

Census of Antarctic Marine Life
SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

► CHAPTER 6.9. SOUTHERN OCEAN EUPHAUSIIDS.

Cuzin-Roudy J., Irisson J.-O., Penot F., Kawaguchi S., Vallet C., 2014.

In: De Broyer C., Koubbi P., Griffiths H.J., Raymond B., Udekem d'Acoz C. d', et al. (eds.). Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp. 309-320.

EDITED BY:

Claude DE BROYER & Philippe KOUBBI (chief editors)

with Huw GRIFFITHS, Ben RAYMOND, Cédric d'UDEKEM d'ACOZ, Anton VAN DE PUTTE, Bruno DANIS, Bruno DAVID, Susie GRANT, Julian GUTT, Christoph HELD, Graham HOSIE, Falk HUETTMANN, Alexandra POST & Yan ROPERT-COUDERT



SCIENTIFIC COMMITTEE ON ANTARCTIC RESEARCH

THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

The "Biogeographic Atlas of the Southern Ocean" is a legacy of the International Polar Year 2007-2009 (www.ipy.org) and of the Census of Marine Life 2000-2010 (www.coml.org), contributed by the Census of Antarctic Marine Life (www.caml.aq) and the SCAR Marine Biodiversity Information Network (www.scarmarbin.be; www.biodiversity.aq).

The "Biogeographic Atlas" is a contribution to the SCAR programmes Ant-ECO (State of the Antarctic Ecosystem) and AnT-ERA (Antarctic Thresholds- Ecosystem Resilience and Adaptation) (www.scar.org/science-themes/ecosystems).

Edited by:

Claude De Broyer (Royal Belgian Institute of Natural Sciences, Brussels)
Philippe Koubbi (Université Pierre et Marie Curie, Paris)
Huw Griffiths (British Antarctic Survey, Cambridge)
Ben Raymond (Australian Antarctic Division, Hobart)
Cédric d'Udekem d'Acoz (Royal Belgian Institute of Natural Sciences, Brussels)
Anton Van de Putte (Royal Belgian Institute of Natural Sciences, Brussels)
Bruno Danis (Université Libre de Bruxelles, Brussels)
Bruno David (Université de Bourgogne, Dijon)
Susie Grant (British Antarctic Survey, Cambridge)
Julian Gutt (Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven)
Christoph Held (Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven)
Graham Hosie (Australian Antarctic Division, Hobart)
Falk Huettmann (University of Alaska, Fairbanks)
Alix Post (Geoscience Australia, Canberra)
Yan Ropert-Coudert (Institut Pluridisciplinaire Hubert Curien, Strasbourg)

Published by:

The Scientific Committee on Antarctic Research, Scott Polar Research Institute, Lensfield Road, Cambridge, CB2 1ER, United Kingdom (www.scar.org).

Publication funded by:

- The Census of Marine Life (Albert P. Sloan Foundation, New York)
- The TOTAL Foundation, Paris.

The "Biogeographic Atlas of the Southern Ocean" shared the *Cosmos Prize* awarded to the Census of Marine Life by the International Osaka Expo'90 Commemorative Foundation, Tokyo, Japan.

Publication supported by:

- The Belgian Science Policy (Belspo), through the Belgian Scientific Research Programme on the Antarctic and the "biodiversity.aq" network (SCAR-MarBIN/ANTABIF)
- The Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium
- The British Antarctic Survey (BAS), Cambridge, United Kingdom
- The Université Pierre et Marie Curie (UPMC), Paris, France
- The Australian Antarctic Division, Hobart, Australia
- The Scientific Steering Committee of CAML, Michael Stoddart (CAML Administrator) and Victoria Wadley (CAML Project Manager)

Mapping coordination and design: Huw Griffiths (BAS, Cambridge) & Anton Van de Putte (RBINS, Brussels)

Editorial assistance: Henri Robert, Xavier Loréa, Charlotte Havermans, Nicole Moortgat (RBINS, Brussels)

Printed by: Altitude Design, Rue Saint Josse, 15, B-1210 Brussels, Belgium (www.altitude-design.be)

Lay out: Sigrid Camus & Amélie Blaton (Altitude Design, Brussels).

Cover design: Amélie Blaton (Altitude Design, Brussels) and the Editorial Team.

Cover pictures: amphipod crustacean (*Epimeria rubrieques* De Broyer & Klages, 1991), image © T. Riehl, University of Hamburg; krill (*Euphausia superba* Dana, 1850), image © V. Siegel, Institute of Sea Fisheries, Hamburg; fish (*Chaenocephalus* sp.), image © C. d'Udekem d'Acoz, RBINS; emperor penguin (*Aptenodytes forsteri* G.R. Gray, 1844), image © C. d'Udekem d'Acoz, RBINS; Humpback whale (*Megaptera novaeangliae* (Borowski, 1781)), image © L. Kindermann, AWI.

Online dynamic version :

A dynamic online version of the Biogeographic Atlas will be available on the SCAR-MarBIN / AntaBIF portal : atlas.biodiversity.aq.

Recommended citation:

For the volume:

De Broyer C., Koubbi P., Griffiths H.J., Raymond B., Udekem d'Acoz C. d', Van de Putte A.P., Danis B., David B., Grant S., Gutt J., Held C., Hosie G., Huettmann F., Post A., Ropert-Coudert Y. (eds.), 2014. Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, XII + 498 pp.

For individual chapter:

(e.g.) Crame A., 2014. Chapter 3.1. Evolutionary Setting. In: De Broyer C., Koubbi P., Griffiths H.J., Raymond B., Udekem d'Acoz C. d', et al. (eds.). Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp. xx-yy.

ISBN: 978-0-948277-28-3.



This publication is licensed under a Creative Commons Attribution-NonCommercial 4.0 International License

6.9. Southern Ocean Euphausiids

Janine Cuzin-Roudy^{1, 2}, Jean-Olivier Irisson^{1, 2}, Florian Penot^{1, 2}, So Kawaguchi³ & Carole Vallet⁴

¹ Sorbonne Universités, UPMC Univ Paris 06, UMR 7093, LOV, Observatoire océanologique, F-06230, Villefranche/mer, France

² CNRS, UMR 7093, LOV, Observatoire océanologique, F-06230, Villefranche/mer, France

³ Australian Antarctic Division, Channel Highway, Kingston Tasmania, 7050, Australia

⁴ Université d'Artois, Laboratoire d'Océanologie et de Géosciences, UMR 8187, Wimereux, France

1. Introduction

1.1. The family Euphausiidae

With 85 species, they are the major family of the order Euphausiacea (86 species). Known since ancient times to be present with baleen whales in Atlantic ocean and Mediterranean Sea (Pliny's *Naturalis Historiae*, circa AD 77-79), they were named "krill" (whale food) by Nordic whalers.

Euphausiidae belong to Crustacea, Malacostraca, Eucarida, Euphausiacea (Martin & Davis 2001) and are morphologically close to Mysida and decapod Natantia. They form a homogenous taxon and show slight differences in morphology, the caryotypes of euphausiids from Mediterranean (*Meganyctiphanes norvegica*) and from the Southern Ocean showed little variation in chromosome morphology, but differed from those of Decapoda or Peracarida, both in number and morphology (Thiriot-Quiévreux *et al.* 1998).

With the aim to relate the speciation of Antarctic and sub-Antarctic euphausiid species to the formation of the actual complex structure of the Southern Ocean (SO) through geological times, Zane & Patarnello (2000), suggested that the formation of the convergence at the northern limit of the Polar Front (PF) may have played a role in the separation of *Euphausia superba* and *E. crystallorophias* from the ancestor of *E. frigida* and *E. vallentini*, during a similar period (27.2 to 24.8 Mya). Jarman *et al.* (2000) proposed a similar cause for the more recent separation (about 10 Mya) of *E. triacantha* and *E. longirostris*. Recent results about euphausiid phylogeny have been revised by Tarling *et al.* (2010).



Photo 1 *Euphausia superba* Dana, 1850. Pelagic female krill feeding on summer phytoplankton. Image © V. Siegel, Thünen Institut für Seefischerei, Hamburg.

1.2. Southern Ocean species of Euphausiidae: diversity and biology

Mauchline & Fisher (1969), Mauchline (1980) have given the list and the global distribution of the 86 Euphausiacea species, among which 85 belonging to Euphausiidae. Baker *et al.* (1990) have produced a detailed key for their determination. Kirkwood (1982) proposed keys and maps of latitudinal distribution for 23 sub-Antarctic and Antarctic euphausiid species, including larval stages (*nauplius* I and II, *calyptopis* I to III, *metanauplius* and *furcilia* I to VI) for the principal species (*Euphausia crystallorophias*, *E. frigida*, *E. superba*, *E. triacantha*, and *Thysanoessa macrura*).

The principal biological characteristics of the 13 species represented in the data base are summarised in Table 1, with the corresponding references. The *Euphausia* species show similar traits concerning morphology, life cycle, behaviour (swarming, migrating), diet, reproduction and predators, but vary widely for adult size, life span, and various adaptations to the range of temperature of the SO.

Genus *Euphausia* Dana, 1852

E. crystallorophias Holt & Tattersall, 1906

This coastal species lives in cold water (below 0°C) and under ice-cover. Behaviour is gregarious in the neritic zone and swarming in the top 500 m of the water column on the shelf. Other biological characteristics are given in Table 1 with references.

E. frigida Hansen, 1911

Aggregating and performing diel vertical migrations (from 250–500 m depth by day to 50 m by night), the species resides in waters warmer than 0°C and has not been found under pack ice.

E. longirostris Hansen, 1908

The species is epipelagic and is known to be among the most carnivorous euphausiids, feeding on the copepod *Oitona* sp.

E. lucens Hansen, 1905

It is mostly distributed out of the SO, in Atlantic, Indian and Pacific Oceans.

E. similis G.O. Sars, 1885

The species distribution extends widely out of the SO. *E. similis* lives at depth during the day (from 0 to 300 m depth, off Japan, and deeper than 500 m in the Indo-Australian Archipelago.

E. similis var. *armata* Hansen, 1911

Distributed further North in the Southern Ocean than the typical form. It was not recorded in the present data set.

E. spinifera G.O. Sars, 1885

Its distribution is mostly out of the SO.

E. superba Dana, 1850 (Photo 1)

It is the largest euphausiid species: adults reach 60 mm and over at the end of their long (5 to 7 years) life cycle. *E. superba* is the most studied euphausiid species in the SO because its abundance and of an evident major role in the SO food web. Its biology and distribution are well documented since Bargmann (1945) and Marr (1962).

E. triacantha Holt & Tattersall, 1906

The species performs diel vertical migrations, from 750 m depth at day to 250 m at night, but does not form large swarms and is not recorded as prey for whales.

E. vallentini Stebbing, 1900

Swarming behaviour and diel vertical migrations from 100 m to 250 m depth by day, to near surface waters at night. Potential preys for small predators (Table 1).

Genus *Nematoscelis* G.O. Sars, 1883

N. megalops G.O. Sars, 1883

The species performs diel vertical migrations down to 300 m at night and is carnivorous, feeding preferentially on copepods, *Oitona* sp. Its distribution extends north in the Pacific and Indian Ocean and is found in north Atlantic.

Genus *Thysanoessa* Brandt, 1851.

The scarcity of *Thysanoessa* records in the SO appears linked to the difficulty to observe the specific characteristics of this small, fragile, species (antennules and elongated predatory legs), which are generally damaged in the net catches. The species determination has to be done by checking the proximal and terminal processes of the *petasma* in males (Kirkwood 1982) and the small body size of *T. vicina* reproducing females compared to larger mature females of *T. macrura* (J. Cuzin-Roudy unpubl. obs.). When recognised, their abundance in the samples raises a doubt about the apparent rarity of the species on the distribution maps, minimising its importance in the diet of top predators and for fisheries.

T. gregaria G.O. Sars, 1883

Most of its distribution is also situated north of the Sub-Antarctic Front (SAF).

T. macrura G.O. Sars, 1883

Aggregating and migrating, the species has an early reproduction in spring, is a prey for whales and is the most common, abundant and widespread circumpolar Southern Ocean species.

T. vicina Hansen, 1911 is a small species (max. length: 17 mm), with an aggregating behaviour. Abundant in catches with *T. macrura*, it is also a prey for whales. In former records, the species was found occasionally from 50° to 65°S, in the Polar Front (PF) and SAF, and more abundantly east of Falkland Islands, South of New Zealand and off Kerguelen Islands (Mauchline & Fisher 1969, Mauchline 1980), but often not distinguished from *T. macrura* and *T. gregaria*.

1.3. General pattern of euphausiid distribution

The present study concerns 13 species of krill living in the Southern Ocean, from which a large amount of data was collected during the last decades by 11 institutions from 7 nations (Table 2). Put together in an international data base, the whole data set cumulates information about the distribution of 13 species living in various sectors of the SO.

The overall distribution of the different species has been related to the circumpolar structure of the Southern Ocean water masses and currents (Bé *et al.* 1969, Kirkwood 1982) and to the sea-ice presence in the Antarctic Ocean.



Table 1 Biological characteristics of *Euphausiidae* living in the Southern Ocean.

	Vertical range	Temperature range	Swarming	Vertical migration	Adult size (mm)	Life span (years)	Spawning period (cycles)	Diet (adults)	Predators	References
Species living south of Antarctic Polar Front										
<i>Euphausia crystallorophias</i> Holt & Tattersall, 1960	Surface to 500 m	-1.8 to 0°C.	+	neritic	34.5(M) 41.5(F)	4(M) 5(F)	Nov.–Dec. (?) 1 to 2 cycles	Phytoplankton, detritus	Whales, seals, birds, fish, squids	1, 2, 3, 4, 5, 6, 7, 10
<i>Euphausia superba</i> Dana, 1850	Surface to 3000 m	-1.8 to 5 °C.	+	+	65		Dec.–April (1 to 3)	Phytopl. (diatoms, flagellates), zoopl. (copepods)	Whales, seals, birds, fish,	1, 2, 3, 4, 7 8, 10, 11, 13
<i>Thysanoessa vicina</i> Hansen, 1911	Surface to >250 m	0 to 8°C	+	+	17	5 to 7	Oct.– ? (1 ?)	Microzooplankton, detritus	Whales, birds fish, squids	1, 2, 7, 11
<i>Euphausia frigida</i> Hansen, 1911	50 to 500 m	-0.7 to 5°C.	+	+	24		Aug.–March	Microzooplankton, detritus	Whales, fish, squids	1, 3, 4, 8, 10, 11, 13,
<i>Thysanoessa macrura</i> G.O. Sars, 1883	Mesopelagic	-1.8 to 8°C	+	+	28.5	2	Sept.–Nov. (2)	Mesozooplankton, detritus	Whales, seals, birds, fish	1, 2, 3, 8 10, 11 8
<i>Euphausia triacantha</i> Holt & Tattersall, 1906	250 to 750 m	1.8 to 11.8°C	-	+	28–34	2+	Oct.– Nov. (1 to 2)	Mesozooplankton, detritus	Birds, fish, squids	1, 3, 7, 8, 10, 11, 13
Species living north of Antarctic Polar Front										
<i>Euphausia vallentini</i> Stebbing, 1900	100 to 200 m	2 to 10°C.	+	+	28	1+	Oct.–Nov.	Phytoplankton, some mesozooplankton	Penguins, birds, fish	1, 2, 3, 9, 11, 12, 14, 15, 17, 21
<i>Euphausia longirostris</i> Hansen, 1908	Epipelagic	3 to 16°C	+	?	21–34		?	Phytoplankton, microzooplankton	Birds, fish	1, 2, 14, 18
<i>Euphausia lucens</i> Hansen, 1905	Epipelagic	5 to 18°C	+	?	18	1+	Aug.–Nov. (multiple)	Phytoplankton dinoflagellates, copepods	Penguins, birds, fish	1, 2, 4, 14, 15, 16, 17
<i>Nematoscelis megalops</i> G.O. Sars, 1883	Epipelagic	Temperate	+	+	20–26	2	Feb.–July	Detritus, phytoplankton, dinoflagellates, zooplankton (larvae)	Whales, penguins, birds, fish	1, 2, 13, 17 1, 2, 11, 12, 18,
<i>Euphausia similis</i> G.O. Sars, 1883	Surface to 400 m	Temperate to Subtropical	+	+	22–26		Dec.–April	Flagellates, coccolithophorids zoopl. (copepods)	Penguins, birds, fish	1, 2, 14, 17, 19, 20
<i>Euphausia spinifera</i> G.O. Sars, 1883	Mesopelagic	6 to 19 °C.	+	+	21–29		?	Phytoplankton microzooplankton.	Birds, fish	1, 2, 9, 14, 16, 19, 20.
<i>Thysanoessa gregaria</i> G.O. Sars, 1883	Epipelagic	3 to 24°C	+	+	11–16		Aug.– Nov.	Phytoplankton, microzooplankton	Penguins	1, 2, 15, 17.

References. (1): Mauchline & Fisher 1969, (2): Mauchline 1980, (3): Siegel 1987, (4): Ross & Quetin 2000, (5): Pakomov & Perissinotto 1996, (6): Kear 1992, (7): Harrington & Thomas 1987, (8): Phleger 2002, (9): Perissinotto *et al.* 2001, (10): Taki *et al.* 2009, (11): Ward *et al.* 1990, (12): Gurney *et al.* 2001, (13): Ono *et al.* 2011, (14): Robertson *et al.* 1978, (15): Croxall *et al.* 1985; (16): Pilar & Stuart, (17): Ramirez *et al.* 1983, (18): Froneman *et al.* 2002; (19): Griffiths 1979, (20): Hirota *et al.* 1990.

