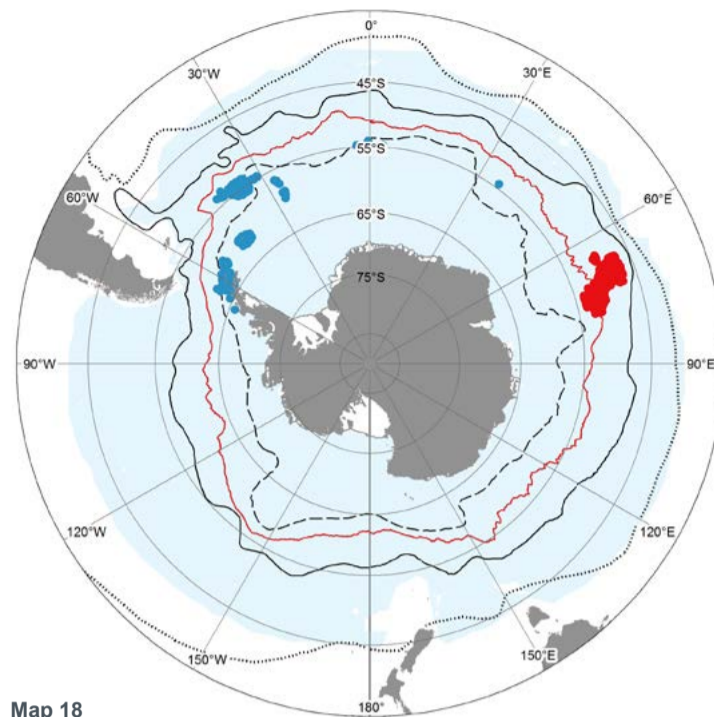


Map 16
 ▲ *Acanthodraco dewitti*
 ▼ *Gymnodraco acuticeps*
 ▲ *Psilodraco breviceps*

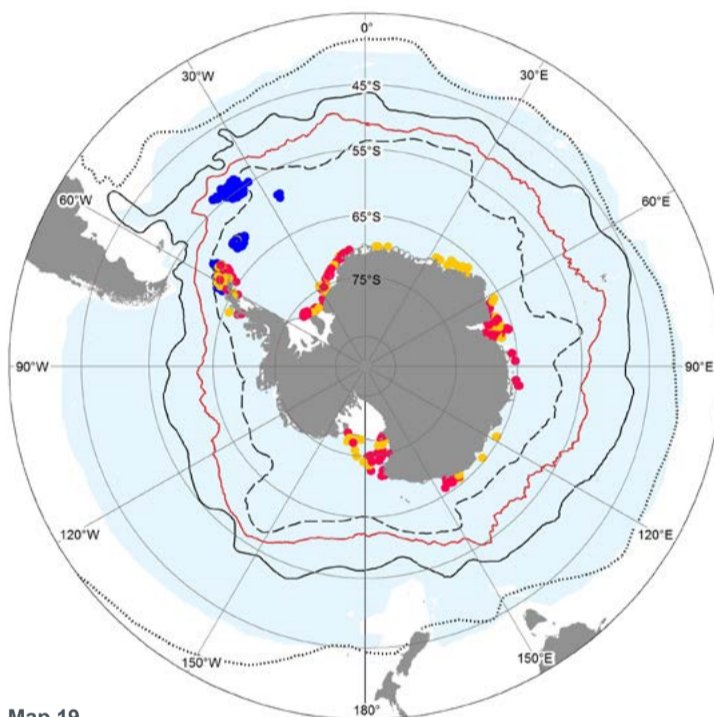
Fish Maps 13–16: Bathydraconinae Map 13. Distribution of *Bathydraco antarcticus* Günther, 1878, *B. marri* Norman, 1938 and *B. joannae* Dewitt, 1985. Map 14. Distribution of *Akarotaxis nudiceps*, *Prionodraco evansi*, *Racovitzia glacialis*, and *Vomeridens infuscipinnis*. Map 15. Distribution of *Cygnodraco mawsoni*, *Gerlachea australis*, and *Parachaenichthys* spp. Map 16. Distribution of *Acanthodraco dewitti*, *Gymnodraco acuticeps* and *Psilodraco breviceps*.



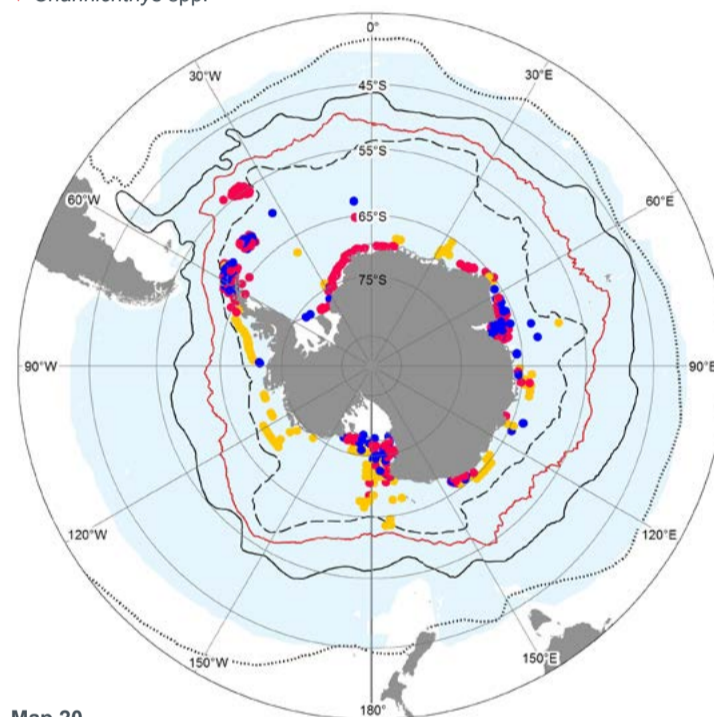
Map 17
 ▼ *Champsocephalus gunnari*



Map 18
 ▼ *Chaenocephalus aceratus*
 ▼ *Channichthys* spp.



Map 19
 ▼ *Chaenodraco wilsoni*
 ▼ *Pagetopsis* spp.
 ▼ *Pseudochaenichthys georgianus*



Map 20
 ▼ *Chionodraco dewitti*
 ▼ *Cryodraco* spp.
 ▼ *Cryodraco* spp.

Fish Maps 17–20: Channichthyinae Map 17. Distribution of *Champsocephalus gunnari* Lönnberg, 1905. Map 18. Distribution of *Channichthys* spp. and *Chaenocephalus aceratus* (Lönnberg, 1906). Map 19. Distribution of *Chaenodraco wilsoni*, *Pagetopsis* spp., *Pseudochaenichthys georgianus* Norman, 1937. Map 20. Distribution of *Chionodraco* spp., *Cryodraco* spp. and *Chionobathyscus dewitti* Andriashev & Neyelov, 1978.

Sea, Dumont d'Urville Sea and the South Shetland Islands. Catches of *Chionobathyscus dewitti* (Map 20) and *C. antarcticus* have been reported in the longline fishery at 600–1600 m depth (Arana & Vega 1999, Kock *et al.* 2006). High abundances of *C. dewitti* and *N. ionah* are recorded as deep as 1700 m in Dumont d'Urville Sea along the continental slope (Causse *et al.* 2011). *C. dewitti* was caught as deep as 2000 m in Weddell Sea (Hureau *et al.* 1990).

The highest diversity with respect to Channichthyinae has been reported for the Antarctic continental shelf (Causse *et al.* 2011). Some species are mobile and seem not to live preferentially in a highly specialized environment (*C. wilsoni*, *C. myersi*, *N. ionah*) (Eastman & Hubold 1999), due to their partially pelagic life (Chen *et al.* 1998, Gutt & Ekau 1996). Indeed, species seem to feed mostly in water column (Eastman & Hubold 1999, Schwarzbach 1988). Evidence for egg brooding and parental care has been reported in some icefish species (Kock *et al.* 2006).

Only the schooling species *C. gunnari* is presently commercially exploited at South Georgia and on the Kerguelen Plateau (Anonymous 2012).

2.2. Liparidae (Maps 21–22)

Liparidae are the most speciose family in the Southern Ocean (Eastman 2005, Duhamel *et al.* 2010). A North Pacific origin of the family was postulated by Andriashev (1977) and bi-polar abundance is noticeable. Molecular studies group the northern and southern hemisphere species into sister clades (Duhamel *et al.* 2010). However two criteria to support the 'species flock' concept (monophyly for the species in the area of interest and predominance in biomass) are not fulfilled by this family (Lecointre *et al.* 2013). Information on

diversity has been recently improved by taxonomic reviews (Andriashev 1986, 2003) and from deep-sea investigations in some areas of the Southern Ocean areas such as the Ross and Weddell Seas, East Antarctica and the Kerguelen Province (Duhamel 1992, Duhamel *et al.* 2010, Stein 2012). Some descriptions of new species from the Ross Sea need re-analysis in light of recent molecular findings (Smith *et al.* 2012).

Liparids currently include 5 genera and 85 species in the Southern Ocean (Maps 21 and 22). Some species such as *Paraliparis devriesi* exhibit a distribution confined to specific inner depressions of the continental shelf (Eastman 2005) or on the slopes such as *P. operculosus* on the Kerguelen Plateau (Duhamel *et al.* 2010). Other species (*P. antarcticus*, *P. leobergi*, *P. mawsoni*, *P. terraenovae*, *P. valentinae*) have a wider circumantarctic distribution. However knowledge of the distribution of Southern Ocean liparids is still limited due to poor coverage of the deep-sea.

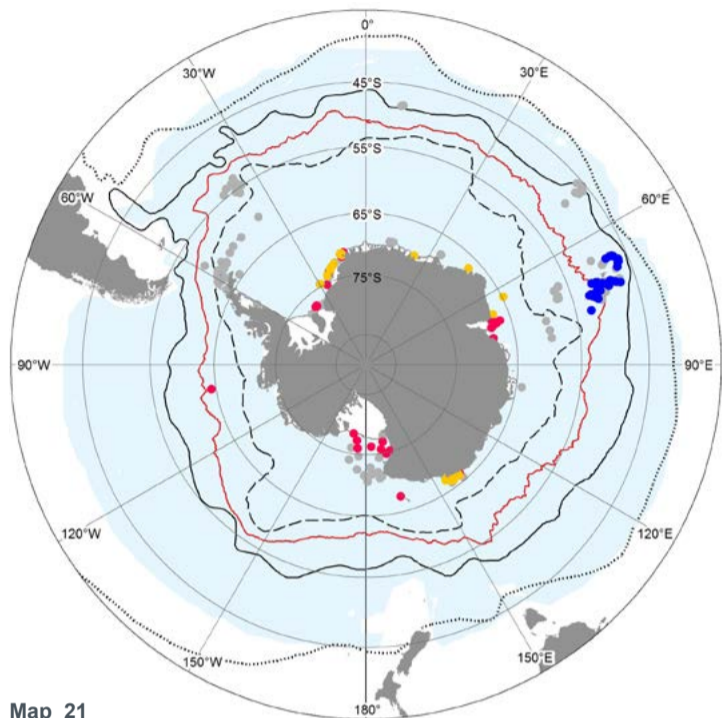
The depth range of the species is between 300–2000 m except for *Careproctus georgianus* which is found in shallow waters (100–250 m). A large number of *Careproctus* species (*C. acifer*, *C. ampliceps*, *C. crozetensis*, *C. discoveryae*, *C. fedorovi*, *C. sandwichensis*, *C. scaphopterus*, *C. valdibeckeri*), some *Paraliparis* species (*P. diplopura*, *P. stehmanni*, *P. wolffi*) and all *Notoliparis* species have been recorded from abyssal depths (2600–5450 m). Most species are benthic/epibenthic but some (*Paraliparis terraenovae*, *P. thalassobathyalis*) are currently caught pelagically (Duhamel *et al.* 2010).

Suspected commensalism or a parasitic reproductive strategy with other benthic organisms such as stone crabs (Lithodidae) has been observed in *Careproctus* sp. (Yau *et al.* 2000).

2.3. Zoarcidae (Maps 23–24)

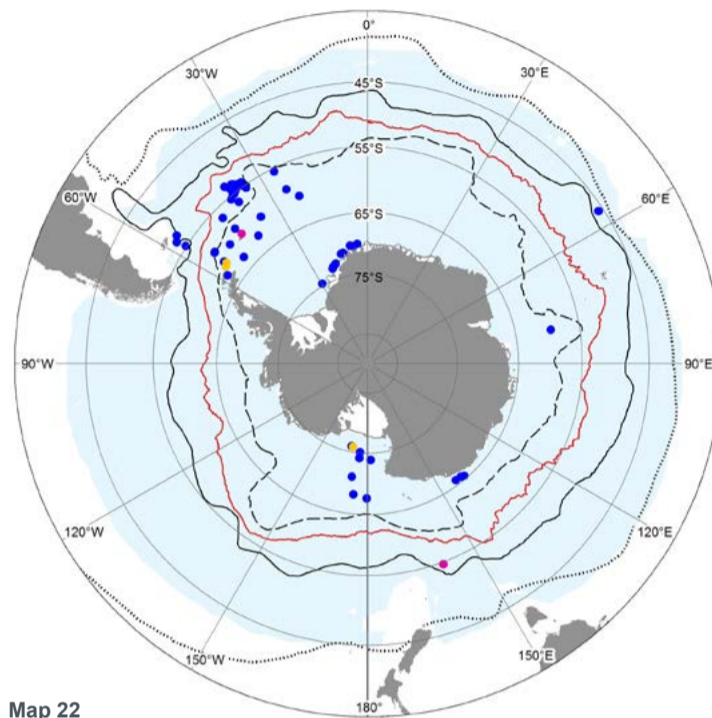
Fifteen genera comprising 40 species make eelpouts the third most diverse family in the Southern Ocean. Zoarcids, like liparids, have their origin in the North Pacific and dispersed to the Southern Hemisphere during the Miocene. They have radiated secondarily in the Southern Ocean (Anderson 1994). The majority of species are endemic to the Southern Ocean. The west Antarctic region of South Georgia, the Scotia Sea, and the Antarctic Peninsula is the most diverse with 28 species (Map 23). They include 17 endemic species. Four species, *Gosztonyia antarctica*, *Ophthalmolycus eastmani*, *Santelmoa*

antarctica, and *S. elvirae* are endemic to the Bellingshausen Sea. *Bothrocara molle*, *Lycenchelys argentina*, *L. bellingshauseni*, and *L. nannospinata* are confined to the Scotia Sea. Outside these areas there are only 10 species, five of which are endemic: *Seleniolycus pectoralis* and *S. robertsi* off Scott Island, *Pachycara cousinsi* and *P. priedei* off Crozet Islands, and *Lycenchelys hureaui* around the Kerguelen Plateau. Some species (*Lycodichthys antarcticus*, *Ophthalmolycus amberensis*, *O. bothriocephalus*, and *Pachycara brachycephalum*) are widely distributed along the continent to the Antarctic Peninsula. Others (*Lycodapus antarcticus*, *Melanostigma gelatinosum*) are recorded in the whole Southern Ocean (Map 24). The record of zoarcid species and



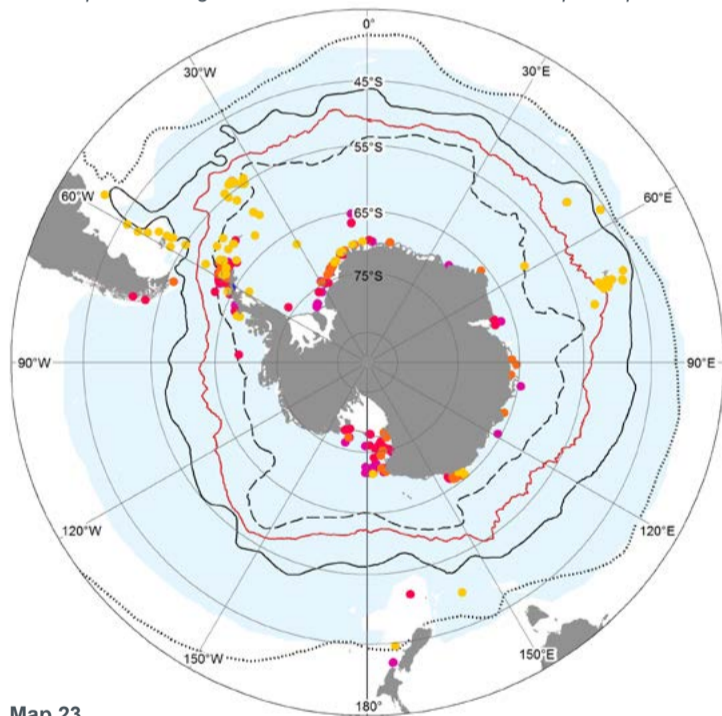
Map 21

▼ Other species
 ▼ *Paraliparis leobergi*
 ▼ *Paraliparis antarcticus*
 ▼ *Paraliparis operculosus*



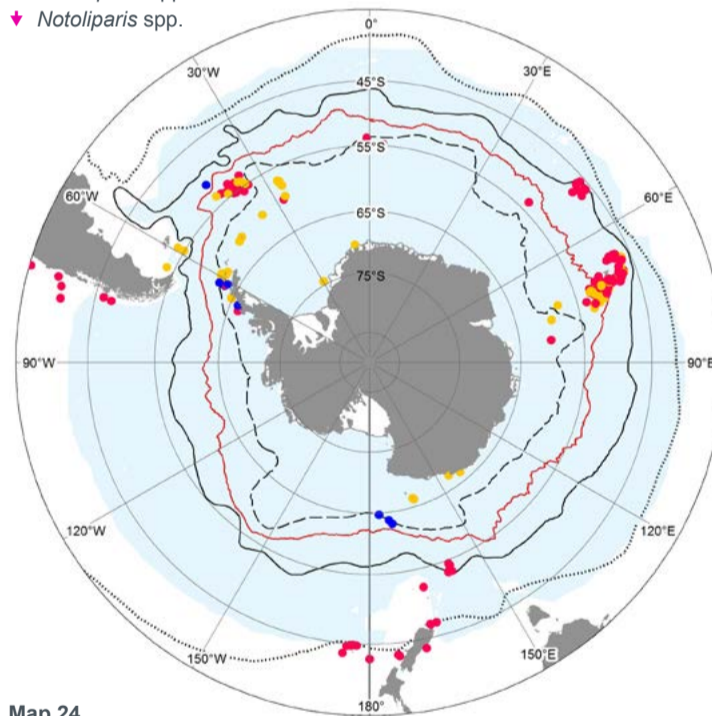
Map 22

▼ *Careproctus/Volodichthys*
 ▼ *Genioliparis* spp.
 ▼ *Notoliparis* spp.



Map 23

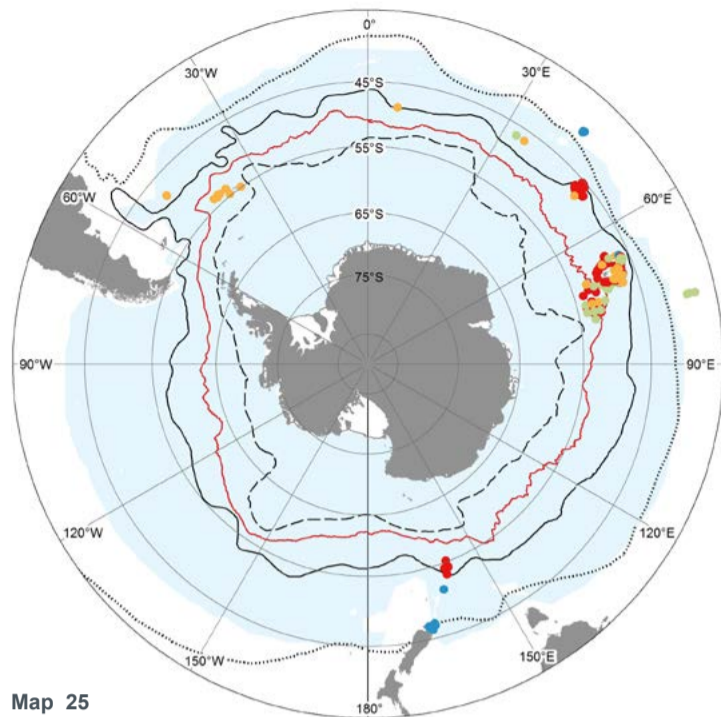
▼ *Lycenchelys* spp.
 ▼ *Lycodichthys* spp.
 ▼ *Ophthalmolycus* spp.
 ▼ *Pachycara* spp.
 ▼ *Santelmoa* spp.



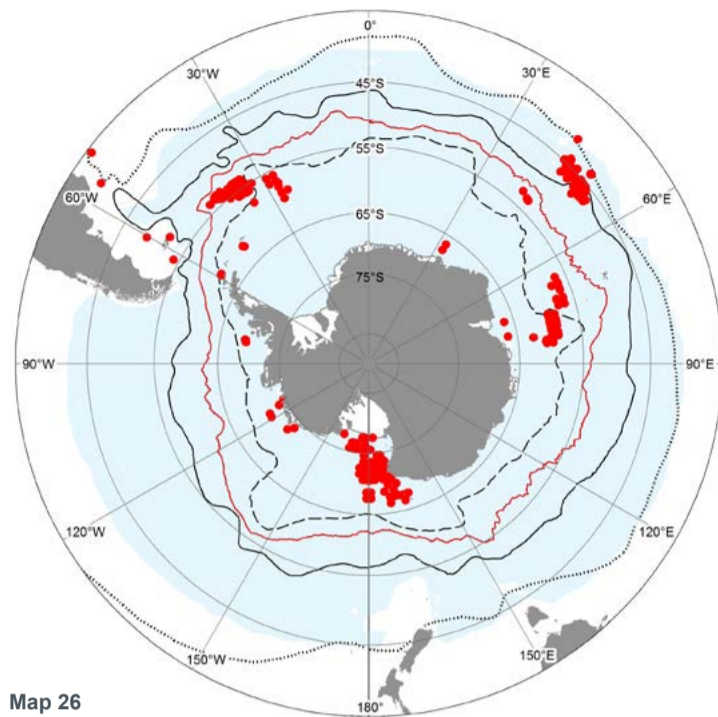
Map 24

▼ *Melanostigma* spp.
 ▼ *Lycodapus* spp.
 ▼ *Seleniolycus* spp.

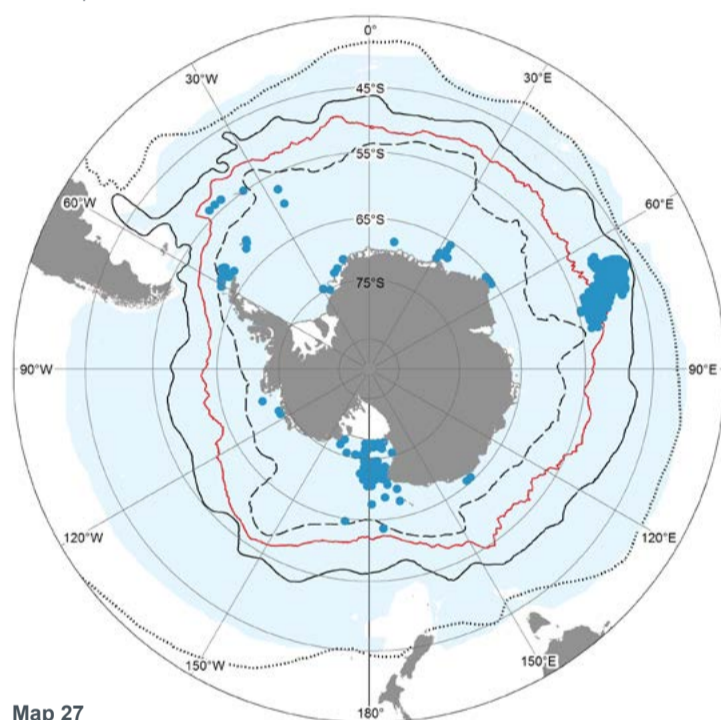
Fish Maps 21–24: Liparidae and Zoarcidae Map 21. Distribution of *Paraliparis* spp. Map 22. Distribution of *Careproctus/Volodichthys* spp., *Genioliparis* spp. and *Notoliparis* spp. Map 23. Distribution of *Lycenchelys* spp., *Lycodichthys* spp., *Ophthalmolycus* spp., *Pachycara* spp., *Santelmoa* spp. . Map 24. Distribution of *Melanostigma* spp., *Lycodapus* spp., *Seleniolycus* spp.



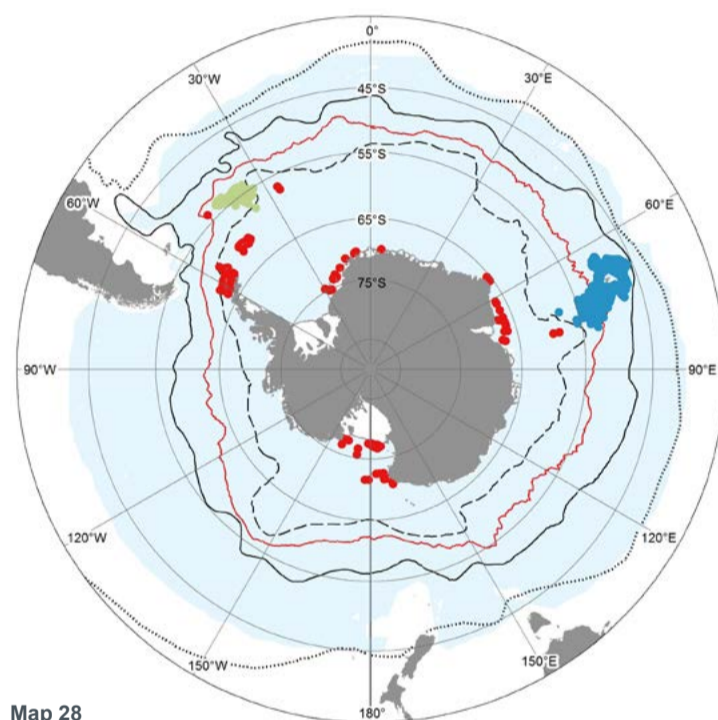
Map 25
 ◆ *Centroscyrnus coelolepis*
 ◆ *Etmopterus vivator*
 ◆ *Lamna nasus*
 ◆ *Somniosus antarcticus*



Map 26
 ◆ *Amblyraja georgiana*



Map 27
 ◆ *Bathyraja eatonii*



Map 28
 ◆ *Bathyraja irrasa*
 ◆ *Bathyraja meridionalis*
 ◆ *Bathyraja maccaini*

Fish Maps 25–28: Chondrichthyes Map 25. Distribution of sharks (excepted *Squalus acanthias*). Map 26. Distribution of *Amblyraja georgiana* Norman, 1938 and *A. taaf* Meissner, 1987. Map 27. Distribution of *Bathyraja eatonii* (Günther, 1876) (Kerguelen Plateau only) and *B. cf. eatonii*. Map 28. Distribution of *Bathyraja irrasa* Hureau & Ozouf-Costaz, 1980, *B. maccaini* Springer, 1971, *B. meridionalis* Stehmann, 1987.

their geographical distribution in the Southern Ocean need to be completed. Species identification is still a problem in some species. For example, very few species have been recorded from East Antarctica except for the Dumont d'Urville and the Ross Seas.

Eelpouts are distributed over a wide bathymetric range from species limited to the shallower waters of the shelves (300–700m) such as *Lycenchelys argentina*, *Lycodichthys antarcticus*, *Ophthalmolycus amberensis*, *O. andersoni*, *O. botriocephalus*, *P. brachycephalum* to species in deep water along the slopes or abyss such as *Lycenchelys antarctica*, *L. nannospinata*, *P. cousinsi*, and *P. priedei*. Most species (*Lycodapus antarcticus*, *M. gelatinosum*) live over a considerable depth range, from 600 to 2600 m for example in *L. bellingshauseni*. While most species are benthic, some genera exhibit a benthopelagic mode of life such as *Seleniolycus* to meso/bathypelagic *Lycodapus* and *Melanostigma* spp. distribution (Map 24).

2.4. Chondrichthyes (sharks and rays) (Maps 25–28)

2.4.1. Lamnidae, Squalidae, Somniosidae (sharks)

Species diversity of sharks was much higher in the Cenozoic Era than in the Holocene. The fossil faunas suggest a circum-Antarctic distribution during the Eocene (Eastman 2005) which disappeared with the changes in the environment (Oligocene cooling eliminating the temperate shallow-water Eocene fauna). Few species of sharks now occur in the Southern Ocean. They are mainly recorded in its northern part, with only one southerly record in the Ross Sea.

The widely distributed porbeagle, *Lamna nasus*, is common on shelves

and slopes of the sub-Antarctic islands (South Georgia, Kerguelen Plateau and Crozet Islands) (Duhamel *et al.* 2005). Four other species occur in the deep-sea: two are small-sized lantern sharks, *Etmopterus vivator* is only known from the Kerguelen Plateau in the Southern Ocean but is wide ranging in the Southern Hemisphere, and *Etmopterus* sp. has recently been recorded in the Ross Sea (Hanchet *et al.* 2013). Radiation in the lantern sharks from the *E. spinax* clade has been recently investigated by molecular phylogeny (Straube *et al.* 2010a, 2010b) and probably additional cryptic species will be discovered. Other shark species occurring in the north of the Southern Ocean are the cosmopolitan Portuguese dogfish *Centroscyrnus coelolepis* at Kerguelen and Crozet Islands, and the sleeper shark *Somniosus antarcticus* from South Georgia, Marion Islands, Crozet Islands, Kerguelen Plateau and Macquarie Island (Map 25). The widespread piked dogfish *Squalus acanthias* is considered to be an occasional migrant to the Kerguelen Islands.

