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SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

▶ CHAPTER 10.3. NEAR SURFACE ZOOPLANKTON COMMUNITIES.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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10.3 Near-surface zooplankton communities

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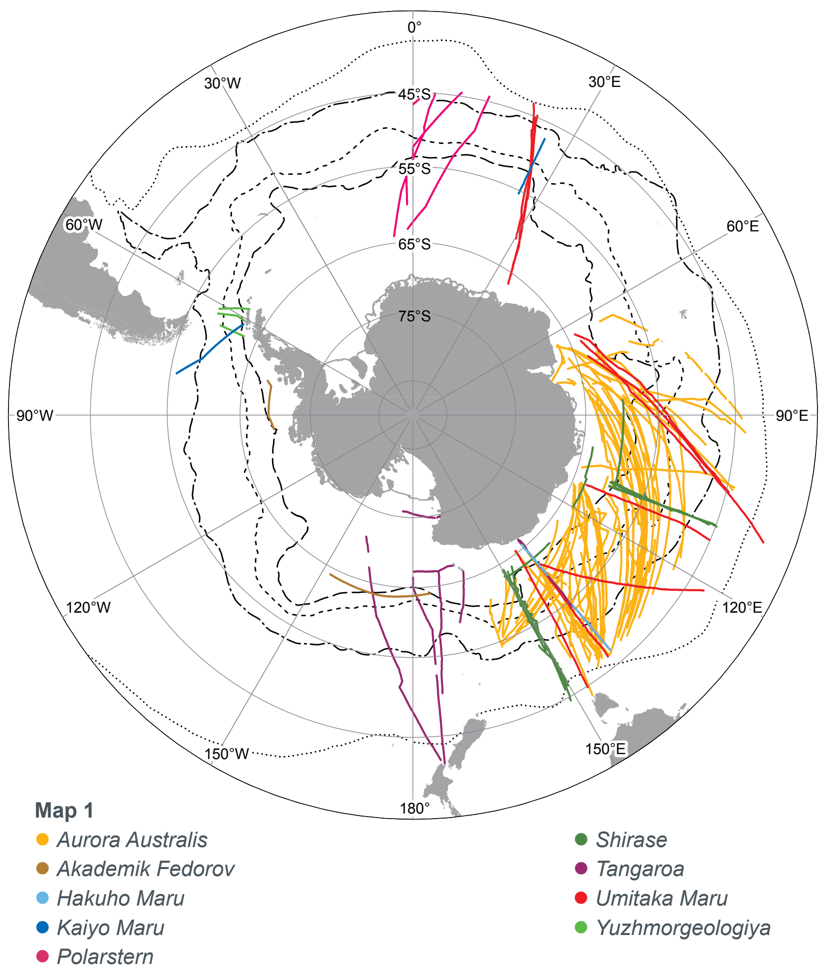
1. Introduction

There have been a number of attempts to define and describe the composition, structure and distribution patterns of zooplankton communities around Antarctica. Early attempts, well prior to the availability of computers and modelling methods, included Mackintosh (1934, 1937), Hardy & Gunther (1936), and Voronina (1972). Mackintosh perhaps provided the first circum-Antarctic description of zooplankton distributions. More systematic attempts to describe zooplankton community patterns started during the BIOMASS (Biological Investigation of Marine Antarctic Systems and Stocks) programme, using a range of computer aided multivariate and quantitative analytical methods. Several studies have focussed on the Atlantic sector, including the Antarctic Peninsula area, Scotia Arc and southern Weddell Sea, e.g. Boysen-Ennen & Piatkowski (1988), Hubold *et al.* (1988) and Piatkowski (1989a,b), Siegel & Piatkowski (1990), Siegel *et al.* (1992), Pakhomov *et al.*, 1997, Ward *et al.* (2005, 2006, 2007). Surveys in the eastern Antarctic sector have covered a wider geographic area including the Lazarev Sea (Pakhomov *et al*. 1993, Hunt *et al*. 2011), Cosmonaut Sea (Pakhomov & Pelevin 1989, Hunt *et al*. 2007), the Prydz Bay region (Hosie 1994, Hosie & Cochran 1994, Hosie *et al*. 1997, Yang *et al*. 2011), from Casey station to the Ross Sea (Chiba *et al*. 2001), and in the Ross Sea (Pane *et al*. 2004). These surveys ranged from small to large scale in area with sampling resolutions of 10s to 100s km between sites. There have been a number of smaller area, finer scale zooplankton surveys have been conducted along the coastal margins of Antarctica, e.g. off Syowa station (Fukuchi *et al.* 1985, Ojima *et al.* 2013), Mawson (Nicol *et al.* 2008), near Dumont d'Urville (*Ono et al.* 2011, Swadling *et al.* 2011), and around Palmer Station (Lancraft *et al.* 2004, Ross *et al.* 2008, Marrari *et al.* 2011), as well as around sub-Antarctic islands, e.g. Marion, Prince Edward, Kerguelen and Heard Islands (e.g. Grindley & Lane 1979, Froneman *et al.* 1999, Fielding *et al.* 2007, Carlotti *et al.* 2008). These finer scale surveys have proved very useful at identifying localised biogeographic patterns but less so for identifying large scale biogeographic patterns, which is the scope of this chapter.

Various sampling methods with different nets have been employed, e.g. Bongo nets, Norpac, Longhurst-Hardy Plankton Recorder, Rectangular Midwater Trawl (RMT) and other midwater trawls. The BROKE (Hosie *et al*. 2000) and BROKE West (Swadling *et al*. 2010) surveys were one of the most extensive geographic surveys, covering the eastern Antarctic region from 30 to 160°E with the same sampling method using an RMT1+8 net system. Collectively the surveys have not been systematic in determining the biodiversity and distribution of zooplankton. For many of the surveys, the zooplankton have been a secondary study to the primary objective of studying the distribution, abundance and ecology of Antarctic krill *Euphausia superba*. Most of these studies have attempted to relate the distribution of the assemblages to hydrology and other environmental conditions in the sampling area. Sea temperature, chlorophyll *a*, and sea ice were the most consistent variables related to zooplankton patterns. The one region that has consistently remained poorly studied has been the Pacific sector between the Ross Sea and the Antarctic Peninsula, i.e. the Amundsen and Bellingshausen Seas.

The SCAR Southern Ocean Continuous Plankton Recorder (SO-CPR) Survey commenced in January 1991 with the purpose of mapping the seasonal, inter-annual, long-term and spatial variation in plankton diversity, as well as to use plankton as sensitive indicators of environmental changes to monitor the health of the Southern Ocean (Hosie *et al*. 2003). The SO-CPR Survey provides the largest comprehensive and systematic Antarctic zooplankton data set, spatially and temporally, using a consistent sampling methodology ideal for biogeographic studies. The Survey to date has towed CPRs for approximately 210,000 nautical miles over about 70% of the Southern Ocean, mainly in the months from September to April when most research and supply ships are operating (Map 1). However, some tows have been conducted in winter: May, July and August. The highest concentration of tows and sampling collection is in the region south and west of Australia (McLeod *et al*. 2010). The application of species distribution modelling techniques to the SO-CPR data set has proved useful for bioregionalisation studies and for predicting the spatial and seasonal distribution and abundance of the cyclopoid copepod *Oithona similis* in the Southern Ocean (Pinkerton *et al*. 2010). The success of the prediction lies in the sensitivity of zooplankton to closely align with and reflect the oceanographic conditions of their environment.

Additional distribution modelling of other species was considered for this Atlas, but a new zooplankton atlas for the Southern Ocean has just been published showing the distribution patterns for the 50 most abundant taxa and developmental stages from the SO-CPR database (McLeod *et al*. 2010). These 50 taxa are the most abundant comprising more than 90% of the total abundance. The next step, therefore, was to produce predictive biogeographic maps of whole zooplankton assemblages, zoogeographic divisions of plankton, using the same 50 taxa used by McLeod *et al*. (2010). Hunt & Hosie (2003, 2005, 2006a,b) have shown the existence of consistent zooplankton assemblages south of Hobart using the CPR data, with strong latitudinal zonation associated with oceanographic fronts. The modelling of the *Oithona* data has predicted the existence of hot-spots of abundance which appear to match predator patterns. Analysis of patterns by month or season will hopefully assist other scientists studying climate change, plankton, predator-prey relationships by providing information on the degree of variation or in fact consistency in zooplankton biogeographic regions. Such information is useful for fisheries and conservation management.