During the austral winter, the sea-ice cover surrounds the whole continent, up to and including the Polar Front. In summer, sea-ice is still present in the Weddell Sea, along the coast west of the Peninsula and around the continent. Sea-ice habitat is favourable to the Antarctic Ocean euphausiids, especially for their larval and juvenile stages that feed on the under-ice small fauna (see Swadling, Chapter 6.12, Map 1, this volume).

Altogether, euphausiids occupy a vast latitudinal range between latitude 40°S, down to 78°S (for the coastal *E. crystallorophias*), in relation with the structure of the SO organised in circumpolar fronts, currents and seasonal sea ice cover (Thorpe *et al.* 2007, Atkinson *et al.* 2008). Few species occupy the entire latitudinal range, others are restricted to latitudinal zones which are, from North to South: the Sub-Tropical Front (STF, about latitude 40°S), the Sub-Antarctic Front (SAF, about 45°S), the Polar Front (PF, about 50°S), the Southern Antarctic Circumpolar Current Front (SACCF) and the Sea Ice Zone (SIZ), down to the shelf zone and coast of the continent (Rintoul *et al.* 2012). This latitudinal organisation is altered by the geography of the Antarctic continent and is particularly restricted between the Antarctic Peninsula and South America, thus enhancing the strength of the eastward Southern Antarctic Circumpolar Current (SACC) and creating the Weddell gyre. A vertical supply of nutrients to a surface mixed layer (Law *et al.* 2003) renders the SACCF suitable for euphausiids, abundant there.

The SACC insures an eastward circulation of the pelagic populations and consequently their mixing and a constant gene flow. Along the continental coast, the westward Antarctic Coastal Current (ACC) interacts in summer with sea ice retreat and transport of the broken coastal ice shelf. Current flows are more complex along the irregular coastline of the continent, where the SACC and the ACC interact with fronts and eddies (Pakhomov 2000). A series of gyres have been mapped around the continent, which are associated with stable concentrations of Antarctic krill (Nicol 2006).

For the different krill species, such concentrations indicate a favourable habitat, at least for part of their life cycle. Actually, for each species, larvae, juvenile and adult stages have different requirements concerning physical and trophic conditions, due to specific physiological, metabolic and functional adaptations. Consequently, they may rely successively on different suitable habitats to complete their life cycle.

The aim of the present study is to better understand which environmental conditions are favourable and to characterise which environmental variables

define suitable habitats, at least for the most abundant and most studied species.

2. Materials and methods

2.1. Data sources

The list of the Institutions contributing to the data base is presented in Table 2.

2.2. Sampling krill

The euphausiid species were sampled with different nets, depending on their body-size at different stages of their development: 1) Mid-water trawls: IKMT (progressive mesh size, up to 4.5 mm), now replaced by RMT 8 (mesh size: 4.5 mm) for catching adults of large species, 2) ORI nets (mesh size: 500 µm) for euphausiids of smaller size: 3 mm) RMT 1 (mesh size: 315 µm), often combined with the RMT 8 for larvae and zooplankton living in the same habitat; 3) WP2, Bongo nets (200 µm) and plankton recorder (CPR) for larvae and zooplankton.

2.3. Modelling spatial distribution of euphausiids

For each species, a multivariate modelling technique, namely “Boosted Regression Trees” (BRTs) was used to predict the “suitable habitat” of a species by regressing the observed presences-absences against biologically sensible local environmental variables (see Chapter 2.3: Distribution modelling).

Such models can capture complex, non-linear relationships between the environment and presences or absences. These relationships will be depicted by plots with a variable on the x-axis and the “marginal effect” of that variable on the logit of the probability of presence on the y-axis. A “marginal effect” means that all other variables are held constant, at their mean, and only the effect of the change in the focal variable is represented. The model is still multivariate and accounts for interactions, but the univariate effect of each variable represented on these plots is easier to understand. The logit transformation is usual for probabilities and brings them from [0, 1] to [-∞, +∞].

Once the relationships are established from observations, they can be used to predict “maps of habitat suitability” over the whole Southern Ocean, provided that the environmental conditions are known. These maps represent the probability of presence of the species based on the environment (i.e. whether the habitat is suitable or not).

Table 2 List of Institutions contributing to the database.

Code	Institution	Country
AAD	Australian Antarctic Division	Australia
AWI	Alfred Wegener Institute for Polar and Marine Research	Germany
TI-SF	Thünen Institut für Seefischerei	Germany
BAS	British Antarctic Survey	UK
CCAMLR	Commission for the Conservation of Antarctic Marine Living Resources	International Commission
LOV	Laboratoire d'Océanographie de Villefranche/mer	France
ULg	Université de Liège	Belgium
US AMLR	U.S. Antarctic Marine Living Resources	USA
WHOI	Woods Hole Oceanographic Institution	USA
YUG / YUGNIRO	Research Institute for Marine Fisheries and Oceanography	Ukraine
Japan Expedition	Not communicated	Japan

The datasets used to relate presence-absence to oceanic environmental conditions were summer climatologies (see Chapter 2.3). The variables as potentially influencing the presence of euphausiid species in a given environment, were: 1) proportion of the year during which the region is covered by sea ice; 2) mixed-layer depth; 3) concentration of surface chlorophyll a; 4) spatial gradient of sea surface height, which marks limits of front; 5) silicates concentrations at 0, 50 and 200 m depth; 6) nitrates concentrations at 0, 50 and 200 m; 7) oxygen saturation at 0, 50 and 200 m; 8) salinity at 0, 50 and 200 m; 9) temperature at 0, 50 and 200 m. For each species, the relevant variables were selected based on whether they make biological sense and, within those, whether they provide good explanatory power in the model. In marginal effects plots, variables were ranked according to the proportion of variance they explain in the model (they sum to 100%).

Some of these variables were only available for the open ocean and not for coastal regions, which explains the white areas on the maps of predicted suitability of habitat. In particular, variables at 200 m depth were not available near the coast. When such a variable was found to be of influence in the model, we could not infer what the prediction would be in the costal regions. This explains some of the white areas on the maps of predicted habitat suitability along the coasts.

The ability of the model to capture the patterns in the observations was quantified by the percentage of variance explained. The performance of the model in accurately predicting presence and absence was quantified by the Area Under the receiver operating characteristic Curve (AUC). An ideal model would predict 100% of presences and would never predict a presence when the species is absent, giving an AUC=1. A model with no discriminatory power would be right 50% of the time on average, just by chance, which would give an AUC of 0.5. A model with an AUC value greater than 0.7 is considered as "useful".

One hundred and fifty bootstraps of the data were used to draw 95% confidence intervals around the marginal effects plots. Bootstraps were also used to quantify the uncertainty in the prediction of habitat suitability. The chosen measure of uncertainty was the coefficient of variation (the ratio between the standard deviation and the mean of the 150 predicted values). The map of this uncertainty is represented next to the map of habitat suitability.

A total of 16,478 unique records of the presence of at least one species of euphausiids were available, at 14,397 unique locations, and all were used to fit the models. Modelling was based on presences and absences only, not abundance, because abundance data is very scarce. Even then, BRT modelling could only be performed for species with enough presence-absence data. Finally, even on these data-rich species, some models were not able to detect significant relationships between presence-absence and the available environmental variables. BRT modelling could be conducted successfully for 5 species.

As most of the data were collected in the pelagic habitat in summer, the habitat suitability model concerned mostly juvenile and adult euphausiids of the pelagic realm and environmental and trophic summer conditions, which generally correspond to the season of reproduction and larval recruitment.

3. Results

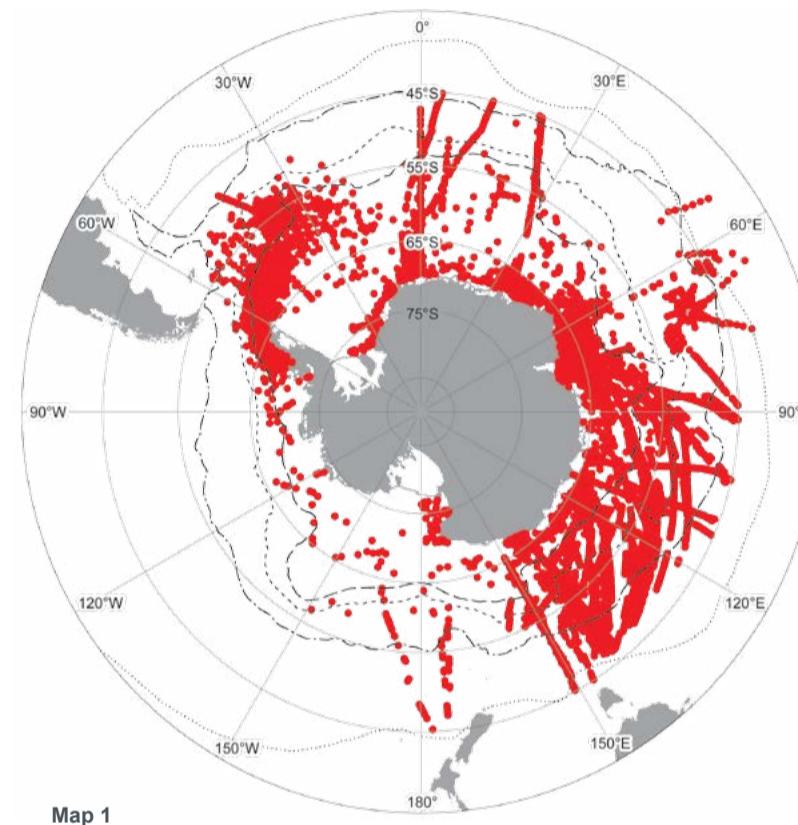
3.1. Overall distribution of euphausiids

Considering the whole set of presence data, the observed distributions for the 13 species were summarised as violin plots in Figure 1.

Two groups of euphausiids species were distinguished:

- the species living mostly in the cold waters of the Antarctic Ocean, distributed from the coast of the continent to the Antarctic Polar Front (PF): numbered from 1 to 6: *Euphausia crystallorophias*, *E. superba*, *Thysanoessa vicina*, *Euphausia frigida*, *Thysanoessa macrura* and *Euphausia triacantha* (Table 1, Maps 2–7).
- the species living north of the PF limit, in the Sub-Antarctic Front and beyond it: *Euphausia vallentini*, *E. longirostris*, *E. lucens*, *Nematoscelis megalops*, *Euphausia similis*, *E. spinifera*, and *Thysanoessa gregaria*, numbered from 7 to 13 (Table 1, Maps 8–14).

When mapping together all the stations with euphausiids present in the catches (Map 1), a continuity of presence was observed from the coast of Antarctica to the Polar Front (PF), the Sub-Antarctic Front (SAF) and up to the



Euphausiacea Map 1 General map combining all records of the 13 species of Euphausiidae living in Southern Ocean. Dotted circumpolar lines (from south to north) limits of: Southern Antarctic Circumpolar Current Front (SACCF), Polar Front (PF), Sub-Antarctic Front (SAF), Sub-Tropical Front (STF).

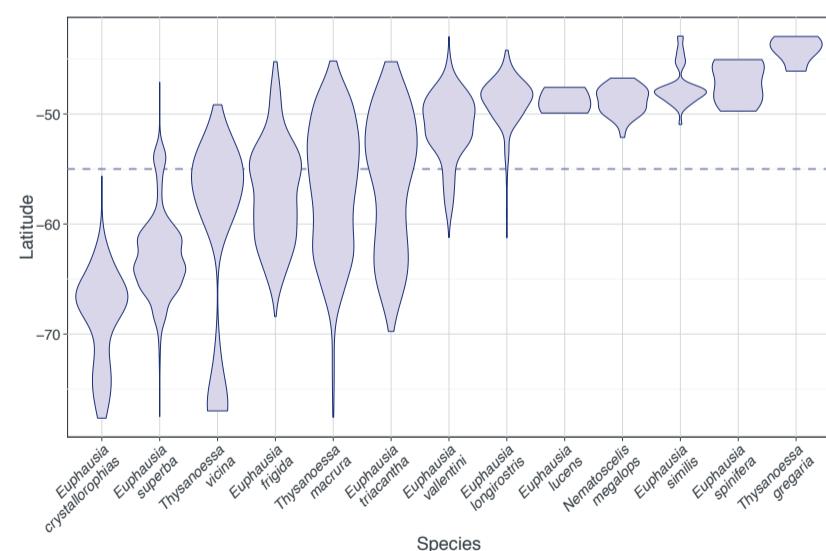


Figure 1 Latitudinal distributions of the 13 euphausiids species sampled at 14,397 stations in the Southern Ocean, represented as violins (the wider the violin, the more presence at this latitude). The dashed line is the average position of the northern limit of the Antarctic Polar Front.

Sub-Tropical Front (STF). Sampled stations were less numerous in the Weddell Sea and in the sector from 90°W to 150°E, including the Ross Sea. These regions were less surveyed due to a difficult accessibility for oceanographic vessels when ice-cover is present, and/or an excessive distance from the research bases.



3.2. Species living south of the Antarctic Polar Front

Euphausia crystallorophias (Map 2: a, b, c) was recorded along Antarctica coasts west of the Peninsula, eastern Weddell Sea and from 60° to 180°E, mostly in Pridz Bay region and Ross Sea (a).

The model fitted the data well (52% of variance explained) and had good predictive power (AUC=0.84). It confirmed only partially the localisation of the species near the coasts (b), but could not represent the large distribution observed west of the Peninsula and in the SAAC. The model suggested also a presence of *E. crystallorophias* along the east coast of the Peninsula and Weddell Sea, and west of the Ross Sea. The uncertainty of the prediction (c) was near zero away from the coast (*E. crystallorophias* is actually not present there), and higher in the western coastal region of the continent, but still acceptable considering that the environmental data did not concern the coast itself.

The environmental variables (Fig. 2) which drove most of the distribution of *E. crystallorophias* were temperature at 0 and 200 m depth (the species is limited to waters below 0°C). *E. crystallorophias* also seemed to prefer richer and fresher waters, with high nitrates, low salinity, and was associated with the sea-ice zone, as expected.

Euphausia superba behaviour is gregarious, with juveniles and adults forming large swarms (Table 1). Fast swimmers, they perform large circumpolar and vertical migrations (from surface down to >3000 m depth).

Euphausia superba (Map 3: a, b, c) observed presence (a) from net hauls data was circumpolar, extending from the continent to the northern limit of the Polar Front (PF), with an occurrence in the SACC Front (SACCF) in the Atlantic sector.

The model of habitat suitability fitted the data well (63% of variance explained) and therefore agreed with those observations, but also allowed inferring the presence of *E. superba* in regions where sampling was scarce. The map (b) shows a high probability of presence almost everywhere in the Polar Front, and a low probability beyond it, with a good confidence overall (AUC=0.94). In particular, it predicts that the region between 90°W and 150°E, in the Polar Front, is favourable to *E. superba*. The species is therefore likely to be possibly present there and the low number of observed presences in that region (a) would be due to the scarcity of the sampling.

In this model *E. superba* was predicted to preferentially inhabit regions with high concentrations of silicates and oxygen near the surface, temperature at depth (200 m) between -1.5 and +1.5°C and shallow to intermediate mixed layer depths (between 30 and 50 m) (Fig. 3). All this points at cold, productive regions where diatoms are abundant.