Depth distribution of the bottom living species (*S. antarcticus*, *E. vivator* and *C. coelolepis*) ranges from slopes to down to 1700–1900 m (with an increasing depth range for each of the above species). The more pelagic species (*L. nasus* and *S. acanthias*) are recorded from shelf and coastal (*L. nasus*) waters to upper slopes.

2.4.2. Rajidae (skates)

The two genera of Rajidae present in the Southern Ocean belong to a taxonomically diverse, but morphologically conservative clade (McEachran & Dunn 1998). They are not morphologically diverse, the morphological characteristics present in modern rajids such as rostral morphology and pelvic

girdle structure being already present in fossil specimens from the Upper Cretaceous. Two subfamilies are present: Rajinae with the genus *Amblyraja* (2 species, Map 26) and Arhynchobatinae with the genus *Bathyrāja* (8 species, Maps 27, 28).

The distribution of the ancestral relatives of rajids was confined to inner shelf waters. Rajids may have made multiple radiations into the deep-sea (McEachran & Dunn 1998). Recent molecular studies (Smith *et al.* 2008) have revealed misidentification in some species which casts doubt on the horizontal and vertical range of the species in question. Some species tentatively described as *Bathyrāja* sp. (dwarf) and *B.* sp. (cf. *eatonii*) need to be fully described before their geographic distributions can be delineated and any biogeographic assignment be proposed. In the genus *Bathyrāja* three species of the genus *Bathyrāja* (*B. maccaini*, *B.* sp. (cf. *eatonii*), *B.* sp. (dwarf)) seem to exhibit a circum-Antarctic distribution. *B. meridionalis* is limited to South Georgia and *B. eatonii*, *B. irrasa*, *B. murrayi* are restricted to the Kerguelen Plateau. In the genus *Amblyraja*, *A. georgiana* is present around islands of the Scotia Arc. *A. taaf* is recorded from the Indian sector and probably also occurs off South Georgia (Endicott *et al.* 2006).

The bathymetric distributions of skates range from shelf waters (*B. murrayi*, *B. maccaini*) to deeper (upper and lower slopes for all other species), and down to 1800 m for *A. taaf*, *B. irrasa* (Duhamel *et al.* 2005). Some species are taken regularly and in some numbers as bycatch in the longline fisheries for toothfish *Dissostichus* spp. (Anonymous 2012).

2.5. Other demersal fish families (Maps 29–38)

2.5.1. Grenadiers - Macrouridae

The grenadier family (rattails) contains about 400 species worldwide. Three genera with 11 species are present in the Southern Ocean. The genera *Macrourus* and *Coryphaenoides* are the most speciose and include some endemic species (*Macrourus whitsoni* and *M. caml*, *Coryphaenoides ferreiri*). The remaining species are widespread in the deep-sea. The recent revision of the genus *Macrourus* (McMillan *et al.* 2012) has suffered from misidentifications made at-sea. The genus *Coelorinchus* does not seem to occur in the Southern Ocean. Therefore records of the species of this genus in the Southern Ocean appear to be misidentifications.

All deep-sea species (*Coryphaenoides filicauda*, *C. armatus*, *C. lecoinctei*) appear to lead a benthopelagic life along the continental slope and down to abyssal depths of 4000–5000 m (Cousins & Priede 2012) (Map 29). Some species appear to be abundant and may in fact dominate the deep-sea slope ichthyofauna such as *Macrourus whitsoni* and *M. caml* in the High Antarctic and South Georgia, and *M. carinatus* and *M. holotrachys* elsewhere) (Smith *et al.* 2011, Causse *et al.* 2011, McMillan *et al.* 2012) (Map 30). *Coryphaenoides* species appear to dominate the abyssal depths (Cousins & Priede 2012) as *Macrourus* in shallower depths.

Localized abundances of *Macrourus* species in the Southern Ocean are also known from by-catches in the longline fishery on *Dissostichus* spp. (see Anonymous 2012) with the largest by-catches occurring in the Ross Sea (Hanchett *et al.* 2008), on the Kerguelen Plateau (Duhamel *et al.* 2005) and around South Georgia (Anonymous 2012). To protect macrourids from overfishing, a by-catch provision has been introduced which makes it obligatory for longliners to change the fishing ground if the by-catch exceeds a certain level.

2.5.2. Myxinidae, Petromyzonidae

The presence of the hagfish, *Myxine australis*, seems exceptional in the Southern Ocean (one record in South Shetlands). The lamprey *Geotria australis* is common around South Georgia, but should be considered as a summer migrant from South America (Fernholm 1990). They appear regularly in epipelagic layers where they are extensively preyed upon by albatrosses (Renaud 2011).

2.5.3. Halosauridae, Notacanthidae, Synphobranchidae, Ipnopidae, Ophidiidae, Bythitidae

These six families are distributed worldwide in the deep sea. Only a few records from the Southern Ocean exist (Map 31). The paucity of records may be partly caused by the low sampling effort of the bathyal/abyssal zones. Not surprisingly, every recent cruise has provided new records or new species. Cousins & Priede (2012) estimated that, on the basis of the 15 deep-sea species (including 6 species of the these families) collected in the Crozet Basin, a total of 19–21 deep sea species might occur in the Basin. Given the limited number of species/individuals of the deep sea species so far collected, no further conclusions on the biogeography of these species can be drawn.

2.5.4. Alepocephalidae, Carapidae, Oreosomatidae, Gempylidae

These four families occur mainly on the upper slopes in the South Georgia and Kerguelen provinces (Maps 32, 33). They are benthopelagic. Larvae, postlarvae and juveniles are epi- to mesopelagic. With increasing age, they migrate closer to the seafloor. The Oreosomatidae are probably oceanic migrants from northern temperate waters. The only species occurring in the high Antarctic appears to be the gempylid *Paradiplospinus gracilis*.

2.5.5. Muraenolepididae

Balushkin & Prirodina (2006) suggested that the Muraenolepididae (eel cods) is the only family of gadiform fishes in which divergence occurred in temperate and cold waters of the Southern Hemisphere. The family includes 2 genera: *Muraenolepis* and *Notomuraenobathys*. Eight species occur in the Southern Ocean. Andriashev (1965) considered the Muraenolepididae as a typically Antarctic family. De Witt (1971), however, believed that they are recent invaders to the Southern Ocean.

The distribution of eelcods seems to be mainly circum-Antarctic (Map 34). *M. marmorata* is found on the continental and islands slope regions of the Southern Ocean (Duhamel *et al.* 2005, Matallanas & Olaso 2007). Some species appear to be widely distributed all along the Antarctic Continent such as *Muraenolepis microps* (Victoria Land, Weddell and Ross Seas, Antarctic Peninsula and Scotia Sea) (Chiu & Markle 1990, Eastman & Hubold 1999, Matallanas & Olaso 2007); *M. evseenkoi* (Commonwealth, Riiser-Larsen, Amundsen and Ross seas) (Balushkin & Prirodina 2010b); and *Notomuraenobathys microcephalus* (Scotia Sea, the northern part of Antarctic Peninsula, the Enderby coast, in Prydz Bay and Macquarie Ridge) (Cohen *et al.* 1990, Balushkin & Prirodina 2010a). Other species seem to have a more restricted geographical distribution. *M. kuderskii* is only caught at South Georgia (Balushkin & Prirodina 2007). *M. orangiensis* occurs in the Indian sector of the Southern Ocean (Marion/Prince-Edward and Heard Islands), and *M. trunovi* in the Lazarev Sea (Balushkin & Prirodina 2006). *M. pacifica* is restricted to the Hercules Ridge (Pacific-Antarctic rise) in the South Pacific sector (Prirodina & Balushkin 2007).

Four new species (*M. andriashevi*, *M. evseenkoi*, *M. pacifica* and *M. trunovi*) have been added the last decade, and a new genus (*Notomuraenobathys*) has been erected, and mixes records of previously described species in this morphologically difficult group. Much uncertainty currently exists surrounding the identification of the Muraenolepididae and a number of genetic studies are being undertaken to address these interrogations. The biogeography is therefore still hypothetical.

2.5.6. Moridae

The deep sea cods form an important component of deep species diversity with 110 different species known to be distributed worldwide (Cohen *et al.* 1990). Only 5 genera and 6 species have been recorded from the Southern Ocean (Maps 35, 36). Species are mainly found on the slope of sub-Antarctic islands: *Guttigadus kongi* at South Georgia, Kerguelen, Crozet, Marion and Prince Edward Islands; *Lepidion ensiferus* at South Georgia, Kerguelen and Crozet Islands; *Notophycis marginata* off the Crozet and Kerguelen Islands; *L. schmidtii* on the Del Cano Rise, Kerguelen and Crozet islands and in the Ross Sea region (Hanchet *et al.* 2013), and is also known in Australia and New Zealand waters, North Pacific and Atlantic Ocean. *Antimora rostrata* and *Halargyreus johnsonii* are cosmopolitan species (Duhamel *et al.* 2005, Smith *et al.* 2012). Specimens collected in the Ross Sea and currently recognized as *H. johnsonii*, could probably be a cryptic species (Smith *et al.* 2011).

2.5.7. Congiopodidae

One species is present in the Southern Ocean: *Zanclorhynchus spinifer*. It is restricted to the sub-Antarctic islands of the Kerguelenian Province (Marion/Prince Edward, Kerguelen, Crozet, Heard, Macquarie Islands) and some oceanic seamounts (Kara-Dag on the Del Cano Rise) north-east of Prince Edward Islands (Map 37). The vertical distribution of this species ranges from 5–400 m depth.

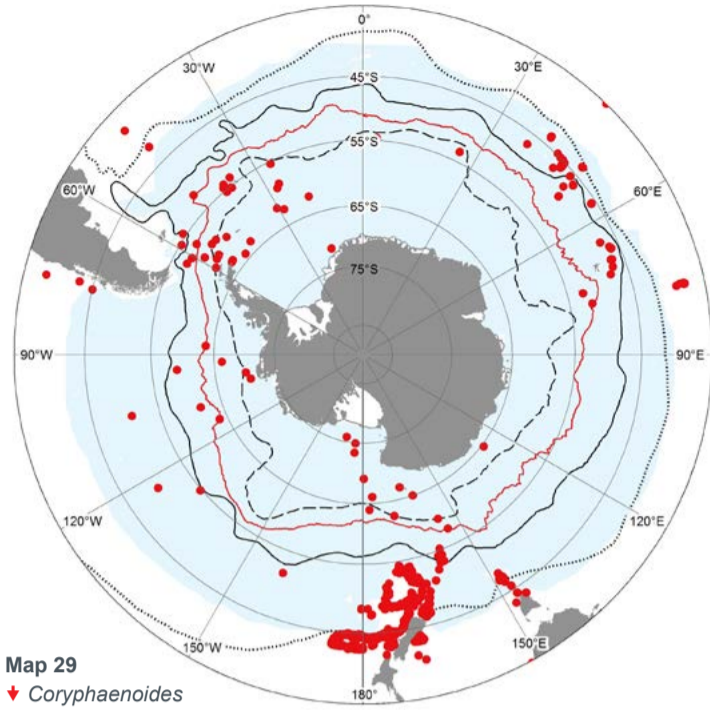
2.5.8. Psychrolutidae, Bathylutichthyidae

The Macquarie blobfish (*Ebinania macquariensis*) is the unique species belonging to the family Psychrolutidae in the Southern Ocean. A few specimens have been recorded at Macquarie Island and the Kerguelen Plateau (Map 37). The genus has been recently recorded from the Ross Sea region (Hanchet *et al.* 2013). This ambush feeder is found on island slopes from 500 m to more than 1100 m depth. The southernmost record of a second species, *Ambophthalmos magnicirrus*, was from the deep-sea region off Macquarie Island, but it has never been found further south.

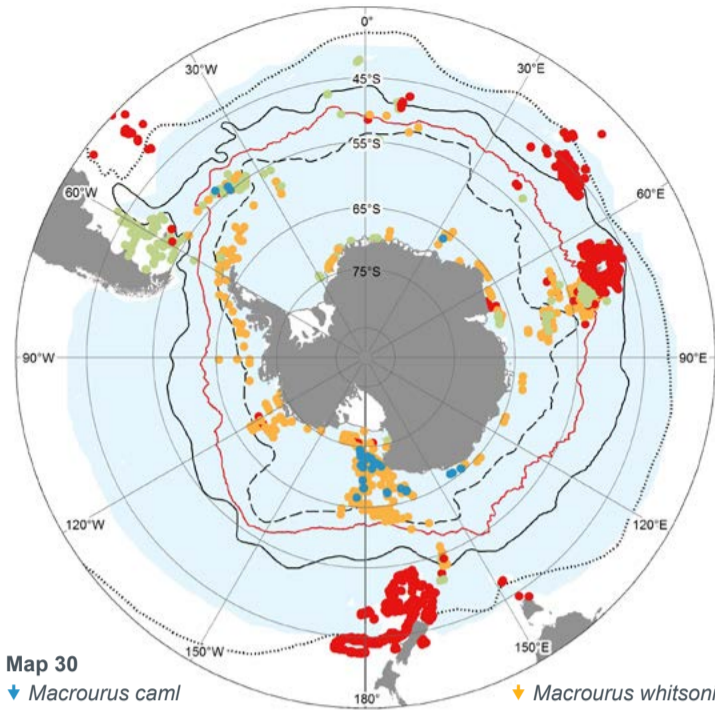
The recently described family Bathylutichthyidae, with the single specimen (holotype) of *Bathylutichthys taranetzi*, belongs to the psychrolutid-liparid branch in the evolution of the Cottoidei (Balushkin & Voskoboinikova 1990). The specimen was recorded in the deep-sea (1650 m) northeast of South Georgia (Map 37).

2.5.9. Tripterygiidae

The family has a widespread distribution in rocky sublittoral habitats in tropical and temperate regions. Only a single species, *Helcogrammoides antarcticus*, has been recorded from inshore waters of the Antarctic Peninsula (Gon 1990) (Map 37).

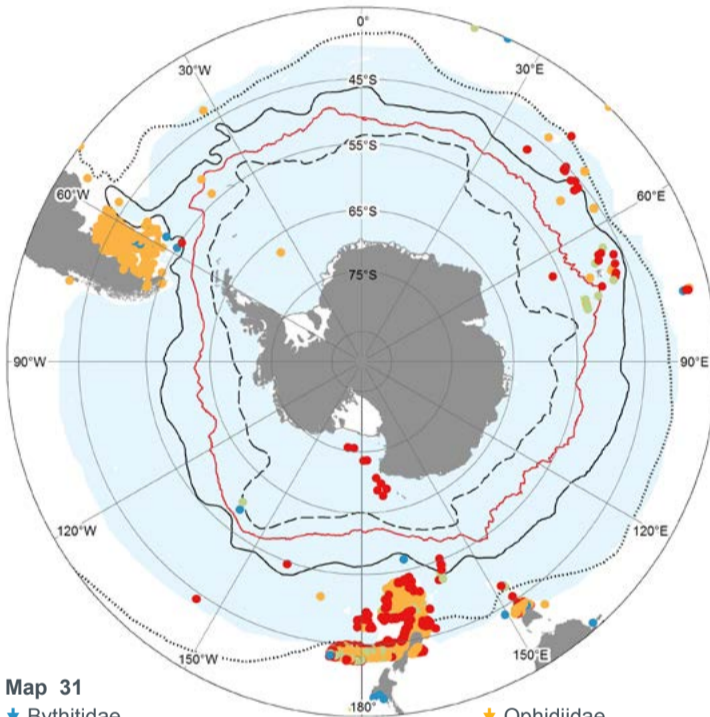


Map 29
 ▼ *Coryphaenoides*

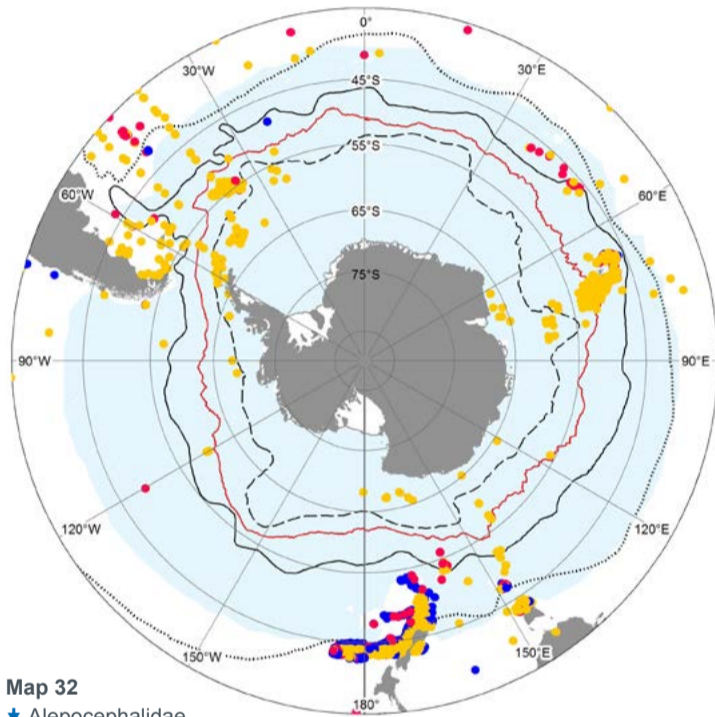


Map 30
 ▼ *Macrourus caml* ▼ *Macrourus whitsoni*
 ▼ *Macrourus holotrachys* ▼ *Macrourus carinatus*

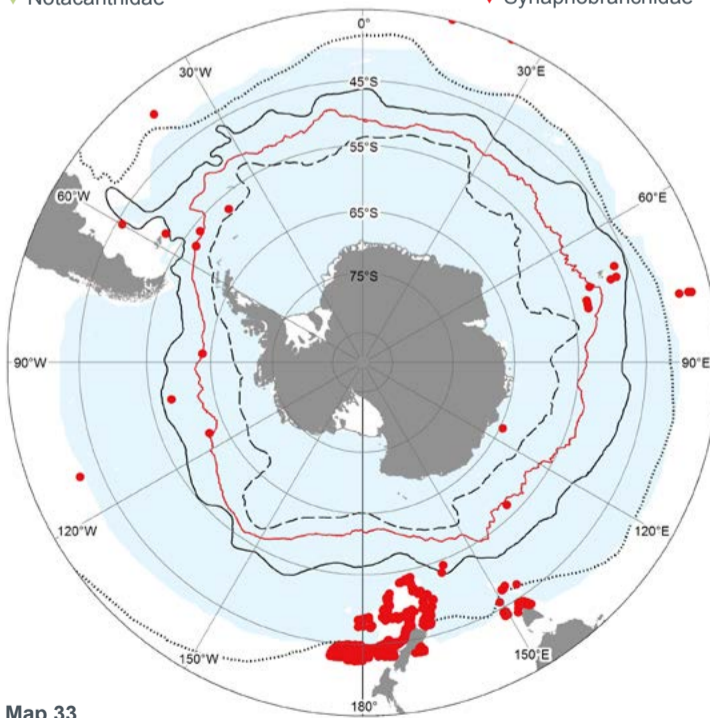
Fish Maps 29–30: Macrouridae Map 29. Distribution of *Coryphaenoides* spp. Map 30. Distribution of *Macrourus caml* Mcmillan, Iwamoto, Stewart & Smith, 2012, *M. holotrachys* Günther, 1878, *M. whitsoni* (Regan, 1913) and *M. carinatus* (Günther, 1878).



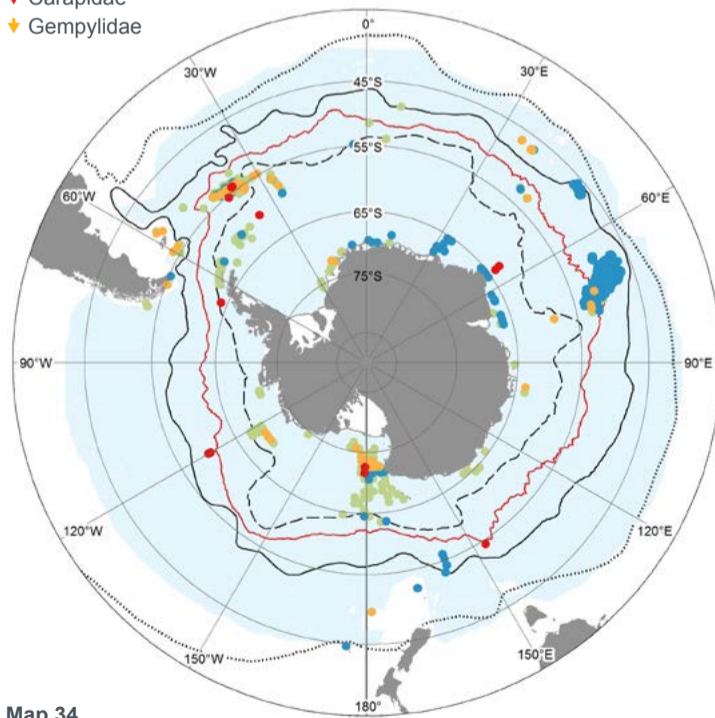
Map 31
 ▼ Bythitidae ▼ Ophiidiidae
 ▼ Notacanthidae ▼ Synphobranchidae



Map 32
 ▼ Alepocephalidae
 ▼ Carapidae
 ▼ Gempylidae

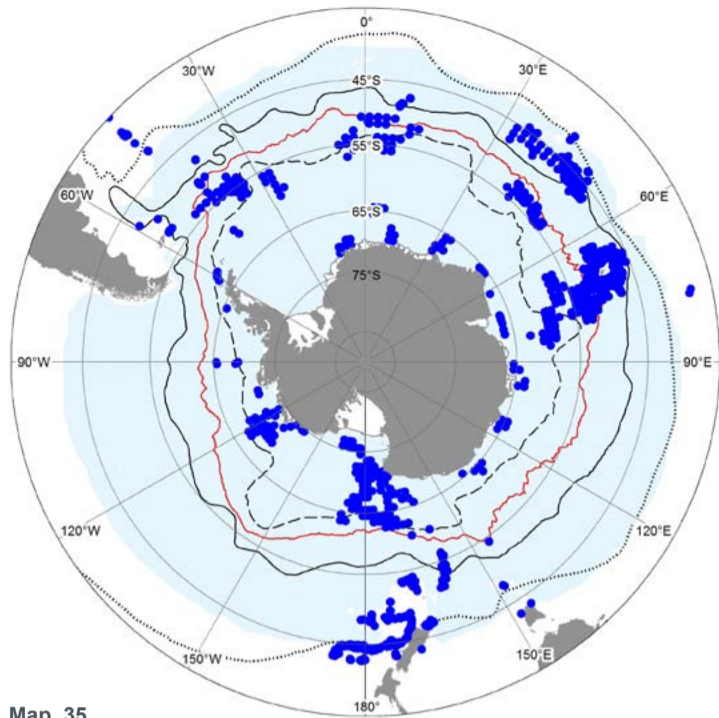


Map 33
 ▼ Oreosomatidae

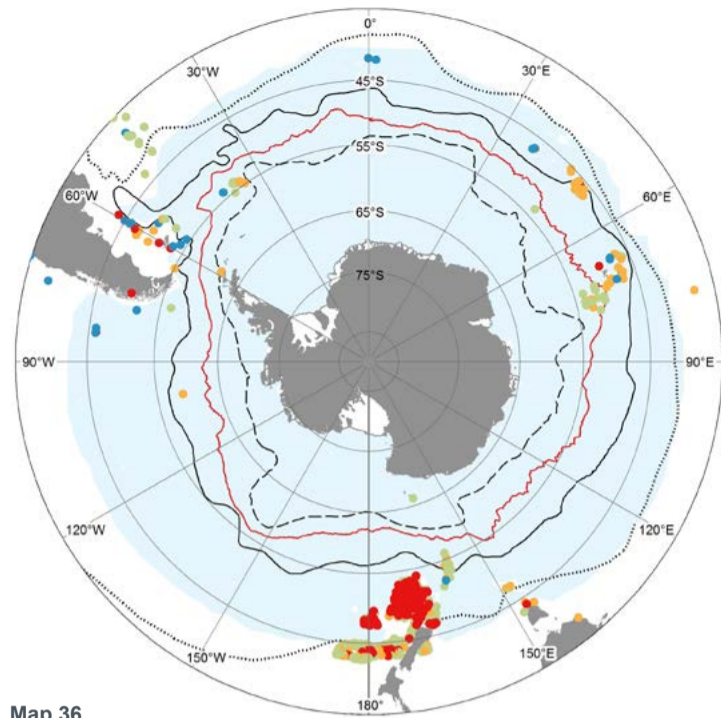


Map 34
 ▼ *Notomuraenobathys microcephalus* ▼ *Muraenolepis marmorata*
 ▼ *Muraenolepis orangiensis* ▼ *Muraenolepis microps*

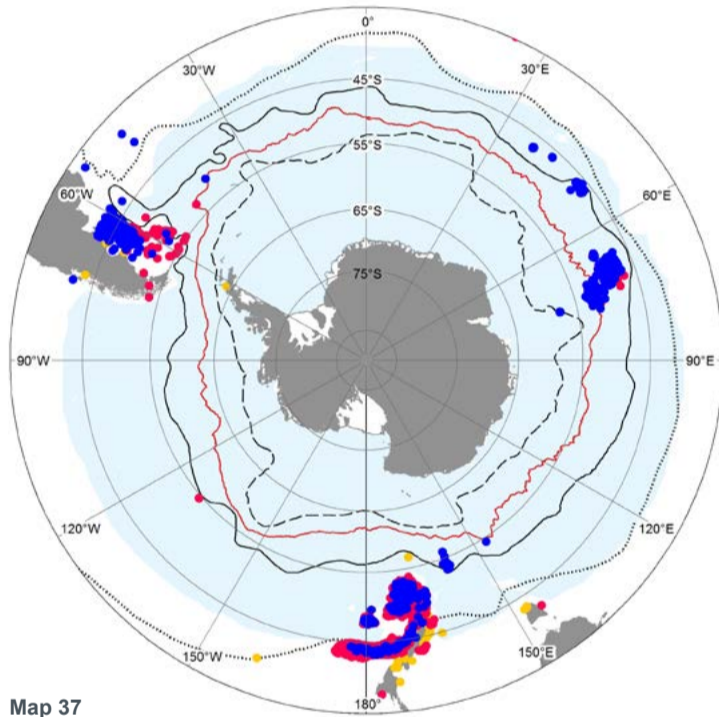
Fish Maps 31–34: Notacanthidae, Synphobranchidae, Ophiidiidae, Bythitidae, Alepocephalidae, Carapidae, Gempylidae, Oreosomatidae and Muraenolepididae Map 31. Distribution of Bythitidae, Notacanthidae, Ophiidiidae and Synphobranchidae. Map 32. Distribution of Alepocephalidae, Carapidae, Gempylidae. Map 33. Distribution of Oreosomatidae. Map 34. Distribution of *Muraenolepis marmorata* Günther, 1880, *M. microps* Lönnberg, 1905, *M. orangiensis* Vaillant, 1888 and *Notomuraenobathys microcephalus* (Norman, 1937).



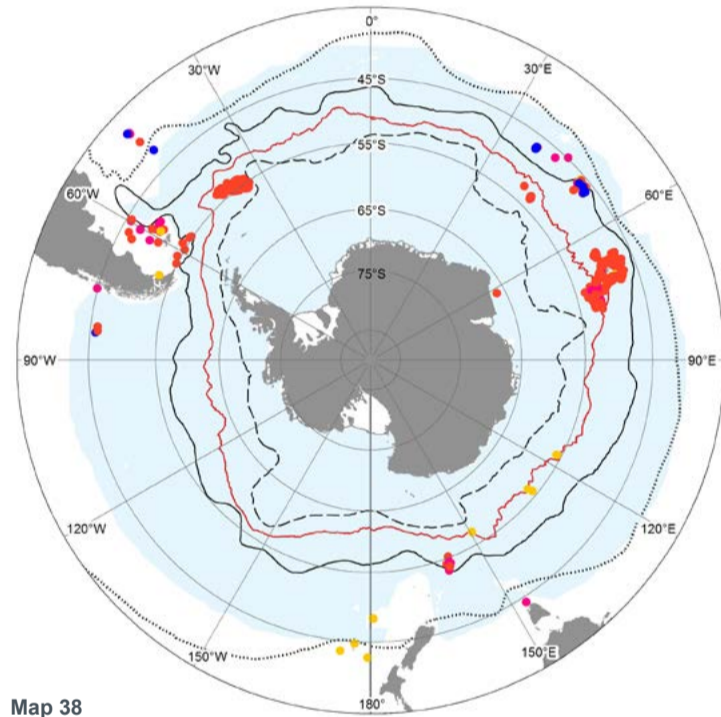
Map 35
 ↓ *Antimora rostrata*



Map 36
 ↓ *Guttigadus kongi* ↓ *Lepidion*
 ↓ *Halargyreus johnsonii* ↓ *Notophycis marginota*



Map 37
 ↓ Tripterygiidae
 ↓ Psychrolutidae
 ↓ Congiopodidae



Map 38
 ↓ *Achiropsetta tricholepis* ↓ *Neochiropsetta milfordi*
 ↓ *Mancopsetta maculata* ↓ *Pseudomancopsetta andriashevi*

Fish Maps 35–38 Moridae, Congiopodidae, Psychrolutidae, Tripterygiidae and Achiropsettidae Map 35. Distribution of *Antimora rostrata* (Günther, 1878). Map 36. Distribution of *Lepidion* spp., *Guttigadus kongi* (Markle & Melendez, 1988), *Notophycis marginata* (Günther, 1878) and *Halargyreus johnsonii* Günther, 1862. Map 37. Distribution of Congiopodidae, Psychrolutidae and Tripterygiidae. Map 38. Distribution of Achiropsettidae.

