

Estimating the biodiversity of the East Antarctic shelf and oceanic zone for ecoregionalisation: Example of the ichthyofauna of the CEAMARC (Collaborative East Antarctic Marine Census) CAML surveys

Philippe Koubbi ^{a,b,*}, Catherine Ozouf-Costaz ^c, Anne Goarant ^{a,b}, Masato Moteki ^d, Percy-Alexander Hulley ^e, Romain Causse ^f, Agnès Dettai ^c, Guy Duhamel ^f, Patrice Pruvost ^f, Eric Tavernier ^g, Alexandra L. Post ^h, Robin J. Beaman ⁱ, Stephen R. Rintoul ^j, Toru Hirawake ^k, Daisuke Hirano ^d, Takashi Ishimaru ^d, Martin Riddle ^l, Graham Hosie ^l

^a UPMC Université Paris 06, UMR 7093, Laboratoire d'Océanographie de Villefranche, BP28, 06234 Villefranche-sur-Mer, France

^b CNRS, UMR 7093, LOV, BP 28, 06234 Villefranche-sur-Mer, France

^c CNRS UMR 7138 Systématique, Adaptation, Evolution, CP26, Muséum National d'Histoire Naturelle, 57 rue Cuvier, 75231 Paris, Cedex 05, France

^d Faculty of Marine Science, Tokyo University of Marine Science and Technology, 4-5-7 Konan, Minato, Tokyo 108-8477, Japan

^e Iziko – South African Museum, P. O. Box 61, 8000 Cape Town, South Africa

^f MNHN, DMPA UMR 5178, 43 rue Cuvier, 75005 Paris, France

^g ULCO, Département Génie Biologique, IUT Calais-Boulogne, Bassin Napoleon Quai Masset B.P. 120, 62327 Boulogne sur Mer Cedex, France

^h Marine and Coastal Environment Group, Geoscience Australia, GPO Box 378, Canberra ACT 2601, Australia

ⁱ School of Earth and Environmental Sciences, James Cook University, PO Box 6811, Cairns QLD 4870, Australia

^j Centre for Australian Weather and Climate Research, Antarctic Climate and Ecosystems Cooperative Research Centre, Wealth from Oceans National Research Flagship, CSIRO Marine Laboratories, Division of Oceanography, PO Box 1538, Castray Esplanade, Hobart, Tasmania 07001, Australia

^k Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido, Japan

^l Department of the Environment, Water, Heritage and the Arts, Australian Antarctic Division, 203 Channel Highway, Kingston, Tasmania 7050, Australia

Received 8 January 2010; revised 19 April 2010; accepted 27 April 2010

Available online 12 May 2010

Abstract

Ecoregions are defined in terms of community structure as a function of abiotic or even anthropogenic forcing. They are meso-scale structures defined as the potential habitat of a species or the predicted communities geographic extent. We assume that they can be more easily defined for long-lived species, such as benthos or neritic fish, in the marine environment. Uncertainties exist for the pelagic realm because of its higher variability, plus little is known about the meso- and bathypelagic zones. A changing

* Corresponding author. UPMC Université Paris 06, UMR 7093, Laboratoire d'Océanographie de Villefranche, BP28, 06234 Villefranche-sur-Mer, France.

E-mail address: koubbi@obs-vlfr.fr (P. Koubbi).

environment and modification of habitats will probably drive new communities from plankton to fish or top predators. We need baseline studies, such as those of the Census of Antarctic Marine Life, and databases like SCAR-MarBIN as tools for integrating all of these observations. Our objective is to understand the biodiversity patterns in the Southern Ocean and how these might change through time.

© 2010 Elsevier B.V. and NIPR. All rights reserved.

Keywords: East Antarctic shelf; Ichthyofauna; Ecoregionalisation; Generalized dissimilarity modeling; Dumont d'Urville Sea

1. Introduction

The Census of Marine Life (COML) has adopted the KUU (the known, unknown and unknowable) approach as an integrative component to its program. The purpose of COML is “to assess and explain the diversity, distribution and abundance of marine life in the world’s oceans, to evaluate what we know and what is within our current limits of understanding”. The Census of Antarctic Marine Life (CAML) is part of COML. Field work were mainly achieved during the International Polar Year (IPY Project 53) with 18 research vessels participating in studies of the state of marine biodiversity and the evolution of marine life using comparable procedures. These studies will help us to understand the impact of climate change on the polar biodiversity. Georeferenced species records from these surveys will be transferred to the SCAR-Marine Biodiversity Information Network (SCAR-MarBIN) which will allow comprehensive large-scale biogeographic studies.

Some of the study areas that were investigated will be legacy sites for future comparability studies. One such site is the Dumont d'Urville Sea ranging from Terre Adélie to the Mertz Glacier Tongue (MGT) in George V Land, East Antarctica, with a northward extension to latitude 62°S and centered along the 140°E meridian. The area was studied during the Collaborative East Antarctic Marine Census (CEAMARC). Three ships from Australia, Japan and France carrying scientists and students from many countries were involved in a sampling network of 132 sites. The main objective of CEAMARC was to gather information on the composition of the marine biota over the East Antarctic continental shelf in relation to environmental parameters, and to establish baseline information that could be used to track changes over time.

The MGT is the largest glacier in the region, though smaller ones like the Astrolabe Glacier (140°E) are also present in the western part of the area. Grounded icebergs are observed north of these glaciers. Large bays are situated along the coastline, such as Commonwealth Bay. A long plateau, the Adélie Bank,

of about 200 metres depth is located between the Astrolabe Glacier and Commonwealth Bay. Inner-shelf depressions (500–1000 m) are observed, with the largest one between Watt Bay and the MGT, known as the Adélie Depression or George V Basin (from 142°E to 146°E). The MGT forms the Mertz Polynya to its west. The MGT has some major fissures running across it which may be signs of an impending rupture. In some places the benthic environment is highly influenced by the scouring of icebergs with the extent of this perturbation being determined by the depth and topography of the seabed. Scars formed by glacial advance across the shelf during the Last Glacial Maximum also form major features on the seabed in areas deeper than the keels of contemporary icebergs. An early outcome of the study was the proposition to Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) by Australia to classify some areas as Vulnerable Marine Ecosystems.

One aim of the sampling network was to conduct a regionalisation of this area. Marine regionalisation is a planning tool using multivariate classification methods based on spatial patterns of mainly abiotic or physical geographic factors. Ecoregionalisation is “a recognizable space which can be distinguished by its abiotic characteristics and associated biological assemblage, operating at particular spatial and temporal scales” (ICES, 2005). The following are three approaches to ecoregionalisation (Vierros et al., 2008).

The first approach is regionalisation based on abiotic and geographic factors and surface chlorophyll distribution, a procedure frequently called ‘bio-regionalisation’ although it includes limited biological information. CCAMLR has undertaken the bio-regionalisation of the Southern Ocean (Grant et al., 2006) following the methodology used by Australia (Lyne and Hayes, 2005). This preliminary bio-regionalisation included surface chlorophyll as the only parameter representing biological activity directly.

However, it is now recognised that it is important to add species distributions as stated by the CCAMLR bio-regionalisation expert group in 2007 in Brussels.

The second approach is then a regionalisation based on the definition of spatial assemblages of species based on multivariate analysis. This methodology is commonly used in marine ecology to describe spatial patterns within a survey network or from a large-scale combination of surveys, such as the ones from the Southern Ocean Continuous Plankton Recorder (SO CPR).

The third approach is a mixed procedure using the two previous ones in order to define ecoregions. It seeks to determine “assemblages of flora, fauna and the supporting geophysical environment contained within distinct but dynamic spatial boundaries” (Welsh, 1994). This is the approach we adopted for this study by sampling both biotic and abiotic features and using generalised dissimilarity modelling (Ferrier et al., 2007) between species assemblages and environmental factors to predict communities in unsurveyed areas. This meso-scale approach was used to plan the CEAMARC sampling network with an emphasis on ensuring representative sampling along most of the environmental gradients that we thought were important to the biodiversity of the region. This approach is quite unique among ecoregionalisations because in most such analyses, classification is based on available existing data obtained using different sampling gear and with varying sampling effort, which creates problems of comparability of data across the area of interest. The objective here was to avoid these problems by using standard procedures for collecting fish. We used the results of one kind of trawl for the pelagic fish (International Young Gadoid Pelagic Trawl – IYGPT) and one for benthic fish (beam trawl).

The distinction between the bioregions/ecoregions approach and that used for defining biogeographic provinces and their subdivisions is that biogeographic provinces are based uniquely on the level of species endemism. This is not the case for bioregions/ecoregions. The methodology is data-driven and can always be improved by adding new information from satellites and other sources once the models are produced.

We believe that Antarctic fish may be particularly effective indicators for delineating ecoregions because they are long-lived, exhibit a range of functional roles in the ecosystem, are adapted to different ecosystem compartments.

On the Antarctic continental shelf, the notothenioids are believed to be a species flock (Lautredou et al., 2010). Ribbink (1984) defined species flocks as “an assemblage of a disproportionately high number, relative to surrounding areas, of closely related species

which apparently evolved rapidly within a narrowly circumscribed area to which all the member species are endemic”. Species flocks have biological characteristics: monophyly of the species flock (which is the case at least for Trematominae within Nototheniidae); high species diversity, ecological and morphological diversity; habitat dominance; and highly endemic fauna. The origin of the notothenioids are thought to be temperate benthic species which started to colonise habitats that were left vacant by other species during the cooling of the Southern Ocean (Eastman and McCune, 2000). In this study, we will focus on ecological diversity as most of these demersal fishes can range from generalist to specialist. In terms of habitat, some of them are associated with perturbed environments due to iceberg scouring and others to stable environments (like those fishes living in glass sponges). But will they allow us to draw meso-scale structures? Beside notothenioids, species of zoarcids and liparids are also dominant.

In the water column, pelagic early life stages of demersal fishes and true pelagic fish are known to be strongly related to hydrology. Early life stages of Channichthyidae are known to be associated with swarms of the Antarctic krill, *Euphausia superba*. In the neritic zone, *Pleuragramma antarcticum* (Nototheniidae) is the dominant pelagic fish representing more than 90% of the ichthyoplankton (Koubbi et al., 1997, 2009). It is believed that, together with the ice krill, *Euphausia crystallorophias*, they dominate their trophic level in the pelagic environment over the shelf forming a “wasp-waist” ecosystem (Bakun, 2006). More offshore, Myctophids (lantern fish) dominate the mesopelagic zone whereas *E. superba* is the emblematic species of the epipelagic layer (Nicol et al., 2000). Very little information exists for the deeper pelagic layers. Myctophids are known to be indicators of water masses and can be used for the regionalisation of the oceanic zone as proposed by Koubbi et al. (submitted for publication).

Fish studies in this part of Antarctica are generally either coast surveys using small workboats or ship-based oceanographic surveys. Survey investigations in the coastal zone of Dumont d’Urville station commenced in the 1960s, and since 2004 ICO²TA (Integrated Coastal Ocean Observations in Terre Adélie) continues a long-term monitoring programme to evaluate the abundance and dynamics of *P. antarcticum* and *E. crystallorophias*. Oceanographic surveys in the region have been designed primarily for the study of *E. superba*, such as the Australian BROKE East (Nicol et al., 2000; Hoddell et al., 2000), but have provided information on pelagic life stages associated with

Antarctic krill in the oceanic zone. CEAMARC gives us the opportunity to conduct both demersal and pelagic fish studies in a unique area of East Antarctica and at the same period.