The only region where *E. superba* was observed (a) and predicted (b) to be absent in the entire Polar Front zone is between 60°E and 150°E. In that region, the ice retreats almost completely to the coast in summer and the

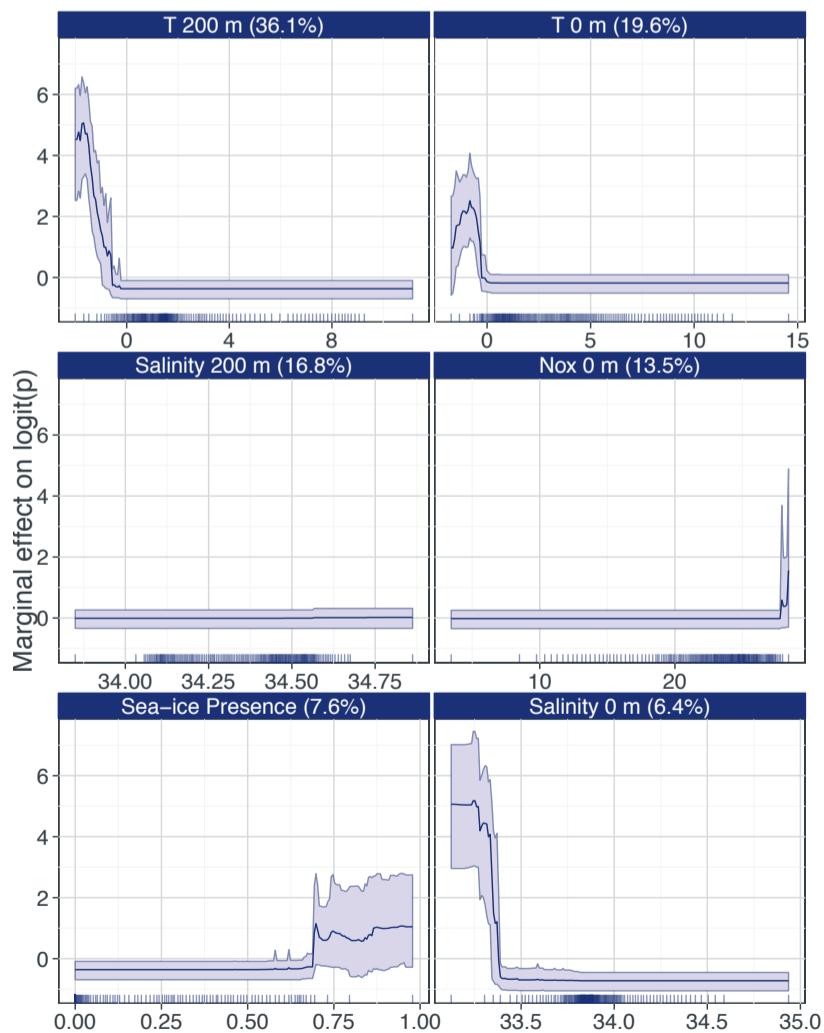
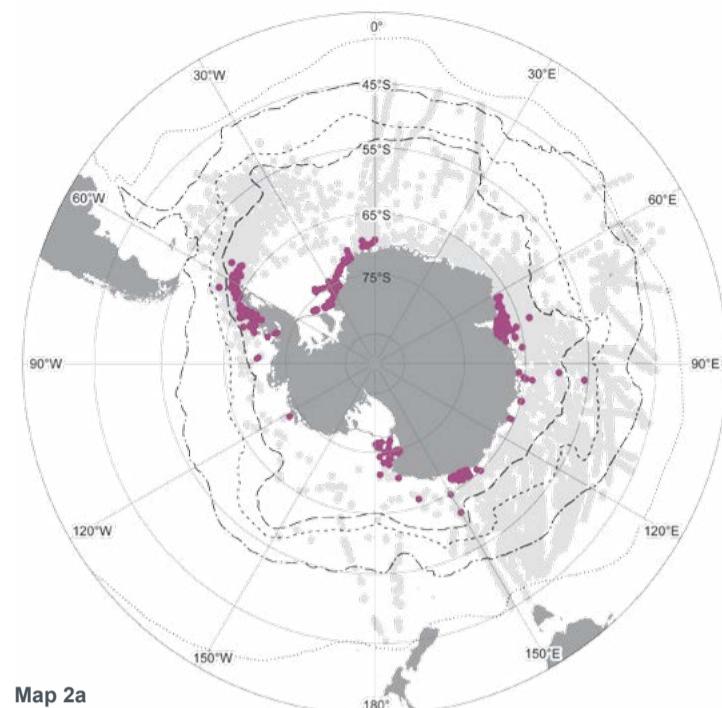
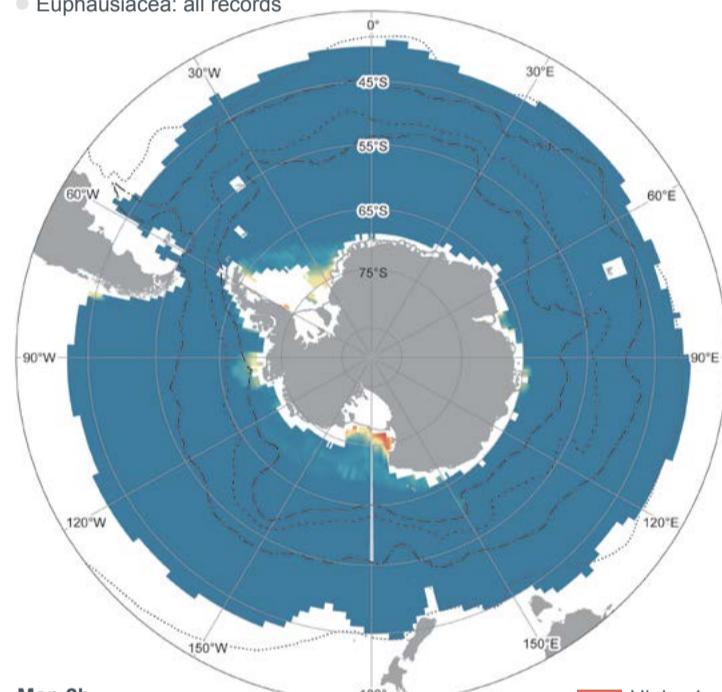


Figure 2 *Euphausia crystallorophias* Holt & Tattersall, 1906. Modelled effects of environmental variables on the probability of presence. Black line: mean effect curve, shaded region: 95% confidence interval computed from 150 bootstraps.



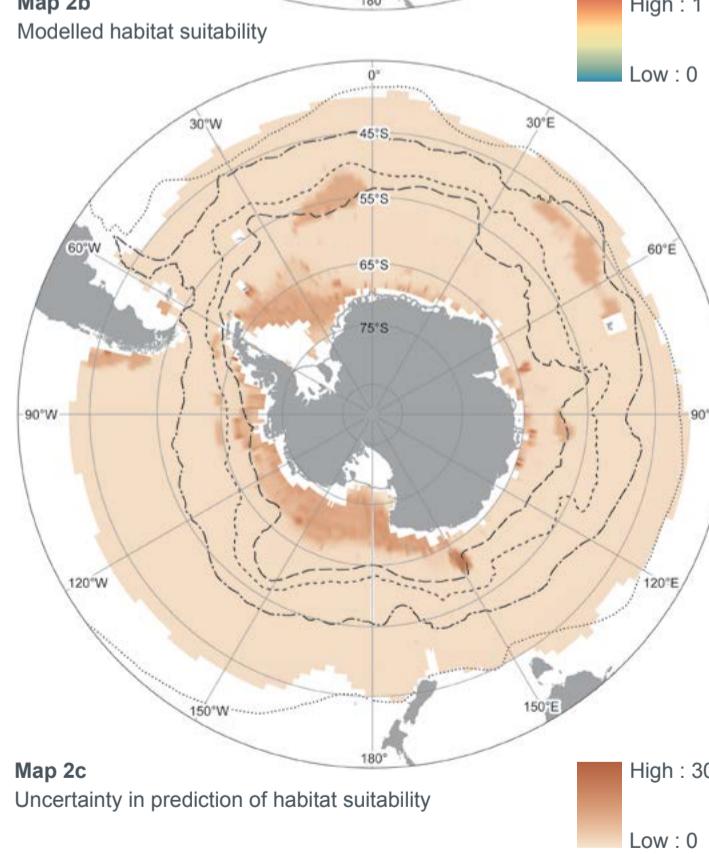
Map 2a

- *Euphausia crystallorophias*
- Euphausiacea: all records



Map 2b

Modelled habitat suitability



Map 2c

Uncertainty in prediction of habitat suitability

Euphausiacea Map 2 *Euphausia crystallorophias* Holt & Tattersall, 1906. (a): presence-absence; (b): modelled habitat suitability; (c): uncertainty in prediction of habitat suitability.

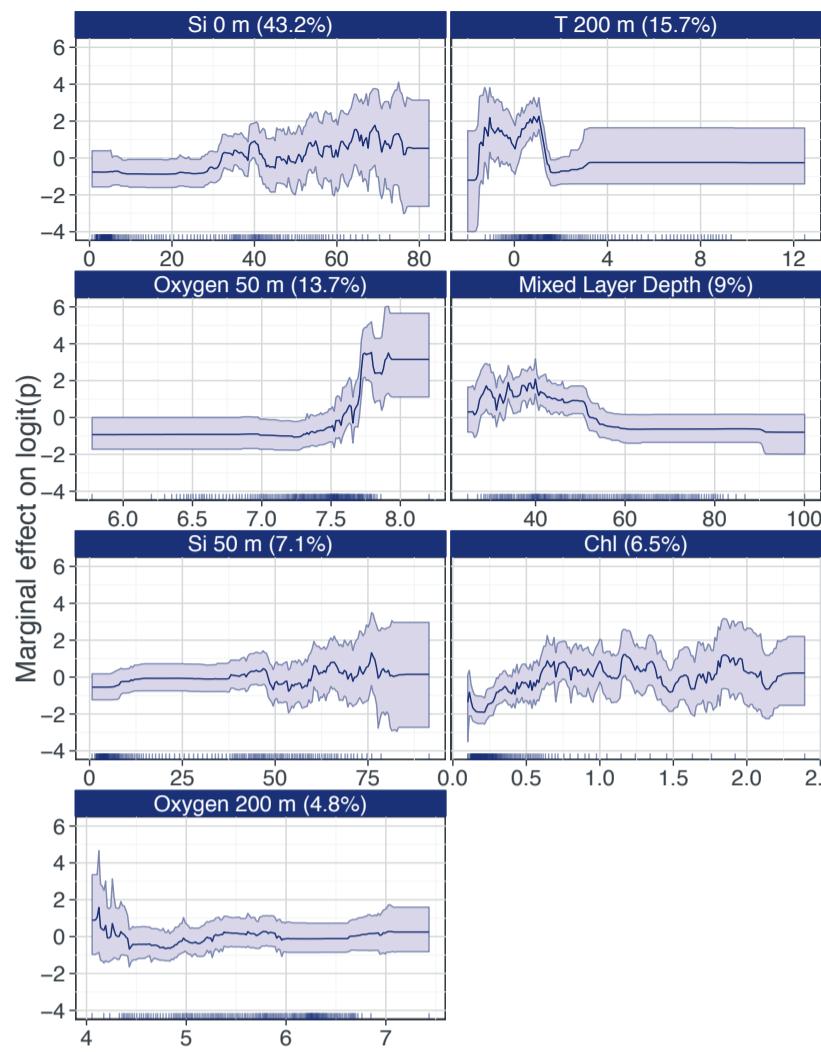


Figure 3 *Euphausia superba* Dana, 1850. Modelled effects of environmental variables on the probability of presence. Black line: mean effect curve, shaded region: 95% confidence interval computed from 150 bootstraps.

hydrologic conditions are also different. The silicates and mixed layer depth are the driving factors to explain the absence of *E. superba* there as the best conditions of habitat are met near the continent.

Chlorophyll is important as an indicator of the presence of phytoplankton blooms, depending on spring light regime and on nitrates presence. Silicates favour diatoms blooms. *E. superba* presence in ice zones is associated with the other species adapted to cold habitats that favour rich mixed layers, but also limit their distributions to cold water masses.

Thysanoessa vicina (Table 1) was occasionally present in former records, in the PF and SAF, from 50 to 60°S, more abundant east of Falkland Islands, between 90°W to 180°E, south of New Zealand and off Kerguelen Islands (Mauchline & Fisher 1969, Mauchline 1980), but often not distinguished from *T. macrura* and *T. gregaria* (Kirkwood 1982).

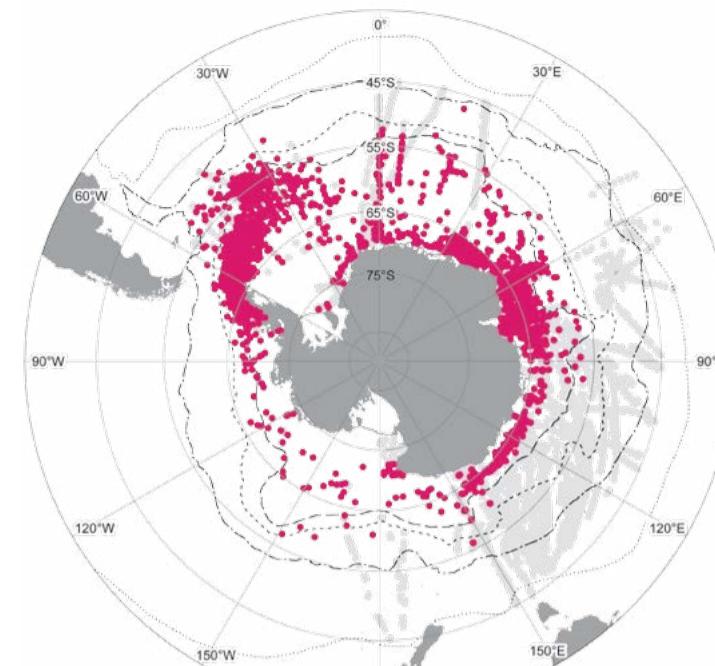
These limited records are due to the difficulty to observe the specific characteristics of this small, fragile species (antennules and elongated predatory legs), which are generally damaged by the net capture. The species determination had to be done by checking the proximal and terminal processes of the petasma in males and the small body size of *T. vicina* reproducing females, conspicuously different from larger *T. macrura* mature females (J. Cuzin-Roudy unpubl. obs.). When recognised, their abundance in the samples raises a doubt about the apparent rarity of the species on the distribution maps, minimising its importance in the diet of top predators and for fisheries.

T. vicina presence-absence map (Map 4) is not in contradiction with former distribution maps for a presence of the species in the PF and the SAF, across the SACC, from 60° to 0°W and around Kerguelen Islands, but limited to this sector and not circumpolar.

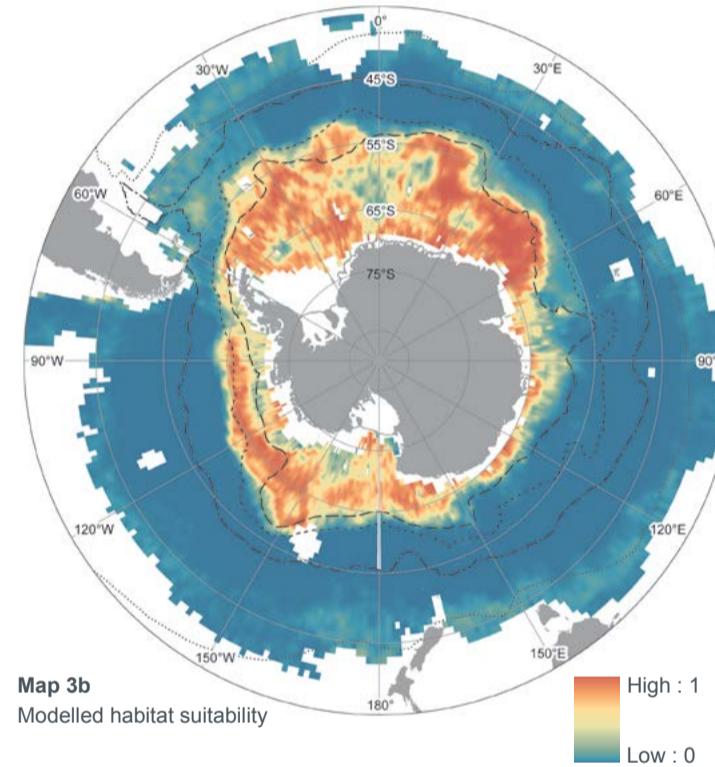
Euphausia frigida (Table 1) was present from the continent to the Polar Front (PF) and in the Sub-Antarctic Front (SAF) and abundant in the samples together with *T. macrura* in its northern habitat. However the species represents only a small proportion of the diet of top predators, due to its small size.

The BRTs model showed a poor fit between the available environmental variables and the presence of that species (only 24% of variance explained). *E. frigida* was associated with low salinities, very high concentrations of nitrates, low surface oxygen and shallow mixed layers. Those relationships tended to predict a circumpolar distribution, mostly between 75°S and 50°S, in the Polar Front, an acceptable result given the presence data. But the model (not presented) also exhibited strong artefacts further north in some regions, which confirmed that the presence of *E. frigida* was mostly determined by variables not considered here.

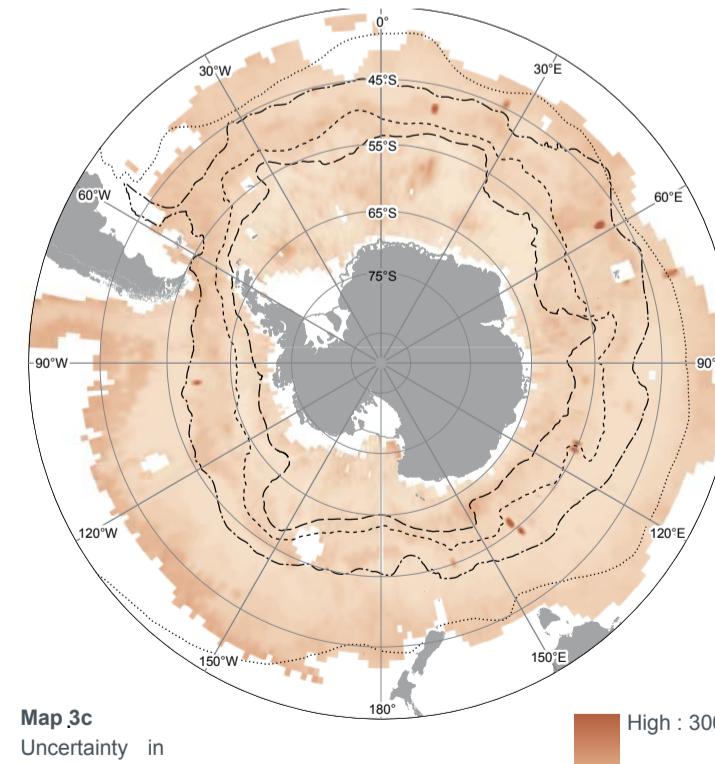
Thysanoessa macrura (Map 6: a, b, c) is the most common, abundant and widespread circumpolar Southern Ocean species, but has a smaller adult size (Table 1). The species was present in net hauls from the continent shelves to the SAF and beyond, except between 120°W to 160°E. It was recorded from the continent to latitude 45°S and up into the Sub-Tropical Front (a). The



Map 3a
● *Euphausia superba*
● Euphausiacea: all records



Map 3b
Modelled habitat suitability



Map 3c
Uncertainty in prediction

Euphausiacea Map 3 *Euphausia superba* Dana, 1850. (a): presence-absence; (b): modelled habitat suitability; (c): uncertainty in prediction of habitat suitability.