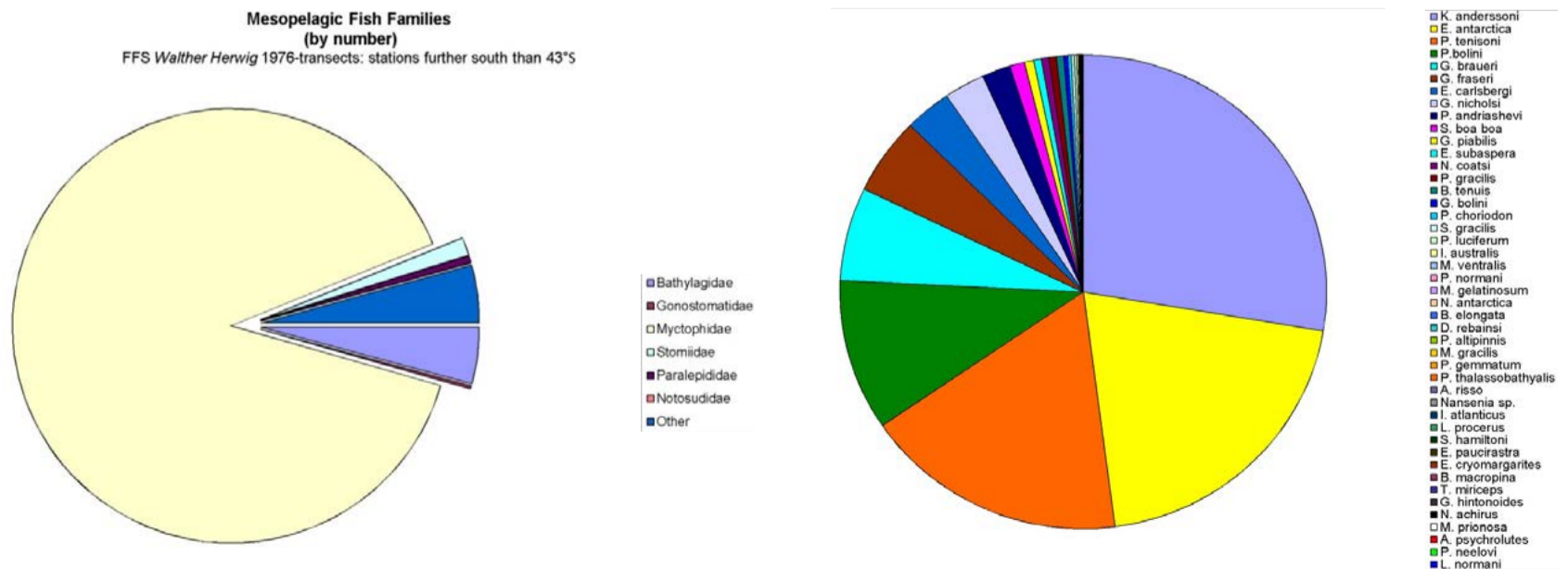


Figure 2 Southern Ocean: (a) Atlantic sector: family representation based on FFS Walther Herwig transect data (November 1975 – January 1976); (b) Indian sector: species representation based on La Curieuse Ichthyoker sampling programme (February 1998 – December 2000).

2.5.10. Achiropsettidae

The family of southern flounders comprises 4 genera and 4 species (+ 1 subspecies). As adults, records of all 4 species are confined to the Sub-Antarctic Region. However, records of larvae indicate dispersion into the high Antarctic. *Mancopsetta maculata* (with two subspecies) is present on the peri-insular shelves of the Kerguelen Plateau, Crozet and Prince Edward Islands and from

Shag Rocks and South Georgia. *Neoachiropsetta milfordi* and *Achiropsetta tricholepis* are restricted to the Indian sector of the Southern Ocean (Kerguelen Plateau, Crozet Islands, Prince Edward Islands and Ob/Lena Banks). *Pseudomancopsetta andriashevi* has only been recorded from the shelves of Crozet and the Prince Edward Islands (Map 38). The distribution of most species extends beyond the boundaries of the Southern Ocean to one or more of the following areas: Patagonian Region, Campbell Plateau and South Africa.

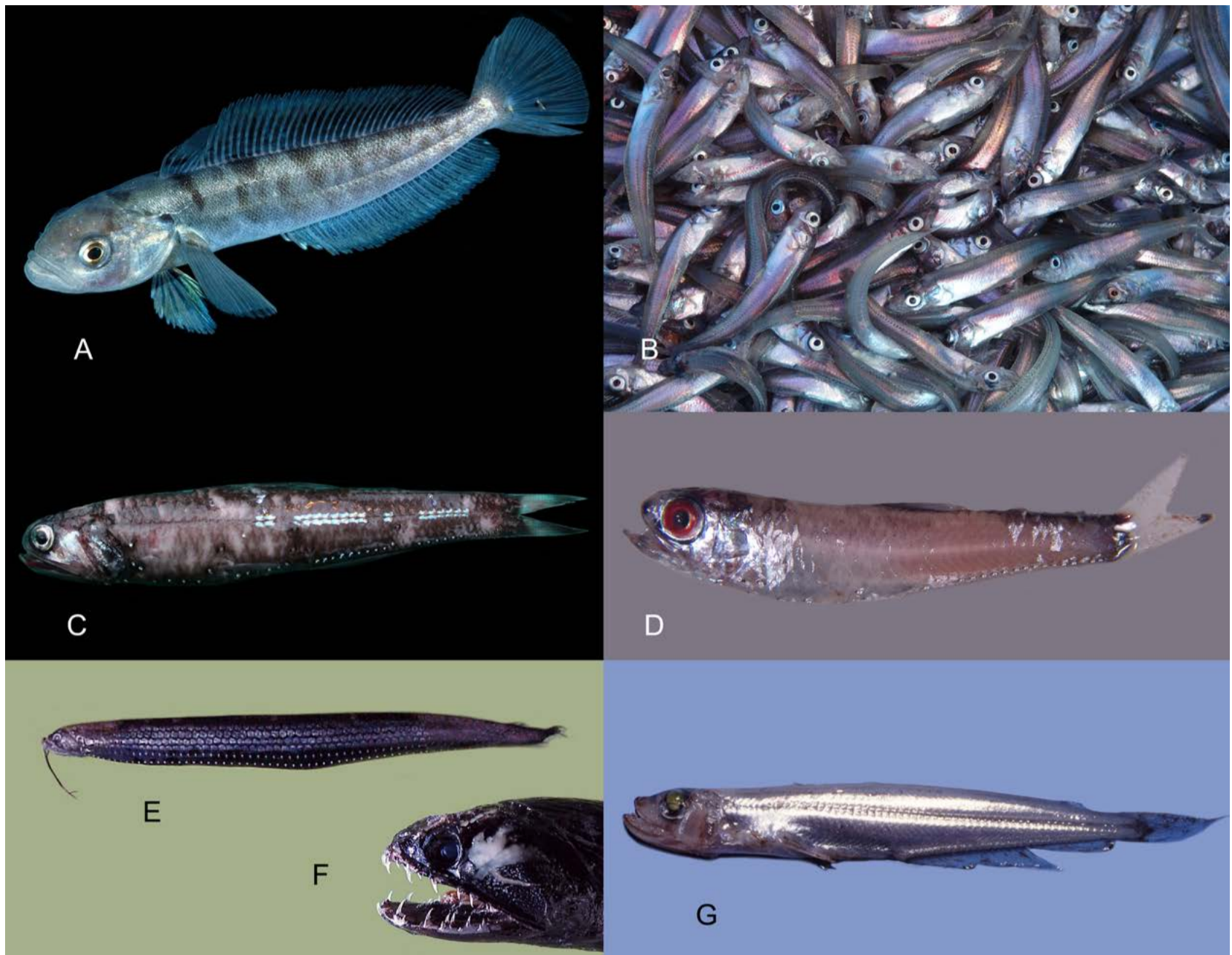
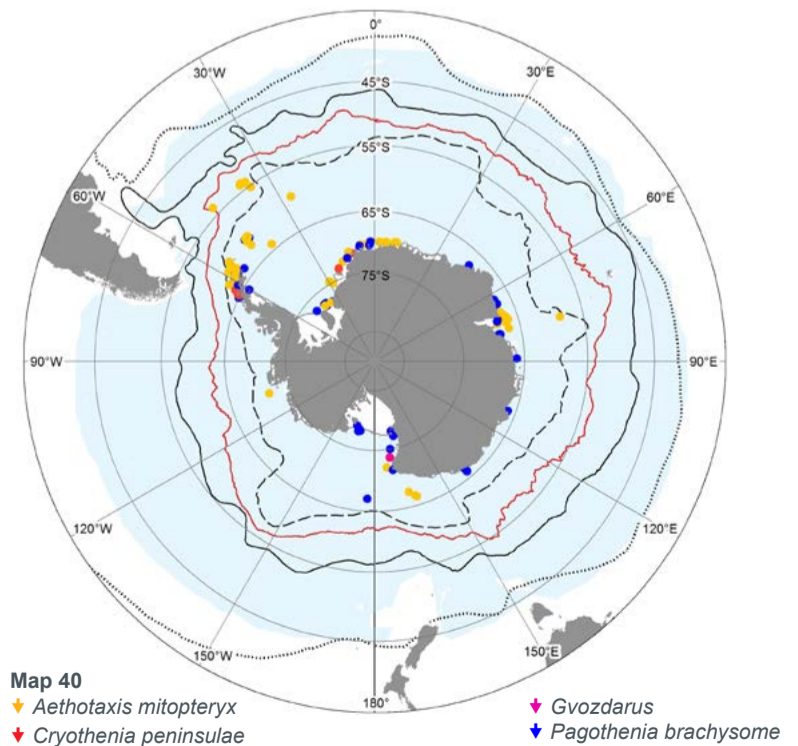
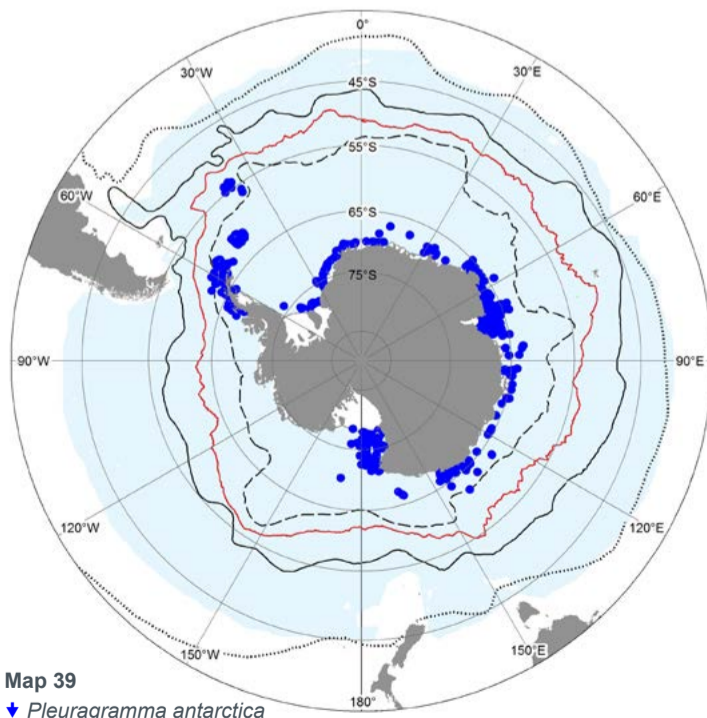


Photo 2 Pelagic fish (A) *Trematomus borchgrevinki* Boulenger, 1902. (B) *Pleuragramma antarctica* Boulenger, 1902. (C) *Gymnoscopelus nicholsi* (Gilbert, 1911). *Krefftichthys anderssoni* (Lönnerberg, 1905). (E) *Stomias* spp. (F) *Trigonolampa miriceps* Regan & Trewavas, 1930. (G) *Benthalbella macropinna*. (A) image © John Macdonald, University of Auckland; (B) (D), P. Koubbi, UPMC; (C), (E), (F), (G), G. Duhamel, MNHN.



Fish Maps 39–40 Pelagic and cryopelagic Notothenioids Map 39. Distribution of *Pleuragramma antarctica* Boulenger, 1902. Map 40. Distribution of *Aethotaxis mitopteryx* DeWitt, 1962, *Gvozdarus* spp., *Pagothenia brachysoma* Pappenheim, 1912, *Trematomus borchgrevinki* Boulenger, 1902 and *Cryothermia peninsulae* Daniels, 1981.

Three of the four species exhibit a depth distribution ranging from about 100 m to 1000 m with occasional records down to 1500 m). *P. andriashievi* appears to be limited to shallower depths (200–365 m).

3. Pelagic fishes

Fishes of the pelagic realm can be divided into two categories:

- true pelagic families including midwater fishes,
- families of benthic origin which have variously adapted to a secondary pelagic mode of life including Nototheniidae, Zoarcidae and Liparidae.

The first group has been mainly investigated in the upper 1000 m (epi- and mesopelagic depth range). Data are still incomplete for depths >1000 m although a few records are available for the typical families of these layers such as the Cetomimidae with three species: *Gyrinomimus andriashievi*, *Gyrinomimus grahami* and *Notocetichthys trunovi*.

The most dominant representative of the secondary pelagic species is *Pleuragramma antarctica* which is described in the following section with cryopelagic Notothenioids. The others have been discussed in 2.1.2, 2.2 and 2.3.

3.1. Pelagic and cryopelagic Notothenioids (Maps 39–40)

Among the holopelagic notothenioids (*Aethotaxis mitopteryx*, *Gvozdarus* spp. and *Pleuragramma antarctica*) (Maps 39, 40), *P. antarctica* is the only abundant species. The Antarctic silverfish *P. antarctica* (Notothenioidei, Nototheniidae, Pleuragramminae) is the most abundant fish in coastal regions of high-Antarctica (White & Piatkowski 1993, Eastmann & Hubold 1999, Hoddell *et al.* 2000, Van de Putte *et al.* 2010, Moteki *et al.* 2011). Its range extends to the South Shetland and South Orkney Islands in the Seasonal Pack-ice Zone (Kock & Stransky 2000, Donnelly & Torres 2008). All life-stages lead a pelagic mode of life in depths ranging from 0 to 900 m (Gerasimchuk 1986, DeWitt *et al.* 1990, Knox 1994, Fuiman *et al.* 2002). Specialization to a pelagic mode of life has been accomplished by a suite of adaptations including the appearance of pedomorphic traits in adults (Albertson *et al.* 2010, La Mesa & Eastman 2012). The mode of life of *P. antarctica* is characterized by ontogenetic shifts in vertical and spatial distributions (Koubbi *et al.* 2011d). Eggs and young larval stages are an important component of the cryopelagic community (Knox 1994, Bottaro *et al.* 2009, Evans *et al.* 2012, Vacchi *et al.* 2012b). Adults are mostly distributed in the water column

Data from the Weddell Sea, Ross Sea, and Dumont d'Urville Sea suggest that geographic and oceanographic features such as the proximity of ice shelves or glacial tongues, underwater canyons, water masses stratification, polynyas and katabatic winds are important for the early life history of the silverfish in that they contribute to the retention of larvae in favorable environments, and/or gradually carry early life stages towards inner-shelf depressions and banks as the fish grow larger. The species plays a pivotal role in the high Antarctic coastal ecosystem as one of the major links from lower to higher trophic levels (La Mesa *et al.* 2004, Eastman 2005, O'Driscoll *et al.* 2011, Pinkerton *et al.* 2012).

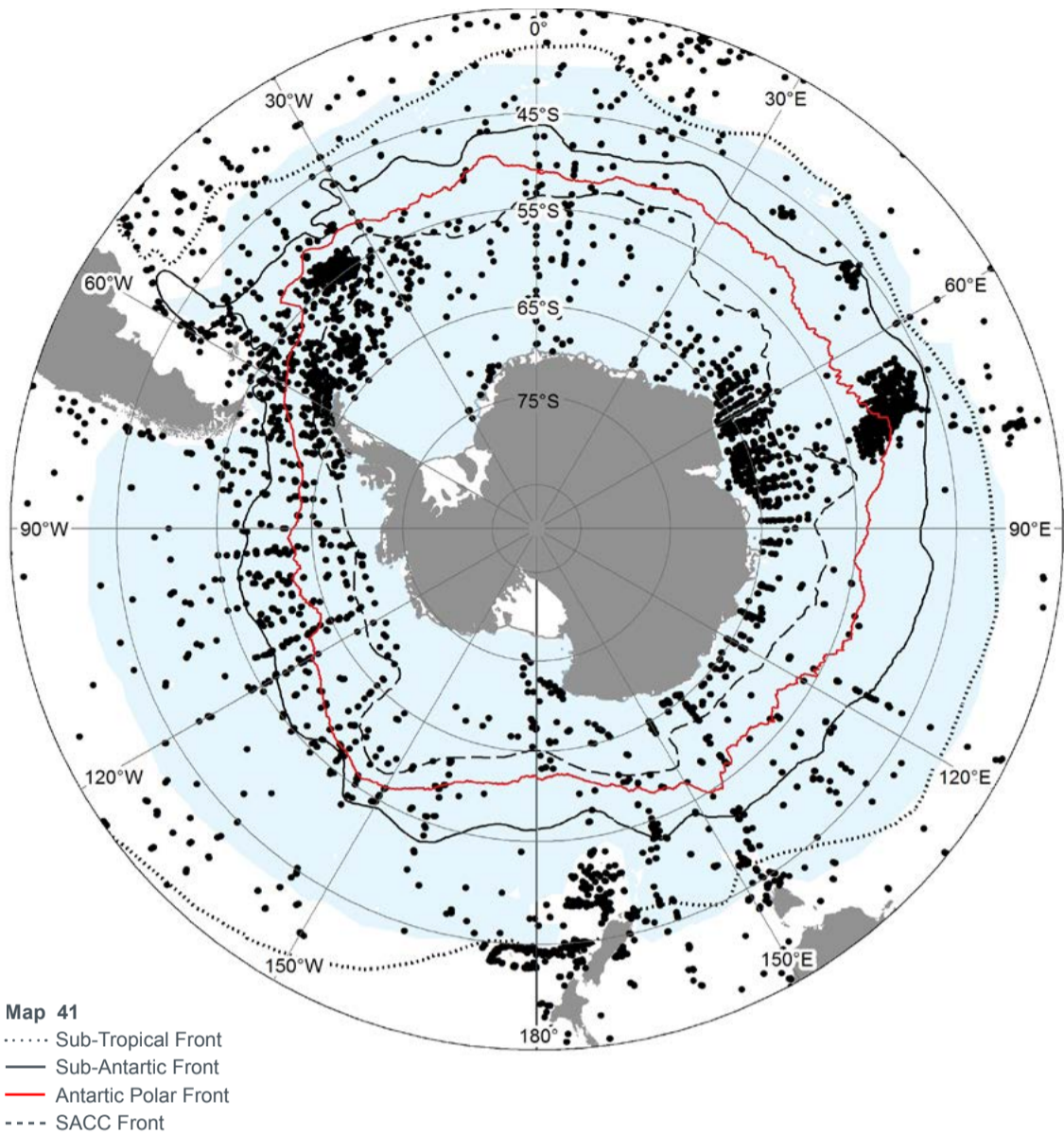
Evidence of direct interaction between the early life stages of the Antarctic silverfish and the sea ice is highly relevant to predictions about possible impacts of environmental changes (in case of warming) on silverfish populations and the implications for the entire coastal Antarctic ecosystem (Moline *et al.* 2008, Vacchi *et al.* 2012a, 2012b).

In addition, there are a few species of Trematominae which are cryopelagic and live in permanent contact with ice. These are *Trematomus borchgrevinki*, *T. amphitrete*, *Pagothenia brachysoma*, and possibly *Cryotheria peninsulae* (Map 40).

3.2. Mesopelagic fishes

3.2.1. Introduction

The mesopelagic (or 'twilight') zone may be better characterized by its ecological processes than by its physical parameters (Robinson *et al.* 2010). It is conventionally regarded as a strictly oceanic division of the water column between about 200 m (depth of the euphotic zone) and 1000 m depth (maximum depth of light penetration). It is located seawards of the continental and peri-insular shelf-breaks (Marshall 1971, Krefft 1974). Mesopelagic fishes undertake regular diel migrations. They spend the daylight hours (or part thereof)



Map 41
 Sub-Tropical Front
 — Sub-Antarctic Front
 — Antarctic Polar Front
 ---- SACC Front

Fish Map 41 Positions of stations sampled for mesopelagic and bathypelagic fishes by international institutions and contributors (see Table 2). The blue area represents the pelagic bioregions 1 to 17 of Raymond (this volume, section 10.1.1.).

in the deeper parts of the mesopelagic zone, and migrate into the upper 200 m at night (Gjøsæter & Kawaguchi 1980).

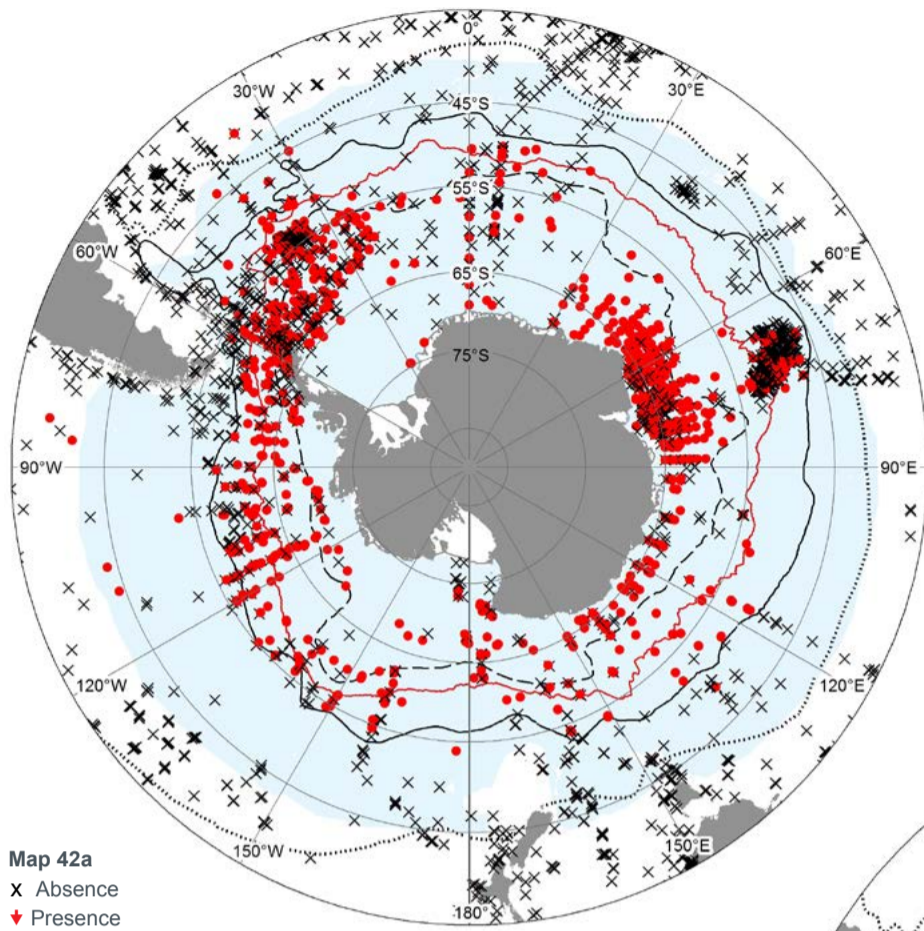
Knowledge of the large-scale distribution and biology of Southern Ocean mesopelagic fishes is mainly based on localized sampling or on multi-year sampling programmes, during which a variety of fishing gears were deployed. Mesopelagic families and species that have been recorded in the Southern Ocean are given in Table 1. The most abundant families include: Bathylagidae, Gonostomatidae, Myctophidae, Notosudidae, Paralepididae and Stomiidae. Representation (% by number) of the families and species from two geographically separated regions of the Southern Ocean are given in Figures 2a, b.

3.2.2. Family Myctophidae (Maps 42–51)

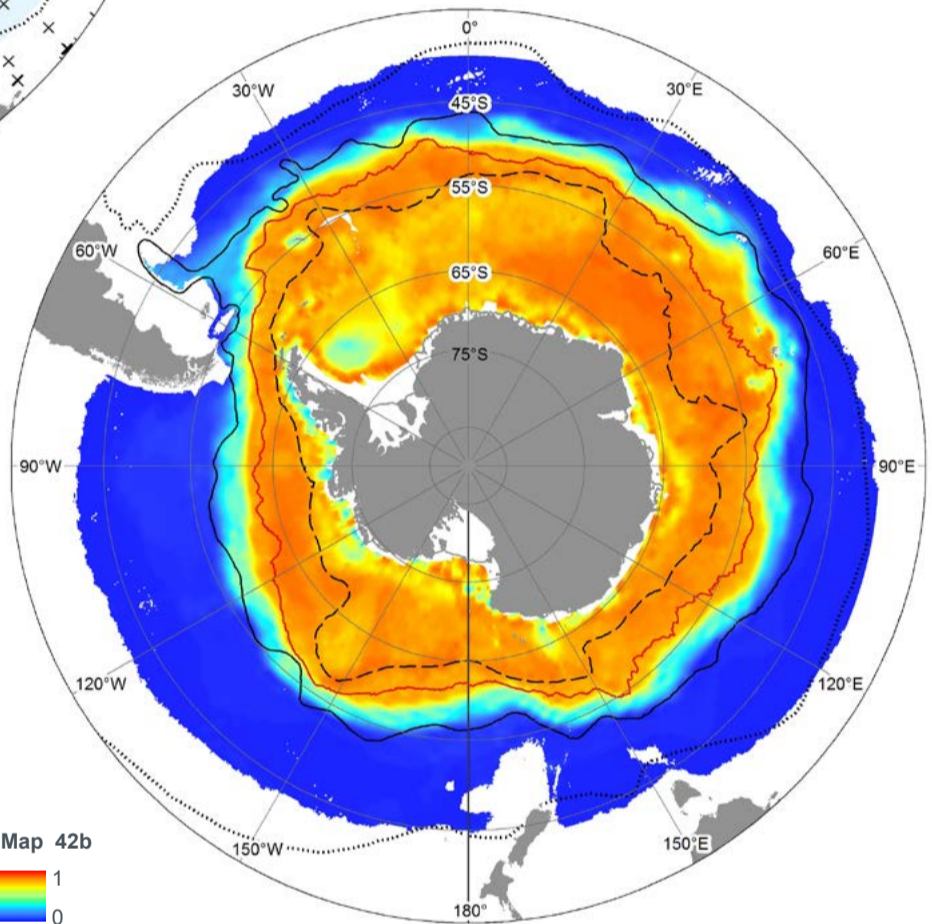
Worldwide, the family Myctophidae comprises at least 33 genera and 240 species. Myctophids are the dominant fish family of the mesopelagic and bathypelagic zones of the Southern Ocean in terms of their species richness, abundance and biomass (Fig. 2) (Hulley 1981, Linkowski 1983, Zemskii 1987, Nevinsky & Efremenko 1989, Donnelly *et al.* 1990, 2004, Filin *et al.* 1990, Kock 1992, Loeb *et al.* 1993, Collins *et al.* 2008, Donnelly & Torres 2008, Koubbi *et al.* 2011c). Juveniles and adults occur in oceanic waters north of the Antarctic Slope Front (ASF) and offshore of the peri-insular shelf breaks (200 m) (Hoddell *et al.* 2000, Flores *et al.* 2008, Ichii *et al.* 2008, Koubbi *et al.* 2011a); larvae may sometimes be found over the peri-insular shelves (Koubbi *et al.* 1991, 2001, 2003, 2009, Loeb *et al.* 1993, Koubbi 1993).

Some 68 species (Table 4) have been recorded from south of Sub-Tropical Front (STF), since analyses of two recently-described species (*Protomyctophum mcginnisi* and *P. kolaevi*) from the region (Prokofiev 2004) suggest that they are junior synonyms of *Protomyctophum bolini* and *P. choriodon* respectively. Of these, 46 species have widespread, broadly-tropical, subtropical, convergence and bi-temperate patterns of distribution. They occur sporadically in the region. 15 species have a Sub-Antarctic Pattern. They are confined mainly to Sub-Antarctic Zone waters between the Sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF). Two species (*Electrona antarctica*, *Gymnoscopelus opisthopterus*) exhibit an Antarctic Pattern and are typically found south of the APF. Five species are distributed from the ASF to the STF (Broadly Antarctic Pattern) (Becker 1963, 1964, 1985, McGinnis 1982, Hulley 1986a, Hulley 1990, Kock 1992, Duhamel *et al.* 2005, Flynn & Williams 2012).

Southern Ocean hydrodynamics result in temporally and spatially patchy,



Map 42a
 X Absence
 ▼ Presence



Map 42b
 1
 0

Fish Maps 42a and b *Electrona antarctica* (Günther, 1878). Plots of (a) occurrence; (b) predicted distribution from BRT-analysis (total deviance explained = 41%; AUC = 0.81) using the following environmental variables (individual contribution in parentheses): summer temperature (°C) at 200 m (67.8%); summer oxygen (ml.l⁻¹) at 50 m (26.9%); bathymetry (m) (5.2%).