Did CEAMARC improve our knowledge on the fish diversity in the Dumont d'Urville Sea compared to historical surveys? We use different approaches to define habitat for pelagic and demersal fish in order to delineate ecoregions. We start with the expectation that the important environmental characteristics for pelagic fish are those that define the characteristics of the water column including the physical, chemical, and biological properties that are used by fish, and that for demersal fish are those which define the substratum, including sediment type, characteristics of hard bottoms, structures underlying the waters, and associated benthic biological communities.

2. Material and methods

2.1. Sampling strategy

T/RV Umitaka Maru conducted a comprehensive survey of the epi-, meso- and bathypelagic zones on and north of the continental shelf (Fig. 1). During the CEAMARC survey, 24 stations were sampled from January 29th to February 12th 2008 using different gears to collect plankton and fish. Oceanographic measurements were also carried out. International Young Gadoid Pelagic Trawl net (IYGPT) is

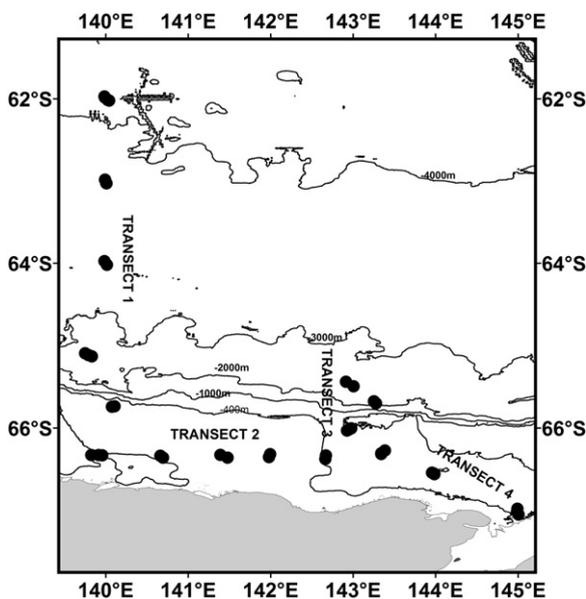


Fig. 1. Positions of the IYGPT samples (during the pelagic survey by the T/RV Umitaka Maru in 2008).

a midwater trawl net designed to catch young cod in the Northern Hemisphere. It has also proved useful for sampling fish in the Southern Ocean that live in the pelagic zone such as the Antarctic Silverfish *P. antarcticum* and myctophids (Duhamel et al., 2000; Collins et al., 2008). The IYGPT net has approximate mouth dimensions of 5.5 m high \times 12 m wide when fishing, with mesh size of 100 mm in the front, then tapering through 80 mm–40 mm–20 mm to 10 mm mesh size in the cod end. The unit effort is 20 min at each standard depth (50, 200, 500 and 1000 m). The IYGPT was used on 16 stations with 47 trawling operations achieved in total (Table 1).

The RV Aurora Australis survey focused mainly on the benthic and demersal sampling, plus a physical-chemical oceanographic survey during December 2007 to January 2008 (Fig. 2). A Beam trawl was used for catching macro benthic invertebrates, benthic and demersal fishes. The duration effort at the bottom was between 5 and 26 min, with depths ranging from 150 m to 2065 m. Two identical beam trawls were used to achieve the 77 events. Each of these trawls were able to take videos or still images during the samples.

2.2. Environmental parameters

On each vessel, temperature and salinity were measured by Conductivity-Temperature-Depth profilers. In the stations where water depths are greater than 2000 m, CTD observations were conducted up to 2000 m. To give an overview of sea surface environment in the investigated area, sea surface temperature (SST) and chlorophyll *a* concentration (chl-*a*) derived from data of a satellite ocean color sensor, Moderate Resolution Imaging Spectroradiometer (MODIS), was obtained from the Goddard Space Flight Center (GSFC), National Aeronautics and Space Administration (NASA). Daily level-2 SST and chl-*a* data during the cruise from January 25th to February 17th, 2009 were compiled over 8 days.

Sediment samples were mostly collected from 52 sites across the shelf with a box corer, though more gravelly sediments were sampled with a Smith-McIntyre or Van-Veen grab. Surface sediment samples were analysed to determine the gravel, sand and silt content by washing through 2 mm and 63 μ m sieves. Sediment values were classified according to a simplified Folk classification (Long, 2006). All sediment properties have been interpolated across the region using kriging to a 0.005° grid.

A bathymetric model based on multibeam swath bathymetry and singlebeam data has been produced at

Table 1

Fish species collected during CEAMARC with pelagic and demersal trawls, and fishes known in the coastal zone around the Pointe Géologie Archipelago in Terre Adélie.

Species	Family	Pelagic trawls	Demersal trawls	Coastal locations (trammel nets, gill nets, traps and longlines)
<i>Mancopsetta maculata maculata</i>	Achiropsettidae	1		
<i>Anotopterus pharao</i>	Anotopteridae	1		
<i>Artedidraco loenbergi</i>	Artedidraconidae	1	1	1
<i>Artedidraco oriana</i>	Artedidraconidae		1	1
<i>Artedidraco shackletoni</i>	Artedidraconidae	1	1	1
<i>Artedidraco skottsbergi</i>	Artedidraconidae	1	1	1
<i>Dolloidraco longedorsalis</i>	Artedidraconidae		1	
<i>Histiidraco velifer</i>	Artedidraconidae		1	
<i>Pogonophryne phyllopogon</i>	Artedidraconidae	1	1	
<i>Pogonophryne</i> sp. Cf. <i>macropogon</i>	Artedidraconidae		1	
<i>Pogonophryne</i> sp. 1	Artedidraconidae		1	
<i>Acanthodraco dewitti</i>	Bathydraconidae		1	
<i>Akarotaxis nudiceps</i>	Bathydraconidae		1	
<i>Bathydraco antarcticus</i>	Bathydraconidae	1	1	
<i>Bathydraco macrolepis</i>	Bathydraconidae		1	
<i>Bathydraco marri</i>	Bathydraconidae		1	
<i>Cygnodraco mawsoni</i>	Bathydraconidae	1	1	1
<i>Gerlachea australis</i>	Bathydraconidae	1	1	
<i>Gymnodraco acuticeps</i>	Bathydraconidae		1	1
<i>Prionodraco evansii</i>	Bathydraconidae	1	1	
<i>Psilodraco breviceps</i>	Bathydraconidae			1
<i>Racovitzia glacialis</i>	Bathydraconidae	1	1	
<i>Vomeridens infuscipinnis</i>	Bathydraconidae		1	
<i>Bathylagus antarcticus</i>	Bathylagidae	1	1	
<i>Bathylagus tenuis</i>	Bathylagidae	1		
<i>Chaenodraco wilsoni</i>	Channichthyidae	1	1	
<i>Chionobathyscus dewitti</i>	Channichthyidae		1	
<i>Chionodraco hamatus</i>	Channichthyidae	1	1	1
<i>Chionodraco myersi</i>	Channichthyidae		1	
<i>Cryodraco antarcticus</i>	Channichthyidae	1	1	
<i>Dacodraco hunteri</i>	Channichthyidae	1	1	
<i>Neopagetopsis ionah</i>	Channichthyidae	1	1	1
<i>Pagetopsis macropterus</i>	Channichthyidae		1	1
<i>Pagetopsis maculatus</i>	Channichthyidae	1	1	
<i>Pseudochaenichthys georgianus</i>	Channichthyidae	1		
<i>Chiasmodon niger</i>	Chiasmodontidae	1		
<i>Paradiplospinus gracilis</i>	Gempylidae	1		
<i>Cyclothone microdon</i>	Gonostomatidae	1	1	
<i>Careproctus continentalis</i>	Liparidae		1	
<i>Careproctus longipectoralis</i>	Liparidae		1	
<i>Paraliparis antarcticus</i>	Liparidae		1	
<i>Paraliparis charcoti</i>	Liparidae		1	
<i>Paraliparis leobergi</i>	Liparidae		1	
<i>Paraliparis mawsoni</i>	Liparidae		1	
<i>Paraliparis terranova</i>	Liparidae	1	1	
<i>Paraliparis valentinae</i>	Liparidae		1	
<i>Cynomacrurus piriei</i>	Macrouridae	1		
<i>Macrourus whitsoni</i>	Macrouridae		1	
<i>Poromitra crassiceps</i>	Melamphidae	1		
<i>Muraenolepis microps</i>	Muraenolepididae	1		
<i>Muraenolepis</i> sp.	Muraenolepididae		1	
<i>Electrona antarctica</i>	Myctophidae	1	1	
<i>Electrona carlsbergi</i>	Myctophidae	1		
<i>Gymnoscopelus bolini</i>	Myctophidae	1		

(continued on next page)

Table 1 (continued)

Species	Family	Pelagic trawls	Demersal trawls	Coastal locations (trammel nets, gill nets, traps and longlines)
<i>Gymnoscopelus braueri</i>	Myctophidae	1		
<i>Gymnoscopelus microlampas</i>	Myctophidae	1		
<i>Gymnoscopelus nicholsi</i>	Myctophidae	1		
<i>Gymnoscopelus opisthopterus</i>	Myctophidae	1	1	
<i>Krefflichthys anderssoni</i>	Myctophidae	1		
<i>Lampanyctus macdonaldi</i>	Myctophidae	1		
<i>Nannobranchium achirus</i>	Myctophidae	1		
<i>Protomyctophum bolini</i>	Myctophidae	1	1	
<i>Scopelosaurus hamiltoni</i>	Notosudidae	1		
<i>Dissostichus mawsoni</i>	Nototheniidae			1
<i>Notothenia coriiceps</i>	Nototheniidae			1
<i>Pagothenia borchgrevinki</i>	Nototheniidae			1
<i>Pleuragramma antarcticum</i>	Nototheniidae	1	1	1
<i>Trematomus bernacchii</i>	Nototheniidae		1	1
<i>Trematomus eulepidotus</i>	Nototheniidae		1	1
<i>Trematomus hansonii</i>	Nototheniidae		1	1
<i>Trematomus lepidorhinus</i>	Nototheniidae	1		1
<i>Trematomus loennbergii</i>	Nototheniidae	1		1
<i>Trematomus newnesi</i>	Nototheniidae	1	1	1
<i>Trematomus nicolai</i>	Nototheniidae	1		
<i>Trematomus pennellii</i>	Nototheniidae	1	1	1
<i>Trematomus scotti</i>	Nototheniidae		1	1
<i>Trematomus</i> sp. 1	Nototheniidae		1	
<i>Trematomus tokarevi</i>	Nototheniidae		1	
<i>Oneirodes notius</i>	Oneirodidae	1		
<i>Notolepis coatsi</i>	Paralepididae	1		
<i>Bathyraja eatonii</i>	Rajidae		1	1
<i>Benthalbella elongata</i>	Scopelarchidae	1		
<i>Benthalbella macropinna</i>	Scopelarchidae	1		
<i>Lycenchelys aratirostris</i>	Zoarcidae		1	
<i>Lycenchelys tristichodon</i>	Zoarcidae		1	
<i>Lycodapus pachysoma</i>	Zoarcidae		1	
<i>Lycodichthys antarcticus</i>	Zoarcidae		1	
<i>Oidiphorus mcallisteri</i>	Zoarcidae		1	
<i>Ophthalmolycus amberensis</i>	Zoarcidae		1	
<i>Pachycara brachycephalus</i>	Zoarcidae		1	
<i>Undescribed species</i>	Zoarcidae		1	
<i>Paraliparis valentinae</i>	Liparidae		1	
<i>Cynomacrurus piriei</i>	Macrouridae	1		
<i>Macrourus whitsoni</i>	Macrouridae		1	
<i>Poromitra crassiceps</i>	Melamphidae	1		
<i>Muraenolepis microps</i>	Muraenolepididae	1	1	
<i>Muraenolepis orangiensis</i>	Muraenolepididae		1	
<i>Electrona antarctica</i>	Myctophidae	1	1	
<i>Electrona carlsbergi</i>	Myctophidae	1		
<i>Gymnoscopelus bolini</i>	Myctophidae	1		
<i>Gymnoscopelus braueri</i>	Myctophidae	1		
<i>Gymnoscopelus microlampas</i>	Myctophidae	1		
<i>Gymnoscopelus nicholsi</i>	Myctophidae	1		
<i>Gymnoscopelus opisthopterus</i>	Myctophidae	1	1	
<i>Krefflichthys anderssoni</i>	Myctophidae	1		
<i>Lampanyctus macdonaldi</i>	Myctophidae	1		
<i>Nannobranchium achirus</i>	Myctophidae	1		
<i>Protomyctophum bolini</i>	Myctophidae	1	1	
<i>Scopelosaurus hamiltoni</i>	Notosudidae	1		