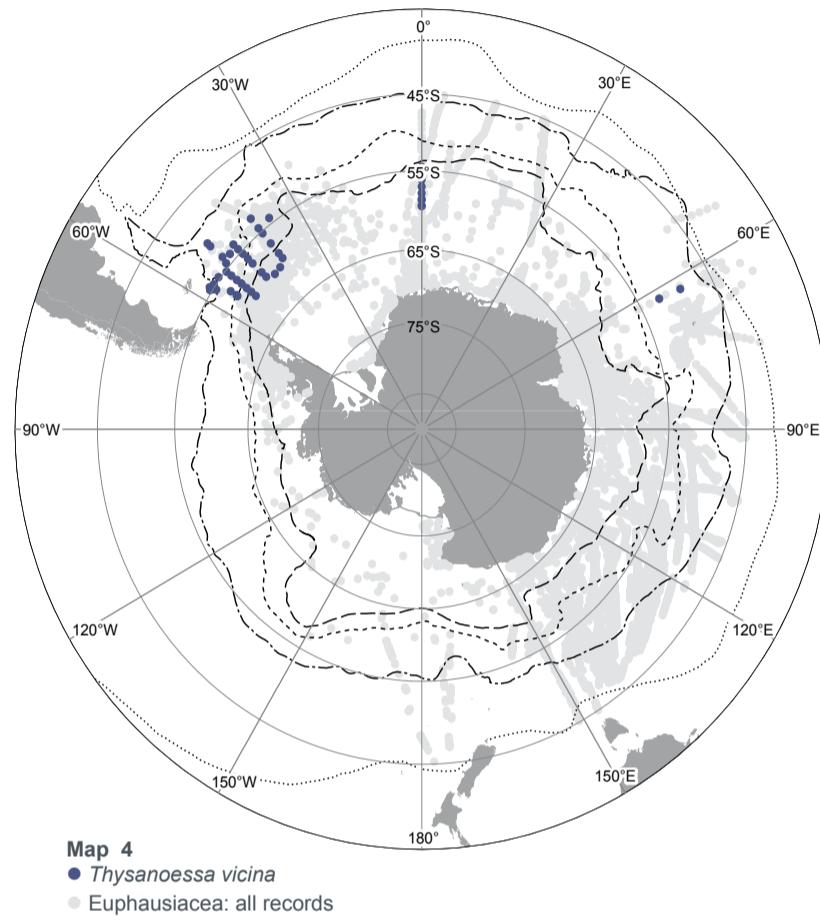


model fit was reasonably good (34% of total variance explained) and predicted a circumpolar presence in the PF and SAF (b), as well as a significant presence in the region between longitudes 90°W and 150°E, where sampling was scarce. The performance of the prediction was good (AUC=0.84) and the uncertainty was low almost everywhere (c).

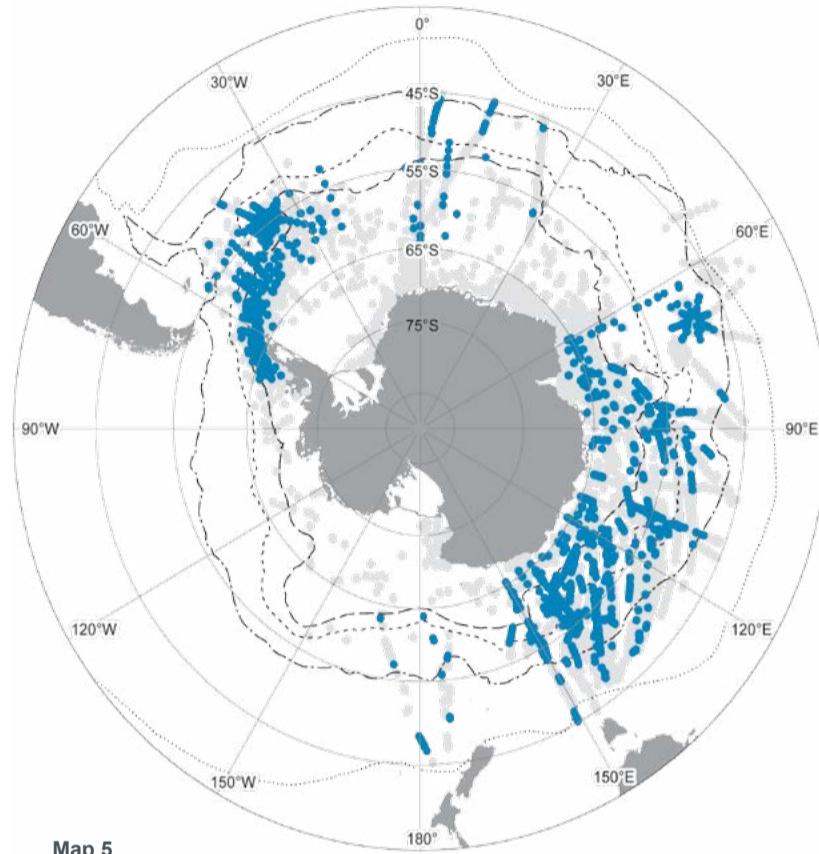
The modelled effects revealed that *T. macrura* seems to favour regions with strong mixing, i.e. where the mixed layer depth is deep, with intermediate concentrations of silicates (Fig. 4). Oxygen and salinity have influences of similar magnitude. *T. macrura* was more present in regions with low to intermediate oxygen concentrations (with a favourable window between 6.5

and 7.7 mL.L⁻¹ at 50 m depth). It seemed to avoid low salinities at the surface, but preferred low salinities at depth.

Euphausia triacantha (Map 7) showed a circumpolar presence mostly south of the Sub-Antarctic Front, from the Peninsula to the islands of the Atlantic sector and from the continent to latitudes north of the Polar Front (PF) and in the Sub-Antarctic Front (SAF) between latitude 50 to 65°S. The BRTs model was ineffective, with only 22% of variance explained. The most influent variable in the model was salinity at 200 m depth: *E. triacantha* was strongly associated with the lowest salinities (< 34.1 PSU).



Map 4
● *Thysanoessa vicina*
● Euphausiacea: all records



Map 5
● *Euphausia frigida*
● Euphausiacea: all records

Euphausiacea Maps 4–5 Map 5. Presence-absence of *Thysanoessa vicina* Hansen, 1911. Map 6. Presence-absence of *Euphausia frigida* Hansen, 1911.

3.3. Species living north of the Antarctic Polar Front

Euphausia vallentini (Map 8: a, b, c) is known to have a circumpolar distribution across the northern limit of the PF and further north, in the South Atlantic, on Argentina shelf, together with *T. vicina*, *E. lucens* and *E. similis*. It was mostly recorded in the eastern part of the Southern Ocean, along the northern limit of the PF and in the SAF, from 60°E to 180°E (a). The model predicted a circumpolar distribution at similar latitudes and longitudes in the Southern Ocean (b), as usually considered for this species in former studies. Habitats of particular suitability seem to be south and west of Kerguelen Islands and for 40 to 50° east and west of the South American continent (c). The explanatory power of the model was not high (30% of variance explained), but the confidence in the prediction was good (AUC=0.87).

The most important factors driving the distribution of *E. vallentini* seemed to be low silicates at 200 m (<35 µM), a characteristic of SAF waters, and low salinities (<34.1 PSU) at 200 m, characteristic of PF waters (Fig. 5). The combination of the two drives the distribution across the PAF and SAF limit. In addition, *E. vallentini* seemed to favour deeper mixed layers (below 60 m). The rest of the variables are characteristic of SAF waters: low silicates at surface, high temperature, low nitrates and low oxygen.

Euphausia longirostris (Table 1) was present in the Sub-Antarctic Front, between 60° and 180°E (Map 9), which confirms previous reports, but present data were too scarce for a valid BRT model.

Euphausia lucens (Table 1) distribution is known to be circumpolar around 40°S. Here, the species was found occasionally in catches south of Tasmania, in sub-Antarctic and sub-tropical waters (Map 10). The data were too limited to allow a meaningful BRTs modelling.

Nematoscelis megalops, from former records (Table 1), has a large distribution in the temperate regions of Atlantic Ocean, in north and south hemispheres, and in South Pacific and Indian Oceans. The species was only recognised here (Map 11), in the Sub-Antarctic Front (SAF) (South of Tasmania, at the limit of its known southern presence (40° to 50°S).

Euphausia similis (Table 1) distribution was described previously as circumpolar in the Southern Ocean from to 30° to 50°S, and up to Arabia in

the Indian Ocean. In the present data, occasional occurrences were found, in the sector 30° to 150°E, north of SAF, in the Sub-Tropical Front (Map 12).

Euphausia spinifera (Table 1) occurs in South Atlantic, Pacific and Indian Oceans, between 35° and 50°S. It was present occasionally between 90° to 150°E, north of the Sub-Antarctic Front and across the limit of the Sub-Tropical Front (Map 13).

Thysanoessa gregaria. The species was only present, at rare occasions (Map 14), at the northern limit of the Sub-Tropical Front and above it, about 60°E, which did not bring enough information for modelling a distribution of presence.

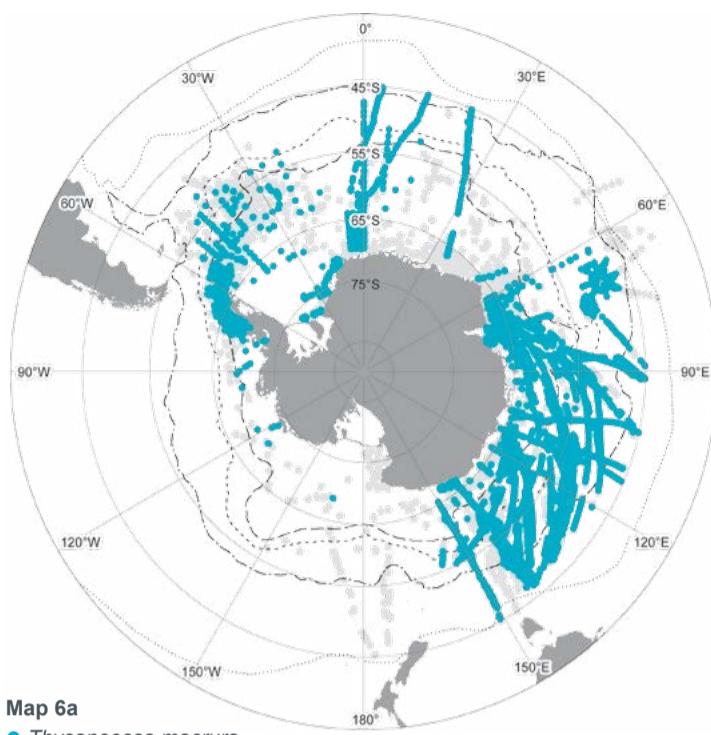
4. Discussion

4.1. Distribution and habitat suitability of Southern Ocean euphausiids

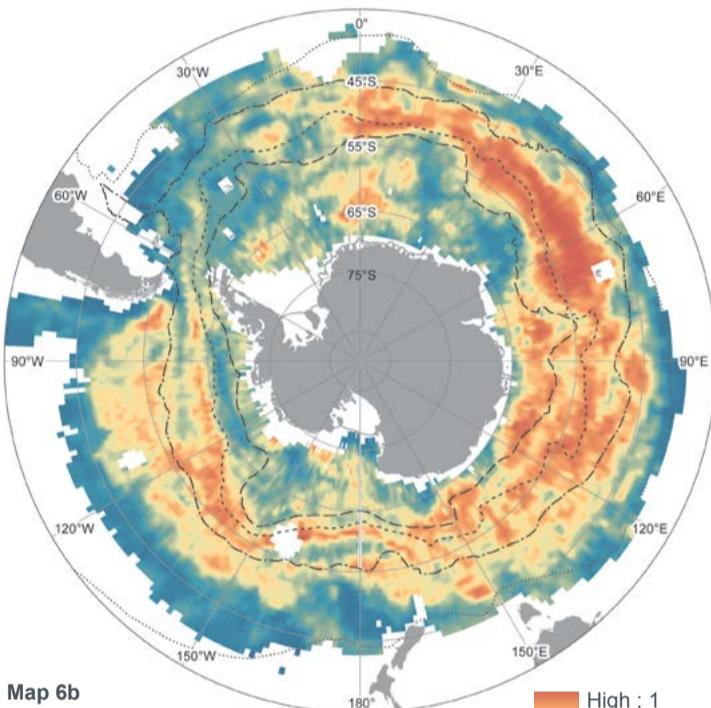
The present study confirms that the distributions of the sub-Antarctic species (Maps 8–14), observed and modelled, are distinct from those of the Antarctic Ocean species (Maps 2–7). Two species appeared limited to the Antarctic Ocean by their adaptation to cold waters and their association with sea ice:

Euphausia crystallorophias (Map 2: a, b, c) showed a distribution limited to inshore waters of the Antarctic continent by an adaptation to cold waters (0°C or less) and an association with sea-ice year round (Table 1) and was absent from the PF and the SAF (a). As our data set for habitat parameters did not cover the coastal area, the model predicting the presence of this species in rich waters, with high nitrates rates and low salinity, concerns only the population of the shelf in summer, but confirms location in chlorophyll rich neritic sites, where the species dominates the mesozooplankton (Swadling *et al.* 2010).

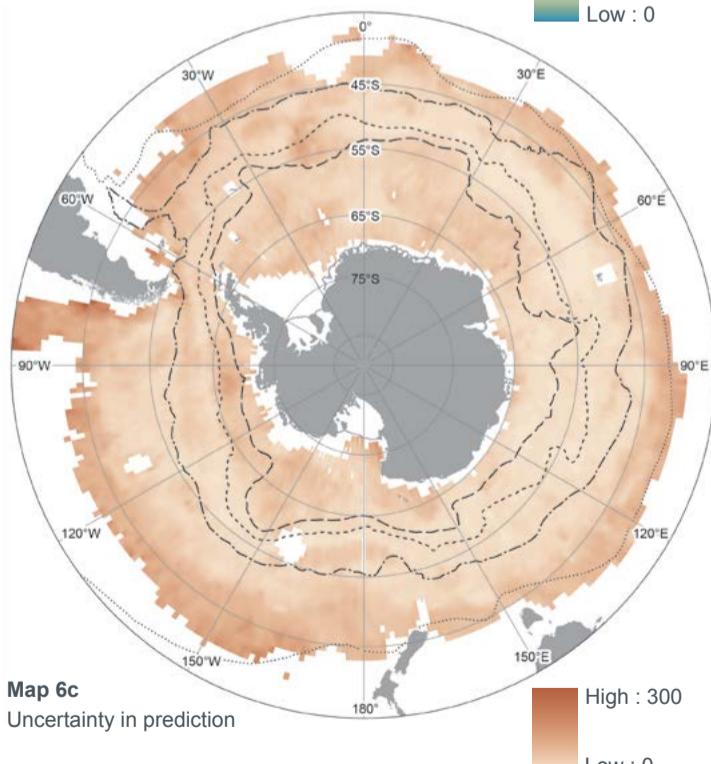
Euphausia superba (Map 3: a, b, c) exhibits an extensive distribution in the Antarctic Ocean. The BRT analysis confirmed that the species presence is limited to the Antarctic Ocean and unequally distributed around Antarctica, with the largest density of presence (observed and predicted) in the PF and SACC of the Atlantic sector, in Scotia-Weddell Sea and from the continental coast to the northern limit of the PF in the whole eastern sector.



Map 6a
● *Thysanoessa macrura*



Map 6b
Modelled habitat suitability



Map 6c
Uncertainty in prediction

Euphausiacea Map 6 *Thysanoessa macrura* G.O. Sars, 1883. (a): presence-absence; (b): modelled habitat suitability; (c): uncertainty in prediction.