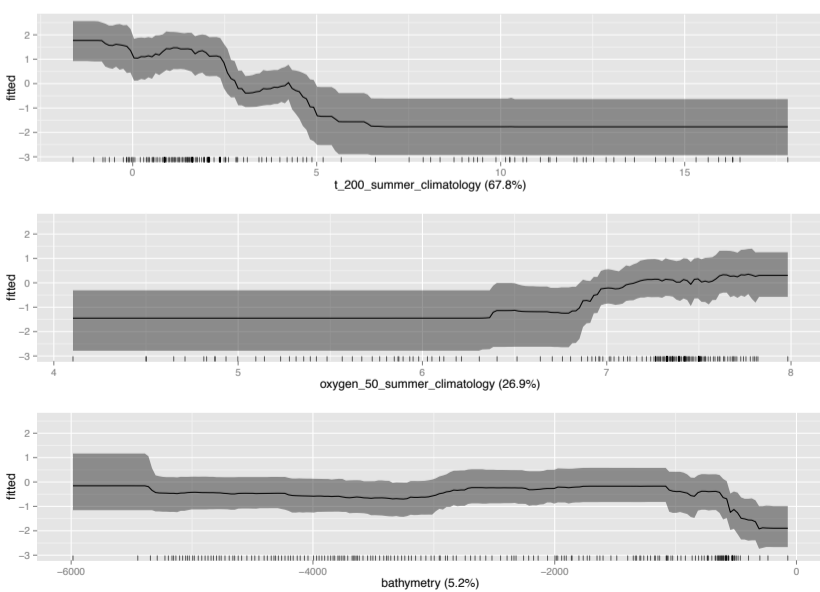


Figure 3 *Electrona antarctica* (Günther, 1878): partial dependence plots of the most influential environmental variables. Mean estimate (black line); 95% confidence limit (grey band); rug plots inside base of plot indicate distribution of data in deciles of x-axis variable.

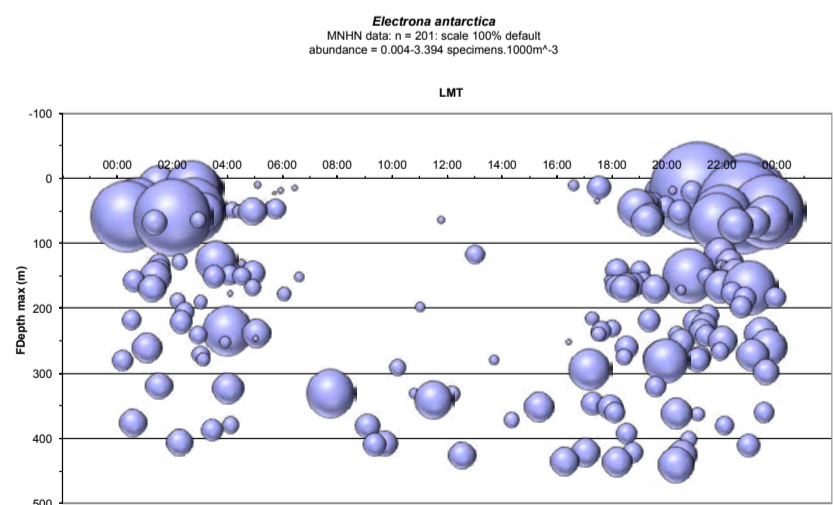
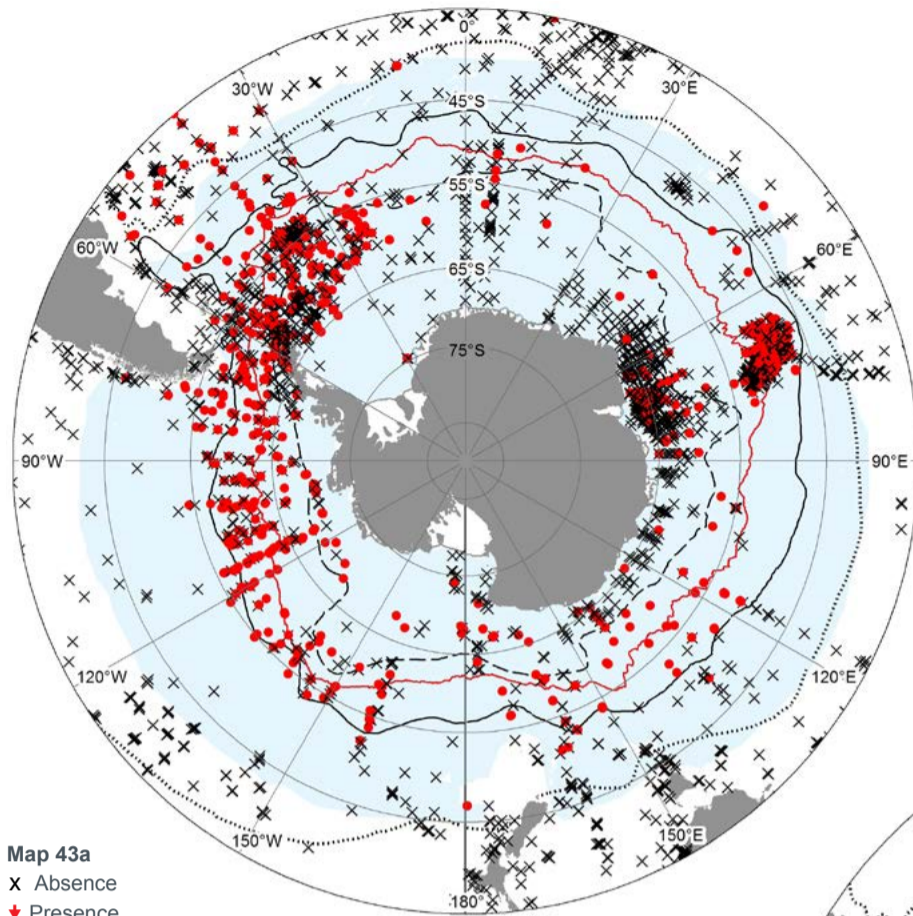
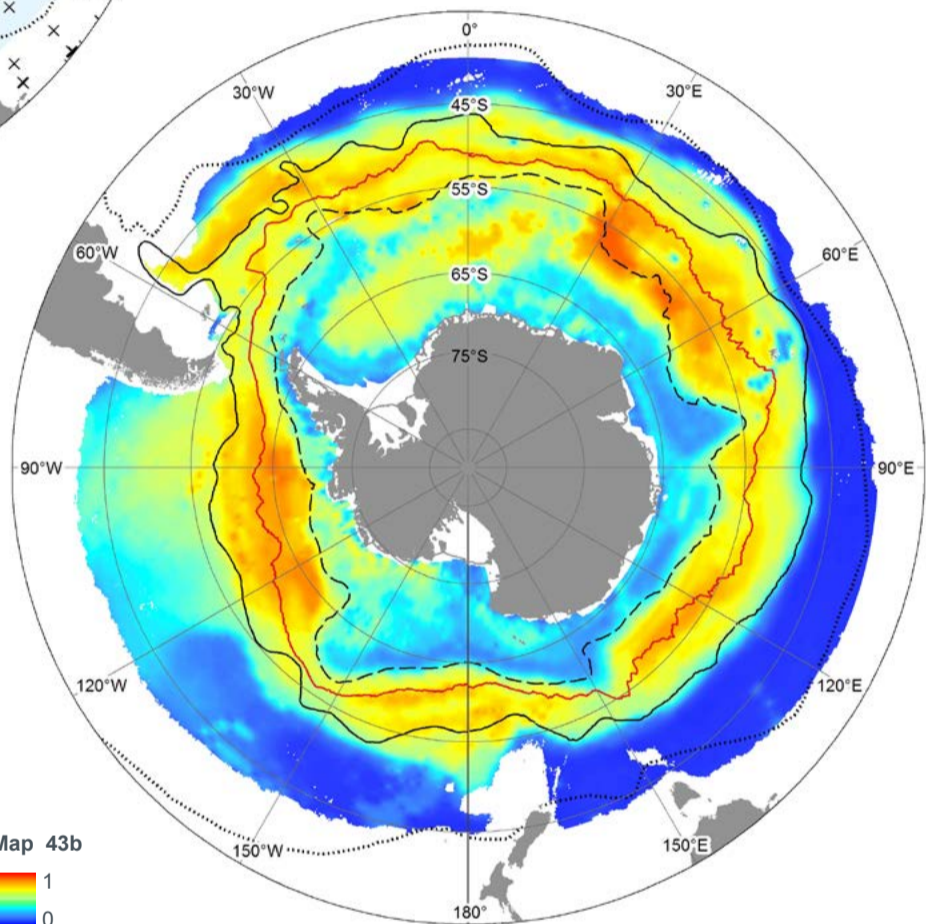


Figure 4 *Electrona antarctica* (Günther, 1878): diel distribution off east coast of Kerguelen Island based on non-closing IYGPT hauls. LMT = local mean time; FDepth (max) m = maximum fishing depth in meters.



Map 43a
 X Absence
 ● Presence



Map 43b
 1
 0

Fish Maps 43a and b *Gymnoscopelus braueri* (Lönnberg, 1905). Plots of (a) occurrence; (b) predicted distribution from BRT-analysis (total deviance explained = 23%; AUC = 0.77) using the following environmental variables (individual contribution in parentheses): summer temperature (°C) at 200 m (43.3%); summer salinity (PPS) at 200 m (37.5%); bathymetry (m) (19.1%).

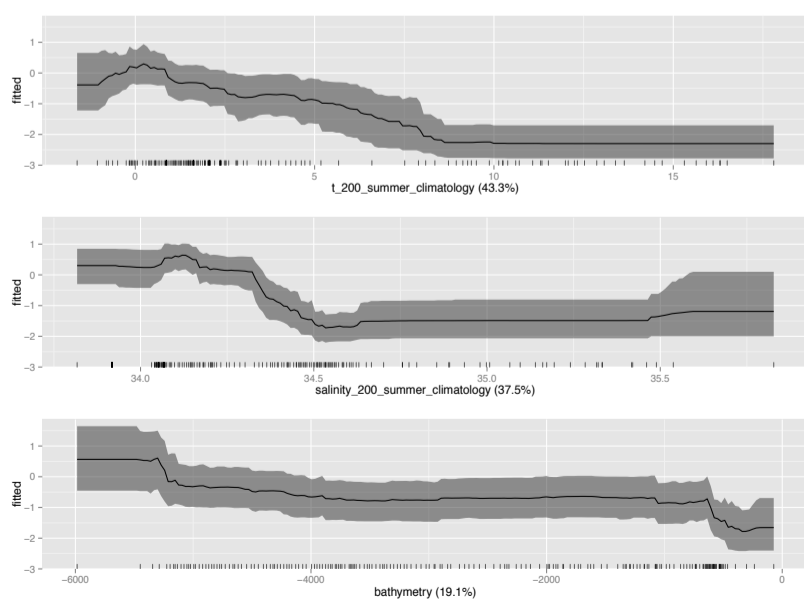


Figure 5 *Gymnoscopelus braueri* (Lönnberg, 1905): partial dependence plots of the most influential environmental variables. Mean estimate (black line); 95% confidence limit (grey band); rug plots inside base of plot indicate distribution of data in deciles of x-axis variable.

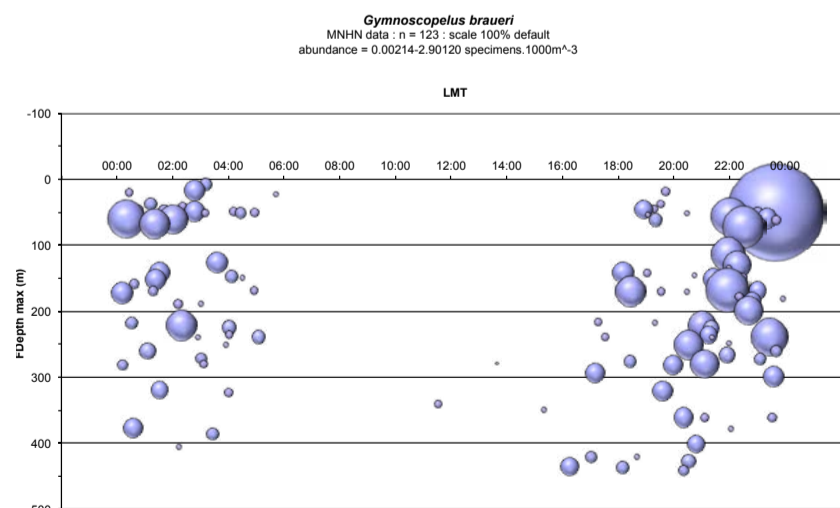
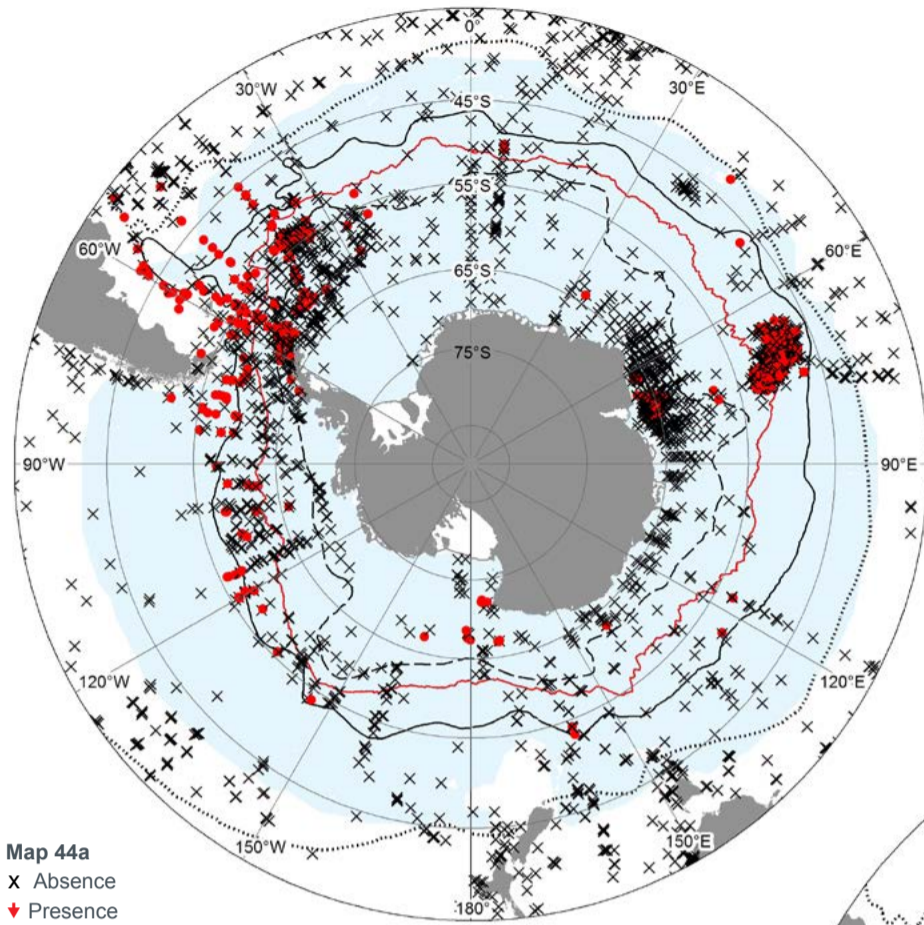
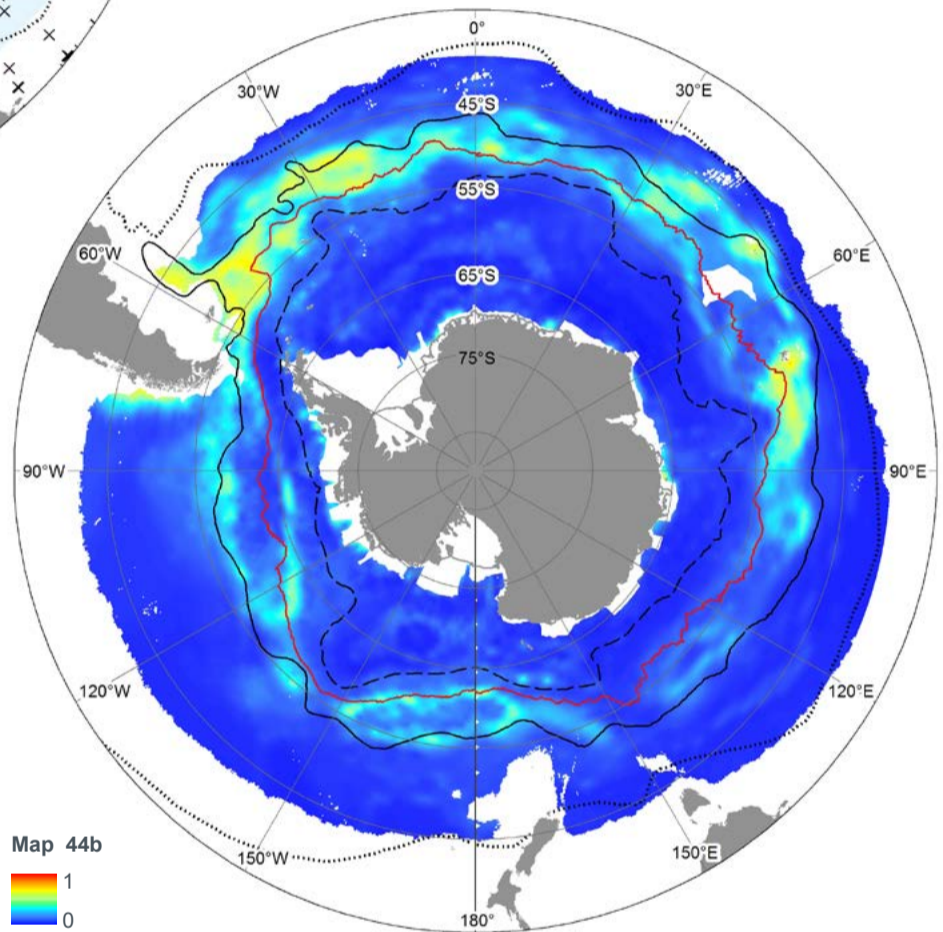


Figure 6 *Gymnoscopelus braueri* (Lönnberg, 1905): diel distribution off east coast of Kerguelen Island based on non-closing IYGPT hauls. LMT = local mean time; FDepth (max) m = maximum fishing depth in meters.



Map 44a
 x Absence
 ◆ Presence



Map 44b
 1
 0

Fish Maps 44a and b *Gymnoscopelus nicholsi* (Gilbert, 1911). Plots of (a) occurrence; (b) predicted distribution from BRT-analysis (total deviance explained = 29%; AUC = 0.8) using the following environmental variables (individual contribution in parentheses): summer salinity (PPS) at 200 m (42.1%); summer chlorophyll-a ($\text{mg}\cdot\text{m}^{-3}$) (30.8%); summer oxygen ($\text{ml}\cdot\text{l}^{-1}$) at 200 m (27.1%).

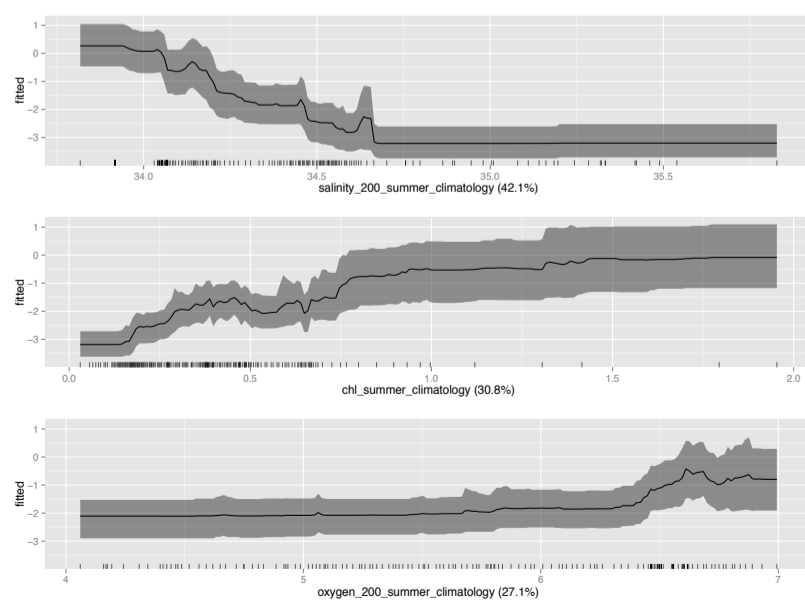


Figure 7 *Gymnoscopelus nicholsi* (Gilbert, 1911): partial dependence plots of the most influential environmental variables. Mean estimate (black line); 95% confidence limit (grey band); rug plots inside base of plot indicate distribution of data in deciles of x-axis variable

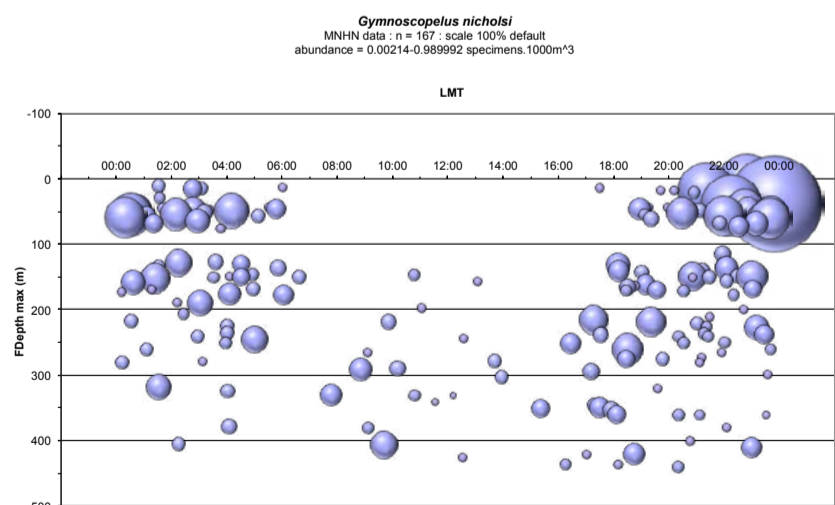
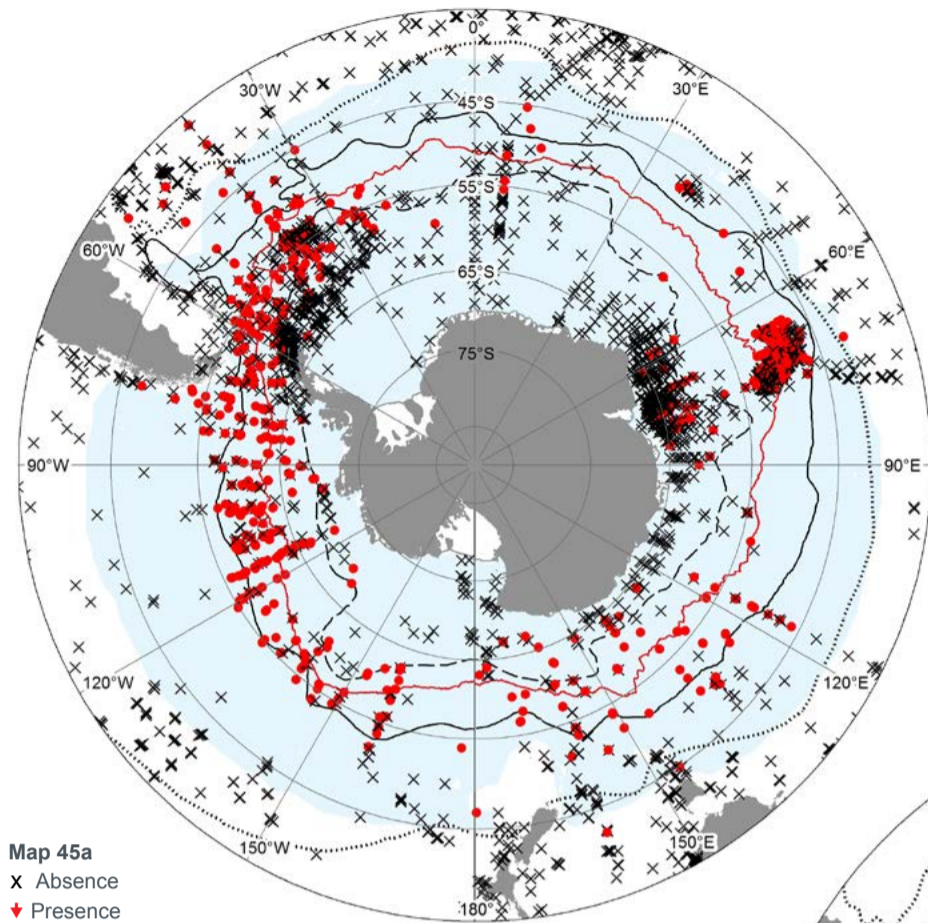
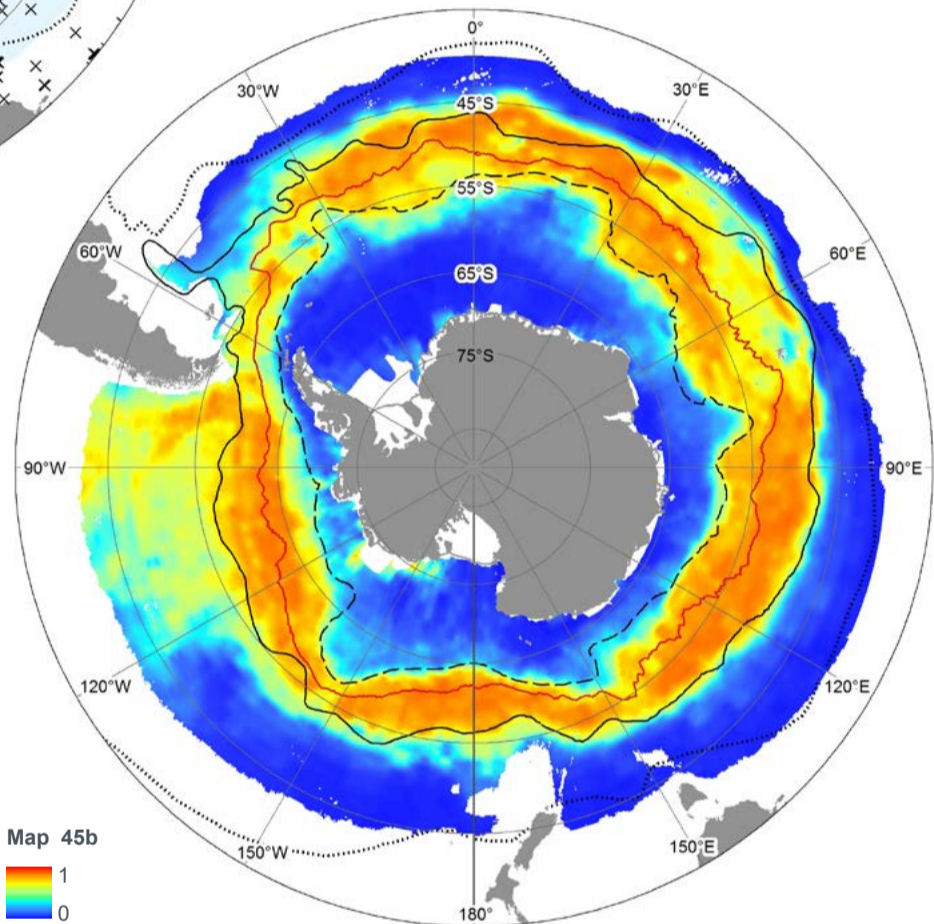


Figure 8 *Gymnoscopelus nicholsi* (Gilbert, 1911): diel distribution off east coast of Kerguelen Island based on non-closing IYGPT hauls. LMT = local mean time; FDepth (max) m = maximum fishing depth in meters.



Map 45a
 X Absence
 ◀ Presence



Map 45b
 1
 0

Fish Maps 45a and b *Krefftichthys anderssoni* (Lönnerberg, 1905). Plots of (a) occurrence; (b) predicted distribution from BRT-analysis (total deviance explained = 38%; AUC = 0.83) using the following environmental variables (individual contribution in parentheses): summer salinity (PPS) at 200 m (69.9%); summer mixed layer depth (m) (14.5%); summer salinity (PPS) at 50 m (9.5%); bathymetry (m) (6.2%).

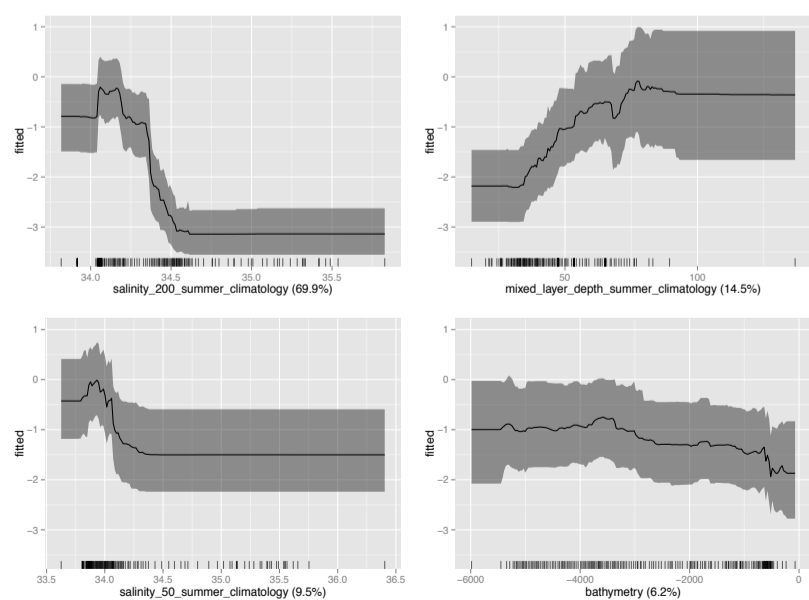


Figure 9 *Krefftichthys anderssoni* (Lönnerberg, 1905): partial dependence plots of the most influential environmental variables. Mean estimate (black line); 95% confidence limit (grey band); rug plots inside base of plot indicate distribution of data in deciles of x-axis variable.