Table 1 (continued)

Species	Family	Pelagic trawls	Demersal trawls	Coastal locations (trammel nets, gill nets, traps and longlines)
<i>Dissostichus mawsoni</i>	Nototheniidae			1
<i>Notothenia coriiceps</i>	Nototheniidae			1
<i>Pagothenia borchgrevinki</i>	Nototheniidae			1
<i>Pleuragramma antarcticum</i>	Nototheniidae	1	1	1
<i>Trematomus bernacchii</i>	Nototheniidae		1	1
<i>Trematomus eulepidotus</i>	Nototheniidae		1	1
<i>Trematomus hansonii</i>	Nototheniidae		1	1
<i>Trematomus lepidorhinus</i>	Nototheniidae	1	1	1
<i>Trematomus loennbergii</i>	Nototheniidae	1	1	1
<i>Trematomus newnesi</i>	Nototheniidae	1	1	1
<i>Trematomus nicolai</i>	Nototheniidae	1		
<i>Trematomus pennellii</i>	Nototheniidae	1	1	1
<i>Trematomus scotti</i>	Nototheniidae		1	1
<i>Trematomus tokarevi</i>	Nototheniidae		1	
<i>Oneirodes notius</i>	Oneirodidae	1		
<i>Notolepis coatsi</i>	Paralepididae	1		
<i>Bathyraja eatonii</i>	Rajidae		1	1
<i>Benthalbella elongata</i>	Scopelarchidae	1		
<i>Benthalbella macropinna</i>	Scopelarchidae	1		
<i>Lycenchelys aratirostris</i>	Zoarcidae		1	
<i>Lycenchelys tristichodon</i>	Zoarcidae		1	
<i>Lycodapus pachysoma</i>	Zoarcidae		1	
<i>Lycodichthys antarcticus</i>	Zoarcidae		1	
<i>Oidiphorus mcallisteri</i>	Zoarcidae		1	
<i>Ophthalmolycus amberensis</i>	Zoarcidae		1	
<i>Pachycara brachycephalus</i>	Zoarcidae		1	
<i>Undescribed species</i>	Zoarcidae		1	

250 m resolution for the shelf, with 500 m resolution over the slope (Beaman, 2008). The key multibeam dataset along the continental slope is derived from the Italian PNRA/MOGAM (Morphology and Geology of Antarctic Margins) survey (De Santis et al., 2007), while smaller areas of swath bathymetry on the shelf are derived from survey NBP0101 on RV Nathaniel B. Palmer. The Bathymetric Digital Elevation Model was processed through the Benthic Terrain Modeler tools from ArcGIS 9 to compute the slope and rugosity (Wright et al., 2005). The rugosity is defined as a measure of terrain complexity.

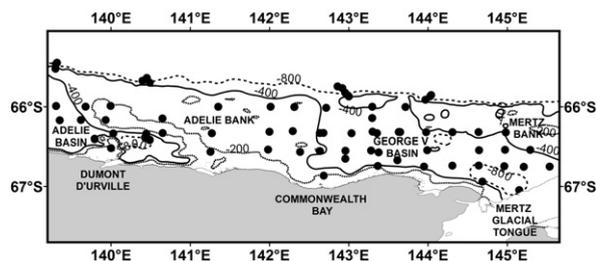


Fig. 2. Location of the beam trawl sample sites during the RV Aurora Australis survey in 2008 on the continental shelf.

2.3. Species identification

Teleost species were either directly identified on board for the most common ones, using either The FAO species identifications sheets (Fischer and Hureau, 1985) or the Fishes of the Southern Ocean (Gon and Heemstra, 1990). As a large and representative sampling was also collected for barcoding, it was possible to compare the identification obtained through morphological means with a preliminary molecular identification (Dettai et al., in press). The Barcoding of Life data system was only moderately useful in this case, because a large proportion of the collected species were not yet present in the database. However, the comparison within our dataset using a distance tree displayed a good correlation between molecular and morphological results for some species which were difficult (Artedidraconidae, Zoarcidae, Liparidae). It allowed us to conclude that there were only a single muraenolepidid species and a single *Macrourus* species collected by RV Aurora Australis, but that there were in fact two *Chionodraco* species (*C. hamatus* and *C. myersi*). The results demonstrate the usefulness of the approach for the reliability of the

identification of Antarctic teleosts, and as a tool for any study needing a reliable species list. Adult liparids were studied and identified on the basis of their morphology according to [Andriashev \(2003\)](#), and all were barcoded and the smallest specimens re-assigned to the right species by comparing their barcoding sequences with those of the adults. Zoarcids are still being studied morphologically : ten species could be separated, and 8 identified after [Gon and Heemstra \(1990\)](#) and [Anderson \(1991\)](#) and two are undetermined.

2.4. Numerical analysis

The goal of this study was to model the fish assemblage as a function of the environmental parameters. Generalized Dissimilarity Modeling functions (GDM) were developed by [Ferrier et al. \(2007\)](#) for terrestrial ecology. This method is an extension of the matrix regression that can accommodate for two types of non-linearity commonly met in ecological studies: (i) the curvilinear relationship between ecological distance and composition dissimilarity through the use of a Generalized Linear Models (GLM) with the proper link and variance function; and (ii) the non-linear response of the community along environmental gradients held with monotonic I-splines functions. The fitting of a GDM first requires the computation of a dissimilarity matrix between each pair of stations ([Ferrier et al., 2007](#)). Then for each environmental predictor, a set of I-splines is fitted to each sampling station. The I-splines coefficients are computed such that they each maximize the reduction in deviance achieved by their inclusion ([Elith et al., 2006](#)) using the dissimilarity matrix as the response variable.

Before analysis only those trawling stations with three or more different species were selected ([Growth, 2009](#)). Locations with less than three different species were excluded because comparing sites with few species results in many dissimilarity values being equal to one (no common species), although this has no ecological meaning and can result in bias in the resulting GDM. As a result, the final dataset was reduced to 51 sampling stations for demersal samplings (including 52 taxa) and 29 observations for pelagic samplings (including 43 taxa).

To identify the environmental variables that contribute most to the change in community composition, GDM were computed by removing one environmental variable at a time. At each step, the explained variance of the model without the considered

variable Var_i was compared to the variance of the complete model Var .

Since the GDM method is sensitive to colinearity between predictors, highly correlated variables were removed from the analyses ([Elith et al., 2006](#)). The Spearman correlation was computed pair-wise between each environmental variable, and variables were considered as highly correlated when showing a correlation coefficient of more than 0.7 as recommended by [Leathwick et al. \(2006\)](#). The selection between two correlated predictors was based on the following procedure: GDM was computed considering one of the two correlated variables; and the environmental predictor having the highest explained variance was retained.

Once the GDM is fitted to the observed data, it can be used to predict the dissimilarity for unobserved locations. The output of the GDM is then a predicted matrix of pair-wise dissimilarity between sites. As the predicted dissimilarity matrix is difficult to visualize, a classification can be computed on the matrix. In this study, the dissimilarity matrix was processed through a non-hierarchical clustering; it achieves a clustering of the data into k clusters around medoids. The optimal number of groups was chosen according to four indexes: Calinski and Harabasz, Xu, Ball and Hall and Hartigan (see definition in [Dimitriadou et al., 2002](#)). This series of tests measures the dispersion of observations within and between clusters.

3. Results

3.1. Environmental parameters

The highest areas of rugosity ([Fig. 3](#)) occur along parts of the inner-shelf, where a complex series of canyons and small glacial basins occur, and on the continental slope which is cut by numerous large submarine canyons. The mid- to outer-shelf has generally low rugosity across the shallow plateaus and in the deep basins, such as the Adélie Depression.

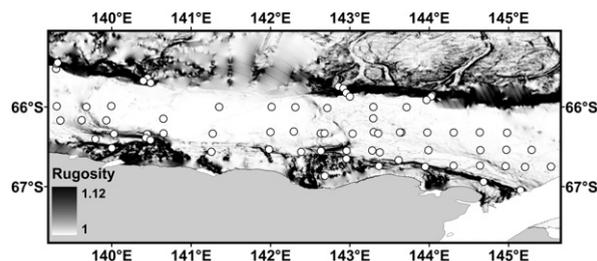


Fig. 3. Rugosity of the bathymetry of the continental shelf.

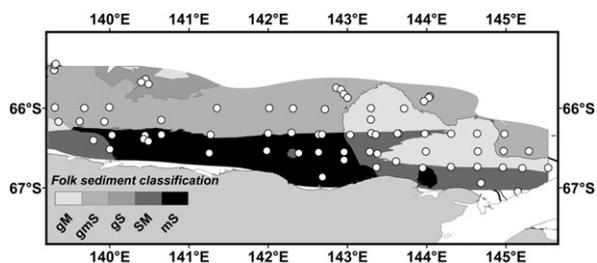


Fig. 4. Simplified Folk sediment classification of the continental shelf. gM = gravelly mud. gmS = gravelly, muddy sand. gS = gravelly sand. sm = sandy mud. mS = muddy sand.

The simplified Folk classification (Fig. 4) indicates that the Adélie Depression and Dumont d’Urville Basins are dominated by muddy, biogenic rich sediments, reflecting the accumulation of thick drapes of diatomaceous ooze and mud throughout the Holocene (Escutia et al., 2003). The Adélie Bank, the Mertz Bank and the shelf edge are all dominated by sandy sediments with minor mud and gravel content. Sandy sediments dominate inner-shelf areas with high rugosity. Only a very few sites are dominated by gravel. Gravelly sediments occur along the upper

continental slope within the Cuvier Canyon and to the west, as well as on the northern margin of the Adélie Depression.

Fig. 5 shows vertical sections of potential temperature and salinity along each transect. Following Orsi et al. (1995), we use sub-surface maximum temperature isotherms $\theta = 1.8$ and 1.5 °C to determine the meridional positions of the southern ACC front (sACCf) and the Southern Boundary of the Antarctic Circumpolar Current (SB) respectively.