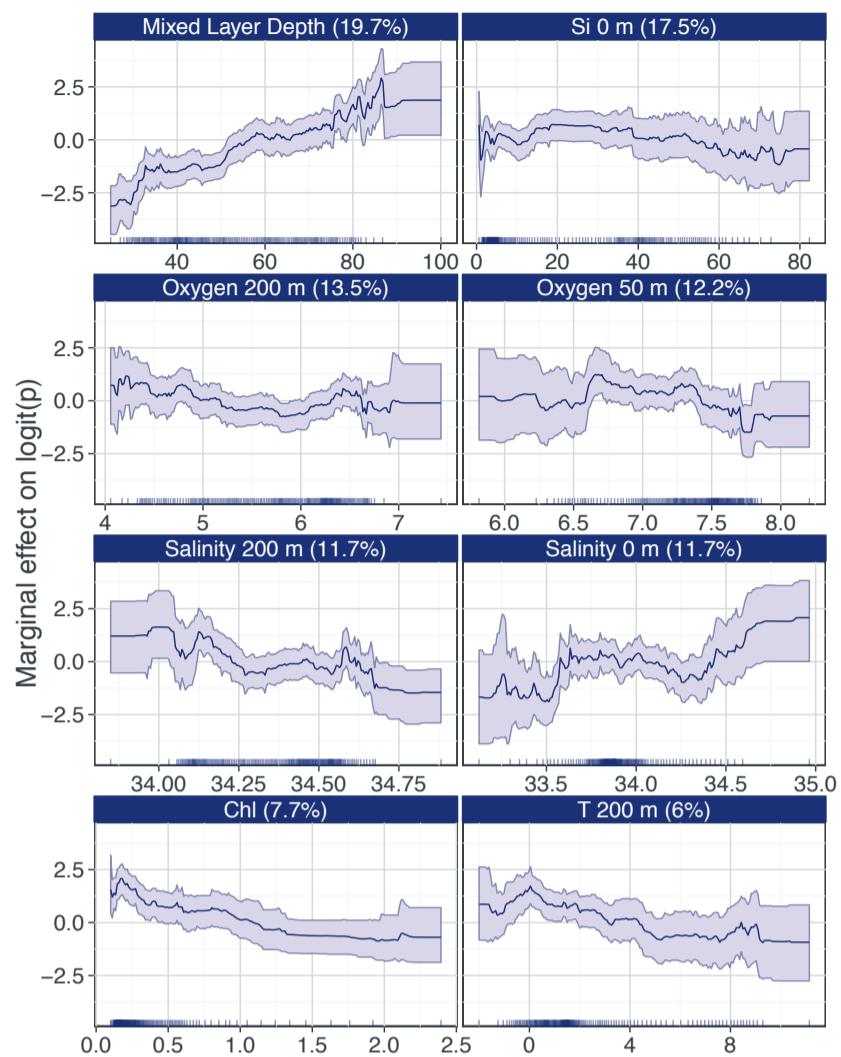
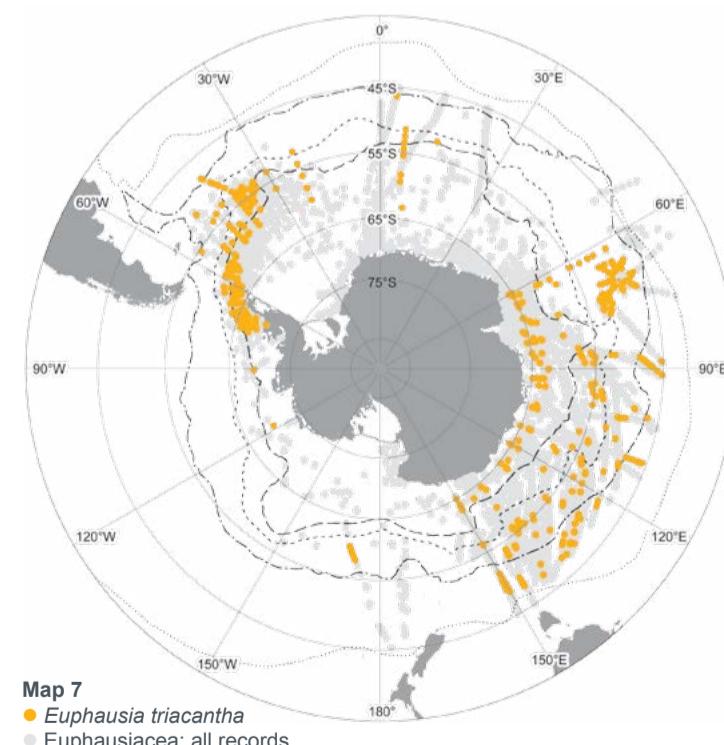
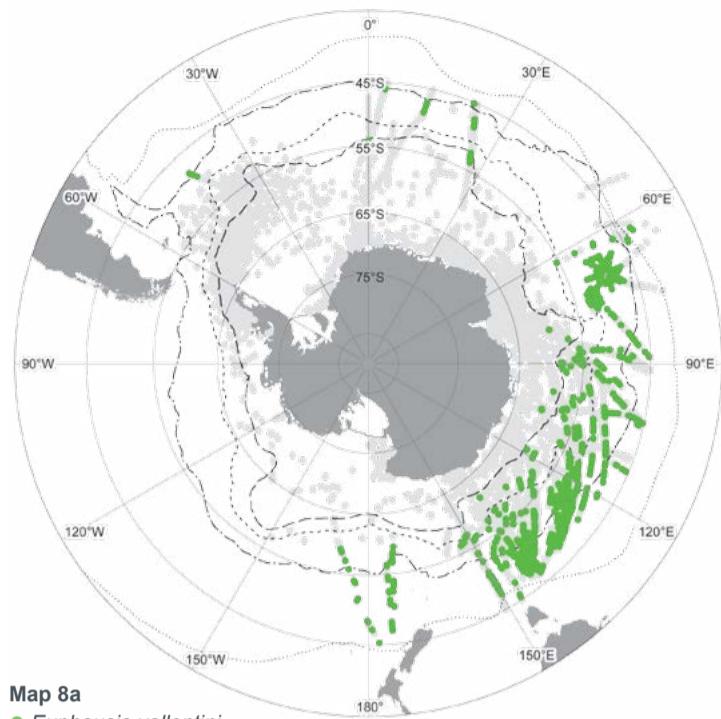


Figure 4 *Thysanoessa macrura* G.O. Sars, 1883. Modelled effects of environmental variables on the probability of presence. Black line: mean effect curve, shaded region: 95% confidence interval computed from 150 bootstraps.

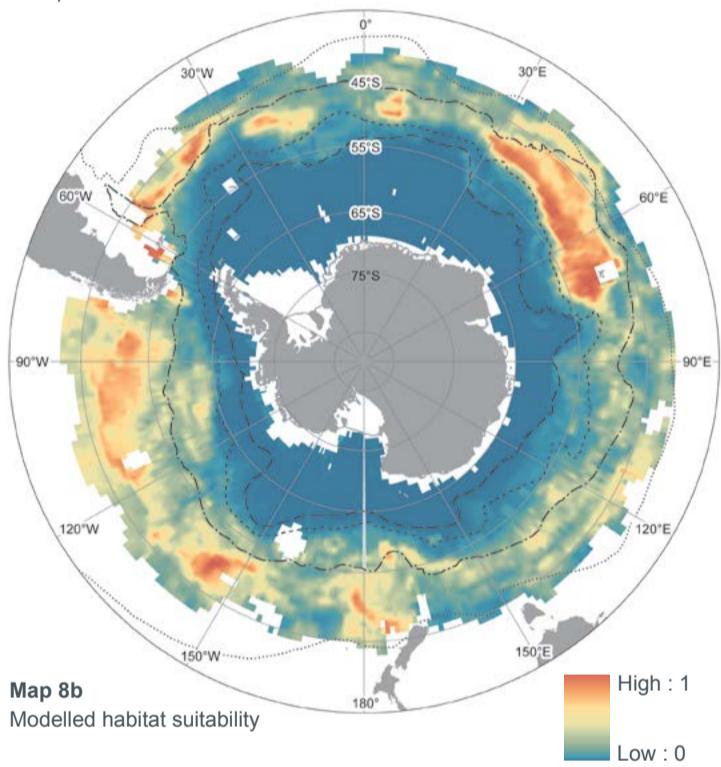


Map 7
● *Euphausia triacantha*
● Euphausiacea: all records

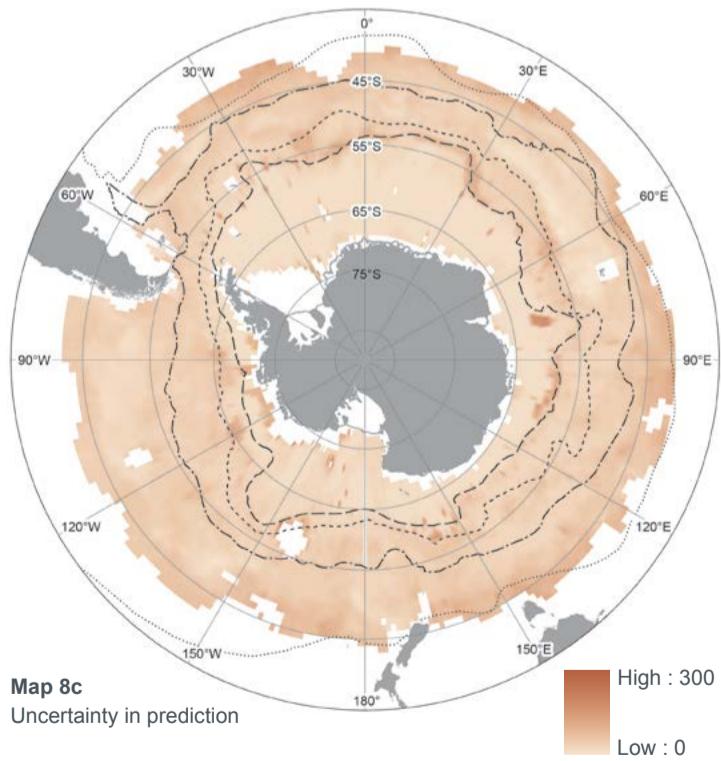
Euphausiacea Map 7 Presence-absence of *Euphausia triacantha* Holt & Tattersall, 1906.



Map 8a
● *Euphausia vallentini*
● Euphausiacea: all records



Map 8b
Modelled habitat suitability



Euphausiacea Map 8 *Euphausia vallentini* Stebbing, 1900. (a): presence-absence; (b): modelled habitat suitability; (c): uncertainty in prediction.

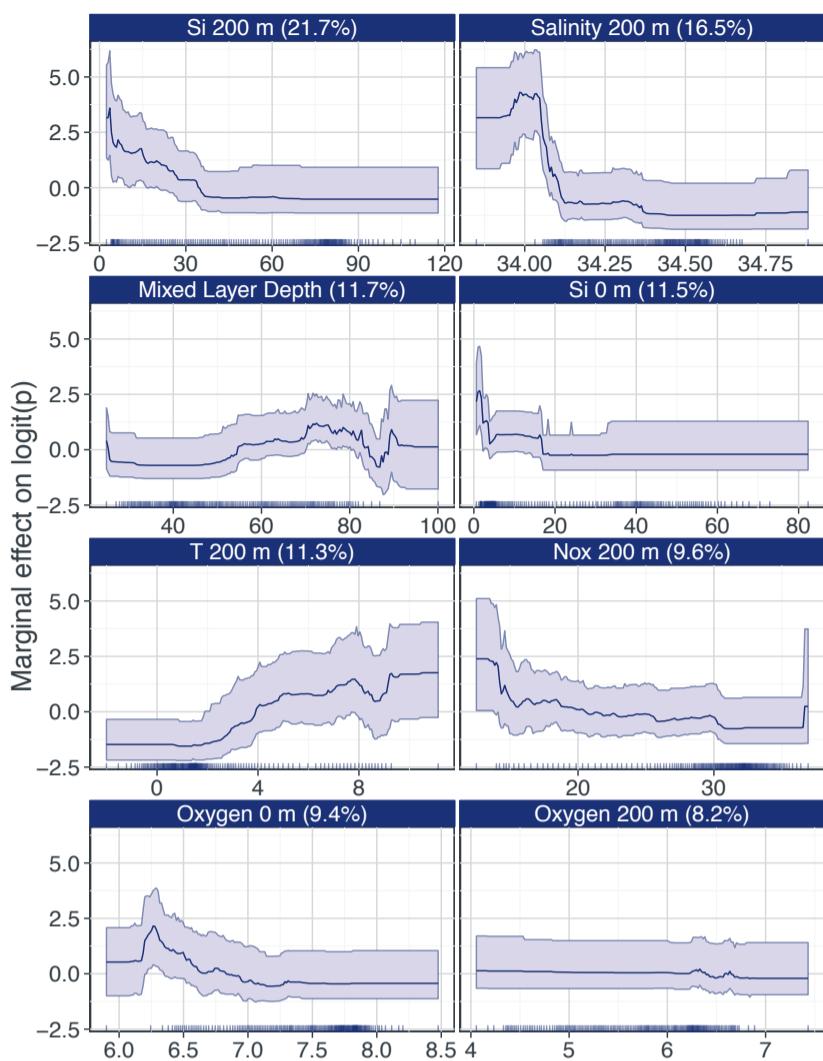


Figure 5 *Euphausia vallentini* Stebbing, 1900. Modelled effects of environmental variables on the probability of presence. Black line: mean effect curve, shaded region: 95% confidence interval computed from 150 bootstraps.

In these zones, chlorophyll is important as an indicator of the presence of phytoplankton blooms, depending on spring light regime and on nitrates presence. *E. superba* presence in ice zones is associated with the other species adapted to cold habitats that favour rich mixed layers.

The continuity of a circumpolar distribution of *E. superba* population around Antarctica in the open ocean, up to the northern limit of the Polar Front and the Southern Antarctic Circumpolar Current Front, was confirmed by the BRT model (b), as well as an interpolated presence in zones with poor data (90°W to 150°E), suggesting a possible presence in habitats that could be suitable, given the parameters chosen.

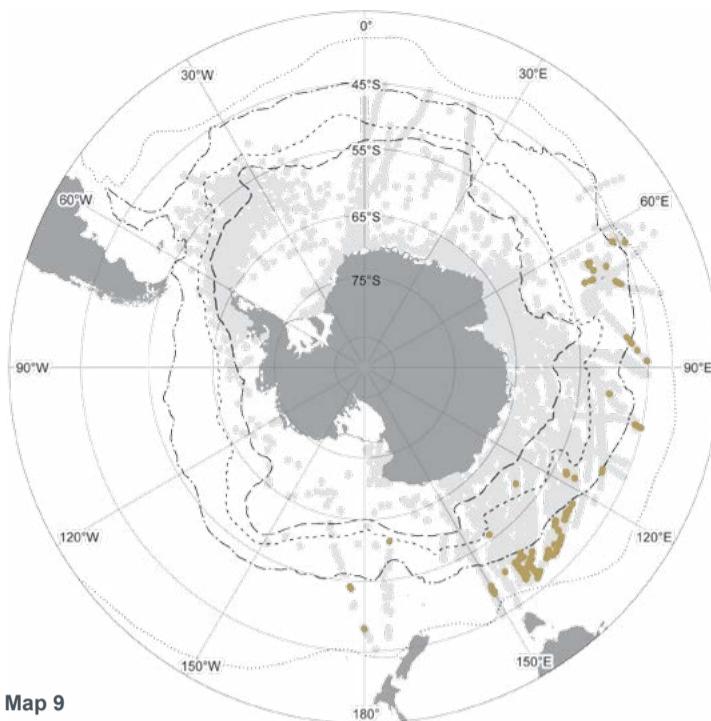
The suitable conditions defined by the model for *E. superba* (cold, oxygenated, productive waters, with high silicates, nitrates and chlorophyll) are met in the marginal ice zone of the retreating sea-ice in spring and near the coast in summer. High silicates rate favours diatoms blooms, an essential food for the lipid metabolism of *E. superba* (Mayzaud et al. 1998), which needs the spring blooms for sexual differentiation of the gonad in late *furcilia* (Cuzin-Roudy 1987a), sexual maturity of adults and the onset of successive reproductive cycles in summer (Cuzin-Roudy 2000). Phytoplankton is also necessary in summer (Photo 1) to maintain a high fecundity (Cuzin-Roudy & Labat 1992, Ross & Quetin 2000).

The concentration of *E. superba* around the continent shown in Map 3a, and predicted by the model (B), concerns mostly pelagic juvenile and adult krill and is in agreement with recent results about distribution and abundance of the species. Atkinson et al. (2008) suggested two populations for *E. superba*, one aligned with the SACC stream (the main population of the Atlantic sector), and the other, in the Antarctic Coastal Current for the remaining 30% of the total stock. Their suggestion of a connexion between the Atlantic sector population and the remaining 30% of the total stock is confirmed by our results (Map 3: a, b, c).

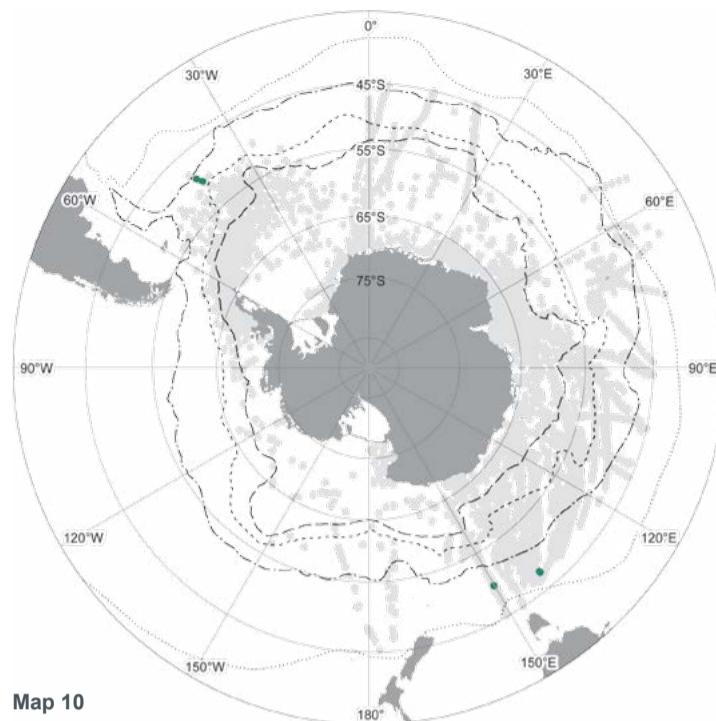
Using another approach to the question of a unique population, a genetic investigation carried out by Zane et al. (1998) at the DNA level on adult specimens of *E. superba* sampled from four sectors of the Antarctic Ocean, found a significant genetic difference between South Georgia and eastern Weddell Sea populations only. In their actual distribution, these two populations are separated by the confluence of the Scotia-Weddell gyre with the SACC, an oceanic barrier possibly limiting gene flow between these two populations.

The association of the life cycle of *E. superba* with sea-ice for overwintering, and with the marginal ice zone in spring, could not be taken into account by the BRT model, mostly based on pelagic data and summer conditions.