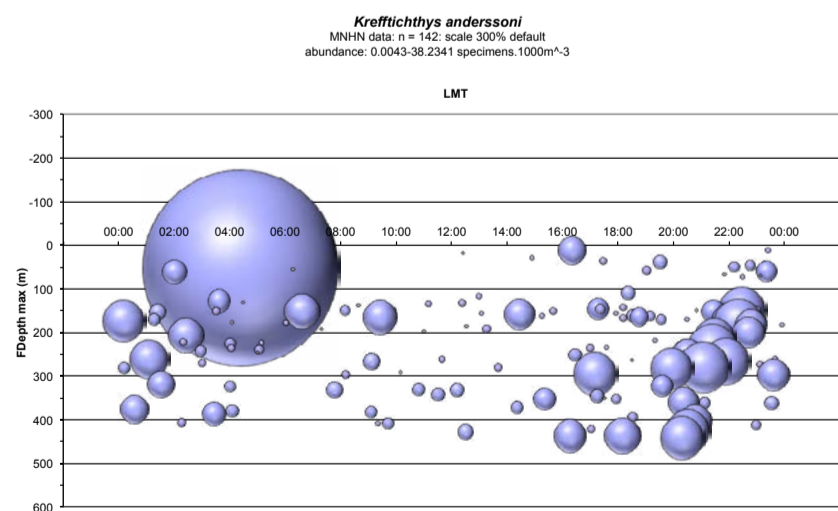
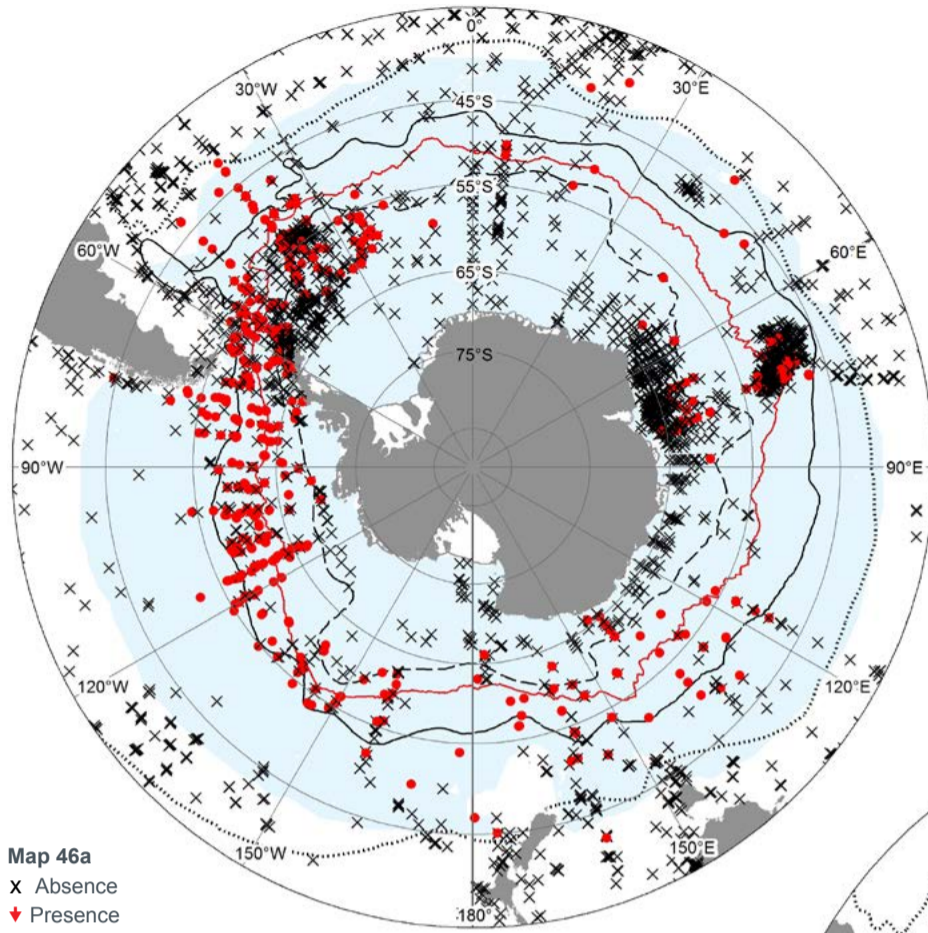
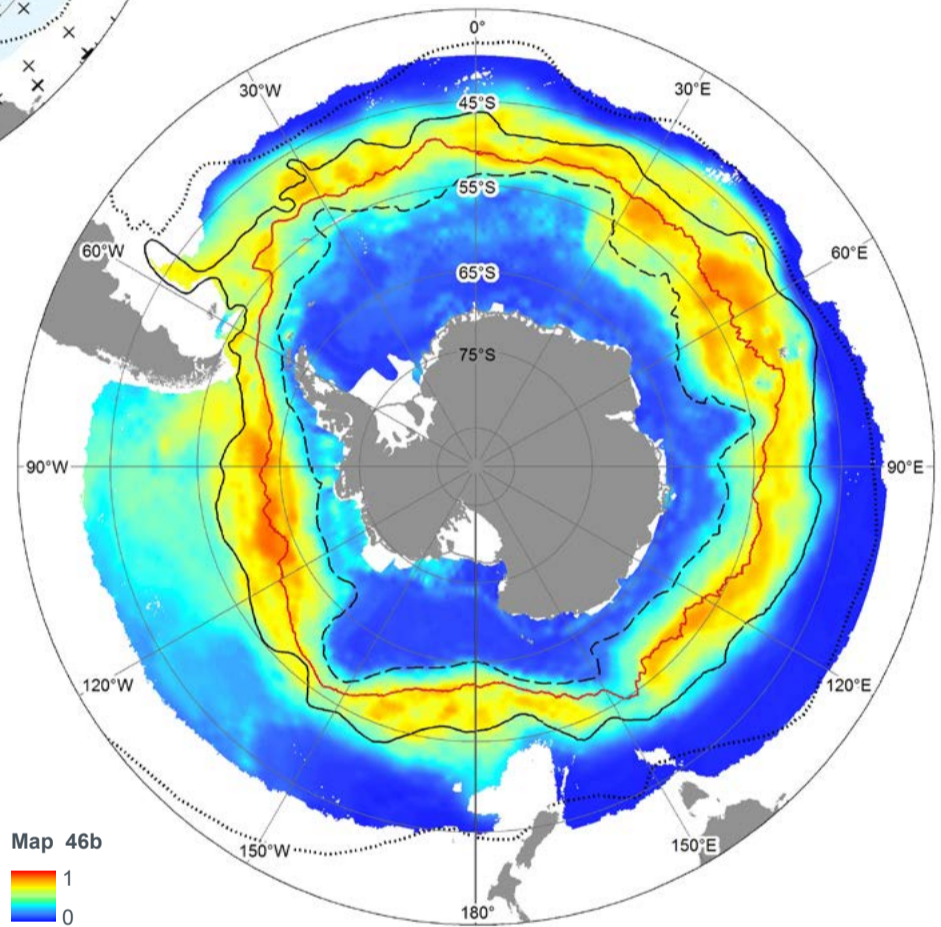


Figure 10 *Krefftichthys anderssoni* (Lönnerberg, 1905): diel distribution off east coast of Kerguelen Island based on non-closing IYGPT hauls. LMT = local mean time; FDepth (max) m = maximum fishing depth in meters.



Map 46a
 X Absence
 ▼ Presence



Map 46b
 1
 0

Fish Maps 46a and b *Protomyctophum bolini* (Fraser-Bruner, 1949). Plots of (a) occurrence; (b) predicted distribution from BRT-analysis (total deviance explained = 31%; AUC = 0.79) using the following environmental variables (individual contribution in parentheses): summer salinity (PPS) at 200 m (70.2%); summer mixed layer depth (m) (9.3%); summer oxygen (ml.l⁻¹) at 50 m (9%); bathymetry (m) (4.6%).

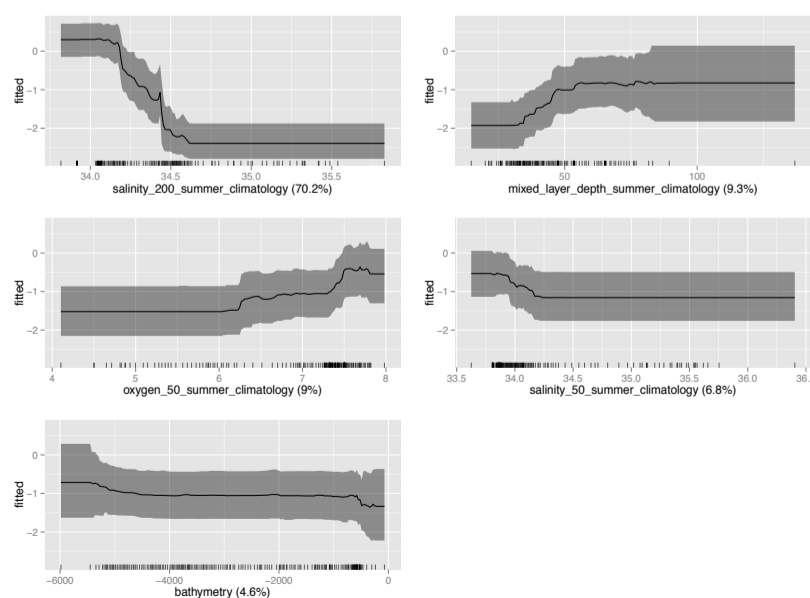


Figure 11 *Protomyctophum bolini* (Fraser-Bruner, 1949): partial dependence plots of the most influential environmental variables. Mean estimate (black line); 95% confidence limit (grey band); rug plots inside base of plot indicate distribution of data in deciles of x-axis variable.

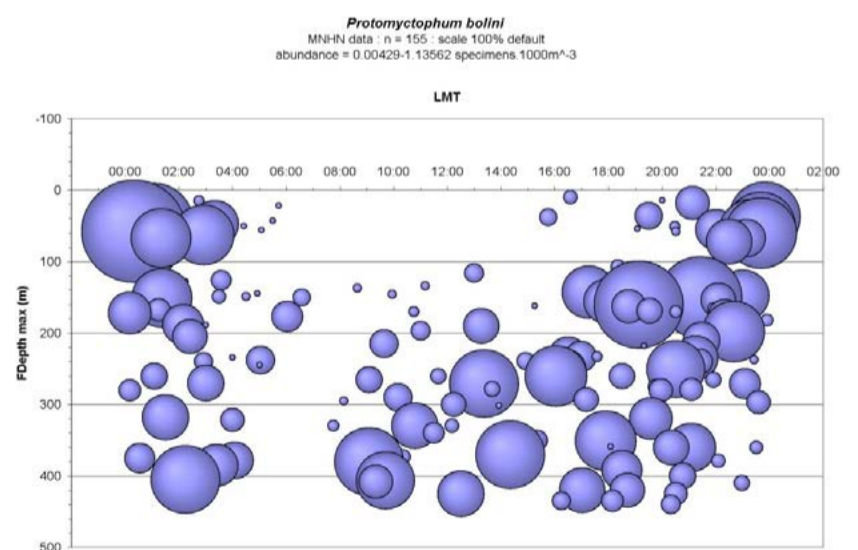
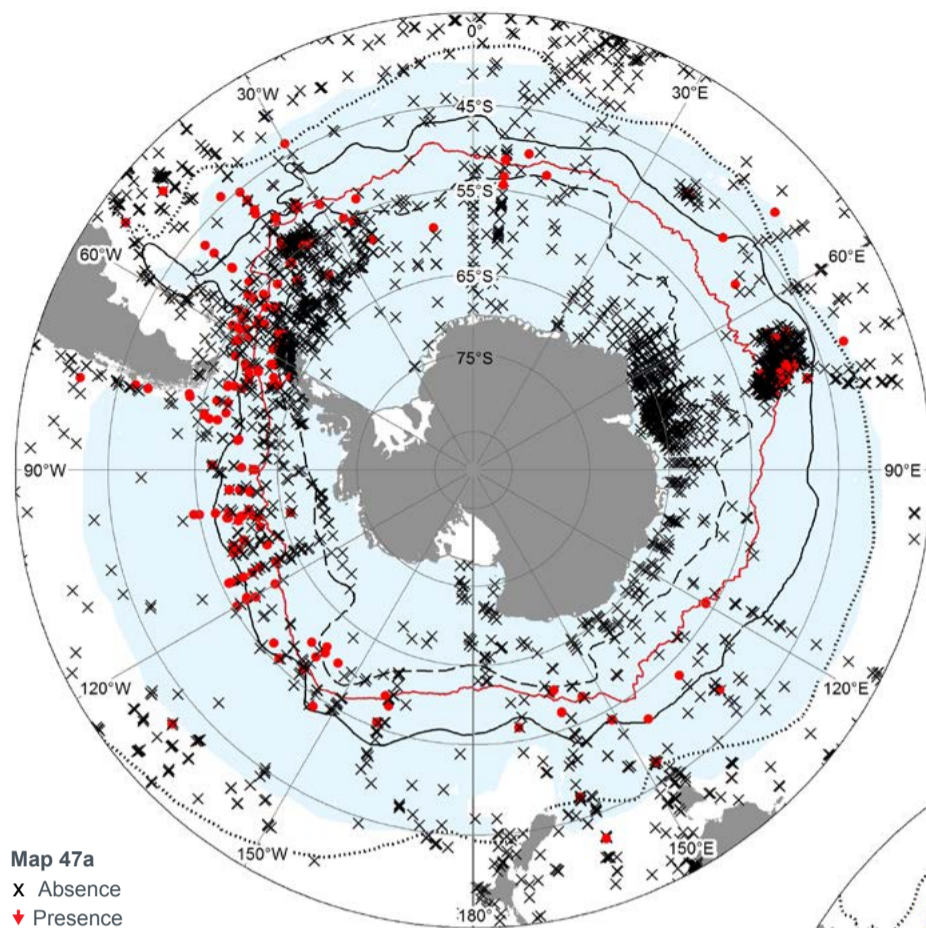
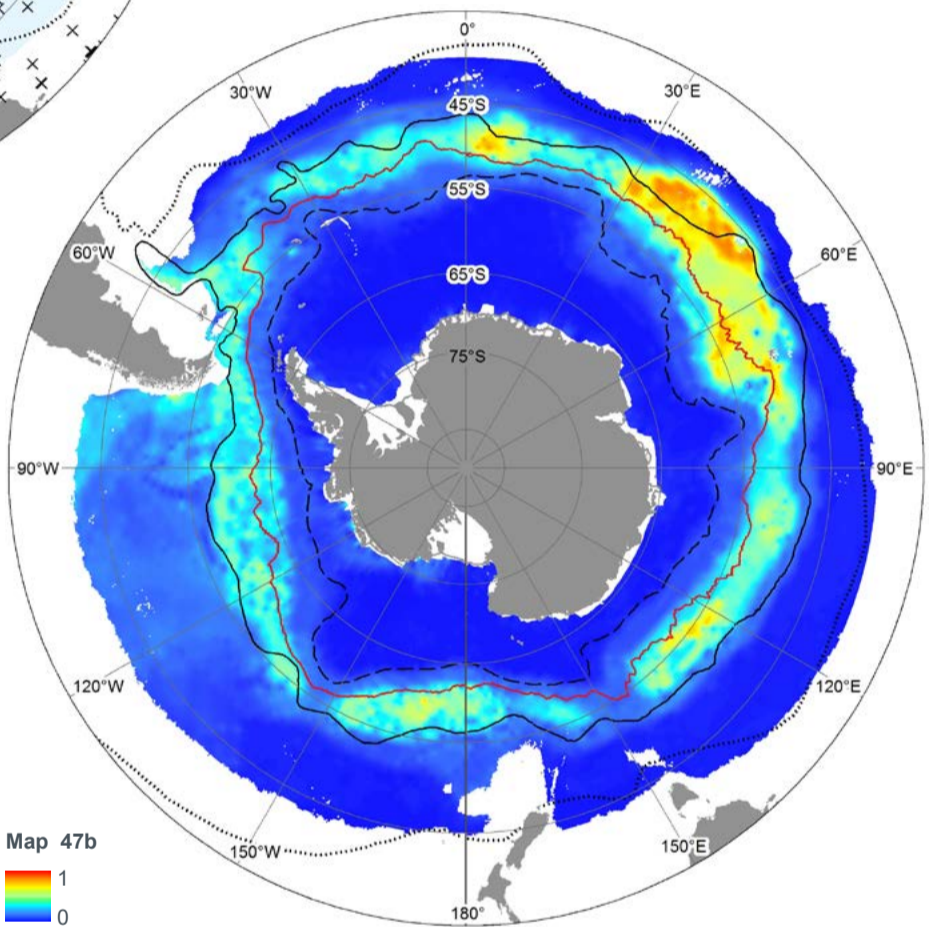


Figure 12 *Protomyctophum bolini* (Fraser-Bruner, 1949): diel distribution off east coast of Kerguelen Island based on non-closing IYGPT hauls. LMT = local mean time; FDepth (max) m = maximum fishing depth in meters.



Map 47a
 X Absence
 ♦ Presence



Map 47b
 1
 0

Fish Maps 47a and b *Protomyctophum tenisoni* (Norman, 1930). Plots of (a) occurrence; (b) predicted distribution from BRT-analysis (total deviance explained = 33%; AUC = 0.88) using the following environmental variables (individual contribution in parentheses): summer salinity (PPS) at 200 m (65.6%); summer oxygen (ml.l⁻¹) at 200 m (23%); bathymetry (m) (11.5%).

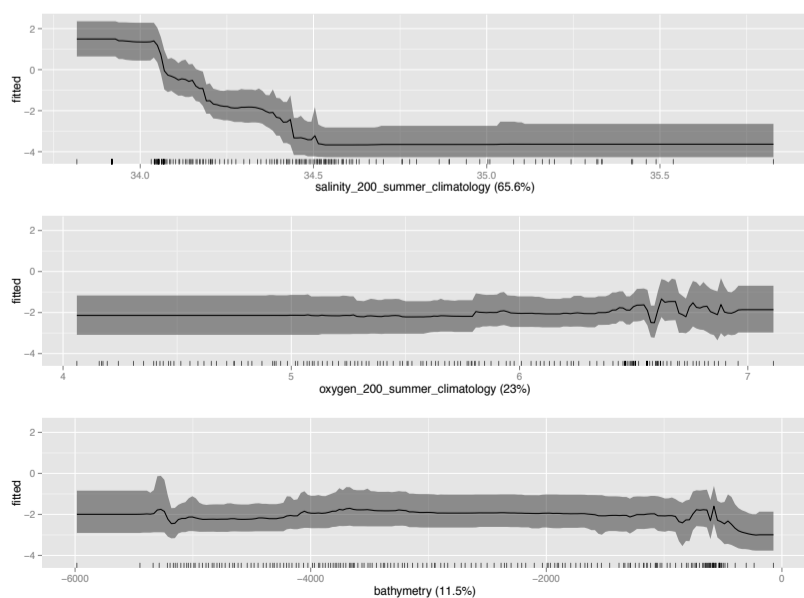


Figure 13 *Protomyctophum tenisoni* (Norman, 1930): partial dependence plots of the most influential environmental variables. Mean estimate (black line); 95% confidence limit (grey band); rug plots inside base of plot indicate distribution of data in deciles of x-axis variable.

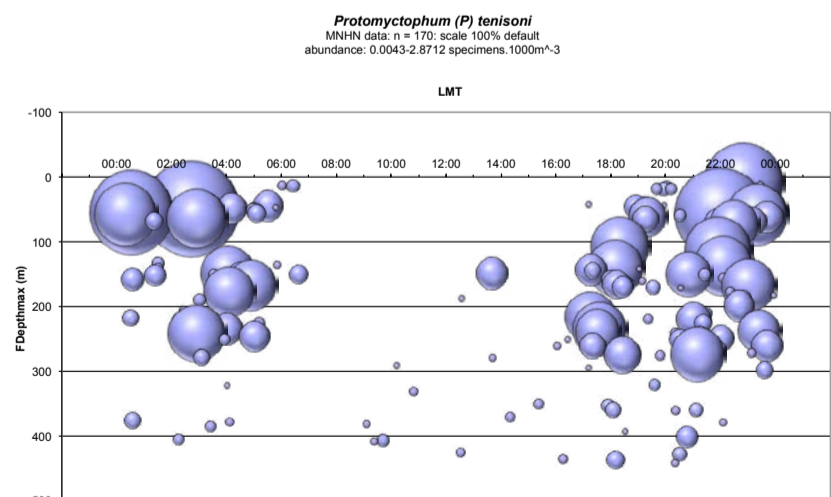
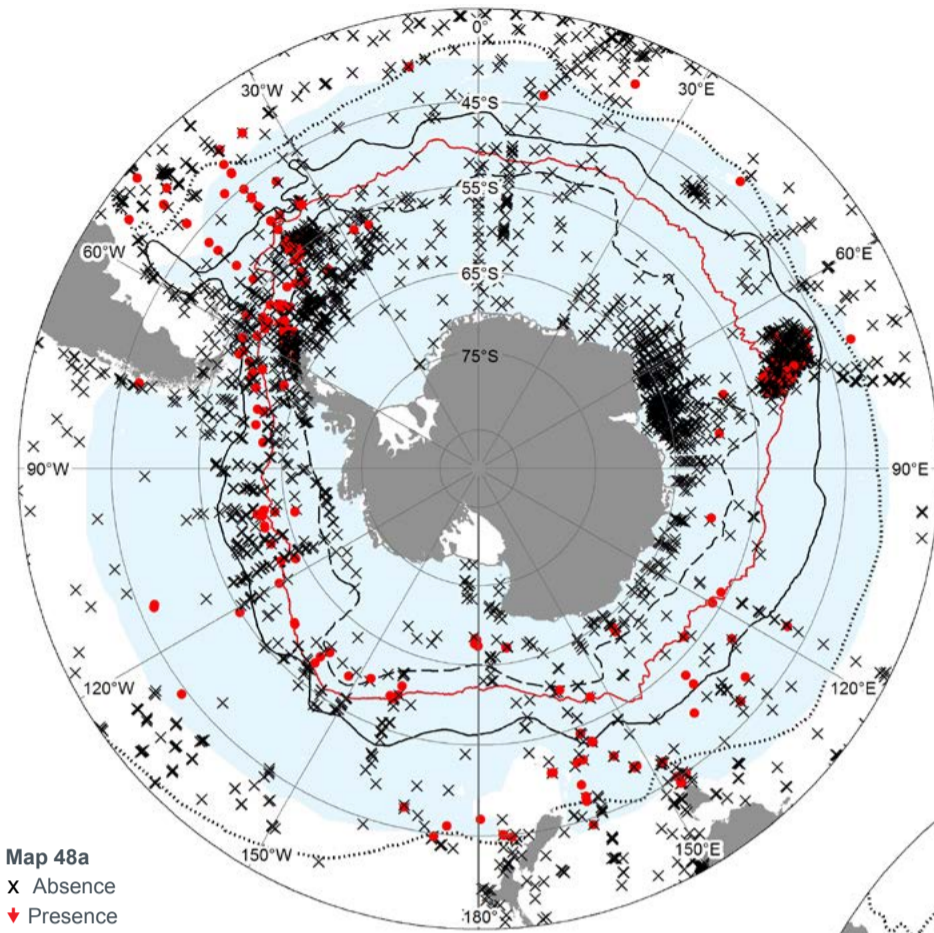
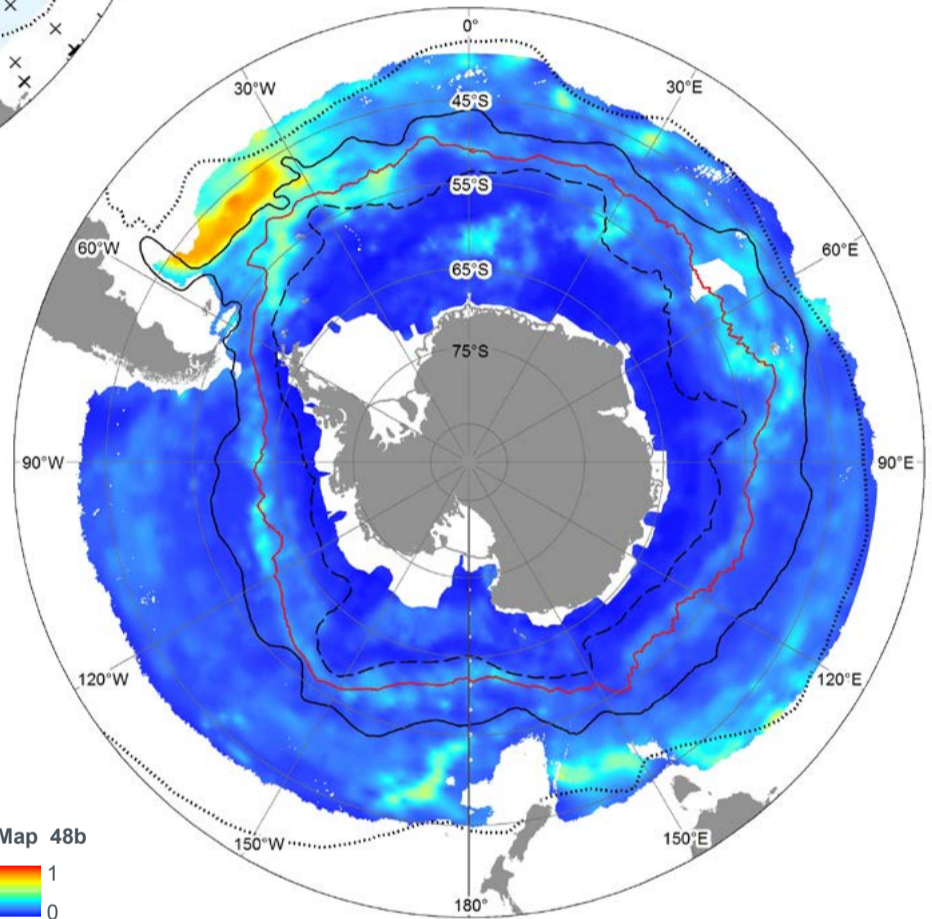


Figure 14 *Protomyctophum tenisoni* (Norman, 1930): diel distribution off east coast of Kerguelen Island based on non-closing IYGPT hauls. LMT = local mean time; FDepth (max) m = maximum fishing depth in meters.



Map 48a
 x Absence
 ★ Presence



Map 48b
 1
 0

Fish Maps 48a and b *Electrona carlsbergi* (Tåning, 1932). Plots of (a) occurrence; (b) predicted distribution from BRT-analysis (total deviance explained = 17%; AUC = 0.74) using the following environmental variables (individual contribution in parentheses): summer temperature ($^{\circ}\text{C}$) at 200 m (21%); chlorophyll-a ($\text{mg}\cdot\text{m}^{-3}$) (20.8%); bathymetry (m) (14.8%); oxygen ($\text{ml}\cdot\text{l}^{-1}$) at 200 m (19.8%); mixed layer depth (m) (12.8%); summer salinity (PPS) at 200 m (11.7%).

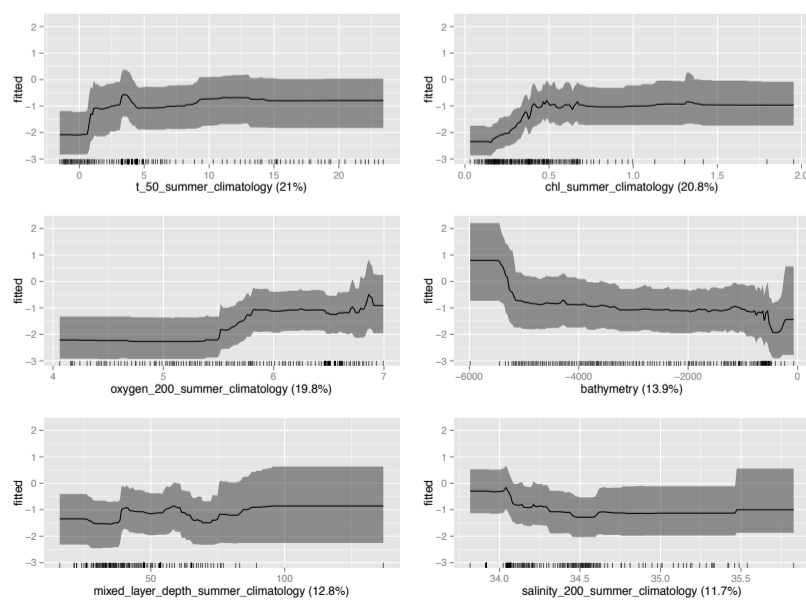


Figure 15 *Electrona carlsbergi* (Tåning, 1932): partial dependence plots of the most influential environmental variables. Mean estimate (black line); 95% confidence limit (grey band); rug plots inside base of plot indicate distribution of data in deciles of x-axis variable.