We use water mass definitions by Whitworth et al. (1998) and neutral density surface γ^n (kg m^{-3}) defined by Jackett and MacDougall (1997) to identify the large-scale water mass distributions. Water masses observed were Antarctic Surface Water (AASW), Circumpolar Deep Water (CDW), Modified Circumpolar Deep Water (MCDW), Antarctic Bottom Water (AABW), and Shelf Water (SW). Near the surface, a shallow layer of fresh water known as AASW (defined by $\gamma^n < 28.03 \text{ kg m}^{-3}$) was found due to ice melting. This AASW layer has the remnant of the previous winter mixed layer, also known as the temperature minimum layer (T_{min} layer) or Winter

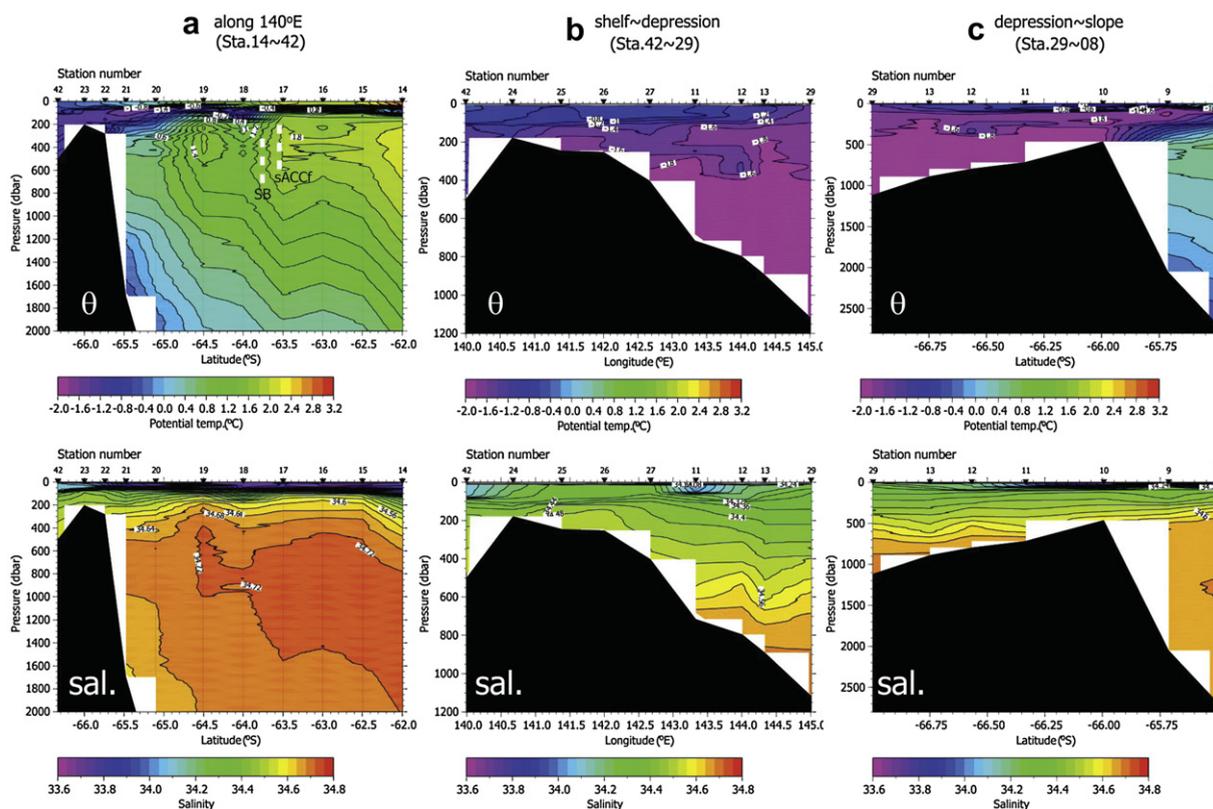


Fig. 5. Vertical profiles of temperature and salinity during the pelagic sampling. Fronts positions are indicated as white vertical dashed lines and the sACCf and the SB were located around Sta.17 and between Sta.17 and 18, respectively.

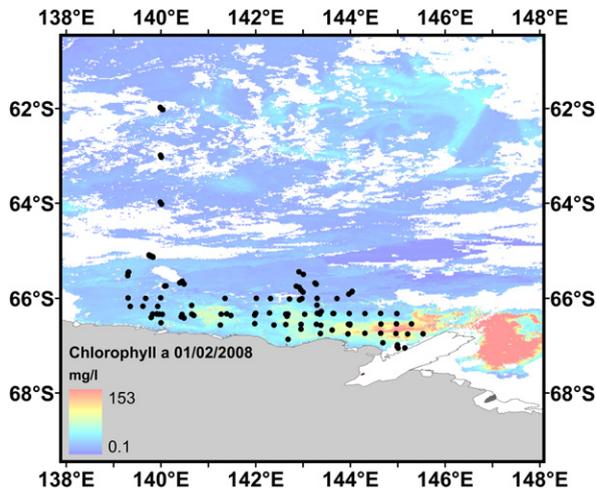


Fig. 6. Chl-a image compiled from 10–17 February 2008.

Water. Cold and relatively fresh AABW ($\gamma^n > 28.27 \text{ kg m}^{-3}$, $\theta > -1.7 \text{ }^\circ\text{C}$) was found offshore of the continental slope. MCDW with a neutral density range $28.03 < \gamma^n < 28.27 \text{ kg m}^{-3}$ occupied most deep layers between AASW and AABW. Only in the Adélie Depression at Stations 29, 13, 12, 11, and 10 was found the coldest and densest SW (defined by $\gamma^n > 28.27 \text{ kg m}^{-3}$ and $\theta < -1.7 \text{ }^\circ\text{C}$).

Chl-a image compiled from 10–17 February 2008 (Fig. 6) shows a high value in the cold water on the shelf south of 66°S on the shelf. Extremely high concentrations are found east of the MGT. Moreover, cyclonic eddies are identified between 62°S and 64°S

around 138°E, as shown in Hirawake et al. (2003) and Aoki and Akitomo (2007).

The shelf area is characterized by strong katabatic winds that influence surface water currents. Two major areas can be observed over the shelf (Fig. 7). The first one is west of Commonwealth Bay, which has less vertical stratification compared to the second zone east of this bay. MCDW enters the Adélie Depression through the sill and follows the eastern side of the basin towards the MGT. The high salinity Shelf Water, produced by cooling and seaice formation in winter, was also found on the eastern side of the basin (deeper than the incoming MCDW) during CEAMARC. Water over the shallow banks was mostly Antarctic surface water (relatively fresh, compared to MCDW and HSSW).

3.2. Species diversity

For the demersal trawling by RV Aurora Australis, 65 species were identified. They mainly belong to the Notothenioidei (including 4 families) followed by Liparidae and Zoarcidae. 49 species were found in the pelagic samplings of which 27 were common with those collected using demersal sampling equipment from RV Aurora Australis. Among them notothenioids (44% of species) were the most diverse with pelagic life stages for each of the four families found in the area. Some species are not only pelagic as larvae but also as juveniles or even as adults. *Pleuragramma antarcticum* dominates at more than 99% over the

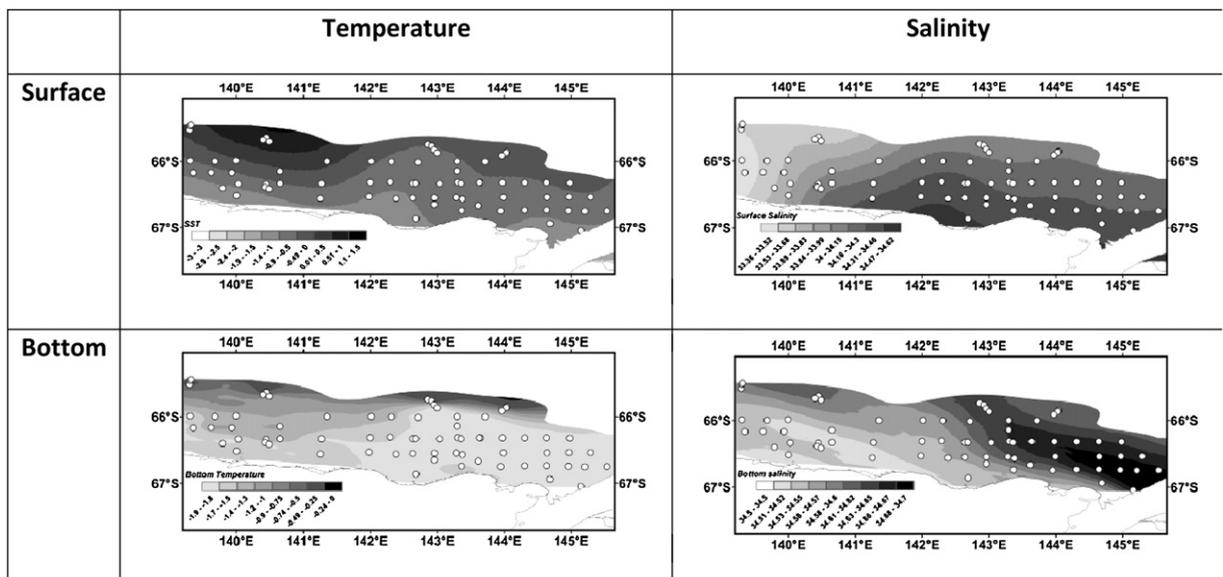


Fig. 7. Spatial distribution of temperature and salinity at surface and near the bottom from the benthic survey of the RV Aurora Australis.

shelf. Myctophid or Lantern fish is the most diverse family with 11 species for the oceanic zone. Many families of the deep oceanic zone had one or two species.

3.3. Numerical analysis

A set of seven non-correlated variables were identified for demersal trawls: depth; rugosity; gravel; surface salinity; mud; chlorophyll concentration; and bottom salinity. The GDM explained 40.7% of the variance and four variables were retained in the model: depth; surface salinity; rugosity; and gravel in order of decreasing importance (Fig. 8). Fish community changed along the depth and rugosity gradients, whereas the other environmental parameters impacted it from a certain threshold: surface salinity from 34.3; and gravel from 10%.

The optimal number of clusters were chosen according to the four indexes. Seven clusters were chosen three times from the following indexes (Calinski and Harabasz, Xu and Hartigan) and three clusters once (Ball and Hall). Clusters three- and four showed the maximum number of species. It corresponds to the depressions and surrounding slopes. At the opposite, clusters 6 and 1 have the lowest number of species.

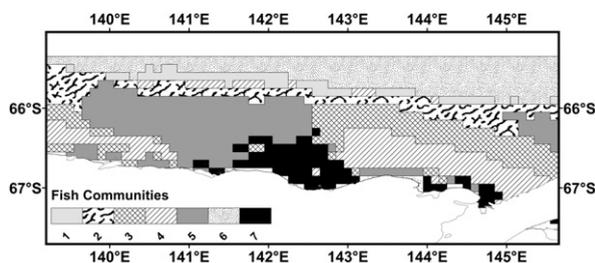


Fig. 9. Benthic ecoregions based on fish assemblages (clusters) and abiotic factors.

They are located on the shelf break (Fig. 9). The other clusters are on the banks and near the coastal zone.