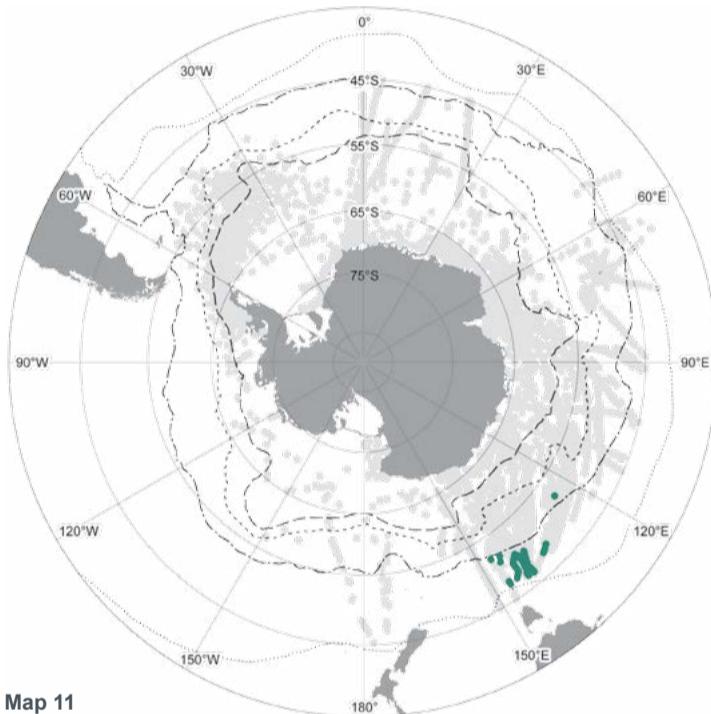
A strong link between *E. superba* and deep benthos, was asserted by recent results (Clarke & Tyler 2008, Schmidt et al. 2011, Kawaguchi et al. 2011a). In the last decade, technical progress for the study of Antarctic



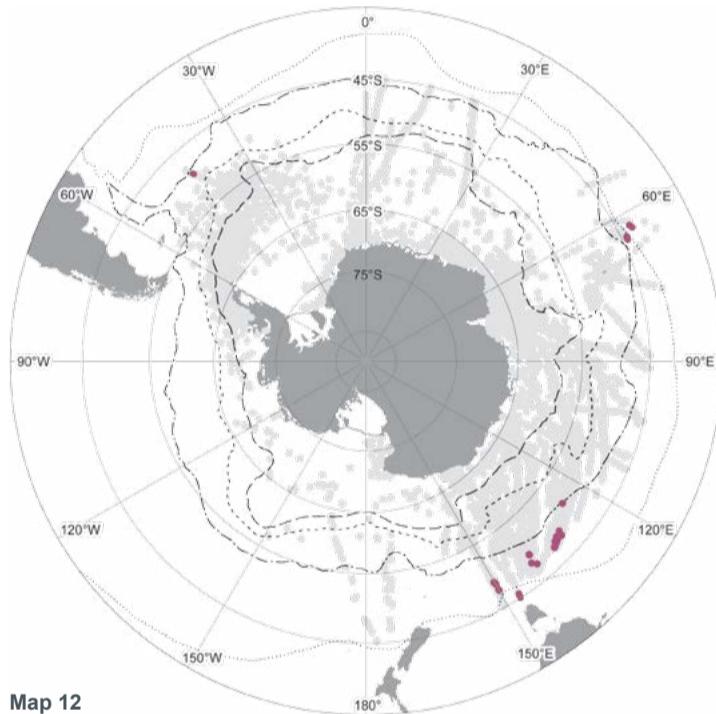
Map 9
● *Euphausia longirostris*
● Euphausiacea: all records



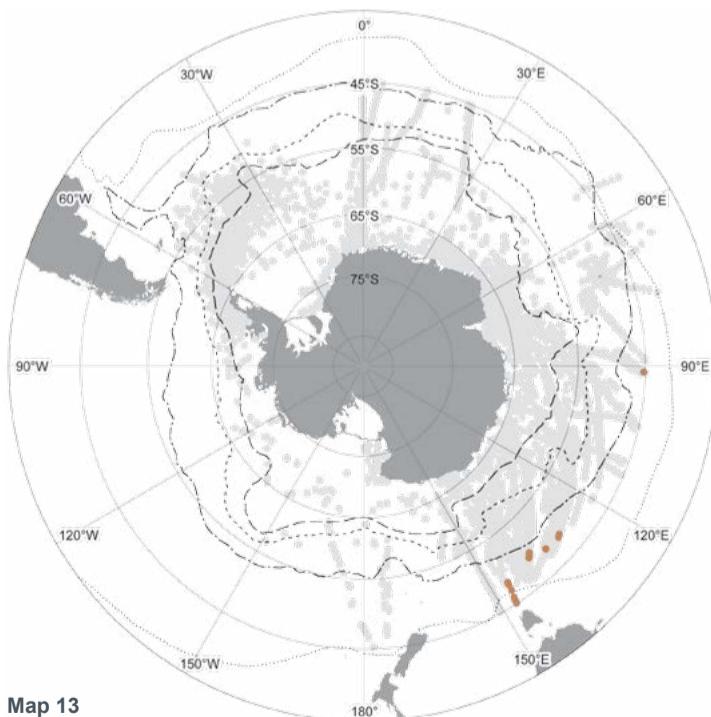
Map 10
● *Euphausia lucens*
● Euphausiacea: all records



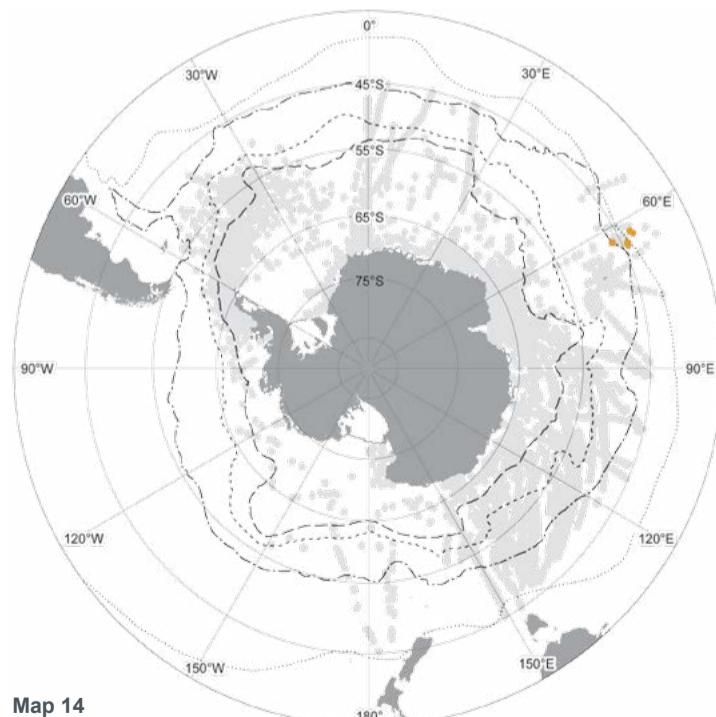
Map 11
● *Nematoscelis megalops*
● Euphausiacea: all records



Map 12
● *Euphausia similis*
● Euphausiacea: all records



Map 13
● *Euphausia spinigera*
● Euphausiacea: all records



Map 14
● *Thysanoessa gregaria*
● Euphausiacea: all records

Euphausiacea Maps 9–14 Maps of presence-absence. Map 9. *Euphausia longirostris* Hansen, 1908. Map 10. *Euphausia lucens* Hansen, 1905. 11. *Nematoscelis megalops* G.O. Sars, 1883. Map 12. *Euphausia similis* G.O. Sars, 1885. Map 13. *Euphausia spinifera* G.O. Sars, 1885. Map 14 *Thysanoessa gregaria* G.O. Sars, 1883.



Ocean deep basins brought a new insight on *E. superba* ecology, as large aggregations of active Antarctic krill were found at great depth on the bottom sediment. Larvae and juvenile krill were present and adults were observed and photographed performing basic activities of their life cycle: feeding, mating (which means also moulting for females) and maturing eggs. This still not explored habitat could not be taken into account in the present study, due to a lack of krill samples and numerical data.

Thysanoessa macrura (Map 6: a, b, c), with a large latitudinal distribution, appeared to favour waters with strong mixing, relatively low oxygen, and low salinities at depth, which are characteristic of the upwelling of deep water in the PF. This carnivorous species does not depend on phytoplankton (Table 1), at least when adult, and is tolerant to low silicates and nitrates. Tolerant to a higher temperature the species is largely distributed in the SAF.

Concerning the other species living north of the Antarctic Polar Front, *E. vallentini*, *E. longirostris* and *E. similis* var. *armata* are known to be associated with sub-Antarctic cold and nutrient rich water masses, while *E. lucens* and *E. spinifera* showed affinity for sub-tropical waters (Robertson & Roberts 1978).

Euphausia vallentini distribution in the SAF, where the species meets low surface silicates concentrations, higher temperature, low nitrates and oxygen, but also in the PF, with a characteristic low salinity at 200 m and a favourable deeper mixed layer depth, is in agreement with former studies.

With the exception of *Euphausia vallentini*, the catches concerning most of the sub-Antarctic species (Maps 9 to 14) were generally too limited in our data set for a meaningful use of the BRTs model to extrapolate habitat suitability maps and to gain new appreciation of their importance in the SO ecosystem.

4.2. Ice habitat and the life cycles of Antarctic euphausiids

Only three species are associated with the ice habitat of the high latitudes, at least for part of their life cycle, but the relationship of *E. superba* with the ice habitat has been the most studied.

Euphausia crystallorophias is associated with ice year round. All stages of development and adults were found from 30 to 150 m depth under the ice in the Gerlache Strait (Nordhausen 1994). It is the dominant species of the inshore waters of Antarctic continent (Swadling et al. 2010) where it forms large neritic aggregations and contribute significantly to the diet of inshore predators (Table 1).

Thysanoessa macrura, the most uniformly distributed species in the Southern Ocean, is found also under solid ice in winter (Nordhausen 1994) and at depth (90–250 m) along Dumont d'Urville Sea coast (Vallet et al. 2011).

Euphausia superba, the Antarctic krill, is present in abundance under the ice in winter, from 15 to 130 m depth in Gerlache Strait (Nordhausen 1994) together with *E. crystallorophias* and *Thysanoessa macrura*. All stages of development of *E. superba* can be associated with sea ice year round (Brierly et al. 2002, Quetin & Ross 2001), with, in summer, under-ice (0 to 2 m depth) concentrations of Antarctic krill (mostly juvenile) estimated larger than in open waters (Flores et al. 2012b).

The winter under-ice population is dominated by larvae and juvenile krill surviving as opportunistic scavengers on the available food sources of the ice biota. A flexible physiology and the capacity to withstand starvation using a body combustion strategy results in a negative growth rate for adults that regress in size and to a sub-adult stage (loosing petasma or thelycum) and to a lesser degree for larvae and juveniles (Daly 1998, Quetin et al. 2003, Ross et al. 2000).

In spring, *E. superba* larvae, juveniles and adults are found at the ice-edge rich in phytoplankton. They need the ice-edge spring blooms of phytoplankton (mostly diatoms) to recover a positive growth rate, sexual differentiation of the gonads in late furcilia stage (Siegel 1987, 2012), and acquisition of sexual maturity and mating for adultst (Cuzin-Roudy 1987b, 1993). Adult females start there the early phase of egg development for the first reproductive cycle of the season (Cuzin-Roudy & Amsler 1991, Cuzin-Roudy & Labat 1992). Intensity of reproduction in summer is the highest under "average" conditions of sea-ice retreat, while late retreat is associated with faster oocyte development (Quetin & Ross 2001).

The juveniles and mature adults migrate next into the pelagic zone (Siegel 2012), with suitable trophic conditions for performing simultaneously swarming and swimming for foraging, moult development and growth, egg production (Cuzin-Roudy 2000) and recruitment (Tarling et al. 2007).

4.3. Species fitness and adaptations

The distribution of euphausiids is not only directed by environmental factors but correspond also to specific strategies developed for their adaptation to the complexity of habitats and the seasonal variability of the Southern Ocean.

There was during the past decades an effort to better understand the adaptive physiology and metabolism of the dominant species, mostly *E. superba*, and the limits of their flexibility concerning the nutritional needs for completing the crucial steps of their life cycle. The species have developed a large panel of adaptations to complete their long life cycle in the pelagic environment, at sea-ice edge, under solid ice and on deep benthos.

Euphausia superba sexual maturity and reproductive period are fitted to the seasonal change in day light and photoperiod (Teschke et al. 2008), but need optimal trophic conditions to maintain through the summer their

reproductive function (Schmidt et al. 2012). Spring phytoplankton blooms (diatoms) of the ice edge permit adult sexual maturity, mating and early development of oocytes (previtellogenesis), but the higher concentrations of phytoplankton found in the open ocean in summer (Photo 1), and other food sources, are necessary for lipid accumulation in eggs (Cuzin-Roudy et al. 1999) and full maturation of egg batches for successive spawning cycles. During their pelagic life in the open Antarctic Ocean, Antarctic krill feed on any preys items, including protists (Schmidt et al. 2006), but the diet may shift preferentially to copepods (Granelli et al. 1993, Mayzaud et al. 1998), and even to the micro-fauna of the sea-bed sediment (Schmidt et al. 2011).

Antarctic krill egg maturation and spawning only occurs in summer in ice-free waters (Cuzin-Roudy 1993, Cuzin-Roudy & Labat 1992), when the various food sources, necessary for the accumulation of lipo-glyco-proteins in large egg-batches reaching up to 46% of the total weight of the female Antarctic krill, are abundant. In South Georgia region, not affected by winter sea-ice and benefiting from an early spring, each female can produce during the summer an average of 12,343 eggs.yr⁻¹ per female, in one to three successive reproductive cycles (Tarling et al. 2007).

In summer, when trophic conditions are insufficient, female *E. superba* rely on oosorption (Cuzin-Roudy & Amsler 1991), a common strategy for crustaceans to retrieve yolk components from developed oocytes to fuel the obligatory energetic expenses of their behaviour (Hamner & Hamner 2000). This is consistent with Quetin & Ross (2003) observation of summers with poor, or null, krill reproduction. Summer oosorption in oligotrophic waters appears as a strategy similar to winter "shrinking", when krill rely on reversible metabolic shifts that allow them to re-metabolise their own cell components to maintain their basic activities of swimming and moulting. Both strategies are reversible and compatible with the long life of the species, which compensate years of poor recruitment resulting from the effects of seasonal sea-ice dynamics linked to ENSO (Quetin & Ross 2003).

In summer, *E. superba* lipid storage is used essentially for reproduction (Cuzin-Roudy et al. 1999). The "fat body", well developed in summer, is completely regressed in winter and lipid storage is then limited to the digestive gland for survival (Cuzin-Roudy 1993, Mayzaud et al. 1998). When this storage is exhausted, survival and maintenance of swimming activity in insufficient trophic conditions rely on oosorption of residual eggs kept in the ovary (Cuzin-Roudy & Amsler, 1991), sexual regression and body "shrinking" at moulting (Cuzin-Roudy et al. 1999).

New data sources, e.g. nuclear coding genes, are bringing new insight on the link between genes expression and physiology. Seear et al. (2012) compared gene expression in two populations of *E. superba* in different seasonal (summer/winter) and environmental conditions (winter ice/permanent free waters). *E. superba* physiology changes with the season in both environments: 1) there was no differential expression for genes involved in respiration, motor activity or absence of vitellogenesis in the two overwintering populations, and 2) vitellogenesis was up-regulated with an insulin-related peptide in summer for both populations.

The different euphausiid species have developed various specific lipid metabolisms (Phleger et al. 2002). The most abundant species (*E. crystallorophias*, *E. superba* and *T. macrura*) are adapted to different water masses and currents (Atkinson et al. 2008, Fach et al. 2006, Thorpe et al. 2007), coastal zones (Tarling et al. 2007), sea ice (Brierley et al. 2002, Daly 1990), and have developed specific strategies for reproduction.

E. crystallorophias and ***T. macrura*** have different requirement concerning habitat suitability, but both start to reproduce before ice breaking and retreat (Table 2).

E. crystallorophias, linked to ice of the coastal habitat, is known to start spawning in early November, before the phytoplankton bloom, to end in December (Pakhomov & Perissinotto 1996; Falk-Petersen et al. 2000), using extensive energy reserves of wax esters accumulated during the previous autumn for survival and reproduction (Kattner & Hagen 1998). Larvae appear in abundance in coincidence with the phytoplankton bloom. *Calyptopis* were abundant together with *furciliae* of *T. macrura* along the coast of Terre Adélie (Vallet et al. 2009, 2011).

The *Thysanoessa* species share with *Euphausia* sp. an adaptation to the pelagic life (larval development, swarming and migrating behaviour), but differ from them by a carnivore trophic mode and by their reproductive physiology.

T. macrura is carnivorous and store lipids in summer for building eggs before the spring period of primary production. Spawning occurs in late winter (in September and October), well before the phytoplankton blooms of November (Falk-Petersen et al. 2000), relying on a storage of polar lipids (Mayzaud et al. 2003, Katner & Hagen 1998) for spawning before the ice break, in time for the *calyptopis* larvae to feed and accumulate lipids from the early phytoplankton bloom of the ice-edge (Vallet et al. 2011).

Antarctic species physiology and metabolism appears to be successfully tuned to the Southern Ocean cold environment, but it is foreseeable that such subtle adaptations, resulting from a very long evolution, may not cope with a rapid climate change. A better knowledge of the complex links between euphausiid species and their environment is still necessary. Predictive models of the response of Antarctic krill and other euphausiids to climate change, ocean acidification by CO₂ (McNeil et al. 2008, Kawaguchi et al. 2013) and human exploitation (Nicol et al. 2012) have to take into account these specific adaptive strategies and their requirements concerning environmental and trophic suitability of the various habitats.

Moreover, Murphy *et al.* (2012) express the necessity of analysis and predicting models for food web structure and function to understand interactions of food web components, from phyto- and zooplankton to top predators, and the possible responses of the different actors of Antarctic communities (Arntz *et al.* 1997) to climate change and human impact on the SO ecosystem.

4.4. Euphausiids conservation

Euphausia superba, as a key species in the Antarctic Ocean food web, provides an efficient energy transfer to highest trophic levels (Van Franeker *et al.* 1997). The species plays a crucial role in the trophic web as feeding on phytoplankton and zooplankton (copepods) and being the major prey for birds, fish, squids, seals and whales, therefore playing a major role in carbon flux and the equilibrium of the Antarctic ecosystem.