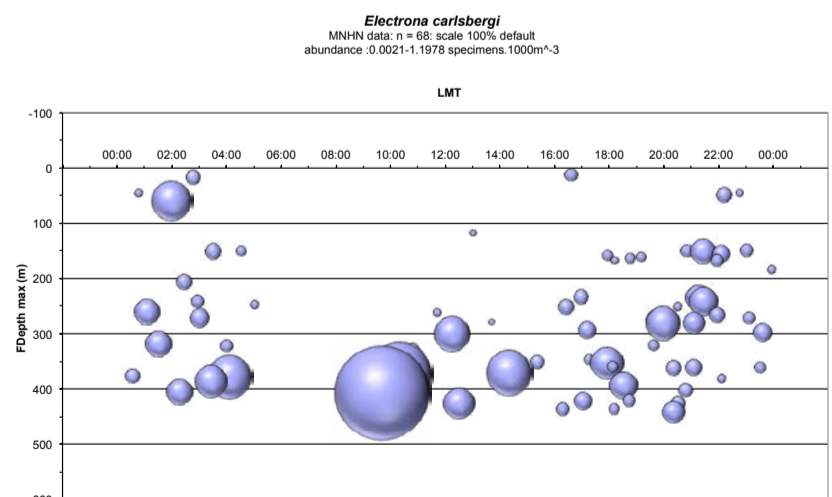
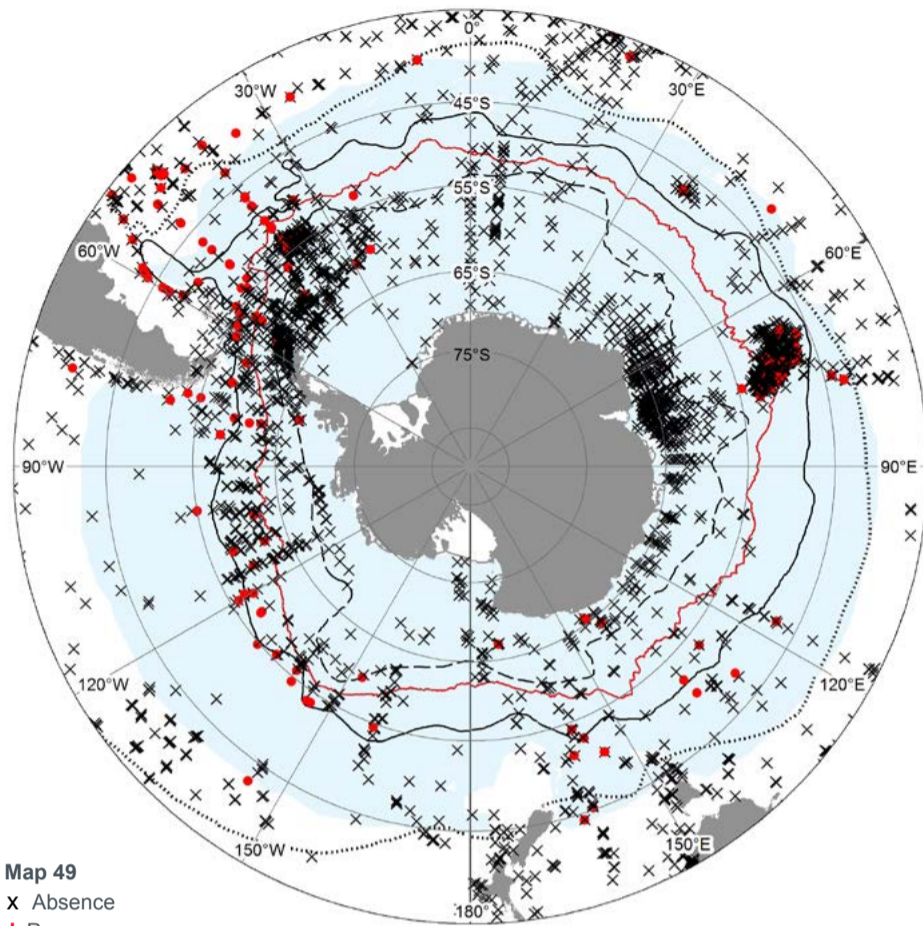


Figure 16 *Electrona carlsbergi* (Tåning, 1932): diel distribution off east coast of Kerguelen Island based on non-closing IYGPT hauls. LMT = local mean time; FDepth (max) m = maximum fishing depth in meters.



Map 49
X Absence
♦ Presence

Fish Map 49 Distribution of *Gymnoscopelus bolini* (Andriashev, 1962).

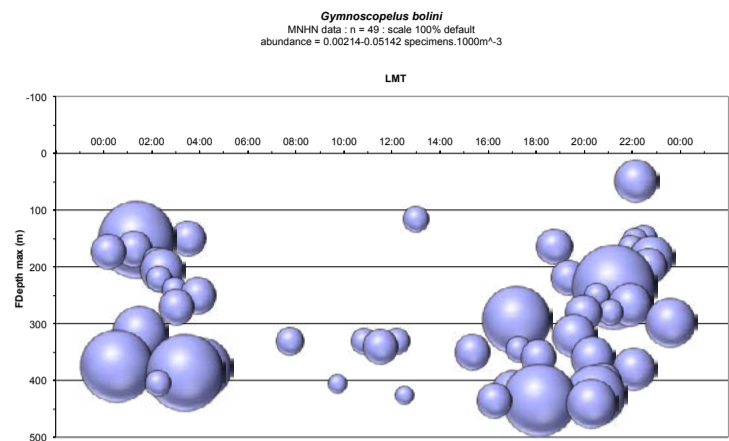
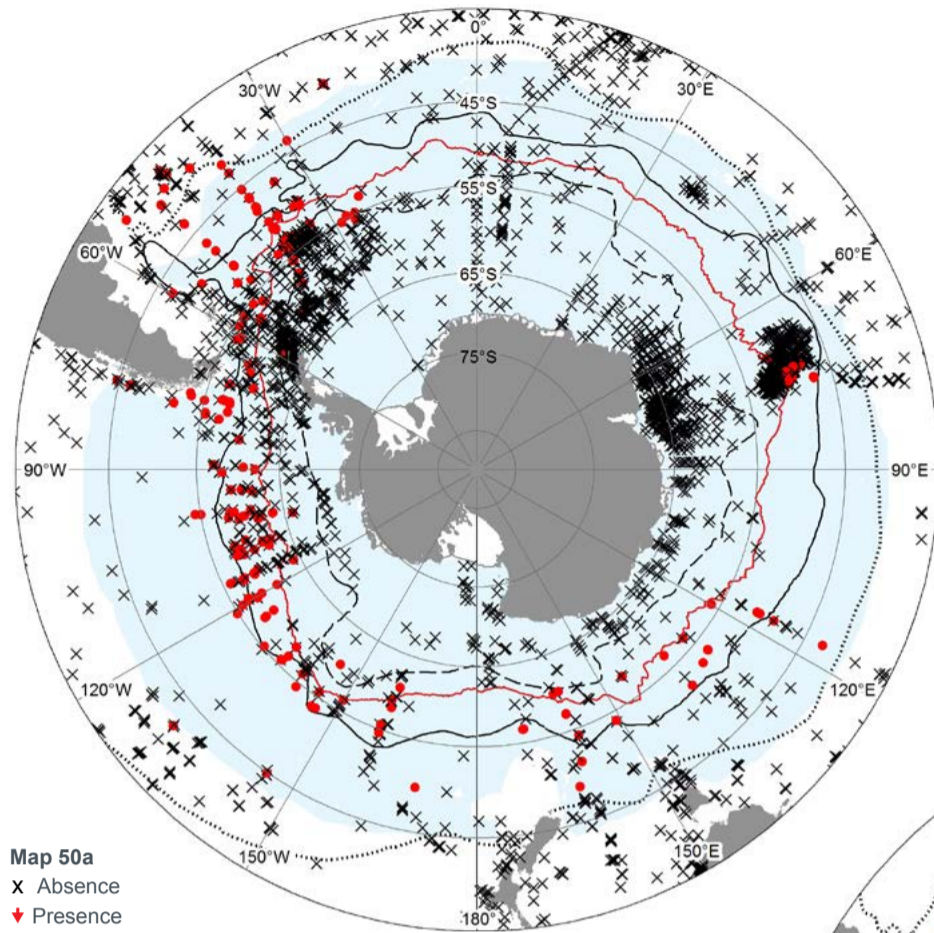


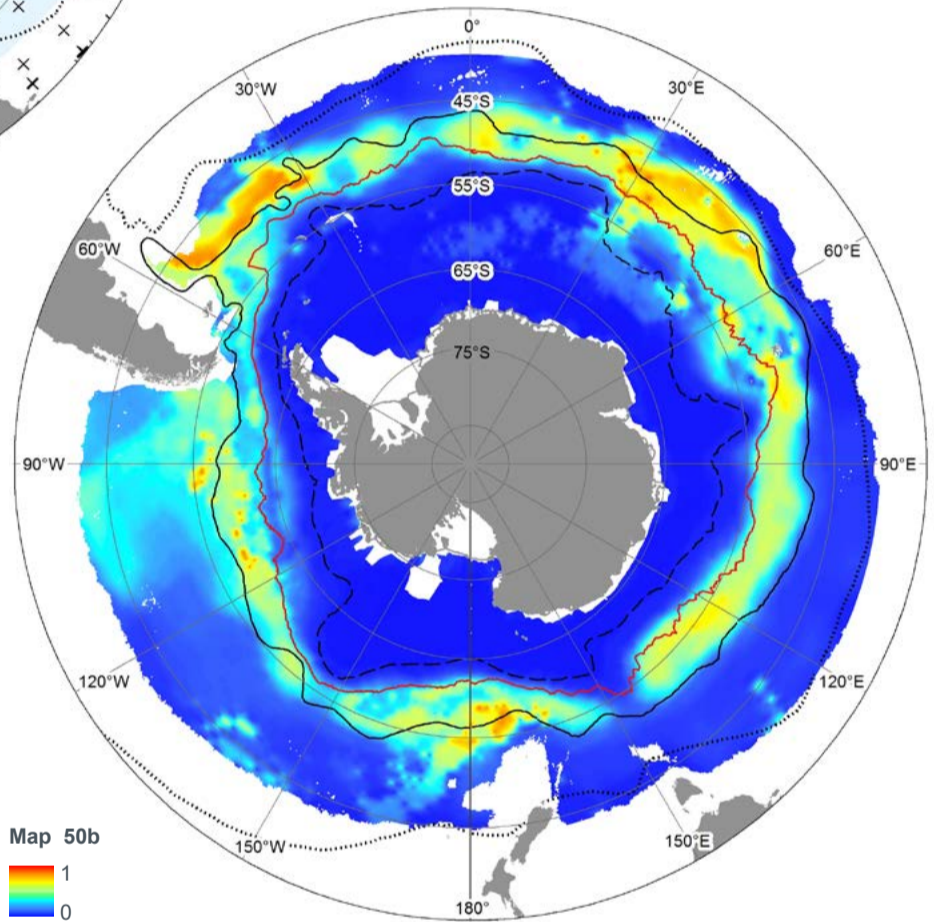
Figure 17 *Gymnoscopelus bolini* (Andriashev, 1962): diel distribution off east coast of Kerguelen Island based on non-closing IYGPT hauls. LMT = local mean time; FDepth (max) m = maximum fishing depth in meters.

Table 4 Species of Myctophidae recorded from south of STF and their associated distribution patterns (Hulley 1981).

SPECIES OCCASIONALLY RECORDED SOUTH OF STF	TRANSITIONAL ZONE SPECIES		SOUTHERN OCEAN SPECIES		
	Convergence Pattern	Bi-temperate Pattern	Sub-Antarctic Pattern	Broadly Antarctic Pattern	Antarctic Pattern
MESOPELAGIC SPECIES					
<i>Benthoosema suborbitale</i>	<i>Diaphus meadi</i>	<i>Lampadena speculigera</i>	<i>Diaphus hudsoni</i>	<i>Gymnoscopelus braueri</i>	<i>Electrona antarctica</i>
<i>Bolinichthys indicus</i>	<i>Diaphus ostentfeldi</i>	<i>Lampanyctus intricarius</i>	<i>Electrona carlsbergi</i>	<i>Gymnoscopelus nicholsi</i>	
<i>Bolinichthys supralateralis</i>	<i>Electrona paucirastra</i>	<i>Lampanyctus macdonaldi</i>	<i>Electrona subaspera</i>	<i>Krefflichthys anderssoni</i>	
<i>Ceratoscopelus warmingii</i>	<i>Gonichthys barnesi</i>	<i>Loweina interrupta</i>	<i>Gymnoscopelus bolini</i>	<i>Protomyctophum bolini</i>	
<i>Diaphus danae</i>	<i>Hintonia candens</i>		<i>Gymnoscopelus hintonoides</i>	<i>Protomyctophum tenisoni</i>	
<i>Diaphus effulgens</i>	<i>Hygophum hanseni</i>		<i>Gymnoscopelus microlampas</i>		
<i>Diogenichthys atlanticus</i>	<i>Lampadena notialis</i>		<i>Gymnoscopelus fraseri</i>		
<i>Electrona risso</i>	<i>Lampanyctus australis</i>		<i>Metelectrona ventralis</i>		
<i>Hygophum bruuni</i>	<i>Lampanyctus lepidolichnus</i>		<i>Protomyctophum andriashevi</i>		
<i>Hygophum hygomii</i>	<i>Lampichthys procerus</i>		<i>Protomyctophum choriodon</i>		
<i>Lampadena chavesi</i>	<i>Metelectrona herwigi</i>		<i>Protomyctophum gemmatum</i>		
<i>Lampadena notialis</i>	<i>Protomyctophum luciferum</i>		<i>Protomyctophum parallelum</i>		
<i>Lampanyctus festivus</i>	<i>Protomyctophum normani</i>		<i>Symbolophorus boops</i>		
<i>Lampanyctus iselinoides</i>	<i>Protomyctophum subparallelum</i>				
<i>Lampanyctus pusillus</i>					
<i>Lampanyctus tenuiformis</i>					
<i>Lepidophanes guentheri</i>					
<i>Lobianchia dofleini</i>					
<i>Myctophum phengodes</i>					
<i>Nannobranchium phyllisae</i>					
<i>Nannobranchium wisneri</i>					
<i>Notolichnus valdiviae</i>					
<i>Notoscopelus resplendens</i>					
<i>Scopelopsis multipunctatus</i>					
<i>Symbolophorus barnardi</i>					
BATHYPELAGIC SPECIES					
<i>Taaningichthys bathyphilus</i>			<i>Nannobranchium achirus</i>		<i>Gymnoscopelus opisthopterus</i>
PSEUDOCEANIC SPECIES					
<i>Lampanyctodes hectoris</i>					



Map 50a
 x Absence
 • Presence



Map 50b
 1
 0

Fish Maps 50a and b *Gymnoscopelus fraseri* (Fraser-Bruner, 1931). Plots of (a) occurrence; (b) predicted distribution from BRT-analysis (total deviance explained = 34%; AUC = 0.83) using the following environmental variables (individual contribution in parentheses): summer salinity (PPS) at 200 m (55.7%); summer oxygen (ml.l⁻¹) at 200 m (18.8%); bathymetry (m) (13.6%); summer temperature (°C) at 50 m (11.9%).

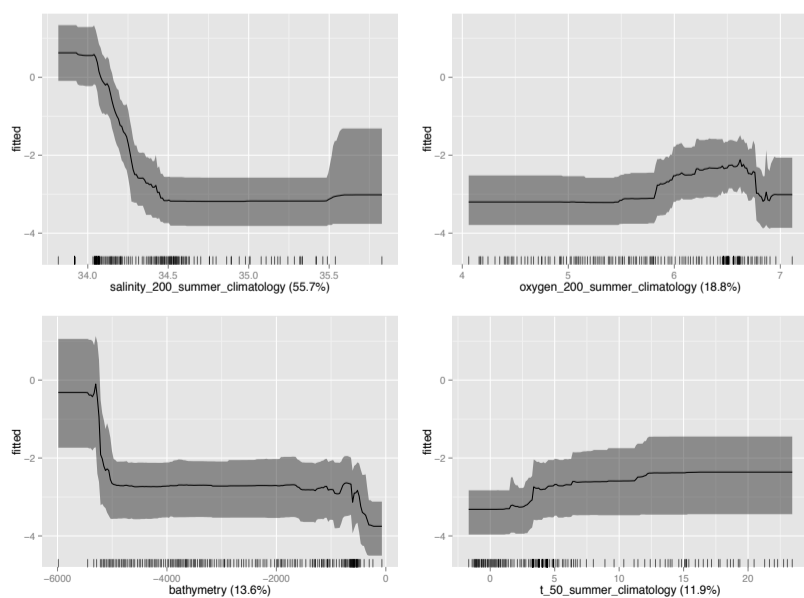


Figure 18 *Gymnoscopelus fraseri* (Fraser-Bruner, 1931): partial dependence plots of the most influential environmental variables. Mean estimate (black line); 95% confidence limit (grey band); rug plots inside base of plot indicate distribution of data in deciles of x-axis variable

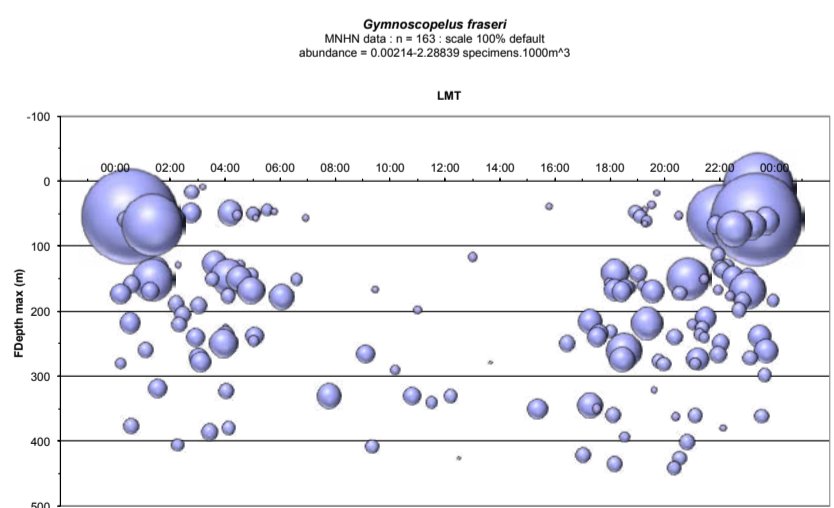
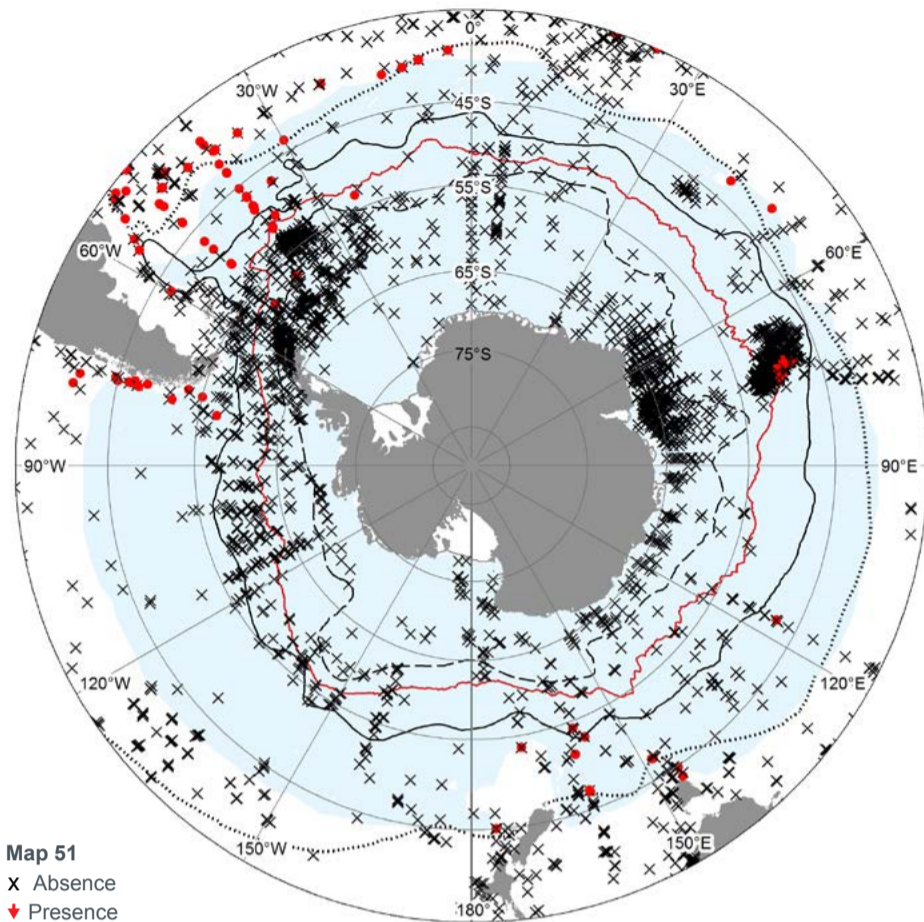


Figure 19 *Gymnoscopelus fraseri* (Fraser-Bruner, 1931): diel distribution off east coast of Kerguelen Island based on non-closing IYGPT hauls. LMT = local mean time; FDepth (max) m = maximum fishing depth in meters.



Map 51
 x Absence
 ♦ Presence

Fish Map 51 Distribution of *Gymnoscopelus piabilis* (Whitley, 1931).

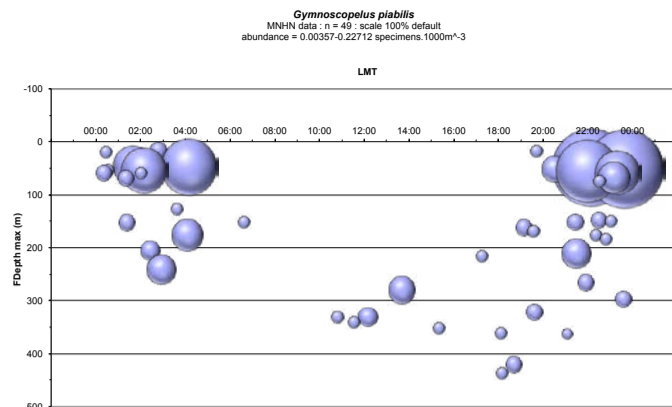


Figure 20 *Gymnoscopelus piabilis* (Whitley, 1931): diel distribution off east coast of Kerguelen Island based on non-closing IYGPT hauls. LMT = local mean time; FDepth (max) m = maximum fishing depth in meters.

zonal (annular) distribution patterns in myctophids (Hulley 1981, 1986a, McGinnis 1982, Hindell 1989, Piatkowski *et al.* 1994, Koubbi *et al.* 2010, Hulley & Duhamel 2011). Unlike the population structuring observed in Antarctic benthic fishes (Ashford *et al.* 2008), year-class analysis (at least in *Gymnoscopelus nicholsi*), and high levels of genetic diversity coupled with a lack of genetic differentiation (at least in *E. antarctica*), indicate large effective population sizes (Linkowski, 1985, Van de Putte *et al.* 2012). Smith *et al.* (2012) have suggested the existence of potentially cryptic species with high intra-specific divergence in *Gymnoscopelus bolini* on the basis of DNA barcode comparisons. Community structure appears to be governed by geographic locality, depth and water mass features at both meso- and submeso-scales (Deacon 1982, Hoddell *et al.* 2000, Pusch *et al.* 2004, Collins *et al.* 2008, 2012, Koubbi *et al.* 2011a).

Mesopelagic species (as far as is known) all undertake diel vertical migration to a greater-or-lesser extent (with the probable exception of *Krefflichthys anderssoni*). Different species and/or different size classes of individual species exhibit a degree of vertical segregation (Torres & Somero 1988, Lancraft *et al.* 1989, Piatkowski *et al.* 1994, Tsarin 1997, Duhamel 1998, Duhamel *et al.* 2000, Collins *et al.* 2012). There is some evidence for the non-migratory behaviour of the deeper living species, *Nannobranchium achirus* and *Gymnoscopelus opisthopterus* (Collins *et al.* 2008, 2012, Hulley & Duhamel 2011).

The energy uptake during nocturnal feeding by myctophids at shallower depths is stored as triacylglycerols and wax esters (Rowedder 1979, Naumov *et al.* 1981, Ascenio & Moreno 1984, Reinhardt & Van Vleet 1986, Kozlov & Tarverdieya 1989, Gerasimova 1991, Kozlov & Shust 1991, Podrazhanskaya & Tarverdieva 1991, Kozlov 1993a, 1993b, 1995, Pakhomov *et al.* 1996, Phleger *et al.* 1997, 1999, Geiger *et al.* 2000, Tierney *et al.* 2002, Pusch *et al.* 2004, Van de Putte *et al.* 2006, Stowasser *et al.* 2009, Schreeve *et al.* 2009, Connan *et al.* 2010, Lenky *et al.* 2012). The energy stored is subsequently partitioned within the water-column by predatory fishes (Bulman *et al.* 2002, Collins *et al.* 2007), squids (Rodhouse *et al.* 1992, Kear 1992, Rodhouse & White 1995, Phillips *et al.* 2001, Bradshaw *et al.* 2003, Phillips *et al.* 2003a, 2003b, 2003c), seabirds (Adams & Brown 1989, Ainley *et al.* 1992, Cherel *et al.* 1993, 1996, Guinet *et al.* 1996, Bost *et al.* 1997, 2002, Casaux *et al.* 1998, 2008, Connan *et al.* 2005, 2007a, 2007b) and mammals (Slip 1995, Kirkman *et al.* 2000, Lea *et al.* 2002, 2006, 2008, Casaux *et al.* 2006, Bailleul *et al.* 2007, Blix & Nordøy 2008) via the dynamic Antarctic trophic-web structure (Cornejo-Donoso & Antezana 2008). Myctophid trophic levels have been estimated to range from 3.8–4.2 (Cherel *et al.* 2008, 2010, 2011). Robison (2003) postulated that predator avoidance might be the principal driver for diel vertical migration, rather than a behavioural response directed towards gaining a metabolic bonus. However, Collins *et al.* (2008) suggest that subtle changes in temperature regimes and prey distributions could also be significant.

The point-data distributions for each species are based on the records of mesopelagic fishes received from a number of international institutions and contributors (Table 2, Map 41). Where possible, predicted distributions for

each species were produced by Boosted Regression Tree (BRT) analyses (Elith *et al.* 2008, Irisson *et al.* 2013), using a subset of these data, namely records from those stations that were fished with mid-water nets (BONGO, IKMT, RMT, Engels-MWT, MT-1000, MT-1600, PT-1088 and IYGPT) (Vigetta *et al.* in preparation). The predicted distributions are given for the species, together with the partial dependence plots of the most influential variables driving the predicted distributions. Plots of species diel distributions based on non-closing IYGPT sampling off the east coast of Kerguelen (Bost *et al.* 2002) are also included. The species are grouped by distribution pattern type.

Antarctic Pattern

Electrona antarctica (Günther, 1878)

Point data indicate that *Electrona antarctica* has a circumpolar distribution mainly between the Antarctic Slope Front (ASF) (as delimited by the continental 500 m isobath) and the APF, although small specimens can be taken in the Sub-Antarctic Zone north of the APF (Map 42a). Records exist for isolated specimens as far north as 33.50°S in association with cold water intrusions to the north of the STF. The southernmost record for the species is at 74.67°S. The paucity of positive records in the Weddell, Lazarev, Ross, Amundsen and Bellingshausen Seas may be a sampling artifact (Map 35a). Except for larval and small juvenile specimens which can occur above the peri-insular shelves (Koubbi *et al.* 2001, 2003, 2009), *E. antarctica* is generally limited to seawards of the peri-insular shelf-breaks (200 m isobath). An upper limiting temperature of 3°C has been proposed (Andriashev 1962, Hulley 1981). The species appears to avoid zones with sea-ice cover, where temperatures in the upper 100 m of the water column are less than -1°C. The results of BRT-analyses are in line with the above findings, with prediction values greater than 0.60 being estimated for regions south of the APF; prediction values are lower north of the APF, as well as in the north-western Weddell Sea (Map 42b). Summer temperature at 200 m is the most important parameter governing the probability distribution of *E. antarctica*. Partial dependence plots (Fig. 3) indicate that the species prefers water temperatures less than 2.5°C, and increases in waters where summer oxygen at 50 m depth is greater than 7 ml.l⁻¹ and where bottom depths are greater than 300 m (with an optimum value at 750 m). These parameters suggest that the distribution (at least at night) is associated with AASW. However on the basis of phylogeny and abundance distributions, Hulley & Duhamel (2011: figs 7, 12–13) have postulated a correlation with UCDW. Vertical distribution suggests that the species is present in the upper 50 m of the water column at night and below 250 m during the day; it has also been taken in nets fished to 2000 m in the region of the STF (Hulley 1981). Diel data off Kerguelen (Fig. 4) reveal a patchy distribution and that the species is present in the upper 50 m between 18:00h – 06:00h, and occurs deeper than 300 m between 08:00h–17:00h.

Broadly Antarctic Pattern

Gymnoscopelus braueri (Lönnerberg, 1905)

Point data indicate that *Gymnoscopelus braueri* has generally been recorded between about 75°S and 34°–35°S, and is distributed in the Polar Frontal, Sub-Antarctic and Antarctic Zones (Map 43a). Probability distribution analyses indicate that the species has a circumpolar distribution between the SACCF and the SAF (Map 43b). Habitat suitability is lower over peri-insular and continental shelves, since *Gymnoscopelus braueri* is essentially an oceanic mesopelagic species. Partial dependence plots (Fig. 5) suggest that the potential habitat increases when the summer temperature at 200 m is lower than 7°C, with an optimal range between 0°C and 1°C (*vide* 5–6°C suggested by Hulley 1981) and where the summer salinity at 200 m is lower than 34.3 PPS - thereby reflecting a distribution correlated with both AASW and AAIW. The species is present in the upper 50 m of the water column at night; and has been taken in depths of 2700 m (Hulley 1981). Diel data off Kerguelen (Fig. 6) reveal a patchy distribution and that the species is present in the upper 10 m between 19:00h–04:00h; it was poorly represented during the day (06:00h–17:00h) below 300 m.

Gymnoscopelus nicholsi (Gilbert, 1911)

Point data indicate that *Gymnoscopelus nicholsi* has been recorded between about 75°S and 38°S, with isolated specimens north to about 36°S. It is distributed mainly north of the SACCF to the STF, but may be found south of the SACCF where this front approaches the continental mass (Map 44a). Larvae and juveniles are oceanic mesopelagic, but adults are typically benthopelagic particularly over the western Antarctic Peninsula slope, around the South Orkneys and South Georgia, the southern Argentinian slope, the Crozet slope and over the Kerguelen Plateau. Probability distribution analyses (which are based on mid-water hauls) (Map 44b) indicate that for pelagic specimens at least, the species occurs between the APF and the STF, especially in those regions with shoaling bottom features (Hulley 1990, Duhamel *et al.* 2005). The habitat is less suitable where such features are less pronounced or widely spread (i.e. between 170°E–100°E). Partial dependence plots (Fig. 7) indicate that the following environmental parameters are important in defining the probability distribution: summer oxygen at 200 m; summer salinity values at 200 m; and summer chlorophyll-a values. The ranges in salinity (<34.1 PPS) and temperature (3°–9°C at 200 m) (Hulley 1981) suggest a pelagic association with AAIW and SAMW. Diel data off Kerguelen (Fig. 8) reveal a patchy distribution, with specimens occurring in the upper 20 m at night (19:00h–06:00h) and generally below about 200 m during the day (07:00h–17:00h).