Fig. 10 shows the ranges of environmental parameters for each cluster. Depth separates clusters 1 and 6 from the others, 6 being the deepest and in the oceanic zone. Cluster 4 corresponds to depressions and is the next deepest one. Clusters 5 and 7 are the shallowest, they correspond to the banks and bays. Rugosity is maximum for cluster 1 corresponding to the shelf break; it is important in clusters 4, 6 and 7. Concerning gravel, the percentage is higher in clusters on the shelf break (1, 2 and 6), which is the opposite for mud that are higher in depressions and bays (clusters 3, 4 and 7). Surface salinity is very high in cluster 7 in the

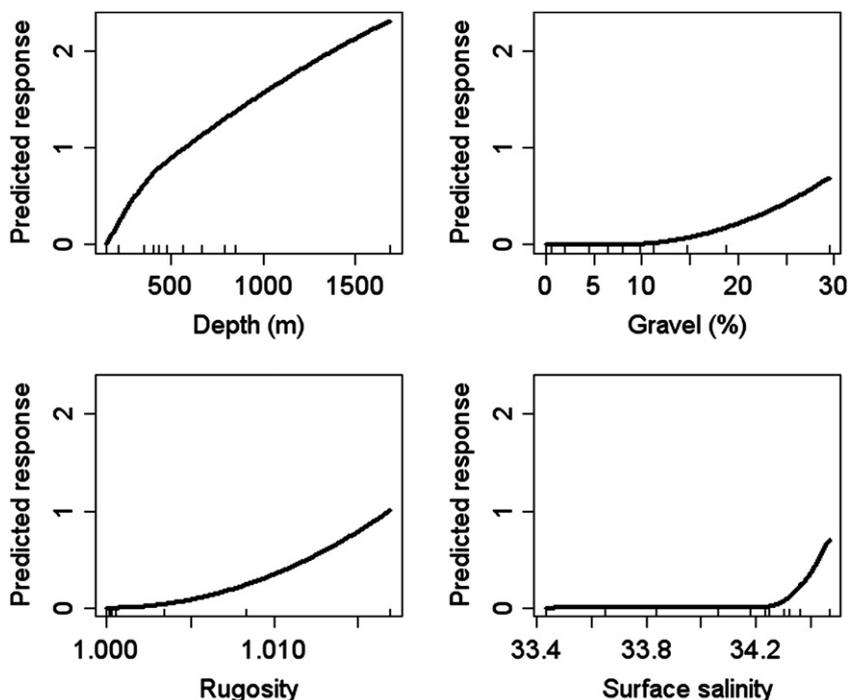


Fig. 8. Predicted response according to GDM towards the environmental factors kept for the analysis.

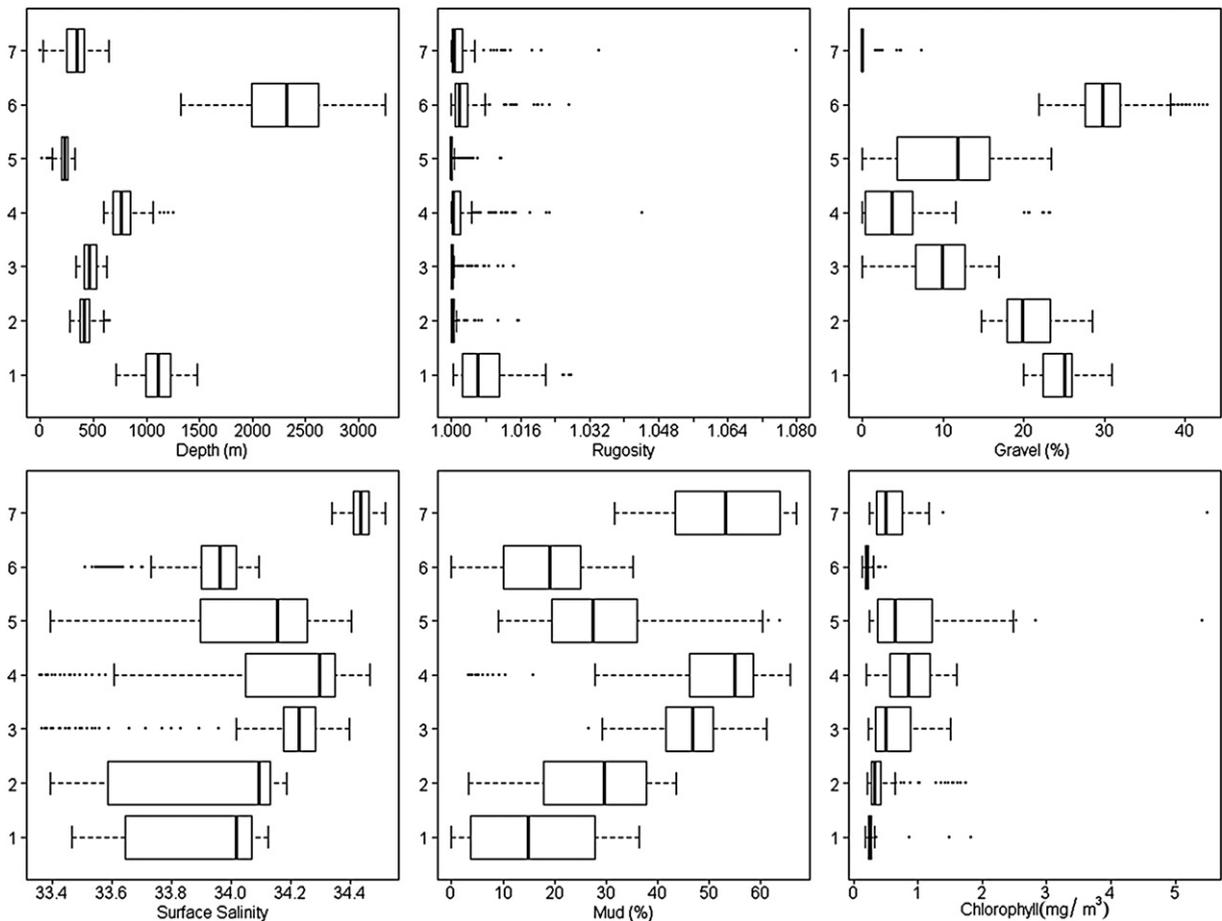


Fig. 10. Tukey plots of environmental factors per benthic ecoregions (clusters from the analysis).

Commonwealth, Watt and Buchanan Bays, and low for the shelf break and oceanic zone but with big ranges of values. Chlorophyll shows some differences between clusters, with the lowest values for the shelf break and oceanic zone (1, 2 and 6).

Table 2 gives the species richness per ecoregions obtained on the RV Aurora Australis demersal fish samples.

Some species are present in every cluster, such as *Pleuragramma antarcticum* or *Trematomus* sp.1 (either *Trematomus lepidorhinus* or *Trematomus loenbergii*) (Table 3). Quite a lot of species are absent from clusters 1 and 6, corresponding to the shelf break and the oceanic zone. Beside the two ubiquitous species, the other species of these two clusters are mainly meso-

Table 2

Number of fish species per benthic ecoregions.

Cluster	1	2	3	4	5	6	7
No. species	9	21	32	39	24	9	16

and bathypelagic fishes belonging to Myctophidae, Bathylagidae and Gonostomatidae. Other families are also present but with one species each (*Channichthyidae*, *Liparidae*, *Zoarcidae*).

For the pelagic samplings, temperature and salinity were kept as explanatory variables in the model. GDM explained 53.7% of the variance (Fig. 11). Salinity was the parameter that explained the most of the change in fish community. Seven clusters were retained as the optimal number. GDM was applied to predict communities along each transect of the pelagic sampling.

The regionalization separates the shelf (Fig. 12), the shelf break and the oceanic zone, showing also differences between surface and deep layers. Clusters 1 and 2 are typical of the shelf and extend to the epipelagic zone to the north (of the study area?). It is replaced by cluster 7 north of 64°S. Clusters 4 and 3 start at the shelf break but extend to the oceanic zone. Cluster 4 forms a band varying in depth between 200 to

Table 3
Distribution of fish species according to the benthic ecoregions.

Cluster	1	6	2	5	4	3	7
<i>Pleuragramma antarcticum</i>	1	1	1	1	1	1	1
<i>Trematomus</i> sp.1	1	1	1	1	1	1	1
<i>Artedidraco loennbergii</i>	0	0	1	1	1	1	1
<i>Chionodraco hamatus</i>	0	0	1	1	1	1	1
<i>Lycodichthys antarcticus</i>	0	0	1	1	1	1	1
<i>Pagetopsis maculatus</i>	0	0	1	1	1	1	1
<i>Racovitzia glacialis</i>	0	0	1	1	1	1	1
<i>Trematomus eulepidotus</i>	0	0	1	1	1	1	1
<i>Trematomus scotti</i>	0	0	1	1	1	1	1
<i>Artedidraco shackletoni</i>	0	0	0	1	1	1	1
<i>Paraliparis leobergi</i>	0	0	0	1	1	1	1
<i>Cygnodraco mawsoni</i>	0	0	1	1	1	0	1
<i>Histiodraco velifer</i>	0	0	0	1	0	1	1
<i>Chionobathyscus dewitti</i>	1	0	0	0	1	0	1
<i>Acanthodraco dewitti</i>	0	0	0	0	0	0	1
<i>Trematomus hansonii</i>	0	0	0	0	0	0	1
<i>Electrona antarctica</i>	1	1	1	0	1	0	0
<i>Macrourus whitsoni</i>	1	1	1	0	1	0	0
<i>Bathylagus antarcticus</i>	1	1	1	0	0	0	0
<i>Cyclothone</i> sp.	0	1	1	0	0	0	0
<i>Careproctus</i> sp.	1	1	0	0	0	0	0
<i>Gymnoscopelus opisthopterus</i>	0	1	0	0	0	0	0
<i>Oidiphorus mcallisteri</i>	0	1	0	0	0	0	0
<i>Cryodraco antarcticus</i>	0	0	1	1	1	1	0
<i>Trematomus tokarevi</i>	0	0	0	1	1	1	0
<i>Pachycara brachycephalus</i>	0	0	1	1	1	0	0
<i>Chaenodraco wilsoni</i>	0	0	0	1	1	0	0
<i>Prionodraco evansii</i>	0	0	1	1	0	1	0
<i>Artedidraco skottsbergi</i>	0	0	0	1	0	1	0
<i>Pagetopsis macropterus</i>	0	0	0	1	0	1	0
<i>Pogonophryne</i> sp.1	0	0	0	1	0	1	0
<i>Gymnodraco acuticeps</i>	0	0	0	1	0	0	0
<i>Trematomus newnesi</i>	0	0	0	1	0	0	0
<i>Trematomus pennellii</i>	0	0	0	1	0	0	0
<i>Neopagetopsis ionah</i>	1	0	1	0	1	1	0
<i>Akarotaxis nudiceps</i>	0	0	0	0	1	1	0
<i>Chionodraco myersi</i>	0	0	0	0	1	1	0
<i>Dacodraco hunteri</i>	0	0	0	0	1	1	0
<i>Dolloidraco longedorsalis</i>	0	0	0	0	1	1	0
<i>Edentoliparis terraenovae</i>	0	0	0	0	1	1	0
<i>Gerlachea australis</i>	0	0	0	0	1	1	0
<i>Lycenchelys aratirostris</i>	0	0	0	0	1	1	0
<i>Ophthalmolycus amberensis</i>	0	0	0	0	1	1	0
<i>Paraliparis antarcticus</i>	0	0	0	0	1	1	0
<i>Paraliparis charcoti</i>	0	0	0	0	1	1	0
<i>Vomeridens infuscipinnis</i>	0	0	0	0	1	1	0
<i>Muraenolepis</i> sp.	0	0	1	0	1	0	0
<i>Paraliparis mawsoni</i>	0	0	1	0	1	0	0
<i>Bathyraco antarcticus</i>	0	0	0	0	1	0	0
<i>Bathyraco macrolepis</i>	0	0	0	0	1	0	0
<i>Bathyraco marri</i>	0	0	0	0	1	0	0
<i>Lycenchelys tristichodon</i>	0	0	0	0	1	0	0
<i>Lycodapus pachysoma</i>	0	0	0	0	1	0	0
<i>Pogonophryne macropogon</i>	0	0	0	0	1	0	0
<i>Cryodraco australis</i>	0	0	0	0	0	1	0
<i>Trematomus bernacchii</i>	0	0	0	0	0	1	0

Table 3 (continued)

Cluster	1	6	2	5	4	3	7
<i>Paraliparis valentinae</i>	0	0	1	0	0	0	0
<i>Protomyctophum bolini</i>	1	0	0	0	0	0	0
<i>Artedidraco orianae</i>	0	0	0	0	0	0	0

400 meters. Cluster 3 is deeper than cluster 4 (from 400 to 600 m), and follows the slope of the continental shelf to the south (into the Adelie Depression). Clusters 5 and 6 are the deepest ones and are found only in the oceanic zone north of 65° 20'S. We can observe a dome in transect 1 where all deep layers are shifted to the surface at 65° 30'S, and a similar pattern is observed at 63°S but it is weaker.