Map 1 CPR tows from January 1991 to March 2008 used in the GDM analysis.

2. Methods

2.1. Continuous Plankton Recorder sampling

A detailed description of the CPR sampling method is given in Hosie *et al*. (2003). A summary of the methods is provided here. The CPR is a robust near-surface towed plankton sampling device that collects regular samples during the austral summer in the Southern Ocean (Hosie *et al*. 2003). The CPR is towed behind research, resupply and fishing vessels typically operating at speeds of 12–15 knots. It is towed at a depth of 10 m, approximately 100 m behind the vessel (Hunt & Hosie 2003, Hosie *et al*. 2003). Water enters through a square aperture of 1.62 cm^2 (1.27 x 1.27 cm), before entering a wider collecting tunnel of 10 x 5 cm. This reduces the speed of water flow by about 30 times before it hits a slowly moving band of silk with an average mesh size of 270 µm. A second band of silk mesh covers the filtering silk to create a sandwich that is then rolled into a storage tank filled with formaldehyde. Regardless of the speed of the vessel, the silk is advanced at a set rate of 1 cm per nautical mile of tow. Each tow lasts about 450 nautical miles (833 km). In the laboratory, each set of silk is unrolled and cut into sections representing 5 nautical mile (9.26 km) samples. The entire contents of each sample is identified and enumerated under a dissecting microscope. Zooplankton are identified to the lowest taxonomic level possible, ideally species, based on the Register of Antarctic Marine Species (RAMS) developed by the SCAR Marine

Biodiversity Information Network (SCAR-MarBIN, De Broyer & Danis 2009). Some zooplankton are easily damaged, notably gelatinous and soft bodied species, and can only be identified to a coarser taxonomic resolution. Antarctic krill and other euphausiids are identified to developmental stage. Copepods (adults and copepodite stages) are identified to species level whenever possible. The database currently holds data for 234 zooplankton taxa and developmental stages.

2.2. Limitations of the data and analysis

There are a number of limitations with the CPR sampling method and data that need to be acknowledged in order to understand what the CPR can and cannot deliver. These include:

- The CPR is towed horizontally at a constant depth, which means that the diurnal vertical migration of some zooplankton taxa may affect abundance variations in the observed data on a 24 hour scale. Normally, this can be taken into account (e.g. by selecting night-time data only, using the ship's light sensor record to distinguish night from day). This was unnecessary for the GDM modelling, and the whole data set was used.
- It has a small aperture and is therefore best suited for mesozooplankton. Nonetheless, it does catch substantial numbers of adult Antarctic krill.
- Gelatinous zooplankton, such as medusae and salps, are poorly sampled. Larvaceans are caught in large numbers and can be identified to genus.
- Consistency in taxonomic skill and identification across different laboratories is an issue (analysts work in different labs in Australia, Japan, Germany and New Zealand). This issue was addressed and tested during the "Southern Ocean CPR Standards Workshop -SCAR Expert Group on CPR Research" in Tokyo November 2011 (Takahashi *et al*. 2012), which noted that a high degree of consistency in taxonomic identification was maintained.
- Some species are too difficult to identify after being trapped on silk. Therefore, many species have to be grouped into coarser taxa.
- Temporal coverage is poor, with the highest volume of data coming after 1997, and there are little winter data.
- The CPR data set is particularly large with the highest density of data coming from the region south and west of Australia, 60–160 ºE (Table 1). When the data set is fragmented into months the data can become somewhat sparse, hence the reason for grouping the early and late seasons months. However, despite the combination of months the number of tows in the early and late seasons period are still limited and predicting patterns around an Antarctica based on just a few samples is obviously tenuous. Nonetheless, there are monthly sub-sets of data sufficient for predicting distributions into other regions not sampled by CPR as demonstrated by Pinkerton *et al.* (2010).

Table 1 Number of CPR samples per month.

Month	Number of samples
July-August-September	763
October	1576
November	2385
December	3882
January	4861
February	4470
March	5930
April-May	1159

2.3. Description of data

All available CPR data up to March 2008 were used. While data have been collected since March 2008, this was taken as the cut-off date when analyses commenced, this being the date when the last CPR tow was conducted during the Census of Antarctic Marine Life. CPR data were analysed by month. July, August, September, were grouped, as were April and May, due to the low number of samples in each of those months. Table 1 lists the number of samples per month. Each sample represents a 5 nautical mile section of CPR track. A total of 25,026 were used in the analyses. All data used in the following modelling and analyses are abundance estimates expressed as the number of individuals per m^3 for each taxon.

The same 50 taxa from the Southern Ocean CPR atlas (McLeod *et al*. 2010) were used for the modelling. Following the "Southern Ocean CPR Standards Workshop – SCAR Expert Group on CPR Research" in Tokyo 2011 (Takahashi *et al*. 2012), it was agree that *Ctenocalanus citer* and *Ctenocalanus vanus* would be combined as the single taxonomic field *Ctenocalanus* spp., because there was a certain degree of uncertainty in distinguishing the two species in the CPR samples.

A number of environmental variables were tested and five were selected for the final models, these being:

- Long-term mean summer sea surface temperature (satellite data)
- Long-term mean summer sea surface chlorophyll-a (satellite data)
- Long-term mean sea-ice extent (satellite data)
- Depth
- Slope

See Table 1 in Chapter 2.3 "Modelling distributions" which describes the details of each of these parameters. The selected parameters produced the most meaningful maps of contiguous groups. Other variables were tested, such as days since ice melt and monthly mean values of the above variables, but these had poor explanatory power and tended to produce maps that were difficult to interpret. These additional variables were not used in the final analyses.

2.4. Modelling

Generalised dissimilarity modelling (GDM) was used for the modelling. It is a technique that models rates of change in species community composition between sites as a function of changing environmental characteristics (Ferrier 2007). Fitting a GDM model to biological and environmental data from a set of survey sites involves calculating the compositional (biological) dissimilarity between pairs of sites in the data frame containing the species information (using the Bray-Curtis index), and then modelling this dissimilarity using the environmental predictors in the environmental predictor data frame. The results from GDM were then classified using the clara clustering method and Manhattan matrix (see Chapter 3 of Kaufman & Rousseeuw 1990). The optimum number of clusters was achieved through maximising average bandwidth. Further details of the GDM modelling are presented in Chapter 2.3 on "Modelling distributions".

Following the production of predictive maps the zooplankton species composition was determined for each group for each month, as well as for the entire dataset (all months combined) by matching the original CPR samples to the GDM cluster groups. In some months, the GDM predicted groups based on environmental parameters alone, for which there was no corresponding CPR samples. This happened in the Antarctic coastal regions and in the subtropics where CPR sampling had not been conducted. For each month the species chiefly responsible for distinguishing a group were identified using the SIMPER analysis tool from Primer V6 (Clarke 1993, Clarke & Warwick 2001, Clarke & Gorley 2006).