There is a special concern about the impact on *Euphausia superba*, and other species exploited by fisheries, of the ongoing environmental changes concerning the Antarctic Ocean (Novacek & Cleland 2001, Atkinson *et al.* 2004, Flores *et al.* 2012b): temperature increase (Hill *et al.* 2013), reduction of ice extent (Quetin *et al.* 2007), acidification (Fabry *et al.* 2008, Kawaguchi *et al.* 2011b, Kawaguchi *et al.* 2013) and human exploitation. Recent developments in harvesting technology and in products derived industrially from krill indicate a renewed interest in exploiting this resource. At the same time, there are changes in the Southern Ocean environment that are affecting both krill and the fishery (Kawaguchi *et al.* 2009).

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) was established by international convention in 1982 with the objective of taking conservation measures for Antarctic marine life in response to increasing commercial interest in Antarctic krill during the 1970s and to prevent over-exploitation (Constable 2000). CCAMLR follows an ecosystem approach in its management because of the essential importance of Antarctic krill in the Antarctic marine ecosystem, in such a way as to minimise potential ecological risks both for krill and krill predators by setting precautionary catch limits for fisheries and therefore manages stocks (Map 15).

Precautionary catch limits on the krill fishery were first introduced by CCAMLR in 1991 and now cover much of the potential and actual fishing grounds in the CCAMLR Area (Map 15). These catch limits are decided based on the best available scientific information, they are under constant review (Miller & Agnew 2000, Nicol *et al.* 2012) and have been updated by CCAMLR on the basis of new information, particularly from large scale scientific surveys. The fishery is currently operating in the South West Atlantic (Areas 48.1, 48.2 and 48.3), but was operated in parts of the South Indian and Pacific Ocean sectors in the 1970s.

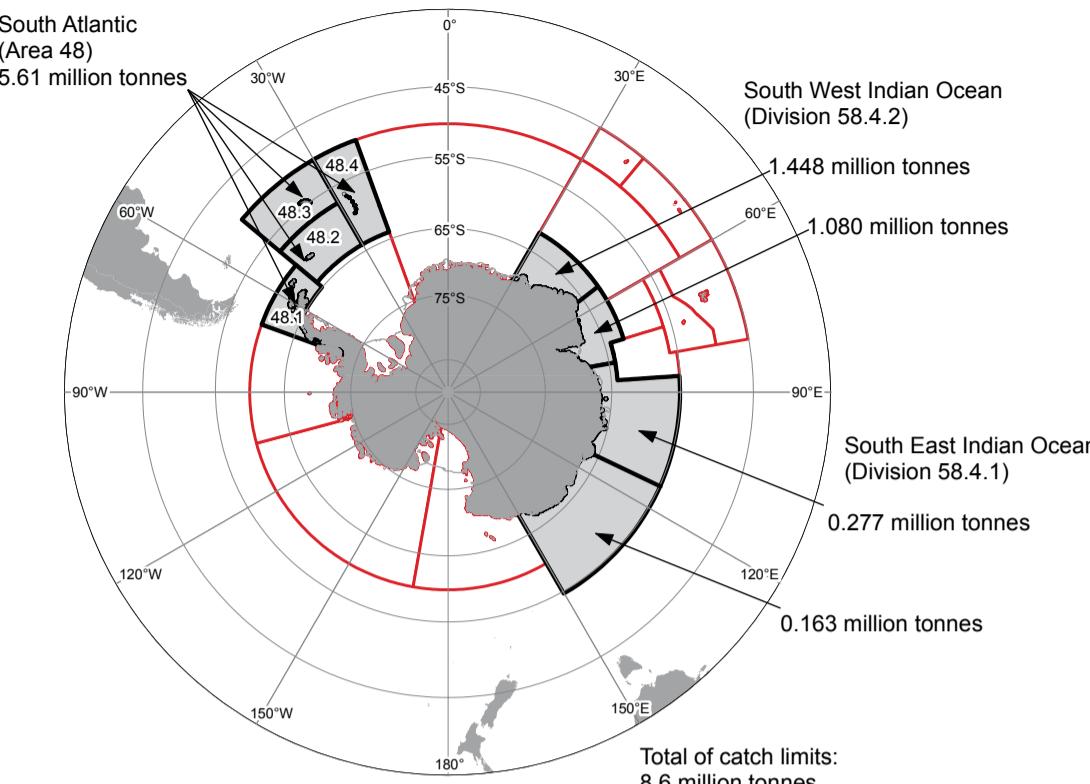
The scientific vigilance has to be reinforced to anticipate the adaptive responses of *E. superba*, and other Southern Ocean euphausiids, to a fast changing ecosystem (Flores *et al.* 2012a) and the limits of their capacity of resilience and survival in the fragile Southern Ocean communities.

Acknowledgements

We thank Dr Volker Siegel for the Antarctic krill picture, Dr Huw Griffiths (BAS, Cambridge) and Dr Anton Van de Putte (RBINS, Brussels) for the preparation of the maps, and Dr Cédric d'Udekem d'Acoz for editing. This research contributes to the programmes of the Laboratoire d'Océanographie de Villefranche-sur-mer, UMR 7093, for J.C-R, J-O I. F.P, and of the Australian Government of Antarctic Division for S.K. This project is part of "Zone Atelier Antarctique" of CNRS, some of the data were obtained thanks to a support from IPEV. It is a contribution to the "Ecoregionalisation project" supported by UPMC, Agence des Aires Marines Protégées and TAAF. We are grateful to Dr Volker Siegel and to an anonymous referee for their comments, which were of great help for the authors. This is CAML contribution #138.

References

- Arntz, M.E., Gutt, J., Klages, M., 1997. Antarctic marine biodiversity an overview. In: Battaglia, B., Valencia, J., Walton, D.W.H. (eds.). *Antarctic communities. Species, structure and survival*. Cambridge, UK: Cambridge University Press, pp. 3–14.
- Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature*, **432**, 100–103.
- Atkinson, A., Siegel, V., Pakhomov, E.A., Rothery, P., Loeb, V., Ross, R.M., Quetin, L.B., Schmidt, K., Fretwell, P., Murphy, E.J., Tarling, G.A., Fleming, A.H., 2008. Oceanic circumpolar habitats of Antarctic krill. *Marine Ecology Progress Series*, **362**, 1–23.
- Baker, A. de C., Boden, B.P., Brinton, E., 1990. *A practical guide to the Euphausiids of the world*. London: British Museum (Natural History), 96 pp.
- Bargmann, H.E., 1945. The development and life history of adolescent and adult krill, *Euphausia superba*. *Discovery Reports*, **23**, 103–176.
- Bé, A.W.H., Bosma, H., Lowe, T.P., *et al.*, 1969. Distribution of selected groups of marine invertebrates in waters South of 35°S latitude. Editor; V.C. Bushnel, Co-edited by JW Hedgepeth, American Geographic Society, New York. Ant Map Folio series, folio **11**, 1–44 (maps 1–29).
- Brierley, A.S., Fernandes, P.G., Brandon, M.A., Armstrong, F., Millard, N.W., McPhail, S.D., Stevenson, P., Pebody, M., Perrett, J., Squires, M., Bone, D.G., Griffiths, G., 2002. Antarctic krill under sea ice: Elevated abundance in a narrow band just south of ice edge. *Science*, **295**, 1890–1892.
- Clarke, A., Tyler, P.A., 2008. Adult Antarctic krill feeding at abyssal depths. *Current Biology*, **18**, 282–285.
- Constable, A.J., De la Mare, W., Agnew, D.J., Everson, I., Miller, D., 2000. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES Journal Marine Sciences*, **57**, 778–791.
- Croxall, J.P., Prince, P.A., Baird, A., Ward, P., 1985. The diet of the Southern rockhopper penguin *Eudyptes chrysocome* at Beauchene Island, Falkland Islands. *Journal of Zoology*, **206**, 485–496. doi:10.1111/j.1469-7998.1985.tb03553.x.
- Cuzin-Roudy, J., 1987a. Sexual differentiation in the Antarctic krill *Euphausia superba* Dana (Crustacea: Euphausiacea). *Journal of Crustacean Biology*, **7**(3), 518–524.
- Cuzin-Roudy, J., 1987b. Gonad history of the Antarctic krill *Euphausia superba* during its breeding season. *Polar Biology*, **7**, 237–244.
- Cuzin-Roudy, J., 1993. Reproductive strategies of the Mediterranean krill, *Meganyctiphanes norvegica* and the Antarctic krill, *Euphausia superba* (Crustacea: Euphausiacea). *Invertebrate reproduction and development*, **23**, 105–114.
- Cuzin-Roudy, J., 2000. Seasonal reproduction, multiple spawning, and fecundity in Northern krill, *Meganyctiphanes norvegica* and Antarctic krill, *Euphausia superba*. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 6–15.
- Cuzin-Roudy, J., Amsler, M.O., 1991. Ovarian development and sexual maturity staging in Antarctic krill *Euphausia superba* Dana (Crustacea: Euphausiacea). *Journal of Crustacean Biology*, **11**, 236–249.
- Cuzin-Roudy, J., Labat, J.P., 1992. Early summer distribution of Antarctic krill sexual development in Scotia-Weddell region: a multivariate approach. *Polar Biology*, **12**, 65–74.
- Cuzin-Roudy, J., Virtue, P., Mayzaud, P., Albessard, A., 1999. The scheduling of spawning with the molt cycle in krill (Crustacea: Euphausiacea): a strategy for allocating lipids to reproduction. *Invertebrate Reproduction and Development*, **36**, 163–170.
- Daly, K.L., 1990. Overwintering development, growth, and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. *Limnology and Oceanography*, **35**, 1564–1576.
- Fabry, V.J., Seibel, B.A., Feely, R.A., Orr, J.C., 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal Marine Sciences*, **65**, 414–432, doi:10.1093/icesjms/fsn048.
- Fach, B.A., Hofmann, E.E., Murphy, E.J., 2006. Transport of Antarctic krill (*Euphausia superba*) across the Scotia Sea. Part II. Krill growth and survival. *Deep Sea Research Part I: Oceanographic Research Papers*, **53**, 1011–1043. doi:10.1016/j.dsr.2006.03.007.
- Falk-Petersen, S., Hagen, W., Kattner, G., Clarke, A., Sargent, J., 2000. Lipids, trophic relationships and biodiversity in Arctic and Antarctic krill. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 178–191.
- Flores, H., Van Franeker, J.A., Siegel, V., Haraldsson, M., Strass, V., Meesters, E.H., Bathmann, U., Wolff, W.J., 2012a. The association of Antarctic krill *Euphausia superba* with under-ice habitat. *PLoS One*, **7**(2), e31775. doi:10.1371/journal.pone.0031775.
- Flores, H., Atkinson, A., Kawaguchi, S., Krafft, B.A., Milneovsky, G., Nicol, S., Reiss, C., Tarling, G.A., Werner, R., Bravo Rebollo, E., Cirelli, V., Cuzin-Roudy, J., Fielding, S., Groeneveld, J.J., Haraldsson, M., Lombana, A., Marschoff, E., Meyer, B., Pakhomov, E.A., Rombolá, E., Schmidt, K., Siegel, V., Teschke, M., Tonkes, H., Toullec, J.Y., Trathan, P.N., Tremblay, N., Van de Putte, A.P., Van Franeker, J.A., Werner, T., 2012b. Impact of climate change on Antarctic krill. *Marine Ecology Progress Series*, **458**, 1–9. doi:10.3354/meps09839.
- Froneman, P.W., Pakomov, E.A., Gurney, L.J., Hunt, B.P.V., 2002. Predation impact of carnivorous macrozooplankton in the vicinity of the Prince Edward Islands archipelago (Southern Ocean austral autumn 1998). *Deep Sea Research Part II: Topical Studies in Oceanography*, **49**(16), 3243–3254.
- Granelli, E., Granelli, W., Rabbani, M.M., Daughberg, N., Fransz, G., Cuzin-Roudy, J., Alder, V.A., 1993. The influence of copepod and krill grazing on the species composition of phytoplankton communities from the Scotia-Weddell sea. *Polar Biology*, **13**, 201–213.
- Griffiths, F.B., 1979. Euphausiids in the Coral and Tasman Seas during May 1972. I. Horizontal and vertical distribution. *Australian Journal of Marine and Freshwater Research*, **30**(5), 551–567. doi:10.1071/MF9790551.
- Gurney, L.J., Froneman, P.W., Pakomov, E.A., Mcquaid, C.D., 2001. Trophic positions of three euphausiids species from Prince Edward Islands (Southern Ocean); implications for the pelagic food web structure. *Marine Ecology Progress Series*, **217**, 167–174.
- Hagen, W., Kattner, G., 1998. Lipid metabolism of the Antarctic euphausiid *Thysanoessa macrura* and its ecological implications. *Limnology and Oceanography*, **43**, 1894–1901.
- Hamner, W., Hamner, P., 2000. Behavior of Antarctic krill (*Euphausia superba*): schooling, foraging, and antipredatory behavior. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**(Suppl. 3), Total of catch limits: 8.6 million tonnes.



Euphausiace Map 15 Precautionary catch limits on Antarctic krill fishery in the CCAMLR Area. Statistical areas are outlined and surveyed areas outlined and labelled (Nicol *et al.* 2012).