There is a sharp transition of temperatures between clusters 1 and 2 over the shelf and the other clusters to the north in the oceanic zone (Fig. 13).

Pelagic fish species is listed for each cluster (Table 4). *Krefflichthys anderssoni* is the only species found in cluster 7. The other species can be divided into two main groups, the ones from the shelf which extend to the shelf break. They are notothenioids and include mainly larval and juveniles stages. Cluster 3 marks the transition between the neritic assemblages and the oceanic ones. The other clusters are mainly dominated by meso- and bathypelagic fishes. Deep species (with very few specimens for each) were observed in cluster 6. We can see that most of the common mesopelagic species occur at all the depths that were investigated.

4. Discussion

Historic surveys had listed about 15 fish species (Blanc, 1961; Hureau, 1962, 1966; Hureau and Arnaud, 1964). In more recent years, the BROKE East survey had found 21 species using pelagic sampling (Hoddell et al., 2000) whereas the French ICO²TA project had identified also 21 species but mainly demersal species. With CEAMARC, the total species number found is 91 species belonging to 21 families. This shows the importance of having integrated surveys dedicated to the census of the marine fauna in order to estimate the species diversity. 51% of the species belonged to the Notothenioids and are followed by Myctophids, Liparidae and Zoarcidae. Several species were caught only occasionally during the survey, such as *Oneirodes notius*, *Anotopterus pharao* or *Mancopsetta maculata*. Their apparent rarity in the survey may reflect a bias towards sampling shallower sites rather than genuine rarity, as some of

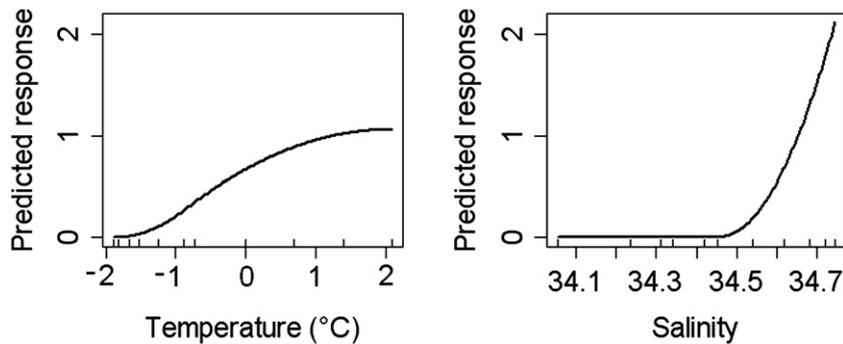


Fig. 11. Predicted response of GDM from temperature and salinity for the pelagic sampling transects.

these species are known to be common in the deep sea of other oceans. However, these intensive surveys were not able to collect all potential species, such as *Dissostichus mawsoni* or skates. Skates were seen on videos over the shelf or in the coastal zone but avoided the beam trawl and none, except one egg, was caught. Another important species for the area is *D. mawsoni*, this species was caught by CCAMLR experimental fishing in the area by longliners. We did not collect it during CEAMARC because the beam trawl is not suitable to catch them; another reason is the limited sampling effort on the continental margin.

The pelagic regionalisation was more relevant for the oceanic zone than for the shelf area, this was clearly related to the different water masses observed. Influence of the vertical structure of the water masses from north to the south was observed on transect 1. It

corresponds to frontal zones associated with the southern boundary and to the shelf break front. Deeper layers are also well separated. Over the shelf, there is only a slight difference between the upper 50 m layer and the rest of the water mass. Transect 3 goes from the Adélie Depression to the shelf break and oceanic zone throughout a sill of 400 m depth. There, the structure of communities is complex, probably due to the particular hydrology of this area; it is where the Adélie Land Bottom Water flows off the Adélie Depression and where the MCDW enters the basin. The diversity is quite important as there is a mixing of different species assemblages in a limited space due to this complex hydrology.

The benthic regionalisation based on demersal fish shows a clear difference between continental margins, inner-shelf depressions, banks and coastal zones. In terms of species, 33 have been recorded in George V Basin and 24 in the Adélie Basin. The two basins dominate the region in fish diversity. There are 20 species that are common to both basins. Seven species were caught specifically in the George V Basin and not elsewhere, namely *Bathyraco antarcticus*, *B. macrolepis*, *B. marri*, *Dacodraco hunteri*, *Dolloidraco longedorsalis*, the rare *Lycodapus pachysoma*, *Pogonophryne* sp.1 (cf. macropogon) which is very rare too. Only few specimens of the genus *Pogonophryne* were sampled in this area. The George V Basin may be richer in species because the sampling effort is three times more than the one of the Adélie Basin. But, we assume that it is not the unique reason. The main difference between these two areas is that George V Basin is a unique place where there is a permanent polyna, and complex water masses due to the formation of Antarctic bottom waters and because it is limited to the north by a sill. For the Adélie Basin, it is the opposite as this depression is not limited by a sill at the level of the continental margin. There, *Lycenchelys tristichodon* and *Trematomus newnesi* have been

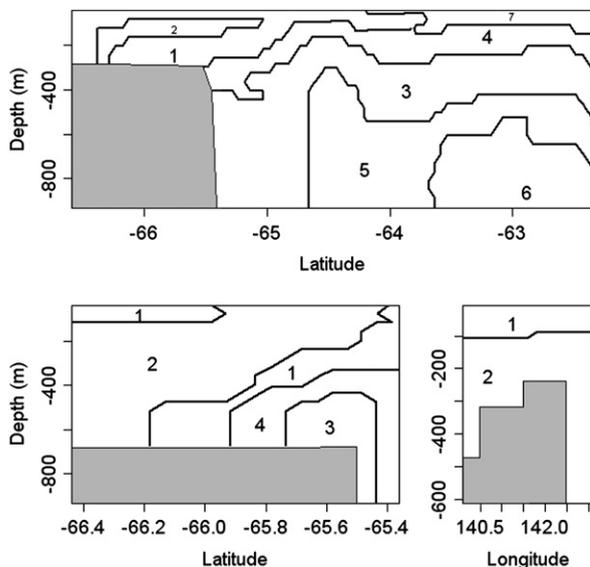


Fig. 12. Pelagic ecoregions based on fish assemblages (clusters) and abiotic factors along transects 1, 2 and 3. Transect 4 is homogeneous vertically and horizontally and was not drawn.

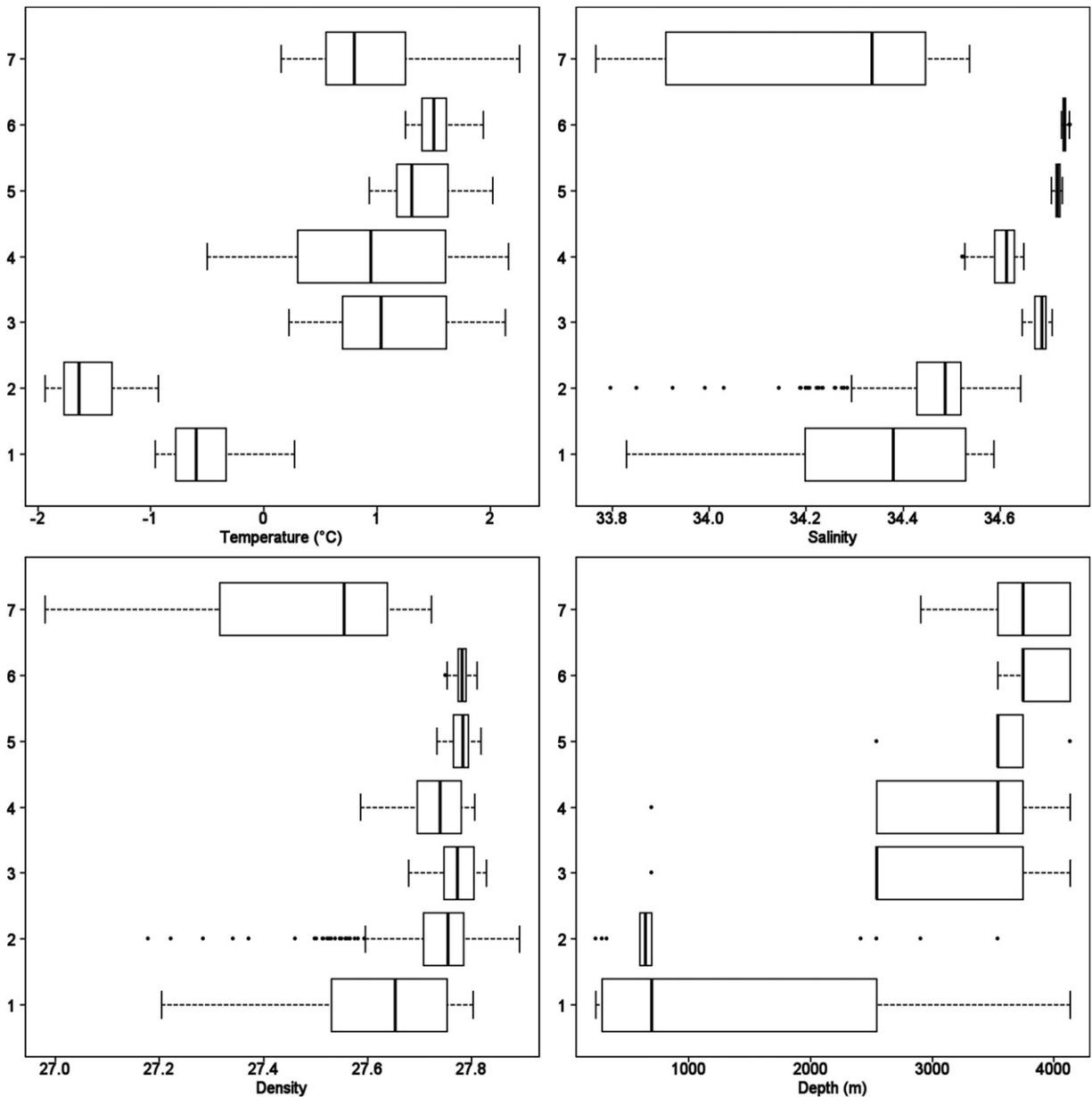


Fig. 13. Tukey plots of abiotic factors of the pelagic ecoregions.

specifically caught. *T. newnesi* was at the lower limit of its bathymetric distribution (400 m). This species is very abundant in the coastal zone of Dumont d’Urville station where we observe schools of juveniles.

The Adélie Bank is the second most investigated area with 17 stations. 23 species have been recorded; two have been specifically caught in this zone : *Gymnodraco acuticeps* and *Trematomus pennellii*. Both species have been caught at low depths (150–230 m) on the southwestern part of the bank (i.e. not far from Pointe Geologie Archipelago). Apart from these two

species, all other species are recorded both on the slopes and on the bottom of Adélie and George V Basins, suggesting a wide range of bathymetric distribution. The Mertz Bank was less investigated compared to the Adélie Bank.

The continental margin includes transects through four canyons (800–2000 m depth). 20 different species have been recorded. Some mesopelagic species were also recorded in these samples. All species are specific to these canyons and are not recorded at equivalent depths inside the basins. This means that they are

Table 4
Fish species according to pelagic ecoregions.