3. Zoogeographic divisions

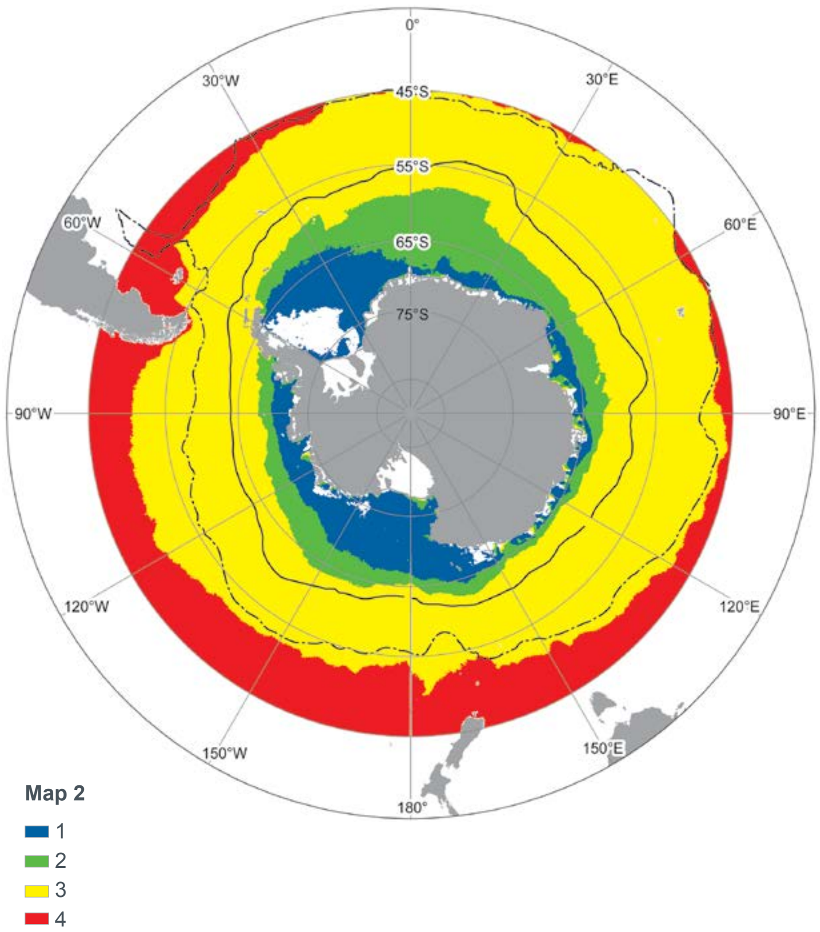
The GDM analyses produced models describing general assemblage patterns that were a good match to our current knowledge and expectations for the region. Four main assemblages or biogeographic zones were identified, as seen in the all-months prediction (Table 2), and evident in each month from December to May (Tables 6 to 10). These four groups more or less matched known geographic regions best described for the current analysis as:

- the Inner Seasonal Ice Zone (ISIZ), a region covering much of the continental shelf and slope area,
- the Outer Seasonal Ice Zone (OSIZ), the rest of the Seasonal Ice Zone south of the maximum sea ice extent,
- the Open Ocean Zone (OOZ), in between the OSIZ and the Sub-Antarctic Front (SAF), which at times includes part of the higher latitudes covered in winter by sea-ice and also the Polar Frontal Zone (PFZ),
- the Sub-Antarctic Zone (SAZ), the region north of the SAF and in some places including the Sub-Tropical Zone (STZ).

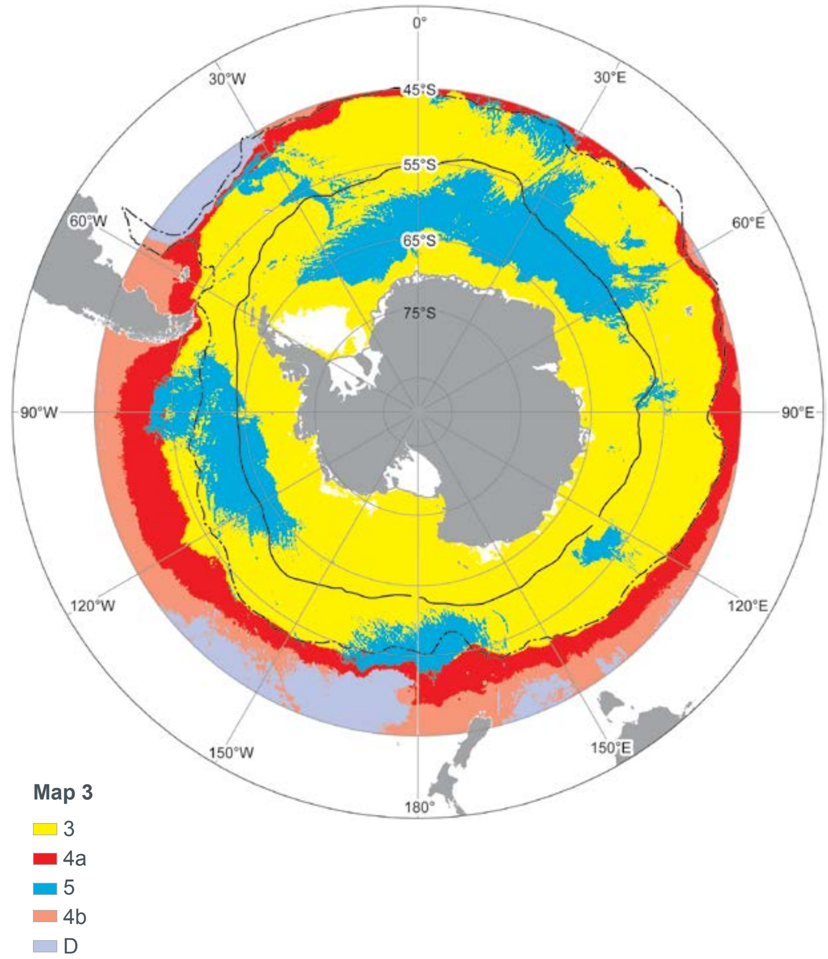
Each of these zones are coloured coded and numbered the same in each map (Maps 2 to 10) and associated table (Tables 2 to 10): ISIZ = 1, blue; OSIZ = 2, green; OOZ = 3, yellow; SAZ = 4, red. Sub-groups were often identified within each basic division and were identified with an alpha-suffix and different shade of the primary colour. For example, the SAZ often comprised subgroups 4a, 4b and 4c (in November). The predicted GDM groups based on environmental parameters alone, with no corresponding CPR samples, were coloured in neutral colours (greys) and identified by letters.

For the months July to November (Maps 3 to 5, Tables 3 to 5) the region south of the SAF was more or less identified as one group which for the convenience of the analyses was identified as Group 3. This corresponds with the OOZ in later months. The inability to distinctly identify the ISIZ and OSIZ in the winter and spring months was primarily due to the inability to tow CPR units when sea-ice was present. This resulted in the GDM model predicting the OOZ zooplankton group into the southern latitudes. For the other months December to May (Maps 6 to 10, Tables 6 to 10), the sea-ice had retreated sufficiently to permit more extensive CPR tows in higher latitudes. Consequently, the four main assemblages of the ISIZ, OSIZ, OOZ and SAZ were identified in these months as seen in the all month analysis (Map 2). There were notable latitudinal variations in the boundaries of the biogeographic zones between months. Hunt & Hosie (2006b) noted that the fronts shift north-south significantly during the year, especially the SAF, but the zooplankton assemblages maintain their association with the fronts and move with the fronts.

Tables 2 to 10 list the taxa identified by SIMPER analysis that characterised the various groups each month. The principal taxa that characterised each group are highlighted. A total of 18 taxa were identified, although not all taxa were considered important in every month. The SAZ was characterised primarily by the calanoid copepod *Neocalanus tonsus*. The copepod *Clausocalanus brevipes*, salp *Salpa thompsoni*, chaetognath *Eukrohnia hamata* and



Map 2 GDM prediction for all months.



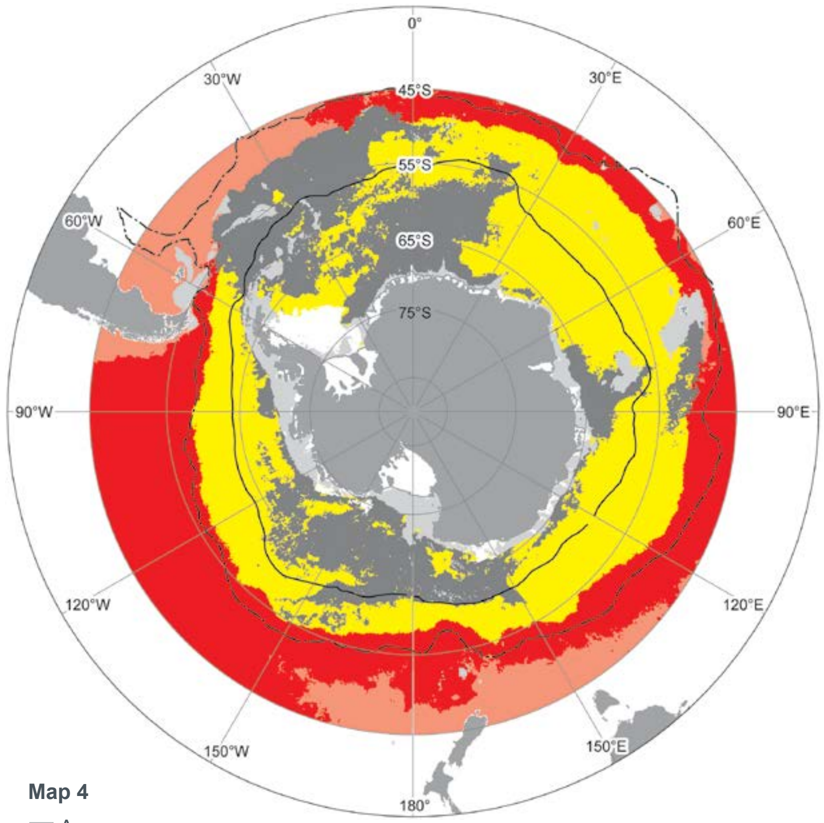
Map 3 GDM prediction for July-August-September.