Krefflichthys anderssoni (Lönnerberg, 1905)

Point data indicate that *Krefflichthys anderssoni* has been recorded between about 70°S and 34°–38°S (Map 45a). It has a circumpolar distribution, occurring mainly in a 20° latitude belt centered on the APF, between the SACCF and SAF. It appears to be absent between about 20°E and 40°E south of about 52°S. Probability distribution analyses (Map 45b) indicate that the species is linked to the APF (Hulley 1981, Koubbi *et al.* 1991, 1992, 1993, 2003). It may be distributed between the STF and the SACCF (Hulley 1981, Duhamel *et al.* 2005) and extends further to the north between 80°W–120°W, off the east coast of South America. It appears to be less common on peri-insular shelves. Although Hulley (1981) and Andriashev (1962) suggested limiting temperatures between 2.6°–5.6°C, more recent and more comprehensive data imply a 0°C limiting temperature. Partial dependence plots (Fig. 9) indicate that the potential habitat of *Krefflichthys anderssoni* is better in water with a summer salinity at 200 m between 33.75–34.3 PPS; a mixed layer depth of less than 30 m; a summer salinity value at 50 m depth between 33.75–34.0 PPS; and bottom depths greater than 750 m. The preferred ranges of temperature and salinity, together with the latitudinal and depth distribution (Hulley 1981: fig. 8) indicate an association with AAIW, as evidenced by its salinity minimum core at 33.75 psu (Tomczak & Liefink 2005). While Becker (1967) has taken the species at depths of 600 m, McGinnis (1974) has recorded the species only to 100 m. Diel data off Kerguelen (Fig. 10) reveal a very patchy distribution with the species occurring in the upper 200 m throughout the 24 h cycle, and with little evidence of extensive vertical migration.

Protomyctophum bolini (Fraser-Bruner, 1949)

Point data indicate that *Protomyctophum bolini* has been recorded between about 70°S and 48°S, with isolated captures north to 42°S (Hulley 1981). It has an oceanic, circumpolar distribution mainly as a belt on both sides of the APF, between the SACCF and SAF (Map 46a). It is generally absent inshore of the shelf breaks and tends to avoid ridge regions where there is a shoaling bottom. There are few records between 10°W–30°W and 0°E–60°E, and no records between 88°E and 117°E; this may be partly due to a sampling artifact. Probability distribution analyses (Map 46b) indicate that the species occurs as an annular band between the SACCF and STF, encompassing the PFZ and parts of the AFZ and SFZ. The BRT-analyses also suggest that it may be less common in the Drake Passage and to the south of the SACCF. Partial dependence plots (Fig. 11) show that the species prefers water with summer salinity at 200 m less than 34.5 PPS; with a mixed layer depth greater than 10 m, and with a 20 m optimum; with a summer oxygen value at 50 m between 7.5–8 ml.l⁻¹; with a summer salinity value at 50 m less than 34 PPS; and with bottom depths greater than 750 m. The preferred temperature (between 1°–7°C) and salinity ranges are indicative of a relationship with AAIW (Hulley 1981, Duhamel *et al.* 2005). Vertical distribution data suggest the spe-

cies occurs between 608–728 m (day) and 364–426 m (night) (Hulley 1990). Diel data off Kerguelen (Fig. 12) reveal a patchy distribution with the species occurring mainly in the upper 50 m at night (19:00h–04:00h), and generally below 140–200 m during the day.

Protomyctophum tenisoni (Norman, 1930)

Point data indicate that *Protomyctophum tenisoni* has been recorded between about 66°S and 38°S–40°S. It has a circumpolar distribution as a band between the APF and the SAF, with fewer records to the north of the SAF, and to the south of the APF (Map 47a). Its apparent absence between 20°E–50°E and from 80°E–110°E may be a sampling artifact. Probability distribution analyses (Map 47b) indicate that the species occurs mainly north of the APF, particularly between 30°E–80°E. It is less common in the western sector of the Southern Ocean. The summer salinity value at 200 m depth (less than 34.4 PPS) is the best explanatory variable for the potential habitat of the species (Fig. 13). Additional environmental variables defining the habitat appear to be higher summer oxygen values at 200 m and bottom depths greater than 750 m. The salinity range preference and the temperature range preference (<5°C: Hulley (1981) indicate that the species distribution could be linked to AAIW. It tends to avoid regions inshore of the shelf break. The species has been taken in the upper 100 m at night (Norman 1930, 1937, Andriashev 1962, McGinnis 1982). Diel data off Kerguelen (Fig. 14) reveal a patchy distribution, with specimens occurring in the upper 50 m at night (18:00h–06:00h). The species is rarely caught during the day and confined to depth horizons below 150–300 m.

Sub-Antarctic Pattern

Electrona carlsbergi (Tåning, 1932)

Point data indicate that *Electrona carlsbergi* has been recorded between about 68°S and 38°S, with isolated captures to 34°–36°S. It occurs mainly alongside the APF (Map 48a). While probability distribution analyses (Map 48b) demonstrate a basic Sub-Antarctic Zone distribution, the pattern may be more complex. It appears as a double-banded pattern, centered along the both the APF and the SAF, with an important area as a potential habitat to the north of South Georgia (Anonymous 2000). It is less common in other parts of Southern Ocean and very rare south of the APF (Hulley 1981). The patchy spatial distribution of *E. carlsbergi* suggests that this species may be extremely gregarious and that its distribution may be linked to the productive regions of the frontal systems themselves. Partial dependence plots (Fig. 15) indicate that the potential habitat of *E. carlsbergi* increases in waters where the summer temperature at 50 m is higher than 2°C (optimal values between 2°–5°C); where the chlorophyll-a value is higher than 0.3 mg.m⁻³, where summer oxygen at 200 m is higher than 5.5 ml.l⁻¹, where bottom depths are deeper than 750 m; where the mixed layer depth is greater than 30 m (optimal values between 30–60 m); and where the summer salinity at 200 m is lower than 34.1 PPS. The habitat seems to be linked to both SAMW and AAIW and to temperate water ecoregions. Krefft (1974) suggested an AAIW association. The species can form dense shoals in the upper 100–250 m and may migrate into the upper 80 m at night (Zasel'skii *et al.* 1985). Diel data off Kerguelen (Fig. 16) reveal an extremely patchy distribution, with some specimens occurring in the upper 10 m at night. During the day, the species generally occurs below about 300 m.

Gymnoscopelus bolini (Andriashev, 1962)

Point data indicate that *Gymnoscopelus bolini* has been recorded between about 67°S and 34°S. It has a circumpolar distribution linked to AAIW (Krefft 1974) and occurs mainly between the STF and the APF, although there are records to the south and north of this region (Map 49). Its apparent absence between 10°W–60°E may be a sampling artifact. Recent data suggest somewhat higher limiting temperatures than the 1.0°–1.5°C range proposed by Hulley (1981). The species has an adult (>100 mm SL) benthopelagic distribution, and is common in bottom trawls (767–800 m) off South Georgia (Hulley 1981). Diel data off Kerguelen (Fig. 17) reveal a relatively constant abundance below 100 m at night (18:00h–04:00h), but the species is poorly represented between 300–450 m during the day (06:00h–16:00h).

Gymnoscopelus fraseri (Fraser-Bruner, 1931)

Point data indicate that *Gymnoscopelus fraseri* has been recorded between 66°S and 38°S, with isolated captures to 34°S. It occurs mainly north of the APF (Map 50a). Despite a noticeable sampling effort, there are no records of the species between 24°W–117°E except around Kerguelen (ca. 72°E). Probability distribution analyses (Map 50b) reveal that the species is distributed mainly in the Sub-Antarctic Zone between the APF and SAF. These limits are exceeded to the north of South Georgia and to the south between 30°E–70°E. Low summer salinity values at 200 m (mainly less than 34.1 PPS) best explain the habitat of this species (Fig. 18), together with high summer oxygen concentrations (between 6–7 ml.l⁻¹) and with bottom depths greater than 750 m. The distribution of *Gymnoscopelus fraseri* seems to be associated with SAMW and AAIW. Diel data off Kerguelen (Fig. 19) reveal a patchy distribution, with specimens occurring in the upper 10 m at night (19:00h–04:00h) and generally below about 300 m during the day (06:00h–17:00h).

Gymnoscopelus piabilis (Whitley, 1931)

Point data indicate that *Gymnoscopelus piabilis* has been recorded between about 57°S and 49°S, with isolated captures north to about 34°S (Map 51). It occurs mainly between the APF and STF, but has been taken north of the STF

in the western South Atlantic off Uruguay (particularly in bottom trawls), and north of the Chatham Rise off New Zealand. Off Chile, it has been recorded south of about 40°S. The fact that the species is taken by bottom trawls on the Patagonian Slope (345–1250 m) suggests a bathypelagic mode of life for older fishes. This fact might account for the paucity of records in the Pacific sector of the Southern Ocean between 80°W–180°W. In our data set *Gymnoscopelus piabilis* represents only 12.78% of the available records. BRT analyses were therefore not undertaken for the species. Diel data off Kerguelen (Fig. 20) reveal a patchy distribution, with specimens occurring in the upper 10 m at night (20:00h–04:00h); occurring below about 150 m during the crepuscular periods; and generally occurring below about 250 m during the day (07:00h–17:00h).

***Metelectrona ventralis* (Becker, 1963)**

Metelectrona ventralis has been recorded between about 52°S and 49°S, with isolated captures north to about 35°S in the eastern South Atlantic (Hulley 1981, 1986b). It occurs between the APF and STF, but more usually is found north of the SAF. It has an apparent circumpolar distribution, although there are few records in the Pacific sector of the Southern Ocean, particularly between about 50°W–135°W. The species represents only 5.87% of the available records. BRT analyses were therefore not undertaken. The small diel data set for this species off Kerguelen reveals that specimens are taken in the upper 10 m at night (18:00h–04:00h), but were never caught in the upper 400 m of the water column during the day.

***Protomyctophum gemmatum* Hulley, 1981**

Protomyctophum gemmatum has been recorded between about 57°S and 49°S, with isolates north to about 38°S in the western South Atlantic (Hulley 1981). It is a circumpolar species and occurs mainly between the APF and STF. The species represents only 0.98% of the records in our data set. BRT analyses were therefore not undertaken. The small diel data set for this species off Kerguelen suggests that the species is uncommon in that area; specimens were taken only at night and only in hauls fished below about 200 m.

3.2.3. Bathylagidae (Map 52)

This family has a worldwide distribution. Individuals dominate the mesopelagic zone and bathypelagic zone from 400 m to greater than 4400 m in all sectors of the Southern Ocean including the Western Antarctic Peninsula (Donnelly & Torres 2008), Scotia Sea (Collins *et al.* 2012) and East Antarctica (Moteki *et al.* 2009, 2011, Koubbi *et al.* 2010, 2011a). There are two genera and four species in the Southern Ocean described by Gon (1990) (Map 52). Recently, Kobylanskii (2006) described a new species, *Bathylagus niger*. The biogeography of *Bathylagus* species is unclear due to morphological similarities, particularly in *Bathylagus tenuis* and *Bathylagus antarcticus*, the two main species observed in the Southern Ocean. These two species are vertical migrants mainly between the bathypelagic zone and the mesopelagic zone. There is an ontogenetic habitat shift to deeper layers as the stalk-eyed larvae of *B. antarcticus* are usually caught from the epipelagic zone to 500 m, while the older stages occur in depths of 4000 m or more (Lancraft *et al.* 1989, Gon 1990, Moteki *et al.* 2011, Collins *et al.* 2012). *B. tenuis* is circum-sub-Antarctic in the southeast Atlantic, and at Crozet and Kerguelen (Duhamel *et al.* 2005) and Macquarie (Gaskett *et al.* 2001); *B. antarcticus* is circum-Antarctic. *Bathylagus gracilis* is described from the Scotia Sea, the south-west Atlantic Ocean and south-east Pacific Ocean, and from the surface to 2700 m (Gon 1990). The three species of *Bathylagus* are present at South Georgia, where *B. tenuis* is the most abundant (Collins *et al.* 2008). Another species, *Bathylagichthys australis* was observed in the Indian and Pacific sectors of the Southern Ocean from 30° to 47°S and from 50 to 1000 m. The Kerguelen and Macquarie records are the most southern ones (Duhamel *et al.* 2005).

3.2.4. Stomiiformes (Gonostomatidae, Phosichthyidae, Sternoptychidae and Stomiidae) (Maps 53–57)

The Stomiiformes comprise 4 families: Gonostomatidae, Phosichthyidae, Sternoptychidae and Stomiidae. All their species lead a meso- and bathypelagic mode of life.

Gonostomatids are distributed in meso- and bathypelagic zones of the World Ocean. It is probably one of the most abundant families in terms of number of individuals in the deep pelagic zone of most oceans. However, few species penetrate as far south as the Southern Ocean (Map 53). Their distribution is restricted to the northern part of the Southern Ocean with the exception of *Cyclothone microdon* and *Cyclothone kobayashii* (= *C. pseudopallida* records in the Southern Ocean; see Miya 1994), which are widely distributed in the Southern Ocean. *C. microdon* is the most abundant species of Gonostomatidae. It is one of the dominant mesopelagic and bathypelagic species at least in parts of the Southern Ocean along with *Electrona antarctica*, *Bathylagus antarcticus* and *Notolepis coatsi* (Moteki *et al.* 2009, 2011). The species live in association with *C. kobayashii* in the region of Marguerite Bay west of Antarctic Peninsula (Donnelly & Torres 2008) and in the Ross Sea (Hanchet *et al.* 2013). There is a vertical segregation of life stages in *C. microdon*: early stages appear to be distributed between 500–1000 m and older stages over a broader depth range of 500–2000 m (Moteki *et al.* 2009). The other gonostomatid species such as *Diplophos rebainsi* have a sub-Antarctic distribution. *Cyclothone pallida* and *Cyclothone braueri* have a subtropical distribution with

some individuals penetrating as far south as Macquarie or Crozet in the northern part of the Southern Ocean (Duhamel *et al.* 2005).

Juvenile specimens of *Vincigueria attenuata* (Phosichthyidae) were recorded in the Transition Frontal Zone and the Sub-Tropical Zone between Crozet and Kerguelen Islands (Koubbi 1993). The species was also recorded by Pakhomov *et al.* (1999) in the sub-Antarctic zone of the Atlantic sector. Gaskett *et al.* (2001) recorded *Photichthys argenteus* at Macquarie Islands and the species has also been recorded as far south as ca. 58°S.

Some species of Sternoptychidae occur in the northern part of the Southern Ocean mainly in the Sub-Tropical Zone. *Maurolicus muelleri* (Map 54) is the only species of Sternoptychidae (subfamily Maurolicinae) that is observed within the Southern Ocean where it is sometimes preyed upon by king penguins (*Aptenodytes patagonicus*). Records off Kerguelen Islands are probably linked to subtropical cyclonic gyres that allow these fishes to drift southward (Duhamel *et al.* 2005).

Five subfamilies of the Stomiidae (as defined by Fink 1985) are recorded from the Southern Ocean. The Chauliodontinae have a worldwide distribution from 60°N to 40°S (Hafner 1952). *Chauliodus sloani* is the most common species in all oceans. It is also present in the sub-Antarctic zone of the Southern Ocean (Map 55).

Two of 11 worldwide species of the subfamily Stomiinae are found in the Southern Ocean (Map 55). *Stomias boa boa* is distributed in subtropical waters. *Stomias gracilis* is found in the sub-Antarctic, with few occurrences in Antarctic waters. *S. boa boa* is separated into different populations, with the southernmost population in the Sub-Tropical Zone. It occurs further north in the cold Benguela and Humboldt Currents (Gibbs 1969). Some specimens were collected south of the SAF and APF at Kerguelen and Heard Islands (Duhamel *et al.* 2005). Moteki *et al.* (2009) captured a *S. boa boa* specimen in the High Antarctic Zone in Lutzom Holm Bay. The depth range of this species varies from 200 to 2630 m (Gibbs 1969). Individuals may migrate into surface waters at night (Gon 1990, Duhamel *et al.* 2005).

S. gracilis occurs from 200 to 1250 m depth (Fink 1985) at Macquarie (Gaskett *et al.* 2001), Kerguelen Islands (Duhamel *et al.* 2005) and South Georgia (Collins *et al.* 2008). *S. gracilis* appears to remain within Antarctic Intermediate Water throughout its vertical migration (Gibbs 1969).

In the subfamily Astronesthinae, *Astronesthes psychrolutes* was observed in the Southern Ocean in the Kerguelen area to 50°S, on the Meteor ridge (48°S–8°E) and at Macquarie Island (Duhamel *et al.* 2005) (Map 56). It belongs to the transitional sub-Antarctic fauna associated with the Sub-Tropical Convergence (Parin & Borodulina, 2003). The species seems to have an ontogenetic depth segregation with juvenile specimens living in the epipelagic zone. Adults live in the meso- and upper bathypelagic zones. They probably migrate diurnally (Duhamel *et al.* 2005).

The other Astronesthinae, *Borostomias antarcticus* is distributed in the temperate and the sub-Antarctic zones at Macquarie (Gaskett *et al.* 2001), Kerguelen and Crozet Islands (Duhamel *et al.* 2005) and South Georgia (Collins *et al.* 2008) (Map 56), but also in the Ross Sea (Hanchet *et al.* 2013). Its depth range varies from 350 to 2630 m. The species is considered to be semi-migrant in the water column (Klimpel *et al.* 2006). It occurs as a regular bycatch in deep bottom trawls, and their habitat appears to be associated with continental and peri-insular slopes, and mid-ocean ridge systems.

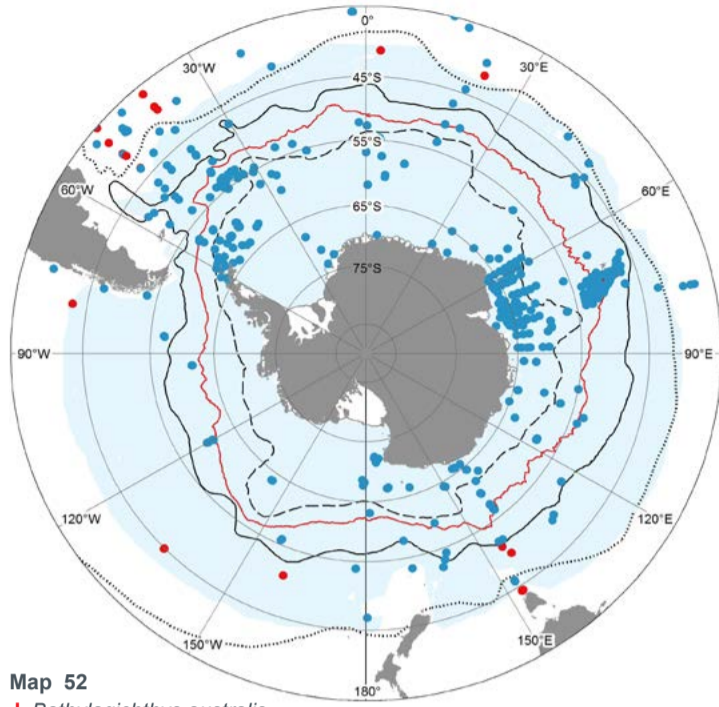
Trigonolampa miriceps (Map 57) is an uncommon species of the subfamily Melanostomiinae living in the Southern Ocean. It has an antitropical distribution. It is recorded from 30°S to the Sub-Tropical Zone north of Kerguelen, Crozet and Macquarie Islands (Gon 1990, Duhamel *et al.* 2005). Its depth range varies between 70 m and 1765 m.

Idiacanthus atlanticus, (subfamily Idiacanthinae), has a subtropical to temperate distribution (Gon 1990). The distributional pattern in the Southern Ocean is similar to those of other Stomiidae. It is observed from 25°S in the north along the South African west coast. It is associated with the Antarctic Intermediate Water (Hulley 1986b). The depth range is from 500 to more than 2000 m (Gibbs 1985). Males live deeper than females.

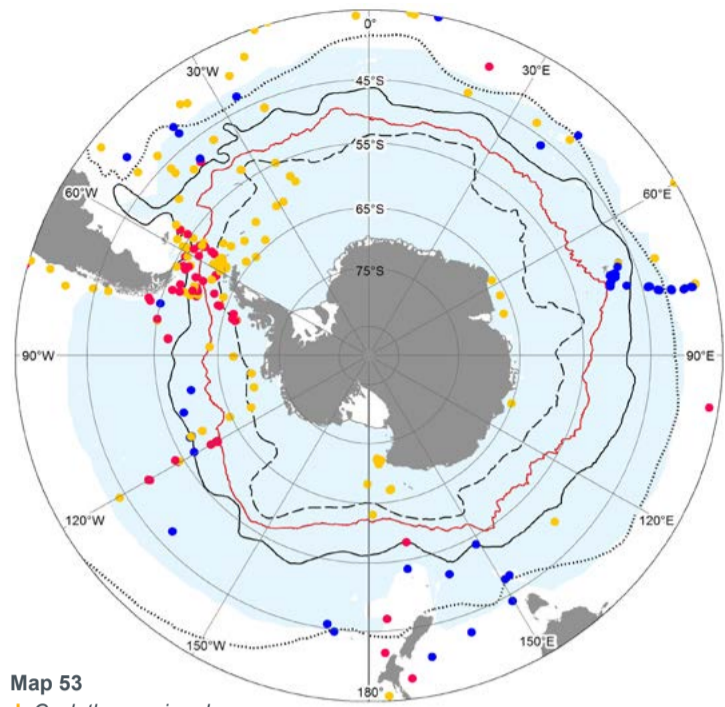
3.2.5. Aulopiformes (Alepisauridae, Anotopteridae, Notosudidae, Paralepididae and Scorpelarchidae). Paralepididae and Scorpelarchidae) (Maps 58–60).

Five families of Aulopiformes with 11 species are present in the Southern Ocean. Two families (Alepisauridae, Anotopteridae) comprise only one species each: *Alepisaurus brevirostris*, a worldwide meso- and epipelagic species is limited to the sub-Antarctic (Gon 1990, Duhamel *et al.* 2005) (Map 58), and *Anotopterus vorax* present from subtropical waters to the Antarctic continental margins (Kukuev 1998).

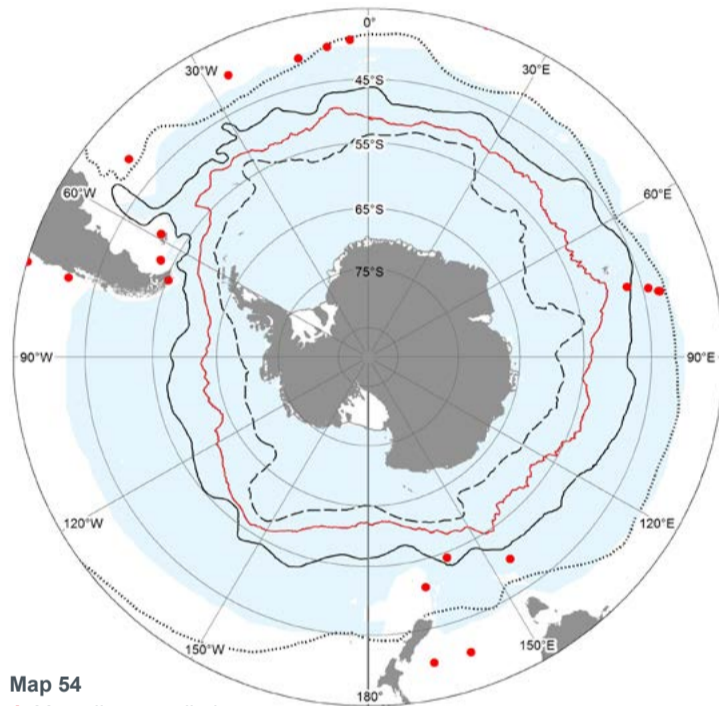
Two species of Notosudidae occur in the Southern Ocean. *Luciosudis normani* is a mesopelagic species generally present in all oceans from 30 to 45°S (Map 58). However, this species has also been recorded from further south, on the north and north-eastern part of the Kerguelen island shelf, on the Meteor Ridge, at Crozet Islands (48°S–8°E), and at Macquarie Island (Duhamel *et al.* 2005). Life stages appear to be segregated by depth, with smaller juveniles in the upper 100–200 m layers, larger juveniles living in the 300–400 m layer, and adults in the 500–800 m layer. The second species is *Scopelosaurus hamiltoni*. It can be observed from 30 to 55°S and is sometimes found even further to the south such as in the Dumont d'Urville Sea (Koubbi *et al.*



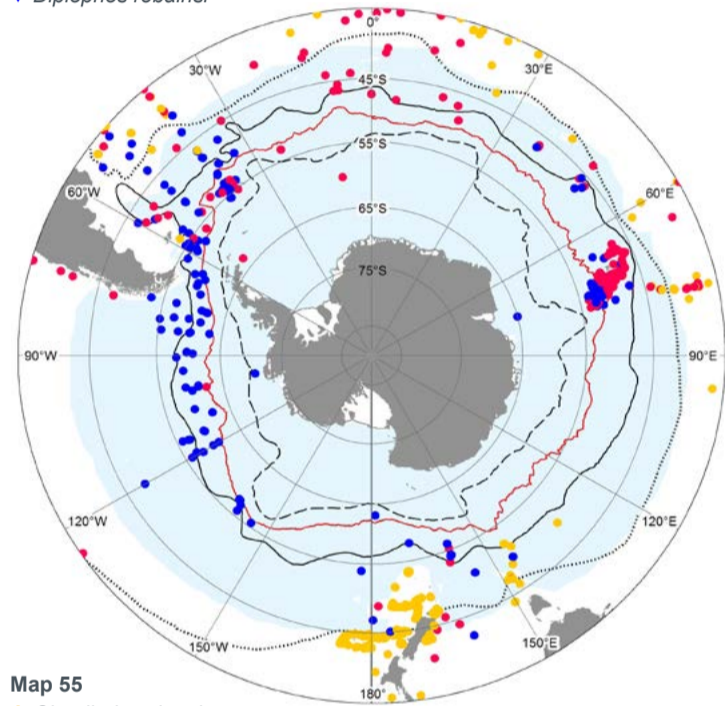
Map 52
 ▼ *Bathylagichthys australis*
 ◆ *Bathylagus*



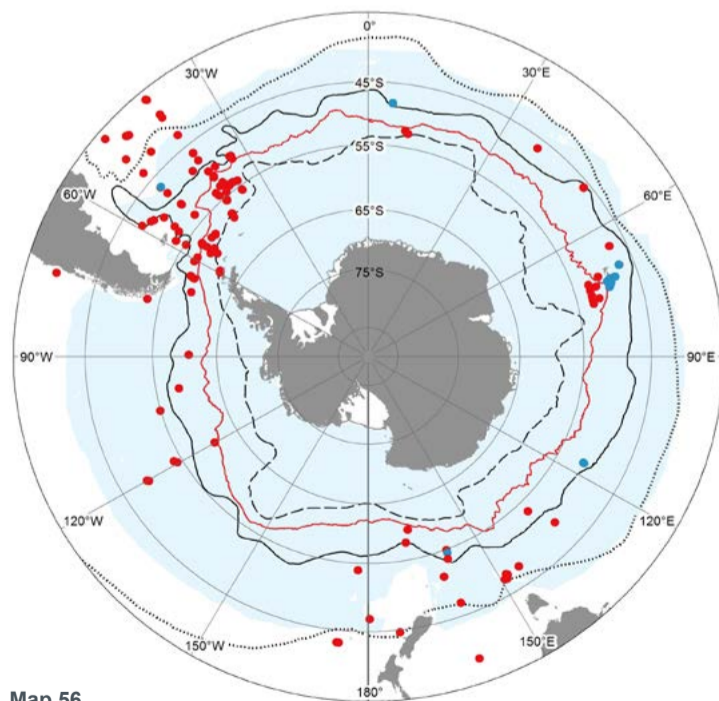
Map 53
 ◆ *Cyclothone microdon*
 ▼ *Cyclothone kobayashii*
 ◆ *Diplophos rebaini*