- 192–202.
- Harrington, S.A., Thomas, P.P.G., 1987. Observation on spawning by *Euphausia crystallorophias* from waters adjacent to Enderby Land (East Antarctica) and speculations on the early ontogenetic ecology of neritic Euphausiids. *Polar Biology*, **7**, 93–95.
- Hill, S.L., Phillips, T., Atkinson, A., 2013. Potential climate change effects on the habitat of Antarctic krill in the Weddell quadrant of the Southern Ocean. *PLoS ONE*, **8**(8), e72246. doi:10.1371/journal.pone.0072246
- Hirota, Y., Nemoto, T., Marumo, R., 1990. Life history of *Euphausia similis* (Crustacea, Euphausiacea) in Sagami Bay, Central Japan. *Journal of the Oceanographical Society of Japan*, **46**, 237–249.
- Hosie, G.W., Schultz, M.B., Kitchener, J.A., Cochran, T.C., Richard, K., 2000. Macrozooplankton community structure off East Antarctica (80°–150°E) during the austral summer of 1995/1996. *Deep-Sea Research II*, **47**, 2437–2463.
- Jarman, S.N., Elliott, N.G., Nicol, S., McMinn, A., 2000. Molecular phylogenetics of circum-global *Euphausia* species (Euphausiacea: Crustacea). *Canadian Journal of Fisheries Aquatic Sciences*, **57**(Suppl. 3), 51–58.
- Jenner, R.A., Dhubhaill, C.N., Ferla, M.P., Wills, M.A., 2009. Eumalacostracan phylogeny and total evidence: limitations of the usual suspects. *BMC Evolutionary Biology*, **9**, 21. doi:10.1186/1471-2148-9-21.
- Kattner, G., Hagen, W., 1998. Lipid metabolism of the antarctic euphausiids *Euphausia crystallorophias* and its ecological implications. *Marine Ecology Progress Series*, **170**, 203–233.
- Kawaguchi, S., Nicol, S., Press, A.J., 2009. Direct effects of climate change on the Antarctic krill fishery. *Fisheries Management and Ecology*, **16**, 424–427. doi:10.1111/j.1365-2400.2009.00686.x.
- Kawaguchi, S., Kilpatrick, R., Roberts, L., King, R.A., Nicol, S., 2011a. Ocean-bottom krill sex. *Journal of Plankton Research*, **33**(7), 1134–1138. doi:10.1093/plankt/fbr006.
- Kawaguchi, S., Kurihara, H., King, R., Hale, L., Berli, T., Robinson, J.P., Ishida, A., Wakita, M., Virtue, P., Nicol, S., Ishimatsu, A., 2011b. Will krill fare well under Southern Ocean acidification? *Biology Letters*, **7**(2), 288–291. doi:10.1098/rsbl.2010.0777.
- Kawaguchi, S., Ishida, A., King, R., Raymond, B., Waller, N., Constable, A., Nicol, S., Wakita, M., Ishimatsu, A., 2013. Risk maps for Antarctic krill under projected Southern Ocean acidification. *Nature Climate Change*, **3**(9), 843–847. doi:10.1038/nclimate1937.
- Kear, A.J., 1992. The diet of Antarctic squid; comparison of conventional and serological gut contents analyses. *Ecology*, **156**(2), 161–178.
- Kirkwood, M., 1982. A guide to the Euphausiacea of the Southern Ocean. *ANARE Research notes*, **1**, 1–45.
- Law, C.S., Abraham, E.R., Watson, A.J., Liddicoat, M.I., 2003. Vertical eddy diffusion and nutrient supply to the surface mixed layer of the Antarctic Circumpolar Current. *Journal of Geophysical Research, Oceans*, **108**, 3272. doi:10.1029/2002JC001604, C8.
- Daly, K.L., 1998. Physioecology of juvenile Antarctic Krill (*Euphausia superba*) during spring in ice-covered Seas. In: Lizotte, M.P., Arrigo, K.R., (eds.). *Antarctic Sea Ice: Biological Processes, Interactions and Variability*. *Antarctic Research Series*, **73**, 183–198. doi:10.1029/AR073p0183.
- Marr, J.W.S., 1962. The natural history and geography of the Antarctic krill (*Euphausia superba*). *Discovery Reports*, **32**, 33–464.
- Martin, J.W., Davis, G.E., 2001. An updated classification of the recent Crustacea. Natural History Museum of Los Angeles County, *Science Series*, **39**, 1–123.
- Mauchline, J., Fisher, L.R., 1969. The biology of euphausiids- Advances in Marine Biology, **7**, 1–454.
- Mauchline, J., 1980. The biology of Mysids and Euphausiids. *Advances in Marine Biology*, **18**, 1–681.
- Mayzaud, P., Albessard, E., Cuzin-Roudy, J., 1998. Changes in lipid composition of the Antarctic krill *Euphausia superba* in the Indian sector of the Antarctic Ocean. *Marine Ecology Progress Series*, **173**, 149–162.
- Mayzaud, P., Boutoute, M., Alonso, F., 2003. Lipid composition of the euphausiids *Euphausia vallentini* and *Thysanoessa macrura* during the summer in the Southern Ocean. *Antarctic Science*, **15**(4), 463–475.
- McNeil, B.I., Matear, R.J., 2008. Southern Ocean acidification: A tipping point at 450-ppm atmospheric CO₂. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 18860–18864.
- Miller, D., Agnew, D., 2000. Management of krill fisheries in the Southern Ocean. In: Everson, I. (ed.). *Krill biology, ecology and fisheries*. Cambridge, UK: Blackwell, pp 300–337.
- Miller, D.G.M., Hampton, I., 1989. Biology and ecology of the Antarctic krill (*Euphausia superba* Dana): A review. *BIMASS Science Series*, **9**, 1–166.
- Murphy, E.J., Cavanagh, R.D., Hofmann, E.E., Hill, S.L., Constable, A.J., Costa, D.P., Pinkerton, M.H., Johnston, N.M., Trathan, P.N., Klink, J.M., Wolf-Gladrow D.A., Daly, K.L., Maury, O., Doney, S.C., 2012. Developing integrated models of Southern Ocean food webs: Including ecological complexity, accounting for uncertainty and the importance of scale. *Progress in Oceanography*, **102**, 74–92.
- Nicol, S., 2006. Krill, currents, and sea ice: *Euphausia superba* and its changing environment. *BioScience*, **56**(2), 111–120. doi:dx.doi.org/10.1641/00063568(2006)056[0111:KCASIE]2.0.CO;2
- Nicol, S., Foster, J., Kawaguchi, S., 2012. The fishery for Antarctic krill – recent developments. *Fish and Fisheries*, **13**, 30–40. doi:10.1111/j.1467-2979.2011.00406.x.
- Nordhausen, W., 1994. Winter abundance and distribution of *Euphausia superba*, *E. crystallorophias*, and *Thysanoessa macrura* in Gerlache Strait and Crystal Sound, Antarctica. *Marine Ecology Progress Series*, **109**, 131–142.
- Novacek, M.J., Cleland, E., 2001. The current biodiversity extinction event: scenarios for mitigation and recovery. *Proceedings of the National Academy of Science*, **10**, 5466–470.
- Ono, A., Moteki, M., Amakasu, K., Toda, R., Horimoto, N., Hirano, D., Ashimaru, T., Hosie, G.W., 2011. Euphausiid community structure and population structure of *Euphausia superba* off Adélie Land in the Southern Ocean during austral summer 2003, 2005, and 2008. *Polar Science*, **5**(2), 146–165. doi:10.1016/j.polar.2011.04.006.
- Pakhomov, E.A., 2000. Demography and life cycle of Antarctic krill, *Euphausia superba*, in the Indian sector of the Southern Ocean: long-term comparison between coastal and open-ocean regions. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**(3), 68–90.
- Pakhomov, E.A., Froneman, P.W., 1999. Macroplankton/microneuston dynamics in the vicinity of the Prince Edwards Islands (Southern Ocean). *Marine Biology*, **134**, 501–515.
- Pakhomov, E.A., Perissinotto, R., 1996. Antarctic neritic krill *Euphausia crystallorophias*: Spatio-temporal distribution, growth and grazing rates. *Deep-Sea Research I*, **43**(1), 59–87.
- Perissinotto, R., Mayzaud, P., Labat, J.P., Razouls, S., 2001. Grazing dynamics of *Euphausia spinifera* in the region of the subtropical convergence and the Agulhas Front. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**(2), 273–281, doi:10.1139/f00-241.
- Phlegler, C.F., Nelson, M.M., Mooney, B.D., Nichols, P.D., 2002. Inter-annual and between species comparison of the lipids, fatty acids and sterols of Antarctic krill from the US AMLR Elephant Island survey area. *Comparative Biochemistry and Physiology*, **131B**, 733–747.
- Pilar, S.C., Stuart, V., 1988. Population structure, reproductive biology and maintenance of *Euphausia lucens* in the southern Benguela current. *Journal of Plankton Research*, **10**(6), 1083–1098. doi:10.1093/plankt/10.6.1083.
- Pliny Secundi. circa 77–79. *Naturalis Historia*. Liber XI. *Aquatilium animalium* in Latin, with French translation by Guérout P.C.B., 1802. *Histoire Naturelle par Pline. Tome 2. Des animaux qui vivent dans l'eau*. 1802, 416 pp.
- Quetin, L.B., Ross, R.M., 2001. Environmental variability and its impact on the reproductive cycle of Antarctic krill. *American Zoologist*, **41**, 74–89.
- Quetin, L.B., Ross, R.M., Frazer, T.K., Amsler, M.O., Wyatt-Evens, C., Oakes, S.A., 2003. Growth of larval krill, *Euphausia superba*, in fall and winter west of the Antarctic Peninsula. *Marine Biology*, **143**, 833–843. doi:10.1007/s00227-003-1130-8.
- Quetin, L.B., Ross, R.M., Fritsen, C.H., Vernet, M., 2007. Ecological responses of Antarctic krill to environmental variability: can we predict the future? *Antarctic Science*, **19**, 253–266, doi:10.1017/S0954102007000363.
- Quetin, L.B., Ross, R.M., 2003. Episodic recruitment in Antarctic krill *Euphausia superba* in the Palmer LTR region. *Marine Ecology Progress Series*, **259**, 185–200.
- Ramirez, F.C., Dato, C., 1983. Seasonal changes in population structure and gonadal development of three Euphausiid species. *Oceanologica Acta*, **6**(4), 427–433.
- Rintoul, S.R., Sparrow, M., Meredith, M.P., Wadley, V., Speer, K., Hofmann, E., Summerhayes, C., Urban, E., Bellerby, R., 2012. *The Southern Ocean observing system: initial science and implementation strategy*. SCAR, SCOR, UTAS, SOOS, IMAS, 76 pp.
- Robertson, D.A., Roberts, P.E., Wilson, J.B., 1978. Mesopelagic faunal transition across the subtropical convergence east of New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **12**(4), 295–312.
- Ross, R.M., Quetin L.B., 2000. Reproduction in Euphausiacea. In: Everson, I. (ed.). *Krill: Biology, Ecology and fisheries*. *Fish and Aquatic Resources Series*, 6. Oxford: Blackwell Science, pp. 150–180.
- Ross, R.M., Quetin, L.B., Baker, K.S., Vernet, M., Smith, R.C., 2000. Growth limitation in young *Euphausia superba* under field conditions. *Limnology and Oceanography*, **45**, 31–43.
- Sala, A., Azzali, M., Russo, A., 2002. Krill of the Ross Sea: distribution, abundance and demography of *Euphausia superba* and *Euphausia crystallorophias* during the Italian Antarctic Expedition (January–February 2000). *Scientia Marina*, **66**(2), 123–133.
- Schmidt, K., Atkinson, A., Petzke, K.J., Voss, M., Pond, D.W., 2006. Protozoans as a food source for Antarctic krill, *Euphausia superba*: Complementary insights from stomach content, fatty acids, and stable isotopes. *Limnology and Oceanography*, **51**, 2409–2427.
- Schmidt, K., Atkinson, A., Venables, H.J., Pond, D.W., 2012. Early spawning of Antarctic krill in the Scotia Sea is fuelled by “superfluous” feeding on non-ice associated phytoplankton blooms. *Deep Sea Research Part II*, **59–60**, 159–172.
- Schmidt, K., Atkinson, A., Steinberger, S., Fielding, S., Lindsay, M.C.M., Pond, D.W., Tarling, G.A., Klevjer, T.A., Allen, C.S., Nicol, S., Achterberg, E.P., 2011. Seabed foraging by Antarctic krill: Implications for stock assessment, benthopelagic coupling, and the vertical transfer of iron. *Limnology and Oceanography*, **56**, 1411–1428. doi:10.4319/lo.2011.56.4.1411.
- Seear, P.J., Goodall-Copestake, W.P., Andrew, H., Fleming, Rosato, E., Tarling, G.A., 2012. Seasonal and spatial influences on gene expression in Antarctic krill *Euphausia superba*. *Marine Ecology Progress Series*, **467**, 61–75. doi:10.3354/meps09947.
- Siegel, V., 1987. Age and growth of Antarctic Euphausiacea (Crustacea) under natural conditions. *Marine Biology*, **96**, 483–495.
- Siegel, V., 2000. Krill (Euphausiacea) life history and aspects of population dynamics. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**(S3), 130–150.
- Siegel, V., 2012. Krill stocks in high latitudes of the Antarctic Lazarev Sea: seasonal and inter-annual variation in distribution, abundance and demography. *Polar Biology*, **35**, 1151–1177.
- Swadling, K.M., Kawaguchi, S., Hosie, G.W., 2010. Antarctic mesozooplankton community structure during BROKE-West (30°E–80°E), January–February 2006. *Deep Sea Research Part II: Topical studies in Oceanography*, **57**(9–10), 887–904.
- Taki, K., Yabuki, T., Noiri, Y., Hayashi, T., Naganobu, M., 2008. Horizontal and vertical distribution and demography of euphausiids in the Ross Sea and its adjacent waters in 2004/2005. *Polar Biology*, **31**, 1343–1356.
- Tarling, G.A., Cuzin-Roudy, J., Thorpe, S.E., Shreeve, S.E., Ward, P., Murphy, E.J., 2007. Recruitment of Antarctic krill (*Euphausia superba* Dana) in the South Georgia region: adult fecundity and the fate of larvae. *Marine Ecology Progress Series*, **331**, 161–179. doi:10.3354/meps331161
- Tarling, G.A., Cuzin-Roudy, J., Wootten, K., Johnson, M.L., 2009. Egg-release behaviour in Antarctic krill. *Polar Biology*, **32**, 1187–1194.
- Tarling, G.A., Ensor, N.S., Fregin, T., Goodall-Copestake, W.P., Frewell, P., 2010. An introduction to the Biology of northern krill (*Meganyctiphanes norvegica* Sars). *Advances in Marine Biology*, **57**, 1–40.
- Teschke, M., Kawaguchi, S., Meyer, B., 2008. Effects of simulated light regimes on maturity and body composition of Antarctic krill, *Euphausia superba*. *Marine Biology*, **154**(2), 215–324.
- Thiriot-Quiévreux, C., Leitão, A., Cuzin-Roudy, J., 1998. Chromosome diversity in Mediterranean and Antarctic euphausiid species. *Journal of Crustacean Biology*, **18**(2), 290–297.
- Thorpe, S.E., Murphy E.J., Watkins, J.L., 2007. Circumpolar connections between Antarctic krill (*Euphausia superba* Dana) populations. Investigating the roles of Ocean and sea ice transport. *Deep-Sea Research I*, **54**, 792–810.
- Vallet, C., Koubbi, P., Sultan, E., Goffart, A., Swadling, K.M., Wright, S.W., 2009. Distribution of euphausiid larvae along the coast of East Antarctica in the Dumont d'Urville Sea (139–145°E) during summer 2004. *Antarctic Science*, **21**, 197–207.
- Vallet, C., Labat, J.-P., Smith, M., Koubbi, P., 2011. Interannual variations in euphausiid life stage distribution in the Dumont d'Urville Sea from 2004 to 2008. *Polar Science*, **5**, 166–178.
- Van Franeker, J.A., Bathmann, U., Mathot, S., 1997. Carbon fluxes to Antarctic top predators. *Deep-Sea Research Part II: Topical studies in Oceanography*, **44**, 435–455.
- Ward, P., Atkinson, A., Peck, J.M., Wood, A.G., 1990. Euphausiid life cycles and distribution around South Georgia. *Antarctic Science*, **2**(1), 43–52.
- Zane, L., Maccatrucci, L., Bargelloni, L., Battaglia, B., Patarnello, T., 1998. Molecular evidence for genetic subdivision of Antarctic krill (*Euphausia superba* Dana) populations. *Proceedings of the Royal Society, London, Ser.B*, **1413**, 2387–2393.
- Zane, L., Patarnello, T., 2000. Krill: a possible model for investigating the effects of ocean currents on the genetic structure of a pelagic invertebrate. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**(3), 16–23.

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



Claude DE BROYER is a marine biologist at the Royal Belgian Institute of Natural Sciences in Brussels. His research interests cover structural and ecofunctional biodiversity and biogeography of crustaceans, and polar and deep sea benthic ecology. Active promoter of CAML and ANDEEP, he is the initiator of the SCAR Marine Biodiversity Information Network (SCAR-MarBIN). He took part to 19 polar expeditions.



Huw GRIFFITHS is a marine Biogeographer at the British Antarctic Survey. He created and manages SOMBASE, the Southern Ocean Mollusc Database. His interests include large-scale biogeographic and ecological patterns in space and time. His focus has been on molluscs, bryozoans, sponges and pycnogonids as model groups to investigate trends at high southern latitudes.



Cédric d'UDEKEM d'ACOZ is a research scientist at the Royal Belgian Institute of Natural Sciences, Brussels. His main research interests are systematics of amphipod crustaceans, especially of polar species and taxonomy of decapod crustaceans. He took part to 2 scientific expeditions to Antarctica on board of the *Polarstern* and to several sampling campaigns in Norway and Svalbard.



Bruno DANIS is an Associate Professor at the Université Libre de Bruxelles, where his research focuses on polar biodiversity. Former coordinator of the scarmarbin.be and antabif.be projects, he is a leading member of several international committees, such as OBIS or the SCAR Expert Group on Antarctic Biodiversity Informatics. He has published papers in various fields, including ecotoxicology, physiology, biodiversity informatics, polar biodiversity or information science.



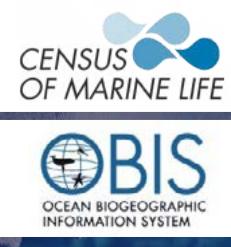
Susie GRANT is a marine biogeographer at the British Antarctic Survey. Her work is focused on the design and implementation of marine protected areas, particularly through the use of biogeographic information in systematic conservation planning.



Christoph HELD is a Senior Research Scientist at the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven. He is a specialist in molecular systematics and phylogeography of Antarctic crustaceans, especially isopods.



Falk HUETTMANN is a 'digital naturalist' he works on three poles (Arctic, Antarctic and Hindu-Kush Himalaya) and elsewhere (marine, terrestrial and atmosphere). He is based with the university of Alaska-Fairbank (UAF) and focuses primarily on effective conservation questions engaging predictions and open access data.



Philippe KOUBBI is professor at the University Pierre et Marie Curie (Paris, France) and a specialist in Antarctic fish ecology and biogeography. He is the Principal Investigator of projects supported by IPEV, the French Polar Institute. As a French representative to the CCAMLR Scientific Committee, his main input is on the proposal of Marine Protected Areas. His other field of research is on the ecoregionalisation of the high seas.



Ben RAYMOND is a computational ecologist and exploratory data analyst, working across a variety of Southern Ocean, Antarctic, and wider research projects. His areas of interest include ecosystem modelling, regionalisation and marine protected area selection, risk assessment, animal tracking, seabird ecology, complex systems, and remote sensed data analyses.



Anton VAN DE PUTTE works at the Royal Belgian Institute for Natural Sciences (Brussels, Belgium). He is an expert in the ecology and evolution of Antarctic fish and is currently the Science Officer for the Antarctic Biodiversity Portal www.biodiversity.aq. This portal provides free and open access to Antarctic Marine and terrestrial biodiversity of the Antarctic and the Southern Ocean.



Bruno DAVID is CNRS director of research at the laboratory BIOGÉOSCIENCES, University of Burgundy. His works focus on evolution of living forms, with and more specifically on sea urchins. He authored a book and edited an extensive database on Antarctic echinoids. He is currently President of the scientific council of the Muséum National d'Histoire Naturelle (Paris), and Deputy Director at the CNRS Institute for Ecology and Environment.



Julian GUTT is a marine ecologist at the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, and professor at the Oldenburg University, Germany. He participated in 13 scientific expeditions to the Antarctic and was twice chief scientist on board Polarstern. He is member of the SCAR committees ACCE and AnT-ERA (as chief officer). Main foci of his work are: biodiversity, ecosystem functioning and services, response of marine systems to climate change, non-invasive technologies, and outreach.



Graham HOSIE is Principal Research Scientist in zooplankton ecology at the Australian Antarctic Division. He founded the SCAR Southern Ocean Continuous Plankton Recorder Survey and is the Chief Officer of the SCAR Life Sciences Standing Scientific Group. His research interests include the ecology and biogeography of plankton species and communities, notably their response to environmental changes. He has participated in 17 marine science voyages to Antarctica.



Alexandra POST is a marine geoscientist, with expertise in benthic habitat mapping, sedimentology and geomorphic characterisation of the seafloor. She has worked at Geoscience Australia since 2002, with a primary focus on understanding seafloor processes and habitats on the East Antarctic margin. Most recently she has led work to understand the biophysical environment beneath the Amery Ice Shelf, and to characterise the habitats on the George V Shelf and slope following the successful CAML voyages in that region.



Yan ROPERT COUDERT spent 10 years at the Japanese National Institute of Polar Research, where he graduated as a Doctor in Polar Sciences in 2001. Since 2007, he is a permanent researcher at the CNRS in France and the director of a polar research programme (since 2011) that examines the ecological response of Adélie penguins to environmental changes. He is also the secretary of the Expert Group on Birds and Marine Mammals and of the Life Science Group of the Scientific Committee on Antarctic Research.