Table 2 SIMPER analysis of each group for all months. The main contributing species are underlined. Abundance values are mean numbers of individuals per m^3.

	Biogeographic zone and group number			
	ISIZ	OSIZ	OOZ	SAZ
Taxa	1	2	3	4
Calanoides acutus	0.050	0.396	0.136	0.001
Calanus propinquus	0.039	0.194	0.052	0
Calanus simillimus	0.017	0.188	1.400	0.156
Clausocalanus brevipes	0.058	0.047	0.270	0.424
Ctenocalanus spp.	0.037	0.465	1.078	0.538
Eukrohnia hamata	0	0.0003	0.023	0.027
Euphausia frigida	0.0004	0.001	0.023	0.009
Euphausia superba	0.052	0.161	0.010	0
Foraminifera	0.610	0.797	2.410	2.186
Fritillaria spp.	4.062	1.475	0.811	0.395
Limacina spp.	1.992	0.647	0.860	0.083
Neocalanus tonsus	0	0	0.056	0.641
Oikopleura spp.	0.189	0.236	0.397	0.446
Oithona similis	2.360	4.163	10.103	2.062
Ostracoda	0.000	0.001	0.071	0.086
Rhincalanus gigas nauplius	0.057	0.160	0.464	0.007
Salpa thompsoni	0.003	0.015	0.014	0.043
Thysanoessa macrura	0.034	0.136	0.095	0.057
Total abundance	11.218	12.600	27.184	12.267
Number of species	26	39	48	44
Number of samples	495	1751	20880	2665

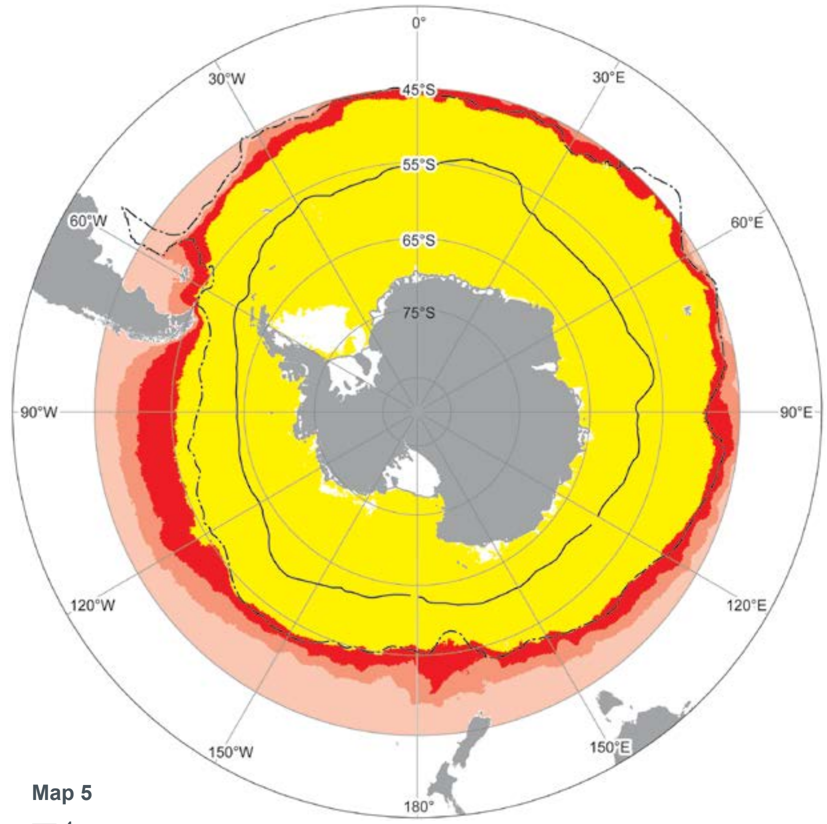
Table 3 SIMPER analysis of each group for July-August-September. The main contributing species are underlined. Abundance values are mean numbers of individuals per m^3.

	Biogeographic zone and group number		
	OOZ	SAZ	SAZ
Taxa	3	4a	4b
Calanoides acutus	0.944	0.001	0
Calanus propinquus	0.040	0	0
Calanus simillimus	0.640	0.374	0.136
Clausocalanus brevipes	0.120	0.385	1.360
Ctenocalanus spp.	0.062	0.038	0.563
Eukrohnia hamata	0.253	0.007	0.012
Euphausia frigida	0.054	0.060	0.136
Euphausia superba	0	0	0
Foraminifera	4.169	16.095	9.178
Fritillaria spp.	1.772	0.126	0.012
Limacina spp.	0.102	0.048	0.099
Neocalanus tonsus	0	0.298	5.079
Oikopleura spp.	0.796	0.137	0.119
Oithona similis	8.642	2.237	0.898
Ostracoda	0.105	0.141	0.062
Rhincalanus gigas nauplius	0.001	0.001	0
Salpa thompsoni	0.020	0.110	0.033
Thysanoessa macrura	0.335	0.192	0.205
Total abundance	18.733	20.797	18.907
Number of species	32	33	28
Number of samples	908	505	163



Map 4
- A
- b
- 3
- 4a
- 4b

Map 4 GDM prediction for October.



Map 5
- 4c
- 4b
- 4a
- 3

Map 5 GDM prediction for November.

Table 4 SIMPER analysis of each group for October. The main contributing species are underlined. Abundance values are mean numbers of individuals per m³.