Species/ Cluster	1	2	3	4	5	6	7
<i>Pagetopsis maculatus</i>	1	0	0	0	0	0	0
<i>Pogonophryne</i> sp.	1	0	0	0	0	0	0
<i>Gerlachea australis</i>	0	1	0	0	0	0	0
<i>Anotopterus pharao</i>	0	1	0	0	0	0	0
<i>Trematomus newnesi</i>	1	1	0	0	0	0	0
<i>Trematomus nicolai</i>	1	1	0	0	0	0	0
<i>Trematomus pennellii</i>	1	1	0	0	0	0	0
<i>Trematomus</i> sp.1	1	1	0	0	0	0	0
<i>Prionodraco evansii</i>	1	1	0	0	0	0	0
<i>Artedidraco shackletoni</i>	1	1	0	0	0	0	0
<i>Artedidraco skottsbergi</i>	1	1	0	0	0	0	0
<i>Cryodraco antarcticus</i>	1	1	0	0	0	0	0
<i>Chaenodraco wilsoni</i>	1	1	0	0	0	0	0
<i>Racovitzia glacialis</i>	1	1	1	0	0	0	0
<i>Pleuragramma antarcticum</i>	1	1	1	0	0	0	0
<i>Dacodraco hunteri</i>	1	1	1	0	0	0	0
<i>Edentoliparis terraenovae</i>	1	1	1	0	0	0	0
<i>Chionodraco</i> sp.	1	1	1	0	0	0	0
<i>Neopagetopsis ionah</i>	1	1	1	1	0	0	0
<i>Pseudochaenichthys georgianus</i>	0	0	1	0	0	0	0
<i>Paradiplospinus gracilis</i>	0	0	1	0	0	0	0
<i>Mancopsetta maculata maculata</i>	0	0	1	0	0	0	0
<i>Muraenolepis</i> sp.	0	0	1	1	0	0	0
<i>Gymnoscopelus opisthopterus</i>	0	0	1	1	1	0	0
<i>Notolepis</i> sp.	0	1	1	1	1	1	0
<i>Protomyctophum bolini</i>	0	1	1	1	1	1	0
<i>Electrona antarctica</i>	0	1	1	1	1	1	0
<i>Bathylagus</i> sp.	0	1	1	1	1	1	0
<i>Cyclothone</i> sp.	0	1	1	1	1	1	0
<i>Krefftichthys anderssoni</i>	0	0	1	1	1	1	1
<i>Cynomacurus pirei</i>	0	0	1	0	1	1	0
<i>Gymnoscopelus braueri</i>	0	1	1	0	1	1	0
<i>Electrona carlsbergi</i>	0	0	0	0	1	0	0
<i>Benthalbella elongata</i>	0	0	1	0	1	0	0
<i>Gymnoscopelus bolini</i>	0	0	1	0	1	0	0
<i>Lampanyctus achirus</i>	0	0	0	0	1	1	0
<i>Poromitra crassiceps</i>	0	0	0	0	1	1	0
<i>Benthalbella macropinna</i>	0	0	0	0	0	1	0
<i>Chiasmodon niger</i>	0	0	0	0	0	1	0
<i>Oneirodes notius</i>	0	0	0	0	0	1	0
<i>Lampanyctus macdonaldi</i>	0	0	0	0	0	1	0
<i>Gymnoscopelus microlampas</i>	0	0	0	0	0	1	0
<i>Gymnoscopelus nicholsi</i>	0	0	0	0	0	1	0

clearly associated with the deep oceanic environment and do not colonize inner-shelf depressions. Many reasons can be given: low temperatures and probably competition with inner-shelf species living at the same depth. Eight species are specific to the canyons, such as *Careproctus longipectoralis*, *Chionobathyscus dewitti*, *Macrourus whitsoni*, *Muraenolepis* sp., *Oidiphorus mcallisteri*, *Pachycara* sp., *Paraliparis valentinae* and *Zoarcididae* sp.

The coastal zone was poorly investigated. Common coastal species occurring in the Pointe Geologie Archipelago are almost totally absent in CEAMARC

records whilst they are very abundant in this area. They are mainly: *Trematomus pennellii*, *T. bernacchii*, *T. hansonii*, *T. newnesi*, *Gymnodraco acuticeps*, *T. nicolai*; *P. borchgrevinki*. Most of them were described by Hureau (1966) and Hureau et al. (2000). We can notice that one of the very common species of the nearshore zone, *Notothenia coriiceps*, is absent from CEAMARC catches.

The benthic regionalisation based on fish was in accordance with previous regionalisation of the eastern part of this area (Beaman and Harris, 2003). Is it related to recent environmental features or to past environment? Probably both. The seabed morphology records the extent and nature of the past glacial ice-sheets (Post et al., in press). Fluting along the axis of Mertz Trough east of Mertz Bank (Barnes, 1987), and the Adélie Depression (Beaman and Harris, 2005) indicates that these shelf troughs were occupied by ice streams during past glaciations. The Mertz moraine, which rims the southern margin of the Mertz Bank, marks the edge of the ice shelf as it advanced across the shelf during the last glaciation (Barnes, 1987; Domack et al., 1989). The over-consolidated nature of the bank-top sediments suggests that the banks may have contained grounded shelf ice for much or all of the last glaciation (Eitrem et al., 1995), however, the occurrence of moraines along the southern margins of the Mertz and Adélie Banks suggests that significant areas of the banks remained ice free during the last glaciation. Any stationary bank ice would have lifted during the early stages of deglaciation as sea-level rose (after ~17 ka) (Ingólfsson et al., 1998). Cores from Mertz Drift, in the western part of the Adélie Depression, indicate that the onset of open marine sedimentation in this part of the basin commenced ~12ka with massively bedded, siliceous mud and diatom ooze deposited as the ice shelf retreated towards the coast (Harris et al., 2001; Presti et al., 2003). Coastal ice may have retreated as late as 8 ka (Ingólfsson et al., 1998). These patterns imply contrasts across this shelf in terms of the timing of ice retreat and in the processes that have created the shelf morphology. After this past glacial maximum, vast inner-shelf depressions were then left open to colonization, and as they are deep and mostly sheltered from iceberg scouring, a rich and diverse fauna developed. It is probably why they are more diverse than the shallower bank areas. The benthic community results are presently being analysed and these results will be used to define species habitat boundaries and the role of disturbance by icebergs on species niches and the consequences on their life traits.

Ecoregionalisation based on fish showed that for the Southern Ocean, fish are good indicators of the pelagic and benthic regions of an oceanic zone. However, if pelagic fish were relevant for the oceanic zone, they were not for the shelf area because of the high dominance of *P. antarcticum* in the samples. The only other pelagic neritic species are larval or juvenile stages of Channichthyidae or Arctedraconidae. Over the shelf, the niche segregation of notothenioids linked to the species flock supposed for this group, gives good results about the benthic regionalization. However, for most of the species, they were found in few areas probably because of their high territoriality and habitat specialization.

This study showed that existing large-scale regionalizations are not adequate for the East Antarctic continental shelf and its surrounding oceanic zone. The marine Ecoregions of the World do not recognize any fine-scale regions within the shelf area (Spalding et al., 2007). We showed that there is an easy way of separating shelf regions based on the separation between inner-shelf depressions, areas of deep water formation, continental margins and banks. The influence of glaciers has to be more studied in more detail as glacial tongues provide sheltered areas when they are stable but they can also become areas of great disturbance due to iceberg release. Our results showed that the intermediate disturbance hypothesis (Gutt et al., 2007) can explain what we observed on fish, with an increase of diversity in deeper layers where disturbance has less chance to occur. For the oceanic zone, Longhurst (1998) considers this area as a unique province, the Austral Polar Province. The bioregionalisation held by CCAMLR provides some information but not at the resolution of the CEAMARC study (Grant et al., 2006). However, our results are in accordance with the findings of the BROKE East surveys (Hoddell et al., 2000).

Ecoregionalisation is a combination of regional oceanographic features and biogeography. We showed here that the past glacial environment is also important for understanding the marine biodiversity of the continental shelf. The recolonisation of the shelf after Last Glacial Maximum is one of the most challenging questions we have to answer in order to determine if the colonization occurred from the continental margin itself or from shelter sites over the shelf that were not covered by ice, as discussed by Thatje (2005). Some questions have to be assessed for the future environmental setting. The Mertz Glacier Tongue showed signs of rupture and broke in February 2010 releasing a large iceberg (IPY n°81 CRAC-ICE – IPEV 1050: Collaborative Research into Antarctic Calving and

ICeberg Evolution). What will happen as it influences the hydrodynamism in the George V Basin.

What have we learned from CEAMARC? We created a network of international experts in different sciences. Three countries have organized the surveys in this area with three ships to study the pelagic and benthic environment. To help explain the diversity, we will share results via SCAR-MarBIN to allow mapping of potential species habitat and communities. This will allow us to predict what will be the consequences of environmental changes in this area. The list of species known for this area increased for all the taxa, especially for fish but also for gelatinous plankton and benthos. However, we are still limited in our knowledge of the environment by what happens in winter or in the very deep layers of the continental margins.

Acknowledgements

We would like to acknowledge crew and captains of RV Aurora Australis and T/RV Umitaka Maru. This research gathers many other scientists and students who worked on plankton and benthos, and they provided us with great help onboard. Alix Post publishes with the permission of the Chief Executive Officer, Geoscience Australia. Funding sources were from CAML, TUMSAT, IPEV (ICOTA: Ichtyologie Côtière en Terre Adélie, PI: Philippe Koubbi and Catherine Ozouf-Costaz), AAD, ANR Antflocks (PI: Guillaume Lecointre), ANR GLIDES (PI: Charles-André Bost), ZA CNRS Antarctique (PI: Marc Lebouvier). This work is a contribution to CAML and SCAR-MarBIN. Philippe Koubbi would like to thank CAML (Michael Stoddart and Victoria Wadley). We would like to acknowledge Professor Mitsuo Fukuchi at National Institute of Polar Research whose previous JARE STAGE program time-series multi-ship survey in the Indian sector of the Antarctic Ocean, which extended into the CEAMARC area, was an important foundation for CEAMARC and encouraged the participation of Japan in this collaborative survey. We also like to thank Prof. Fukuchi and the local organizing committee of the SCAR Biology Symposium for their support.

References

- Anderson, M.E., 1991. Studies on the Zoarcidae, (Teleostei:Perciformes) of the southern hemisphere. V. Two new species from the Weddell Sea, Antarctica. *Cybius* 15, 151–158.
- Andriashev, A.P., 2003. Liparid fishes (Liparidae, Scorpaeniformes) in the Southern Ocean and adjacent waters. In: Results of the Russian Antarctic Expeditions. 9. Exploration of the Fauna of the Seas, vol. 53. Zool. Institute, St Petersburg, p. 475 (61).