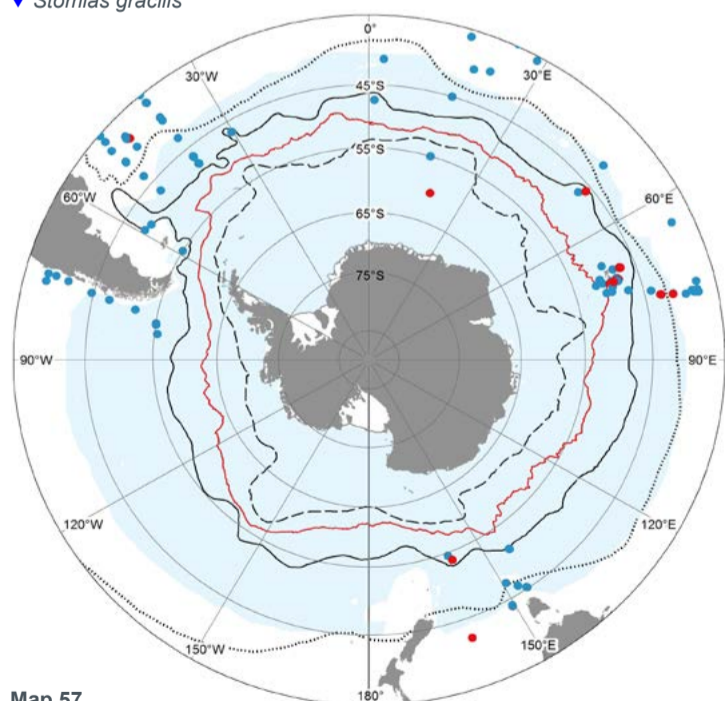
Map 54
 ▼ *Maurolicus muelleri*



Map 55
 ◆ *Chauliodus sloani*
 ▼ *Stomias boa boa*
 ◆ *Stomias gracilis*

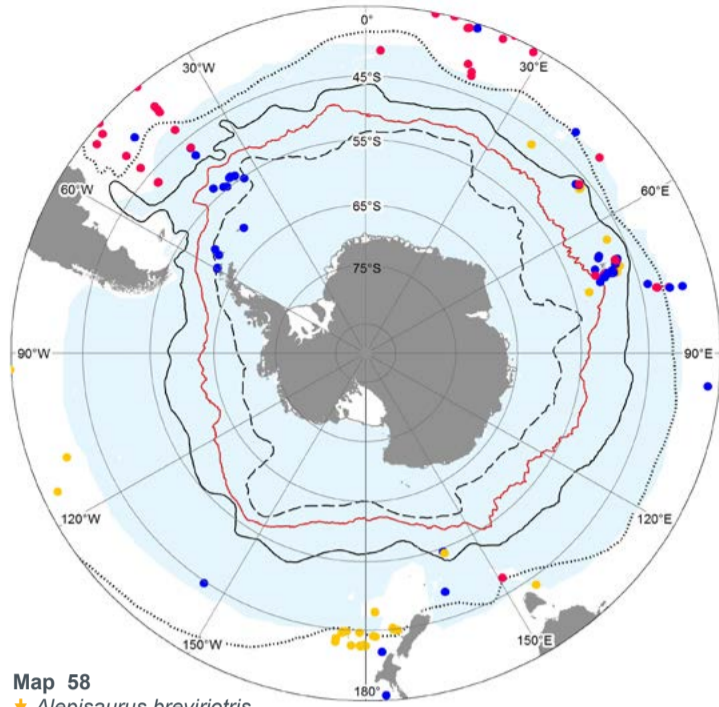


Map 56
 ◆ *Astronesthes psychrolutes*
 ▼ *Borostomias antarcticus*

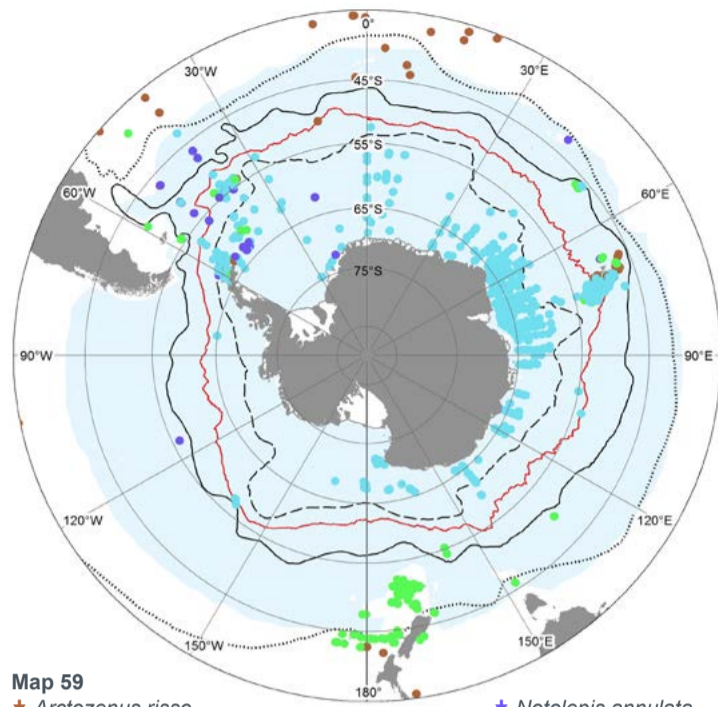


Map 57
 ◆ *Idiacanthus atlanticus*
 ▼ *Trigonolampa miriceps*

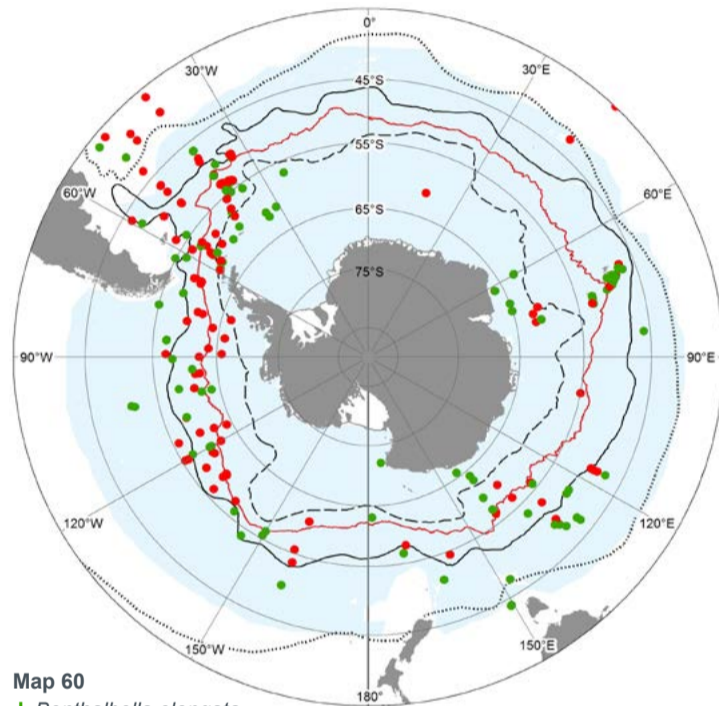
Fish Maps 52–57: Bathylagidae and Stomiiformes Map 52. Distribution of *Bathylagus* spp. and *Bathylagichthys australis* Kobylansky, 1990. Map 53. Distribution of Gonostomatidae. Map 54. Distribution of *Maurolicus muelleri* (Gmelin, 1789). Map 55. Distribution of *Stomias gracilis* Garman, 1899, *Stomias boa boa* (Risso, 1810) and *Chauliodus sloani* Bloch & Schneider, 1801. Map 56. Distribution of Astronesthinae. Map 57. Distribution of Melanostomiinae.



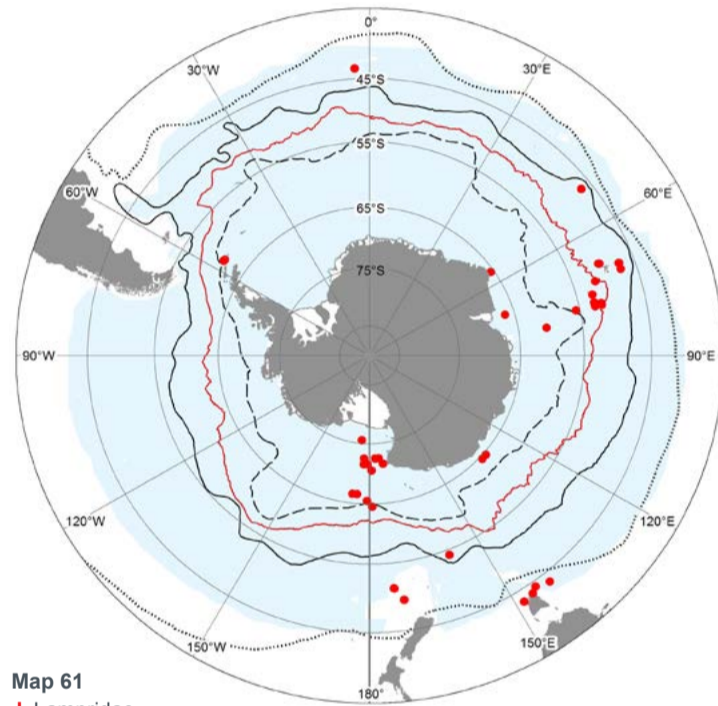
Map 58
 ▲ *Alepisaurus brevirostris*
 ▼ *Luciosudis normani*
 ◆ *Scopelosaurus hamiltoni*



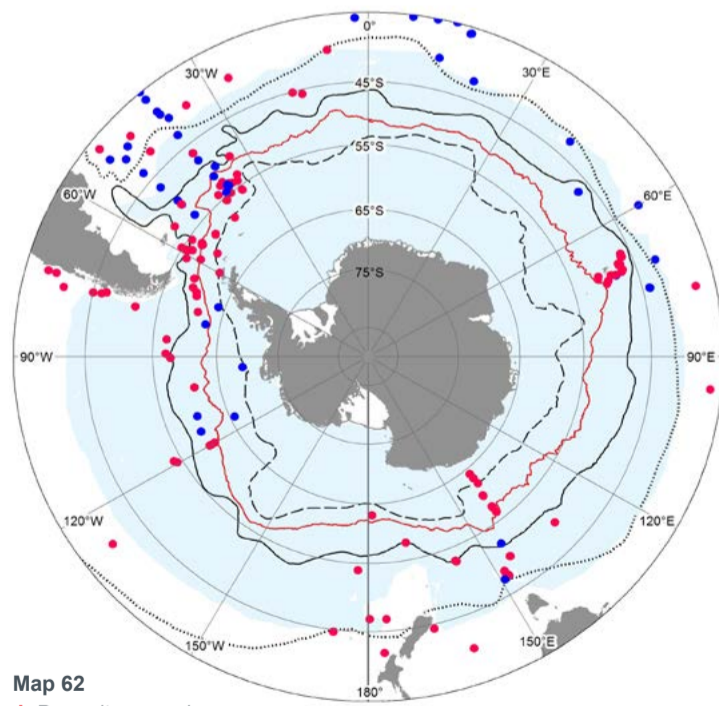
Map 59
 ▲ *Arctozenus risso*
 ▼ *Magnisudis prionosa*
 ◆ *Notolepis annulata*
 ◆ *Notolepis coatsi*



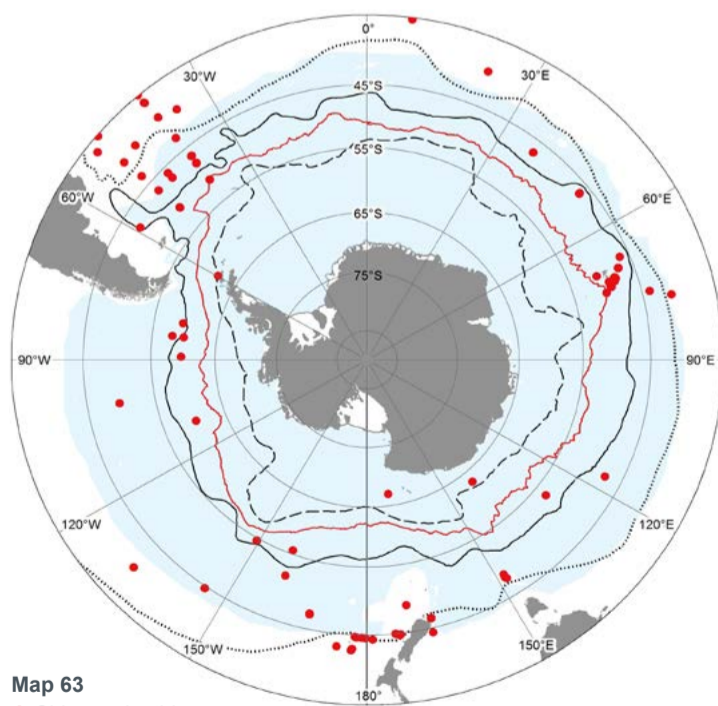
Map 60
 ◆ *Benthabella elongata*
 ▼ *Benthabella macropinna*



Map 61
 ▼ Lampridae

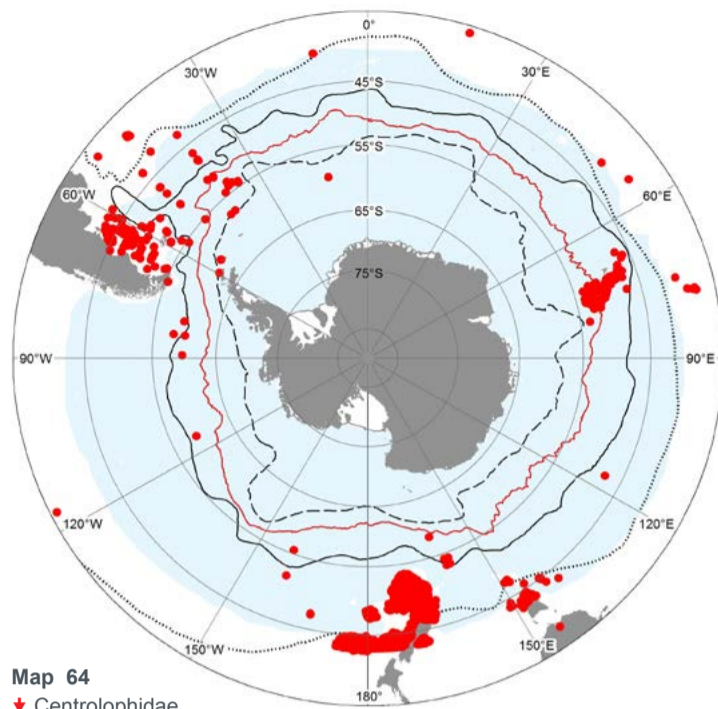


Map 62
 ▼ *Poromitra crassiceps*
 ◆ *Sio nordenskjoeldii*

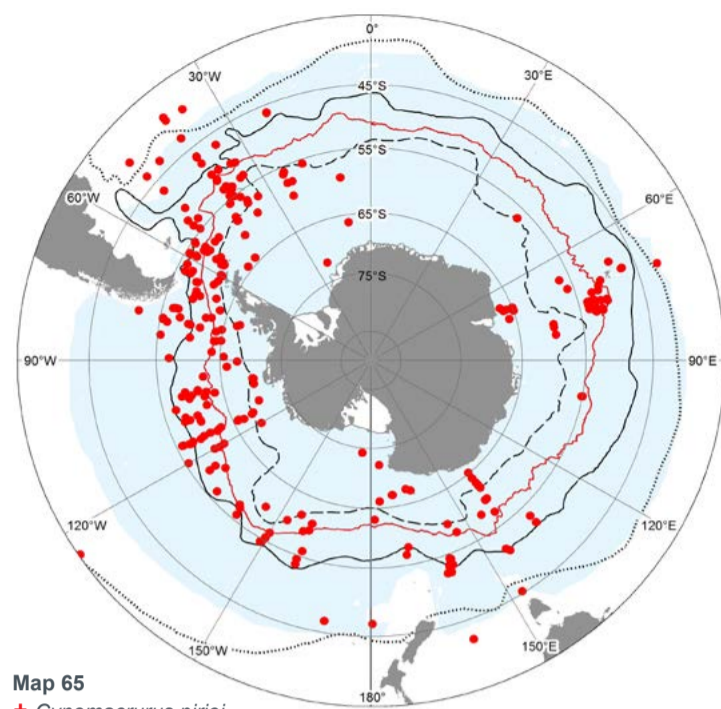


Map 63
 ▼ Chiasmodontidae

Fish Maps 58–63: Aulopiformes, Lampridae, Melamphaidae and Chiasmodontidae Map 58. Distribution of *Alepisaurus brevirostris* Gibbs, 1960, *Luciodus normani* Fraser-Bruner, 1931 and *Scopelosaurus hamiltoni* (Waite, 1916). Map 59. Distribution of Paralepididae. Map 60. Distribution of Scopelarchidae. Map 61. Distribution of Lampridae. Map 62. Distribution of Melamphaidae. Map 63. Distribution of Chiasmodontidae.



Map 64
▼ Centrolophidae



Map 65
▼ *Cynomacrus piriei*

Fish Maps 64–65: Centrolophidae and pelagic Macrouridae Map 64. Distribution of Centrolophidae. Map 65. Distribution of *Cynomacrus piriei* Dollo, 1909.

2010) (Map 58). Records are available from South Georgia and Macquarie Island. It occurs frequently in the Kerguelen and Crozet regions (Duhamel *et al.* 2005). Young fish live mainly in the upper mesopelagic layer in the subtropical area between 30 and 40°S. Adults are found deeper than 750 m (Krefft 1990). This species is likely to undertake vertical migrations into the epipelagic zone.

The Paralepididae is another family abundant in the Southern Ocean (Map 59). *Arctozenus risso* is a pelagic species distributed worldwide and mainly in the epi- and mesopelagic zones of temperate waters. Some of the identifications of another Paralepididae species, *Notolepis coatsi* were probably may be mistaken for *A. risso* as both species prefer a similar habitat. If identifications are correct however, *N. coatsi* is one of the most abundant oceanic species south of the Antarctic Polar Front (Pakhomov *et al.* 1999) and from the surface to 2000 m. Very few specimens have been collected over the shelf break (Hoddell *et al.* 2000, Van de Putte *et al.* 2010, Moteki *et al.* 2011). There is an ontological shift to deeper waters in *N. coatsi* (Moteki *et al.* 2009). Their larvae are one of the predominant species in oceanic waters of the Southern Ocean south of the APF (Efremenko & Pankratov 1988, Morales-Nin *et al.* 1995, Hoddell *et al.* 2000, Fisher *et al.* 2004, Van de Putte *et al.* 2009). *Notolepis annulata* has been caught in the western Atlantic sector (43°S–62°S). Its distribution is probably circum-Antarctic because it has been recorded off the Kerguelen Islands (Duhamel *et al.* 2005). Another (but rarer) species is *Magnisudis prionosa* which has been found in the western Atlantic sector and around Kerguelen, Crozet and Marion/Prince Edward Islands (Duhamel *et al.* 2005) and in the Ross Sea (Hanchet *et al.* 2013).

The family Scopelarchidae includes meso- and bathypelagic predatory fishes observed in all oceans except the Arctic Ocean and the Mediterranean Sea (Davis & Fielitz 2010). Two species of Scopelarchidae which belong to a single genus occur in the Southern Ocean: *Benthalbella elongata* and *Benthalbella macropinna* (Map 60). Both species are circumpolar in the southern hemisphere from 35°S–40°S to the Antarctic. *B. elongata* is mesopelagic with adults living below 500 m. Both species are diel vertical migrators. *B. macropinna* appears to have a deeper distribution compared to *B. elongata* (Gon & Heemstra 1990, Duhamel *et al.* 2005), and *B. elongata* migrates to shallower depths than *B. macropinna*.

3.2.6. Other mesopelagic fish (Maps 61–65)

Microstomatidae

One species (*Nansenia antarctica*) of the family is present in the northern part of the Southern Ocean. This circum-sub-Antarctic species is deep-living (down to 1000 m) and exhibits diel migrations into the lower epipelagic zone (about 150 m) (Duhamel *et al.* 2005).

Melanonidae

One species of pelagic cod, *Melanonus gracilis*, is found in both sub-Antarctic and Antarctic waters. The distribution is circumpolar in the sub-Antarctic. It is known from Crozet, Kerguelen, and Macquarie Islands, the south-east Atlantic along the Meteor Ridge and Discovery Banks. Its occurrence appears to be rarer south of the AFP. Catches have been made off Prydz Bay. This meso- to bathypelagic species is distributed vertically from epi- to mesopelagic layers at night (Duhamel *et al.* 2005) to 3500 m depth (Chiu & Markle 1990).

Lophiiformes (Ceratiidae, Oneirodidae, Melanocetidae, Gigantactinidae)

Four families of Lophiiformes are known from the Southern Ocean. Catches are rare despite the fact that some species have a cosmopolitan distribution

in meso- and bathypelagic layers (Pietsch 1990). Koubbi *et al.* (2010) found a specimen of *Oneirodes notius* at 1000 m in the outer Dumont d'Urville Sea, as did Collins *et al.* (2008) off South Georgia in 600–800 m depth. Hanchet *et al.* (2013) caught representatives of all four families in the Ross Sea.

Lampridae

Lampris immaculatus is a large pelagic fish with a circumglobal distribution in the subtropical and temperate waters of the Southern Hemisphere (Map 61). It is recorded from Kerguelen, Crozet, Macquarie, South Georgia and Elephant Island. It was also caught recently in the Ross Sea (Hanchet *et al.* 2013) and once in the Bellingshausen Sea (Gon 1990). This species is taken along the shelf break and down to 1450 m (Duhamel *et al.* 2005) but is more frequent in depths of 50–485 m (Gon 1990). The more subtropical congener *L. guttatus* has been recorded once at South Georgia (Parin & Kukuev 1983).

Melamphaidae

Three species of Melamphaidae are found in the meso- and bathypelagic zones of the Southern Ocean (Gon & Heemstra 1990) (Map 62). *Melamphaes microps* has an anti-tropical type of distribution. It lives in temperate to Antarctic waters. *Poromitra crassiceps* is a bathypelagic species and has a worldwide distribution. It was caught in the sub-Antarctic zone at Kerguelen and Crozet Islands (Duhamel *et al.* 2005), at South Georgia (Collins *et al.* 2008) and in various locations in the Antarctic zone (Koubbi *et al.* 2010, Hanchet *et al.* 2013). The third species of this family, *Sio nordenskjoeldii* is distributed from the Sub-Tropical Front to the Antarctic shelf, and from 200 to 3000 m (Kotlyar 2002).

Chiasmodontidae

The family Chiasmodontidae is known from the northern part of the Southern Ocean to about 50°S (Map 63). Three species are observed in the Southern Ocean. They are meso- to bathypelagic species. *Chiasmodon niger* was recorded as bycatch in bottom trawls at 505–675 m depth on the Kerguelen and Crozet slopes (Duhamel *et al.* 2005). A second species, *Pseudoscopelus altipinnis*, lives in oceanic waters. It occurs from 50 to 340 m at night and deeper than 1000 m during the day. *Kali* sp. has been recently noted in the Ross Sea (Hanchet *et al.* 2013).

Centrolophidae

The family is represented in the Southern Ocean by one species, *Ichthyos australis*. The distribution is probably circum-Antarctic (Map 64). The species is known to conduct diel vertical migrations from 12 to more than 450 m depth.

Pelagic Macrouridae

Cynomacrus piriei is a bathypelagic species, occurring to 2000 m depth, and is endemic to the Southern Ocean. It has a circumpolar distribution and extends north of the Convergence in some areas (Map 65).

4. Shelfbreak ecotone

The shelf-break represents a marked change between the oceanic and the shelf-associated species assemblages in both demersal fishes and pelagic fishes (Efremenko & Pankratov 1988, Kock 1992, Ekau 1990, White & Pitkowski 1993, Hoddell *et al.* 2000, Granata 2002, Duhamel *et al.* 2000, 2005, Flores *et al.* 2008, Van de Putte *et al.* 2009, Koubbi *et al.* 2010, 2011a). The Southern Ocean pelagic neritic assemblages are dominated by notothenioids like the Antarctic silverfish (*P. antarctica*), icefish and fish larvae, whereas oceanic near-shelf assemblages are dominated by meso- and

bathypelagic fish of the following abundant families: Myctophidae, Bathylagidae, Gonostomatidae and Paralipidae. There are often transitional assemblages along the deeper continental or peri-insular shelf margins (>300 m), the composition of which often changes rapidly with depth, the closer one approaches the shelf margin at 500m. These mixed assemblages comprise of several nototheniids and channichthyids on the one hand, and myctophids such as *Electrona antarctica* and *Gymnoscopelus nicholsi* on the other, and with both groups often feeding on krill (*Euphausia superba*) (Kock 1992, Hoddell *et al.* 2000, Koubbi *et al.* 2010, Moteki *et al.* 2011).

Most of the above studies underline the importance of the shelf break as a pronounced boundary for separating meso- and bathypelagic species from shelf-associated species, although bottom depths do allow some species to migrate from the oceanic zone into either deep inner-shelf depressions, as found in East Antarctica (Andriashev 1965, Koubbi *et al.* 2010, 2011a), or into deeper parts (500–300 m) of the shelf. There are a few exceptions to this pattern of distribution as has been observed in Marguerite Bay in the Western Antarctic Peninsula where both types of assemblages are mixed (Donnelly & Torres 2008). At the Kerguelen Islands, Koubbi *et al.* (1991, 2003) showed that larvae of myctophids such as *K. anderssoni* can temporarily dominate the ichthyoplankton over the island shelf and in the coastal zone, when mixing between assemblages of the oceanic and neritic zones occur in winter. However, this seems to be limited to fish larvae and the survival of these individuals is not sure.

What are the causes for the existence of an ecotone separating the shelf from the oceanic assemblages? Three different hypotheses have been proposed to explain it. The first is associated with the presence of fronts such as those present over the slope; the second is linked to adaptation to the environment; and the third takes account of the possibility of an interspecific interaction between micronektonic species.

Some of the oceanic species are closely linked to particular water masses, as is shown by the latitudinal gradient in their distribution. While the influence of the Sub-Tropical Front, the Sub-Antarctic Front and the Antarctic Polar Front is well described, there are fewer studies related to the influence of other frontal zones like the Southern Boundary and the Southern Antarctic Circumpolar Current Front. In the Dumont d'Urville Sea, Koubbi *et al.* (2010, 2011a) and Moteki *et al.* (2011) showed that the area has a complex system of underwater canyons located on the continental slope. They favour the upwelling of Modified Circumpolar Deep Water which transports the meso- and bathypelagic assemblages in the direction of the shelf. Furthermore, the continental and island slopes and underwater ridges are regions of high water mass dynamics influencing the Antarctic Slope Front, and thereby clearly influencing the distribution of pelagic fish assemblages (Hoddell *et al.* 2000, Flores *et al.* 2008, Van de Putte *et al.* 2010, Koubbi *et al.* 2010, 2011a). These dynamic processes are less obvious in the West Antarctic Peninsula where no clear distinction exists between oceanic and neritic assemblages (Donnelly & Torres 2008). In the Dumont d'Urville Sea, Moteki *et al.* (2011) found that mesopelagic fish were not present south of ASF, except for two specimens of *N. coatsi*.

Results were similar in studies conducted around other islands/island groups of the Southern Ocean. Studies around King George Islands (Pusch *et al.* 2004), Kerguelen Islands (Koubbi *et al.* 1991, 2001, 2003, 2009, Duhamel 1998, Duhamel *et al.* 2000, 2005, Loots *et al.* 2007), and South Georgia (Piatkowski *et al.* 1994, Collins *et al.* 2008) showed not only the importance of the slope front and island mass effect in creating highly productive areas, but also the retention by this front. This obviously has a profound effect on the diversity of mesopelagic fish assemblages.

Some abiotic factors such as water masses, fronts and the presence of sea-ice could explain why the colonization of inner-shelf depressions is not possible because of differences in the ecological niche between epi-, meso- and bathypelagic species. Over the continental shelf, sea surface conditions change drastically during winter when sea-ice starts to form. Only species adapted to these conditions are able to survive in such a harsh environment. Antarctic notothenioids including the Antarctic silverfish *P. antarctica* possess antifreeze glycoproteins (AFGPs) which protect them from freezing.

Cullins *et al.* (2011) found that oceanic midwater fishes (*E. antarctica*, *G. nicholsi*, *G. braueri*, *Melanostigma gelatinosum*, *Paradisoplinus gracilis*, *Notolepis coatsi*, and *Bathylagus antarcticus*) do not contain AFGPs or AFPs. As a consequence, the distribution of meso- and bathypelagic species is mainly correlated with higher temperatures as observed in habitat modeling (Van de Putte *et al.* 2009, Koubbi *et al.* 2011a). It suggests that oceanic midwater fishes cannot live over the continental shelf or in the Weddell and Ross Seas, where a clear transition between oceanic and shelf break fauna is observed (DeWitt 1970, Donnelly *et al.* 2004). Oceanographic conditions are somewhat different west of the Antarctic Peninsula (Klinck *et al.* 2004). There is a mix of neritic and mesopelagic species over the shelf at 200 to 400 m depth (Donnelly & Torres 2008, Cullins *et al.* 2011).

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope

Biogeographic information is of fundamental importance for discovering marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future distributions, monitoring biodiversity, or supporting conservation and sustainable management strategies.

The recent extensive exploration and assessment of biodiversity by the Census of Antarctic Marine Life (CAML), and the intense compilation and validation efforts of Southern Ocean biogeographic data by the SCAR Marine Biodiversity Information Network (SCAR-MarBIN / OBIS) provided a unique opportunity to assess and synthesise the current knowledge on Southern Ocean biogeography.

The scope of the Biogeographic Atlas of the Southern Ocean is to present a concise synopsis of the present state of knowledge of the distributional patterns of the major benthic and pelagic taxa and of the key communities, in the light of biotic and abiotic factors operating within an evolutionary framework. Each chapter has been written by the most pertinent experts in their field, relying on vastly improved occurrence datasets from recent decades, as well as on new insights provided by molecular and phylogeographic approaches, and new methods of analysis, visualisation, modelling and prediction of biogeographic distributions.

A dynamic online version of the Biogeographic Atlas will be hosted on www.biodiversity.aq.

The Census of Antarctic Marine Life (CAML)

CAML (www.caml.aq) was a 5-year project that aimed at assessing the nature, distribution and abundance of all living organisms of the Southern Ocean. In this time of environmental change, CAML provided a comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. CAML was initiated in 2005 as the regional Antarctic project of the worldwide programme Census of Marine Life (2000-2010) and was the most important biology project of the International Polar Year 2007-2009.

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS, www.iobis.org), under the aegis of SCAR (Scientific Committee on Antarctic Research, www.scar.org). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with biodiversity.aq provided free access to more than 2.9 million Antarctic georeferenced biodiversity data, which allowed more than 60 million downloads.

The Editorial Team



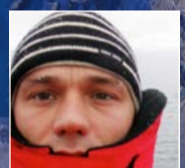
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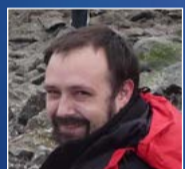
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