	Biogeographic zone and group number		
	OOZ	SAZ	SAZ
Taxa	3	4a	4b
Calanoides acutus	0.944	0.001	0
Calanus propinquus	0.040	0	0
Calanus simillimus	0.640	0.374	0.136
Clausocalanus brevipes	0.120	0.385	1.360
Ctenocalanus spp.	0.062	0.038	0.563
Eukrohnia hamata	0.253	0.007	0.012
Euphausia frigida	0.054	0.060	0.136
Euphausia superba	0	0	0
Foraminifera	4.169	16.095	9.178
Fritillaria spp.	1.772	0.126	0.012
Limacina spp.	0.102	0.048	0.099
Neocalanus tonsus	0	0.298	5.079
Oikopleura spp.	0.796	0.137	0.119
Oithona similis	8.642	2.237	0.898
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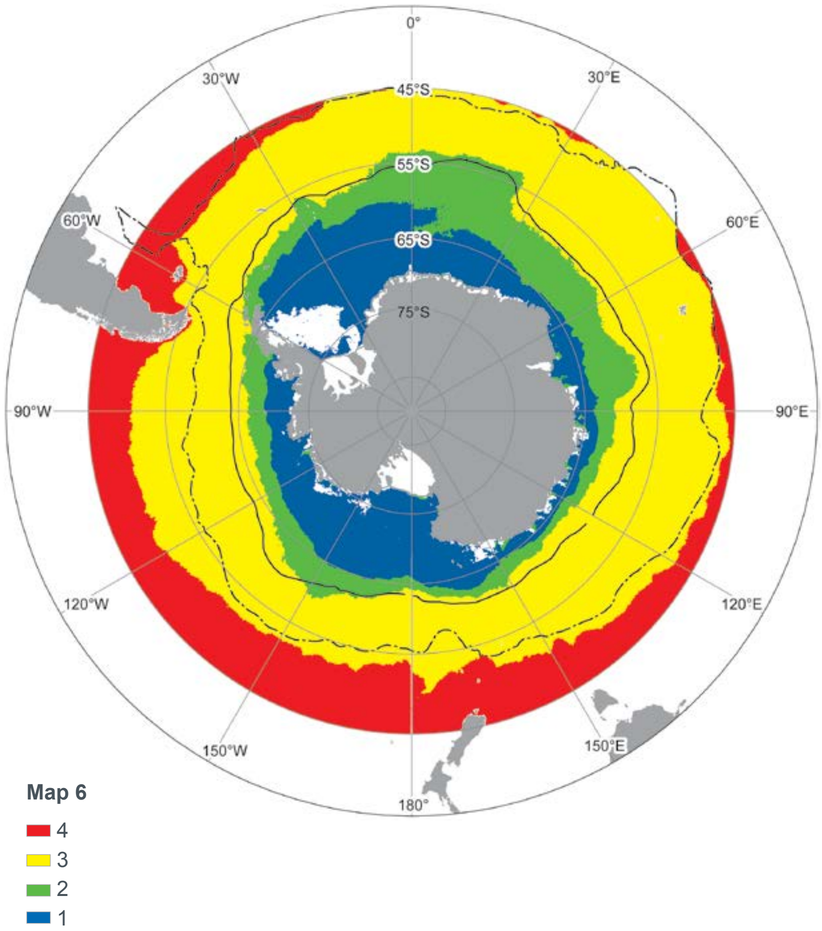
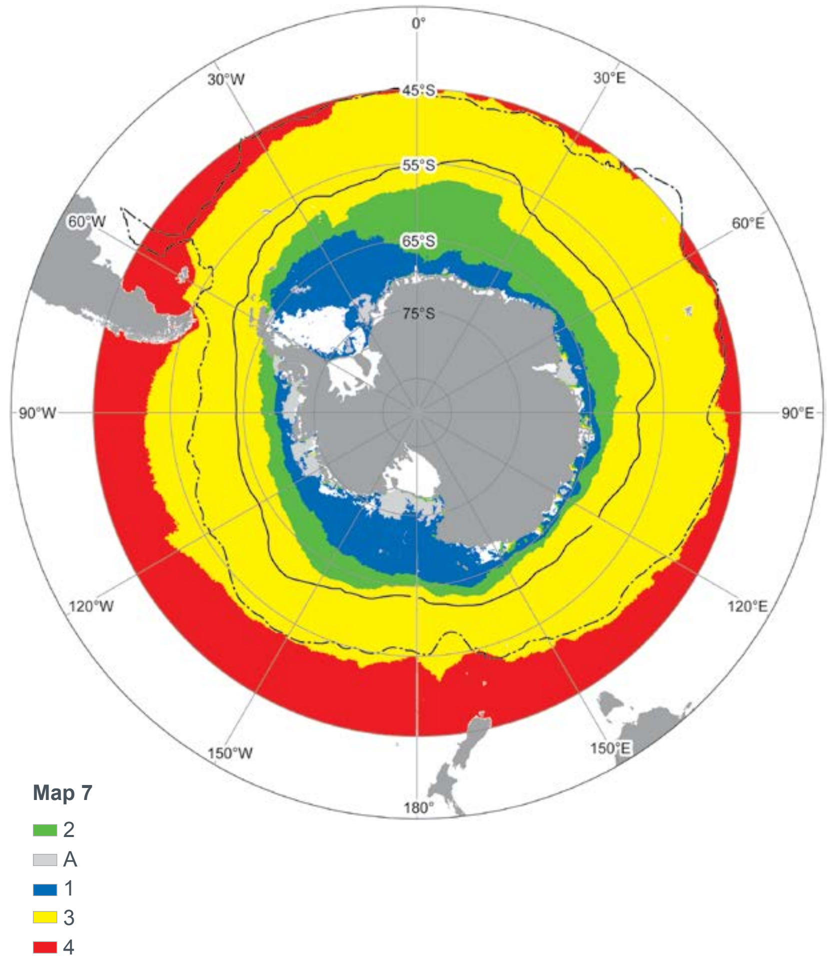
Salpa thompsoni	0.020	0.110	0.033
Thysanoessa macrura	0.335	0.192	0.205
Total abundance	18.733	20.797	18.907
Number of species	32	33	28
Number of samples	908	505	163

Table 5 SIMPER analysis of each group for November. The main contributing species are underlined. Abundance values are mean numbers of individuals per m³.

	Biogeographic zone and group number			
	OOZ	SAZ	SAZ	SAZ
Taxa	3	4a	4b	4c
Calanoides acutus	0.415	0.011	0.011	0
Calanus propinquus	0.012	0	0	0
Calanus simillimus	1.900	0.469	0.056	0.022
Clausocalanus brevipes	1.595	1.018	1.495	0.112
Ctenocalanus spp.	3.737	0.863	2.026	0.647
Eukrohnia hamata	0.049	0.058	0.034	0.112
Euphausia frigida	0.178	0.042	0.026	0
Euphausia superba	0	0	0	0
Foraminifera	17.246	2.356	0.324	0.112
Fritillaria spp.	3.459	0.704	0.135	0.067
Limacina spp.	1.438	0.168	0.102	0
Neocalanus tonsus	0.009	0.365	3.006	5.879
Oikopleura spp.	1.236	0.480	0.401	0.156
Oithona similis	43.615	7.046	5.135	4.379
Ostracoda	0.269	0.180	0.128	0.045
Rhincalanus gigas nauplius	5.387	0.214	0	0
Salpa thompsoni	0.035	0.158	0.324	0.029
Thysanoessa macrura	0.337	0.032	0.053	0
Total abundance	82.457	15.319	15.297	12.480
Number of species	40	31	32	17
Number of samples	1877	301	177	30



Map 6 GDM prediction for December.



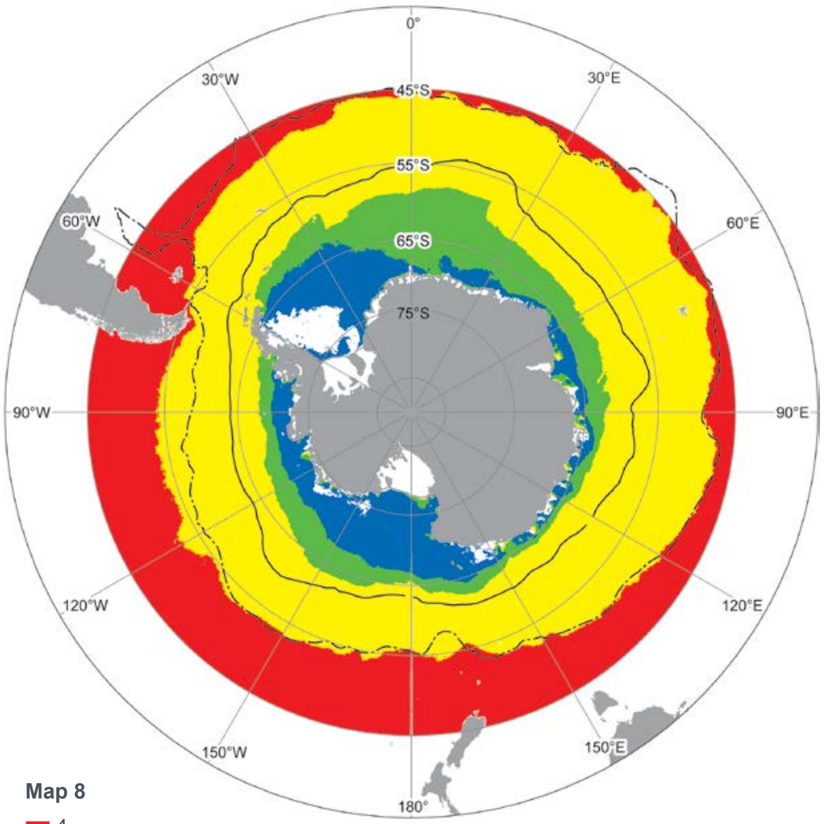
Map 7 GDM prediction for January.