- Aoki, S., Akitomo, K., 2007. Observations of small-scale disturbances of the Subantarctic Front in the Indian Ocean sector. *Deep-Sea Res. Part I* 54, 320–339.
- Bakun, A., 2006. Wasp-waist populations and marine ecosystem dynamics: navigating the “predator pit” topographies. *Prog. Oceanogr.* 68, 271–288.
- Barnes, P.W., 1987. Morphological studies of the Wilkes Land continental shelf, Antarctica - glacial and iceberg effects. In: Eitrem, S.L., Hampton, M.A. (Eds.), *The Antarctic Continental Margin: Geology and Geophysics of Offshore Wilkes Land*, CPCEMR Earth Science Series. Circum-Pacific Council for Energy and Mineral Resources, Houston, TX, pp. 175–194.
- Beaman, R.J., Harris, P.T., 2003. Seafloor morphology and acoustic facies of the George V Land shelf. *Deep-Sea Res. II* 50 (8–9), 1343–1355.
- Beaman, R.J., 2008. A bathymetric Digital Elevation Model (DEM) of the George V and Terre Adélie continental shelf and margin. CAASM: http://gcmd.nasa.gov/KeywordSearch/Home.do?Portal=amd_aud&MetadataType=0. (Data Set Text Search = GVdem_2008).
- Beaman, R.J., Harris, P.T., 2005. Bioregionalization of the George V Shelf, East Antarctica. *Continent. Shelf Res.* 25, 1657–1691.
- Blanc, M., 1961. Poissons récoltés par le Dr. J. Isel au cours de la 8e expédition Antarctique française en Terre-Adélie (1957–1959) (Expéditions polaires françaises. Missions Paul-Emile Victor). *Bull. Muséum nat. Hist. Nat. Paris* 33 (4), 380–383. série 2.
- Collins, M.A., Xavier, J.C., Johnston, N.M., North, A.W., Enderlein, P., Tarling, G.A., Waluda, C.M., Hawker, E.J., Cunningham, N.J., 2008. Patterns in the distribution of myctophid fish in the northern Scotia Sea ecosystem. *Polar Biol.* 31 (7), 837–851.
- De Santis, L., Brancolini, G., Accettella, A., Cova, A., Caburlotto, A., Donda, F., Pelos, C., Zgur, F., Presti, M., 2007. New Insights into Submarine Geomorphology and Depositional Processes along the George V Land Continental Slope and Upper Rise (East Antarctica). 10th International Symposium on Antarctic Earth Sciences. U.S. Geological Survey, Santa Barbara, California, USA.
- Dettai, A., Lautredou, A.-C., Bonillo, C., Goimbault, E., Busson, F., Causse, R., Couloux, A., Cruaud, C., Duhamel, G., Denys, G., Hauteocour, M., Iglesias, S., Koubbi, P., Lecointre, G., Moteki, M., Pruvost, P., Tercier, S., Ozouf, C. The actinopterygian diversity of the CEAMARC cruises: Barcoding and molecular taxonomy as a multi level tool for new findings. *Deep Sea Res.*, in press.
- Dimitriadou, A., Dolnicar, S., Weingessel, A., 2002. An examination of indexes for determining the number of clusters in binary data sets. *Psychometrika* 67, 137–160.
- Domack, E.W., Jull, A.J.T., Anderson, J.B., Linick, T.W., Williams, C.R., 1989. Application of tandem accelerator mass-spectrometer dating to late Pleistocene–Holocene sediments of the east Antarctic continental shelf. *Quaternary Res.* 31, 277–287.
- Duhamel, G., Koubbi, P., Ravier, C., 2000. Day and night mesopélagique fish assemblages off the Kerguelen islands (Southern Ocean). *Polar Biol.* 23, 106–112.
- Eastman, J.T., McCune, A., 2000. Fishes on the Antarctic continental shelf: evolution of a marine species flock? *J. Fish. Biol.* 57, 84–102.
- Eitrem, S.L., Cooper, A.K., Wannesson, J., 1995. Seismic stratigraphic evidence of ice-sheet advances on the Wilkes Land margin of Antarctica. *Sediment. Geol.* 96, 131–156.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McCOVERTON, J., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Sobero'n, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Escutia, C., Warnke, D., Acton, G.D., Barcena, A., Burckle, L., Canals, M., Frazee, C.S., 2003. Sediment distribution and sedimentary processes across the Antarctic Wilkes Land margin during the Quaternary. *Deep Sea Res. II* 50, 1481–1508.
- Ferrier, S., Manion, G., Elith, E., Richardson, K., 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Divers. Distribut.* 13, 252–264.
- Fischer, W., Hureau, J.C., 1985. FAO Species Identification Sheets for Fishery Purposes: Southern Ocean, vol. II. FAO, Rome, Italy.
- Gon, O., Heemstra, P.C., 1990. Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa.
- Grant, S., Constable, A., Raymond, B., Doust, S., 2006. Bioregionalisation of the Southern Ocean: Report of Experts Workshop, Hobart, September 2006. WWF-Australia and ACE CRC.
- Growns, I., 2009. Differences in bioregional classifications among four aquatic biotic groups: implications for conservation reserve design and monitoring programs. *J. Environ. Manage.* 90, 2652–2658.
- Gutt, J., Koubbi, P., Eléaume, M., 2007. Megaépibenthic diversity off Terre Adélie (Antarctica) in relation to disturbance. *Polar Biol.* 30/10, 1323–1329.
- Harris, P.T., Brancolini, G., Armand, L., Busetti, M., Beaman, R.J., Giorgetti, G., Presti, M., Trincardi, F., 2001. Continental shelf drift deposit indicates non-steady state Antarctic bottom water production in the Holocene. *Marine Geol.* 179 (1–2), 1–8.
- Hirawake, T., Kudoh, S., Aoki, S., Rintoul, S.R., 2003. Eddies revealed by SeaWiFS ocean color images in the Antarctic Divergence zone near 140°E. *Geophys. Res. Lett.* 30 (9), 1458.
- Hoddell, R.J., Crossley, A.C., Williams, R., Hosie, G.W., 2000. The distribution of Antarctic pelagic fish and larvae (CCAMLR Division 58.4.1). *Deep-Sea Res. II* 47, 2519–2541.
- Hureau, J.C., Arnaud, P., 1964. Complément à la faune de poissons de Terre Adélie. *Bull. Inst. Océanogr. Monaco* 62 (1295), 14.
- Hureau, J.C., 1962. Poissons antarctiques récoltés au cours de la XIe expédition française en Terre Adélie (1960–1962). *Bull. Muséum Hist. Nat.* 34 (3), 228–238.
- Hureau, J.C., 1966. Biologie comparée de quelques poissons antarctiques (Nototheniidae). *Bull. Inst. Océanogr. Monaco* 68 (1391), 244.
- Hureau, J.-C., Koubbi, P., White, M., Vacchi, M., 2000. Ecological data on *Trematomus hansonii*, a coastal fish from Terre Adélie (Antarctica). In: Davison, W., Howard-Williams, C., Broady, P. (Eds.), *Antarctic Ecosystems: Models for Wider Ecological Understanding*. New Zeal. Nat. Sci., Canterbury University, Christchurch, pp. 96–100.
- ICES, 2005. Report of the Working Group on Habitat Mapping (WGMHM), 5–8 April, Bremerhaven, Germany. ICES CM 2005/E:05 87 pp.
- Ingólfsson, O., Hjort, C., Berkman, P.A., Björck, S., Colhoun, E., Goodwin, I.D., Hall, B., Hirakawa, K., Melles, M., Möller, P., Prentice, M.L., 1998. Antarctic glacial history since the Last Glacial Maximum: an overview of the record on land. *Ant. Sci.* 10, 326–344.

- Jackett, D.R., MacDougall, T.J., 1997. A neutral density variable for the world's oceans. *J. Phys. Oceanogr.* 27, 237–263.
- Koubbi, P., Hureau, J.-C., Vacchi, M., White, M., 1997. Results of the preliminary survey on the coastal distribution of fish larvae in Adelie land (Southern Ocean) during January–February 1996. *Cybiurn* 21 (4), 381–392.
- Koubbi, P., Duhamel, G., Hecq, J.H., Beans, C., Loots, C., Pruvost, P., Tavernier, E., Vacchi, M., Vallet, C., 2009. Ichthyoplankton in the neritic and coastal zone of Antarctica and Subantarctic islands 38th International Liège Colloquium on Ocean Dynamics – Revisiting the role of zooplankton in pelagic ecosystems, Liège (Belgique). *J. Mar. Syst.* 78 (4), 547–556.
- Koubbi, P., Moteki, M., Duhamel, G., Goarant, A., Hulley P.-A., O'Driscoll, R., Ishimaru, T., Pruvost, P., Tavernier, E., Hosie, G. Ecoregionalisation of myctophid fish in the Indo-Pacific sector of the Southern Ocean: results from generalized dissimilarity modeling. *Deep Sea Res.*, submitted for publication.
- Lautredou, A.-C., Bonilla, C., Denys, G., Cruaud, C., Ozouf-Costaz, C., Lecointre, G., Dettai, A., 2010. Molecular taxonomy and identification within the Antarctic genus *Trematomus* (Notothenioideae, teleostei): How valuable is barcoding with COI? *Polar Sci.* 4 (2), 333–352.
- Leathwick, J.R., Elith, J., Hastie, T., 2006. Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. *Ecol. Model.* 199, 188–196.
- Long, D., 2006. BGS detailed explanation of seabed sediment modified Folk classification. Accessible online at: http://ec.europa.eu/maritimeaffairs/emodnet/documents/standards/mesh_geology.pdf.
- Longhurst, A., 1998. *Ecological Geography of the Sea*. Academic Press, San-Diego.
- Lyne, V., Hayes, D., 2005. *Pelagic Regionalisation: National Marine Bioregionalisation Integration Project*. Australian Government National Oceans Office and CSIRO Marine Research.
- Nicol, S., Pauly, T., Bindoff, N.L., Strutton, P.G., 2000. “BROKE” a biological/oceanographic survey off the coast of East Antarctica (80–150°E) carried out in January–March 1996. *Deep-Sea Res. II*, 2281–2297.
- Orsi, A.H., Whitworth III, T., Nowlin Jr., W.D., 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Research* 42, 641–673.
- Post, A.L., Beaman, R.J., O'Brien, P.E., Eléaume, M., Riddle, M.J. Community structure and benthic habitats across the George V Shelf, East Antarctica: trends through space and time. *Deep Sea Res. II*, in press, doi: 10.1016/j.dsr2.2010.05.020.
- Presti, M., De Santis, L., Busetti, M., Harris, P.T., 2003. Late Pleistocene and Holocene sedimentation on the George V Continental Shelf, East Antarctica. *Deep Sea Res. II* 50, 1441–1461.
- Ribbink, A.J., 1984. Is the species flock concept tenable? In: Echelle, A.A., Kornfield, I. (Eds.), *Evolution of Fish Species Flocks*. University of Maine at Orono Press, Orono, pp. 21–25.
- Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Roberston, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* 57 (7), 573–583.
- Thatje, S.C.-D., 2005. Hillenbrand and R. Larter, On the origin of Antarctic marine benthic community structure. *Trends Ecol. Evol.* 20, 534–540.
- Vierros, M., Cresswell, I., Briones, E.E., Rice, J., Ardrón, J., 2008. *Global Open Oceans and Deep Seabed (GOODS) biogeographic classification*. UNEP/CBD/COP/9/INF/44, 92pp.
- Welsh, H.H., 1994. Bioregions: an ecological and evolutionary perspective and a proposal for California. *California Fish Game* 80 (3), 97–124.
- Whitworth, T., Orsi, A.H., Kim, S.J., Nowlin Jr., W.D., 1998. Water masses and mixing near the Antarctic Slope Front. In: Jacobs, S.S., Wiess, R.F. (Eds.), *Ocean, Ice, and Atmosphere: Interactions at the Antarctic Continental Margin*. Antarctic Research Series. American Geophysical Union, Washington, pp. 1–27.
- Wright, D.J., Lundblad, E.R., Larkin, E.M., Rinehart, R.W., Murphy, J., Cary-Kothera, L., Draganov, K., 2005. ArcGIS Benthic Terrain Modeler, Corvallis, Oregon, Oregon State University, Davey Jones Locker Seafloor Mapping/Marine GIS Laboratory and NOAA Coastal Services Center. Accessible online at: <http://www.csc.noaa.gov/products/btm/>.