Table 6 SIMPER analysis of each group for December. The main contributing species are underlined. Abundance values are mean numbers of individuals per m^3.

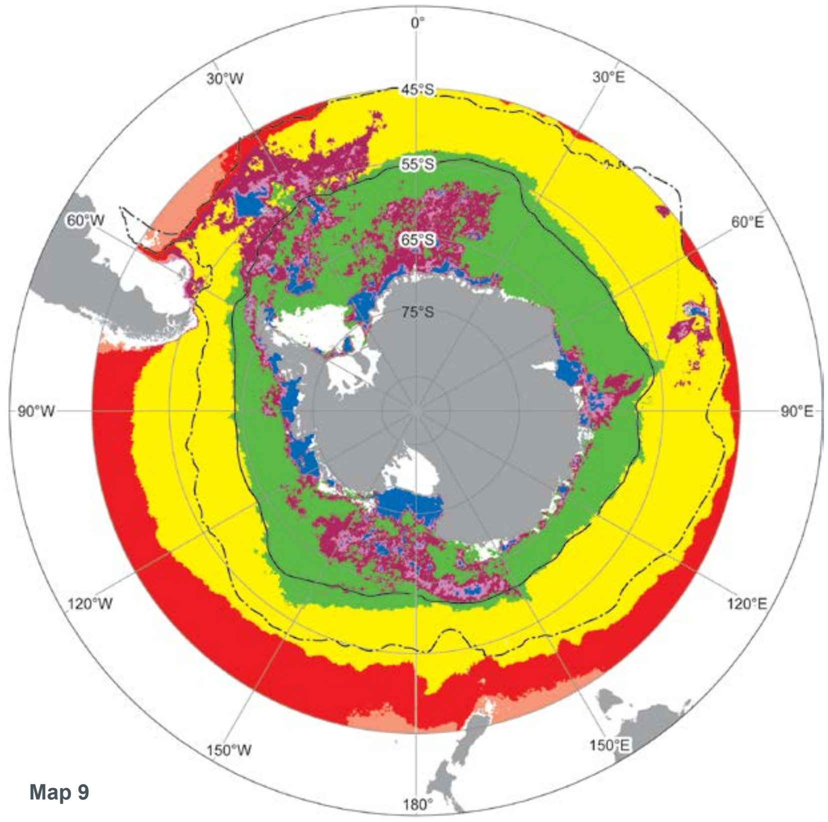
	Biogeographic zone and group number			
	ISIZ	OSIZ	OOZ	SAZ
Taxa	1	2	3	4
Calanoides acutus	0.022	0.056	0.177	0
Calanus propinquus	0.019	0.093	0.002	0
Calanus simillimus	0.022	0.085	2.731	0.485
Clausocalanus brevipes	0	0.156	0.895	0.924
Ctenocalanus spp.	0.043	0.131	6.463	1.699
Eukrohnia hamata	0	0	0.032	0.042
Euphausia frigida	0	0.005	0.027	0.006
Euphausia superba	0.472	0.360	0.008	0
Foraminifera	5.144	3.722	10.878	2.778
Fritillaria spp.	0.043	1.075	3.590	0.391
Limacina spp.	0.022	0.023	2.673	0.249
Neocalanus tonsus	0	0	0.119	5.476
Oikopleura spp.	0.022	0.136	1.893	1.922
Oithona similis	3.045	14.829	61.838	11.940
Ostracoda	0	0	0.258	0.213
Rhincalanus gigas nauplius	0.043	0.013	3.373	0.039
Salpa thompsoni	0.043	0.013	0.065	0.499
Thysanoessa macrura	0.420	0.302	0.234	0.203
Total abundance	9.403	21.167	96.572	28.789
Number of species	15	30	47	34
Number of samples	31	369	3242	240

Table 7 SIMPER analysis of each group for January. The main contributing species are underlined. Abundance values are mean numbers of individuals per m^3.

	Biogeographic zone and group number			
	ISIZ	OSIZ	OOZ	SAZ
Taxa	1	2	3	4
Calanoides acutus	0.875	1.977	0.556	0
Calanus propinquus	0.130	0.048	0.105	0
Calanus simillimus	0.075	0.537	6.114	2.361
Clausocalanus brevipes	0.011	0.182	0.593	0.599
Ctenocalanus spp.	0.572	1.165	3.737	0.860
Eukrohnia hamata	0	0.001	0.049	0.051
Euphausia frigida	0	0	0.019	0.021
Euphausia superba	0.454	0.574	0.069	0
Foraminifera	1.544	4.707	10.316	6.924
Fritillaria spp.	12.362	4.415	3.882	1.289
Limacina spp.	0.151	1.019	1.866	0.241
Neocalanus tonsus	0	0	0.043	1.326
Oikopleura spp.	0.032	0.428	1.020	1.209
Oithona similis	8.722	21.321	46.344	5.713
Ostracoda	0.011	0.002	0.160	0.114
Rhincalanus gigas nauplius	0	1.266	1.544	0.052
Salpa thompsoni	0.022	0.015	0.055	0.077
Thysanoessa macrura	0.551	0.357	0.257	0.274
Total abundance	26.320	38.864	78.003	22.769
Number of species	23	30	45	38
Number of samples	62	758	3566	475



Map 8
- 4
- 3
- 2
- 1



Map 9
- z
- 4b
- 7
- 6
- 4a
- 3
- 2
- 1

Map 9 GDM prediction for March.

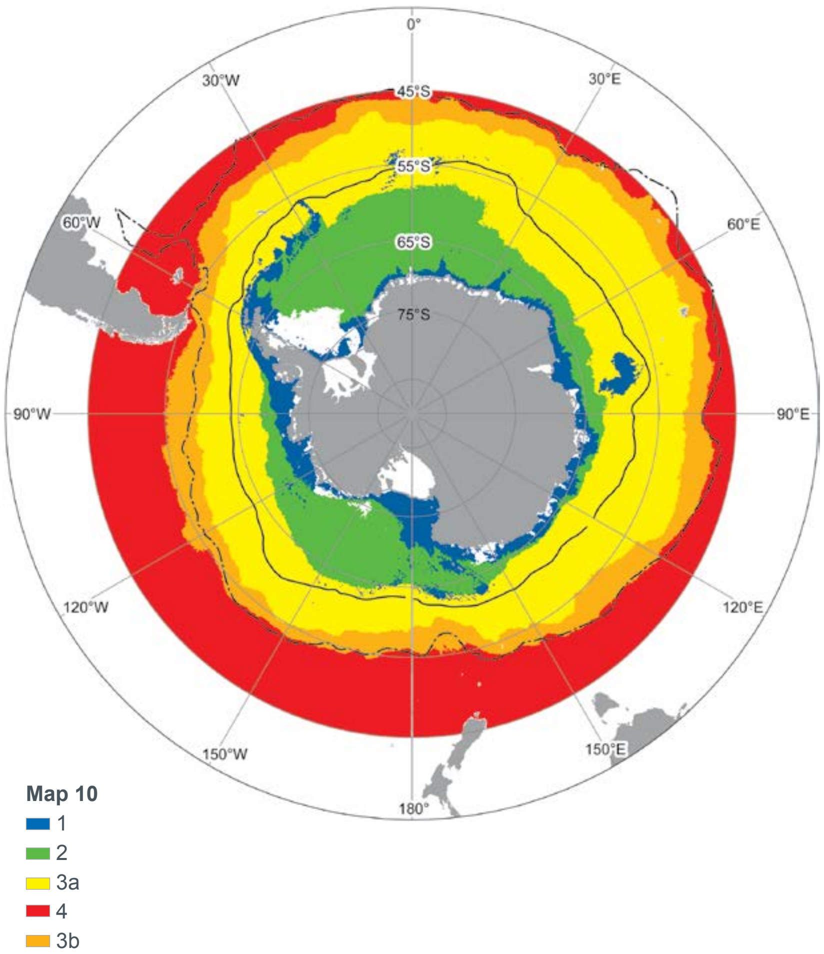
Map 8 GDM prediction for February.

Table 8 SIMPER analysis of each group for February. The main contributing species are underlined. Abundance values are mean numbers of individuals per m^3.

	Biogeographic zone and group number			
	ISIZ	OSIZ	OOZ	SAZ
Taxa	1	2	3	4
Calanoides acutus	0.169	0.487	0.730	0.012
Calanus propinquus	0.060	0.064	0.027	0
Calanus simillimus	0.063	0.088	8.745	1.000
Clausocalanus brevipes	0.478	0.011	1.075	2.265
Ctenocalanus spp.	0.116	1.865	3.495	2.567
Eukrohnia hamata	0	0	0.053	0.211
Euphausia frigida	0	0.005	0.034	0.014
Euphausia superba	0.222	0.701	0.012	0
Foraminifera	2.680	5.039	6.227	20.072
Fritillaria spp.	22.211	17.133	3.832	7.009
Limacina spp.	11.011	5.623	5.803	1.500
Neocalanus tonsus	0	0	0.092	2.869
Oikopleura spp.	0.345	3.189	2.101	3.848
Oithona similis	4.872	19.888	37.932	11.956
Ostracoda	0	0.008	0.223	0.277
Rhincalanus gigas nauplius	0.204	0.469	0.856	0.651
Salpa thompsoni	0.024	0.150	0.033	0.074
Thysanoessa macrura	0.031	0.368	0.420	0.165
Total abundance	43.408	56.907	73.038	56.798
Number of species	23	32	45	40
Number of samples	190	411	3197	672

Table 9 SIMPER analysis of each group for March. The main contributing species are underlined. Abundance values are mean numbers of individuals per m^3.

	Biogeographic zone and group number						
	ISIZ			OSIZ	OOZ	SAZ	SAZ
Taxa	1	6	7	2	3	4a	4b
Calanoides acutus	0.136	0.156	4.066	1.390	0.057	0.002	0
Calanus propinquus	1.056	0.571	8.104	0.916	0.176	0	0
Calanus simillimus	1.659	2.265	3.035	3.122	7.965	0.941	0.030
Clausocalanus brevipes	0.015	0.391	1.368	1.378	1.125	2.210	0
Ctenocalanus spp.	0.271	0.416	8.855	4.523	4.014	3.281	0
Eukrohnia hamata	0	0	0.017	0.049	0.154	0.145	0.015
Euphausia frigida	0	0	0.017	0.055	0.091	0.009	0.298
Euphausia superba	0.134	0.195	0.084	0.089	0.007	0	0
Foraminifera	1.141	2.277	3.470	1.719	5.925	5.747	0.825
Fritillaria spp.	0.030	1.172	2.628	1.646	0.860	0.747	0
Limacina spp.	0.029	0.165	20.883	5.339	2.796	0.337	0.074
Neocalanus tonsus	0	0	0.023	0.003	0.635	0.254	0
Oikopleura spp.	0.122	0.212	0.199	0.803	1.511	0.709	0.149
Oithona similis	5.409	15.731	26.460	23.436	14.613	9.475	5.080
Ostracoda	0	0	0.003	0.016	0.533	0.482	0
Rhincalanus gigas nauplius	0.015	0.524	2.829	0.703	0.091	0.005	0
Salpa thompsoni	0	0	0.007	0.059	0.041	0.083	0
Thysanoessa macrura	1.523	1.162	1.075	0.278	0.467	0.247	0.015
Total abundance	11.836	25.675	83.753	47.291	42.323	27.143	8.018
Number of species	16	19	31	42	49	43	16
Number of samples	44	60	202	1804	3146	629	45



Map 10 GDM prediction for April-May.

Table 10 SIMPER analysis of each group for April-May. The main contributing species are underlined. Abundance values are mean numbers of individuals per m^3.

	Biogeographic zone and group number				
	ISIZ	OSIZ	OOZ	OOZ	SAZ
Taxa	1	2	3a	3b	4
Calanoides acutus	0	0.008	0.010	0.077	0
Calanus propinquus	0	0.182	0.259	0.149	0
Calanus simillimus	0	1.135	1.887	2.289	0.276
Clausocalanus brevipes	0	0	0	0	0
Ctenocalanus spp.	0	0.004	0	0	0
Eukrohnia hamata	0	0	0.187	0.706	0.118
Euphausia frigida	0	0	0.087	0.285	0.236
Euphausia superba	0	0.939	0.112	0	0
Foraminifera	0.223	1.222	0.778	1.001	1.575
Fritillaria spp.	0.893	2.320	0.649	1.049	1.142
Limacina spp.	0	0.314	0.754	3.453	0.118
Neocalanus tonsus	0	0	0	0.054	0
Oikopleura spp.	0.893	0.013	0.679	0.621	0.118
Oithona similis	4.910	10.980	18.452	7.553	10.989
Ostracoda	0	0	0.10	0.986	0.670
Rhincalanus gigas nauplius	0	0.080	0.364	0.017	0.039
Salpa thompsoni	0	0.004	0.009	0.019	0
Thysanoessa macrura	0	0.091	0.321	0.200	0
Total abundance	7.142	18.451	25.289	19.353	15.912
Number of species	5	21	32	28	14
Number of samples	3	160	822	157	17

larvaceans of the genus *Oikopleura* were often more abundant in the SAZ but were also found in southern biogeographic zones.

The Antarctic krill *Euphausia superba*, copepods *Calanoides acutus* and *Calanus propinquus* and larvaceans of the genus *Fritillaria* typically characterised the southern-most zones ISIZ and OSIZ in the summer months. The krill and two copepod species have been identified previously as typical of the sea-ice zone, usually dominating the region north of the shelf slope equivalent to the OSIZ (Hosie 1994, Hosie *et al*. 2000). The big-eye krill *Thysanoessa macrura* is recorded as having a broad circumpolar distribution south of the SAF. In this analysis the species was often more abundant in the ISIZ and OSIZ, than the open zone (OOZ). The neritic ice krill *Euphausia crystallorophias* has been identified previously as the dominant species of the shelf region equivalent to the ISIZ group (Hosie 1994, Hosie *et al*. 2000). However the CPR rarely captures *E. crystallorophias* for two main reasons. Firstly, the CPR usually cannot be towed in the shelf region because of ice, with the neritic zone being free of ice for just a few weeks. Secondly, the adults of the species prefer very cold waters of <-1°C and will not be found in the surface warmed waters sampled by the CPR (Hosie 1994).

The thecosome pteropods of the genus *Limacina* were very abundant in the ISIZ in February and OSIZ March, notably Group 7, but for the rest of time were more abundant in the OOZ.

The Open Ocean Zone was characterised by a number of taxa including the copepods *Calanus simillimus*, *Ctenocalanus* spp., *Rhincalanus gigas* nauplii, euphausiid *Euphausia frigida* and ostracods. *Ctenocalanus* spp. was more abundant in the open waters of the OOZ and occasionally the OSIZ and to some degree in the SAZ, e.g. in February. Ostracods were often reasonably common in the SAZ. The cyclopoid copepod *Oithona similis* was consistent the numerically most abundant and dominant taxa in the OOZ. *O. similis* was in fact abundant and numerically dominant in all zones of the Southern Ocean, which is to be expected for this cosmopolitan species, but was most abundant in the OOZ. This follows the boosted regression tree (BRT) distribution modelling of Pinkerton *et al*. (2010) who predicted this species as being consistently most abundant in the mid ocean band ice free region of the Southern Ocean. Similarly, foraminferans were abundant in all zones but were usually more abundant in the OOZ. In October and February much higher abundances were observed in the SAZ, and these are likely to be different species south of the SAF. South of the SAF the foraminiferans most likely belong to just one species *Neogloboquadrina pachyderma* (Scott & Marchant 2005). More species are expected north of the SAF (Darling & Wade 2008), with *Globigerina bulloides* being the likely dominant species of the SAZ (Moy *et al*. 2009, McLeod *et al*. 2010).

Similarly, it is likely there are a number of species in each of the larvacean genera of *Fritallaria* and *Oikopleura* (O'Sullivan 1983). They are extremely difficult to identify to the species level with any certainty in CPR or plankton net samples. While both genera were common in all zones, there was a general trend of *Fritallaria* being more abundant in the south in the sea-ice region, then decreasing in abundance to the north, whereas *Oikopleura* showed the opposite pattern, being more abundant towards the north.

In general, the highest total zooplankton abundances and numbers of species were consistently observed in the OOZ. The number of species dropped slightly in the SAZ but there was a clear decrease in abundance in this zone. The SIZ was notable for both low abundances and low number of species, especially in the ISIZ, as per previous observations (Hosie *et al*. 2003, Hunt & Hosie 2005, 2006a). In relation to seasonal patterns, total zooplankton abundance in the OOZ increase rapidly in spring from very low winter abundances to reach a peak in December, remaining high in January and February before declining in March, April, May. Zooplankton abundances in the ISIZ and OSIZ peaked two months later, which coincides with the approximate one to two month period of being ice free. Zooplankton abundances also peaked in February in the SAZ. The numbers of species (of the original selected 50) increased over summer and declined in autumn. The number of species peaked in January-February in the ISIZ, March in the OSIZ, remained high from December to March in the OOZ and increased steadily in the SAZ, peaking in March before declining rapidly in April–May.

3.1. Variations from the norm

The July-August-September prediction (Map 3) produced an additional group (5) within the OOZ. This group had low total zooplankton abundance and fewer species than the other groups. This may be an analyses artefact with just 42 samples identifying this group. In October (Map 4), large areas of the OOZ were identified as Group A. There was no CPR data associated with this prediction. In January (Map 7) Group A was predicted as being close to the Antarctic coast, but was not associated with any CPR data. Two additional and intermingled groups 6 and 7 were predicted in the March model (Map 9). These were primarily located with the OSIZ and partly in the OOZ of the Atlantic sector. Group 6 had both lower zooplankton abundances and number of species than the OOZ and OSIZ groups. However, Group 7 had the highest total abundance and notably high abundances of *O. similis* and *Limacina* spp. Groups 6 and 7 are most likely sub-groups of the OOZ and OSIZ caused by the typical patchiness of zooplankton. Group 3b in April-May is approximately in the position of the Polar Frontal Zone between the Polar Front and the Sub-Antarctic Front. The species composition of Group 3b was more similar to 3a than Group 4 in the SAZ. Notable is the complete absence of the usually dominant species *N. tonsus* in the SAZ.

4. Factors and processes influencing geographic distributions

The two most important variables affecting the prediction for the entire data set were (in order) sea surface temperature (SST) and sea-ice. Chlorophyll *a* (Chl *a*) and slope were interchangeably the third most important variable. However there is considerable variation between months. SST was generally the top variable explaining patterns in the months from July to December, was less important than Chl *a* and sea-ice in January and February, and became more important again in March and April-May. Chl *a* increased in importance from winter to November and remained high throughout summer. It was the variable explaining most of the pattern in March and was not important at all in April-May. Sea-ice did not correlate with the patterns during the early part of the season, when sea-ice was still covering most of the region, but became more important from December onwards when ice would have been melting rapidly. The other variables depth and slope explained some of the distributions but were often not important.

Interpretations of the fitted environmental dependencies from these models can sometimes be challenging. The large extent of the region of interest, coupled with the fact that we require predictions across its entirety, means that the modelling process is dependent on predictor variables with synoptic coverage. These typically come from remote-sensed or modelled sources. Unfortunately, the information available from these variables is typically not directly related to the conditions experienced by the animals. This mismatch may reflect scale issues (e.g. zooplankton may be affected by oceanographic features on scales of metres, yet satellite-derived oceanographic data is generally on scales of kilometres or larger), and the inability of satellite sensors to measure sub-surface conditions. SST is probably best interpreted as a general indicator of water mass properties, although it may also reflect the influences of more localised phenomena such as upwelling, sea-ice, and eddy activity. Sea-ice (specifically included here as the average proportion of the year a given location is covered by sea-ice) provides general characterisation of a location in terms of its position within the seasonal ice cycle, but also has reasonable spatial resolution (AMSR-E data at 6.25 km) and so can resolve medium-scale features such as polynyas. Chlorophyll-*a* also has reasonable spatial resolution (9 km source data used here) but suffers from coverage issues where cloud or sea-ice are present. Depth and slope also provide general indices that reflect a variety of processes, such as upwelling and nutrient availability.

Note: the effect plots of each environmental variable for each month are too numerous to reproduce here. They are available on line at share.biodiversity.aq/.

5. Conclusion

All the GDM predictions identified the Sub-Antarctic Front (SAF) as a distinct boundary between the assemblages to the south and the SAZ assemblage typically characterised by *Neocalanus tonsus*. The zooplankton assemblages associated with the region of the Sea Ice Zone and the continental shelf within, typified by species such *Euphausia superba, Calanus propinquus, Calanoides acutus*, were predicted in months from December when the sea-ice had retreated sufficiently to permit CPR sampling in the high latitudes. The Southern Ocean south of the SAF was more-or-less one zooplankton community in the near-surface. It was variations in the relative abundances of the zooplankton taxa that separated the near-surface assemblages more than substantial major changes in species composition between the biogeographic zones. While there were distinct species dominating the SAZ and SIZ, most of the taxa had wide circumpolar distributions; some tended to more abundant in the south and decreasing towards the north (e.g. *Fritallaria* spp., *Thysanoessa macrura*), more abundant towards the north (e.g. *Oikopleura* spp., *Ctenocalanus* spp., *Clausocalanus brevipes*) or more abundant in the mid-latitudes (e.g. *Oithona similis*, *Calanus simillimus*, *Euphausia frigida*). This confirms the previous analyses by Hunt and Hosie (2003, 2005, 2006 a,b) who also identified the SAF as a major biogeographic boundary for zooplankton south of Tasmania. Their studies using cluster analysis regularly identified sub-assemblages in the Open Ocean Zone, and a different assemblage in the SIZ, which again were based on subtle variation in the proportion of species, rather than major changes in species. Their conclusions were based on a single transect sampled multiple times in one season. The GDM models in this study predicted the same biogeographic zones, in terms of species composition and distribution, as being consistent uniform bands around Antarctica, and that these are also consistent for most of the year. Nonetheless, there can still be distinct latitudinal and longitudinal variation and possibly consistent localised hotspots of abundance for individual species as demonstrated with the BRT spatial-temporal models for *Oithona similis* (see Fig. 12 in Pinkerton *et al*. 2010).

There are definite warm-water species in the north (SAZ), *N. tonsus*, and cold-water species in the south, *E. superba, C. propinquus, C. acutus*, and in particular *E. crystallorophias*, but as noted above there are large number of species with broad circumpolar distributions which indicates a reasonably wide temperature tolerance. Moderate increases in sea-water temperature are predicted to have a severe impact on the survival of sea-ice species like Antarctic krill *E. superba* (Hill *et al*. 2013), and the same is most likely to apply to the neritic ice krill *E. crystallorophias.* However, for many species increases in temperature may not be as problematic, other than a predicted poleward shift in their distribution (Mackey *et al*. 2013). *Oithona similis*, for example, is a cosmopolitan species that seems to occur in most marine environments and therefore seems unlikely to be negatively affected by temperature increases. Potentially, there may be high tolerance to temperature increase in the near-surface zooplankton communities at least. The effects of ocean acidification are potentially more disruptive (Kawaguchi *et al*. 2013, Bednaršek *et al*. 2012). This warrants further autecological studies of the major Southern Ocean zooplankton species, and in concert with other potentially detrimental environmental stressor such as ocean acidification and UV, to determine the degree of impact of or resilience of plankton to environmental changes.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope

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

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

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

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

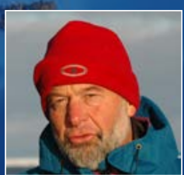
The Census of Antarctic Marine Life (CAML)

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

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

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

The Editorial Team



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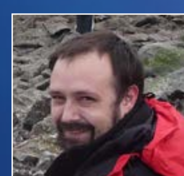

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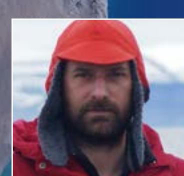
Graham HOSIE is Principal Research Scientist in zooplankton ecology at the Australian Antarctic Division. He founded the SCAR Southern Ocean Continuous Plankton Recorder Survey and is the Chief Officer of the SCAR Life Sciences Standing Scientific Group. His research interests include the ecology and 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.